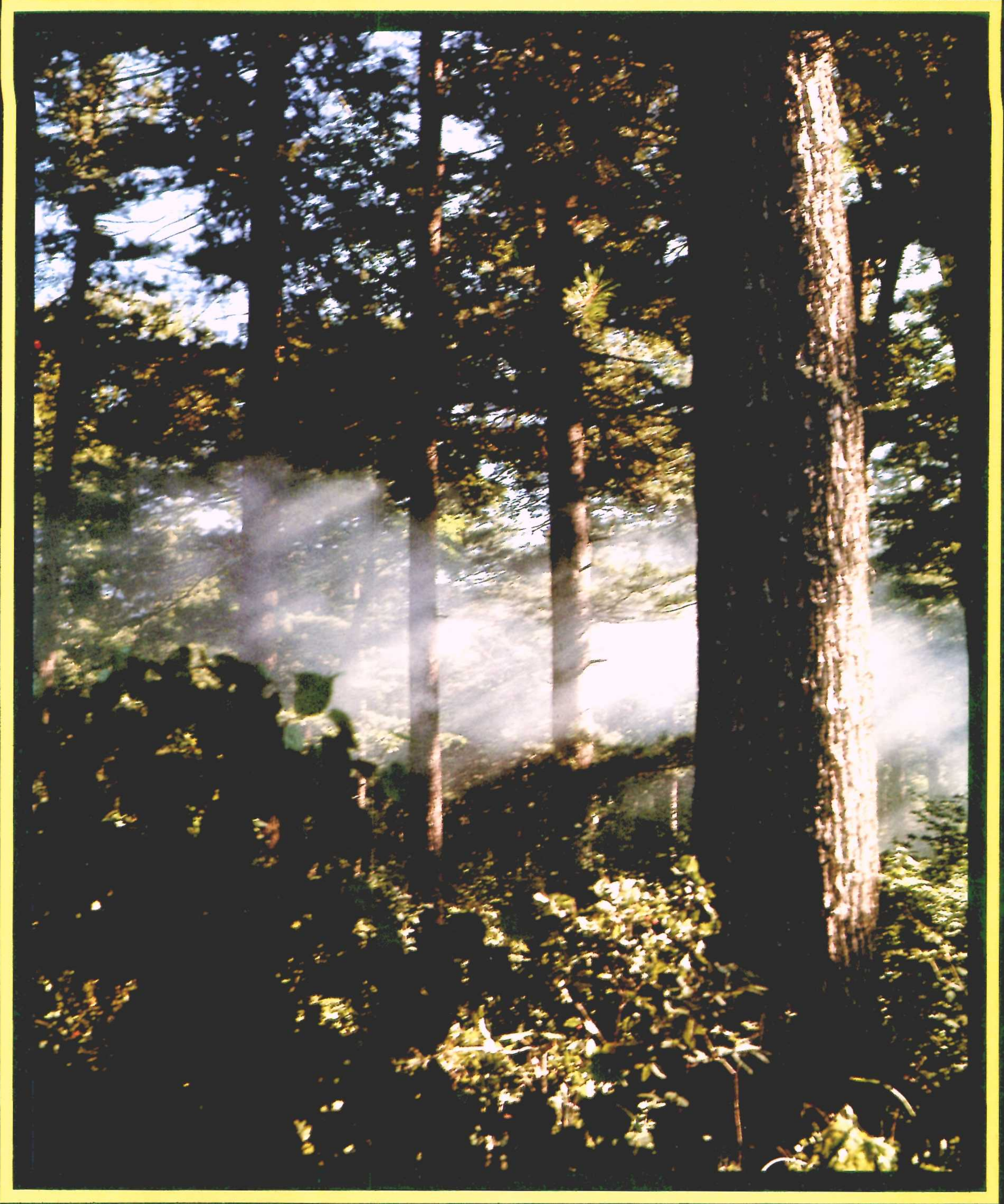
THE
TEMPERATE FOREST
ECOSYSTEM



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and
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COVER ILLUSTRATION
View of temperate forest in Changbai Mountain Biosphere Reserve, north-east China (Photograph Wang Ying)

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Preface

The Symposium on temperate forest ecosystems was jointly sponsored by the National Committee of the People's Republic of China for Man and the Biosphere (MAB), the Academia Sinica Institute of Forestry and Soil Science, the Natural Environment Research Council's Institute of Terrestrial Ecology (ITE), the United Nations Educational, Scientific and Cultural Organization (UNESCO) and the Changbai Mountain Nature Reserve Bureau. This Symposium was held on 5–11 July 1986 at the Changbai Mountain Research Station of Academia Sinica, in Jilin Province, north-east China, close to the Korean border. Despite the very remote area in which the Symposium was held, 31 foreign delegates attended, together with 74 Chinese scientists drawn from a wide selection of organizations, institutes and universities throughout China.

The Changbai Mountain range stretches along the boundary between China and Korea in the south-east of Kirin Province, and covers an area of 8000 km^2, with elevations ranging from 500 m to 2691 m. The highest peak – Baiyun – is a magnificent volcano situated on the wide lava plateau. It is not only the best-known mountain in NE China, but is also one of the most famous volcanoes in the world. The Symposium began with a series of excursions to the top of the volcanic crater which forms the physical base of the Changbai Mountain Reserve. The Reserve was established as an international Biosphere Reserve by UNESCO in 1979, and covers an area of 190 000 ha. Within the crater, there is an extensive lake, Tianchi – 'Sky Lake', with a surface area of 9.4 square kilometres. There are many peaks round the lake, and the only gap is to the north, through which the Changbai waterfall runs out, falling 68 m to the valley below. Three rivers rise in the Mountain, the Song Hua, Ya Lu and Tu Men.

The climatic characteristics in Changbai Mountain are of cold weather during the long winter, and a short and cool summer. It is frequently windy, and often foggy. The mean annual temperature ranges from 3°C to −7°C, and at the mountain peak it is even colder. The average maximum temperature does not reach 10°C in July, and the minimum temperature recorded is −44°C. The precipitation is abundant in the mountains, with an annual average of between 700 mm and 1400 mm. Precipitation at the top of the Mountain is mainly in the form of snow, and occasionally, particularly in June–August, falls as hail.

The animal and plant resources in Changbai Mountain are rich and abundant. Over 50 species of mammals, 200 species of bird and 1000 insect species have been recorded, and reptiles, amphibians and fish together total about 300 species. The vascular plants represent about 1300 species, belonging to 122 families and 430 genera. The forest ecosystem is an original forest vegetation which has not been exploited or managed for production. The biological resources of the area are also rich, and the ecosystem plays an important role in water and soil conservation, and in environmental protection.

There is a distinct vertical zonation, and 4 different natural zones can be seen, ranging from the bare volcanic rock and ash at the summit of the Mountain (see centre spread).

In the upper part of the volcanic cone, above 2000 m, lies the alpine tundra zone, where only the specially adapted perennial cushion plants and creeping shrubs manage to survive. The area is divided into 2 types – dwarf shrub tundra where the main species are *Rhododendron* (rhododendron) and *Vaccinium* (cranberry), and the alpine semi-desert, where vegetation is thin, with few plant species. The soil is an alpine meadow soil, and animals are rare, mainly the alpine hare (*Lepus mandschuricus* Radde) and some birds.

Betula ermanii Cham. (Erman's birch) occurs between 1800 m and 2000 m, forming a pure forest. In this zone, the soil is a mountain soddy forest earth, with rather poor fertility. The trees are sparse, short and crooked at the upper limit, mainly because of the strong winds. At the highest part, the trees become prostrate. Animals and birds are rare.

Between 1100 m and 1800 m is the coniferous forest zone, where the main species are *Picea jezoensis* (Sieb. et Zucc.) Carr. (Yezo spruce), *Abies nephrolepis* (Trautv.) Maxim. (East Siberian fir) and *Larix olgensis* A. Henry (Olga Bay larch). The soil is a brown Taiga.

Below 1100 m is found a mixed forest of broadleaved and coniferous trees. The main species present is *Pinus koraiensis* Sieb. et Zucc. (Korean pine), but other major species include *Tilia amurensis* Rupr. (Amur linden), *Quercus mongolica* Fisch. ex Turcz. (Mongolian oak), *Acer mono* Maxim. (painted mono maple), *Fraxinus mandshurica* Rupr. (Manchurian ash), *Ulmus propinqua* Koidz. (white elm), and *Abies holophylla* Maxim. (Manchurian fir). The soil of this zone is mainly a brown forest earth, and the soil layer is fertile and deep. Many different species of animals are found here, including the valuable *Rana chensiensis* David (Chinese forest frog). Rare medicinal plants are also found in this area, eg *Panax ginseng* C.A. Mey (ginseng), and many edible fungi.

The papers presented at the Symposium covered all aspects of the research in the Reserve, together with papers by the foreign delegates on various topics related to temperate forest ecosystems. Many of the papers presented by the Chinese delegates illustrated the tremendous development of ecosystem science in China that has taken place in recent years. Nevertheless, there is still a need for greater integration of the research on the Reserve if the full potential of this research is to be attained.

The contacts established between the Chinese and the overseas scientists in the discussions which followed the papers, both formally and informally, should greatly strengthen and accelerate the progress of Chinese science in temperate forest ecosystems. The delegates from outside China were greatly appreciative of the warmth of the welcome and hospitality extended to them. Any visit to the Changbai Mountain Reserve must be regarded as the highlight of an ecologist's experience: the opportunity to see a textbook series of ecological systems related to altitude can probably not be equalled anywhere else in the world.

The proceedings are to take 2 forms. This book, published by the Institute of Terrestrial Ecology, represents the English version. A Chinese version will follow the style of the English version as far as possible, but is likely to take a little longer to appear.

The importance of research in temperate forests

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1 Introduction

Why should we continue to do research in the temperate forests of the world? Many of the temperate forests exist in some of the wealthiest countries in the world, and there are long traditions of forest research in such countries. We might reasonably assume, therefore, that most of the important problems of forest ecology and management have already been solved, leaving very little that still needs to be done. It is true, of course, that large areas of temperate forest also exist in countries which have less well-developed economies, or which experienced long periods of economic or social disturbance. In such countries, forest research, with its long timescale for experiments and surveys, has been difficult, if not impossible, and it is only recently that many such countries have been able to establish forest research institutes, or even to survey the forest lands which may themselves have been devastated by warfare or by ill-advised utilization. In such situations, can we simply transfer some of the knowledge gained by those countries with long traditions of forest research?

The dependence on past research stressed above is only possible if we can assume that the influences on temperate forest have changed relatively little during the last century. In fact, of course, there are many negative influences on temperate forests and woodlands which have operated over the last 100 years, and which, if anything, have increased during the last 30 years. Perhaps the most important of these influences is the wholesale clearance of woodland for agriculture, urban expansion, industrial sites, and communications (roads, power lines, railways, etc). In many areas, land which even in recent history carried temperate woodland has been cleared for agriculture, often pushing the woodland remnants back on to the poorer land unsuitable for agriculture, and probably also unsuitable for the growth of high-quality timber. Where forest lands have been retained, such forests have often been subjected to overcutting or selective fellings, removing the more valuable species, but leaving damaged or poor growth of the less useful timber trees.

On such forest land as has been left after conversion to agriculture or other uses, and on areas brought back into forest, sometimes many years after they were originally felled, man has introduced fast-growing exotic species as alternatives to the often slower-growing native species, thus changing the composition of the forests. The redevelopment of a forest ecosystem is a slow process, especially where the species introduced to improve the rates of growth or the value of the timber for particular purposes do not have their full complement of associated organisms, such as mycorrhizas, from their original habitats. Many of the present-day temperate forests consist of species which have yet to establish an ecological balance with their environment, so that outbreaks of pests or diseases may be more difficult to control or predict.

Changes in land ownership and management, especially through traditional forms of inheritance, have also led to the fragmentation of temperate forest lands in many countries. The effects of such fragmentation have not been widely studied, but are clearly also influenced by hunting practices and sporting interests, and by the harvesting of plants and animals for medicinal or decorative purposes, in addition to their use as foods. In recent years, the marked growth of interest in wildlife conservation has also had a profound effect on forest lands, not merely on nature reserves and in national parks, but also in the more extensive areas of commercial and recreation woodlands. Thus, while the growth of timber and wood fibre may remain the primary purpose of temperate woodland, the management of the woodland for such purposes has to be modified to accommodate other interests and values.

Finally, and for many countries most importantly, temperate forests have shown themselves to be sensitive to many of the pollutants which have become an apparently essential part of our economic life. In many industrialized countries, the effects of acidic inputs to the atmosphere, from power stations driven by fossil fuels, from industrial plants, and from motor vehicles, are currently causing particular concern. We now talk of 'forest decline', a phrase unheard of until quite recently. In the search for increasingly rapid growth in an attempt to beat the disadvantages of the long rotations of the discounting techniques of the economists' models, the use of greater quantities of nitrates in agriculture and forestry may have particularly unfortunate effects on the quality of future water supplies. Our use of pesticides and herbicides to control pests and diseases is often careless and uncontrolled, with results that were not foreseen at the time of application. We know very little about the possible effects of radionuclides released into the atmosphere by nuclear reactors, reprocessing plants or by accidents like Chernobyl.

All of these influences on temperate forest involve a wide range of scientific disciplines and expertise. In no sense can forest research be regarded as a narrow academic topic, fit only to be pursued in isolation from the wider biological, ecological and environmental issues, as well as the economic and social factors that impinge on those issues. Forests, whether in the temperate or tropical regions of the world, play an essential role in the biosphere. If most attention has been given recently to the problems of tropical forest, for example in the Man and the Biosphere Programme of UNESCO, because of the rapid disappearance of that biome, we should not allow ourselves to be deluded into thinking that the problems of temperate woodland are trivial by comparison. For both temperate and tropical forests, the timescale necessary for scientific research into long-lived organisms like trees imposes a difficulty that can only be overcome by equally long-term planning and financial support.

2 Resource conservation

The rational development of a strategy for research and management of temperate forest, as for the other major biomes, requires a set of clear objectives for the future. Fortunately, we need look no further than the World Conservation Strategy (Allen 1980) for objectives that give a sharp focus for our present and future research. This strategy defines 3 main areas of activity.

i. Maintaining essential ecological processes and life-support systems. The essential ecological processes range from global phenomena, such as the cycling of oxygen and carbon, to local ones such as the production and dispersal of seed by trees and other forest plants. In between these 2 extremes, there are many other processes essential for the survival of the forest, notably soil formation, the cycling of nutrients, and vegetation succession following the clearance of forest or damage by fire. All of these processes are part of the complex system of plants, animals, micro-organisms and the non-living components of the forest ecosystem, and our understanding of this ecosystem is essential for the survival and wise management of our forest resources.

ii. Preserving genetic diversity. The range of genetic variation present in the temperate forest ecosystem includes all of the species, subspecies, varieties, strains and forms of plants, animals and micro-organisms. We need to keep the widest possible range of this variation to sustain and improve timber and fibre production, through breeding programmes for forest crops and forage plants, as well as for plants that have medicinal or decorative uses. The preservation of genetic diversity is a vital form of insurance, and an investment against harmful environmental change. It requires the prevention of the extinction of species and the preservation of as much of the variation within species as possible. Many species are highly variable, occurring in many different forms, and the continuing availability of these different forms is important. Research is necessary, therefore, to characterize variability and to find ways in which that variability can be preserved in living plants and animals.

iii. Utilizing species, and the forest ecosystem as a whole, sustainably. The concept of sustainability is a simple one: we should utilize the species and the ecosystem at levels and in ways that allow them to go on renewing themselves for all practical purposes indefinitely. How to achieve sustainability is less easily defined because the difference between sustained use and exploitation leading to extinction is sometimes very small, particularly in ecosystems which suffer periodic fluctuations because of climate or succession. Research is therefore necessary to define the limits within which the exploitation of the forest resources can be permitted so as to ensure that the forest itself, and the many species making up that forest, will survive. Such research also has to be linked to the economic and social factors which govern the use of the forest and its resources.

In implementing such a strategy of research and management, it should be clear that the forest resources extend far beyond those of wood and wood fibre that are the more obvious products of forestry. They include fuelwood, often important to the local community, water, the food provided by forest animals and plants, the wildlife for which the forest provides the necessary habitat, and areas for recreation and visual amenity. In the pursuit of these resources and their continuing availability in the future, the interaction of policies and programmes for individual areas of forest with factors of ownership and with state policies for land use and the protection of resources will often impose critical constraints. To make matters even more complicated, these constraints may alter several times in a single rotation of the forest. Everyone engaged in forest research must, therefore, have a very clear idea of the objectives of that research so as to ensure its relevance against a changing political, social and economic background.

3 Research topics

Within the framework of the broad strategy outlined above, it is relatively easy to identify the individual research topics that will make up a programme of forest research. Beginning with the regeneration of existing forest as it reaches the end of its rotation, or the reafforestation of land that has not carried forest, perhaps for many years, study of the early years of the growth of the forest stand, and the succession of forest types during the period of rapid growth and change, poses many practical problems in forest ecology and silviculture. Clear understanding of the processes of decomposition and nutrient cycling help in the unravelling of variations in productivity on different sites, or even in different parts of the same site. From such knowledge of the potential and actual productivity, effective silvicultural management of the growing forest, from the closure of canopy to maturity, guides the development of the long-term resource.

Throughout the life of the forest, protection against pests and pathogens will often be necessary, especially where natural cycles of succession or development are controlled or inhibited in the interests of productivity. However, maintaining forest development in close harmony with the ecology of the area may do much to reduce the harmful effects of pests and diseases, partly by ensuring that the chain of predators and secondary consumers is kept intact, rather than being truncated. Effective forest research, therefore, requires knowledge about the whole of the forest ecosystem and not just about the trees which are the most obvious components of that ecosystem. The old English saying about not being able to 'see the wood for the trees' is especially relevant to research and management of temperate forest.

Once the forest has reached maturity, it has to be harvested, and, in temperate forest in particular, there is much research that still needs to be done to make the harvesting and extraction of timber from the forest less damaging to the forest ecosystem. The last few decades of cheap energy, in the form of oil, have placed an undue emphasis on large-scale clearances of forest as the most 'economic' form of harvesting. When the effects of loss of soil through erosion, compaction of soil by the use of heavy vehicles, and destruction of humus with burning are added to the negative side of the balance, however, it may be necessary for us to reconsider our harvesting and extraction practices, both in terms of scale and of methods. The felling of the forest and the extraction of the timber are not the end of the process, but the start of the process of forest renewal.

4 The role of Changbai Mountain

We are gathered together for this Symposium near a site which is perhaps unique. Not far from where we are now, the Changbai Mountain rises steeply from the surrounding plain, and, since 1702, the vegetation on that mountain has been disturbed only minimally. As we have seen, there is a complete succession of vegetation from bare rock at the summit, through alpine tundra and dwarf shrub communities, to *Betula* (birch) woodland. From the *Betula* woodlands, the progression through various mixtures of conifers follows altitudinal zones marked by transitions within only a few metres. Finally, we emerge in the broadleaved woodlands of the plains.

There can be few places in the world where all of these woodland types are in such close proximity and so undisturbed by man's activities or by the grazing of man's domestic animals. Changbai offers an opportunity for forest ecology, and for the study of the essential life-support systems of the different types of forest so that they can be compared and contrasted within a relatively narrow range of soil and site types. Some of this work has already been done, and has been described at this Symposium, but there remains much that can still be done, and we look forward to working with our Chinese colleagues on extensions of this work in the future. Those of us who are visitors to Changbai have been privileged to share these days with our hosts in this very special place.

It would also be appropriate, perhaps, to say something about the UNESCO Man and the Biosphere Programme, and its role in promoting this Symposium and the collaboration of scientists of many countries with their Chinese colleagues at Changbai. It was under the auspices of MAB that many of us first heard of Changbai, and were invited by the National Committee for MAB of the People's Republic of China to visit Beijing and the research sites of the MAB Programme in China. The general objective of the MAB Programme is to develop the basis within the natural and social sciences for the rational use and conservation of the resources of the biosphere, to predict the consequences of today's actions on tomorrow's world, and thereby to increase man's ability to manage efficiently the natural resources of the biosphere. This Symposium is an expression of those objectives, and it is heartening that, despite all the differences that divide the nations of the earth, the scientists participating in MAB can meet as colleagues intent on finding solutions to the ecological, social and economic problems which affect all of us on the planet Earth.

5 Reference

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BACKGROUND TO THE FOREST ECOSYSTEM AND PROTECTION OF NATURAL RESOURCES

Tree composition, age structure and regeneration strategy of the mixed broadleaved/*Pinus koraiensis* (Korean pine) forest in Changbai Mountain Reserve

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Abstract

The age structure and regeneration strategy of 6 major species of the broadleaved/*Pinus koraiensis* Sieb. et Zucc. (Korean pine) forest in Changbai Mountain Reserve are discussed in detail. Two types of regeneration strategy are identified. *P. koraiensis, Fraxinus mandshurica* Rupr. (Manchurian ash), and *Quercus mongolica* Fisch. ex Turcz. (Mongolian oak) belong to the discontinuous regeneration type, while *Tilia amurensis* Rupr. (Amur linden), *Acer mono* Maxim. (painted mono maple) and *Ulmus propinqua* Koidz. (Japanese elm) are of a continuous type. A tolerance scale of the major species is suggested: *Q. mongolica* → *F. mandschurica* → *P. koraiensis* → *U. propinqua* → *T. amurensis* → *A. mono* (in increasing order of shade tolerance).

1 Introduction

The mixed broadleaved/*P. koraiensis* forest is distributed between 500 and 1000 metres above sea level (asl) at Changbai Mountain Reserve in Jilin Province, north-east China. It is the most important and the widest distributed forest type among the 3 types of *P. koraiensis* forest. Numerical classification and pattern analysis of the forest have been described in earlier papers (Yang *et al.* 1979, 1984). This paper describes the composition of tree species, age structure and regeneration strategy of the forest.

At Changbai Mountain Reserve, small patches of pure *P. koraiensis* stands can occasionally be seen on the slope and ridge top, but, in general, the conifer is mixed with more than 10 species of broadleaved trees on the gentle slopes and in the valley, including *T. amurensis, T. mandshurica* Rupr. et Maxim. (Manchurian lime), *F. mandshurica, Juglans mandshurica* Rupr. (mountain walnut), *Acer mandshuricum* Maxim. (Manchurian maple), *A. mono, U. propinqua, U. laciniata* Mayr. (large-leaved elm), *Phellodendron amurense* Rupr. (Amur cork tree), *Betula costata* Trautv. (yellow birch) and *Q. mongolica*. Occasionally, *Populus ussuriensis* Kom. (Ussuri poplar) and *P. koreana* Rehd. (Korean poplar) can be found in the forest, as pioneer trees. *Populus davidiana* Dode (Chinese aspen) and *Betula platyphylla* Suk. (Manchurian birch) usually appear in a gap or on the edge of the forest, but are few in number and not important species.

2 Study methods and sites

2.1 Sites

The sample plots were located in the mixed broadleaved/*P. koraiensis* forest on the mountain, behind the Bureau of the Changbai Mountain Reserve, 42°25′N and 128°6′E, at an elevation of 740 m asl and on a slope of about 5°. The soil is a dark brown forest earth, formed by volcanic ash, with a pH value of 6.2 and a depth of about 130 cm. The soil fertility is rich. In the canopy of the forest, *P. koraiensis* comprises 33.8% of the total tree species. The important species of mixed broadleaved trees include *T. amurensis, A. mono, F. mandshurica, U. propinqua, B. costata, Q. mongolica*, with some *P. davidiana* and *B. platyphylla*.

2.2 Layout of sample plots

Transects were chosen at random about 200 m from the edge of the forest stands. Each transect measured 50 m by 10 m, and contained 5 recording quadrats of 10 m^2. Fourteen transects were investigated, totalling 0.7 ha in area.

2.3 Delimiting the boundary of a tree crown

The projection of tree crown in the main storey (over 16 m high) was encircled by ropes. If the gap between 2 crowns was less than 10 m^2, it was divided by the 2 neighbouring crowns. When the area of the gap was larger than 10 m^2, it was regarded as a gap (Figure 1). This method has the advantage of not only considering the saplings under the canopy, but also including those around the canopies.

2.4 Recording items

The diameter breast height (dbh), total height (by estimation), and health of each tree over 10 cm dbh were recorded.

2.5 Measuring tree age

The age of standing trees was measured using an

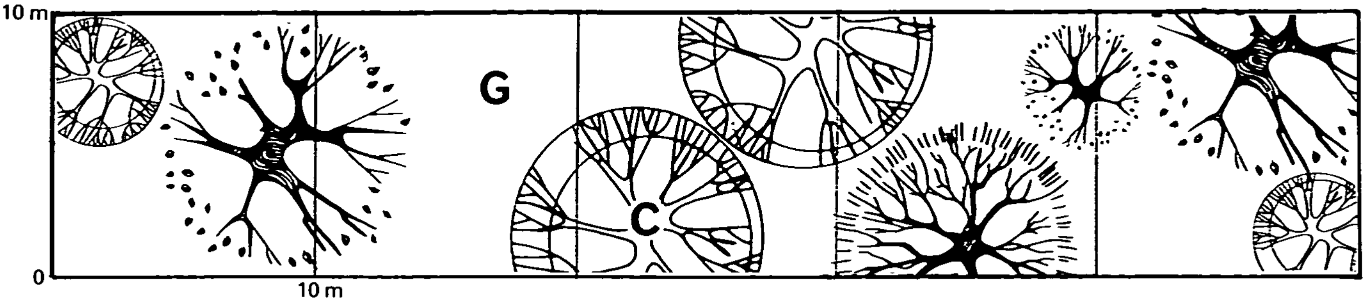

Figure 1. Definition of the boundaries of tree crowns (C = crown projection; G = gap)

increment borer. This method can lead to errors when a tree is larger than 1 m dbh or if pseudo-rings appear, and cannot be used in tropical or subtropical regions, because trees there probably have 2 or more rings in a year, and much of the timber is too hard to bore. However, in the mixed broadleaved/*P. koraiensis* forest studied, few trees are larger than 60 cm dbh, the annual ring appears clearly, and the timbers of the major species are not too hard. The method is labour intensive, so only a certain proportion of trees were sampled, from different dbh classes. Regression equations were calculated for tree age on dbh, and tested for significance, and the results show a highly significant correlation. Altogether, 85 trees of different species were measured, 27% of the total trees surveyed in the main storey.

3 Results and analysis

3.1 Composition of tree species

The canopy can be divided into 2 storeys. The first storey has an average height of about 25 m and contains 4 species: *P. koraiensis*, *T. amurensis*, *F. mandshurica* and *Q. mongolica*. The second storey is 16–20 m high, and includes all species in the first storey, together with *A. mono*, *A. mandshuricum*, *U. propinqua*, *U. laciniata* and *B. costata*. Sometimes, the transition between the 2 storeys does not appear very sharp. Below the main storey (16 m), there is a layer of small trees about 10 m high, which includes several *Acer* spp. (*A. barbinerve* Maxim. (hair maple), *A. tegmentosum* Maxim. (Manchu striped maple), and *A. tschonoskii* Maxim. var. *rubripes* Kom. (small maple)), *Syringa amurensis* Rupr. (white lilac), *Philadelphus schrenkii* Rupr. (north-east mock-orange) and *Maackia amurensis* Rupr. et Max. (Amur maackia) (Figure 2). The number and basal area at breast height of the major species in the main storey are shown in Table 1.

Table 1. The number and basal area at breast height of major species in the main storey

Species	Number	% of number	% of basal area
P. koraiensis	92	33.8	30.2
T. amurensis	67	23.6	23.4
F. mandshurica	24	8.4	14.8
A. mono	34	12.0	6.3
Q. mongolica	34	12.0	18.7
U. propinqua	12	4.6	4.0
B. costata	3	1.1	1.2
Populus spp.	12	4.5	1.4

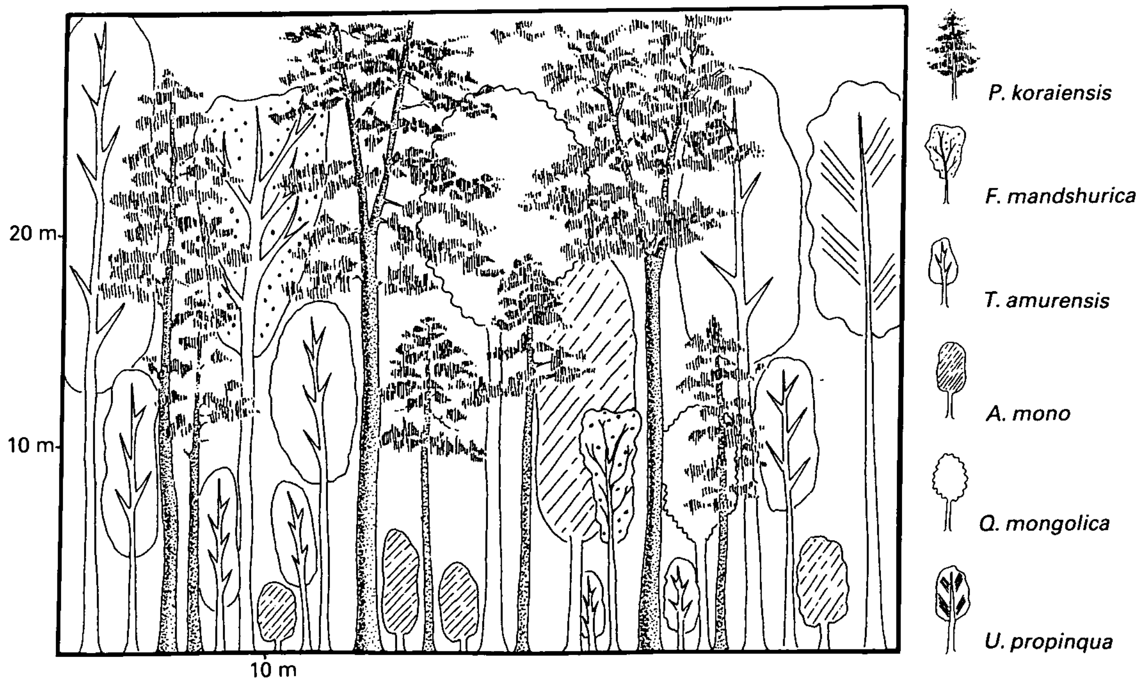

*Figure 2. A profile of the mixed broadleaved/*P. koraiensis *forest at Changbai Mountain Reserve. In the main storey,* P. koraiensis *accounts for 33% of the stems and* T. amurensis *for 23%*

It can be seen from the Table that *P. koraiensis* makes up 33.8% and 30.2% respectively of the total percentage of numbers of trees per hectare and of total basal area, and is clearly the most important species in the forest. The second dominant tree is *T. amurensis*, which amounts to 23% both in number and in basal area. *Q. mongolica* and *A. mono* each account for 12% in number, but the trees of the former species are much larger, with a basal area of 18.7%, 3 times more than that of *A. mono*, which makes up 6.3% of the total. *U. propinqua* comprises 4.6%, and has a basal area of 4%. Compared with the other species, *U. propinqua* does not hold a very important place in the forest. *B. costata* accounts for only 1.1% and 1.2% in number and basal area respectively.

The number and basal area of *P. davidiana* and *B. platyphylla* amount to 4.5% and 1.4% respectively. These are pioneer species appearing in the gap of the forest. No large tree of *P. ussuriensis* was seen, but there were 4 seedlings, 2–5 m in height.

In summary, the mixed broadleaved/*P. koraiensis* forest consists of 5 principal tree species: *P. koraiensis*, *T. amurensis*, *F. mandshurica*, *Q. mongolica* and *U. propinqua*. *P. koraiensis* ranks first in the forest, with *T. amurensis* second. The other species are not of comparable frequency.

3.2 Structure of the major tree species in the main storey

In order to understand the regeneration of the major species in the main storey, attention must be paid to the distribution of seedlings, saplings and small trees of each important species under the different canopies. The results are given in Table 2.

Table 2. The distribution of seedlings, saplings and small trees of each important species under different canopies (number ha^{-1})

Canopy species	*Pinus koraiensis*	*Tilia amurensis*	*Fraxinus mandshurica*	*Acer mono*	*Quercus mongolica*	*Ulmus propinqua*	*Populus & Betula*	Total
P. koraiensis	22	116	76	799	34	34	35	1116
T. amurensis	23	93	61	291	26	13	9	516
F. mandshurica	6	42	36	166	34	6	0	290
A. mono	12	28	43	59	9	3	1	155
Q. mongolica	37	170	74	370	52	1	3	707
U. propinqua	4	8	21	39	7	3	4	86
Populus & Betula	17	33	49	121	17	9	10	256
Total	121	490	360	1845	179	69	62	3126

Only 121 individuals of *P. koraiensis* per hectare are present under their own canopies and those of other species, compared with 1845 individuals ha^{-1} of *A. mono*. *T. amurensis* and *F. mandshurica* account for 490 and 360 individual plants respectively, and there are 179 individuals of *Q. mongolica*, all more numerous than *P. koraiensis*. *U. propinqua* has 69 plants, and *Populus* and *Betula* species together account for only 62 individuals.

Saplings and seedlings of different species are abundant under the canopies of only 121 individuals of *P. koraiensis*, with a total of 1116 plants. Between 120 and 160 years of age, *P. koraiensis* begins to spread out its crown, creating suitable conditions for seedlings and saplings of various shade-tolerant species. The oldest *P. koraiensis* trees in the forest are between 260 and 280 years old. Another interesting fact is that more individuals of *P. koraiensis* grow under the shade-intolerant species – *Q. mongolica*, *Populus* and *Betula*. There are 37 individual plants of *P. koraiensis* under the canopies of *Q. mongolica*, amounting to 30.6% of the total number for this species under canopies of all species. Also, *Populus* and *Betula* comprise only 4.5% of the total trees in the main storey, but have 17 individuals of *P. koraiensis* under their crowns.

If seedlings (<2.5 cm dbh) are excluded, the result is different, as shown in Table 3. The proportion of *P. koraiensis* increases significantly, while *A. mono* decreases, indicating that one third of the individual plants of *P. koraiensis* are present as small trees. The seedlings of *A. mono* are numerous, but there are few saplings. A large number of seedlings will not grow because of the biological characteristics of the species.

Table 3. The number of saplings and small trees of different species under canopies of each species in the main storey (number ha^{-1})

Canopy species	*Pinus koraiensis*	*Tilia amurensis*	*Fraxinus mandshurica*	*Acer mono*	*Quercus mongolica*	*Ulmus propinqua*	*Populus & Betula*	Total
P. koraiensis	12	7	7	10	1	9	1	47
T. amurensis	2	29	4	8	1	0	1	45
F. mandshurica	2	3	0	4	0	0	0	9
A. mono	2	6	6	5	10	0	2	31
Q. mongolica	21	24	4	9	0	0	0	58
U. propinqua	0	0	3	6	0	1	4	14
Populus & Betula	1	7	4	4	0	6	2	24
Total	40	76	28	46	12	16	10	228

Table 3 also shows that there are 21 saplings and small trees of *P. koraiensis* under the canopies of *Q. mongolica*, whereas there are few saplings and small trees of *Q. mongolica*, *Populus* or *Betula*. Although the proportion of *Q. mongolica* is high in the main storey, the numbers of saplings and small trees are far fewer than for *F. mandshurica*.

The basal area of the different species under the canopies of each major species are listed in Table 4. *P. koraiensis* has the largest basal area under the canopies of *Q. mongolica*, amounting to nearly 28% of the total basal area of the major species under the main storey.

Table 4. The basal area and percentage of each major species under the canopies of different species (number ha^{-1})

Under canopy/ in canopy	*Pinus koraiensis*	*Tilia amurensis*	*Fraxinus mandshurica*	*Acer mono*	*Quercus mongolica*	*Ulmus propinqua*	*Populus & Betula*	Total
P. koraiensis	1786	838	367	1053	12	94	99	4244
T. amurensis	544	1091	35	267	13	2	86	2038
F. mandshurica	167	124	1	77	0	0	0	368
A. mono	121	74	326	350	454	1	39	1364
Q. mongolica	5556	2480	212	1567	0	0	0	9815
U. propinqua	0	3	16	48	3	32	23	124
Populus & Betula	718	111	616	315	2	177	11	1951
Total	8892	4721	1573	3677	484	306	258	19903
%	44.7	23.7	7.9	18.5	2.4	1.5	1.3	100

The proportion of *T. amurensis* species growing under the canopies, accounting for 23.7%, is very close to that found in the main storey, 23.4%, while the proportion of *P. koraiensis* species amounts to 44.7%, which is much higher than that of the other species. The reason lies in the large number of small trees.

In addition, the proportion of basal area of *Populus* and *Betula* is very low, only 1.3%, while those of *P. koraiensis* and the shade-tolerant species, *T. amurensis* and *A. mono*, have a high proportion of basal area. The striking similarity between the ratio of basal areas of each species under canopies to that in the main storey indicates the natural regeneration processes in the mixed broadleaved/*P. koraiensis* forest. It seems that *P. koraiensis* may regenerate in considerable proportions, and maintain its position as the dominant species, while the shade-tolerant species, *T. amurensis*, *A. mono* and *F. mandshurica*, will maintain their role in the forest. The shade-intolerant trees, *Q. mongolica*, *Populus* and *Betula* species, will continue to be minor components.

3.3 Age structure and regeneration strategy of the major species

Analysis of data on the age structure of tree populations is a useful method for studying the regeneration strategy of the species and the actual state of the forest. Each of the major species, *P. koraiensis*, *T. amurensis*, *F. mandshurica*, *A. mono*, *Q. mongolica* and *U. propinqua*, is discussed.

3.3.1 *P. koraiensis*

Twenty-nine trees, 10–71 cm dbh, have been measured using an increment borer. The regression equation of age on dbh is given as:

$$A = 86.0360 + 1.8607D$$
$$F = 28.76$$
$$N = 29,\ F(1,28) = 7.64$$
$$R = 0.72^{**}\ (^{**} = \text{highly significant}) \qquad (1)$$

where A = age, and D = diameter breast height. The equation is plotted in Figure 3.

The correlation coefficient is slightly lower than in the mixed *Picea/Abies/P. koraiensis* forest, which is 0.77. On checking the data, we found some variations among the 11 sample trees between 10–20 cm dbh, which represent an irregular age distribution from 80 to 160 years. This irregularity may be explained by the varying degrees of suppression in that period of their growth. However, the regression of age on dbh of 29 trees is still highly significant. *P. koraiensis* will resume normal growth after it passes the suppression stage and grows into the main storey. From the scatter diagram, it seems that in some individual trees dbh may not be closely correlated with age, and an average slope for the whole group of *P. koraiensis* trees is still warranted.

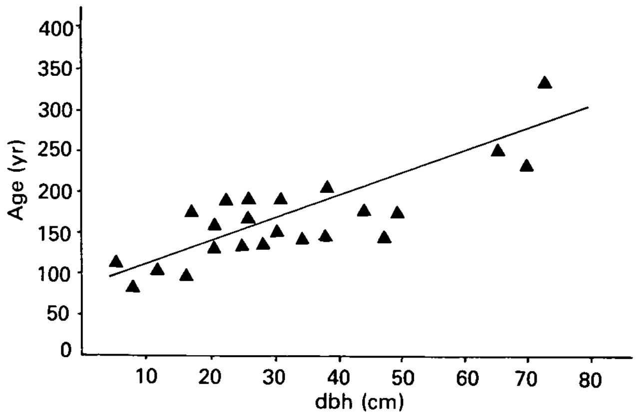

Figure 3. The regression of age on dbh for P. koraiensis

The distribution of individual plants of *P. koraiensis* in the different age classes (each class = 20 years) is shown in Figure 4. The Figure shows clearly that the population lacks 3 age classes, ie II, III and IV (from 21 to 80 years), which means that there are no saplings of this species in the forest at this time. It can also be

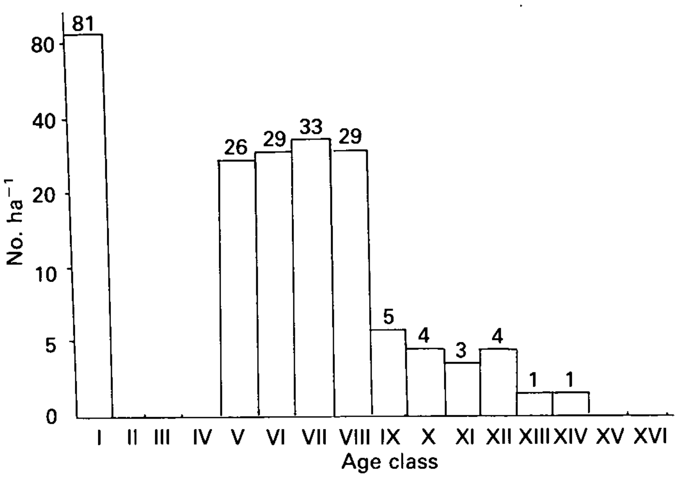

Figure 4. The age structure of the P. koraiensis *population*

seen that there are 81 seedlings of no more than 20 years old and 1.3 m high. This result seems to confirm the general statement that *P. koraiensis* has 'only seedlings and no saplings' in the forest.

Figure 3 also shows that *P. koraiensis* is a species with discontinuous regeneration, and enters the forest in 'waves'. The latest wave is from 80 to 160 years. In this period, large numbers of trees emerge, with a concentrated distribution – there are 117 standing trees in this period. Forty small trees have not yet grown into the main storey, and will not resume normal growth until the old overhead trees of *P. koraiensis*, *T. amurensis* and *Q. mongolica* fall down. Then, they will grow up rapidly to enter the main storey. In this latest wave, another 77 trees have taken an important place in the main storey, accounting for 81% of the total number of *P. koraiensis*. The oldest tree is 260–280 years old, the oldest in the forest, but only 2 individuals are left. There is another wave from 180 to 240 years old, when 16 trees are present.

It appears that the regeneration process covers a period of 40–60 years. Bai (1965) pointed out that *P. koraiensis* can be divided into generations of 60 years, and that there are 3 generations in a mature forest at the same time. This observation was confirmed by our study.

According to literature and field investigations, *P. koraiensis* in natural stands begins to bear fruit at about 80 years old, and increases gradually to a peak period of fruiting at 180–220 years, but will not lose its capability for fruit bearing until its death. Every 3–5 years, there is a heavy harvest. Seeds can germinate in mineral soil and on rotten logs. In the first 20 years, seedlings can endure shade, but grow very slowly under direct overhead shade. As soon as the shade disappears, they will recover to grow at a normal rate. This pattern of growth is clearly indicated by ring measurement. At about 160 years of age, the tree spreads out its crown horizontally. *P. koraiensis* appears to be a neutral to slightly shade-intolerant species.

The rate of survival of the species is difficult to estimate, but Figure 4 shows the age structure of trees at different stages (also named waves). The younger stage, between 80 and 160 years, has 117 trees, while the older stage, 160–240 years, has 16 individuals. Each stage lasts for 80 years between the 2 stages. The rate of survival may be estimated as follows:

Rate of survival in 80 years =

$$\frac{\text{individuals in older stage}}{\text{individuals in younger stage}} = \frac{16}{117} = 0.1368 \qquad (2)$$

Therefore, the rate of survival in a 10-year period =

$$8\sqrt{0.1368} = 0.7798$$

It is worth noting that, according to equation (2), the average rate of survival in each 10-year period from 160–240 years to 240–280 years, when 2 individuals are present, is 0.7711. The 2 values are nearly the same, and the average is 0.7755. There appears to be a regular decrease of individuals with age.

At the peak stage, there are 117 trees with an average age of 120 years, and an average number of 11.7 trees in each 10-year period. Using the survival rate of 0.7755, only one tree will be left after 330 years. This calculation can be used to estimate the maximum lifespan of *P. koraiensis* as 450 years.

The analysis of the height growth data shows that *P. koraiensis* takes about 30 years to reach 1.3 m, and 90 years to enter the main storey, over 16 m.

3.3.2 T. amurensis

From the age measurements of 15 trees, 9.5–68.4 cm dbh, the regression equation of age on dbh is as follows:

$$A = 2.8D + 8.4$$
$$F = 113.4,\ N = 15,\ F(1,14) = 8.86$$
$$R = 0.96^{**} \qquad (3)$$

The regression equation is plotted in Figure 5, and the distribution of individual plants in each age class is

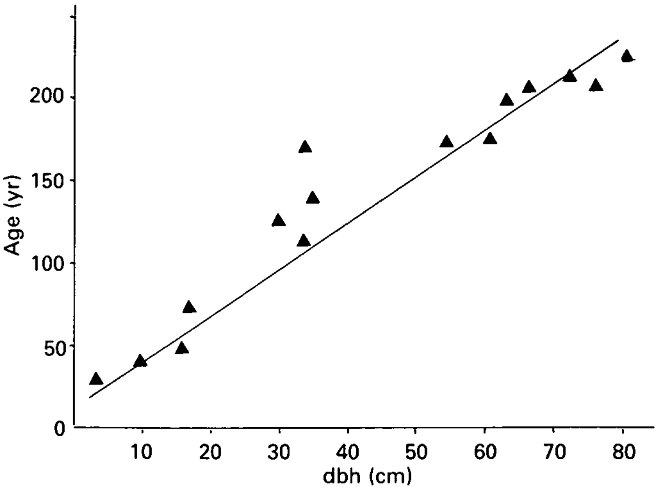

Figure 5. The regression of age on dbh for T. amurensis

shown in Figure 6. *T. amurensis* appears to be a stable species, with a continuous regeneration strategy, and is highly shade tolerant. It entered the forest at 220 years of age, 60 years later than *P. koraiensis*. Since then, the number of individuals has increased gradually. The age structure presents an inverse j-form, and can be fitted by a negative exponential equation:

$$N = 20.2809 \exp(-0.0450t)$$
$$F = 71{,}30,\ N = 7,\ F(1{,}6) = 13.74$$
$$R = 0.96^{**} \qquad (4)$$

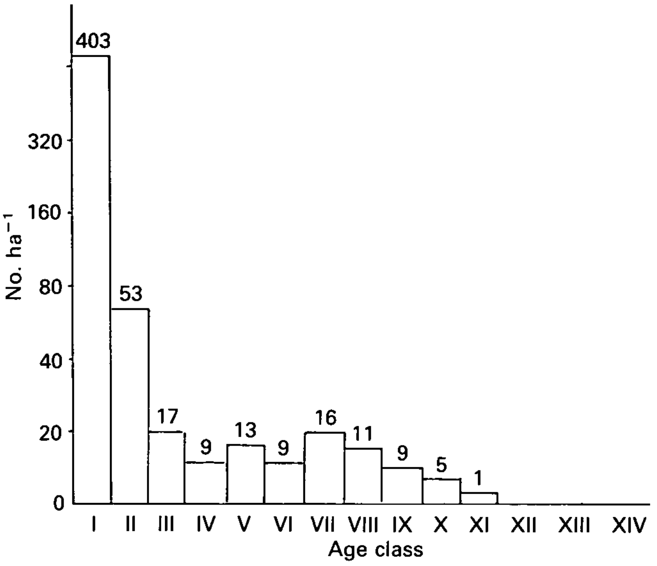

Figure 6. The age structure of the T. amurensis *population*

From equation (4), the average rate of survival in each 10-year period (Lr) can be estimated as:

$$Lr = \frac{B \exp(-At(2))}{B \exp(-At(1))} = \exp(-A(t(2)-t(1)))$$
$$= \exp(-10A)$$
$$= \exp(-10 \times 0.0450) = 0.6376 \quad (5)$$

and the integral equation is:

$$Nr = \int_x^{\infty} B \exp(-At)\,dt < 0.01 \qquad (6)$$

where Nr = number of trees after x years.

If Nr is less than 0.01, no more than one tree remains in 100 ha after x years, so x years is the maximum lifespan of the species.

According to equations (4) and (6):

$$Nr = \int_{240}^{\infty} B \exp(-At)\,dt = 0.0092 < 0.01$$

Thus, it is obvious that the maximum lifespan of *T. amurensis* is about 240 years, which agrees well with general observations.

Based on growth analysis, it appears that *T. amurensis* can grow to a height of 1.3 m in 6–9 years and will enter the main storey in about 60 years.

3.3.3 *F. mandshurica*

Eleven trees of *F. mandshurica*, 2.7–59.5 cm dbh, have been measured, and a regression equation of age on dbh is estimated as:

$$A = 3.8379D + 6.2522$$
$$F = 126.51,\ N = 11,\ F(1{,}10) = 10.04$$
$$R = 0.97^{**} \qquad (7)$$

The equation is plotted in Figure 7, and the age structure of *F. mandshurica* in the broadleaved/*P. koraiensis* forest is shown in Figure 8. The Figure gives a clear picture of *F. mandshurica* as a species of discontinuous regeneration. The species appeared in the forest between 160 and 240 years ago, slightly later than *P. koraiensis*. The first wave lasted as long as 80 years, and the second wave came in the last 60 years. Saplings and seedlings are limited in number, and usually grow in a moist site. The characteristics of discontinuous regeneration for *F. mandshurica* make it difficult to estimate its survival rate. Using equation (2) and the numbers of trees in age classes X, XI and XII, we estimated the survival rate in each 10-year period

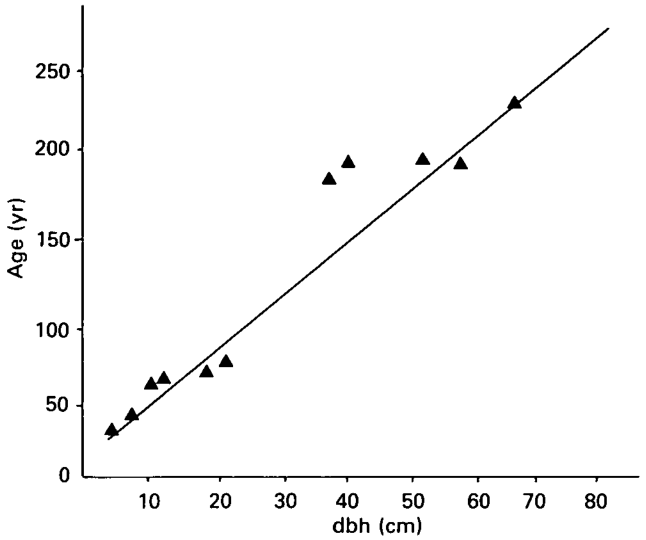

Figure 7. The regression of age on dbh for F. mandshurica

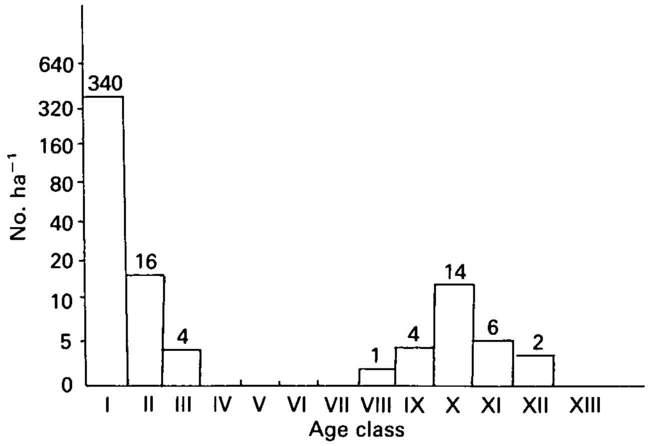

Figure 8. The age structure of the F. mandshurica *population*

from class X to class XI as 0.6547, and from class XI to class XII as 0.6148, giving an average of 0.6348. The maximum lifespan of *F. mandshurica* is estimated as 280 years.

Growth analysis also shows that *F. mandshurica* takes 5–7 years to reach a height of 1.3 m, and 50 years to grow into the main storey.

3.3.4 *A. mono*

The age of 11 sample trees of 2.5–36.9 cm dbh has been determined, and the regression equation of age on dbh is as follows:

$$A = 4.4085D + 5.7428$$
$$F = 97.76,\ N = 11,\ F(1,10) = 10.04$$
$$R = 0.96^{**} \qquad (8)$$

Using the regression equation plotted in Figure 9, the age structure of the species in the forest is shown in Figure 10. It appears to be a negative exponential distribution. From the numbers of saplings and seedlings, the species is clearly more shade tolerant than *T. amurensis*. *A. mono* became established in the forest 220 years ago, at the same time as *T. amurensis*, but is not abundant. The growth analysis reveals that it appears to need 6–7 years to reach 1.3 m and about 50 years to enter the main storey.

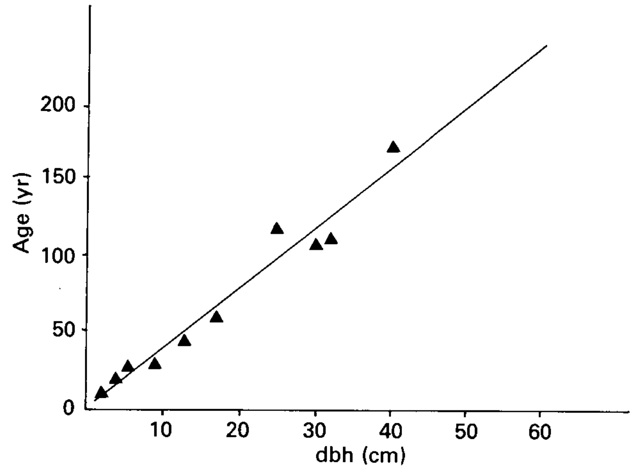

Figure 9. The regression of age on dbh for A. mono

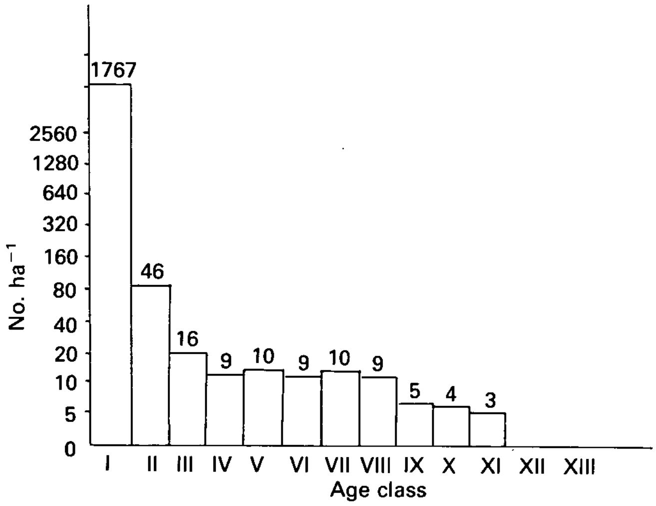

Figure 10. The age structure of the A. mono *population*

From the distribution of trees in each age class, we can fit a negative exponential equation:

$$N = 83.6132 \exp(-0.0477t)$$
$$F = 34.58,\ N = 9,\ F(1,8) = 11.26$$
$$R = 0.91^{**} \qquad (9)$$

The survival rate of *A. mono* in each 10-year period can be estimated by equations (5) and (9) as:

$$Lr = 0.6208$$

and the following integral equation as:

$$N = \int_{250}^{\infty} 83.6132 \exp(-0.477t)\, dt = 0.0069 < 0.01$$

As a result, the maximum lifespan of *A. mono* is estimated at 250 years, which agrees with field observations.

3.3.5 *Q. mongolica*

We sampled 11 trees of *Q. mongolica* and determined their ages to obtain the following regression equation of age on dbh:

$$A = 3.1530D + 15.0629$$
$$F = 61.53,\ N = 11,\ F(1,10) = 10.04$$
$$R = 0.93^{**} \qquad (10)$$

According to equation (10) (plotted in Figure 11), the age structure of *Q. mongolica* in the forest is shown in Figure 12. Obviously, it is a species of discontinuous regeneration, and its age structure appears to be similar to that of *F. mandshurica*. The species emerged in the forest at 2 different periods: the first wave appeared 160–220 years ago, 20 years later than *F. mandshurica*, and the second 60 years ago. Its seedlings and saplings number half those of *F. mandshurica*, indicating that it is a shade-intolerant species.

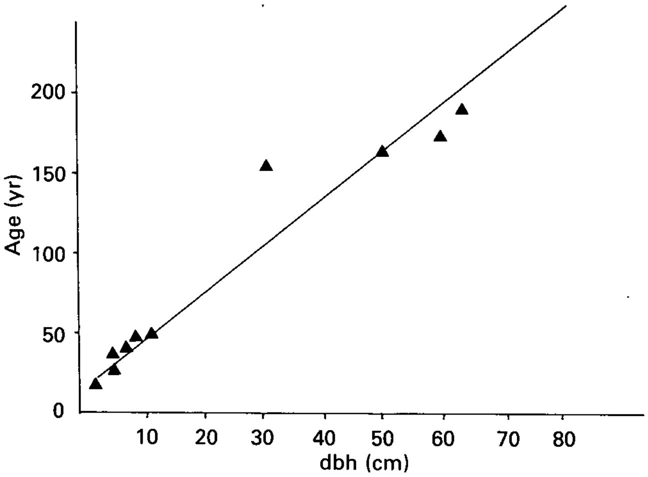

Figure 11. The regression of age on dbh for Q. mongolica

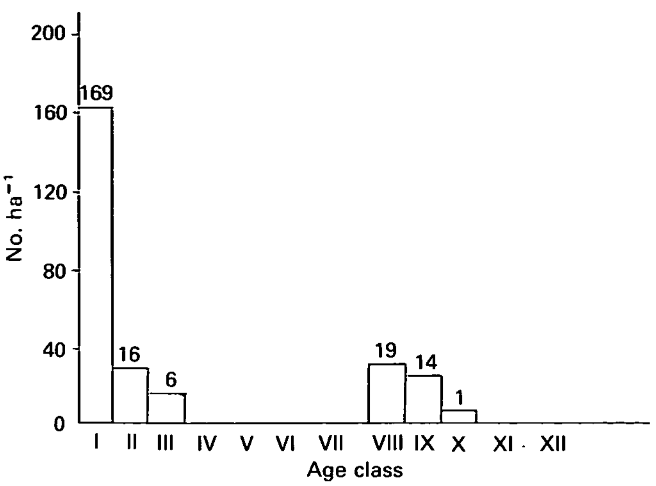

Figure 12. The age structure of the Q. mongolica *population*

Its survival rate in each 10-year period is estimated as 0.6687, and its maximum lifespan is 270 years.

From the growth analysis, we know that *Q. mongolica* grows 1.3 m high in 7–10 years and into the main canopy in about 60 years.

3.3.6 U. propinqua

The regression equation of age on dbh for *U. propinqua* is based on 11 sample trees of 1.2–35 cm dbh:

$$A = 3.9274D + 5.0031$$
$$F = 208.66, N = 11, F(1,10) = 10.04$$
$$R = 0.98^{**} \qquad (11)$$

and is plotted in Figure 13.

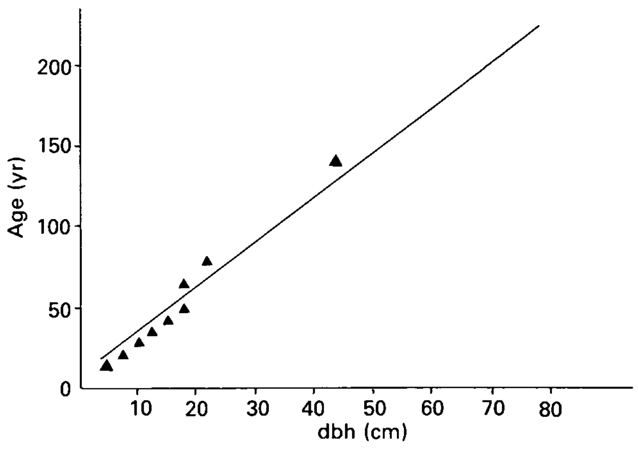

Figure 13. The regression of age on dbh for U. propinqua

U. propinqua is a wind-dispersed species, with continuous regeneration. A negative exponential curve can be fitted to the distribution of individuals in the different age classes (Figure 14).

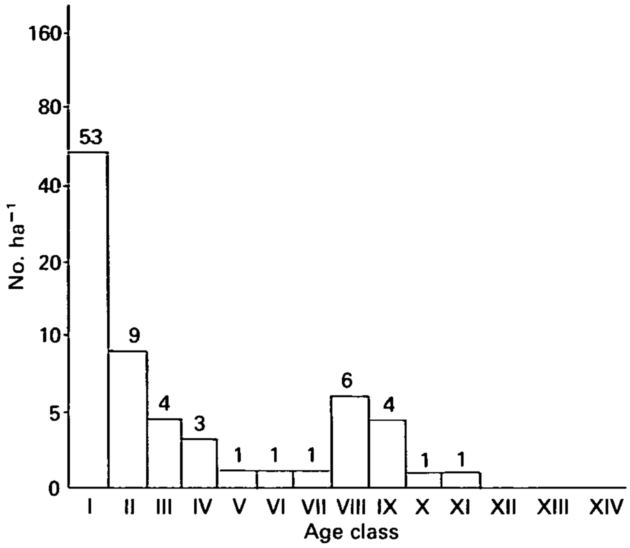

Figure 14. The age structure of U. propinqua

$$N = 4.8903 \exp(-0.0371t)$$
$$F = 32.46, N = 7, F(1,6) = 13.74$$
$$R = 0.96^{**} \qquad (12)$$

Together with *Q. mongolica*, *U. propinqua* entered the forest 220 years ago. There was a small wave between 140 and 180 years, since when the species has emerged continuously into the forest, growing up into the main storey.

In accordance with equations (6) and (12), the species survival rate in each 10-year period is 0.6898, and its lifespan is estimated by equations (6) and (12) as 260 years.

From the growth analysis, *U. propinqua* appears to need 4–5 years to grow 1.3 m, and 60 years into the main storey.

3.4 Comprehensive analysis of the forest

In order to understand the regeneration strategy in the forest, we carried out a comprehensive analysis on the age structure of the 5 major species (Figure 15). It is clear that the mixed broadleaved/*P. koraiensis* forest is uneven-aged and multi-layered. Because of the optimal temperature and water conditions, it is probably the richest in floral composition of the world's temperate mixed and conifer forests. *P. koraiensis* is the oldest tree, and was the first species to enter the forest 260–280 years ago. Two old trees still remain. At 240–280 years of age, the species is still in its prime. Why no more individuals of the species have survived is unknown.

Q. mongolica and *F. mandshurica* entered the forest about 40 years later than P. koraiensis (200–240 years ago), followed by *T. amurensis* and *A. mono*. It is remarkable that, of the 5 species, *P. koraiensis*, *T. amurensis*, *A. mono*, *Q. mongolica* and *F. mandshurica*, the latter 2 species accounted for 64% of the total number in the 160–240 year age class. In the 80–160 year age class, or 80 years later, *P. koraiensis*,

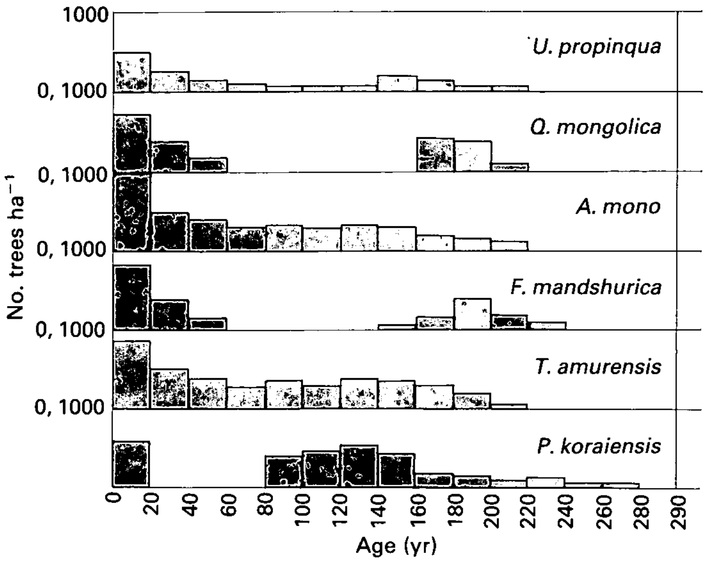

Figure 15. The age structure of the 5 major species

T. amurensis and *A. mono* comprised 58% of the main storey, whereas *A. mongolica* and *F. mandshurica* have rapidly decreased in number. The reason for the decrease seems to be that the canopies became denser, limiting the growth of these shade-intolerant species. In the main storey, *T. amurensis* and *A. mono* retained their position, as shown by the numbers of their saplings and seedlings, which grew up continuously into the canopy layer. The number of *A. mono* in the main storey is limited and their dbh is much smaller, so that this species is less important in the community than *T. amurensis*. It is important to point out that there is no *P. koraiensis* in the 20–80 year age classes.

Figure 14 also shows clearly that the 5 major species can be divided into 2 regeneration types. The first are the discrete or discontinuous regeneration species, such as *P. koraiensis*, *Q. mongolica* and *F. mandshurica*. They enter the forest in waves and show a concentrated age distribution, the length of a wave for *P. koraiensis* being 40–80 years. The second type are the continuous regeneration species, eg *T. amurensis* and *A. mono*. They have trees of all age classes, as shown by the negative exponential equation. *U. propinqua* shows more affinity with the continuous regeneration species.

The species have a different regeneration strategy. Obviously, this strategy is closely related to their ability to grow under the shade of their own canopies or those of other species. *Q. mongolica* and *F. mandshurica* are both shade-intolerant species, *T. amurensis* and *A. mono* are shade tolerant, *P. koraiensis* neutral to shade intolerant, and *U. propinqua* neutral to shade tolerant. In increasing order of tolerance, the scale is as follows:

Q. mongolica → *F. mandshurica*→ *P. koraiensis* → *U. propinqua* → *T. amurensis* → *A. mono*

The analysis of the age structure in the forest is time-consuming, but is the only method which can reflect the actual state of the forest, and shed some light on its past history.

Only some of the major species have been mentioned in the mixed broadleaved/*P. koraiensis* forest, yet the pattern of different combinations of variety and number of species is quite diverse. This spatial variation is shown clearly by numerical classification (Yang *et al.* 1979). Therefore, an analysis of the age structure of the stand at different sites will undoubtedly provide useful information for predicting future development of the forest. In the absence of serious disturbances like volcanic eruption, forest fire, felling, etc, the forest community will develop by autogenic succession. The future of the mixed broadleaved/*P. koraiensis* forest will be discussed in a future paper.

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Preservation of the forest resource of Changbai Mountain in relation to human activities

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Abstract
The rich natural resources of Changbai Mountain have been seriously disturbed by human activities. In order to improve this situation, we must (i) increase the forest cover to 80% of the total land area, (ii) give priority to forestry in the economic development of the region, (iii) introduce advanced methods of science and technology, and (iv) control population growth.

1 Introduction

1.1 Natural resources of Changbai Mountain

The characteristics of Changbai Mountain area have already been described. The area's main natural resource is forest, and *Pinus koraiensis* Sieb. et Zucc. (Korean pine) is the major species. The mixed coniferous and broadleaved forests contain a multi-storeyed canopy, with a high yield and quality of wood production. Because of the high mountains, dense forests and numerous springs, many rivers rise in this area, eg the Songhua, Yalu, Tumen, Mudan and Suifen Rivers. Runoff and water reserves make up 70% and 88.3% respectively of the total area. There are 127 plant genera, including 1477 species of higher plants and 510 species of lower plants. There are several valuable tree species, such as *P. koraiensis*, *Larix* (larch), *Picea* (spruce) and *Abies* (fir), and many kinds of medicinal herbs, such as *Panax ginseng* C.A. May (ginseng), *Codonopsis pilosulae* Nannfeldt (Dangshen), *Asarum heterotropoides* Fr. Schmidt. var. *mandshuricum* (Maxim.) Kitag. (wild ginger), *Schisandra chinensis* (Turcz.) Baill. (Chinese magnolia vine), *Fritillaria ussuriensis* Maxim. (Ussuri fritillary), etc. The flowering plants include *Chamaenerion angustifolium* (L.) Scop. (rosebay willow herb), *Lychnis fulgens* Fisch. (senno campion), *Lilium distichum* Nakai (wheel-leaf lily), and *Iris dichotoma* Pall. (golden-fringed iris). More than 300 vertebrate species have been recorded in the area, including *Pantha tigris longipilis* L. (north-east tiger), *Cervus nippon* Temminck (Sika deer), *Felis lynx* L. (lynx), *Moschus moschiferus* L. (musk deer), *Martes zibellina* L. (marten), *Lutra lutra* L. (otter), *Sciurus vulgaris* L. (grey squirrel), *Mustela sibirica* Pallaë (yellow weasel), *Agkistrodon halys* Pallas (Pallas pit viper), *Rana chensiensis* David (Chinese forest frog), etc. Many precious drugs are obtained from the area, such as ginseng, pilose antler, tiger bone, musk, bear's gall bladder, frog oil, and deer's tail.

2 Effects of human activities on the forestry resource

About 3000 years ago, a minority nationality – the Sushen – lived in the area and were in close contact with the people of central China. The members of the Bohai dynasty from 698 AD were the first to exploit the Changbai area. Fishing, hunting and animal husbandry were the main activities, and people began to reclaim and cultivate waste land for agriculture. The use of drawn ploughs and iron tools expanded the cultivated area, and increased the effectiveness of agricultural production. The crops grown were mainly chestnut, wheat, beans and rice, and hand industries included textiles, pottery mining and ship-building. Reclamation and cultivation were carried out mainly in the river basins.

Along with the development of agricultural production, people had to cut increasing numbers of trees for building houses, making ships, and for energy, but these activities did not affect the stability and basic condition of the forest ecosystem.

However, at the end of the 19th century and during the Qing dynasty, when the administrative system was set up, land was being cultivated at an unprecedented rate. Almost all the river valleys, flat lands and hillside fields were reclaimed for farmland, and forests were cut on a large scale, including the area along the rivers.

In 1907, there were 89951 people living in Tonghua county, 107767 in Jian county, and 9551 in Linjiang county. At present, the total population in the Changbai Mountain area (including Tonghua and Yanbian areas) is about 5 million, 52.8% of which is employed in agriculture. The population density of the area is 76 people per square kilometre, and industry makes up 75.4% of the total output for the area.

The total area of forestry in the Changbai area is 9.3 Mha, covering 49% of Jilin Province. The annual increment of standing stock is about 24 million m^3, with a growth rate of 3.6%. The annual cutting rate is now controlled at 3.06%, and the total consumption of timber is about 21 million m^3 yr^{-1}.

3 Developing a balance between ecology, technology and the economic society

In the Changbai Mountain area, the forest is the most important natural resource, although, at present, its importance has not been fully recognized. Destruction of the forest in the past has had serious consequences. In Yanbian, 10.5% of the total land area suffers from soil erosion, the main causes being the destruction of the forest cover and the cultivation of the hillsides. According to statistics, the annual loss of soil nutrients exceeds the chemical fertilizer applied to the whole agricultural area. Changes in soil utilization structure (the proportion of agriculture, forestry and animal husbandry) and in the ecological resources (plants and animals) have restricted development.

In order to improve the whole ecosystem, to make proper use of the natural resources of light, heat, water and soil, and to give priority to forestry, it is necessary to establish a correct balance between the economic, social, ecological and technological needs of the area, by well-balanced planning and comprehensive assessment.

To protect the natural resources and to make rational use of them, and to improve the present low level of energy flow through the ecological system, the following measures are suggested.

i. Forest cover should be increased, while improving the forest structure and quality of the plant community. To ensure the stability and balance of the ecological system, no cutting should be permitted in the mountain area, but selective cutting may be allowed in the basin area.

ii. The present use of land is irrational, and the area devoted to farmland is too great. Some of the cultivated land on the hillsides should be returned to woodland or pasture for grazing. The remaining areas of farmland should be cultivated intensively to increase agricultural productivity.

iii. Advanced methods of science and technology should be introduced for the development of the area. Advantage should be taken of existing achievements in scientific research, ie remote sensing, computing and systems engineering, in preparing an overall management plan. Forest cutting in the eastern part of the area should be selective and the broadleaved/*P. koraiensis* forest should be managed rationally so as to increase forest productivity. A management plan should be prepared for the forest industry to ensure the continued utilization of this valuable resource.

iv. The rate of population growth should be strictly controlled. The high population growth rate and the large-scale destruction of the forest are serious threats to the preservation of the area's natural resources. For instance, the amount of fuelwood required each year for one family is about 7 m^3. At present, the amount of wood burnt annually is about 2.63 million m^3 for the whole area, which is about 50% of the amount of annual wood production cut by state operations in the region. Population control and careful management of productivity are the most important measures to be adopted in the protection of the forest resources in the Changbai Mountain area.

Historical eruptions of the Changbai volcano resulting in large-scale forest devastation (deduced from widespread tephra)

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Abstract
A sheet of volcanic ash has been studied from various archaeological sites in northern Japan, as well as from several piston cores in the northern Sea of Japan. Physical and chemical features of this ash indicate that it represents the youngest major eruption of the Changbai (Baegdu) volcano. The stratigraphic position of several sites in northern Japan suggests that the major eruption of the Changbai volcano occurred some time around the end of the 10th century. It is known that vegetation at the summit of the Changbai volcano has not yet recovered completely after being buried by pumice falls and flows. Buried forests are reported at several localities high above the present tree-line. Case histories from northern Japan, northern Korea and north-eastern China illustrate the importance of this volcanic activity to ecologists, as well as to geologists.

1 Introduction

In highly volcanic areas like Japan, the impact of exploding volcanoes on human life and on the environment must be great. In fact, it has been documented that a number of historical eruptions have severely damaged volcanic areas. Generally speaking, the amount of such damage depends on the nature and magnitude of the eruptions, the distance from the volcano centre to inhabited areas, and the type and density of the settlements within the range of damaging effects. The damage caused by effusive and mixed-type eruptions is usually fairly local or of short range. In contrast, the highly explosive activity of plinian and ignimbrite-forming types has not only had severe local or short-range effects but also long-range and semi-global ones, even though their occurrence is infrequent. Such events are exemplified in historic times by the Santorini (1500 BC), Vesuvius (79 AD), Tambora (1815 AD) and Krakatau (1883 AD) eruptions, all of which had severe effects on human beings and their environments, resulting in a lack of cultural continuity.

This paper presents case studies on the cataclysmic eruptions of the Changbai volcano and assesses the probable ecological significance of such events for the surrounding area. Our studies started with discoveries in northern Japan of extensive ash deposits derived from eruptions of the Changbai volcano, and are still in progress, but we have little evidence from the Changbai Mountain area itself. The magnitude of the eruption will be described, first, on the basis of tephra correlation between the local area around the Changbai volcano and the more distant areas in the northern Sea of Japan and in northern Japan, and, second, from the large-scale forest devastation on the slopes of the volcano. Finally, we will comment on the age and nature of the eruption, from observation of the ash and archaeological records in Japan.

2 Identification of the volcanic ash derived from Changbai (Baegdu) volcano in northern Japan and the northern Sea of Japan

2.1 Baegdusan-Tomakomai ash (B-Tm ash) in northern Japan

In northern Honshu, 2 volcanic ash layers comprising abundant micropumice and glass shards can be found within strata, bearing the human remains of the Heian age (794–1192 AD). Both layers were previously thought to have come from the Towada caldera in northern Honshu, but have recently been shown to be completely different from each other in their petrographic properties (Machida *et al.* 1981).

The lower layer of ash is pyroxene-bearing rhyodacite, assigned to the phreatomagmatic eruption of the Towada caldera, and is found almost everywhere in the Tohoku (northern Honshu) district (Figure 1). The upper layer is characterized by fine-grained pumiceous and bubble-walled glass shards and by small amounts of alkali feldspar, which is generally lacking in Japanese ashes. It is significant that the major elemental composition of the glass in this ash has a high alkali content, approximately 8.5 wt % (K_2O + Na_2O). Most Japanese ashes are not as rich in alkali, normally less than 7%. Moreover, the (Na_2O + K_2O) – FeO – (CaO + MgO) plot in the glass of some widespread ashes in Japan shows that this ash occupies a particularly characteristic field. It is poor in MgO (0.01–0.02 wt %) and CaO (0.2–0.3 wt %), but rich in FeO (3.8–4.2 wt %). Japanese ashes are entirely different in their composition.

This ash is also conspicuously characteristic in its trace elements. We noticed that the glass presents a chondrite normalized trace element pattern, with high amplitude. For example, the content of rare earths is the highest, except for Eu (europium), which is lowest. Furthermore, we analysed the refractive index of volcanic glass for identification. The variation of the

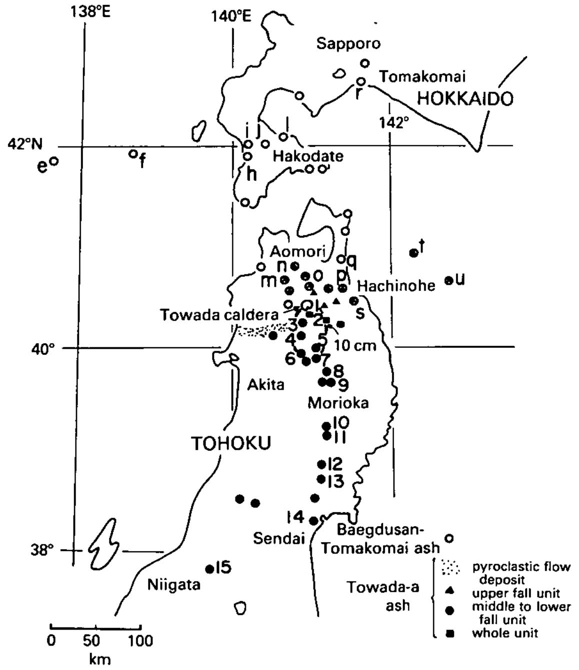

Figure 1. Map showing localities where Towada-a ash and Baegdusan-Tomakomai ash have been identified (source: Machida et al. *1981)*

index in this ash was wide, 1.506–1.516, suggesting a heterogeneous composition of magma.

Extensive investigations revealed that the upper ash occurs not only in the northern Tohoku district, but also in the southern half of Hokkaido. The fact that its thickness and grain size vary little in spite of widespread occurrence clearly suggests that the ash was derived from major eruptions of a very distant volcano.

2.2 B-Tm ash in the northern part of the Sea of Japan

In order to reveal the source volcano of the upper layer of ash, we analysed many deep-sea piston core samples collected by Japanese, American and Soviet research vessels in the Sea of Japan. As a result, we found a fine-grained ash within the sediment a few decimetres below the bottom surface in the northern part of the Sea of Japan (Figures 2 & 3). The physical and chemical properties of the ash were similar to those of the upper ash in northern Japan. The thickness and grain size gradually increase toward the west, where the Changbai volcano lies on the bound-

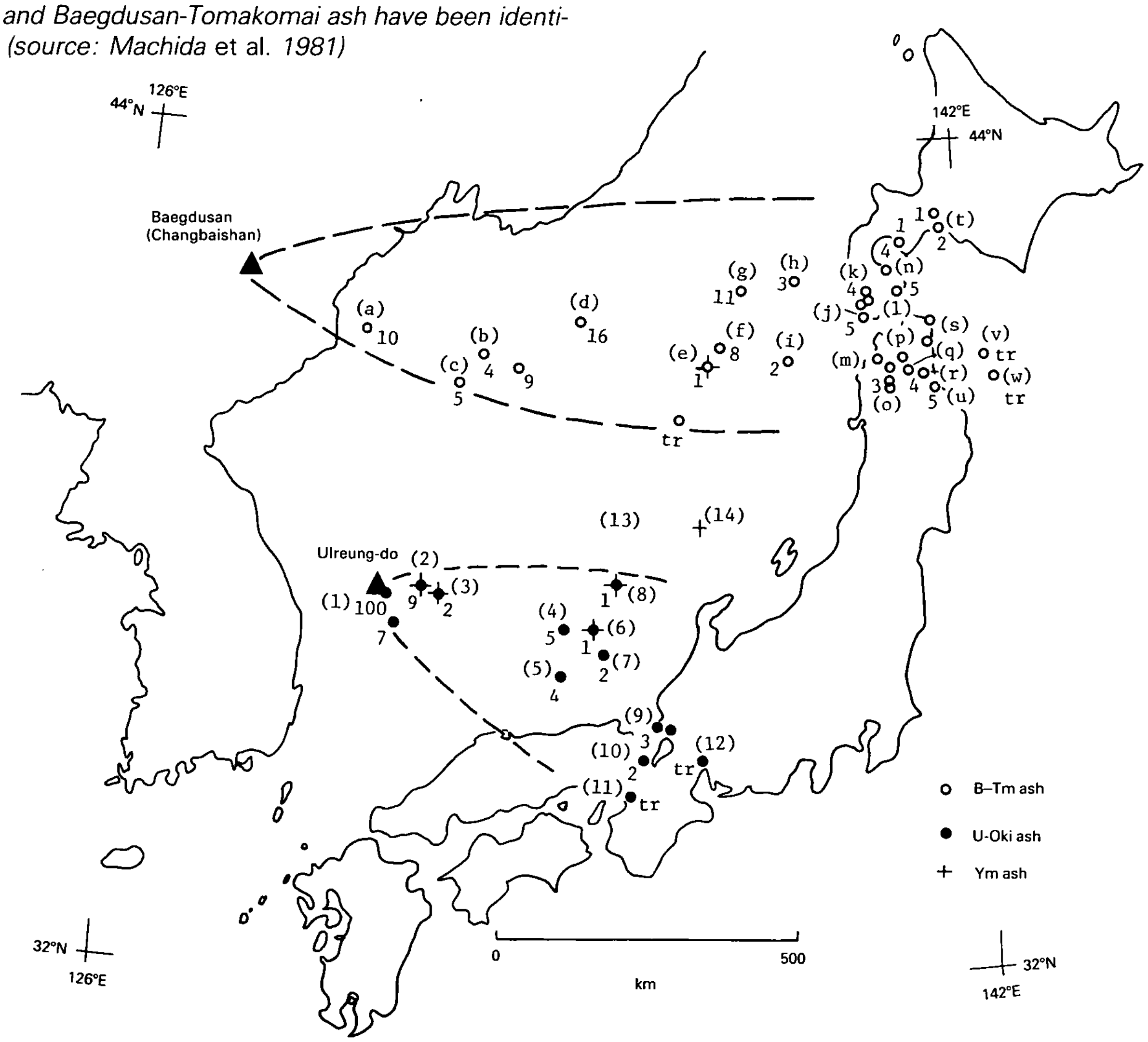

Figure 2. Map showing localities where the marker-tephras from the Korean volcanoes have been identified. Thickness of the B-Tm ash and the U-Oki ash are shown in cm by numerals. Localities are shown by numerals in parenthesis: a=St.6913; b=KH69-2-25; c=St.6920; d=KH69-2-23; e=P129; f=KH77-3-M5; g=KH79-3-C2; h=P130; i=V28-271; j-u=several localities in northern Japan; v=P82; w=P83. 1=To-dong, Ulreung; 2=P106; 3=KH77-3-M3; 4=KT79-6-19; 5=KH77-3-M2; 6=KH79-3-C3; 7=0124; y=KH77-3-L4; 9=Torihama site; 10=Mizorogaike, Kyoto; 11=south port of Osaka; 12=Yatomi; 13=P127; 14=V28-268 (source: Machida & Arai 1983)

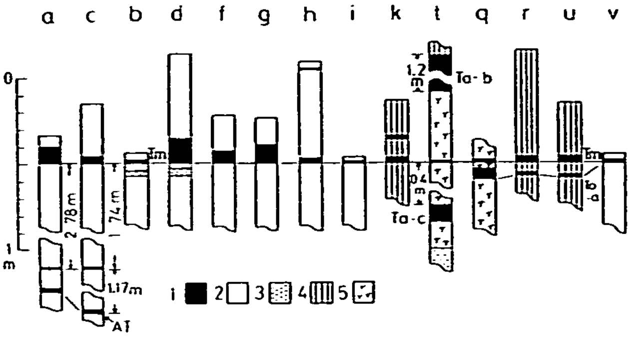

Figure 3. Representative cores and columnar sections bearing the B-Tm ash from the northern part of the Sea of Japan, northern Japan and the Pacific Ocean. Localities are shown in Figure 2. Tm=Baegdusan-Tomakomai ash; Ta-b=Tarumai-b pumice; To-a=Towada-a ash; Ta-c=Tarumai-c pumice; AT=Aira-Tn ash. 1=tephra layer; 2=marine clay; 3=sand; 4=andosol; 5=peat

ary between North Korea and China (42°N, 128°10'E). It was previously known that this volcano had erupted several times in the course of history.

Thus, the evidence strongly suggests that the ash was supplied by the large-scale eruption of the Changbai (Baegdu) volcano. The ash has been named after the volcano, Baegdusan, and the type locality, Tomakomai, Hokkaido, about 1000 km from the source (ie B-Tm) (Machida *et al.* 1981; Machida & Arai 1983).

3 Gigantic eruption of Changbai volcano

3.1 Pumice falls and flows occurring around the Changbai volcano

The Changbai volcano has a prominent caldera, Tianchi (Sky Lake), with an approximate diameter of 4.5 km, and is extensively covered by thick pumice falls and 'mud lava', which is interpreted as pyroclastic flow deposits (ignimbrite) (Asano 1948) (Figure 4). It seems probable that these ejecta represent the youngest major eruption of this volcano. Pumice blocks were found by Asano (1948) to be alkali rhyolite, with alkali feldspar and microphenocryst of aegirine-augite. Correlation between the Changbai (Baegdusan) pumice and the distal B-Tm ash is highly probable because of the similarity of the petrographic and stratigraphic features. The total volume of the pumice falls and ignimbrite sheets, including the distant fallout ash, is estimated at more than 50 km^3. Therefore, the recent eruption of Changbai volcano was probably one of the largest in the world.

Buried forests consisting of *Pinus* spp. (pine), *Picea* spp. (spruce) and broadleaved trees were found in the pumice falls and ignimbrite sheets at several localities high above the present timber-line (Figure 5), as well as in the present forest area around the volcano (Koyama 1943; Asano 1948; Takahashi 1963; Zhao 1981). It is evident, therefore, that large-scale forest devastation was caused by these eruptions.

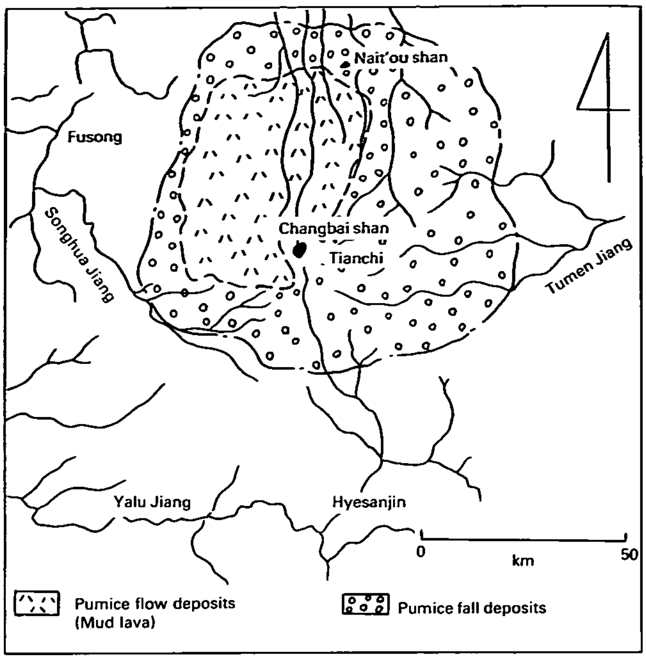

Figure 4. Map showing approximate distribution of recent pumice fall and flow deposits around the Changbai volcano (source: Asano 1948)

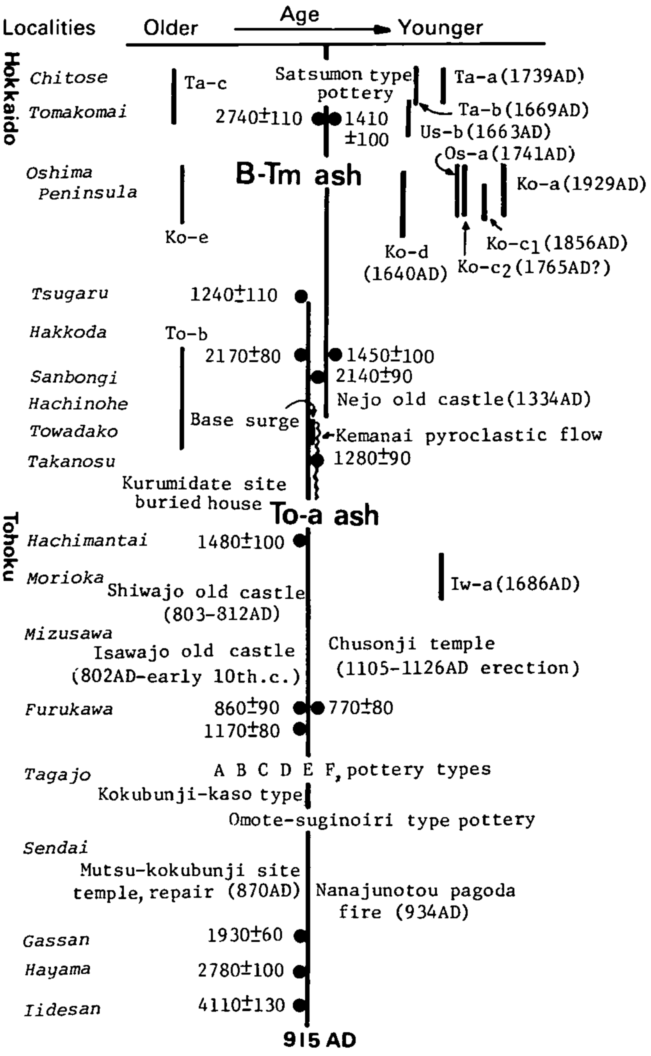

Figure 5. Map showing localities where buried forests were found above the timber-line

3.2 Age of eruption

Opinions vary on the age of the pumice eruptions of the Changbai volcano: most geologists believe that the eruptions producing pumice fall occurred before those producing mud lava, and that both eruptions preceded the last glacial age (Asano 1948). In contrast, forest ecologists are of the opinion that these eruptions occurred more recently, probably within recorded history (Koyama 1943). Zhao (1981) reported the 2 radiocarbon ages of the buried forests, 1050±70 and 1120±70 years, supporting the hypothesis that the eruptions of Changbai volcano occurred in recent times.

There are reliable archaeological and chronological data on the age of the Changbai eruptions in northern Japan (Figure 6). As mentioned earlier, the B-Tm ash occurs immediately above Towada-a ash, which has been dated exactly from archaeological remains, from historical documents, and by radiocarbon dating of remains at Sendai: 915 AD is the most probable age. The Towada-a ash occurs within the peat bogs above the remains of the 870 AD earthquake and below those of the 934 AD fire of an ancient temple (Shiratori 1980). In addition, there is an old document describing the ashfall in the summer of 915 AD, around the time when the Towada-a ash eruption should have occurred. In Hachinohe, northern Honshu, the remains of an old castle, Nejo, were excavated from the soil above the B-Tm ash. Hence, this ash is clearly younger than 915 AD and older than 1334 AD, the documented age for the construction of Nejo. The stratigraphic position suggests that it occurred some time between the end of the 10th century and the 11th century.

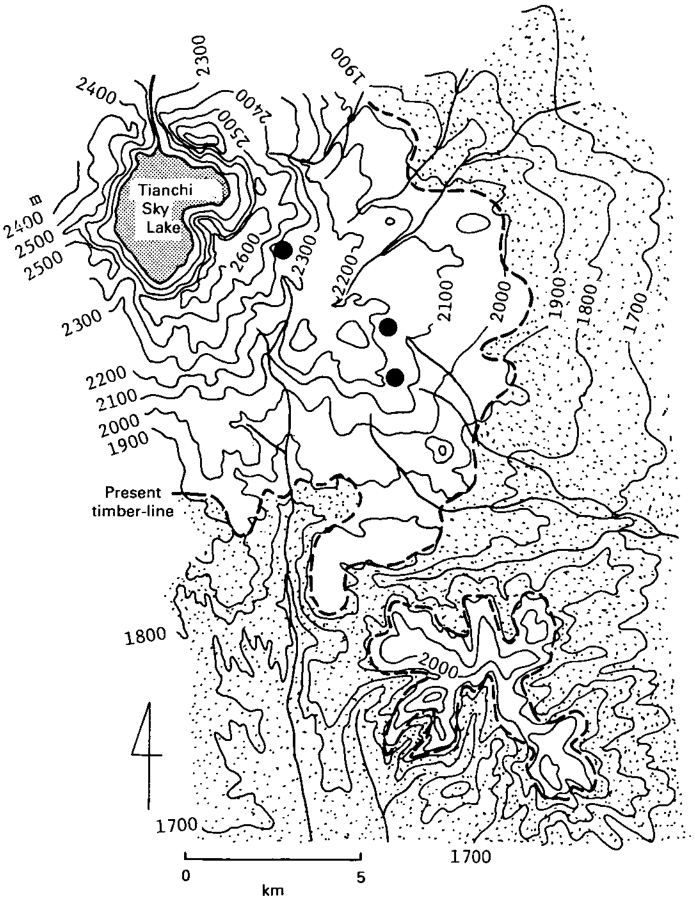

Figure 6. Chronological relationship between Towada-a ash, B-Tm ash, human remains and radiocarbon dating (source: Machida et al. *1981)*

Historical documents indicate that the Changbai volcano has erupted 4 times since the 15th century, in 1413, 1597, 1668, 1702 AD. However, these activities do not correspond with the major eruptions generating the B-Tm ash and pumiceous deposits, but could have been minor ones. More detailed investigation of historical documents in China, North Korea and Japan will be needed to determine the timing of the major eruptions.

The recent major eruption of the Changbai volcano is also suggested by the fact that vegetation at the summit has not yet completely recovered from a burial caused by pumice falls and flows (Zhao 1981).

3.3 Nature of eruptions

Previous geological studies (eg Asano 1948) of the ejecta have shown that paroxysmal activity of the Changbai volcano started with a plinian-type eruption, producing the voluminous pumice falls, and was followed by an ignimbrite-forming eruption. The second type of eruption was caused by the collapse of a huge column forming thick and highly mobile ash flows, which spread largely toward the north and west from the caldera of the volcano.

It is not yet certain, however, whether the B-Tm ash is associated with the pumice fall, the ignimbrite, or with both.

From the viewpoint of volcanic hazards, it seems likely that hot ash flows might cause the greatest destruction to the area covered. The ash falls generated as co-ignimbrite or phreatoplinian type, however, might also have a heavier impact, because they occur over a greater area and usually fall when wet.

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Preliminary studies on volcanic eruptions and historical vegetation succession in the eastern mountain area of north-east China

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1 Introduction

The eastern mountain forest of north-east China belongs to the temperate coniferous and deciduous mixed forest zone, and the climax vegetation is a mixed forest of *Pinus koraiensis* Sieb. et Zucc. (Korean pine) and broadleaved trees (Figure 1).

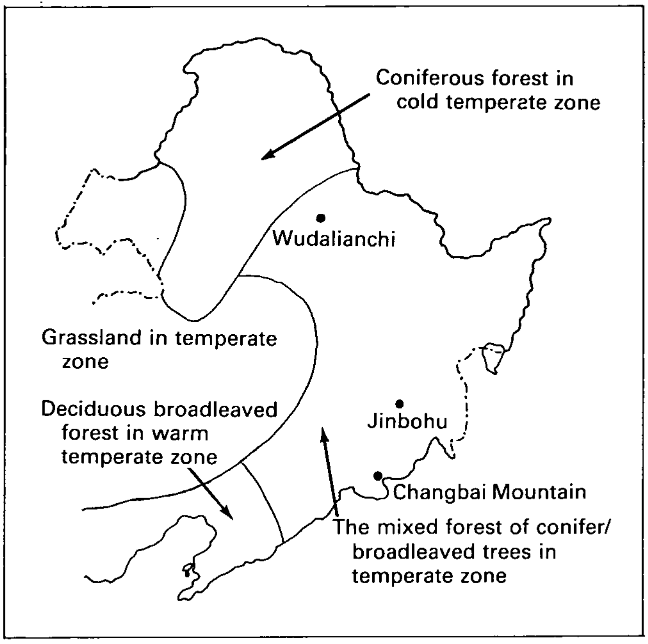

Figure 1. Vegetation zones in north-east China

The landscapes of Wudalianchi, Jinbohu and Changbai Mountain were all formed by volcanic eruptions, and the vegetation is closely related to the volcanic action. In this paper, the author expresses opinions about the dates of the eruptions and about the previous vegetation in 3 areas, based on measurements by radiocarbon dating techniques, and identification of tree species from carbonized wood samples.

2 Wudalianchi

In the region of Wudalianchi, the volcanic eruption occurred in 1720, according to historical evidence. A dense growth of lichens and mosses now covers basaltic lava plateaux, and only a few pioneer tree species (such as *Larix davurica* Ledeb. (= *Larix gmelini* (Rupr.) Litvinov) (Dahurian larch), *Betula platyphylla* Suk. (Manchurian birch), etc) have invaded the plateaux, where soils have begun to develop. The present vegetation, therefore, is in an early successional stage to a mixed forest of broadleaved/*P. koraiensis* trees.

3 Jinbohu

There is no evidence available for estimating the date of the volcanic eruption in the Jinbohu region. The forests are well developed and consist of *Pinus koraiensis*, *Picea jezoensis* (Sieb. et Zucc.) Carr. (Yezo spruce), *Abies nephrolepis* (Trautv.) Maxim. (East Siberian fir), *Betula costata* Trautv. (yellow birch), *Tilia* (lime) and *Acer* (maple). These species are all typical components of the mixed forest of broadleaved/*P. koraiensis* trees.

By radiocarbon analysis of the carbonized wood from *P. koraiensis* trees, their age has been estimated as 4380±90 years. It is, therefore, assumed that the volcano erupted about 4380 years ago, destroying the former mixed forests.

4 Changbai Mountain

According to historical records, the volcano of Changbai Mountain erupted in 1597, 1668 and 1702. However, there is some question about the validity of these dates. For example, the diameter at breast height of the largest *P. koraiensis* tree, which is growing in the volcanic ash, is about 120–140 cm, so that the tree must be at least 400 years old. It is believed, therefore, that the latest eruption took place some 400 years ago. According to the radiocarbon analysis of the carbonized wood, the age of the samples from the northern slope is 1050±70 years and 1120±70 years, and of the samples from the western slope about 1410±80 years (Figure 2).

The samples of carbonized wood found on the eastern slope have been identified as *P. koraiensis*, *Picea jezoensis*, *Abies holophylla* Maxim. (Manchurian fir), *Larix olgensis* A. Henry (Olga Bay larch), *Betula costata*, *Fraxinus mandshurica* Rupr. (Manchurian ash), *Tilia amurensis* Rupr. (Amur linden) and *Padus asiatica* Kom. (Asian cherry), and, on the western slope, *Acer mono* Maxim. (painted mono maple), *Quercus mongolica* Fisch. ex Turcz. (Mongolian oak), and *Populus* (poplar) species were also found. These species are all major components of the mixed forests of

Figure 2. Map showing the dates of eruption from historical records and from radiocarbon analysis of carbonized wood

broadleaved/*P. koraiensis* forest. Therefore, it can be assumed that the volcanic eruption in the Changbai Mountain occurred about 1100 years ago, destroying the mixed forest of *P. koraiensis* and deciduous trees (Figure 3).

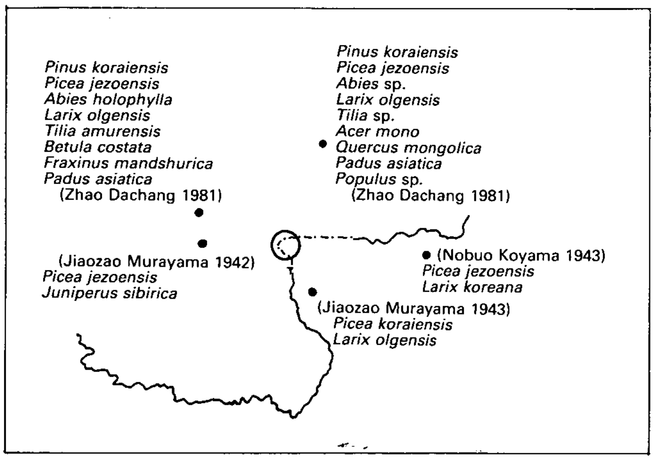

Figure 3. Species of carbonized wood samples found in Changbai Mountain region

In 1940–42, Jiaozao Murayama and Nobuo Koyama, 2 Japanese scientists, found carbonized wood on Changbai Mountain, and identified 2 tree species. According to Chinese historical records, carbonized wood was also found on Changbai Mountain in 1911. In fact, samples have been collected on almost every slope of the Mountain, and, therefore, have provided evidence for studying the dates of volcanic eruptions and of vegetation present in former times (Figure 4).

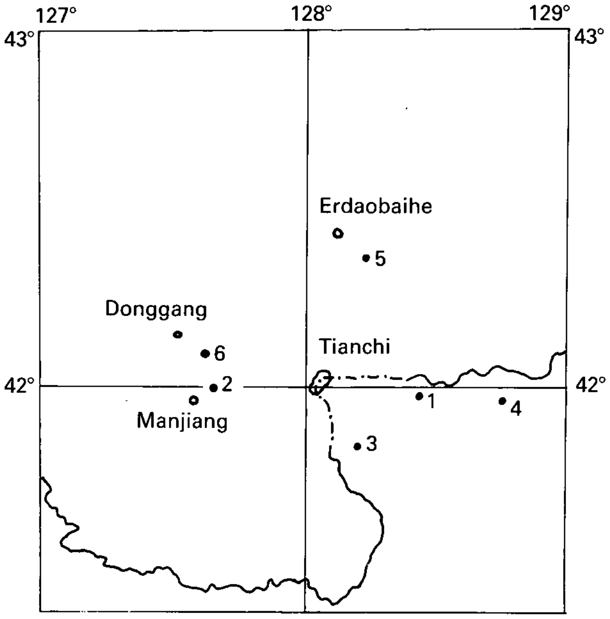

Figure 4. Sites where carbonized wood has been collected in Changbai Mountain region
1 = According to historical records (1911)
2/3 = Jiaozao Murayama (1942, 1943)
4 = Nobuo Koyama (1943)
5/6 = Zhao Dachang (1981)

5 Conclusion

In our research in the 3 areas of Wudalianchi, Jinbohu and Changbai Mountain, the process of vegetational succession following destruction of the former vegetation cover by volcanic eruptions is similar, even though the dates of the destruction differ. The 3 destroyed areas are recovering their former mixed forests of broadleaved and *P. koraiensis* trees, which comprise the climax vegetation in the eastern mountain region of north-east China.

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The moss flora of the Baektu Mountain area

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Abstract
The mosses of the Baektu Mountain area have been divided into 38 families, 84 genera and 173 species. Because of the favourable natural conditions, the moss flora seems rich, even if the formation history of the flora in the Baektu Mountain is not long.

The mosses are more widely distributed in the subarctic coniferous forest zone (83.3%) than in the alpine tundra zone (26.6%), and a distinction can be drawn between these 2 zones. There is a further distinction between the mosses on the side of the Baektu Bridge and around the volcanic lake, named Sky Lake, in the alpine tundra zone.

The mosses growing only on soil are more numerous (71) than those growing on rock or stone (20), because the area surveyed was covered almost entirely with forest or alpine tundra. The moss flora in the Baektu Mountain area has been studied since 1978, and the results are summarized briefly in this report.

1 Conditions of physical geology and study material

The study area is the Baektu Mountain situated in Samjiyon County in the Ryanggang Province. The highest peak is 2750 m above sea level (asl). Many high mountain peaks surround the area, such as Sobaek Mountain, Ganbaek Mountain, Wasabong, etc, together with famous plain plateaux reaching over 2000 m.

As a result of volcanic action, basalt and alkalic tracyte have been overlain with pumice stone in the Baektu Mountain area. The thickness of the pumice stone varies: 7 m on the plateau from Yonjibong to Mudubong, 1.6 m around Samjiyon, and 1.5–2 m at Mubog. Being the highest area in Korea and far from the sea, the climate of the area is of a cold continental type, with average annual temperatures at Samjiyon of −0.3°C, ranging from 16.4°C in July to −17.6°C in January. The average annual precipitation is 894.4 mm, but varies greatly throughout the year. In the period June–August, over 130 mm falls each month. The relative humidity at Samjiyon is about 72%.

The higher plant flora falls mainly into 2 groups: the subarctic coniferous forest zone below about 2000 m asl (the tree-line) and the alpine tundra zone above 2000 m. The subarctic coniferous forest can be divided further into 2 groups: the middle coniferous forest below about 1500 m asl (by Samjiyon) and the upper coniferous forest above 1500 m asl. The alpine tundra zone is again divided into 2 groups: the side of the Baektu Bridge and the side of Sky Lake. Both the Bukpotae Mountain and the Nampotae Mountain have been divided separately.

- I Subarctic coniferous forest zone
  - Ia Middle coniferous forest
  - Ib Upper coniferous forest
- II Alpine tundra zone
  - IIa Side of the Baektu Bridge
  - IIb Side of the Sky Lake
- III Bukpotae Mountain and Nampotae Mountain

For study material, the author used about 1500 of his own specimens, collected in the area and held in the Herbarium of the Research Institute of Botany (Table 1).

Table 1. Division of observation

Group		Points of observation (m asl)	Vertical height (m)	Variation
I	Ia	Rimyongsu (1300) Chongbong (1450) Gonchang (1300) Begaebong (1610) Samjiyon (1340–1380) Below Sinmusong (1500)	1300–1500	Middle coniferous forest
	Ib	Above Sinmusong (1500) Below 2000 m on Baektu Mt, Sobaek Mt, Ganbaek Mt, Wasabong	1500–2000	Upper coniferous forest
II	IIa	The side of Baektu Bridge above 2000 m	2000–2750	Alpine tundra zone
	IIb	The side of Sky Lake	2190–2750	Alpine tundra zone
III		Bukpotae Mt and Nampotae Mt	1300–2000	Middle and upper forest

2 Discussion of results

2.1 Combination of species in Baektu Mountain area

A total of 31 families, 62 genera and 99 species have already been described in the Baektu Mountain area (Gao & Chang 1983; Horikawa 1935, 1936; Kashimura 1939, 1941; Noguchi 1954; Osada 1958). In this study, a further 7 families, 22 genera and 74 species have been included, giving a total of 38 families, 84 genera, 173 species (Hoang 1986) (Table 2).

Because of the favourable natural conditions, the moss flora seems rich, even if the history of the flora in the Baektu Mountain area is not long.

Table 2. Combination of species in the Baektu Mountain area

Number	Order	Family	Genus	Species
1	Sphagnales	1	1	5
2	Andreaeales	1	1	1
3	Dicranales	3	14	25
4	Fissidentales	1	1	2
5	Pottiales	3	4	4
6	Grimmiales	1	2	10
7	Funariales	2	2	2
8	Tetraphidales	1	1	1
9	Bryales	5	14	35
10	Isobryales	7	10	15
11	Hypnobryales	10	28	55
12	Buxbaumiales	2	2	3
13	Polytrichales	1	4	15
Total	13	38	84	173

2.2 Results of study

The distribution of mosses in the Baektu Mountain area shows several characteristics, according to the different ecological conditions. The numbers of species in the various groups are shown in Table 3.

Table 3. Number of species according to variation

Variation			Number of species	
I	II	III	121	
I		Ia	100	67
		Ib		64
II		IIa	32	18
		IIb		23
	III		48	

One hundred (83%) species grow in the subarctic coniferous zone, and most are found there because of the lower temperature, frequent summer rainfall and the higher atmospheric humidity in the area, although total precipitation is not so high. The mosses growing in the middle coniferous forest number 67 species, and in the upper coniferous forest 64 species. The numbers of species are similar because the ecological conditions are similar. In the alpine tundra zone, only 32 species of mosses are found because the thin surface layer is unfavourable for moss growth, although the area is covered with pumice stone. Within this zone, more mosses are found on the side of Sky Lake, where ecological conditions are more favourable, ie more mist and cloud.

On the Bukpotae Mountain and Nampotae Mountain, only 48 species have been collected, but further observations will be made in the future. Eighteen species have a wide distribution in the Baektu Mountain area, such as *Ceratodon purpureus* (Hedw.) Brid., *Drepanocladus uncinatus* (Hedw.) Warnst., *Plagiothecium cavifolium* (Brid.) Iwats., *Dicranum scoparium* Hedw., *Ptilium crista-castrensis* (Hedw.) De Not., *Pohlia elongata* Hedw., *P. nutans* (Hedw.) Lindb. and *Rhytidium rugosum* (Hedw.) Kindb. These species are mostly those with a wide ecological amplitude.

In the subarctic coniferous forest zone, 20 species are to be found in the middle and upper coniferous forest, the essential ones being *Tetraphis pellucida* Hedw., *Mnium heterophyllum* (Hook.) Schwaegr., *Aulacomnium palustre* (Hedw.) Schwaegr., *Hylocomium splendens* (Hedw.) Br. Eur., *Climacium japonicum* Lindb. and *Pleuroziopsis ruthenica* (Weinm.) Kindb. These species can be said to be typical of the subarctic coniferous forest. Within this zone, 15 species are collected only in the middle coniferous forest and 29 species in the upper coniferous forest, but as yet we can see no clear distinction between them.

The species with a cushion form are *Rhacomitrium canescens* var. *tortuloides* Moenk. and *R. lanuginosum* (Hedw.) Brid., while the species growing in the valley with some humus, and therefore a little nourishment and moisture, is *Dicranum spadiceum* Zett.

A few typical species are collected on the northern slope of Sky Lake: *Messia longiseta* Hedw., *Bryoxiphium norvegicum* ssp. *japonicum* (Berggr.) Love et Love, *Cinclidium arcticum* (B.S.G.) Schimp., *Hypnum pratense* (Kabenh.) Koch ex Hartm., *Rhytidiadelphus*

Table 4. Habitats of mosses

Number	Order	Number of species	Soil, rock, tree	Soil, rock	Soil, tree	Rock, tree	Soil	Rock	Tree
1	Sphagnales	5					5		
2	Andreaeales	1						1	
3	Dicranales	25	8	6	1	2	6	1	1
4	Fissidentales	2		2					
5	Pottiales	4		2			1	1	
6	Grimmiales	10		2				8	
7	Funariales	2		1			1		
8	Tetraphidales	1			1				
9	Bryales	35	2	3		1	29		
10	Isobryales	15		2	1		5	2	5
11	Hypnobryales	55	6	21	11		10	5	2
12	Buxbaumiales	3					2	1	
13	Polytrichales	15		2			12	1	
Total	13	173	16	41	14	3	71	20	8

squarrosus Warnst., *Polytrichum sphaerothecium* (Besch.) C. Müll. These species grow on or under wet rocks.

The habitats of mosses found on the Baektu Mountain are shown in Table 4. The species growing only on soil are much more numerous (71) than those growing on rock or stone (20), because the area examined is covered almost entirely with forest or alpine tundra.

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Three different types of forest dynamics

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Abstract

Three different types of change in forest vegetation have been analysed, the primary method employed being the careful age determination of the trees and saplings present in relatively small plots. The first concerns primary succession on a rising seashore on the island of Skabbholmen in the Baltic. Regressions of tree age on elevation suggest that individuals became established continuously downwards as new land became available, and that *Alnus* (alder) is being replaced by *Fraxinus* (ash).

The second is concerned with dynamics related to the formation of storm gaps in the primeval forest of Fiby urskog, where the time estimated by Sernander (1936) for the complete disintegration of fallen trunks of *Picea abies* (L.) Karst. (Norway spruce) proves to be something of an overestimate.

The final example concerns a study plot, at 460 m above sea level (asl) in northern Sweden, in which there was no evidence of storm gaps involving several trees, as occur in Fiby urskog. Here, production of seed by *Picea* is low and uneven, while initial mortality is high. In all 3 types of dynamics, environmental and biotic factors are mutually interacting, and no change can be classified as solely autogenic or allogenic.

1 *Introduction*

Studies of vegetation dynamics have long been an important part of ecological science, but during the last decade ecologists have shown an even greater interest (Miles 1979; White 1979; McIntosh 1980; West *et al.* 1981; Pickett & White 1985; Fanta 1986). The reasons for this increased interest are probably manifold: obviously, landscape types are constantly changing and this factor, in combination with the development of new methods in modelling and ordination techniques, has increased the possibility of predicting rates and direction of change and of differentiating between short- and long-term changes (Cramer & Hytteborn 1987). Also, the present interest in population biology has introduced new approaches to the study of vegetation change (Peet & Christensen 1980).

In this paper, I will discuss 3 different types of dynamics in forests. The first type deals with the changes occurring in connection with primary succession on rising seashores. The second type is usually called gap dynamics. It occurs when a single tree, or a group of trees, falls, and thereby makes it possible for smaller individuals of the same or other species to grow up into the tree layer. The last example is from a stand near to the forest-line, where regeneration is highly dependent on the amount of germinable seeds; good seed years rarely occur at this high altitude.

2 *Vegetation change on a shore with land upheaval: primary succession*

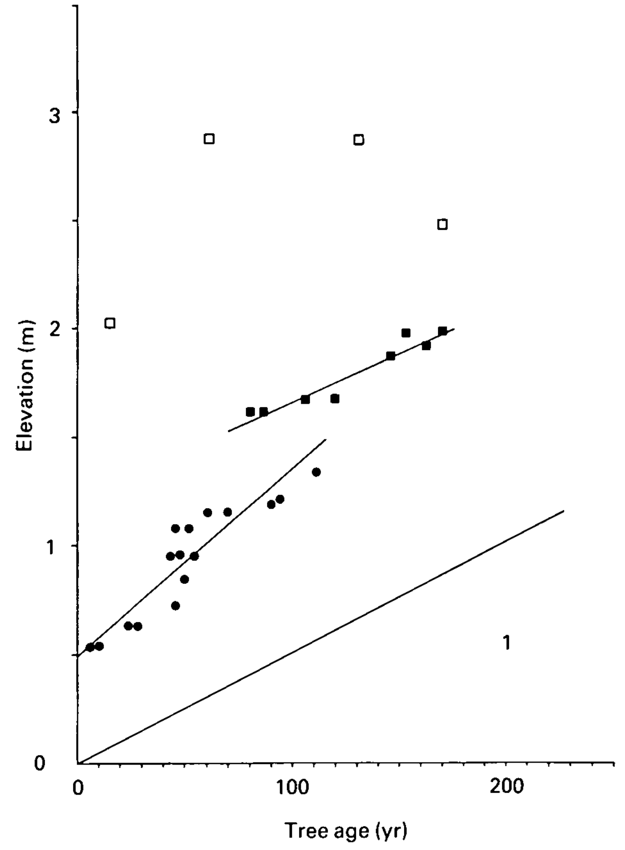
Since the beginning of the Flandrian interglacial, most of Sweden has been rising isostatically. This rise is most evident at the seashore. Nowadays, the land upheaval varies between 0.9 cm yr^{-1} and zero (Ericson & Wallentinus 1979). In fact, in southern Sweden, a small subsidence is noticeable. During this process, new land is continuously made available for germination and establishment.

Accumulation and erosion are additional processes influencing the sum of the change, the so-called seashore displacement, which is different from theoretical seashore displacement calculated from land upheaval values only. On a seashore exposed to waves, erosion is the main additional factor. Part of the eroded material may accumulate, at least for a while, further down on the shore. In sheltered places, eg bays, organic material accumulates on the shore, and material suspended in the water can also be deposited on the sea bottom. Another important process is ice-pushing, which can transport material and raise the ground considerably during a short period of time. Higher up on the shore, litter accumulation and subsequently soil formation will raise the ground to a higher level than would be caused by land upheaval alone.

As land becomes available, vegetation should, in theory, be able to invade and migrate down the shore, as has been shown by several investigations in Finland and Sweden. In the short term, this process is hindered by variations in water levels between years (Ericson 1980). Cramer and Hytteborn (1987), however, have shown that it is possible to distinguish between short-term fluctuations and long-term successional change, even if the investigation period is short. In the long term, over 10 years, on the other hand, such a process should be more clearly distinguishable. A Finnish study on a few shoals, which rose 16 cm and 25 cm during the investigation period of nearly 20 years, showed a continuous increase in species number (Schwanck 1974). In a series of annual investigations over a 12-year period, Ericson (1980) showed that vegetation zones were each taken over by the zone previously located at a higher elevation, and that the main vegetational gradient remained unchanged. This long-term dynamic method is too time-consuming for most scientists, and so-called static methods have been used instead (Austin 1977).

Verwijst and Cramer (1986) used relationships between tree age and elevation in a successional study of a shore with land upheaval, assuming that the above-mentioned additional factors were of little importance to seashore displacement. The advantage of using trees in a static study is obvious: tree individuals are relatively long-lived and their age can, in most cases, be accurately determined. A disadvantage is that the age determination can, of course, only be made on those individuals which have survived. The method tells us nothing about the individuals which, for one reason or another, have died since establishment.

In a similar way, material from the small island of Skabbholmen in the Baltic (59°47'N, 19°12'E) is represented in Figure 1. Three transects with different exposure were investigated. Change in the field layer has been discussed earlier by Cramer and Hytteborn (1987) and by Hytteborn (1986). Ten-metre wide transects were laid out from the seashore up into the forest, and all tree individuals within the transects were mapped, measured and their age determined using borings taken at the trunk base. *Alnus glutinosa* (L.) Gaertn. (common alder) borders the open shore and, on this nutrient-rich site, *Fraxinus excelsior* L. (common ash) is growing at a slightly higher level. Higher up, other species such as *Picea abies* and *Sorbus aucuparia* L. (rowan) are found.



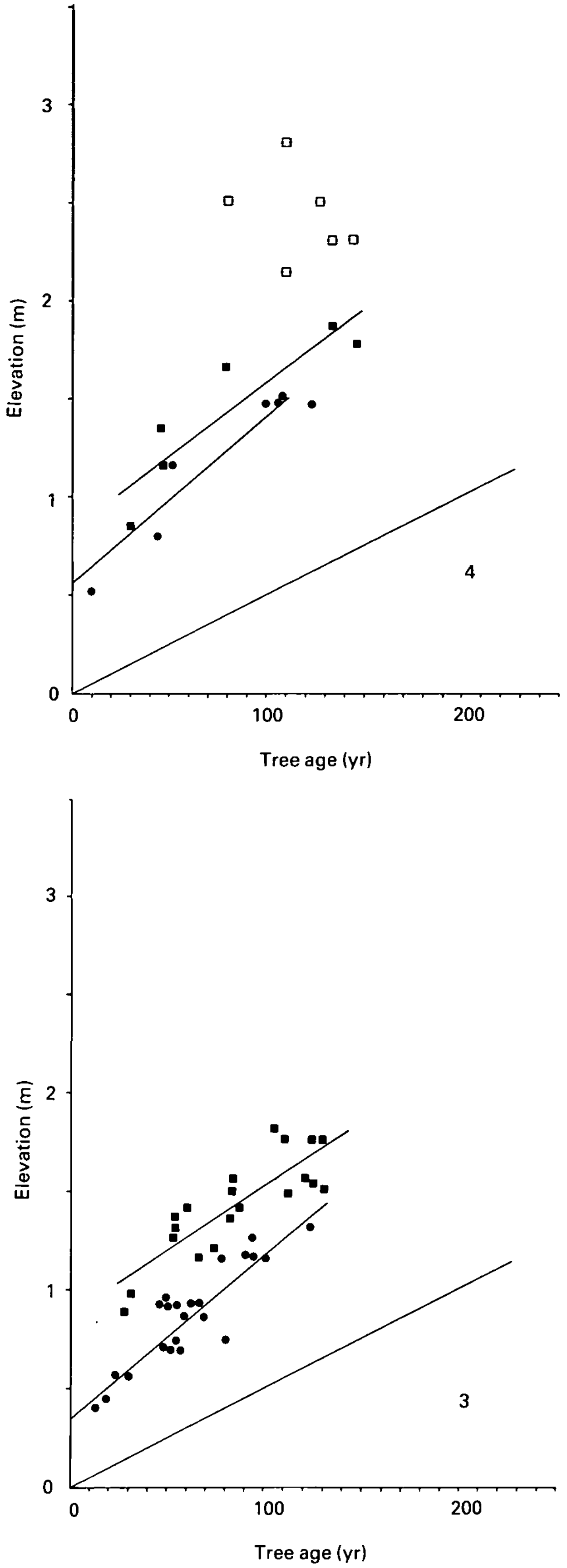


Figure 1. The regression of tree age on elevation in profiles 1, 3 and 4 on the island Skabbholmen. (● Alnus glutinosa; ■ Fraxinus excelsior) Fraxinus *individuals 2 m above water level are not used in the regressions but marked as open squares. The line through origin shows the rate of land upheaval*

Table 1. Regression of tree age on elevation and the intercept at age = 0

Tree species	Profile	n	Regression	r^2	P	Elevation at age = 0
Alnus	L1	25	a = 100.6 e − 35.9	0.85	0.0001	0.36
	L3	25	a = 96.7 e − 16.3	0.80	0.0001	0.17
	L4	8	a = 103.6 e − 42.8	0.86	0.0005	0.41
Fraxinus	L1	8	a = 203.6 e − 221.4	0.90	0.0002	1.09
	L3	20	a = 108.4 e − 62.9	0.70	0.0001	0.58
	L4	6	a = 107.3 e − 66.4	0.77	0.013	0.62
Alnus	All	58	a = 93.3 e − 23.2	0.78	0.0001	0.24
Fraxinus	All	34	a = 118.6 e − 77.4	0.79	0.0001	0.65

a = age; e = elevation (m)

The regressions of tree age on elevation are, in all cases, significant (Table 1), suggesting that the individuals have established continuously downwards as new land became available. In all 3 examples, the regression lines for *Alnus* have a lower intercept with the elevation axes than the lines for *Fraxinus*. These intercepts can be taken as a preliminary establishment level for the different species. The zonation illustrated by the regressions also suggests a replacement of *Alnus* by *Fraxinus*, as the oldest *Alnus* trees are growing among the youngest *Fraxinus* trees.

The rate of land upheaval in the investigation area is about 0.5 cm yr^{-1}. If the downward process of tree establishment on the shore is at the same rate as the land upheaval, the slope of the regression lines should not differ significantly from the land upheaval. Only for *Fraxinus* in profile L1 is the slope about the same as for the land upheaval rate (200 yr m^{-1}); for all the others, the slopes indicate a faster downward process. Verwijst and Cramer (1986) found a somewhat better agreement between the land upheaval and the establishment rates.

The assumption that the age of the growing place of the trees (site age) could be accurately estimated from the elevation using the land upheaval rate is likely to be true only if the additional factors are negligible. Besides erosion, the processes already mentioned, ie the accumulation of drift material, ice-pushing and soil formation, lead to an estimation of site age that is higher than that estimated from the land upheaval rate only. Ugolini (1968) gives an example where the humus layer increased in thickness by 20 cm during primary succession over a period of 150 years, after which time an increase was no longer observed. Cramer and Hytteborn (1987) observed a new drift accumulation, including stones, 20 cm thick, after a storm with an exceptional high water in January 1983. The drift was concentrated about 1.4 m asl. These additional processes are even more complicated, as accumulation and erosion can occur on the same transect, but at different heights above the mean water level.

The intercepts for *Alnus* (Figure 1, Table 1) on the elevation axis are not significantly different between the 3 profiles. The most exposed transect, L4, has the highest intercept with the elevation axis, and the least exposed profile, L3, had the lowest intercept, which is as expected (Brenner 1916). The numbers of individuals are rather low, but significant differences are found between the intercepts for *Alnus* and *Fraxinus*, except for profile L4.

3 Gap dynamics

The landscape of Sweden is dominated by forests, but there is only a limited number of primeval forests, apart from those in mountainous areas, where natural processes can be studied.

Over many years, especially in the 1930s, the small primeval forest, Fiby urskog, has been studied by ecologists (Hesselman 1935; Sernander 1936). In his research, Sernander formulated the 'storm gap' theory of *Picea* forest regeneration. He produced maps of a few plots in the forest, some of which have been relocated. It is possible to use them in a dynamic study of change in the tree layer, even if 50 years have elapsed between the 2 investigations.

Figure 2a is redrawn from Sernander (1936) over part of his plot III, and Figure 2b is from a remapping in 1983–85. Besides the position and the species of each tree, the maps also show the fallen stems, and an index has been given to indicate the degree of necrotization, according to a scale proposed by Sernander (see Hytteborn & Packham 1987). Score 1 means a newly fallen stem, and score 6 a completely decomposed stem forming a raised line of humus on the ground. The numbers of stems and logs are given in Table 2. Three of the 9 fallen trees in 1935 were still recognizable in 1985 (Table 3). They had changed their necrotization score from 3 to 6 or from 2 to 5 or 6, whereas the others with scores from 2 to 6 had disappeared.

According to Sernander (1936), the first necrotization stage will last about 4 years, and it will take about 25 years to end stage 2. These intervals were based on real observations, but Sernander's statement that it takes 90 years before no remains can be observed does not seem to be based on any real age determination.

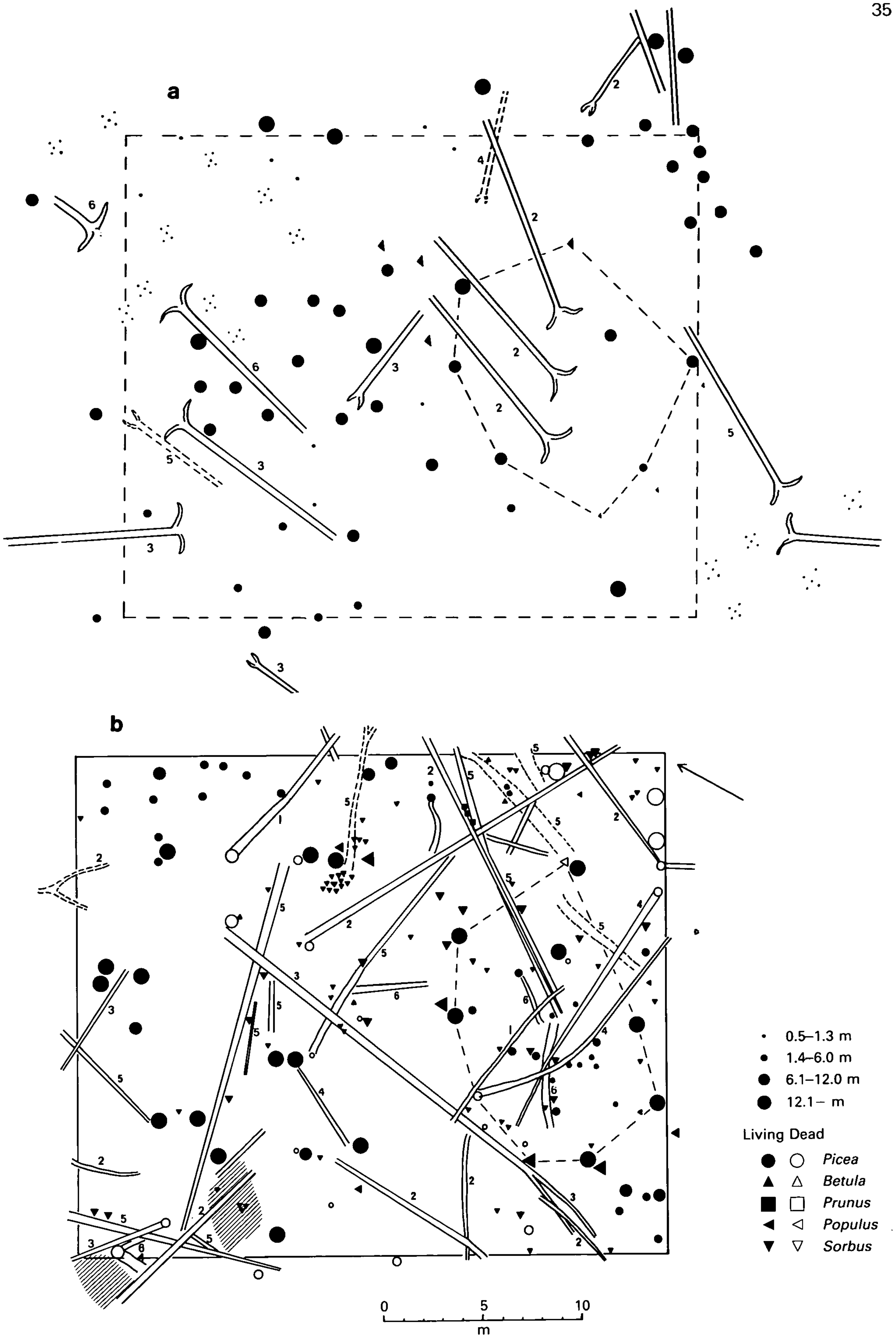


Figure 2. Map of a plot 25 m × 30 m, a part of plot III in Sernander (1936): a. mapped in 1935 and redrawn from Sernander (1936). Besides the tree and the fallen stems, regrowths are shown with a pattern of small dots. b. mapped in 1985. The size of the symbols reflects the height classes. A few big boulders are marked. On both maps the necrotization degree of the fallen stems are marked according to a scale in Sernander (1936, p167). Fallen Populus *are dashed. A gap, rather new in 1935, is delimited in both maps with a broken line.*

Table 2. Numbers in the tree layer and of fallen trees in 1935 (source: Sernander 1936) and 1985

	Number
Living trees in 1935	46
Living trees in 1935, still living in 1985	27
Living trees in 1935, log in 1985	18
Living trees in 1935, unrecognizable in 1985	1
Living trees in 1985	32
New trees	5
Dead logs in 1935	9
Dead logs in 1985	24
Dead logs in 1935, recognizable in 1985	3

Of the 3 stems with a necrotization degree of 2 in 1935, one had completely disappeared, but 2 were still recognizable with scores of 5 and 6. As stages 1 and 2 are supposed to last about 4 + 20 years, it took 55–75 years for one stem to disappear. For the other 2, it will take the same period, plus the time period from stage 5 or 6 to complete disappearance. Eight of the stems that had fallen since 1935 had reached stage 5. In these cases, it took 50 years or less to reach stage 5. It is not possible, from these few observations, to estimate the complete decomposition time precisely, but obviously Sernander's statement of 90 years for complete decomposition is somewhat of an overestimate. Decomposition rates will, in any case, differ in particular cases.

Table 3. Number of stems in each necrotization stage

Year	1	2	3	4	5	6	Σ
1935	—	3	3	1	1(2)	1	9 (10)
1983–85	1	6	4	2	9	2	24

The number of trees in the tree layer has decreased from about 46 to 32 (Table 2). It is not clear from Sernander's description how he separated the tree layer from the shrub layer, as he only mapped the trees and what he called the regrowth. A height of 6 m was used as a limit for the tree layer in the remapping, but the lower number of trees mapped now is likely to represent a real loss of large individuals. Since 1935, 19 individuals from the previous tree layer have fallen, and only 5 individuals have grown up into the tree layer. It is often assumed that, on average, in a forest one fallen tree should be succeeded by one new tree (Horn 1975), thus keeping the mean number more or less constant over time. There are several reasons for questioning this hypothesis, but, in this case, the investigation plot is too small, related to the gap structure, to give a reliable mean number at a specific point in time.

On the 1935 map, 2 patches with regrowth are shown, one in the north corner and one in the south. A gap created by the fall of 3 stems lying in a NNE direction is also distinguishable and marked with a broken line. This gap was created within a time period of 25 years before the plot was investigated, but it is still possible to recognize the gap in the field (Plate 3). From the necrotization degree of the fallen stems (5–6), the 2 other patches are considerably older.

No peak in the age distribution of the individuals growing in the patches (Table 4) was observed. Only a few individuals below 0.5 m in height were found in the northern patch and in the gap, and none in the southern patch. The mean ages were about the same in the 2 regrowth patches, about 80 years, and the mean age in the gap about 30–35 years lower. The establishment has not occurred at a single point in time, when the gaps were created, but continuously over a rather long period. It is only the survivors, of course, whose age has been determined. If the gap formation was followed by a high degree of germination, the seedlings have not survived. As several of the individuals in the marked gap were younger than 50 years (the time difference between the first map and the present), there was a continuous recruitment for several decades after gap formation.

Table 4. Age distribution in 1985 in 4 groups of individual trees 1.3–6 and 0.5–1.3 m in height

Patch	Height class (m)	$\bar{x}$	Minimum	Maximum	n
Northern group	1.3–6	76.8	54	102	11
Southern group	1.3–6	80.5	40	111	5
In the gap	1.3–6	49.8	36	70	6
	0.5–1.3	40.8	35	55	8

Small saplings, excluding the current year's seedlings (0.5 m), are numerous in the plot (Table 5), mainly on boulders and logs. There are significantly more saplings growing on boulders than on the soil. More saplings are growing on boulders and on *Picea* and *Populus tremula* L. (aspen) logs in open places, than on such substrates below tree crowns. On the other hand, significantly more saplings are growing on soil below the crowns of tree layers than in open places. More saplings are growing on *Populus* logs than on *Picea* logs; this last comparison is only made for the necrotization stage 5.

Table 5. Number of small saplings <0.5 m and their growing places

	Below tree crown	In open places	Σ	Not mapped	Approx cover of plot (%)
On soil	60—*—	28	88	0	67
On boulder	89—*—	133	222*	3	32
On *Picea* log	32—*—	98	130	0	
On *Populus* log	10—*—	159	169*	0	
On ND log	11	1	12	2	
On rootplate	0	27	27	0	1
Not stated	1	0	1	0	
Σ	203	446	649	5	
Cover %	52	48			100

ND = not determined; * significant at 1% level

Significant differences are also found in the height increments for certain cases. The growth of the saplings on logs is higher in well-lit areas than below tree crowns. There is also a higher growth rate on *Populus* logs than on *Picea* logs, but no significant differences were found between saplings growing on boulders and on soil.

On the boulders and on the decomposing stems, the saplings escape competition from the established trees and also from a dense field layer. The vegetation on boulders and stems consists mainly of bryophytes. The fact that saplings growing on soil were found more often below the tree crowns than in the open probably results from reduced competition from the field layer. The grasses and herbs are better developed in the open spots than below the tree crowns. If the shade is deep, as in the 3 above-mentioned regrowths, few small saplings were found. An interesting review of the importance of logs and other coarse woody debris in forest ecosystems has been published by Harmon *et al.* (1986).

4 Vegetation change near the forest-line

The last example is from a forest in northern Sweden, situated north of the Arctic Circle at about 67°N, near the village of Kvikkjokk. The coniferous forest-line is situated about 580 m asl and the study plot is at 460 m asl. The forest consists of *Picea abies, Pinus sylvestris* L. (Scots pine) and *Betula pubescens* Ehrh. (downy birch). The plot is open, with a crown cover of only 15%, but there is no evidence of storm gaps involving several trees, as occurs in Fiby urskog. Figure 3 compares trees from this plot, which measured 20 m × 20 m and is Plot 2 on the diagram (also in Hytteborn *et al.* 1987), with those from the Fiby urskog plot illustrated in Figure 2 and Plate 1.

The cumulative age distributions of *Picea* and *Betula* are plotted in a semi-logarithmic diagram, with age classes of 10 years (Figure 3). For the plot with the gap structure (cf Figure 2b), the cumulative age distributions can be interpreted as static survivorship curves. In any 10-year period, there is probably at least one year in which an adequate supply of germinable seeds is produced. Initially, *Picea* mortality is very high, but later it becomes relatively lower, probably an effect of its ability to survive as a so-called dwarf or suppressed tree (a more complete discussion is given in Hytteborn *et al.* 1987).

For plot 2, the cumulative age distribution of *Picea* cannot be interpreted as a survivorship curve. The number of cones at this latitude (67°N) is very low (Simak 1974). Cone production in *Picea* is very irregular (Hagner 1958), even if cones are also produced between the good cone years. It is not certain that a year with high cone production yields a high number of germinable seeds (Sarvas 1957). Several investigations (Kujala 1927; Eide 1930; Mork 1933) have shown that mature and fertile seeds are produced in

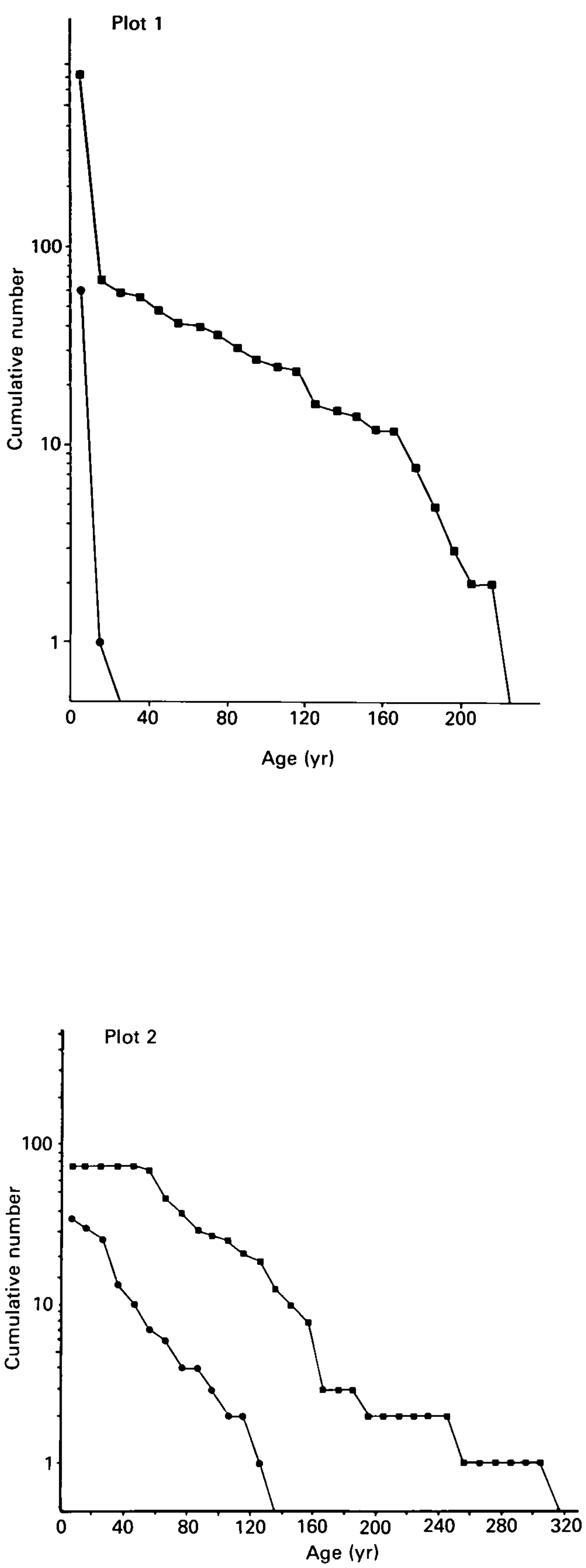


Figure 3. Cumulative age distributions of all individuals of (●) Betula pendula *plot 1,* Betula pubescens *plot 2, and* (■) Picea abies
Plot 1: Fiby urskog; Plot 2: near the coniferous forest-line in northern Sweden

years with a mean summer temperature (June–September) higher than 10°C. Temperature measurements were made in the village of Kvikkjokk, but not in plot 2, which is about 130 m higher. Based on a reduction of the mean temperature in Kvikkjokk between 0.7° and 1.0°C (Liljequist 1970; Alfjorden & Remröd 1975), it is possible to estimate the mean temperature in our plot. Only in about 6 years during the period 1950–80 did the mean summer temperature exceed 10°C, and none of these years were known as years with a high number of cones.

In such mountainous areas, the ability of a young tree to reach full size depends largely on its relationship with snow. The most difficult period is when the shoots become higher than the snow cover. Kullman (1981) discusses the complex of factors which are detrimental to the regeneration of *Pinus* in the Swedish mountains. He mentions the length of the growing season, the insolation conditions during snowmelt, strong winds, and damage from pathogenic fungi. Exposed foliage may also be grazed.

5 *Conclusions*

In the primary succession described, the 'driving force' was probably not the modification of the environment by the early species, but the different susceptibility to the strong environmental factor, inundation, and the different survivorship patterns in the forest in the early stages. The first tree species to invade the shore do not become established in the forest. A large seed source was available, and several tree species germinated on the open shore, but died shortly afterwards.

The gap dynamics described did not involve a succession in the tree layer, but in other cases, in the same forest, deciduous trees can be involved. Many cones were observed. The dynamics is determined by the gap formation, which, in turn, depends on a combination of environmental factors, strong winds, an unstable substrate, namely a very bouldery soil, and biotic factors, such as the height of the trees and the shallow root system. The shallow root system is characteristic of *Picea*, and also of the bouldery soil where most of the nutrients are in the humus layer. The bouldery ground and the shallow root system make the trees susceptible to strong winds, and most of the trees, therefore, never grow old. In most of the literature, the main emphasis has been given to the light factor. The forest described is rather open, with a 50% crown cover. From the number of *Picea* saplings surviving, it is evident that light is important, but it is also clear that competition for water and for nutrients plays a major role.

In the plot from the northerly region of the montane boreal forest, changes are very slow, with seed production depending totally on the frequency of a sequence of years with warm weather. From flower bud formation to germination, it takes 4 years for *Pinus* species and 3 years for *Picea*.

In all 3 examples, environmental and biotic factors are involved, in different combinations. Up to now, the results have been based largely on field observations; carefully designed experiments are needed in the future to identify the separate factors involved in the natural dynamics.

6 *Acknowledgement*

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International co-operation in the Man and the Biosphere Programme of UNESCO

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1 Introduction

In the past 15 years, since the launching of the Man and the Biosphere Programme (MAB) by UNESCO in 1971, there has been a considerable amount of environmental field research and experimentation which has had both successes and failures. This work has led to changes in perception and priorities in recent years as regards environmental matters. Hence, MAB, together with other international scientific programmes, provides the focus of a new situation, with a new order of importance and new opportunities for international co-operation.

Some of the relevant changes which MAB must take into account are described below. These topics were examined by the MAB General Advisory Panel, an independently appointed group of experts, which met twice in 1985 and 1986 to make recommendations to the MAB International Co-ordinating Council (ICC) about future MAB research and about the most suitable forms of international collaboration. For example, in 1986, a main perceived need is the application of existing knowledge, rather than the simple collection of data, modelling or systems analysis, which were the predominant topics of interest when MAB was launched in 1971.

Another important change is the scale at which environmental problems need to be examined. In the 1970s, emphasis was laid on small-scale phenomena with a rapid rate of response, whereas large-scale, regional to global, phenomena have become a major target of environmental research in 1986. Slow global changes in the biosphere may produce unexpected changes and discontinuities at a local level. One example is the catastrophic impacts of the 'El Nino' current which are now related to global climatic changes. Fifteen years ago, emphasis was laid on gradual changes, on the equilibrium state of the biosphere, and on global stability, while, today, the scientific world believes in a much higher rate of significant change, and underlines the importance of rare events in shaping environmental systems. Disequilibrium and multi-stable states are common. There is a belief in global instability.

In the 1970s, there was a considerable emphasis on interdisciplinary research to find solutions to real-world problems, using complex models, depending on many variables, which attempted to fill the still-existing gaps in knowledge. Today, there is a tendency to seek a more simplified understanding of the complexity of the real world.

In some countries, one can also perceive significant changes in the social aspect of environmental matters. In the 1970s, public confrontation and polarization on single issues characterized the social climate when environmental issues were discussed. Today, societal learning and consensus will hopefully lead to a new ethic of shared responsibilities for the environment.

One of the most important changes in the perception of environmental questions has been triggered off by technological development.

Fifteen years ago, there was an increase in the use of large main-frame computers, of aerial photography, and particularly of satellite imagery. Today, there have been dramatic changes in these fields through the large-scale introduction of smaller, more powerful and portable computers, and through the development of interactive computer programs and expert systems. Satellite imagery, improved photography and laser radar are becoming more widely used, and offer new, exciting possibilities for ecological research.

These trends provide new opportunities for international co-operative research from now into the 1990s, with new objectives, a different combination of knowledge, and a new *modus operandi*. Consequently, the General Advisory Panel has recommended to the MAB ICC that the future MAB research programme should be comprised of 4 major research themes:

i. ecosystem functioning under different intensities of human impact;
ii. management and restoration of human impacted resources;
iii. human investment and resource use;
iv. human response to environmental stress.

This proposed new research programme should be implemented through complementary networks of MAB pilot projects and MAB comparative studies.

2 The MAB research programme

Let us now consider in more detail the 2 categories of MAB research.

2.1 Category 1: MAB pilot projects

Traditionally, the major focus for international co-operation in MAB has been provided by pilot projects. Ideally, these problem-oriented projects have the following characteristics:

- they deal with land use problems of interest at the regional and international, as well as the local and national, levels;
- they address land use problems at a manageable scale (eg an alpine river valley), while placing them within their broader context;
- they involve the participation of scientists from the range of natural and social science disciplines needed to study the interplay between natural and social systems, as well as planners and local populations.

There is no room here to describe fully the large number of current MAB pilot projects. Let me, therefore, briefly mention one of them.

The MAB pilot project in the Mayombe (Congo) aims to develop the scientific bases for regional planning in this forested mountain chain in south-west Congo. The practical working hypothesis of the project is that the process of rural depopulation can be halted by new strategies of development to increase regional productivity, services and food self-sufficiency. These strategies include the diversification of agricultural production – such as agroforestry – and emphasis on developing local resources of renewable energy.

At the same time, a number of challenging scientific issues are being addressed within the project. These issues include the study of the mechanisms involved in the breakdown of organic matter by soil fauna, and the role of fog and mist in maintaining the dense tropical forest in a region with an annual rainfall of only 1300 mm, and a 5-month dry season.

2.2 Category 2: MAB comparative studies

Comparative studies are intended to develop a better theoretical and operational basis for understanding the replicability and comparability of ecological information, and thus to advance ecology as a more predictive science. The specific aim of MAB comparative studies is to test a range of hypotheses under different ecological situations and human impacts.

The MAB international networks of pilot projects represent a valuable approach to comparative research: that of extracting the essence from studies of processes, and identifying the elements of situations that are either similar or different.

Such comparative studies should help to re-establish links between ecology and the natural and social science disciplines and subdisciplines. They should encourage better use of modern technology (eg use of remote sensing for identifying similar ecosystem types or comparable research sites in different regions). They should help to develop collaborative links between scientists in different countries. Soil characteristics and site history must be taken into account in selecting sites, in addition to climatic factors. An alternative research strategy is to choose contrasting sites in order to advance our understanding by comparing differences rather than by searching for similarities.

Let me give as an example one comparative study being undertaken jointly by MAB and the International Union of Biological Sciences. The comparative study on soil biological processes and tropical soil fertility aims to develop management options for improving tropical soil fertility by biological processes. The programme of field work is based on a series of hypotheses which have been grouped under the following 3 general experimental principles.

i. The release of nutrients from above- and below-ground litter can be synchronized with plant growth demand.

ii. Soil organic matter acts as both a source and sink for nutrients in the soil – its quantity and quality can be regulated by the management of its litter inputs.

iii. Litter and soil organic matter influence soil water characteristics.

As in other comparative studies, the focus is on explanation rather than description, with mechanisms established for substantive review and evaluation of the overall programme, and exchange of information between the participating national projects.

2.3 MAB networks

May I now give a brief overview of the third mode of implementation of the future MAB research programme through the MAB networks.

MAB supports international co-operation in research through its international networks, where the sharing of information and resources is mutually beneficial to the co-operating countries. These networks differ in character and in objective, as well as in their regional or international extent. Some are based on geographical proximity, such as the countries of the southern cone of South America, and others on common linguistic or sociocultural background, such as the francophone African countries. Wider in scope are the MAB pilot project networks and the international Biosphere Reserve network, where common research frameworks and scientific information exchange are encouraged.

As Biosphere Reserves are considered to be the 'backbone' of the MAB Programme, please allow me to digress to explain their origin and development. I recall that, when the MAB Programme was launched in 1971, Project 8 was aimed at the conservation of natural areas and the genetic material they contain. This theme was developed subsequently in 1974 by a task force, which drew up a set of objectives and characteristics for special sites designated for this purpose, called 'Biosphere Reserves', to identify them with the rest of the MAB Programme. The objectives for Biosphere Reserves stated in 1974, which have since been endorsed and refined by the Scientific Advisory Panel for Biosphere Reserves, are as follows:

- — to conserve for present and future use the diversity and integrity of biotic communities of plants and animals within natural and semi-natural ecosystems, and to safeguard the genetic diversity of species on which their continuing evolution depends;
- — to provide areas for ecological and environmental research, including baseline studies, both within and adjacent to such Reserves;
- — to provide facilities for education and training.

At that time, Biosphere Reserves were unusual as conservation sites, in that man and human activities were considered to have a constructive role in environmental protection, and that, *vice versa*, the Biosphere Reserve was to contribute to the development of its region. The emphasis on combining multiple functions within a single given site and on linking these Reserves into an international network based on a common understanding of scientific purpose also made the concept different from other more traditional means of establishing protected areas. In 1984, an Action Plan for Biosphere Reserves was adopted by the International Co-ordinating Council to improve and expand the Biosphere Reserve network within the overall context of the MAB Programme. As of May 1987, the international Biosphere Reserve network consists of 266 sites located in 70 countries. These Biosphere Reserves serve as the locus for all MAB activities, as every effort is made to place MAB pilot projects and comparative studies within them.

All MAB networks, either regional or international, are linked through information dissemination, the exchange of scientists and research workers, and through joint meetings. In addition, some networks are linked through newsletters, joint training programmes, comparability of research design, and data collection. The networks are also characterized by newly established facilities for research, permanent exhibits, specialist training programmes and environmental education.

These characteristics are fully displayed at China's most advanced Biosphere Reserve – Changbai Mountain – notably in terms of logistic facilities for research and environmental education and training.

The most important factor for international co-operation, however, is the will to co-operate with ecologically analogous Biosphere Reserves around the world. In China, this potential for international co-operation can be mobilized through the permanent presence of a large number of scientists working in the Changbai Mountain Biosphere Reserve. In this respect, there is no doubt that Changbai is on the way to becoming a model within the international MAB networks.

FOREST ECOSYSTEM AND FOREST MANAGEMENT

Physiography as an integral part of forest ecosystems

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Abstract
Forestry is active at local, regional, national and continental levels, and uses knowledge and understanding of the distribution and dynamics of forest ecosystems, the vegetation/soil/climate complexes which are the primary production systems.

This paper outlines the principles and relevance of a site classification system or model, in which selected physiographic features of soil and climate provide a relatively stable framework for considering the more dynamic vegetation/land relationships both in space and time. Significant characteristics of this system are forest succession in relation to physiography, feature continua, normality rather than average as a reference criterion in such continua, and also the establishment of classes within continua by concurrent reference to vegetation rather than *a priori*. The selected features of local climate, soil moisture regime and soil nutrient regime are related to more easily recognizable features of the landscape.

The classification comprises 4 inter-related levels, with increasing differentiation and detail of feature classes. They include (climatic) site or ecoregion based on differing relationships among tree species and position in the landscape, relevant geological material classes in the rooting zone of trees, physiographic site type being the stable basis of the ecosystem at the practical level of forestry operations, and, finally, site condition comprising the more variable surface soil and ground vegetation.

This hierarchical system, developed in Ontario, Canada, during the past 40 years, is valuable for interdisciplinary research, for evaluating relative productivity, for management planning at various levels of complexity, and for information transfer, even among widely separated areas.

1 Introduction

Forest management – being part of land management – is engaged in the manipulation of ecosystems at various levels of complexity, ie from planting a crop on a specific site, to management of large tracts of land, to national policy development. To be most effective, the management planning and operations at the various levels should be inter-related in an ecological framework so that decisions made at one level are compatible with those at other levels. The development of this framework requires a knowledge of ecosystems, their composition, their distribution and their dynamics.

The forest ecosystem is a dynamic complex of interacting and inter-related biotic and abiotic factors or subsystems. Forest managers must consider both the vegetation and the important soil and other physical environmental factors. Without an understanding of this complex ecosystem, we can exploit the forest but not manage it as a crop towards renewed and improved production.

Once we acquire knowledge of local ecosystems, through scientific investigations and by experience gained during management practices, we must organize it within a classification framework of ecosystem types, based on an appreciation of cause/effect relationships, ie how various factors affect the performance of tree species. This procedure allows the forest manager to select, consider and use only the relevant knowledge and experience from previously treated areas, when making new decisions about treating another specific area. The most relevant knowledge comes from ecosystems of the same type as that about to be treated.

For purposes of classification to facilitate the transfer of management knowledge, scientists and managers have used information on factors such as climate, topography, geology, land form, soil, flora and fauna, sometimes separately with the intent to combine these various factors at a later stage. However, we must remember that the relevance of any one factor for tree growth depends on the combined effect of all other factors. For example, in a humid region, tree growth on a clay soil may be better than on sand, but, in a more arid region, trees may grow mainly on the sandy soils while the clay soils support grass. Tree species usually have a considerable range of distribution, but within this range their occurrence and vigour in relation to specific land form features, such as slope position and aspect, as well as soil drainage, vary considerably. This variation reflects a compensation among climate and soil factors.

Because the significance of the variation in any one factor is dependent upon the total effect of all the other factors in the ecosystem complex, it is logical to approach the evaluation of the relevance of factors through a classification of ecosystems as a whole.

Such an integrated approach has been developed for Ontario by Hills (1952, 1960, 1976) and a team of researchers (see Burger 1972b). It has resulted in a hierarchical system originally oriented towards forestry, but later broadened to provide an ecological basis for land use planning, including uses other than timber production. The system has 4 inter-connected levels, based on an increasing completeness in considering the detail of ecological relationships.

The purpose of this paper is to describe how the Ontario classification system integrates knowledge of vegetation, soil and climate to provide an ecological framework which is useful for the management of forest ecosystems.

2 Concepts and principles

Forest management requires the management of an ecosystem, the whole local biological production system, which Hills (1953) has also called 'total site' or just 'site'. The general approach used in this classification of 'total sites', or ecosystems, is based on the principle that, although ecosystems include all environmental features, they may be classified by a single feature or by a combination of features (Hills 1953), depending on the purpose. In Ontario, that purpose was to provide an ecological basis for forest management for an area about the size of north-east China or of France and Spain together, within which ecosystems range from northern tundra to deciduous broadleaved forests in the south.

Because ecosystems are dynamic systems, physiographic features have been chosen to constitute the logical frame of reference, because these features remain most stable in a world of constant change (Hills 1952).

Three physiographic features which directly affect plant growth have been chosen. They include:

- ecoclimate regime, which refers to the variations in the atmosphere (effective temperature and effective humidity) of local areas between ground surface and tree tops;
- soil moisture regime, which refers to the soil moisture supply during a complete vegetation cycle;
- soil nutrient regime, which refers to nutrients available in the rooting zone of trees.

These 3 features are related to readily observable features in the landscape, namely relief (slope, aspect, relative mass elevation and relative position of bodies of water), soil pore size distribution pattern (combinations of soil texture and structure), and mineral composition of soil materials.

Used in combination, these features comprise the so-called physiographic site, which is the most stable component of the local forest ecosystem.

The relative level of each of these features – ecoclimate, soil moisture and soil nutrient regime – is ranked during field investigations on the 11-class scale, covering the complete continuum from extremely low (θ) to extremely high (9) as follows:

θ, 0, 1, 2, 3, 4, 5, 6, 7, 8, 9

For some management purposes, these 11 classes have been grouped into broader classes. Thus, for example, the soil moisture regime scale in Ontario ranges from 'extremely dry' (θ) to 'saturated' (9), with broader groupings: 'dry' (θ,0), 'fresh' (1,2,3), 'moist' (4,5,6) and 'wet' (7,8,9).

As an important reference point, Hills (1945) applied the term 'normal' as used by Marbut (1927) in his concept of normal soil profile development. Normal does not equal average, modal, or optimum, but, instead, it is a standard well-defined reference point. On the above-mentioned continuum scale, the normal is positioned somewhere near the middle to provide adequate numbers of classes on both sides to suit the above purpose. Thus, a 'normal physiographic site' has a normal ecoclimate regime, a normal moisture regime and a normal soil nutrient regime. The primary land form reference point is a gently undulating, well-drained deep loam, with no significant deficiencies or excesses of nutrients, and a gently undulating topography which imparts no extreme influence on the ecoclimate. This is a useful practical reference point during field investigations. On such a normal physiographic site, vegetation development reflects the unmodified effectiveness of the macro- (or regional) climate. Thus, in a humid region, the normal site provides adequate moisture for a mesophytic vegetation, but, in an arid region, only xerophytes can survive on the normal site.

On any one physiographic site, vegetation is not stable. Given the opportunity, it tends to develop in a succession from a pioneer stage through intermediate stages to a climax or least disturbed stage. A pioneer vegetation type – as characterized by its tree species – may occur over a considerable range of physiographic sites within one climatic region, and even across 2 or more regions, whereas a climax vegetation has a more restricted range.

When relating forests to physiographic sites, Hills (1960) argues that neither physiographic nor biotic types can be established independently, but that groups of features must be classified concurrently. Forest types are often established independently, on the assumption that similar forests have similar environmental controls, but that assumption does not take into account the compensation of factors. Similarly, independent classification of climate or soil is not adequate either, as these are only one portion of the total productivity complex.

The above principles were used in the development of a hierarchical physiographic classification system comprising 4 inter-related levels; they include, from the broad to the local level, site region, land type, physiographic site type and site condition.

3 Site regions

It is well recognized that vegetation changes with latitude within a continent, and changes with altitude at a given latitude, such as on a mountain. For example, on Mount Washington in the White Mountains of the State of New Hampshire, USA, using the physiognomy of the vegetation, one can easily recognize 4 vegetation zones, from deciduous forest to alpine tundra, over an approximately 1.5 km range in altitude. The distance from the base of this mountain to the comparable subarctic zone in the north is about 1300 km. For a similarly great latitudinal distance in Ontario, Rowe (1972), using physiognomy and the presence of some tree species as criteria, recognized 4 forest regions. However, over that great distance with a relatively low relief, changes occur not only in the physiognomy and tree species occurrence, but also particularly in the relationships between species and physiography which are relevant to forest management. In site regions, we recognize such particular changes, and 6 site regions have been distinguished in the above south–north Ontario example.

Site regions in Ontario are defined as regions within which specific plant successions occur upon specific land form positions. Conversely, similar land forms (relief and geological materials) within different site regions will support different plant successions. The different vegetation/land form relationships in various site regions are a reflection of differences in regional climate (Hills & Pierpoint 1960).

The characterization of any one site region in Ontario can be demonstrated on a simple grid (Table 1) comprising 2 continua, namely ecoclimate (ie effective local temperature as influenced by local topographic position) and soil moisture (as influenced by soil materials and local drainage conditions). The characterization is based mainly on the most stable vegetation type on the normal physiographic site type, plus the most stable vegetation type on each of the 8 important deviations from the normal. In addition, the less stable (pioneer and intermediate) types indicate successional trends. These relationships have been published by Hills (1950, 1966, 1976) and Burger (1976). Table 2 demonstrates how, for the same normal moisture regime but with 3 different ecoclimates (temperature only) – ie normal, hotter than normal and colder than normal – 3 species (*Picea glauca* (Moench) Voss (white spruce), *Acer saccharum* H. Marsh. (sugar maple) and *Carya ovata* (Mill.) K. Koch (hickory)) change their preferred positions in the 7 most eastern site regions in Ontario, trending north to south. With these changes, there are also related changes in the vigour of other tree species, ecosystem productivity, and type of ground vegetation which competes with forest regeneration. Shifts such as those shown here for macroclimatic temperature gradients occur also in the east–west air humidity gradient. Similarly, humidity-related shifts are very likely important in north-east China, as well as any temperature-related shifts.

Table 1. The 'grid' of 9 physiographic sites which provide the basis for the characterization of vegetation/site relationships in site regions of Ontario

		Ecoclimate regime		
		Hotter	Normal	Colder
Soil moisture regime	Drier			
	Normal			
	Wetter			

Table 2. Change of preferred positions of 3 tree species on the normal moisture regime, but with 3 different ecoclimates for the 7 most easterly site regions of Ontario

	Ecoclimate		
Site region	Hotter	Normal	Colder
1E	P		
2E	P	P	
3E	P	P	
4E	A P	P	
5E	A	A	P
6E	C	A	P
7E		C A	

P = *Pica glauca*; A = *Acer saccharum*; C = *Carya ovata*

In site regions, we have thus placed ecosystems in a macroclimatic context or continental continuum. These regions could be called gradient-defined regions, and differ from the original geographical regions which can be called areal-described regions (Hills 1960). Both are important for the distribution of knowledge; their functions, however, differ.

The concept of site regions was developed in Ontario to recognize important gradients in species/site relationships over long distances where altitudes range mainly from 0 m to 500 m. In mountains with greater ranges in altitude, forest zones have been recognized. It seems quite possible that the concept of site regions could be applied within such altitudinal zones, particularly in such mountains as in north-east China and the eastern USA, where there is a strong north–south trend, and where altitudinal zones occur as high plateaux rather than as steep mountain slopes.

For the characterization of site regions, knowledge is required of the distribution of tree species in relation to land form positions, ie physiographic site types; for mapping these regions, information on distribution ranges of tree species, climatic gradients, relief, soil and geology is very useful. Where vegetation has been severely disturbed, remnants of ecosystems, or scattered occurrences and performance of individual forest trees or domesticated fruit-bearing trees may offer clues regarding important regional gradients. Historical records would also be valuable.

The boundaries of site regions are based on the manner in which more than one species adapt themselves to the gradients in the macroclimate. No 2 species act in exactly the same manner, but many show similarities. Regional boundaries are therefore transition zones; they are not sharp, but serve as warning signs that relationships between species and sites are changing, the closer the boundary is approached. Sometimes the boundaries are fairly sharp where the physiography changes abruptly. Furthermore, in Ontario, boundaries based on north–south temperature gradients are somewhat more easily recognizable than those indicating the east–west air humidity gradients.

It should be realized that the soil moisture continuum in a moist climate will differ in absolute terms from one in a dry climate, although the same 11 class scale (0–9) can be used. The concept of 'normal' is the same for all regions; in a humid region, the normal may be called fresh, ie suitable to support a mesophytic forest, but in a dry climate the normal is much drier, with the optimum site for mesophytes occurring in a lower position in the topography. Moisture regime ratings are thus specific for each site region. The use of a universal moisture regime scale has been discussed by Hills (1952).

Figure 1 and Table 2 show and characterize the 13 site regions of Ontario. Beyond Ontario, preliminary site regions have been recognized in the lake states of the USA (Burger 1976); the term 'forest ecosystem region' was proposed, because ecosystem is synonymous with 'total' site, and because ecosystem region might be a more convenient term for international, and perhaps intercontinental, communication than 'site region'. Studies to characterize and map such regions covering all of Canada and eastern USA are in progress.

4 Land type, physiographic site type and site condition
Within site regions, the classification system recognizes 'land type' as the second level. This is defined in terms of taxonomic classes of texture and petrography of geological materials which occur within the normal rooting depth of trees (Hills & Pierpoint 1960). To be

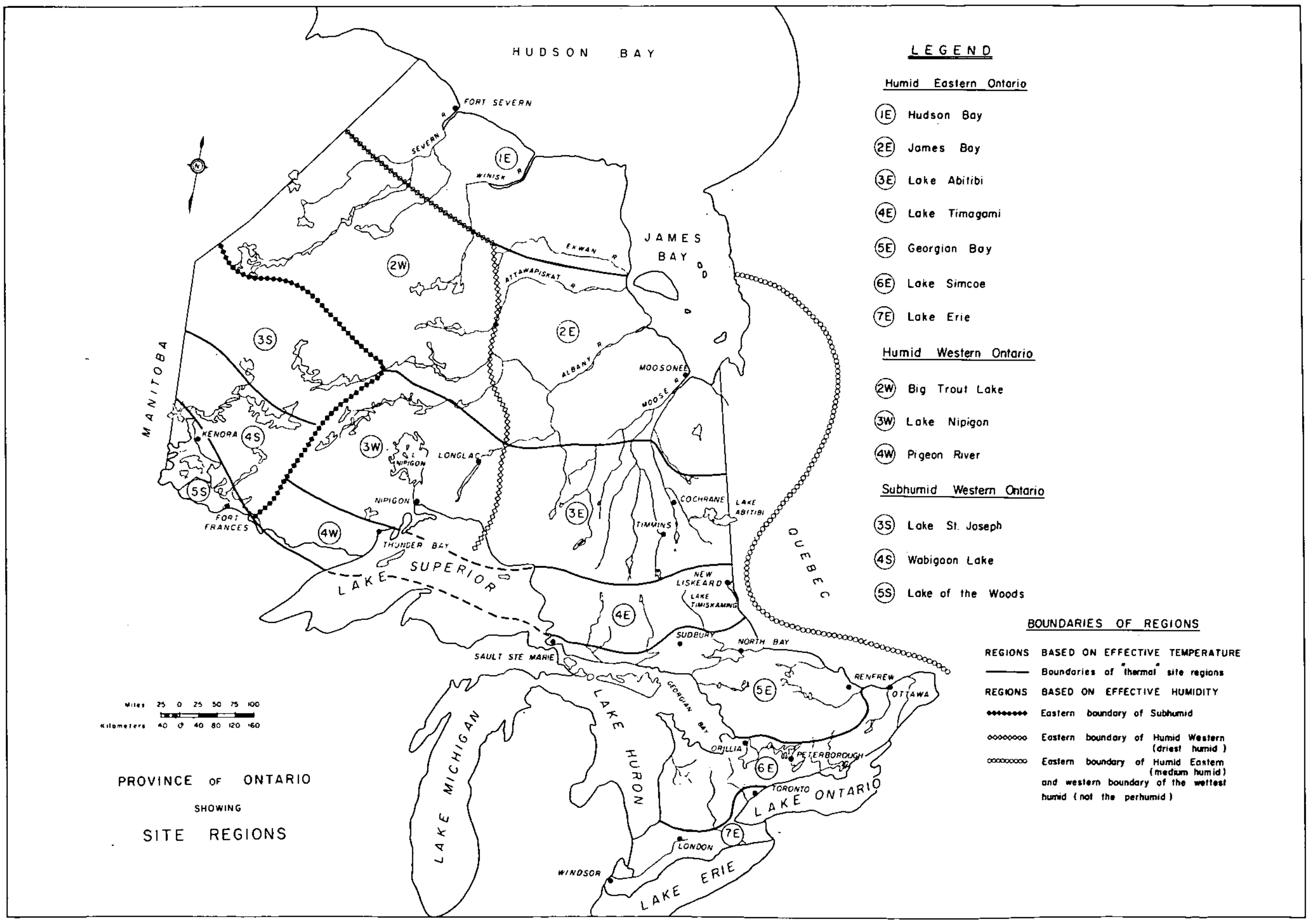

Figure 1. The site regions of Ontario (source: Hills 1966)

useful for large areas of land, the texture and petrography classes of these geological materials (Burger 1967, 1972a) are usually broader than those used in establishing catenas in agricultural soil surveys.

The third, and most important, level in the Ontario classification system is the 'physiographic site type', a subdivision of the 'land type'. It is defined by relatively narrow ranges in (i) depth of geological materials occurring in the rooting zone, (ii) soil moisture regime, and (iii) local climate. An example of a physiographic site type is: a dry shallow (30–120 cm), very low base (granitic), medium sand over a very low base bedrock, with a hotter than normal ecoclimate. The physiography/vegetation relationships studied at this level provide the basis for the establishment of site regions and the classification of significant land types. The ecosystem as defined by tree species and physiographic site type provides a convenient level to summarize descriptive information and ecological knowledge. This is the level at which the potential productivity is rated, and at which the forester usually has to manage his forest stand.

The fourth and last level is called 'site condition'; it refers to the forest floor and upper soil horizons. Variations in site conditions within any one particular physiographic site type reflect differences in history of forest growth and disturbance (eg fire and soil erosion), and influence both the actual forest production and the competition from undesired vegetation during forest establishment. Currently important 'forest ecosystem classification' programmes are in progress in northern Ontario (Jones 1984; Jones *et al.* 1983a,b). Extensive sampling of vegetation and soil, computer-based data analyses and modelling, and close co-operation between researchers and forest managers have resulted in the establishment of classes of mature forest ecosystems. These classes provide the basis for considering the results of past management activities, making interpretations and developing prescriptions for harvesting and related forest regeneration operations. These ecosystem classes may also serve fire management activities and wildlife management.

5 Mapping and evaluation

This Ontario site classification system – also called the physiographic site classification system because physiography is used as a basis for ecosystem ('total

Table 3. The characteristic forests of Ontario, simplified after Hills (1966)

THE MAJOR PHYSIOGRAPHIC SITE CLASSES

Site Regions	ECOCLIMATE (TEMPERATURE)								
	HOTTER			NORMAL			COLDER		
	SOIL MOISTURE								
	DRIER	NORMAL	WETTER	DRIER	NORMAL	WETTER	DRIER	NORMAL	WETTER
Humid Eastern Ontario									
1E	BETULA-POPULUS pa t PICEA-PINUS m bn	PICEA-BETULA g,m pa POPULUS t	OPEN PICEA-LARIX m l	PICEA m	OPEN PICEA m	OPEN PICEA-LARIX m l	MOSSES AND LICHENS		
2E	(OPEN) PINUS-BETULA bn pa	PINUS-PICEA bn m,g	OPEN PICEA m,g	PINUS-PICEA bn m,g	ABIES–PICEA ba m,g POPULUS t	OPEN PICEA-LARIX m l	OPEN PICEA-LARIX m l	MOSSES AND LICHENS	
3E	PINUS-PICEA bn m	PINUS-PICEA bn m	POPULUS-THUJA b o	PINUS-BETULA bn pa	ABIES-PICEA ba g POPULUS-BETULA t,b pa	PICEA-ABIES m ba	PICEA-PINUS m bn	(OPEN) PICEA-LARIX m l	MOSSES AND LICHENS
4E	PINUS-BETULA st,r,bn pa -POPULUS t,gd	ACER-BETULA s,ru al PINUS-ABIES-PICEA st ba g	BETULA-THUJA al o	PINUS st,r,bn	ABIES-PICEA ba g PINUS st	ABIES-PICEA ba g,m	ABIES-THUJA ba o	PICEA-LARIX m l	OPEN PICEA-LARIX m l
5E	QUERCUS-PINUS ra st	ACER-QUERCUS s ra -FAGUS gf	ULMUS-ACER am ru -FRAXINUS n	PINUS-TSUGA st,r c	ACER-BETULA s al TSUGA-PINUS c st	FRAXINUS-ACER n ru PICEA-ABIES g ba	PICEA-ABIES g ba -PINUS st	ABIES-PICEA ba g PINUS st	ABIES-PICEA ba m -LARIX l
6E	FAGUS-TSUGA gf c QUERCUS ra	QUERCUS-CARYA a,ra ov	ACER-BETULA s,st,ru al -JUGLANS ci	ACER-QUERCUS s,ru ra -FRAXINUS-ULMUS am d	FAGUS-ACER gf s -QUERCUS-TSUGA ra c	TSUGA-BETULA c al	PINUS st,r FRAXINUS-ULMUS am a	PICEA-ABIES g ba	ABIES-PICEA ba m,g LARIX l
7E	QUERCUS-CASTENEA v,ra,cc d CARYA-JUGLANS gl,ov ci	LIRIODENDR-JUGLANS tu n,ci QUERCUS-CARYA a,ra to,gl	PLATANUS- o FRAXINUS-BETULA pe,n al	QUERCUS-CARYA ra,a ov,gl	ACER-FAGUS s gf -QUERCUS-CARYA a,ra ov	QUERCUS-FRAXINUS bi,p pe,n ULMUS-CARYA a cr	TSUGA-FAGUS c gf -BETULA-PINUS al st	ULMUS-FRAXINUS a n QUERCUS-ACER bi ru	PICEA-ABIES g,m ba ACER-BETULA s,ru al
Humid Western Ontario									
2W	(OPEN) PINUS bn	PICEA-PINUS m,g bn	OPEN PICEA m,g	PINUS-PICEA bn m -POPULUS t	PICEA m	OPEN PICEA-LARIX m l	OPEN PICEA-LARIX m l	MOSSES AND LICHENS	
3W	PINUS-PICEA bn m,g	PINUS bn POPULUS-BETULA t pa	POPULUS-ABIES b ba	PINUS bn BETULA-POPULUS pa t	PICEA-ABIES g ba PINUS bn	PICEA-LARIX m l	PICEA-PINUS m bn	OPEN PICEA m	MOSSES AND LICHENS
4W	PINUS-BETULA bn,r pa	PINUS-POPULUS st t BETULA-ACER al ru	THUJA-ABIES o ba	PINUS st,r,bn	PICEA g PINUS-ABIES st ba	ABIES-PICEA ba g	PINUS bn ABIES-THUJA ba o	PICEA-ABIES m ba	OPEN PICEA-LARIX m l
Subhumid Western Ontario									
3E	PINUS-BETULA bn pa	PINUS-POPULUS m,g t	PICEA-ABIES m ba	PINUS-PICEA bn m	POPULUS-PICEA t m,g	POPULUS-PICEA t m,g	(OPEN) PICEA-PINUS m bn	PICEA-PINUS m bn	OPEN PICEA-LARIX m l
4E	PINUS-BETULA bn,st pa	PICEA-POPULUS g t,gd	POPULUS-FRAXINUS b n	PINUS-PICEA bn,st,r g	PICEA-ABIES m ba POPULUS t	PICEA-ABIES m ba	PICEA-PINUS m bn	PICEA-PINUS m bn	PICEA-LARIX m l
5E	QUERGUS-ULMUS ma a	PINUS-POPULUS st,r t,gd	FRAXINUS-ULMUS pe,n a	PINUS-POPULUS st,r t,gd	PICEA-ABIES m ba POPULUS-BETULA t,gd pa	PICEA-POPULUS m,g b THUJA o	PICEA-ABIES g,m ba	ABIES-THUJA ba o	PICEA-LARIX m l

ABBREVIATIONS

a	alba
al	allegheniensis
am	americana
b	balsamifera
ba	balsamea
bi	bicolor
bn	banksiana
c	canadensis
cc	coccinea
ci	cinerea
cr	cordiformis
d	dentata
g	glauca
gd	grandidentata
gf	grandifolia
gl	glabra
l	laricina
m	mariana
ma	macrocarpa
n	nigra
o	occidentalis
ov	ovata
p	palustris
pa	papyrifera
pe	pennsylvanica
r	resinosa
ra	rubra
ru	rubrum
s	saccharum
si	saccharinum
st	strobus
t	tremuloides
to	tomentosa
tu	tulipifera
v	velutina

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site') classification – provides the taxonomic units within which knowledge can be organized. However, land areas are not always sufficiently homogeneous to allow the mapping of single taxonomic units. Therefore, a number of broader units have been developed for mapping at several scales, each with fairly specific purposes in mind. These units include 'land type components' (scale 1 : 50 000) which are patterns of physiographic site types (Pierpoint 1962) useful for management operations, and 'land type pattern' at a scale of 1 : 125 000 (Burger 1972a) for broad forest land management planning. 'Land units', segments of landscapes each of at least 10 km^2, and the even larger 'landscape units' (Hills *et al.* 1970) comprising several land units were developed for multiple land use planning. Finally, a 'site district' (scale 1 : 4 000 000 to 1 : 10 000 000) is a subdivision of a site region based on a characteristic pattern of physiographic features, such as relief, type of bedrock, and soil parent materials.

For use in forest and land management, both taxonomic and mapping units have been evaluated with respect to potential production and degree of effort required to obtain a desired crop (Hills & Pierpoint 1960) and for rating forest use capability (Hills 1966). Site regions are used as seed zones and provide regional boundaries for silvicultural treatments.

6 *Acknowledgement*

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Studies on the ecological characteristics and management of *Pinus sylvestriformis* (Changbai pine)

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Abstract

Pinus sylvestriformis T. Wang (Changbai pine) is a 2-needled pine, which is an endemic species on the north slope of Changbai Mountain. By studying its photosynthesis and the relationships between growth and environmental factors, *P. sylvestriformis* was found to be a pioneer tree species which tolerates dry and poor soil conditions, and grows fast. According to the community investigation, the current *P. sylvestriformis* forest is divided into 2 types: (i) *Lespedeza/P. sylvestriformis* (bush clover/Changbai pine) forest; and (ii) *Vaccinium/Larix/P. sylvestriformis* (*Vaccinium*/larch/ Changbai pine) forest. The 2 types differ in composition, structure and primary productivity. According to research on succession and regeneration, the *P. sylvestriformis* forest vegetation is not in a steady state in the Changbai Mountain area. Human activities are important factors affecting its succession and regeneration. Some management options are suggested.

1 Introduction

P. sylvestriformis is a 2-needled pine, endemic on the north slope of Changbai Mountain, between latitude 42°06′–42°32′N and longitude 128°7′–128°20′E, and between 650 m and 1600 m above sea level (asl). The centre of its distribution is near Erdaobaihe and at Prevent Area, at 1100 m asl, and the forest covers 100 ha at each site. Information on the species' taxonomy is given by Tackenouchi (1958), Tackenouchi and Zhu (1959), Liou (1955), Zheng (1983) and Gu (1985). Until now, there has been no systematic study of its ecological characteristics. This paper discusses its native distribution and ecological features, and makes suggestions for its future preservation and management.

2 Ecological factors in relation to growth

It is evident that relationships exist between tree growth and climate, soil conditions, and, especially, light. We have studied these aspects, therefore, to determine growth rate.

2.1 Light

According to our investigations and experiments, *P. sylvestriformis* is a shade-intolerant tree species, which cannot regenerate under its own canopy. Measurements of photosynthesis of 3-year-old seedlings have shown that the species' light compensation point is about 300 Lux at 15°C, 500 Lux at 20°C and 2000 Lux at 25°C. The light saturation point is about 30 000 Lux (see Figure 1). The net photosynthesis rate is about 4.1 mg CO_2 fg^{-1} h^{-1}, and the respiration rate is 1.0 mg CO_2 fg^{-1} h^{-1}.

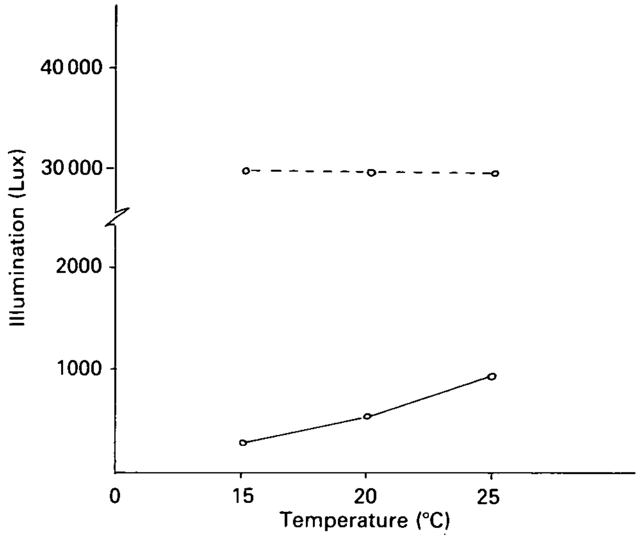

Figure 1. The light saturation point (o——o) and light compensation point (o– – –o) at different temperatures

The species has many physiological features which are related to its intolerance of shade.

2.2 Temperature

Temperature is an important factor which not only determines the species' natural distribution, but also affects its growth. When mean temperatures exceed 10°C for periods over 5 days, the buds of *P. sylvestriformis* begin to expand. Because of changes in temperature, productivity varies at different elevations. At 690 m, a 136-year-old tree has the following measurements: volume 2–4 m^3, mean height 23.5 m, mean diameter 50 cm, whereas, at 1100 m, a 339-year-old individual has a volume 3 m^3, 21.4 m height, and a mean diameter of 51.6 cm. Studies on premature *P. sylvestriformis* forest have revealed that diameter growth changes in relation to annual temperature, with continuous low temperatures in the growing season restricting growth.

Temperature also affects *P. sylvestriformis* seed development. At 690 m, an individual tree produced 305 g of seeds (the weight of 1000 seeds is 5.2 g), while, at 1260 m, an individual tree produced seeds weighing only 18 g (the weight of 1000 seeds is 3.9 g). According to our experiments at different elevations, where seeds were sown on the forest floor, temperature also affects seed germination.

P. sylvestriformis can tolerate temperatures as low as −44°C. Although seedlings in the nursery were often injured by low temperature, no evidence of injury was found among the seedlings regenerating naturally under the forest canopy.

2.3 Moisture

P. sylvestriformis has no strict water requirements. In its native range, mean annual precipitation varies between 670 mm and 1333 mm, with large fluctuations in soil moisture and air humidity. At 690 m, the forest site is very dry, as indicated by the presence of such species as *Quercus mongolica* Fisch. ex Turcz. (Mongolian oak), while at 1100 m the *Vaccinium/Larix/ P. sylvestriformis* forest mixture is evidence of a moist site, with a layer of moss 6–9 cm thick. *P. sylvestriformis* grows well at both sites.

2.4 Soil

P. sylvestriformis grows well in different soil types on the north slope of Changbai Mountain, and is able to tolerate poor soil conditions.

3 Growth analysis

P. sylvestriformis is a fast-growing tree species, according to stem analysis. At 690 m, the largest tree is about 28 m high, the largest diameter at breast height (dbh) is 69 cm, and the volume is 2–3 m^3 in a stand 136 years old. At 1100 m asl, the largest dbh ever recorded is 106 cm, the maximum height is 22 m, and the volume is 3 m^3, when trees are 339 years old. The variation in growth rate results from the different temperatures, humidity, radiation and soil conditions at the different elevations.

3.1 Height growth

Height growth rate is evidently faster at lower elevations. At 690 m, *P. sylvestriformis* grows faster after reaching 5 years of age, while at 1100 m it accelerates after 10 years. The rate of growth begins to slow down when trees reach 80 years of age (Figures 2 & 3).

3.2 Diameter growth at breast height

The stem analysis confirmed that *P. sylvestriformis* is a fast-growing tree species, and that its high rate of diameter growth lasts for a long time. At 690 m elevation, no reduction in dbh growth is found in the natural stands. The fastest growth period is between 10 and 68 years (Figure 4), while at 1100 m it is between 10 and 70 years (Figure 5).

3.3 Volume growth

The volume growth rate is quite fast and is maintained over a long period. No reduction in growth rate was evident (Figures 6 & 7).

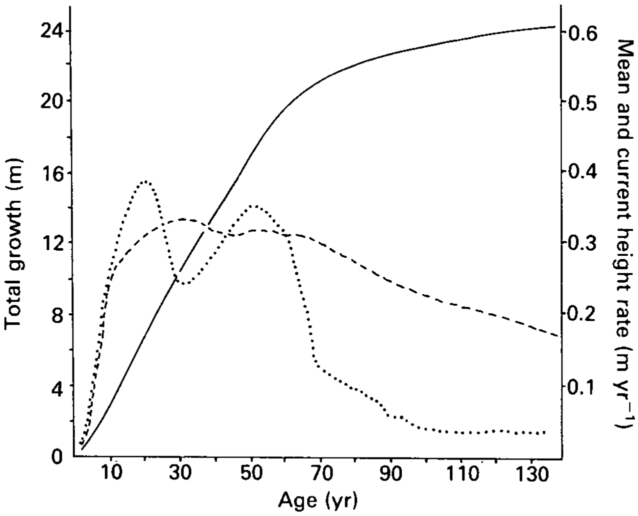

Figure 2. Height growth of P. sylvestriformis *at 690 m asl (—— accumulated growth; --- mean growth rate; ··· current growth rate)*

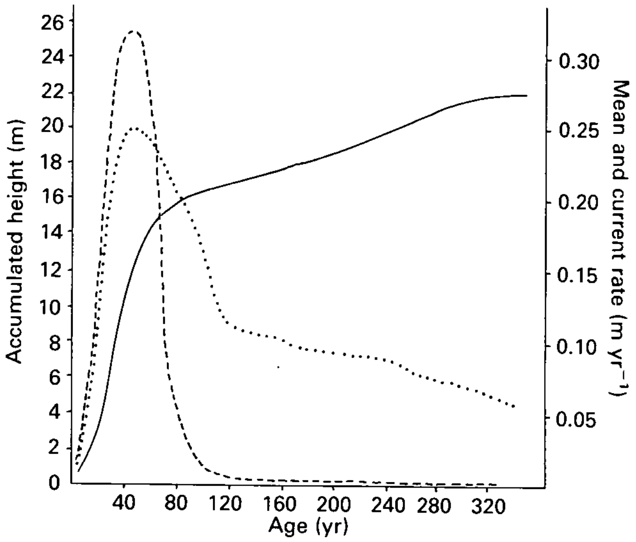

Figure 3. Height growth of P. sylvestriformis *at 1100 m asl (—— accumulated growth; --- mean growth rate; ··· current growth rate)*

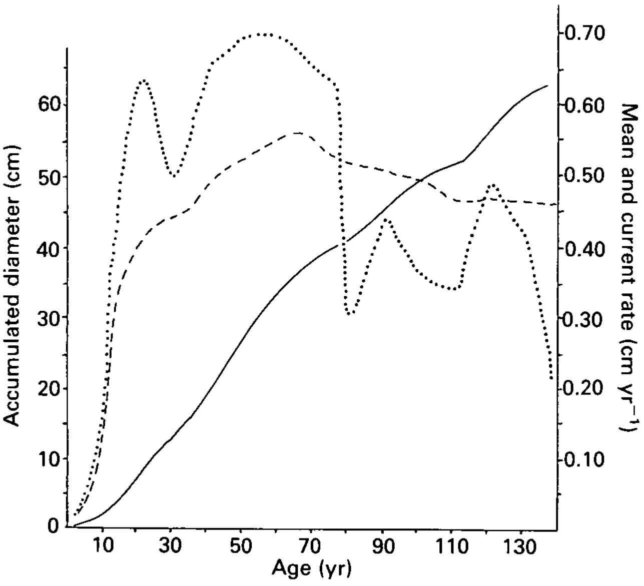

Figure 4. Diameter growth of P. sylvestriformis *at 690 m asl (—— accumulated growth; --- mean growth rate; ··· current growth rate)*

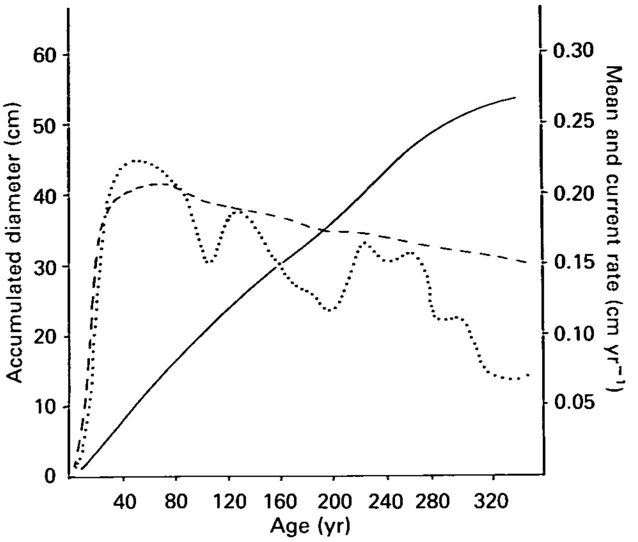

Figure 5. Diameter growth of P. sylvestriformis *at 2200 m asl (—— accumulated growth; --- mean growth rate; ··· current growth rate)*

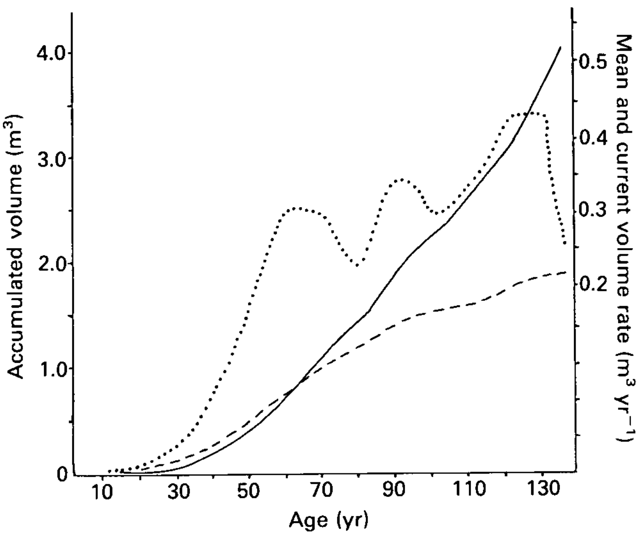

Figure 6. Volume growth of P. sylvestriformis *at 690 m asl (—— accumulated growth; --- mean growth rate; ··· current growth rate)*

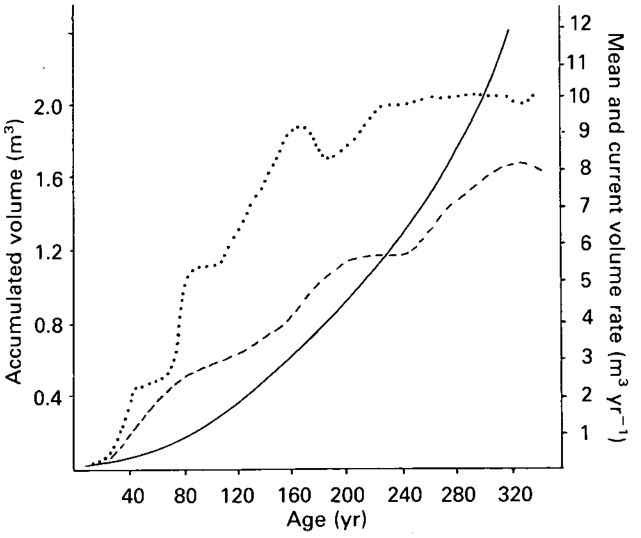

Figure 7. Volume growth of P. sylvestriformis *at 1100 m asl (—— accumulated growth; --- mean growth rate; ··· current growth rate)*

At 690 m, a reduction in growth rate was recorded, but is not a normal phenomenon, and probably resulted from human activity.

4 Community characteristics

The current *P. sylvestriformis* forest can be divided into 2 types, according to its composition, structure, and distribution: (i) *Lespedeza/P. sylvestriformis* forest, and (ii) *Vaccinium/Larix/P. sylvestriformis* forest.

4.1 Stand composition

4.1.1 Lespedeza/P. sylvestriformis forest

This is a very important type, only found at 690 m altitude, and covers about 100 ha near Erdaobaihe Town. It is a pure stand on a very dry site, and contains species such as *Q. mongolica*, etc. It shows evidence of serious damage. It can be further divided into 2 sub-types: (i) *Lespedeza/P. sylvestriformis* forest, and (ii) *Lespedeza/P. sylvestriformis* premature forest.

i. Lespedeza/P. sylvestriformis forest

This type is almost solely composed of *P. sylvestriformis*, although some *Larix* trees are present. The canopy cover is 0.7 and the stocking density is about 258 m^3 ha^{-1}. The mean age of the forest is about 136 years (see Table 1).

ii. Lespedeza/P. sylvestriformis premature forest

This type is a pure *P. sylvestriformis* stand, with a mean age of 36 years. The largest dbh is 24 cm, with a mean value of 13.4 cm, and the mean height is 12.1 m. There are 1538 trees ha^{-1}, and the stocking density is about 269 m^3 ha^{-1} (Table 2).

The *Lespedeza/P. sylvestriformis* forest has a rich understorey, which includes *Lespedeza bicolor* Turcz. (bush clover), *Lonicera ruprechtiana* Regel (honeysuckle), *Rubus crataegifolius* Bunge (hawthorn-leaf raspberry), *R. sachalinensis* Leveile (sachalin raspberry) and *Schisandra chinensis* (Turcz.) Baill. (Chinese magnolia vine), etc.

The growth of herbs is limited by the shrub species and the mean cover is only 40–50%. The main species are *Carex lanceolata* Boott (lanceolate sedge), *Spodiopogon sibiricus* Trin. (Siberian spodiopogon), *Deyeuxia angustifolia* (Kom.) Chang (narrow-leaved reedgrass) and *Melampyrum roseum* Maxim. (cow-wheat). These herbs can be divided into sub-layers, according to their heights.

4.1.2 Vaccinium/Larix/P. sylvestriformis forest

This is a moist type of *P. sylvestriformis* forest, at 1100 m asl, and covers an area of about 100 ha. The forest floor has a 6–9 cm layer of thick moss. *Vaccinium vitis-idaea* L. (cowberry) grows well. The type can be divided into 2 sub-types: (i) *Vaccinium/Larix/P. sylvestriformis* forest, and (ii) *Vaccinium/Populus* (poplar)/*Betula* (birch)/*P. sylvestriformis* forest.

Table 1. Composition of *Lespedeza/Pinus sylvestriformis* forest

		Composition		dbh (cm)		Height (m)		1 ha	
Tree species	Layer	Number (%)	Vol. (%)	Max	Mean	Max	Mean	No.	Volume (m^3)
P. sylvestriformis	I	96.0	99.8	69.0	37.0	28.1	22.1	162	256.3
Larix olgensis	I	4.0	0.2	41.0	16.5	28.8	16.8	7	2.0
Total		100	100					169	258.3

Table 2. Composition of *Lespedeza/Pinus sylvestriformis* premature forest

		Composition		dbh (cm)		Height (m)		1 ha	
Tree species	Layer	Number (%)	Vol. (%)	Max	Mean	Max	Mean	No.	Volume (m^3)
P. sylvestriformis	I	100	100	24.0	13.4	17.9	12.1	1538	269.3
Total								1538	269.3

Table 3. Composition of *Vaccinium/Larix/Pinus sylvestriformis* forest

		Composition		dbh (cm)		Height (m)		1 ha	
Tree species	Layer	Number (%)	Vol. (%)	Max	Mean	Max	Mean	No.	Volume (m^3)
P. sylvestriformis	I	64.5	67.0	106.0	41.1	23.0	22.0	248	396.8
Larix olgensis	I	35.5	33.0	50.0	19.4	30.0	24.6	137	129.9
Total		100	100					385	526.7

i. Vaccinium/Larix/P. sylvestriformis forest

This area of forest is composed of *Larix olgensis* A. Henry (Olga Bay larch) and *P. sylvestriformis*. The canopy cover is about 0.8, mean dbh is 33.4 cm, mean height is 23.0 m, and there are 248 plants ha^{-1}. The stocking density is 526.7 m^3 ha^{-1} (Table 3).

ii. Vaccinium/Populus/Betula/P. sylvestriformis forest

This is a secondary forest type. The major tree species are *Populus ussuriensis* Kom. (Ussuri poplar), *Betula platyphylla* Suk. (Manchurian birch), *Larix olgensis* and *P. sylvestriformis*. The site is drier than the previous type, and the moss is not too thick. Canopy cover is about 0.8 (Table 4).

Tree species in the subcanopy include *Salix raddeana* Laksch. (yellow willow) and *Acer tegmentosum* Maxim. (Manchu striped maple), with *Schisandra chinensis*. Herb species are present on the forest floor.

4.2 Diameter changes

According to our studies, the *P. sylvestriformis* forests differ in composition, height and diameter. At 690 m, the species forms a pure stand and its diameter changes reflect its hereditary features and soil conditions (Figures 8 & 9).

The diameter variation is particularly marked in the *Vaccinium/Larix/P. sylvestriformis* forest at 1100 m,

Table 4. Composition of *Vaccinium/Populus/Betula/P. sylvestriformis* forest

		Composition		dbh (cm)		Height (m)		1 ha	
Tree species	Layer	Number (%)	Vol. (%)	Max	Mean	Max	Mean	No.	Volume (m^3)
P. sylvestriformis	I, II	16.9	40.3	50.0	18.1	21.0	13.8	152	73.4
Larix olgensis	I, II	21.4	14.2	47.0	16.0	30.0	16.6	193	25.6
Populus ussuriensis	II	32.0	32.0	25.0	12.3	19.0	11.5	183	57.6
Betula platyphylla	II	20.3	10.2	25.0	12.3	19.0	11.5	183	18.3
Picea jezoensis (Sieb. et Zucc.) Carr.	II	6.7	2.2	15.0	10.4	12.0	9.5	60	3.9
Abies holophylla Maxim.	II	1.2	0.3	12.0	10.0	9.0	8.0	11	0.5
Pinus koraiensis Sieb. et Zucc.	II	1.5	0.3	12.0	11.0	8.6	8.0	14	0.5
Total								901	179.8

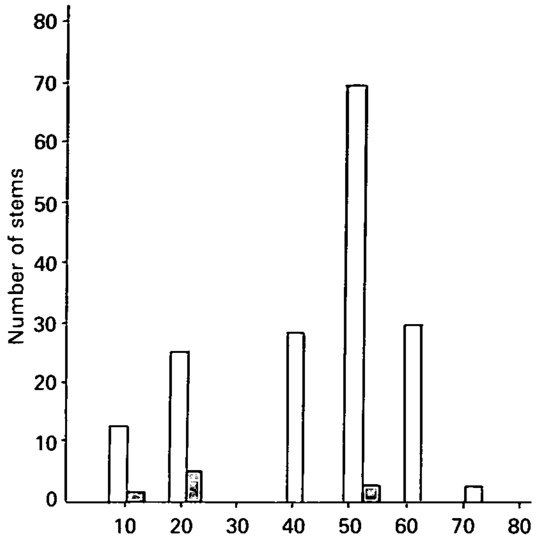

Figure 8. Stem number distribution in dbh classes of P. sylvestriformis *forest (*□ Pinus sylvestriformis*;* ■ Larix olgensis*)*

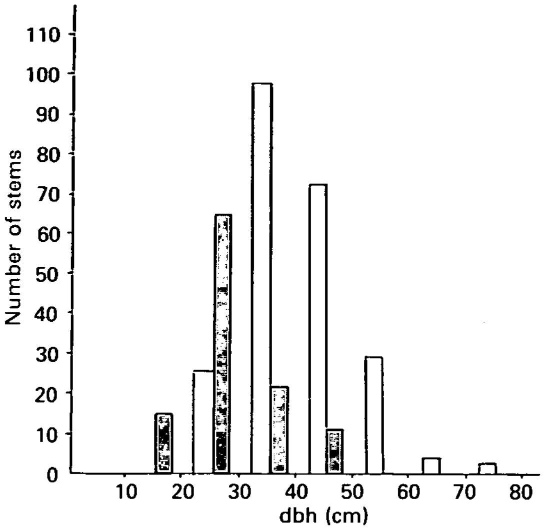

Figure 10. Stem number distribution in dbh classes of Vaccinium/Larix/P. sylvestriformis *forest (*□ Pinus sylvestriformis*;* ■ Larix olgensis*)*

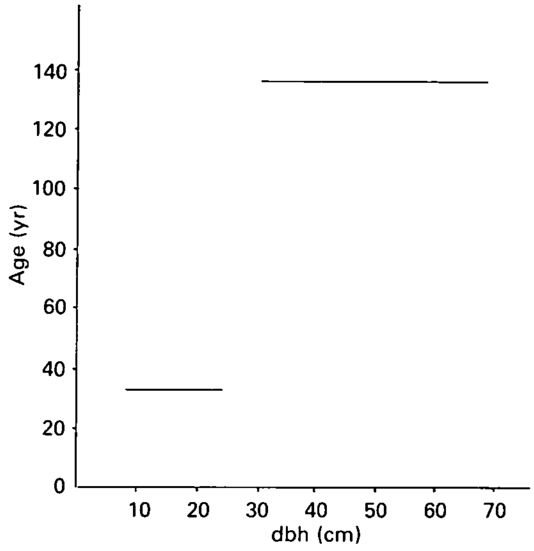

Figure 9. The relationship between diameter and age of Lespedeza/P. sylvestriformis *forest*

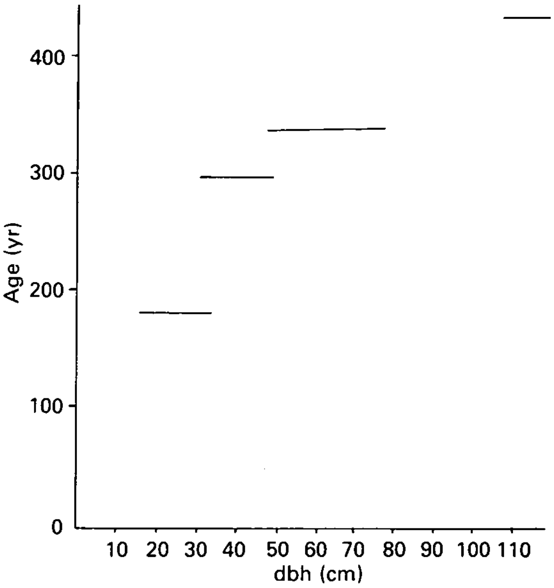

Figure 11. The relationship between diameter and age of Vaccinium/Larix/P. sylvestriformis *forest*

where there is clear evidence of 4 distinct generations (Figures 10 & 11).

5 Succession and regeneration

P. sylvestriformis is an intolerant tree species, with poor natural regeneration. According to seedling experiments in different forest types, *P. sylvestriformis* can germinate under a canopy at 690–1260 m, but many seedlings die because of insufficient light. Table 5 shows the natural regeneration of the *Lespedeza/P. sylvestriformis* forest.

At 1100 m, the *Vaccinium/Larix/P. sylvestriformis* forest has a closed canopy, so natural regeneration is poor, as shown in Table 6.

From Table 5, we can see that the *Lespedeza/P. sylvestriformis* forest will be gradually replaced by broadleaved species, such as *Quercus mongolica*. We also find that *Vaccinium/Larix/P. sylvestriformis* forest will eventually become *P. sylvestriformis/Picea* (spruce)/*Abies* (fir)/*Pinus koraiensis* forest.

6 Management

P. sylvestriformis is an endemic tree species of Changbai Mountain; it grows fast and adapts to dry and poor soil conditions. Because it represents a scarce resource which has been seriously damaged in the past, we must protect the remaining stands and encourage future development. On the basis of its ecological features, we must encourage the rational

Table 5. The natural regeneration of *Lespedeza/P. sylvestriformis* forest

Tree species	Seedlings	Young trees	Large young trees	Nos ha^{-1}	Percentage
P. sylvestriformis	160	248	—	408	11.9
Quercus mongolica	—	—	1778	1778	52.1
Betula platyphylla	340	—	160	500	14.6
Ulmus japonica (Rehd.) Sarg.	—	—	245	245	7.2
Tilia amurensis Rupr.	—	—	245	245	7.2
Betula davurica Pall.	—	—	160	160	4.7
Acer mono Maxim.	—	—	80	80	2.3
Total	500	248	2668	3416	100.0

Table 6. Census of natural regeneration of *Vaccinium/Larix/P. sylvestriformis* forest

Tree species	Regeneration frequency (%)	Seedlings	Young trees	Large young trees	Nos ha^{-1}	Percentage
P. sylvestriformis	22	225	725	—	950	11.7
Pinus koraiensis	39	600	1325	525	2450	30.1
Picea jezoensis	25	50	275	425	750	9.2
Abies holophylla	35	400	1950	50	2400	29.4
Larix olgensis	20	1000	400	0	500	6.1
Betula davurica	3	0	50	25	75	0.9
Acer spp.	19	0	1025	0	1025	12.6
Total		1375	5750	1025	8150	100.0

use of the present resources of the premature *P. sylvestriformis* forest, and improve its conditions for growth. Fire is an important factor for the species' natural regeneration, and we must encourage its natural regeneration using controlled fires. To expand the *P. sylvestriformis* resource, we must plant seedlings on open sites.

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Current ecosystem research topics in the United States

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Abstract
Research on forests as ecosystems began in earnest with the International Biological Programme (IBP) in the late 1960s. Some significant activities certainly preceded IBP, including studies of nutrient compartments and cycles and of flows of materials and energy through small catchments or watersheds. Nevertheless, it was during IBP that the methodology of describing and modelling the structure and function of forest ecosystems was developed and widely applied.

Ecosystem science has progressed markedly in the decade following the completion of IBP. The descriptive studies which dominated much of this programme in the United States have given rise to subsequent generations of ecosystem studies which are built around testable hypotheses, and which utilize experimental approaches (see, for example, Waring & Schlesinger 1985). Many of the hypotheses are the direct outgrowth of the IBP efforts, including methodological developments.

Research topics receiving major consideration by ecosystem scientists are discussed in this paper. Although the topics reflect much of the North American activity, the material presented does have some regional (north-western North American) bias. Most of my current experience is with the joint USDA Forest Service—Oregon State University ecosystem research group, which works at the H J Andrews Experimental Forest in western Oregon.

1 Ecosystem research topics

1.1 Old-growth ecosystems

I would like to begin by mentioning our studies of old-growth forests, from which several of the other topics have been derived. These are primary forests which are, in my region, greater than 200 years of age. Old-growth temperate forests dominated by coniferous species, such as *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir), once covered more than 6 million hectares in western Washington and Oregon alone. Now, only 2 Mha of old-growth forests remain in this region, of which 400 000 ha are reserved.

A typical temperate old-growth forest in this region is composed of *P. menziesii*, *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), and *Thuja plicata* D. Don (western red cedar), with little or no hardwood tree component (Franklin *et al.* 1981). The old-growth trees are typically 100 cm in diameter, 75 m in height, and 400–500 years old. Stand biomass and volume values typically exceed 1000 Mt ha^{-1} and 1000 m^3 ha^{-1}, respectively. Leaf areas of 12 m^2 m^{-2} are common.

Although the forests are very valuable commercially, the disposition of the remaining old growth has become highly controversial. Research is increasingly showing its importance for a variety of wildlife species, including birds (such as *Strix occidentalis* Xantus (spotted owl)), small mammals (including several species of bats), and amphibians (including several species of salamanders). Old-growth forests are also valued for watershed protection and aesthetic enjoyment.

We have discovered that these old, primary forests are also a very important scientific resource. Serious study began in 1969 with the initiation of the Coniferous Forest Biome Project, which was part of the US IBP. Since then, the old-growth forests have provided us with many basic and applied ecological lessons.

1.2 Coarse woody debris

The behaviour and ecological importance of coarse woody debris (CWD) or dead wood structures is one important topic that has emerged from our studies of old-growth forests. CWD includes standing dead trees (or snags) and down logs (or boles). These structures fulfil many ecosystem functions; as I tell my students, 'a tree has fulfilled only half its functions when it dies' (Plate 1).

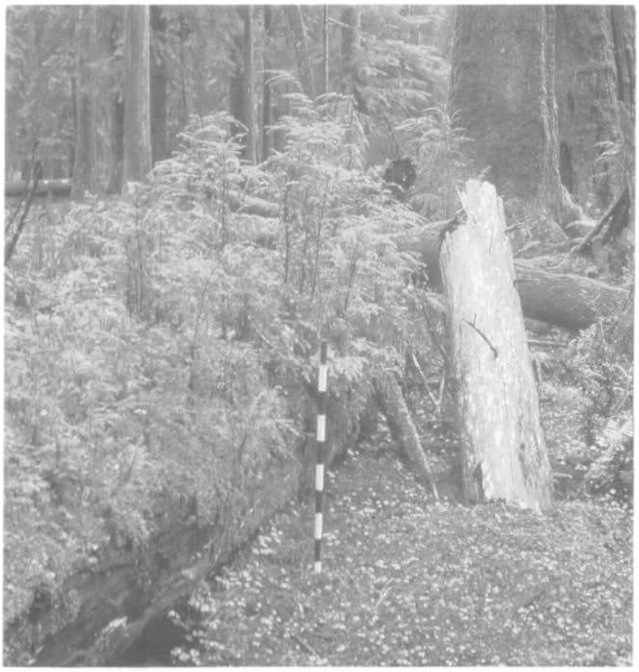

Plate 1. Downed log which has been heavily colonized by seedlings of *Tsuga heterophylla, Picea sitchensis* and *Thuja plicata,* at Quinault Research Natural Area, Olympic Peninsula, Washington (Photograph J F Franklin)

CWD is both prominent and functionally important in the coniferous forests of north-western North America. Between 80 and 200 Mt ha^{-1} of dead wood are commonly present in the primeval forests, including young forests, as most catastrophes which initiate seres do not consume large amounts of wood. This wood plays important roles in material cycles (Harmon *et al.* 1986). It is a long-term source of nutrients and energy, as well as a site where microbial nitrogen fixation occurs. Dead wood structures are also critically important as wildlife habitat for a large proportion of the native vertebrate species (see, for example, Brown 1985), and as factors in stability and biological diversity of stream ecosystems (Triska *et al.* 1982).

1.3 Forest canopies

Another timely topic in ecosystem research is that of forest canopies and their interactions with the atmosphere. These are very important interfaces between the biological and physical world, certainly in our old-growth forests where the surface areas of green leaves alone are huge. It is common in the north-western North American coniferous forests to have leaf areas of 10, 12 or 14 $m^2\ m^{-2}$. A single *Pseudotsuga* tree may have a total leaf surface area of 4000 m^2.

Forest canopies carry on many important ecosystem functions, in addition to their role as primary sites for photosynthesis. Canopies may scavenge large amounts of moisture, nutrients, and pollutants from the atmosphere. In one study in Oregon, condensation on old-growth forest canopies resulted in a net addition of 387 mm to the annual precipitation on a mountain watershed (Harr 1982). Canopies are also important sites of biological diversity, providing habitat for a large variety of plants, such as epiphytic lichens and mosses, and animals from a wide range of trophic levels. A recent study found exceedingly high numbers of invertebrate species in a tropical forest canopy; one result has been a drastically revised estimate of the total number of species in the world (Wilson 1985). Studies in our coniferous forests have shown that some of the canopy organisms, such as epiphytic lichens, can play important functional roles in their ecosystems; the lichen *Lobaria oregana* (Tuck.) Müll., for example, is a species which adds 3–5 kg $ha^{-1}\ yr^{-1}$ of fixed nitrogen to the forest.

1.4 Below-ground processes

Below-ground processes are another important topical area in ecosystem research. This is the other major interface between the biological and physical world. It is a remarkably complex and biologically active area which generally comprises only 20% of the biomass in a forest, but which may require 50%, or even 70%, of the photosynthate for maintenance due to high rates of turnover. Symbiotic interactions are of critical importance in this topical area; biological linkages, such as through mycorrhizae, may sometimes bypass the physical soil matrix.

1.5 Successional research

In successional research, linkages between the old ecosystem and the new are increasingly being emphasized. Studies at Mount St Helens have reminded us of the importance of biological legacies, biological influences that survive a major catastrophic event (Franklin *et al.* 1985). Biological legacies include (i) surviving organisms, (ii) structures, such as dead wood, and (iii) imprints that have been created on soil chemical and microbiological properties by the predisturbance biota.

1.6 Landscape ecology

Landscape ecology is an emerging field which addresses the importance of spatial pattern in the ecological behaviour of the landscape, such as the productivity and diversity of the landscape (Forman & Godron 1985). Many aspects of an ecosystem can only be addressed at a broader geographical scale. Examples include (i) productivity or carrying capacity for larger herbivores, (ii) assessment of the cumulative effects of management on water and sediment yields, and (iii) aquatic (including fish) productivity in drainage basins.

My studies on the effects of forest cutting patterns have demonstrated that the size, shape, and distribution of cutover patches are critical in determining many attributes of a forest landscape, including its vulnerability to catastrophes, such as windthrow, and various biological attributes, such as total diversity and carrying capacity for wildlife species (Franklin & Forman 1986).

2 Long-term ecological research

There is currently a major emphasis on long-term ecological research in the United States. It is believed that long-term observations and experiments (Plate 4) are absolutely essential to formulation and testing of ecological theory, and to the development of rational management schemes. Results from short-term studies can, as we all know, be extremely misleading. Long-term studies are particularly important in dealing with gradual processes, such as changes in ecosystem productivity, and episodic phenomena. Tree mortality is a process that may fall into either of these 2 categories, and typifies one major class of long-term study that is under way in north-western North America.

The National Science Foundation, the major agency funding ecological research in the USA, has selected 11 sites on which it is sponsoring long-term research (Halfpenny & Ingraham 1984), and 3 or 4 more sites will be selected in 1986–87. Total support for these programmes amounts to about $6M each year. The sites cover a wide range of ecosystems, including coniferous forest, deciduous forest, alpine tundra, desert, grasslands, swamp, estuary and lakes (Plate 2).

3 Integration and synthesis

A great deal of interest in integration, the interdisciplinary synthesis of scientific findings, has been

Plate 2. Interior of coastal *Picea sitchensis/Tsuga heterophylla* forest along the Hoh River, in Olympic National Park, Washington (Photograph J F Franklin)

expressed at this Conference. Synthesis of this type is critical to both ecological science and society. Most of the important problems simply cannot be solved by individual scientists or single disciplines. These problems typically lie at the interfaces between traditional fields. A good example in our region is the riparian zone, which is of critical importance in our forested landscapes but which has been ignored because of its position at the interface between terrestrial and aquatic ecology.

True integration in the biological sciences is extremely difficult. Such integration goes against our formal training and our institutional structures and reward systems, all of which are orientated toward disciplinary, and not interdisciplinary, approaches.

Our experience is that there is no magic formula, no specific methodology or technology, which will ensure integration and synthesis. There are many devices which can help, however. Examples include (i) the use of a common research site for much of the research; (ii) use of conceptual and mathematical models; (iii) identification of common research objectives (and the more specific the better); and (iv) continuity of a core research group.

Scientists and their attitudes are ultimately of the utmost importance in determining whether or not integration will be achieved. Interdisciplinary synthesis is a social phenomenon in which the scientists are the most important component. To be successful, team scientists must put aside their specialities and related emphases; they must listen to other scientists with the objective of creating a mutually acceptable and exciting set of goals which will sometimes have limited disciplinary interest. Additionally, the group must find leaders who can catalyse the identification and definition of objectives.

4 Forests of the Changbai region

I want to conclude with some comments on the extreme importance of the primary deciduous hardwood/*Pinus koraiensis* Sieb. et Zucc. (Korean pine) of the Changbai region. Similar forests once existed in Europe and, especially, in eastern North America, but, except for small tracts, these forests have now been cut down. These regions are today beset with serious problems, such as acid rain and other pollutants.

The natural forests of the Changbai region are, therefore, of incalculable value to the world. They are important as natural baselines for mankind, baselines against which the effects of pollutant impacts can be measured. They are equally important for ecological studies of natural processes, such as succession, within primary temperate hardwood/conifer forests. There is no other region in the world with this potential scientific value.

Preservation of some extensive examples of these forests is essential to the realization of their potential value to the world. Hence, I want to commend the Chinese people for their efforts to preserve examples of these forests for scientific study. I also want to urge the greatest efforts to preserve additional samples, and to establish long-term studies and baseline measurements, of pollutants and other materials, in these ecosystems. Scientists throughout the world stand ready to co-operate in such efforts.

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Rational management of broadleaved/*Pinus koraiensis* (Korean pine) forest and improvement of woodland productivity in north-east China

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*1 The geography of broadleaved/*Pinus koraiensis *(Korean pine) forest and its related environment*

The broadleaved/*P. koraiensis* Sieb. et Zucc. forest is a special forest type in the temperate zone, and is the zonal climax community locally. It covers a fairly wide area, 40°20′–44°40′N and 134°–125°45′E, and is the dominant forest type in Changbai, Wanda and Lesser Xingan Mountains in north-east China. It stretches further north into the far eastern part of USSR and south into North Korea and Japan. It occurs at altitudes between 500 m and 1100 m or above on Changbai Mountain, and 300–600 m on Lesser Xingan Mountain. The climate is warm and humid, with an annual average temperature between 0°C and 6°C. The temperature in January ranges between −14°C and −28°C. The frost-free period when the daily average temperature is over 10°C lasts for 4–4.5 months. Annual precipitation is 500–1000 mm. The area, therefore, has a typical temperate monsoon climate. The growing period is 100–120 or even 150 days (Wang & Xu 1981).

The area is mountainous and hilly. The soil is a dark brown forest earth, with thick depth, rich humus and high fertility, and is moist and well drained. The forest has a high biomass per unit area, but, as virgin forest that has become overmature, much timber is lost as rotten wood. Its productivity, therefore, is not very high.

As a source of timber, the broadleaved/*P. koraiensis* forest is significant to the country's economy, as it provides a great deal of construction timber and saw-wood for furniture. The forest also serves other functions: it protects the watershed at the source of the Song-hua, Ya-lu and Tumen Rivers; it prevents soil erosion; it regulates water supply and the regional ecological balance; and it guarantees agricultural yield and animal husbandry.

However, because of disturbance from human activities, especially from the ravages of imperialists before the liberation, many of the high-quality *P. koraiensis* trees were felled, and the present area of broadleaved/*P. koraiensis* forest continues to decrease. The virgin forest is being replaced by low-value secondary growth of species such as *Populus* (poplar), *Betula* (birch) and other hardwoods. The natural resources are being used wastefully, and the protective function of the forest is declining, so that various kinds of natural calamities are frequently occurring in agriculture. However, current attention is now being given to the management of the forest in north-east China to conserve the broadleaved/*P. koraiensis* forest, and to improve the productivity of the woodland.

2 Structure and related characteristics of broadleaved/ P. koraiensis *forest*

In order to manage the forest rationally and to improve its productivity, it is necessary to study its structure and related characteristics. A comprehensive survey and analysis were carried out, and the results emphasized the following features of broadleaved/*P. koraiensis* forest.

2.1 Rich flora and fauna diversity

A total of 122 families, 545 genera and 1337 species has been recorded for pteridophytes and embryophytes in the Changbai Mountain, of which 75% are found in the broadleaved/*P. koraiensis* forest zone, 55.7% in the deciduous forest zone, 26.9% in the coniferous forest zone, 20.8% in the *Betula ermanii* Cham. (Erman's birch) forest zone, and 13.1% in the tundra zone (Li 1985; Yang & Qu 1983).

The birds recorded in Changbai Mountain belong to 11 orders, 33 families and 120 species. Among them, there are 45 species of resident birds and 75 species of summer migrants. Table 1 shows that most of the birds occur in the broadleaved/*P. koraiensis* forest (Li 1985). Ten thousand samples of insects have been collected, and 500 species have been identified. They belong to 15 orders and 60 families, with Coleoptera and Lepidoptera being dominant. Again, the insect fauna population is most abundant in the broadleaved/*P. koraiensis* forest: 46% of the 500 species are found

Table 1. Distribution of bird species among different types of vegetation on Changbai Mountain

Type of forest	Summer migratory birds	Resident birds	Total	Characteristic species
Broadleaved	25	22	47	8
Broadleaved/ *P. koraiensis*	37	25	62	11
Coniferous	17	26	43	12
B. ermanii	5	5	10	1
Forest edge brush	29	4	33	14
Along river	9	1	10	10
Populus & *Betula*	17	9	26	0

there, 30% in the *B. ermanii* forest, fewer in the coniferous forest, and least of all in the tundra zone (Yang & Qu 1983).

The altitudinal distribution of the soil animals, especially the dominant and common groups such as Nematoda, Collembola, Enchytraeidae, Lumbricidae, Acarina, Coleoptera, Diptera, Araneae and Protozoa, shows a similar trend to the plants, birds and insects, being most abundant in the broadleaved/*P. koraiensis* forest, followed by the coniferous forest, *B. ermanii* forest and tundra (Zhang *et al.* 1980; Zhang & Chen 1981; Chen *et al.* 1983; Cui 1983).

Soil micro-organisms, including bacteria, fungi and actinomycetes, are also most abundant in the broadleaved/*P. koraiensis* forest (Li & Liu 1983).

2.2 High biomass

Many types of forest occur in north-east China, such as *Picea/Abies* (spruce/fir), *Larix* (larch), *Populus/Betula*, *Quercus* (oak), etc, but the broadleaved/*P. koraiensis* forest has the highest stocking density. The stocking of virgin broadleaved/*P. koraiensis* forest is usually 400–500 m^3 ha^{-1}, and sometimes as much as 600 or 800 m^3 ha^{-1}, while the other forest types have only 300–400 m^3 ha^{-1}. The biomass study on Changbai Mountain shows that broadleaved/*P. koraiensis* forest has a biomass of 328 t ha^{-1}, the coniferous forest 285 t ha^{-1}, the *B. ermanii* forest 130 t ha^{-1}, the *Populus* and *Betula* forest 92 t ha^{-1}, and the *Larix* forest 251 t ha^{-1} (Li *et al.* 1981).

2.3 Complex structure

The broadleaved/*P. koraiensis* forest occurs in a favourable environment in which a variety of plants are found. Its structure is more complex than other coniferous forests. *P. koraiensis* is the dominant tree species, and its companion species are *Tilia amurensis* Rupr. (Amur linden), *T. mandshurica* Rupr. et Maxim. (Manchurian lime), *Acer mono* Maxim. (painted mono maple), *Quercus mongolica* Fisch. ex Turcz. (Mongolian oak), *Betula costata* Trautv. (yellow birch), *Picea koyamai* var. *koraiensis* Shirasawa (Koyama spruce), *P. jezoensis* (Sieb. et Zucc.) Carr (Yezo spruce), *Abies nephrolepis* (Trautv.) Maxim. (East Siberian fir) and *A. holophylla* Maxim. (Manchurian fir). All the species are organized in an irregular uneven-aged mixed forest, and pure *P. koraiensis* forest is rarely seen. Under the mixed forest canopy, there is a well-developed understorey, herbaceous layer and moss ground cover. Lianas are also well developed in some stands.

2.4 High soil fertility

The humus layer of the soil is as thick as 5–12 cm, and the litter stock is 11–14 tonnes (dry weight) in Changbai Mountain, with the broadleaved/*P. koraiensis* having the maximum density, the *Larix* forest and *B. ermanii* forest the average, and the *B. ermanii/Picea/Abies* forest the minimum. Enzyme activity and metabolic rate are also much higher in the soils of broadleaved/*P. koraiensis* forest than in those of the other coniferous forests. The organic matter decomposes fast, and there is a greater availability of nitrogen to the plants (Cheng *et al.* 1981; Zheng *et al.* 1981, 1983).

The high soil fertility is a result of the complicated internal structure of the forest and is maintained by a special mechanism. The irregular, uneven-aged and mixed forest structure enables the nutrients to be taken up by the plants in the different layers, and released periodically to meet the requirements of tree growth.

2.5 High resistance to stress

As the stands are multi-storeyed and mixed with both coniferous and deciduous species, the ecosystem is in a state of equilibrium. The forest has developed a self-defence function, so that it is more resistant to natural disasters than pure *P. koraiensis* plantations. For example, *Cronartium ribicola* J. C. Fischer (white pine blister rust) and *Pissodes nitidus* Roelofs (pine yellow-spotted weevil) occur widely in pure plantations, but are not seen in the broadleaved/*P. koraiensis* forest.

The logical conclusion is that the broadleaved/*P. koraiensis* forest should be treated as the main forest type in the mountainous area of north-east China. More attention should be paid to develop such forest, to ensure the optimum use of the land resource, and to provide high and stable productivity of the whole forest ecosystem.

*3 Rational management of the broadleaved/*P. koraiensis *forest and improvement of the woodland productivity*

3.1 Selective (partial) cuttting as part of a main felling and generation cycle

For the irregular, uneven-aged forest, large-scale clearfelling is wasteful of the forest resource. Many trees which still have great growth potential are cut down, large areas of land are uncovered, and the watershed-protecting ability of the forest is lost. As a result, soil erosion occurs; landfalls, earth slides and mud-rock flows in some areas cause serious damage to the forest environment, and provide opportunities for the secondary growth of such species as *Populus*, *Betula* and shrubs, which will hinder the natural regeneration of *P. koraiensis*. The value of the forest is reduced and the use of the woodland limited. Methods of artificial planting of *P. koraiensis* are expensive of both manpower and capital, and cannot keep pace with the speed of forest clearing.

Past experience has shown that, in the pure *P. koraiensis* plantation, the trees bear flowers and cones and fork much earlier, thus lowering the technological value of the timber. The pure plantation is also susceptible to a great variety of diseases and pests. For example, *Cronartium ribicola* spreads rapidly, and, in some areas, 43.5% of young trees are attacked by the disease. In other regions, the young *P. koraiensis* has been attacked by *Pissodes nitidus* for years, with the result that 96% of the trees are forked at a height of 3–4 m, and the tree growth seriously affected (Wang & Xu 1981).

In order to encourage the potential productivity of the woodland, it is necessary to manage the existing broadleaved/*P. koraiensis* forest in accordance with local conditions. In such an irregular, uneven-aged forest, there are many trees at various stages of growth, and the middle- or small-sized trees will grow fastest. The most rational management would be a system of selecting (partial) cutting; clearfelling is reasonable only in small, island-like, even-aged stands of overmature trees. To make optimum use of the woodland, it is necessary to improve the quality of the stand and to promote the regeneration of *P. koraiensis* forest by planting trees under the canopy after selective felling. The tree species planted should mainly be *P. koraiensis*, but other rare conifers and deciduous species can also be used. To encourage early canopy closure and to shorten the cutting cycle, some fast-growing trees, such as *Populus ussuriensis* Kom. (Ussuri poplar), *P. koreana* Rehd. (Korean poplar) and *Larix olgensis* A. Henry (Olga Bay larch), can be planted to fill large gaps in the forest on logging roads, and on the forest fringe. According to our investigations, such trees are fast growing and can be cut after 20–30 years.

The advantages of selective cutting are as follows.

i. It is suited to the biology of *P. koraiensis* and associated tree species, and makes the best use of the species' potential for natural regeneration. *P. koraiensis* and associated tree species show a certain shade tolerance, growing well under canopy, especially under *Populus* and *Betula* and other deciduous forest.

ii. It is suited to the irregular, uneven-aged structure. In broadleaved/*P. koraiensis* forest, there are a great number of middle- and small-sized trees which can be used to restore the stands and shorten the felling cycle.

iii. It is the best method for conserving mixed coniferous/deciduous forest, with valuable species such as *P. koraiensis*, *Fraxinus mandshurica* Rupr. (Manchurian ash), *Tilia amurensis*, etc. Their timber has a high quality and commercial value; they are shade tolerant and difficult to grow after clearfelling. By selective cutting, the structure of the remaining stands can be regulated, and, by replanting with valuable conifers and deciduous trees, the uneven-aged species mixture can be maintained, so that soil fertility and the stability and high productivity of the forest can be preserved.

iv. It encourages the forest's self-defence mechanism and its environmental protection functions. Selective cutting ensures a continuous woodland cover, and combines exploitation of the natural resource with the maintenance of its role in environmental protection.

v. It makes the best use of naturally regenerating seedlings, reducing expenditure on reafforestation after clearfelling. The savings in manpower, materials and capital can be used to increase forest cover in other open areas.

vi. It secures the woodland for ever, providing shelter for various forest animals and a natural environment for edible and medicinal plants. It increases the secondary productivity of the forest.

However, the success of selective cutting depends on the correct choice of trees to cut and of cutting cycle. Generally, the less intensive the harvest cutting, the shorter the cycle, and the less lost by natural wood decay, the greater the yield from the same managing unit. On the other hand, if the cutting cycle is too short, the output will be too small and the cost too high.

Taking as an example the management unit – the owner of a forest resource with an average stocking density of 180 m^3 ha^{-1}, 10.46 million m^3 can be harvested annually in a 78-year period. Quantitative evaluation of the economics of different harvesting systems shows an obvious advantage in the selective cut over clearfelling. Table 2 shows that a 30% selective cutting system provides the maximum economic gain: the average annual gain is 3.03–3.68 billion Chinese Yuan. If we include compound interest, the annual gain is more than 13.63–23.07 billion Yuan, ie between 10 and 100 times the amount invested to extend the transport line in a selective cutting system. Therefore, a 30% intensity would give maximum gain, but the gain reduces with increasing intensity of selective cutting.

The data in Table 2 show that the selective cut makes best use of the growth potential of the remaining stand, and greatly reduces loss from timber decay. Therefore, a selective cut not only provides high economic benefit, but also encourages the growth of the forest resource.

The intensities of selective cutting currently being practised in broadleaved/*P. koraiensis* forest far exceed the recommended percentage of 30%, and should be reduced to minimize further destruction of the forest.

In a rational management of broadleaved/*P. koraiensis* forest, the diameters of trees to be cut or left standing should be determined according not only to the cutting intensity, but also to the duration of the cutting cycle, the growth rate, the self-thinning rate, and the disease in the remaining stands. The trees to be cut should be those whose age and diameter have passed their fast-growing phase. In order to choose which trees to fell, thousands of *P. koraiensis* and associated trees have been measured on the Changbai, Lesser Xingan and Wanda Mountains, and a series of regressions have been fitted to determine their growth rates and vulnerability to disease. Using the data from Wanda Mountain as an example, regressions of wood volume increment on tree age are fitted as follows:

$$V_p = 0.14 - 0.0076t + 0.00013t^2 - 0.00000015t^3 \qquad 30 \leqslant t \leqslant 550 \quad r = 0.85$$
$$V_j = 0.038 - 0.00514t + 0.000169t^2 - 0.00000029t^3 \qquad 20 \leqslant t \leqslant 370 \quad r = 0.84$$
$$V_a = 0.26 - 0.0182t + 0.000381t^2 - 0.00000125t^3 \qquad 30 \leqslant t \leqslant 180 \quad r = 0.87$$
$$V_{ti} = 0.21 - 0.0111t + 0.000187t^2 - 0.00000031t^3 \qquad 30 \leqslant t \leqslant 370 \quad r = 0.86$$
$$V_b = 0.07 - 0.0057t + 0.000167t^2 - 0.00000037t^3 \qquad 20 \leqslant t \leqslant 280 \quad r = 0.95$$
$$V_m = 0.02 - 0.002t + 0.000068t^2 - 0.0000015t^3 \qquad 20 \leqslant t \leqslant 290 \quad r = 0.92$$

Table 2. Economic benefit of harvest cut system

Calculating factors	Unit	Intensity of cutting (%) 10	30	50	70	90
Annual cut	1 km^3	15820	17110	16060	14160	11580
Period of cutting management	Year	78	78	78	78	78
Annual area of cutting	Hectare	830000	276380	166000	118690	92130
Increment of remaining stand	m^3 ha^{-1} yr^{-1}	3.57	4.13	3.71	3.00	2.49
Cut-number in cutting cycle	Time	15.6	6.0	3.2	1.9	1.2
Cutting cycle	Year	5.0	13.1	24.3	42.0	65.1
Standing stock of remaining stand	1 billion m^3	11.18	10.11	8.84	7.86	6.50
Economic gain of remaining stand at end of management period*	1 billion Yuan	101.70	91.99	80.42	71.50	59.12
Economic gain of remaining stand at end of management period**	1 billion Yuan	72.0	65.10	56.92	50.60	41.84
Area of plantation	Thousand ha	10899	11653	10358	8610	6992
Total increment of plantation	1 billion m^3	3.486	4.022	3.575	2.972	2.413
Economic value of plantation	1 billion Yuan	258.66	298.46	265.30	220.53	179.08
Economic gain in increment of forest resource*	1 billion Yuan	197.78	202.80	178.91	153.36	125.60
Economic gain in increment of forest resource**	1 billion Yuan	168.03	175.91	155.40	134.46	108.32
Economic gain in reduction of self-thinning*	1 billion Yuan	21.77	26.06	17.88	9.96	2.87
Economic gain in reduction of self-thinning**	1 billion Yuan	15.41	18.44	12.65	7.05	2.03
Compound interest gain in reduction of self-thinning*	1 billiion Yuan	1026.72	1144.65	727.86	435.76	92.85
Compound interest gain in reduction of self-thinning**	1 billion Yuan	726.60	810.06	515.10	304.58	65.71
Reducing cost of timber production	Yuan m^{-3}	5.62	5.04	3.20	1.60	0.43
Economic gain caused by reducing cost of timber production	1 billion Yuan	4.58	4.11	2.61	1.30	0.35
Compound interest gain caused by reducing cost of timber production	1 billion Yuan	121.90	113.68	68.41	38.82	9.45
Economic gain caused by raising prises of timber*	1 billion Yuan	9.93	9.62	6.11	2.82	0.82
Economic gain caused by raising prices of timber**	1 billion Yuan	7.03	6.81	4.32	2.00	0.56
Compound interest gain caused by raising prices of timber*	1 billion Yuan	43.66	27.48	24.53	23.00	15.12
Compound interest gain caused by raising prices of timber**	1 billion Yuan	30.90	19.45	17.36	16.97	10.70
Increment of investment for extending logging road	1 billion Yuan	10.74	2.68	2.33	2.84	1.39
Compound interest investment for extending logging road	1 billion Yuan	1630.79	944.12	462.38	230.53	46.92
Economic gain of timber production*	1 billion Yuan	38.07	47.19	39.77	26.23	7.95
Economic gain of timber production**	1 billion Yuan	26.94	33.40	28.14	18.56	5.63
Compound interest gain of timber production*	1 billion Yuan	1012.50	1255.14	1057.70	697.71	21.18
Compound interest gain of timber production**	1 billion Yuan	716.54	888.25	748.53	493.77	14.97
Total economic gain of select cut*	1 billion Yuan	261.38	287.09	242.95	190.84	136.20
Total economic gain of select cut**	1 billion Yuan	211.45	235.98	200.81	158.53	115.52
Total compound interest gain of select cut*	1 billion Yuan	771.75	1799.63	1595.03	1129.11	217.26
Total compound interest gain of select cut**	1 billion Yuan	113.17	1063.23	1042.42	756.08	162.23
Annual average economic gain of select cut*	1 billion Yuan	3.35	3.68	3.12	2.45	1.75
Annual average economic gain of select cut**	1 billion Yuan	2.71	3.03	2.57	2.03	1.48
Annual average gain of select cut calculated according to compound interest*	1 billion Yuan	9.89	23.07	20.45	14.48	2.79
Annual average gain of select cut calculated according to compound interest**	1 billion Yuan	1.71	13.63	13.63	9.69	2.08
Annual average investment increment for extending logging road	1 billion Yuan	0.14	0.03	0.03	0.03	0.02

*based on timber price 130 Yuan m^{-3}

**based on timber price 92 Yuan m^{-3}

Table 2. Economic benefit of harvest cut system (continued)

Calculating factors	Unit	Intensity of cutting (%) 10	30	50	70	90
Compound interest of annual average investment for extending logging road	1 billion Yuan	20.91	12.10	5.93	2.96	0.60
The ratio between investment increment for extending logging road and economic gain of select cut*	1 billion Yuan	24.28	107.32	103.83	67.97	97.00
The ratio between investment increment for extending logging road and economic gain of select cut**	1 billion Yuan	19.63	88.19	85.80	56.44	82.28
Ratio between investment increment for extending logging road and economic gain of select cut according to the compound interest*	1 billion Yuan	0.47	1.91	3.45	4.90	4.63
Ratio between investment increment for extending logging road and economic gain of select cut according to the compound interest**	1 billion Yuan	0.08	1.13	2.25	3.28	3.46
Annual average gain ha^{-1}*	Yuan ha^{-1} yr^{-1}	5.18	5.69	4.81	3.78	2.70
Annual average gain ha^{-1}**	Yuan ha^{-1} yr^{-1}	4.18	4.67	3.98	3.14	2.29
Compound interest of annual average gain ha^{-1}*	Yuan ha^{-1} yr^{-1}	1528	3564	3159	2236	430
Compound interest of annual average gain ha^{-1}**	Yuan ha^{-1} yr^{-1}	264	2105	2064	1497	321

*based on timber price 130 Yuan m^{-3}
**based on timber price 92 Yuan m^{-3}

In these equations, V = wood volume, t = tree age, p = *Pinus koraiensis*, j = *Picea jezoensis*, a = *Abies nephrolepis*, ti = *Tilia amurensis*, b = *Betula costata*, m = *Acer mono*, and $t = t_o + t_n$, where t_0 = relative age of trees to be left standing, calculated from the regression of wood volume at time of cutting, t_n = age of trees to be left after selective cutting, and r = correlation coefficient.

The data show that the self-thinning process in a stand is reflected in the stem distribution along an age or diameter gradient. Logarithmic regressions of stem number (Y) on age (t) are fitted as follows:

$$Y_p = 11826 - 4261\log(t) \quad 1 \leq t \leq 596 \quad r = 0.94$$
$$Y_j = 18213 - 6375\log(t) \quad 1 \leq t \leq 243 \quad r = 0.95$$
$$Y_a = 18415 - 8371\log(t) \quad 1 \leq t \leq 158 \quad r = 0.97$$
$$Y_{ti} = 16018 - 6877\log(t) \quad 1 \leq t \leq 213 \quad r = 0.94$$
$$Y_b = 14729 - 6073\log(t) \quad 1 \leq t \leq 266 \quad r = 0.95$$
$$Y_m = 13626 - 5384\log(t) \quad 1 \leq t \leq 339 \quad r = 0.92$$

P. koraiensis shows the lowest rate of natural self-thinning which is related to its longevity, whereas *Abies* shows the highest rate, and *Picea* falls in the middle.

The survival coefficient of trees (H) after selective cutting is correlated with t (age of tree to be left) and t_0 (age from the time of last cut) in the following ratios:

$$H_p = \frac{11826 - 4261\log(t)}{11826 - 4261\log(t_0)}$$

$$H_j = \frac{15213 - 6375\log(t)}{15213 - 6375\log(t_0)}$$

$$H_a = \frac{18415 - 8374\log(t)}{18415 - 8374\log(t_0)}$$

$$H_{ti} = \frac{16018 - 6877\log(t)}{16018 - 6877\log(t_0)}$$

$$H_b = \frac{14729 - 6073\log(t)}{14729 - 6073\log(t_0)}$$

$$H_m = \frac{13626 - 5384\log(t)}{13626 - 5384\log(t_0)}$$

The rate of heart rot (P) increased with age (t) as in the following equations:

$$P_p = 1.414e^{-\frac{139.5}{t}} \quad r = 0.94$$

$$P_j = 0.544e^{-\frac{92.2}{t}} \quad r = 0.93$$

$$P_a = 1.977e^{-\frac{174.0}{t}} \quad r = 0.95$$

$$P_b = 1.208e^{-\frac{97}{t}} \quad r = 0.97$$

$$P_m = 1.264e^{-\frac{157.7}{t}} \quad r = 0.94$$

The volume of heart rot (V) was correlated with age (t) as follows:

$$V_p = 2.5 \times 10^{-10}t^{3.535} \quad r = 0.94$$
$$V_j = 0.0000019t^2 \quad r = 0.88$$
$$V_a = 0.00000427t^{1.823} \quad r = 0.92$$
$$V_{ti} = 7 \times 10^{-11}t^{3.889} \quad r = 0.92$$
$$V_b = 1.9 \times 10^{-10}t^{3.856} \quad r = 0.87$$
$$V_m = 0.000000223t^{2.165} \quad r = 0.97$$

In summary, the net volume increment of trees of different sizes (and related ages) within a cutting cycle and the threshold diameters (above which the trees should be cut and below which they should be left standing) are determined according to the following formula:

$$V' = HV - PV - V_0 + P_0V_0$$

where V' = net volume increment in a cutting cycle, V = current wood volume, H = survival coefficient of trees, P = rate of heart rot, P_0 = rate of heart rot at last cutting, and V_0 = volume of trees remaining after last cutting.

As an example, for cutting cycles of 20–30 years, the threshold diameters are shown in Table 3. In fact, many trees cut in the past were too small, so that a great deal of growth potential has been lost. *P. koraiensis* grows well in its later life, and only trees with a diameter of over 44 cm should be felled.

Table 3. Threshold diameter for selective cutting

Cutting cycle	Species	Remaining wood diameter	Maximum remaining wood diameter	Diameter with maximum production	Cutting wood diameter	Absolute cutting wood diameter
20 years	*Pinus*	≤40	64	40	≥44	68
	Picea	≤28	40	28	≥32	44
	Abies	≤20	28	20	≥24	32
	Tilia	≤24	36	24	≥28	40
	Betula	≤24	40	24	≥28	44
	Acer	≤20	32	20	≥24	36
30 years	*Pinus*	≤40	64	40	≥44	68
	Picea	≤28	40	28	≥32	44
	Abies	≤16	28	16	≥20	32
	Tilia	≤24	36	24	≥28	40
	Betula	≤24	40	24	≥28	44
	Acer	≤20	32	20	≥24	38

In selective cutting, the valuable deciduous species, such as *Fraxinus mandshurica, Tilia amurensis, Juglans mandschurica* Rupr. (mountain walnut), etc, should be left to improve the composition of the soil organic matter, and to maintain soil fertility and the stability of the forest.

Our study shows that selective cutting produces excellent results. In a 20–30 years' cutting cycle, the volume increment of the remaining stands is 3.5–5 m^3 ha^{-1} yr^{-1}, and over 100 m^3 ha^{-1} can be cut again within 20–30 years. This would not be possible in pure plantations of *P. koraiensis* or *Larix*. In addition, natural regeneration under the remaining stands is good, with numbers of seedlings and saplings reaching 19 000 ha^{-1} in some areas. In other stands, the number of seedlings may be only 3500 ha^{-1} (Wang & Xu 1981), but with artificial planting the regeneration rate is satisfactory. The simulation shows that, if selective cutting is used instead of clearfelling and replanting, in all the broadleaved/*P. koraiensis* forests in north-east China, over 1000 million Yuan would be saved which could be used for afforestation purposes.

3.2 Development of multiple use forestry and improving the protective function of the woodland

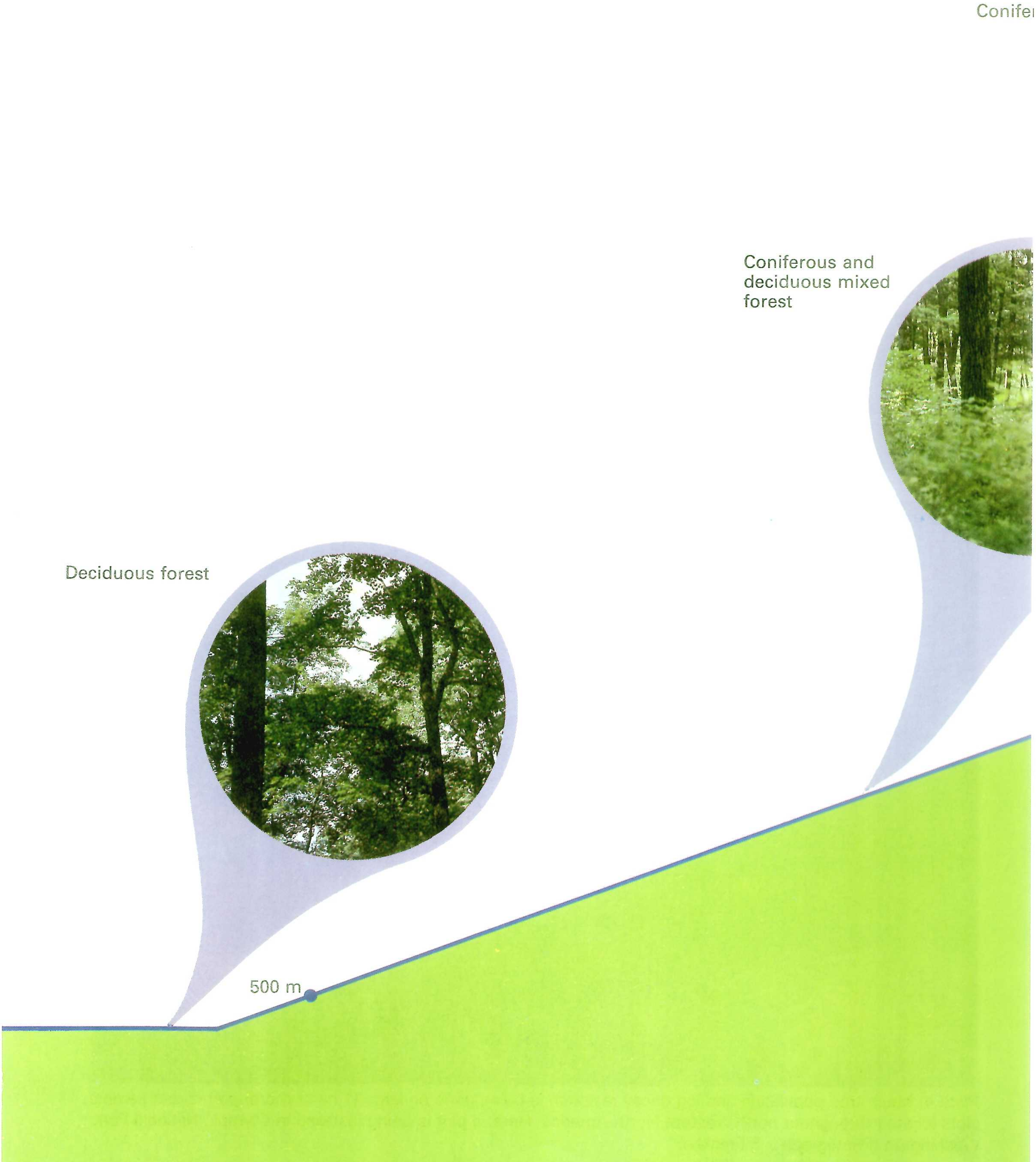
P. koraiensis is not only a valuable timber species, but also an important source of edible oil. The seeds are edible and have an oil content as high as 69.2%. The broadleaved/*P. koraiensis* forest provides many other by-products. Tiger bone, *Panax ginseng* C. A. Mey (ginseng), pilose antler, *Rana chensiensis* David (Chinese forest frog), *Gastrodia elata* Blume (tall gastrodia), *Boschniakia rossica* (Cham. et Schlect) Fedisch. (Russian boschniakia), *Gymnadenia conopsea* R. Br. (conic gymnadenia), and *Fritillaria ussuriensis* Maxim. (Ussuri fritillary) are all sources of valuable traditional Chinese medicines. Mushrooms, honey, nuts of *Corylus mandshurica* Maxim. ex Rupr. (Manchurian hazel), fruits of *Vitis amurensis* Rupr. (Amur grape) and *Actinidia kolomikta* (Rupr.) Maxim. (bear actinidia), shoots of some pteridophytes, and *Aralia*, etc, are also famous local products. Furthermore, many wild animals live in these forests: *Martes zibellina* L. (marten), *Sciurus vulgaris* L. (grey squirrel), *Mustela sibirica* Pallaë (yellow weasel), *Panthera tigris longipilis* L. (north-east tiger), *Cervus nippon* Temminck and *C. elaphus* L. (sika and red deer), *Sus scrofa* L. (European wild boar), *Selenarctos thibetanus* Cuvier (black bear) and various birds, and they are all sources of meat and fur. Therefore, we should encourage the multiple use of the forest – not only of its wood, but also of its many other products. We should also remember that its value lies not only in its material products, but also in its role in protecting the natural environment.

3.3 Reshaping the overcut stands and promoting recovery of the *P. koraiensis* forest

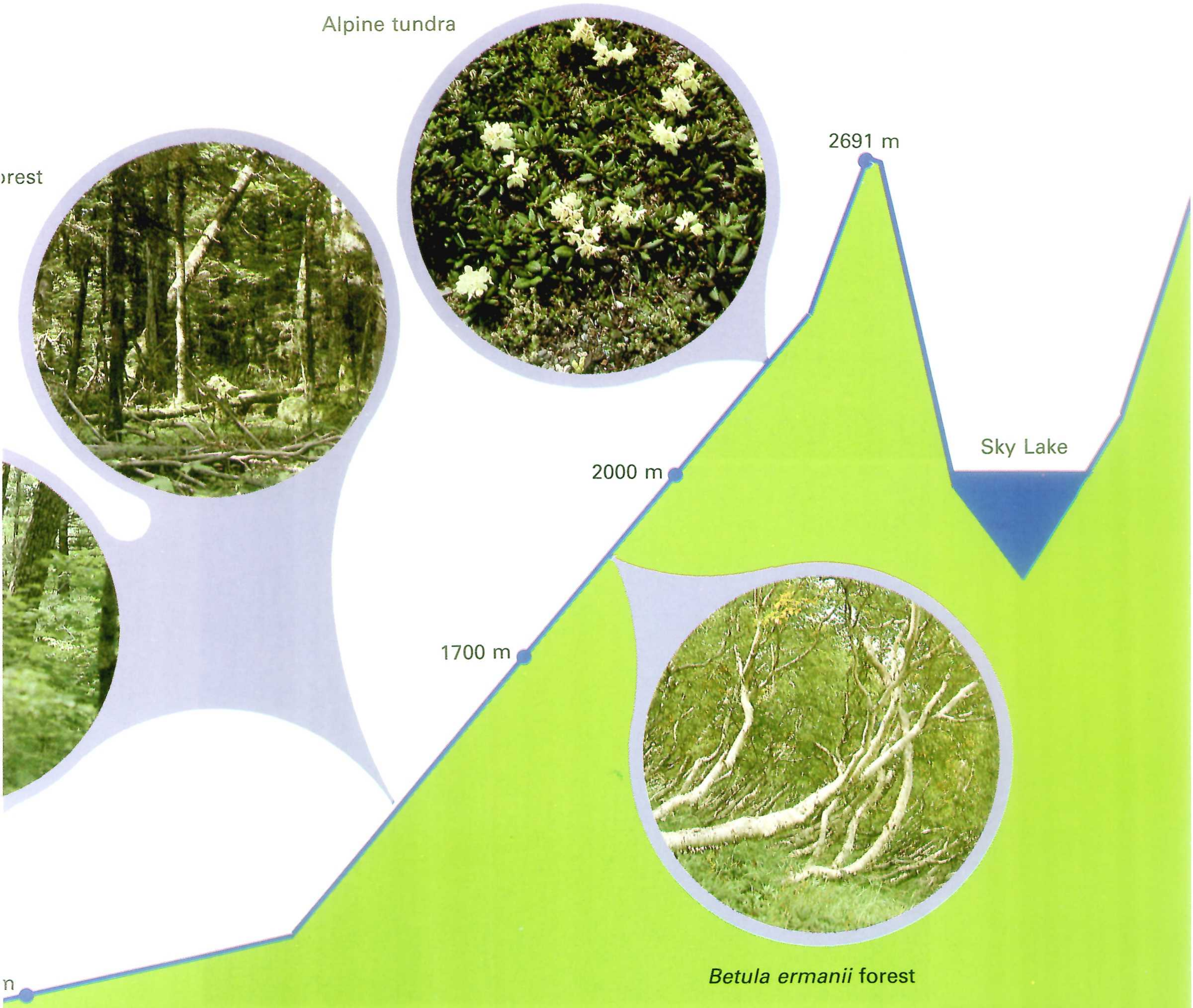
The felled areas are regenerating mostly with *Populus* and *Betula* species and with other low-value deciduous trees. The stocking density is thin, and there

Plate 3. A gap created more than 50 years ago in Fiby urskog, central Sweden, the same as in Figure 2 of Hytteborn's paper (p 35). The regrowth of *Picea abies* is still below 1.3 m in height. The fallen stems are not the original gap creators – view towards south-east in 1985 (Photograph H Hytteborn)

Plate 4. Much tree population and log decay research is being done on large (1 ha or more) permanent sample plots located throughout north-western North America. Here, a plot is being installed in Olympic National Park, Washington (Photograph J F Franklin)



Altitudinal zonation of vegetation c



he north slope of Changbai Mountain

Plate 5. Changbai Mountain Reserve in north-east China (Photographs Wang Ying)
Centre: Long distance view of Changbaishan – the 'ever white mountain'
Top left: Tianchi – Sky Lake – in the volcanic crater
Top right: Panax ginseng C. A. Mey, the ginseng plant, famous for its medicinal properties
Bottom left: Panthera tigris longipilis L. (north-east tiger)
Bottom right: The Changbai waterfall, falling 68 m from Sky Lake

are many decaying trees. The natural recovery of *P. koraiensis* forest in such areas requires a long period of succession. If the current situation continues, not only will the potential productivity of the woodland be wasted, but the pathogens and pests will spread quickly. Every effort should therefore be made to encourage the stand to revert to broadleaved/*P. koraiensis* forest. One method is to liberate the suppressed trees, especially *P. koraiensis* and *Abies*, by thinning the decaying trees. Another method is to plant *P. koraiensis* and other valuable trees under the canopy. According to our study and experience in forestry practice, *P. koraiensis* grows well under a deciduous forest canopy, and abnormalities such as early forking, early cone-bearing and severe disease do not occur as in the pure plantation.

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Some ecological aspects of forest conservation in temperate Australia

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Abstract

The native forests of southern Australia are still being actively cleared for agriculture and plantations. The forest types that form the main base for the timber industry are poorly preserved within National Parks and equivalent Reserves, and have been overexploited for sawlogs. They are now widely used as a source of pulpwood, and are usually managed by broad-acre clearfelling, followed by slash burning and the sowing of seed of commercially preferred species.

This silvicultural system usually ensures the regeneration of *Eucalyptus* species and the survival of fire-adapted and adventitious native species. However, the age class composition of the dominant stratum is usually dramatically changed, the rainforest element in the understorey, where present, is markedly diminished, and there is often invasion by species exotic to Australia. The ecological problems that result from these consequences could largely be avoided by a reversal to the group selection system. However, there seem to be no practical ways to counter the massive ecological and economic effects of the invasion of a root-rotting pathogen *Phytophthora cinnamomi* Rands into much of the *Eucalyptus* forest of southern Australia. A major problem in forests that are both outside the pathogenic range of *P. cinnamomi* and unavailable to the timber industry is fire management. In this respect, computer models of fire-related fuel dynamics and the expert systems that they sire are no substitutes for hypothesis-directed data collection, and conservative and variable management aimed to ensure the perpetuation of native species.

1 Introduction

Conservation is the wise use of resources in the long term. This paper assumes that one of the wise uses of native forest is to maintain the primeval composition and functioning of a wide range of ecosystems, primeval being defined as the absence of changes resulting from the economic activities associated with agriculture and industry. Even in the best of conditions, the primeval can only be approximated, but this goal provides a research and management direction as strong as that provided by the profit motive of economic man. This paper presents a brief review of the ecological problems of conservation management in the remaining approximately primeval forests in temperate Australia. The politics and science of reserve selection are ignored, but the interaction of the forest industries with the native communities cannot be dismissed, as most Australian temperate forests are primarily devoted to wood production.

2 Forest

There is no sharp break in Australian forest types at the Tropic of Capricorn. The dominant genera of the northern part of the geographical temperate zone all extend well into the tropics, with little or no latitudinal variation in physiognomic characteristics, or patterns of association. For statistical and heuristic convenience, this paper considers only the forests of southern Western Australia, South Australia, Victoria and Tasmania (Figure 1). For the purposes of discussion, these forests are broadly divided on the basis of their dominant genera and the nature of the understorey.

Dry forests dominated by species of *Eucalyptus* cover the largest area (9.8 Mha) (Figure 1; Plate 6). Recent reviews of their characteristics and ecology have been written by Gill (1981a) and Christensen *et al.* (1981). They are water-limited (Bowman & Kirkpatrick 1986b) and have adapted to fire (Gill 1981b). Natural and man-induced fires cause the death of individual trees by basal attrition (Mount 1979; Bowman & Kirkpatrick 1986a). Each fire also creates conditions suitable for the recruitment of seedlings, many of which linger as suppressed plants in the understorey until a tree collapse frees moisture for their release (Abbot & Loneragan 1984). The high flammability of both the dominants and the understorey species (Dickinson & Kirkpatrick 1985), the ability of *Eucalyptus* to propagate fire up to 30 km ahead of the main front (Cheney 1981), and the high probabilities of ignition (Gill 1981b) combine to create an uneven-aged natural forest, usually with a relatively short understorey. The dry forests extend on to soils highly deficient in potassium, nitrogen and a variety of trace elements, these poor soils being characteristic of Australia as a whole (Charley & Cowling 1968).

Topographic (Kirkpatrick & Nunez 1980), edaphic (Ashton 1976a) and climatic (Churchill 1968) moisture gradients strongly influence the floristic composition and biomass of the *Eucalyptus* forest understorey. The wet *Eucalyptus* forests, which cover 1.3 Mha (Figure 1), have understoreys dominated by ferns, broad-leaved shrubs, or rainforest species. The fine green fuel in these forests is relatively non-flammable (Dickinson & Kirkpatrick 1985), and dead fine fuel is usually moist, reducing the probability of ignition resulting in conflagration. If fire is absent for more than 400 years, the *Eucalyptus* trees die out, leaving the tolerant elements of the understorey as dominants. However, highly frequent fire can also eliminate some of the wet forest *Eucalyptus*, because, unlike most members of their genus, they do not recover readily

Plate 6. Dry forest dominated by *Eucalyptus pulchella* Desf. (white peppermint) with an understorey dominated by grasses (Photograph S Harris)

from severe fire damage (Ashton 1976b). The literature on the ecology of these forests has been well reviewed by Ashton (1981a,b).

In the drier parts of the temperate zone, there are also some small areas of forest dominated by trees of the genera *Callitris* (Cupressaceae) and *Casuarina* (Casuarinaceae), which may be self-perpetuating in the absence of fire (Withers & Ashton 1977; Harris & Kirkpatrick 1982). In the wetter parts of the zone, *Acacia* (Mimosaceae), *Melaleuca* (Myrtaceae), *Leptospormum* (Myrtaceae), *Agonis* (Myrtaceae) and *Banksia* (Proteaceae) all form some small areas of forest. The establishment of most of these taxa in large stands seems to require the environmental perturbation of fire.

In areas of high and continuous moisture availability and low fire frequency, temperate rainforest covers approximately 700 000 ha (Jarman & Brown 1983) (Figure 1). This forest is dominated by species in the genera *Nothofagus* (Fagaceae), *Atherosperma* (Monimiaceae), *Eucryphia* (Eucryphiaceae), *Phyllocladus* (Podocarpaceae), *Anodopetalum* (Cunoniaceae), *Athrotaxis* (Taxodiaceae), *Lagarostrobus* (Cupressaceae) and *Diselma* (Cupressaceae). These species are all capable of successful establishment in shade or small gaps (Read 1985; Cullen 1987), but most of them are easily killed by fire (Kirkpatrick & Dickinson 1984b), and they are normally incapable of long-distance dispersal (Gilbert 1959; Jackson 1968; Bowman & Jackson 1981).

3 The impact of logging

The forests of Australia have been mined since the early decades of settlement in New South Wales, when *Toona australis* (F. Muell.) Harms. (red cedar) was exported from the coastal rainforest (Webb 1968). There being few people and vast areas of forest, the lack of any concern for the future of the forest resource was not surprising, especially as forest was an obstacle to agricultural expansion. The tallest hardwood forests in the world were ignominiously ring-barked in the late 19th century to provide space for grass for dairy cows in South Gippsland and the Otway Ranges. Clearing of forest for other purposes still continues. In Tasmania alone, approximately 10 000 ha of forest were inundated or cleared per annum in the period 1972–80 (Kirkpatrick & Dickinson 1982).

As the mirage of endless forest gave way to a perception of the reality of interminable shrublands, grasslands dominated by *Triodia* and *Plechtrachne* species (spinifex) and pasture, State Forest was declared, and foresters were first imported and then trained locally. In 1979, State Forest covered almost 13 Mha of the 42 Mha of forest in Australia, mostly in the temperate zone. Twenty per cent of all forest was privately owned and half was on Crown Land, most of which was used for commercial rather than conservation purposes. Most (98%) of this forest was dominated by native species, and over most of Australia trees were selectively harvested for domestic use as timber. *Eucalyptus* is the major timber

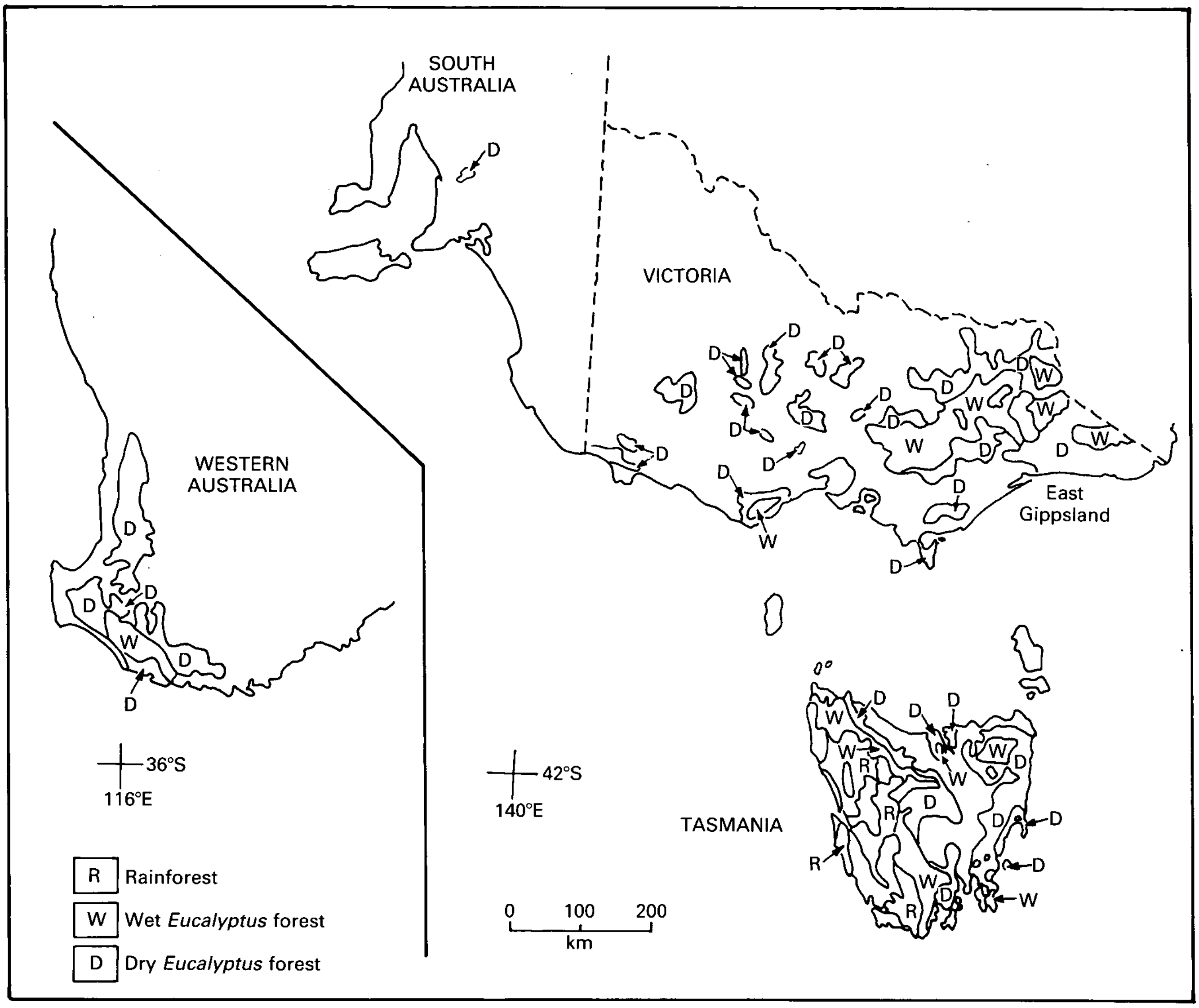

Figure 1. The present distribution of temperate forest types in Tasmania, Victoria, South Australia and Western Australia. Some very small areas of rainforest are found in Victoria, but cannot be shown at this scale

resource of Australia. It includes some of the fastest-growing temperate zone trees in the world, and species that will grow on the poorest of soils. They are destroyed only with difficulty. If a small group of *Eucalyptus* trees are removed from dry forest, they are likely to be replaced rapidly by saplings and seedlings previously suppressed, or by new trees establishing in disturbed ground.

A silvicultural system that was based on the removal of small groups of trees (group selection) worked well, and still works well, in most dry *Eucalyptus* forests. However, *Eucalyptus* regeneration failed in the wet forests under selective logging, because this silvicultural method seldom created a large enough gap in wet forests for successful seedling establishment (Cunningham 1960). The *Eucalyptus* seedlings germinated but were soon destroyed by fungi.

Research on the problems of wet forest regeneration led to the adoption of a system of clearfelling (Plate 7). In this system, merchantable trees are removed, the understorey is felled by bulldozer, and then the slash burned. Aeroplanes are used to broadcast seed after the slash burn. An occasional baiting or shooting of the marsupials attracted to the regenerating forest completes the management procedure.

There is no doubt that this slash and burn silviculture has solved the *Eucalyptus* regeneration problem in wet forests. However, most forests now clearfelled and burned are not naturally even-aged, and certainly do not require such drastic treatment to induce *Eucalyptus* regeneration (Kirkpatrick & Bowman 1982; Bowman 1986). The clearfell and burn system is attractive to the forest industries because it is easy to administer, and because it may have some initial economies when compared to the alternative of group selection. However, it is new and relatively untested, considering that the second crop is decades away in the shortest of conceived rotations, and that the oldest clearfell coupes in dry forest were regenerated less than 2 decades ago.

Plate 7. A clearfelled coupe in 40 m tall mixed forest dominated by *Eucalyptus obliqua* L'Herit. (messmate) (Photograph P Blackwell)

The ecological impact of the new silviculture promises to be substantial. Patterns of dominance, structure and floristic composition are likely to change in both wet and dry forest types.

The planned rotation times for the wet forests are between 40 and 90 years. Thus, the wet forests will be burned more frequently than was likely to have been the normal practice under aboriginal occupancy of Australia. The burns are also far more severe than natural fires, because of increased fire fuel loads near the ground. One effect of increased frequency and increased severity seems likely to be a shift from rainforest species to fire-adapted species in the understorey. Forests of giant *Eucalyptus* trees with understoreys of rainforest species will become exceedingly rare. In another 70 years, these mixed forests will survive only in a few small parts of National Parks, where they are very much under-represented. The National Park managers will be faced with a terrible problem. The only way that they will be able to perpetuate the giant mixed forests will be to burn them before the *Eucalyptus* trees die of old age. Yet the areas of these forests that they control are so small and usually so old that there is little prospect of maintaining all the stages of mixed forest development at the same time. If they do not burn these forests, and if the trees are not burned by accident, rainforest will replace the mixed forest. The continuous perpetuation of natural mixed forests dominated by giant *Eucalyptus* can only occur if large areas of these forests, in different stages of their life cycle, are preserved in different areas. The preserving of 1–2 ha around particular forest giants has no long-term conservation value.

The wet forests may experience a long-term deterioration in soil fertility as a result of clearfelling and regeneration burning (eg Raison 1980, 1981; Neilsen & Ellis 1981). However, there are few or no data on the inputs of nutrients from dust and seawater precipitated in rain, of the rate of release of nutrients through the weathering of the bedrock, or of the amount of nutrients lost in runoff and groundwater after fire.

Acclerated soil erosion may be a greater potential cause of vegetation change on some of these mixed forest sites than any decline in nutrient status. Forests are felled on extremely steep slopes and on shallow limestone soils. However, the situations in which clearfelling and regeneration burning will reduce the physical soil resource are yet to be determined.

In most wet forests, the seeds sown on the coupe after burning are from the same *Eucalyptus* species that grew there previously, and are often from the best of the felled trees. However, in dry forests, *Eucalyptus* species that have little or no commercial value are omitted from the seed mixture, and more economically desirable species, not naturally present on a coupe, are sometimes included (Kirkpatrick & Bowman 1982). Whether these attempts to change the forests will succeed in producing almost pure stands of commercial species is uncertain. The non-commercial species often occupy the driest or worst-drained parts of the coupes, where commercial species cannot flourish in the long term. Also, the amount of regeneration that actually results from sown seed varies enormously. Many suppressed seedlings survive regeneration burns, and they often constitute the bulk of the new *Eucalyptus* growth (Dickinson 1985).

Nevertheless, some *Eucalyptus* species are having their ranges extended beyond their natural bounds, both within the small area of a coupe and through the State Forest as a whole. These local and regional range extensions may result in an increased incidence of hybridization, as species that are not normally juxtaposed are sown in mixture. The prospect of *Eucalyptus* forests consisting of complex hybrid swarms between 2 or more species is one that has already been realized in second-generation plantations in California (Kirkpatrick 1977).

The relatively few data that are available suggest that clearfelling and slash burning do not eliminate native understorey plant species in dry forests, but do encourage the invasion of exotic weed species (Loyn *et al.* 1983; Duncan 1981; Dickinson 1985). Grazing by native marsupial herbivores strongly influences the relative abundances of species in the regenerating understorey (Dickinson & Kirkpatrick 1986).

Some of the effects of clearfelling and burning on dry forest will only become apparent after each coupe has been cut several times. At least some old trees whose hollows are so essential for the breeding of many birds and larger animals have been left in many clearfelled coupes. However, their lives are limited and there is no prospect of their replacement, as the trees now growing are destined for industry at a relatively tender age. The birds and animals that require these old trees, and those that require the varied resources of a forest consisting of many size classes of trees, will decline in abundance, while species adapted to the new conditions will be favoured. These shifts in the animal population will certainly lead to changes in the vegetation. These changes are virtually impossible to predict, as we know very little about the functioning of the dry forest ecosystem and of the role of various bird and animal species in plant dispersal and pollination.

Eucalyptus and *Pinus radiata* D. Don (Monterey pine) account for most of the forestry activity in Australia today. However, some of the woods of highest value per unit volume are extracted from rainforest. About one third to one half of the area of rainforest in Australia has been destroyed for farmland, and much of the remainder has been favoured for inclusion in National Parks (Webb & Tracey 1981). However, much rainforest is still found within State Forest and uncommitted Crown Land, especially in Tasmania. These forests are logged selectively for speciality woods (Calais & Kirkpatrick 1983) (Plate 8).

The temperate rainforest is largely confined to Tasmania, where it extends on to some of the coldest, wettest and most acid ground in Australia. Consequently, the breakdown of organic matter does not keep pace with its accumulation, and rainforest often grows on red fibrous peats (Brown & Podger 1982). These peats will burn during the more extreme dry spells of summer, and such fires are only extinguished by prolonged and soaking rain. Little of the temperate rainforest has been cleared for agriculture, but it covers only one tenth of the area it could cover if fire were absent from the Tasmanian environment (Jackson 1968). The peat fires cause the death and collapse of trees, creating a jumble of wood ripe for fuelling the next fire.

There seems to have been an acceleration of the destruction of the temperate rainforest by fire in the last 30 years. The vegetation map of Tasmania (Kirkpatrick & Dickinson 1984b) shows 56 000 ha of recently burned rainforest, compared to 166 000 ha that was burned 30–200 years ago and is now dense scrub, and 682 000 ha that is still rainforest. As men light virtually all the fires in Tasmania (Jackson & Bowman 1982), there is no hope of a decrease in this rate of attrition, unless the incidences of incendiarism and escapes from authorized fires decrease drastically.

Most temperate rainforest is now free from any logging. Yet, the major proportion of its area is within State Forest or Crown Land that could easily become State Forest. If a pulpwood market ever developed for rainforest tree species, there is a strong likelihood that the rainforest on reasonable soils would be clearfelled and sown to *Eucalyptus*, as this genus produces much more wood than any of the rainforest species.

4 Problems with exotic species

Australia has been one of the places most affected by the recent massive exchange of biotas between continents. Most taxa that have naturalized in Australia are not significantly degrading the native forest ecosystems. However, there are a few species that have the potential to transform much of the temperate forest.

The most significant of these organisms is *Phytophthora cinnamomi*, a root-rotting fungus. This species

Plate 8. Selective logging in temperate rainforest (Photograph P Crowther)

has killed most trees and understorey shrubs wherever it has invaded. It has had its major impact on the *E. marginata* Donn. ex S. M. (jarrah) forest of western Australia and the *E. sieberi* L. A. S. Johnson (silvertop) forests of eastern Victoria (Old 1979). The tree and understorey species that are most susceptible to damage have their major period of root growth at the time of maximum activity of the fungus. Symptoms are also more pronounced on nutrient-poor soils than on good soils, and may be moderated within the *E. marginata* forest by the encouragement of nitrogen-fixing species, such as *Acacia* spp. (acacia), rather than susceptible taxa, such as *Banksia* (honeysuckle).

There is little practical that can be done to preserve native communities from the spread of *P. cinnamomi*, once the species has been introduced into a locality. However, infested areas can be quarantined, and islands and large areas free of fungus can be protected from its ingress by stringent hygiene measures. The main dispersal vector has been machinery, particularly where it has been used to spread infested gravel, as was frequently the case before the cause of dieback was diagnosed. However, the organism has also been widely disseminated by the boots of walkers in the muddy ground of south-west Tasmania (M Neyland, pers. comm.). The natural spread of the species is relatively sedate: 3 m yr^{-1} upslope, 18–171 m yr^{-1} across slope, and up to 400 m yr^{-1} downslope (Weste *et al.* 1973).

P. cinnamomi is no immediate threat to the wet *Eucalyptus* forests or rainforest, as soil temperatures are too low to support pathogenic activity. However, canopy breaks can raise soil temperatures sufficiently to allow the fungus to become a cause of plant death (F Podger, pers. comm.) (Plate 9).

There are few other exotic high plant species that are capable of invading the poorest of the Australian forest soils. However, once these soils are fertilized with phosphorus and trace elements, whether purposely or inadvertently, the exotics quickly displace the natives (Heddle & Specht 1975). On moderately fertile and fertile soils, there are many species pre-adapted to invade forests. The most notable of these taxa include the South African invader of dry forest, *Chrysanthemoides monilifera* (L.) T. Norl. (South African boneseed) (Weiss & Noble 1984), a collection of species from English woods and moors, including *Ulex europaeus* L. (gorse) and *Rubus fruticosus* L. (bramble), and a wide range of species in the Poaceae.

It is possible to manage Reserves to mitigate the impact of these species on the native biota, and many taxa such as *Hypochaeris radicata* L. (cat's ear) and

Plate 9. Xanthorrhoea australis R. Br. (grass tree), one of the first victims of invasion by *Phytophthora cinnamomi* (Photograph F Bolt)

Aira spp. (hair-grass) have insinuated themselves into the more nutrient-rich forest communities, without any apparent severe impact on the native species. The few data available suggest that forests and woodlands on the better soils may be more resilient to disturbance than those on poorer soils (Kirkpatrick 1986b).

The impact of introduced animal species on Australian temperate forest is mostly unquantified, although there is some qualitative evidence that *Oryctolagus cuniculus* L. (rabbit) has prevented *Eucalyptus* regeneration in parts of the dry forest and mallee (Parsons 1968).

5 Fire management

Fire presents the most severe immediate conservation management problem in the temperate forest Nature Reserves and National Parks of Australia (Plate 10). The degree of danger that unplanned fires present to lives, wood values and property cannot be ignored by park managers. Thus, there is a tendency to consider fire management largely in terms of reduction of hazard. Fire simulation programmes are used as a means of reducing the likelihood of severe and widespread fire, by planning the reduction of hazard, as well as being used as a means of predicting fire spread to aid suppression activities. The widespread use of hazard reduction burning in National Parks and Nature Reserves has a major conservation disadvantage, in that there is a high likelihood of local extinction of those species not adapted to any particular regime. Some of the rarest species in Victoria are those that respond best to late summer/autumn fire (Scarlett & Parsons 1982), because spring/early summer fire has prevailed, and frequent low-intensity fire has been shown to affect adversely obligate seed regenerators (Fox & Fox 1986), which usually include the species most important in nitrogen fixation (Adams & Attiwill 1984).

Fuel levels and rates of fire spread under different conditions can be modelled relatively easily at a planning level, and with some degree of universality. However, the modelling of vegetation response to fire (eg Shugart & Noble 1981) must be site-idiosyncratic, because of genecological variation, the feedback between fire and flammability, and the influence of vegetation patterning on fire hazard.

Genecological differentiation has been found in most species for which data are available (eg Pryor 1957; Kirkpatrick 1975; Potts & Reid 1985). In some cases, it is known that forest dominants vary in their adaptation to fire. For example, *Nothofagus cunninghamii* Oerst. (myrtle) commonly resprouts from a basal burn after fire in Victoria (Howard 1973) and highland Tasmania (Kirkpatrick 1983a), but usually fails to recover vegetatively from fire in lowland Tasmania (Howard 1973).

If prescribed fire increases fire frequency, it is likely also to increase the flammability of the vegetation,

Plate 10. Structural modification of dry forest resulting from a high frequency of intense fire in a coastal environment (Photograph J B Kirkpatrick)

because those species that survive high fire frequencies tend to be much more flammable than those that require lower frequencies for survival (Mount 1964; Jackson 1968; Dickinson & Kirkpatrick 1985), and because the structure of the vegetation becomes more favourable for the propagation of fire (Jackson 1968).

The spatial patterning of flammable and non-flammable vegetation types has also been shown to have an influence on fire incidence and effects. In north-west Tasmania, Jackson (1981) has demonstrated that ridges have an increasing probability of carrying *Eucalyptus* within those rainforest regions with increasing windward proximity to large areas of *Eucalyptus* forest.

Like much else in the area of nature conservation, an appropriate fire policy for Nature Reserves might best be decided on the basis of the ecological requirements of the rarer species (Kirkpatrick 1986a). Where relative rarity or ecological requirements are not known, spatial and temporal variability in firing patterns would seem highly desirable, until such knowledge is obtained. In some cases, such as rainforest (Howard 1981), there is little doubt that fire exclusion is the appropriate management goal.

6 General discussion

Although much of the remaining temperate forest of Australia is in danger of elimination or transformation by economic activities, the invasion of alien species, and changes in fire regimes, there are few temperate forest plant species that are considered to be extinct or endangered (Leigh *et al.* 1984), and substantial proportions of the original areas of most forest types are probably on land presently devoted to uses that are likely to maintain a large native plant cover. We have yet to determine the full conservation status of forest communities and species, a large task that is just commencing (Kirkpatrick 1983b; Jarman *et al.* 1984; Leigh *et al.* 1984; Duncan & Brown 1985). We also lack the detailed ecological investigations that would allow rational management of our Reserves for conservation purposes. Even large-scale vegetation maps are lacking for most forests dedicated to nature conservation. Conservative management and accelerated research effort could, and should, mitigate the effects of this information dearth.

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The importance, exploitation and utilization of China's forest in arid mountainous regions

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In the special geographical areas and ecological conditions of the arid regions of north-west China, the trees on the Qi Lianshan, Tianshan and Altaishan Mountains belong to the shelterbelt forest, protecting the headwaters of rivers which have an important role in conserving water reserves and adjusting the moisture regime. The mountainous forest and alpine 'ice-source reservoir' provides the water for agriculture, animal husbandry and industry, as well as acting as the lifeblood of oasis construction and human existence. The destruction of the mountainous forest ecosystem causes an insufficient supply of water, water loss, erosion, silting up of river courses, desertification and flood. An extremely urgent danger existing at present is that the ecological balance in the arid areas is being seriously upset. The continuous deterioration of the natural ecological environment leads directly to a deficiency of water supply and a yield reduction in agriculture and animal husbandry, because of the irrational exploitation and utilization of the mountainous forest resource.

Because of its extreme importance in arid regions, the mountainous forest is the major component of the land ecosystem in such areas, and the whole ecosystem will be out of balance and heading towards collapse if the forest is lost. For example, the drying up of sources, water loss, soil erosion, damage resulting from drought and flood, desertification, as well as the deterioration of farm- and pasture-land, etc, are all consequences of disorder, confusion of structure, and weakening of stability in the arid ecosystem. Therefore, the exploitation of the mountainous forest must be controlled. The following measures are proposed.

1. A China Comprehensive Exploitation Centre of Natural Resources in Arid Areas should be established. Under the unified leadership of the Land Bureau of the State Planning Commission of the State Council, the various departments should collaborate to produce a unified plan for the comprehensive exploitation and manage-

Table 1. The natural and forest characteristics of arid mountainous regions in north-west China

		Forest region	
	Upstream forest of Qi Lianshan Mountains	Upstream forest of Tianshan Mountains	Upstream forest of Altaishan Mountains
Landscape characteristics	Desert	Desert	Desert–steppe
Natural features			
Geographical location	36°30′–39°30′N 93°30′–103°E	36°18′–49°10′N 85°50′–95°25′E	44°51′–49°10′N 85°50′–95°25′E
Total area (10 kha)	1070.1	4011.1	801.9
Percentage of country's land area (%)	1.11	4.18	0.84
Snow-line (m)	4200–5200	3800–4200	3000–3400
Main maximum (m)	5564	7439	4374
Climate	Continental frigid semihumid and semi-arid climate	Continental frigid semihumid and semi-arid climate	Continental frigid semihumid and semi-arid climate
Forest soil	Grey–drab forest soil	Grey–drab forest soil	Grey forest soil
Glacier number	2859	8900	416
Glacier area (km^2)	2062.7	9549.7	293.2
Glacier volume (100 Mm^3)	81.1	3600	165
Percentage of the country's glacier (%)	3.49	16.92	0.52
Main water system	Shiang Xo, Xei Xo, Beido Xo, Shurhen Xo, etc	i Li Xo, Malas Xo, etc	Ercis Xo, etc
Forest characteristics			
Main tree species	*Picea crassifolia*	*Picea schrenkiana*	*Larix sibirica*
Forest distributional zone (m)	2500–3200	1500–2900	1400–2300
Total forest land area (10 kha)	50.18	72.11	47.62
Total forest stock (10 km^3)	1390.65	13739.40	8075.89
Total forest land (10 kha)	12.09	43.06	31.62
Stand volume (10 km^3)	1269.25	11538.39	7274.59
Forest coverage (%)	12.4	26.9	25.5
Forest growth rate (%)	2.51	1.82	1.42
Forest annual mortality (10 km^3 yr^{-1})	Unknown	77.0	94.9
Forest disease decay rate (%)	10.0	17.4	45.0
Forest productivity (m^3 ha^{-1})	100.5	290	160

ment of the natural resources in such areas, in order to obtain a co-ordinated balance between ecological, economic and social benefits.

2. The principles of ecology and economics must be followed in the exploitation and utilization of the mountainous forest resource. Protection must be of over-riding concern. Cutting limits that do not exceed the natural rate of growth should be set, and the principle of sustained utilization should be followed. Forests should be protected by law, and destructive felling prohibited. A rational policy of felling should be maintained, with a reduction in the amounts cut.

3. A scientific system of forest management should be practised. Improved silvicultural methods (timely forest regeneration, forest management, grass and tree planting) in the mountainous regions should be adopted and forest investment increased.

4. A policy for grazing in forests should be formulated, and a correct balance established between the competing aims of forestry and animal husbandry.

5. A forestry foundation system should be set up, so that the expense of constructing shelterbelts to protect the headwaters of the rivers is shared by those benefiting from the improved forest conditions.

6. Increased collaboration with UNESCO should be encouraged for international co-operation, the free exchange of information, and technical training in environmental studies.

Problems of draining excessively moist forests in the temperate zone of the USSR

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Abstract
The problems of establishing scientific measures to increase the productivity of excessively moist forests and of forested peatlands by drainage are highlighted, and the consequences for the natural environment are discussed. An expedient scale of draining and preserving excessively moist forests and peatlands is suggested.

Different approaches to the optimal management of peatland forests are analysed by considering the inter-relations in a biogeocoenosis that change in the process of drainage. Information is given on the development of a model of groundwater dynamics in the inter-ditch space, which is used to select the optimal parameters of a forest drainage network.

1 Introduction

Waterlogging of soils is an extremely widespread process in the USSR and in other countries with a humid climate. Being one of the main causes of low forest productivity, it greatly hinders the development of such areas. As a result, these countries have implemented expensive programmes for draining the excessively moist (waterlogged and peatland) forests.

Even though scientists in various countries have made substantial contributions to solving this problem during the past few decades, and although a special branch of forest science ('peatland forestry') has emerged, a number of important aspects of forest drainage still require investigation. This lack of knowledge can only result in an incomplete picture of the effect of drainage on forest growth and doubt about its potential negative effects on the environment.

The present paper presents some examples of forest drainage schemes in the USSR. Attention is given to the most important unsolved scientific problems in establishing a rational method of forest drainage, that are currently being studied.

2 Certain results of forest drainage

Although forest drainage operations were started in Russia early in the 19th century, this work has been carried out on a large scale only since the 1950s upon the creation of a scientific, design, institutional, and production base. The volume of work has been increasing constantly, reaching a maximum area of 320 000 ha yr^{-1} in 1975. The rates of forest reclamation have decreased gradually to 180 000–200 000 ha yr^{-1} in 1983–85, associated with increasing distance between the areas to be reclaimed and the reclamation stations, and the need to restore the old drainage network. There are currently about 5.2–5.5 million hectares of forests with operational drainage networks in the USSR.

Attempts have been made to evaluate the efficiency of forest reclamation in large areas. It has been established that forest drainage efficiency differs in various regions because of the differences in quality of work and the intensity of the drainage. Attempts to drain greater areas more cheaply, less intensively, and without the need for road construction, have proved to be more expensive in the long term. In regions with a high level of forest management (the Baltic republics, the Ukraine, and some other areas), the efficiency of the drainage operation was acceptable, whereas in some regions of the RSFSR it was 30–40% below the expected level. Notwithstanding all the drawbacks of putting theoretical ideas of forest reclamation into practice, its expediency has been universally recognized (Vompersky 1986).

The practical implementation of forest drainage is hindered mainly by the lack of specialized machinery for constructing new networks and, especially, for restoring old ones. General-purpose machinery is clumsy for operation in forested peatlands, and requires cutting wide passages that reduce the area of productive land. The effect of drainage is also reduced by the delay in the establishment of forests on the newly drained lands, by the absence of a special service responsible for the operation of drainage systems, and by insufficient scientific substantiation of the methods and requirements of drainage.

3 The impact of forest drainage on the environment

Until recently, little attention was paid to this problem. However, public criticism of certain cases of irrational drainage has resulted in a more careful approach to the reclamation of peatlands, in order to minimize the negative side-effects on the natural environment, which has stimulated relevant research (Sabo 1972; Ivanov 1977; Boch & Mazing 1979).

Figure 1 attempts to define the consequences and chains of impacts of forest drainage on the natural environment (Vompersky 1982). Seven levels of consequence have been identified, taking account of the time and magnitude of their occurrence. Possible feedbacks have been omitted for the sake of simplicity. In all, 31 consequences have been highlighted, some of which incorporate minor after-effects.

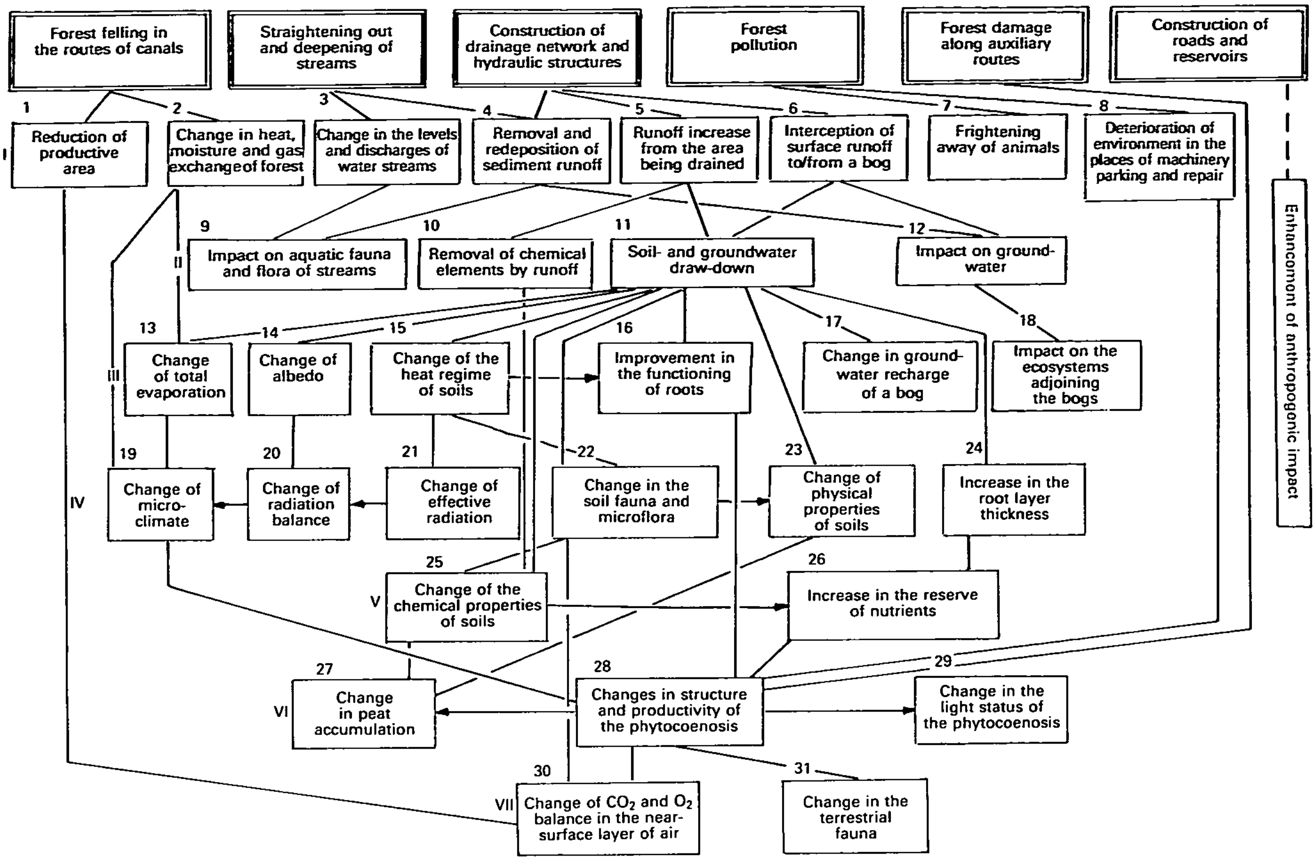

Figure 1. The chains of direct impact of peatland forest drainage on the environment (and its consequences), without the feedback links. The upper row = types of drainage operations; Roman numerals indicate successive levels of consequences, whereas the numbers of consequences are shown as Arabic numerals. The chains of impacts extend from top to bottom, with horizontal chains indicated by an arrow

Unfortunately, the majority of consequences have been insufficiently studied in quantitative experiments, eg the changes in total evaporation (13 in Figure 1), radiation balance in a peatland (20), $CO_2 + O_2$ balance in the near-surface layer of air (30), groundwater inflow and outflow to/from the drained area (17); possible impacts on the aquatic fauna and flora in water-receiving streams (9), etc.

The impact of draining peatland forests on the water resources and regime of runoff, as well as on the natural conditions and productivity of naturally drained lands adjoining the drained areas, is being studied extensively both in the USSR and in other countries (Heikurainen 1972; Aire 1977; Laine 1980; Pisar'kov 1981; Starr & Päivänen 1981). The effect of forest drainage on peat accumulation and peat deposits is also being studied (Vompersky & Smagina 1984). The impact of forest drainage on runoff distribution with time and on the volumes and peaks of floods remains unclear.

4 The scale of drainage and preservation of waterlogged forests and peatlands

This problem has so far been resolved with respect to economic and other general considerations. In the USSR, it is prohibited to drain the following areas: extremely poor, woodless oligotrophic bogs where forest growth is inefficient without fertilization; peatlands producing good yields of *Vaccinium oxycoccus* L. (cranberry); small scattered peatlands that are inconvenient for drainage operations; and peatlands and bogs preserved for various reasons. Prohibited peatlands account for more than 1% of their total area.

The concept of harmonic utilization of nature presupposes a balanced exploitation and protection of all the natural resources in a forest river basin. Unfortunately, as far as we know, there are no proven methods for the integrated utilization of nature. It is assumed that drainage should not be carried out in a river basin where peatlands occupy up to 10% of the area. If peatlands comprise 20–30% or more than 40% of a basin, it is permitted to drain up to one third or between one and two-thirds, respectively. However, no assessment has been made of the negative after-effects of large-scale drainage operations on the environment, and one is guided only by the need to protect the natural diversity of biogeocoenoses, valuable *Vaccinium* patches, or hunting grounds. This problem requires further study.

In the USSR, the areas not to be drained till the end of the century range from 45% to 80% of the total area of excessively moist forest lands (including those with insignificant peat deposits or on mineral, hydromorphic soils).

5 The intensity of drainage of forested lands

Cheaper methods of drainage, coupled with the growing price of wood, require the sound ecological drainage of forests. First, it is necessary to determine whether the soil- and groundwater table is lowered or maintained, and to assess the annual effects of precipitation. Second, we need to define what kind of drainage network will maintain soil- and groundwater at a certain level. We shall discuss the solution of the second problem below.

In the USSR, the drainage network designs used are based on semi-empirical calculations and on the past experience of certain experts. The network parameters (spacing of ditches and their depth) approved for the central regions of the country are also recommended for other regions, with corrections for changing hydroclimatic conditions (Anon 1971). However, no agreed level of drainage has yet been determined. Therefore, experimental drainage sites in the different regions of the USSR are being monitored at intervals, according to a single methodical instruction. This experimental work is aimed at drawing up instructions for draining forested land to varying degrees.

6 Theoretical analysis of optimal forest drainage

In general, the criterion of optimal forest drainage

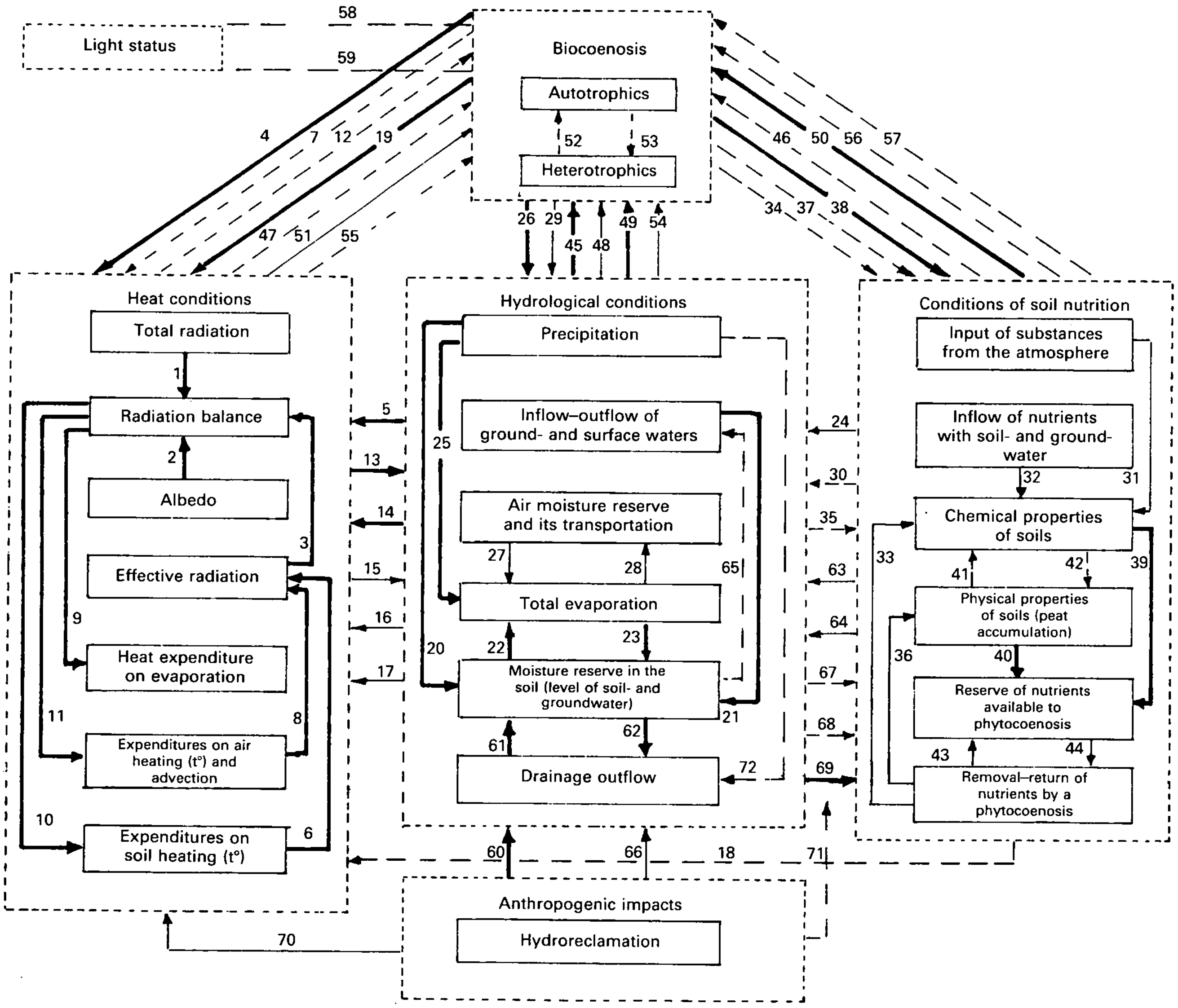

Figure 2. A more detailed flow diagram of the inter-relationships in a biogeocoenosis affected by forest drainage (——— most important; —— significant; – – – – secondary inter-relations); 1–59 are the inter-relations typical of natural excessively moist forests and peatlands that condition the functioning of the following blocks: 'thermal conditions' (1–19); 'hydrological conditions' (20–30); 'conditions of soil nutrition' (31–44); and 'biocoenosis' (45–59). The inter-relations (60–72) result from forest drainage, in addition to those which already existed in a peatland

Various impacts and inter-relations are indicated as follows: the impact of the in-coming short-wave direct and scattered radiation on the radiation balance of forest (or peatland) (1), the effect of albedo (2) and effective radiation (3) on the radiation balance; the impact of the vegetation structure on albedo (4), moistening of the soil surface (5); the effects of the soil surface temperature (6), plants (7), and air (8) on the effective radiation; expenditure of the radiation balance (residual radiation) on total evaporation (9) and heating of soil (10), near-surface layer of air (11), and bodies of plants (12); the effects of heat resources on the amount of evaporating water (13) and vice versa *(14); the inter-relation of heat expenditure on the heating of air (its temperature) with its humidity, taking into account the process of advection (15,16); the impact of soil moisture reserves (17), soil structure and properties of its skeleton (18) on the heating of soil and its thermal properties; the impact of the specific features of phytocoenosis on the heat transfer (gas composition) in the near-surface layer of air (19); the effect of precipitation reaching the soil surface (20), and of the inflow (outflow) of ground- and surface water (21) on soil moisture reserves in a forest (peatland); 22 and 23 designate the reciprocal influence of the soil moisture content and total evaporation; the effect of the physical properties of soil on the moisture content in the aeration zone (24); the amount of rainfall, retained by vegetation, to be spent on evaporation (25); the effect of the phytocoenosis structure on total evaporation (on transpiration and physical evaporation) (26); the effect of the moisture content in the near-surface layer of air and its transfer, as well as air humidity, on the evaporation value (27) and* vice versa *(28); the effect of the phytocoenosis structure on moisture transfer in the near-surface layer of air (29); the effect of capillary moisture expenditure (soil structure) on evaporation (30); the impact of substances introduced to the peatland from the atmosphere (31), brought by ground- and surface water (32), and returned by phytocoenosis with litterfall and forest debris (33), as a result of the activities of soil microflora, mesofauna and surface organisms (34), and that of the gas exchange and aeration regime in soils (35) on the chemical properties of soils; the impact of litterfall and forest debris (36) and the effects of soil microflora and mesofauna (37) on the physical properties of soils; the effects of the depth of penetration of roots (and their distribution) (38), chemical properties (39) and bulk density (40) of soil on the reserves of soil nutrients available to phytocoenosis; the reciprocal influence of the chemical and physical properties of soil (41, 42); the reciprocal influence of the reserves of available nutrients and their consumption by phytocoenosis (43, 44); the impact of groundwater table (45) and physical properties of soil (46) on the depth of penetration and distribution of roots in the soil; the effects of temperature (47) and humidity (48) of air, aeration (49), reserves of nutrients in the root zone (50) and of soil temperature regime (51) on the physiological processes, structure and productivity of phytocoenosis; the impact of heterotrophic organisms on the net productivity of phytocoenosis (52) and its properties on the complexes of animals and micro-organisms (53); the effects of the humidity and aeration regimes (54), temperature (55), soil fertility (56) and physical properties (57) on the group composition, amount and activity of soil fauna and microflora; the inter-relation of illumination with the structure of phytocoenosis (58, 59); the effect of forest drainage methods on runoff volume and regulation (60); the reciprocal influence of runoff volume in a drainage network and the groundwater table (moisture reserves in soil) (61, 62); the effect of soil permeability characteristics, its water-yielding capacity and gradient on rate of runoff (63) and on the depression curve of groundwater in the inter-ditch space (the heterogeneity of a water regime) (64); the impact of groundwater level draw-down in a drained peatland (forest) on the inflow (outflow) of the recharging groundwater (65); the effect of drainage on the termination of the surface water inflow to the drained peatland (forest) (66); the effect of changes in the volume and quality of the inflowing ground- and surface water on the amount of substances brought to the peatland in the course of reclamation (67); the effect of water discharge through the drainage network on the removal substances (68); the impact of groundwater table lowering on peat deposition, ie on the increase in the bulk density of soil (69); the impact of ditches (gaps in the stand canopy) on the turbulent heat and moisture exchange in the near-surface layer of air between the ditches (70); the effect of local technical damage on biocoenosis (along auxiliary routes, sites of machinery repair, etc) (71); precipitation reaching the drainage network directly (72).*

implies the achievement of maximum (or economically conditioned) forest growth with minimum disturbance of the water regime and the least adverse effects on the environment. The optimal design of each drainage network should, strictly speaking, be unique. An increase in peatland forest productivity, as well as the required water regime, is not only achieved by varying the design of a drainage network, but also as a result of the complex inter-relationships in a biogeocoenosis affected by reclamation (Figure 2). An analysis of these inter-relationships illustrates that a similar state can be achieved for separate components in a peatland forest ecosystem by various management strategies and by stimulating different mechanisms responsible for its functioning. It should also be noted that, at different sites in the same type of waterlogged forest, an identical drainage network will not necessarily produce quantitatively similar changes in its functioning and productivity, because of individual differences between these sites.

As shown in Figure 2, the development of a mathematical model of productivity in a drained forest, including drainage work parameters, is impossible at present because it would require quantitative assessment of the dynamics in time of more than 70 (or at least 19 major) inter-relationships (Vompersky 1982), and the applicability of such a model (as well as its verification) for other analogous objectives is of doubtful validity. For this reason, it is preferable to use simpler models to establish methods of managing waterlogged and peatland forests, and to resort to well-tested natural experiments and mathematical modelling. In this way, we will be able to assess the dependence of the final states of a certain biogeocoenotic parameter ('output') on the impacts ('input'), but without becoming involved in the details of the analytical process.

7 Modelling of soil- and groundwater dynamics and determination of forest drainage network parameters

It has already been stated that experimental sites for draining forests and peatlands have been established in different regions of the USSR, and statistical analysis is being carried out on the long-term (8–10 years) dynamics of the soil- and groundwater table. Such monitoring takes account of the distances between boreholes and ditches in similar types of forests (peatlands), and under different designs of drainage network. By modelling the soil- and groundwater table dynamics at an experimental site in the

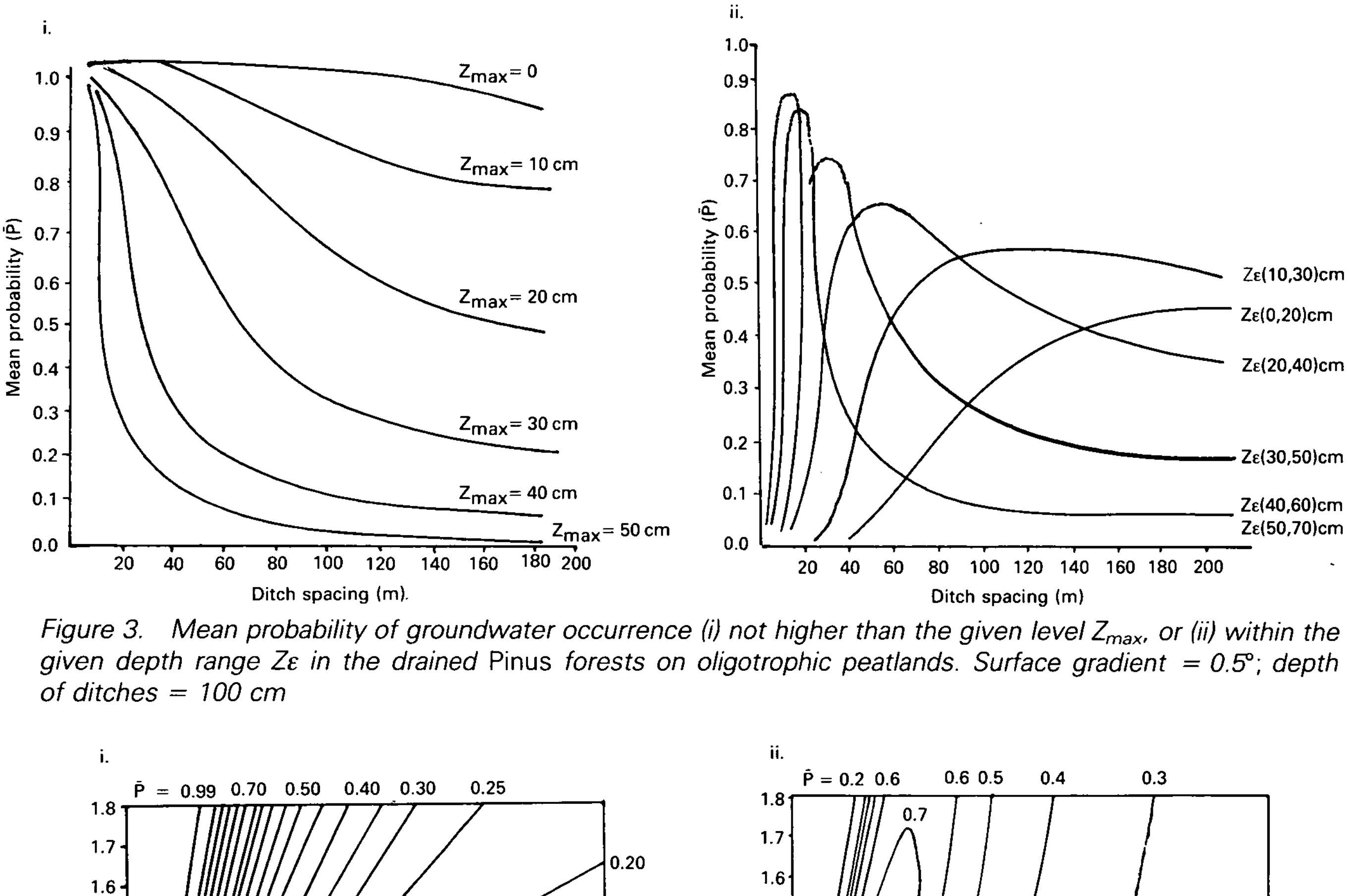

Figure 3. Mean probability of groundwater occurrence (i) not higher than the given level Z_{max}, or (ii) within the given depth range Zε in the drained Pinus *forests on oligotrophic peatlands. Surface gradient = 0.5°; depth of ditches = 100 cm*

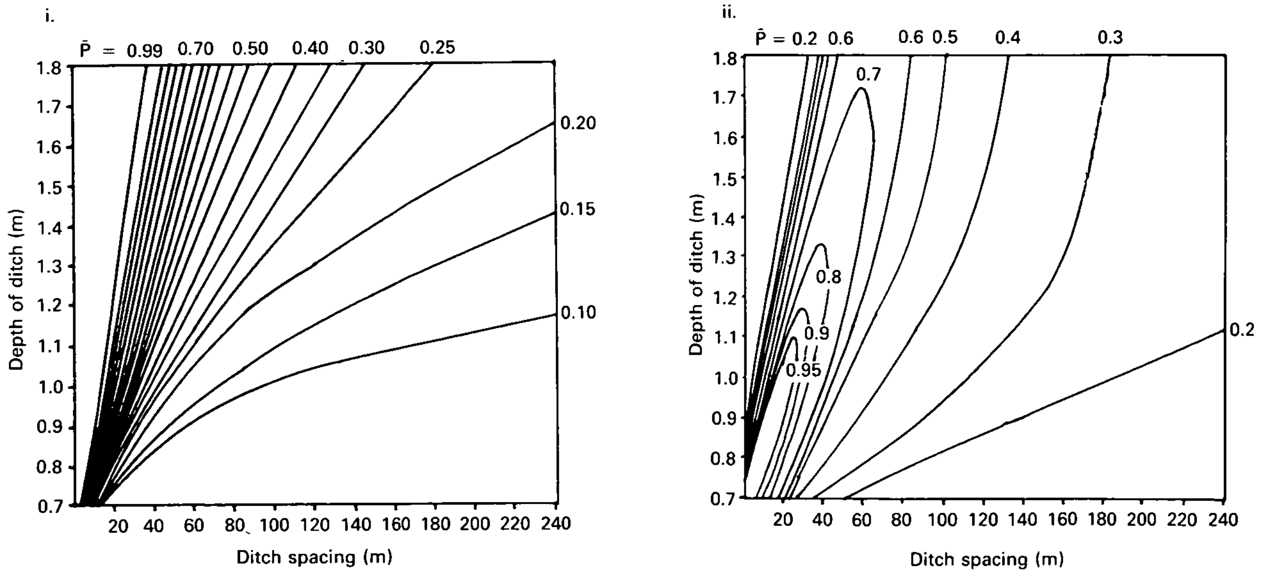

Figure 4. Combinations of ditch spacing (L) and depth (H_d) to ensure, with mean probability (P), that the groundwater table does not fluctuate (i) above the given level of 40 cm, or (ii) within the depth range of 30–60 cm in an oligotrophic bog in a Pinus *forest on* Sphagnum *peat*

Zapadnaya Dvina region of the Kalinin area (Vompersky *et al.* 1984), it has been possible to predict the soil- and groundwater table occurrence in time at an arbitrary point of inter-ditch space, depending on the ditch spacing and depth, and taking into account the surface gradient.

This model enables the selection of the optimal parameters of a drainage network which, according to the probability criterion, will ensure the required regime of soil- and groundwater table fluctuation in the inter-ditch space during the growing season. Figure 3 presents the graphs of the probable ($\bar{P}$) levels of the groundwater table (in the inter-ditch space of the oligotrophic bogs in a dwarf shrub/*Sphagnum*/*Pinus* (pine) forest being drained) below the present level (Z_{max}) or within a given depth interval ($Z\varepsilon$), depending on the spacing of ditches at constant depth. Using similar data, we have constructed appropriate nomograms for selecting the parameters of a drainage network which will maintain the required levels of soil- and groundwater (Figure 4).

The models of soil- and groundwater dynamics developed in this manner are applicable in regions with heat and moisture regimes similar to those where the experimental material was obtained. Therefore, work is in progress to extend the models, incorporating other data on experimental drainage obtained in various regions, which will enable us to predict more accurately the effects of climatic factors on changes in forest drainage parameters in different natural zones.

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FOREST SOILS

Review of the study on soil animals during the past 6 years (1979–85) on Changbai Mountain

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Abstract

According to recent estimates, the soil animals found in the study area belong to 7 phyla, 14 classes and over 20 orders. Acarina, Collembola and Nematoda are the main groups distributed over all the vertical zones of vegetation.

Some aspects of the ecological investigation are reviewed, including (i) the ecological distribution of certain groups, (ii) an analysis of the habitats of the various soil animals, and (iii) an experiment on litter disappearance.

1 Introduction

The present paper describes the main results of a soil zoological study carried out during 1979–85, as part of a larger study of the forest ecosystem on Changbai Mountain, in north-east China. Because there is no professional body in the field of soil zoology, and only a few published reference works, it is hoped that this study will be of interest to pedologists, biologists and ecologists, hopefully encouraging further development, and opening up possibilities for co-operation with related disciplines within the larger programme, in order to understand the role of one of the most important elements, the decomposers, in the forest ecosystem.

2 Preliminary survey of soil fauna

Using Berlese or Tullgren and Baermann funnels ('dry' and 'wet') for micro-arthropods and nematodes and cultivating media for soil protozoa, together with hand sorting, the soil animals collected were identified as belonging to 7 phyla, 14 classes and over 20 orders, as follows:

Protozoa
- Phytomastigophora
- Zoomastigophora
- Rhizopoda
- Ciliata

Platyhelminthes
- Turbellaria

Nemathelminthes
- Nematoda
  - Rhabditida
  - Chromadorida
  - Enoplida
  - Teratocephalida

Trochelminthes
- Rotatoria

Annelida
- Oligochaeta

Mollusca
- Gastropoda

Arthropoda
- Myriapoda
  - Symphyla
  - Diplopoda
  - Chilopoda
- Arachnoidea
  - Chelonethida
  - Araneida
  - Opiliones
  - Acarina
- Tardigrada
  - Eutardigrada
- Crustacea
  - Cladocera
- Insecta
  - Protura
  - Collembola
  - Diplura
  - Orthoptera
  - Thysanoptera
  - Hemiptera
  - Lepidoptera
  - Diptera
  - Coleoptera
  - Hymenoptera

Unfortunately, there is no identification literature available on soil animals in China, except for protozoa and earthworms, so that most of the specimens could not be identified at genus or family level. Among the 4 groups, Acarina, Collembola, Nematoda and Annelida, however, we were able to identify some at species level (Yin *et al.* 1985; Zhang *et al.* 1980; Zhang & Chen 1981).

Acarina
- Cryptostigmata
  - Hypochthonioidae
    - *Poecilochthonius*
  - Phthiracaroidea
    - *Hoplophthiracarus*
  - Euphthiracaroidea
    - *Protoribotritia aberrans*
  - Eulohmanniidae
  - Nothridae
    - *Nothrus*
  - Camisiidae
    - *Platynothrus*
    - *Camisia*
  - Tectocepheidae
    - *Tectocepheus*
  - Oppiidae
    - *Oppiella nova*
  - Suctobelbidae
    - *Suctobelbella naginata*
  - Liacaridae
    - *Liacarus*
  - Nanhermanniidae
    - *Nanhermannia nova*
  - Ceratozetidae
    - *Perlohmannia*
  - Damaeidae
    - *Hypodamaeus*
  - Oribatulidae
    - *Scheloribates latipes*
  - Palaeacaridae
  - Hermanniidae
    - *Hermannia*
  - Tenuialidae
- Mesostigmata
  - Epicriidae
    - *Epicrius*
  - Parasitidae
    - *Poecilochirus*
    - *Parasitus*
  - Ologamasidae
    - *Gamasiphis pulchellus*
  - Trachytoidea
    - *Trachytes*
  - Veigaiaidae
    - *Veigaia slonovi*
  - Pachylaelaptidae
    - *Pachylaelaps*
    - *Pachyseius*
  - Blattisocidae
    - *Cheiroseius*
    - *Blattisocius*
  - Rhodacaridae
    - *Gamasellus vibrissatus*
    - *G. montanus*
  - Parholaspidae
    - *Parholaspulus bregetovae*
  - Uropodidae
    - *Uropodina*
- Astigmata

Collembola
- Entomobryidae
  - *Entomobrya*
  - *Lepidocyrtus*
  - *Sinella*

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*Graduate students Cui Zhendong and Yang Faizhu were also involved in the study

  - *Homidia*
- Tomoceridae
  - *Tomocerus* sp.
  - *T. varius*
- Onychiuridae
  - *Onychiurus*
  - *Tullbergia*
- Isotomidae
  - *Folsomia octoculata*
  - *Desoria*
  - *Isotoma*
  - *Isotomiella minor*
  - *Folsomides*
- Hypogastruridae
  - *Hypogastrura*
  - *Willemia*
- Neanuridae
  - *Neanura*
  - *Lobella*
  - *Micranurida*
  - *Friesea*
  - *Pseudachorutes*
- Oncopoduridae
  - *Oncopodura*
- Sminthuridae
  - *Ptenothrix*
  - *Sminthurinus*
  - *Sphaeridia*
  - *Dicyrtoma*
  - *Arrhopalites*
  - *Sphyrotheca*
  - *Deuterosminthurus*
- Neelidae
  - *Neelus*
  - *Megalothorax*
- Poduridae

Nematoda

- Rhabditida
  - Rhabditidae
    - *Rhabditis brevispina*
    - *Bunonema*
  - Diplogasteridae
    - *Tylopharynx foetidus*
    - *Diplogaster*
- Chromadorida
  - Monhysteridae
    - *Monhystera vulgaris*
    - *Prismatolaimus intermedius*
  - Plectidae
    - *Plectus*
    - *Haliplectus*
    - *Rhabdolaimus*
    - *Pseudohobdolaimus*
- Enoplida
  - Mononchidae
    - *Mononchus papillatus*
    - *Prionchulus muscorum*
  - Dorylaimidae
    - *Dorylaimus*
    - *Actinolaimus*
    - *Oionchus*
- Teratocephalida
  - Teratocephalidae
    - *Teratocephalus*
- Tylenchida
  - Tylenchidae
    - *Tylenchus*

Annelida

- Oligochaeta
  - Moniligastridae
    - *Drawida gisti*
  - Megascolecidae
    - *Pheretima*
  - Lumbricidae
    - *Allolobophora*
    - *Eisenia rosea*
    - *E. foetida*
  - Enchytraeidae

Although these lists are far from complete, the survey shows the tremendous abundance and species richness of the soil animals that exist on Changbai Mountain. However, how can future soil zoological research be carried out, unless the soil fauna can be identified with certainty? It seems probable that, for the next few years at least, most soil zoologists, as well as some of the taxonomists working on invertebrates, will be obliged to devote some time to describing new taxa and to compiling identification keys for the different taxonomic levels of the soil fauna in as much detail as possible, so as to enable further ecological investigations of their role in the ecosystem. The dominant species should be identified, with the help of the taxonomists concerned. Today, all ecologists are aware of the fact that the higher taxa (genera and families) have no uniform ecological characteristics.

3 Study on the ecological distribution and habitat of soil animals

The distinct changes in vegetation and climate on the northern slope of Changbai Mountain are believed to be exerting great influence on the distribution of soil animals. From a comparative study carried out in 1979, the numbers collected in the different vegetational zones are summarized in Figure 1, which shows the relative abundance of the main groups in each zone. Most of the groups have been found in all of the zones. However, because insufficient numbers were collected, the results of this study only provide a rough picture which will be refined by future collections.

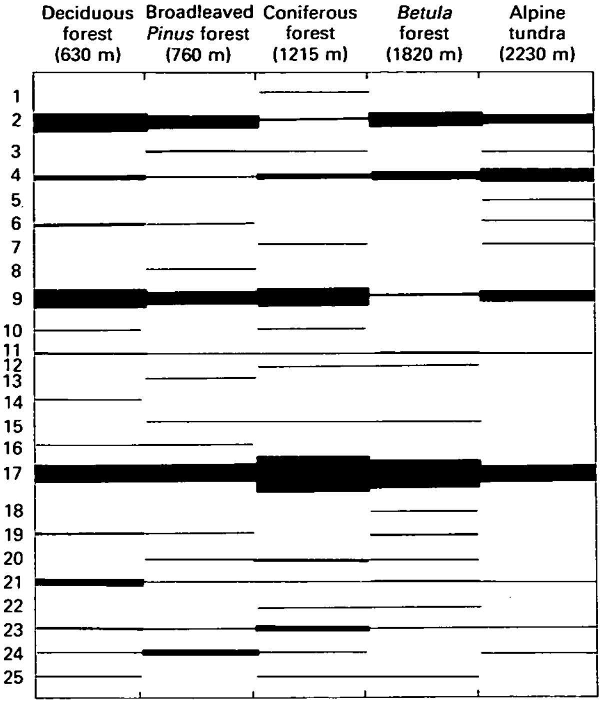

Figure 1. Relative abundance of soil animals on the northern slope of Changbai Mountain (1 = Turbellaria; 2 = Nematoda; 3 = Gastropoda; 4 = Enchytraeidae; 5 = Eutardigrada; 6 = Pseudoscorpiones; 7 = Araneida; 8 = Phalangida; 9 = Acarina; 10 = Crustacea; 11 = Diplopoda; 12 = Lithobiomorpha; 13 = Scolopendromorpha; 14 = Geophilomorpha; 15 = Symphyla; 16 = Diplura; 17 = Collembola; 18 = Orthoptera; 19 = Thysanoptera; 20 = Hemiptera; 21 = Diptera; 22 = Lepidoptera; 23 = Coleoptera; 24 = Hymenoptera; 25 = larvae of Arthropoda)

Except in the broadleaved forest at the lower elevations, the total number of individual soil animals decreased with increasing altitude, but numbers of groups did not show the same trend. A significant decline in number of groups was found only in the alpine tundra zone.

The Acarina, Collembola and Nematoda are widely distributed and are the dominant groups in all the zones. A study of mite distribution carried out in June 1983 and 1984 revealed that the highest number of species was recorded in the broadleaved/*Pinus* (pine) forest. A mathematical analysis showed that this high number coincided with the highest diversity index and evenness degree (Table 1), suggesting that the broadleaved/*Pinus* ecosystem provides an optimal habitat, with varied food sources. Apart from the broadleaved forest, number of species and number of individuals increased with increasing altitude, with the highest individual number of soil animals occurring in the alpine tundra zone (Yang & Ma 1983), in spite of the generally unfavourable climatic conditions.

Table 1. Diversity index and evenness degree of mites in the 4 sample plots (June 1983 & 1984)

	Species number	Individual number m^{-2}	Simpson's diversity index	Index of evenness degree
Pinus densiflora var. *sylvestriformis* forest (690 m)	80	13 398	18.8	0.23
Broadleaved/*Pinus koraiensis* forest (740 m)	119	6 170	42.2	0.37
Coniferous forest (1380 m)	93	14 695	14.9	0.15
Alpine tundra (2100 m)	105	15 287	25.7	0.21

Generally speaking, soil animal diversity gradients down the profile tend to exhibit a significant decline, as do the number of individuals with increasing depth from the top of the A_{00} or A_0 layer. In broadleaved/*Pinus* forest and in *Betula* (birch) forest, the maximum number of groups and individuals occurs in the A_0 layer, while in the deciduous coniferous forest and in alpine tundra it occurs in the A_{00} layer (Figure 2). Except for Annelida, only the Collembola of micro-arthropods can move to the B layer of the soil profile.

A micromorphological study of the soil habitat in the broadleaved/*Pinus* forest showed that the micro-structures can be examined in detail from the litter layer down to the humus horizon. The most complex micro-environment occurs just above the interface between the A_0 and humus layers (A_1). In this area, deposits of fragmented litter and indigestible remains of droppings constitute a spongiform microstructure with numerous biopores, providing varied, favourable, microhabitats. Below the A_{00} layer, which acts as a buffer, the A_0 layer retains a more stable temperature regime and the highest water content throughout the whole year (Zhang & Chen 1981). There is a fair correlation between variation in water content and the soil animal population in the soil profile (Figure 3).

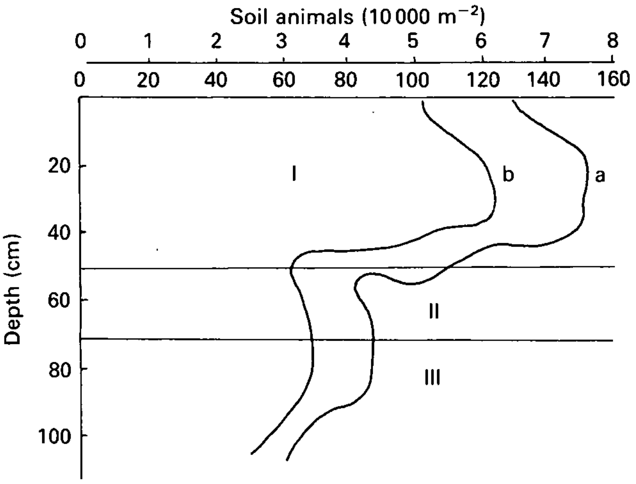

*Figure 3. Vertical changes in soil animal numbers correlated with water content and temperature regime in the soil profile of the broadleaved/*Pinus *forest*
(a = water content; b = number of soil animals
I = freezing layer; II = transitive layer; III = unfreezing layer)

At a local scale, a study (Zhang & Chen 1981) of the ecological distribution of Annelida in the broadleaved/*Pinus* forest was carried out. Three typical sites were selected for study, ie a sunny slope with deciduous trees, a shadowy slope with mixed trees, and a flat area of grass and shrubs with gradual changes in ecological condition. The records of collecting, hand sorting and mapping the species' occurrence show that the different sites with different soil temperature and water content regimes and food materials have a considerable role to play in the ecological distribution of earthworms. Each land form site was inhabited by all 3 species, but each species showed different densities in the different sites (Table 2; Figure 4). Within a site, a more uniform habitat generally carries a population with an irregular distribution, as reported by western colleagues (Satchell 1958). Our mapping records, however, reveal that sites with dense plant roots, and a high water content, appear to be more popular with adultoids, while sites with less water content are favoured by adults.

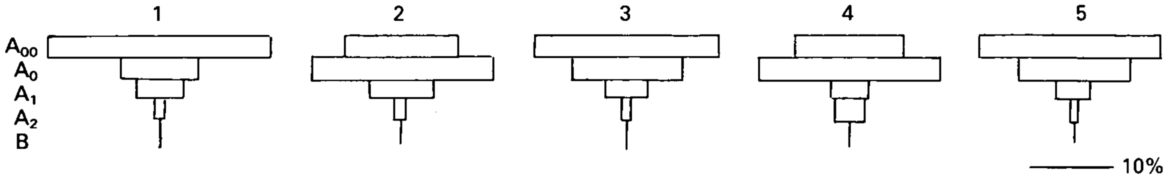

Figure 2. Percentage of soil animal numbers in the soil profiles of each vegetational zone on the northern slope of Changbai Mountain
*(1 = deciduous forest; 2 = broadleaved/*Pinus *forest; 3 = coniferous forest; 4 =* Betula *forest; 5 = alpine tundra)*

Table 2. Population of earthworms in broadleaved/*Pinus* forest (sampled within 1 m × 20 m)

	Mixed forest		Grassland in gully		Deciduous forest		Total	
	Number	Density m^{-2}	Number	Density m^{-2}	Number	Density m^{-2}	Number	Density m^{-2}
Drawida gisti	86	4.3	22	1.1	15	0.8	123	6.2
Pheretima sp.	23	1.4	67	3.4	6	0.3	101	5.1
Eisenia rosea	3	0.2	54	2.7	26	1.3	83	4.2
Total	117	5.9	143	7.2	47	2.4	307	15.4

4 Experiment in litter disappearance

An exclusion experiment was set up in the broadleaved/*Pinus* forest and in a *Populus* (poplar) woodland to study the disappearance of litter. For comparison, 3 sites were selected: (i) dominated by *Pinus koraiensis* Sieb. et Zucc. (Korean pine), (ii) dominated by *Fraxinus mandshurica* Rupr. (Manchurian ash), and (iii) dominated by *Populus davidiana* Dode (Chinese aspen). Litter samples were collected at the beginning of October, soon after the end of litterfall. Two types of litter were chosen: single leaves of the 3 dominant trees, which were placed in separate bags, and mixed leaves selected from the litter layer. The natural percentage of different leaves was determined from random samples and used as a standard for sampling square quadrats. The samples were placed in 160 nylon bags of different mesh size. Each sample weighed 10 g when fresh, and was weighed again when dry, after the action of soil animals, to calculate the standard correlation. The separate bags were half-buried under natural litter on the F layer for 1, 2 and 3 years respectively. The bags were made of the following mesh sizes, which only allowed certain organisms to enter.

10 mm	All micro-organisms and invertebrates, including earthworms
1 mm	All micro-organisms and invertebrates, except earthworms
0.2 mm	Only micro-organisms, small mites and springtails, enchytraeids and other small invertebrates
0.005 mm	Very small micro-organisms, including invertebrates
0.005 mm	(with naphthalene) in an attempt to exclude all soil animals.

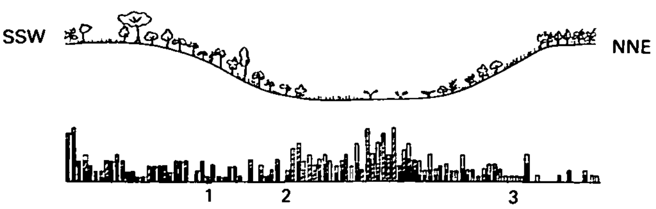

*Figure 4. Ecological distribution of earthworms in the broadleaved/*Pinus *forest (1 m × 20 m)*
(1 = Drawida *sp.; 2 =* Pheretima *sp.; 3 =* Eisenia rosea*)*

This experiment was used as a basis for estimating the contribution of soil fauna to decomposition in the different environments selected. The disappearance of litter in the bags can be considered a result of decomposing action by each entire group of soil invertebrates associated with microbial activities. The bags with 10 mm mesh represent equivalent conditions in the natural environment. This method has been widely used by soil zoologists and botanists. We are trying to determine the successive occurrence of soil animals in litter placed in the bags at different periods of time.

After one year, the preliminary results show that the litter in the bags lost weights ranging from 31% to 66%. The soil animals present in the litter of the bags have been extracted, and the results are summarized in Figure 5. In general, a higher number of animals were found in the mixed samples set at sites (i) and (ii) in the broadleaved/*Pinus* forest, presumably because those sites most closely resembled natural litter. The greatest number of nematodes among the groups collected in the bags may indicate that this group plays a significant role in decomposition during the first year.

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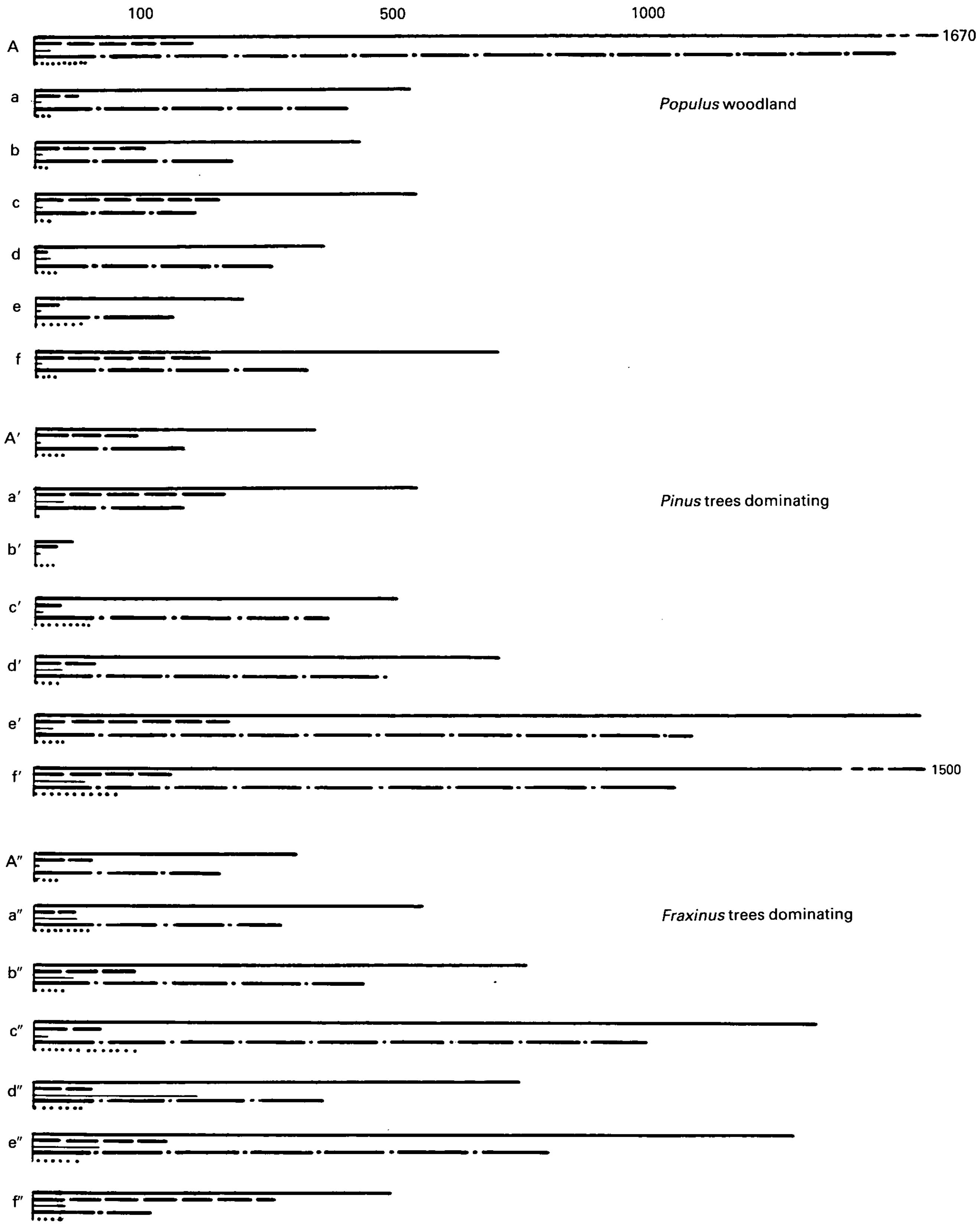

Figure 5. The individual numbers of dominant groups of soil animals extracted from the bags semi-buried (1984–85) and natural litter
(A,A′A″ from natural litter;
a,b,c from Pinus koraiensis *litter;*
a′,b′,c′ from Fraxinus mandshurica *litter;*
a″,b″,c″ from Populus davidiana *litter;*
d,e,f from mixed litter
a,d mesh size 2 mm; b,e 1.0 mm; c,f 10 mm)

━━━ *Total number*
— — *Acarina*
─── *Collembola*
—·— *Nematoda*
········· *Others*

The family Parholaspidae (Acarina, Mesostigmata) in Japan

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1 Introduction

The family Parholaspidae is commonly found in free-living soil mesostigmatid mites in the temperate forests of Japan. The members feed on nematodes and collembolans, and it is generally accepted that they play an important role in the forest ecosystem. In this paper, the ecology of the family Parholaspidae in Japan is described.

2 Materials and methods

Samples of litter, humus and/or soil containing mites were brought back to the laboratory in cotton bags. The mites were extracted from the samples using Tullgren apparatus.

3 Distribution

Examining about 3000 specimens collected at 600 different localities all over the Japanese islands, the author has concluded that 27 species, belonging to 7 genera, exist in Japan (Table 1). The genus *Parholaspulus*, the largest of the parholaspid genera, is widely distributed in England, Germany, eastern Europe, east Siberia, Japan, North Vietnam, Malaysia and North America. The number of known species is largest in east Siberia and Japan. Present knowledge suggests that all the species recorded from Japan, with the exception of *P. alstoni* Evans, are endemic to the Japanese islands and have a strong affinity to the east Siberian fauna.

The genus *Gamasholaspis* is recorded from east Siberia and Japan, and also from Malaysia. Of the 6 Japanese representatives, *G. browningi* (Bregetova et Koroleva), *G. communis* Petrova and *G. asiaticus* Petrova are common to east Siberia, and the remainder are endemic to Japan.

The genus *Euparholaspulus* contains only one species, *E. primoris* Petrova, which occurs in both east Siberia and Japan.

The genus *Neparholaspis* is widely distributed, and it is interesting that 2 Japanese representatives have a closer affinity to the North American *N. evansi* Krantz, than to the east Siberian species.

Parholaspis is a small genus, containing 2 described species from Japan and one species each from Singapore, east Siberia and England. Of the 2 Japanese species, *P. mordax* Petrova occurs also in Sakhalin, while *P. meridionalis* Ishikawa is endemic to Japan; both species have a strong resemblance to *P. desertus* Berlese of Singapore. This genus is believed to have originated in tropical Asia.

Table 1. Distribution of Parholaspidae in Japan

Species	Hokkaido	Honshu	Shikoku	Kyushu
Parholaspulus ochraceus	+	+	+	+
P. trifurcatus	+	+	+	+
P. dentatus	+	+	+	+
P. shigaensis	−	+	+	−
P. alstoni	−	+	+	−
P. communis	+	+	+	−
P. arboreus	−	+	+	−
P. extremiorientalis	−	+	+	−
P. marinus	−	−	+	−
P. yakushimaensis	−	−	−	+
Proparholaspulus suzukii	+	−	+	+
Gamasholaspis akimotoi	+	+	+	−
G. browningi	+	+	+	+
G. asiaticus	−	+	+	+
G. communis	−	+	−	+
G. pygmaeus	−	−	+	−
G. serratus	−	+	+	+
Neparholaspis monticola	+	+	+	+
N. shinanonis	−	+	−	−
N. serratichela	−	+	+	+
Parholaspis mordax	+	+	+	+
P. meridionalis	−	−	+	+
Euparholaspulus primoris	−	+	+	+
Holaspulus tweediei	−	+	+	+
H. tenuipes	−	+	+	−
H. serratus	−	−	+	+
Number of species	9	20	23	16

The genus *Proparholaspulus* contains 2 species: *P. suzukii* Ishikawa from Japan, and *P. pasohensis* Ishikawa from Malaysia.

Holaspulus is a small genus which may be regarded as of southern origin.

None of the parholaspid genera hitherto known are endemic to the Japanese islands, whereas 19 of the 27 species recorded from the same region, or 70.3% of the known species, are restricted to the island country.

4 Quantitative investigations of mesostigmatid mites

In order to study the density and composition of the mesostigmatid mites in Japan, 5 different areas were intensively surveyed during the years 1969–71. These areas are as follows:

1. Mt Daisetsu (Hokkaido) – 700–1800 m above sea level (asl)
   Vegetation: *Tsuga diversifolia* (Maxim.) Mast.

(northern Japanese hemlock), *Abies mariesii* Mast. (Maries' fir), *Betula ermanii* Cham. (Erman's birch).

2. Mt Shigayama (Nagano Prefecture) – 1650–1750 m asl
   Vegetation: *Tsuga diversifolia*, *Abies mariesii*, *Betula ermanii*, etc.

3. Mt Ishizuchi (Shikoku) – 800–1980 m asl
   Vegetation: *Abies veitchii* var. *shikokiana* Lindl. (Veitch's silver fir), *Betula ermanii*, *Fagus crenata* Blume (Japanese beech), *Tsuga sieboldii* Carr. (Japanese hemlock), *Abies firma* Sieb. et Zucc. (Japanese fir), etc.

4. Yanase national forest (Shikoku) – 800–1200 m asl
   Vegetation: *Castanopsis cuspidata* (Thunb.) Schottky (pasania), *Cryptomeria japonica* D. Don (Japanese cedar), *Tsuga sieboldii*, etc.

5. Mt Kirishima (Kyushu) – 1000–1650 m asl
   Vegetation: *Pinus densiflora* Sieb. et Zucc. (Japanese red pine), *Fagus crenata*, *Quercus mongolica* var. *grosseserrata* Rehd. et Wils. (Japanese oak), etc.

Nineteen families of mesostigmatid mites are known to occur in Japan. The total number of mites from all the areas surveyed amounted to 24 717 individuals per metre square. Of the 19 mesostigmatid families, the largest individual number m^{-2} belonged to Parholaspidae – 6636 m^{-2} (26.8%), followed by Rhodacaridae – 3563 m^{-2} (14.4%), Uropodidae – 2845 m^{-2} (11.5%), Zerconidae – 2632 m^{-2} (10.6%), and Parasitidae – 2467 m^{-2} (10.0%). Therefore, the Parholaspidae are seen to be a distinctly predominant group among the mesostigmatid families.

Within the Parholaspidae, individual numbers per metre square varied according to the different areas. The largest number was found in Mt Ishizuchi – 2413 m^{-2}, followed by Mt Kirishima – 1556 m^{-2}. Thus, the number found on Mt Ishizuchi was 10 times than on Mt Daisetsu.

5 Behaviour

5.1 Life history

The life history of mites was studied using *Parholaspulus ochraceus* as an example.

5.1.1 Egg: the egg is oval in shape (352 μ × 258 μ), with a smooth surface, and is pearly white in colour.

5.1.2 Larva: the larvae are milky white in colour, have a soft body surface, and are slow in movement; the dorsal shield is 365 μ long and 237 μ wide.

5.1.3 Protonymph: just after casting off the skin, the protonymph is semi-transparent and soft on the surface of its body. It gradually begins to move and feed.

5.1.4 Deutonymph: the dorsal shield is slightly sclerotized; the dorsum measures 750 μ × 530 μ.

5.2 Predation

The mites' sensory setae, which are well developed at the tops of the tarsi I, feel for the nematodes or micro-arthropods in the soil, and they then catch them

Table 2. Individual number of the family level of mesostigmatid mites collected from 5 areas in Japan (number m^{-2})

Families	Mt Daisetsu		Mt Shigayama		Mt Ishizuchi		Yanase		Mt Kirishima		Total	
		%		%		%		%		%		%
Parholaspidae	257	15.7	1370	36.7	2413	40.9	1040	37.1	1556	14.6	6636	26.8
Rhodacaridae	539	33.0	360	9.7	582	9.9	710	25.4	1372	12.9	3563	14.4
Zerconidae	279	17.1	320	8.6	469	8.0	230	8.2	1334	12.4	2632	10.7
Uropodidae	136	8.3	20	0.5	232	3.9	330	11.8	2127	20.0	2845	11.5
Parasitidae	46	2.8	760	20.4	523	8.9	250	8.9	888	8.3	2467	10.0
Ascidae	89	5.4	280	7.5	792	13.4	20	0.7	842	7.9	2023	8.2
Veigaiidae	164	10.0	110	2.9	223	3.8	100	3.6	521	4.9	1118	4.5
Digamasellidae	14	0.9			137	2.3			1605	15.1	1756	7.1
Neoparasitidae	28	1.7	100	2.7	200	3.4	110	3.9	225	2.1	663	2.7
Polyaspidae	39	2.4	290	7.8							329	1.3
Pachylaelapidae	25	1.5			209	3.5	10	0.4	21	0.2	265	1.1
Macrochelidae	4	0.3	100	2.7	86	1.5			46	0.4	236	1.0
Trachytidae	14	0.9	20	0.5							34	0.1
Phytoseiidae					18	0.3			67	0.6	85	0.3
Podocinidae					5	0.1			13	0.1	18	0.1
Epicriidae					5	0.1					5	0.02
Laelaptidae									17	0.2	17	0.07
Eviphididae									17	0.2	17	0.07
Eutrachytidae									8	0.1	8	0.04
Total	1634		3730		5894		2800		10651		24717	

by stretching the chelicerae beyond the tops of the pedipalps. The fixed digit of each chelicera has a *pilus dentilis*, and, although the chemical component of the secretion from the *pilus dentilis* is not yet known, it is sufficiently strong to paralyse the micro-animals. The parholaspid mites hold their prey with the chelicerae, then penetrate them with their mouth parts and suck up the prey's body fluid.

5.3 Natural enemies

Pseudoscorpiones are the only natural enemies of the parholaspid mites, so far as is known. Small pieces of dorsal shield and legs of parholaspid mites were seen under the microscope in the intestines of some symphylans and lithobiomorphs.

Soil pseudoscorpions in the cool temperate forests of Japan

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Abstract
The structure of Pseudoscorpiones communities was investigated in the cool temperate forests of Japan. The number of *Mundochthonius japonicus* Chamberlin increased in proportion to development of the forest (from young secondary to natural), although the value of the β-index of diversity in the natural forests was lower than in the secondary forests.

1 Introduction

As stressed by Sato (1984), pseudoscorpions are one of the important groups of soil fauna in the cool temperate forests of Japan. Their density sometimes exceeds 1500 individuals per metre square in climax forests, ie 1648 m^{-2} at Mt Takao (Sato 1984), but lower densities are often found in the other types of forest. The aim of this study is to provide basic information on the population density and species composition under various types of forests (particularly secondary and natural forests).

2 Method

The study was carried out in 8 cool temperate forests, which were classified into 3 types, namely young secondary forests, mature secondary forests, and natural forests, ranging in altitude from 500 m to 1500 m above sea level. Sampling periods and environmental information are shown in Table 1. Between 4 and 8 samples of litter and humus (each of 4 l) were collected monthly at each site, the size of each sample varying between 400 cm^2 and 625 cm^2. The animals were extracted using a modified Tullgren funnel of 50 cm diameter, and were preserved in 70% alcohol. Heat was supplied by a 60-W bulb above the funnel, and the samples were kept warm for 4 days. Only pseudoscorpions were selected for examination under the microscope.

3 Results

3.1 General information

A total of 21 213 individuals (9 species belonging to 5 genera of 2 families) was collected from 8 sites during the study. The numbers of individuals and species are given in Table 2. The mean population density was 1034 ± 699 per 100 l (range 244 in KZ — 2503 in TB), but no significant relationship was found between altitude and pseudoscorpion density. The number of species found at the various sites were in the following order:

Marukawa-toge (8) = Sakeishi (8) > Saiki-rindo (7) > Yanagisawa-toge (6) > Ohgi-yama (5) = Karuizawa (5) = Takao-A (5) = Takao-B (5)

No relationship was found between altitude and number of species, but densities varied with the different forest types, more numbers of pseudoscorpions being found in the natural forests than in the young secondary forests (Table 2).

3.2 Species composition

The individual numbers of animals found per 100 l soil collected during the sampling period are shown at

Table 1. Environmental information and sampling periods at the 8 sites

Sampling station	Altitude (m)	Forest type	Vegetation	Sampling period
Marukawa-toge (MK)	1500	Natural	*Fagus crenata*	May–December 1983 April 1984
Yanagisawa-toge (YS)	1500	Mature	*Fagus crenata* *Quercus crispula*	June 1983–January 1984 May 1984
Saiki-rindo (SR)	1500	Mature	*Quercus crispula*	June 1983–January 1984 May 1984
Karuizawa (KZ)	1000	Secondary	*Quercus crispula* *Pinus densiflora*	April–December 1978
Sakeishi (SI)	1000	Mature	*Fagus crenata* *Bonzoin leptolepis*	May–December 1983 May 1984
Ohgi-yama (OY)	1000	Secondary	*Fagus crenata* *Quercus crispula*	June 1984–January 1985
Takao-A (TA)	500	Natural	*Fagus japonica* *Prunus dorarium* *Abies firma*	February 1978–January 1979
Takao-B (TB)	500	Natural	*Fagus japonica* *Prunus dorarium*	June 1983–May 1984

species level in Table 2. Species with individual numbers of more than 10% of the total for each site were as follows:

Marukawa-toge (MK)	
Mundochthonius japonicus	87%
Yanagisawa-toge (YS)	
M. japonicus	58%
Microcreagris pygmaea Ellingsen	25%
Allochthonius opticus (Ellingsen) Morikawa	11%
Saiki-rindo (SR)	
M. japonicus	82%
A. opticus	10%
Karuizawa (KZ)	
A. opticus	54%
M. japonicus	27%
Roncus japonicus (Ellingsen) Morikawa	16%
Sakeishi (SI)	
M. japonicus	55%
Neobisium anagamidensis Morikawa	18%
A. opticus	10%
Ohgi-yama (OY)	
Microcreagris japonica Ellingsen	49%
A. opticus	38%
Takao-A (TA)	
M. japonicus	87%
Takao-B (TB)	
M. japonicus	82%

Consequently, *Mundochthonius japonicus* was seen to be dominant in all the sites studied, except Ohgi-yama (OY). This species accounted for more than 80% of the total in 3 natural forests and one mature forest, but less than 50% in the young secondary forests. From this evidence, it may be concluded that *M. japonicus* increases as the forest grows older and reaches its climax.

3.3 Diversity

The complexity of the animal community is expressed using the β-index of Morishita (1967) in the following formula:

$$\beta = \frac{(\Sigma n_i - 1)\Sigma n_i}{\Sigma n_i\,(n_i - 1)}$$

where n_i is the number of individuals of species i. When the number of species is low in relation to the number of individuals, β is low, and *vice versa*. From the index value in Table 2, it is clear that the values of complexity increase in the secondary forests.

4 Discussion

In general, the life of Pseudoscorpiones, which are carnivorous animals, may not be affected by vegetation types, although *M. japonicus* prefers a mature soil environment, consisting of deep leaf litter and thick humus, to a young unstable soil which is easily affected by wind and flowing water (Sato 1980). In contrast, the densities of the other Pseudoscorpiones species are not influenced by the forest types (secondary or natural). In the natural forests, the pseudoscorpion fauna shows a high density of *M. japonicus* and a low value of the β-index. Figure 1 shows the percentage of *M. japonicus* and the β-index at the 8 sampling sites. Three distinct types of fauna are evident:

Type 1. *M. japonicus* comprises over 80% in number and the β-index is below 1.5 (TA, TB, MK and SR)

Type 2. *M. japonicus* attains 50–60% in number and the β-index is 2–3 (YS and SI).

Type 3. *M. japonica* attains less than 30% and the β-index is 2–3 (KZ and OY).

Table 2. Density, species number and β-index of Pseudoscorpiones communities at the 8 sampling sites

			Number 100 l⁻¹ soil sample									
Station	Mean no. 100 l⁻¹ soil per month	Species no.	*Microcreagris pygmaea*	*Microcreagris macropalpus*	*Microcreagris japonica*	*Neobisium anagamidensis*	*Neobisium pygmaeum*	*Roncus japonicus*	*Allochthonius opticus*	*Mundochthonius japonicus*	*Tyrannochthonius japonicus*	β-index
MK	1614.4 ± 1291.0	8	52.0	1.0	34.4	2.9	5.8	31.1	96.0	1412.9	0	1.36
YS	1118.9 ± 540.6	6	284.8	0	0	48.4	11.8	4.0	125.9	644.0	0	2.44
SR	1350.3 ± 717.0	7	20.3	0	0.6	56.4	28.4	2.8	134.4	1106.8	0	1.45
KZ	244.1 ± 133.4	5	0	0.8	0	0	6.0	40.1	131.3	66.3	0	2.57
SI	355.0 ± 199.6	8	18.6	20.1	2.3	62.7	1.4	8.4	35.3	194.9	0	2.85
OY	318.4 ± 289.2	5	0	0	156.2	0	4.4	7.4	121.1	28.9	0	2.53
TA	1216.0 ± 663.2	5	0	0	85.7	0	5.3	0	40.8	1056.2	27.7	1.31
TB	2503.0 ± 1069.2	5	0	0	196.7	0	12.9	0	194.8	2043.3	55.6	1.47

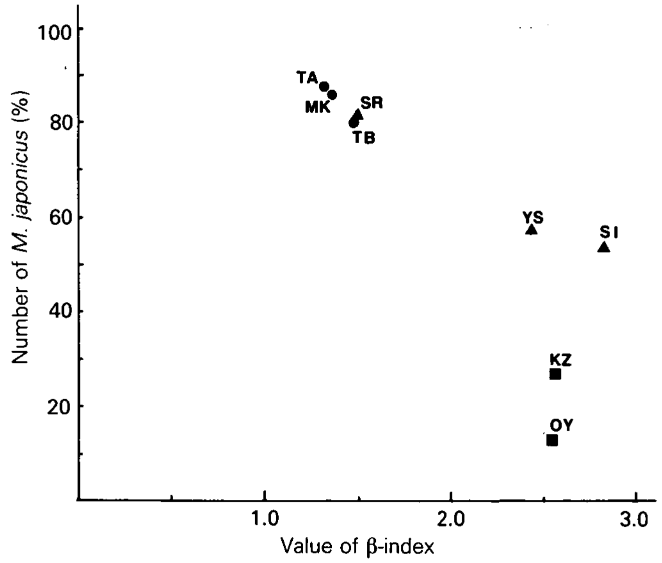

Figure 1. The relationship between number of M. japonicus *and the β-index at the 8 sample sites (● natural forest; ▲ mature secondary; ■ young secondary forest)*

Types 1, 2 and 3 correspond to the natural, mature and young secondary forests, respectively. One exception, Saiki (SR), a site in a mature forest, fell into Type 1. The soil environment of this site appears very old and has a thick layer of litter and humus which resembles that of a natural forest.

5 Acknowledgement

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The role of herbivores in forest ecosystems: the case for Biosphere Reserves

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Abstract
Defoliating herbivores in forest ecosystems can cause considerable alteration in system function, but this natural impact is seldom studied and is little known. Direct and indirect effects are known to govern productivity and watershed behaviour of various elements in biogeochemical cycles.

Impacts of herbivores are non-linear, and they can therefore contribute a considerable source of variation to forest watershed production and nitrogen cycles, for example. If this source of variability approaches the levels known to be contributed by grassland grazers, the cause and effect relationships in Biosphere Reserves, which have been set aside for determining anthropogenic effects in the landscape, remain in considerable doubt. It will not be until levels of herbivory and their effects are fully known that this uncertainty can be adequately described.

1 *Introduction*

Herbivory, the process of animals consuming live plant tissue, and its associated processes are considered among the most important ecological subjects. In the past decade, studies have resulted in an explosion of information about herbivores and plants (cf Gilbert & Raven 1975; Harper 1977; Crawley 1983; Wallace & Mansell 1976; Denno & McClure 1983; Hopkinson & Hughes 1982; Mitton & Sturgeon 1982; Rosenthal & Janzen 1979). Scores of papers are presented that, in turn, summarize hundreds of others about genetics, phytochemistry, plant and animal population biology, and evolutionary aspects of the associates, as well as information on feedbacks and regulating mechanisms that herbivores and plant communities impose on one another in large-scale ecosystems and landscapes (eg Sinclair & Norton-Griffiths 1979; Estes *et al.* 1982; Lowrance *et al.* 1984). These latter reports on whole-system problems are relatively scarce in relation to the earlier cited reports on autecological relationships. Thus, it is my intent to examine herbivory in the larger context, specifically in relation to a temperate forest ecosystem such as at Coweeta Hydrologic Laboratory in North Carolina, USA, where much of the work on herbivore/community impacts is being conducted (Seastedt & Crossley 1984; D A Crossley, pers. comm.). The work at Coweeta serves an an example for other Biosphere Reserves, such as Changbai Mountain, the subject of this Symposium.

By 'larger context' in herbivorous events, I specifically mean ecosystem research conducted on a watershed- or catchment-sized landscape unit, rather than on individual organisms. The main focus will be on processes known to regulate carbon and nutrient interactions, and on the dynamics of water flow, which acts as an integrator of ecosystem response to varying levels of herbivory in the watershed.

1.1 Effects of insect defoliation on forest ecosystem dynamics

Swank *et al.* (1981) have reported how herbivory can change ecosystem behaviour during an insect outbreak. *Alsophila pometaria* Harris (fall cankerworm) invaded at least 2 high-elevation watersheds at Coweeta Hydrologic Laboratory in outbreak conditions in the early to mid-1970s. (Coweeta is one of the oldest US Department of Agriculture Forest Service research sites and is both a National Science Foundation long-term ecological research site and a Biosphere Reserve.) One of the first responses noted was an increase in NO_3-N in streamwater chemistry at weirs measuring watershed behaviour. Process-level research conducted at that time did not link the defoliation with the hydrologic events precisely, but there was sufficient evidence to suggest indirect effects. Swank *et al.* (1981) concluded that it was highly likely that the cankerworm defoliation of the canopy set in place a series of events which eventually resulted in changes in streamwater chemistry, as mediated through intervening biogeochemical processes.

Changes in several other ecosystem processes were also reported by Swank *et al.* (1981). At the outset of the outbreak, there was increased leaf-fall, which was followed by an increase in leaf production associated with a decrease in wood production. There were large inputs of frass and contained elements to the forest floor, increases in soil metabolism (CO_2 efflux), increases in standing crops of soil microbial populations (ATP measures), and increased levels of nitrifying bacteria (MPN). Overall, there were increases in above-ground net primary production (NPP) and nutrient cycling rates, resulting in significant increases in mineral nitrogen in the upper soil horizons, all synchronized with the period of cankerworm feeding in the canopy.

A more recent study on infestations of *Dendroctonus ponderosae* Hopkins (mountain pine beetle), in the Front Range of Colorado, serves as a second example (Kovacic 1983; Kovacic & Dyer, unpublished). These workers found that total soluble organic N (NO_2, NO_3 and NH_4 fractions) increased on the forest floor for 2 years following beetle attack, after which levels dropped to below pre-attack conditions. Soil fractions showed a considerable lag effect, nearly doubling over a 4- to 5-year period, then returning to pre-infestation levels in 8- to 10-year-old sites. The data also suggest a complex series of ecosystem processes following a major biotic influence. This ecosystem behaviour appears to be much different from that recorded for physical perturbation, such as fire or clearcutting, and lends support to hypotheses proposed by Mattson and Addy (1975). They proposed that forest insects are not always detrimental, as they might seem to be initially, and suggested that herbivores and plants interact to influence critical community or ecosystem processes, thus developing a variety of system feedbacks which would not ordinarily exist.

Such feedbacks have been discussed by Owen and Wiegert (1976, 1981), Petelle (1982) and others, who hypothesized that sap-feeding insects cause increases in nutrient-rich throughfall in the canopy. This theme was picked up at Coweeta later by Seastedt and Crossley (1984) for defoliators. In a theoretical model, Dyer *et al.* (1986) show how nutrients and biomass can interact to optimize the rate at which recycling occurs. This idea has been introduced as the herbivore optimization hypothesis in grassland ecosystems by McNaughton (1979) (Figure 1) (see also Hilbert *et al.* 1981), but it is not known whether this phenomenon applies to forest ecosystems, even though some workers suggest it may (see Mattson & Addy 1975). Thus, because of these multi-faceted responses in any ecosystem, it is necessary to know, first, the degree of herbivory, and then the system's response, eg whether it is monotonic or non-linear, in respect to various herbivory levels. These responses have been documented for native grasslands and graminoid agricultural cultivars (McNaughton 1979; Dyer 1975; Dyer *et al.* 1982; Coppock *et al.* 1983), but not for forests.

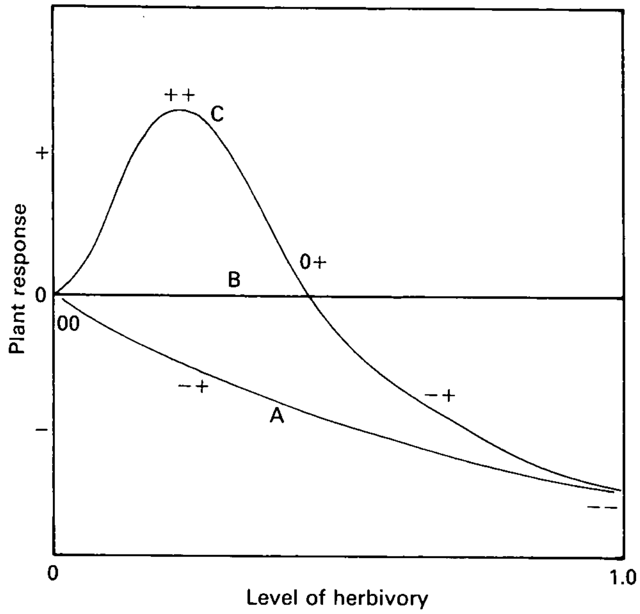

Figure 1. The herbivore optimization curve or hypothesis' (source: McNaughton 1979; Hilbert et al. *1981). Three potential responses are presented which depend upon the type of response that the plant, or the entire community, may exhibit after being eaten by herbivores:*

A a monotonically decreasing level of productivity at the outset of herbivory
B a curve traced from 00 to 0+, where it then becomes −+ and eventually − − in extreme herbivory
C a curve traced from 00 to ++, after which it then follows the curve noted by hypothesis B

Note that both hypotheses B and C involve compensatory growth of the individual plant or those within the community, as a function of increasing herbivory for at least part of the overall response: hypothesis B involves compensatory growth accounting for lost tissue, hypothesis C suggests over-compensation for part of the reaction

As there is evidence that herbivory may have significant direct negative or positive effects on plants, significant indirect effects should be expected elsewhere in the system (Wiegert & Kozlowski 1984). Changes in reduction of litter, rates at which microbial populations can decompose organic material, rates at which these fractions re-enter biotic elements of the community through nutrient uptake, and loss of elements in groundwater are all examples of such indirect effects. Few of these processes have been investigated in sufficient detail to predict what might happen during and after herbivory in any ecosystem, a point emphasized by Wiegert and Kozlowski (1984) in their discussion on indirect causality.

Finally, because intense defoliation is often fatal to individual trees, one important physiological and population-oriented response that must be considered is the degree to which plants may develop protection from intense defoliation. A large number of herbivore defence strategies has been identified in the reports cited earlier (cf Wallace & Mansell 1976; Rosenthal & Janzen 1979; Rhoades 1983a,b; Baldwin & Schultz 1983). The evolutionary consequences of natural selection in secondary compounds, which tend to regulate the herbivore load on a particular plant species in time and space, is widely accepted (Rhoades 1985). However, what is not known is the degree to which herbivore-induced defences detract from tree or plant growth (Mooney & Gulmon 1982), and thus from community dynamics, as production of these compounds is quite expensive of energy and nutrients (Gulmon & Mooney 1985).

1.2 Hierarchical association and analysis of herbivory effects

Allen and Starr (1982) point out that problems in ecology have an inherent hierarchical nature, in that there are several levels of resolution that can be invoked to explain events observed in every study. For instance, with herbivory, it is not always clear what the total effects are on an individual plant, beyond the obvious direct effect of loss of leaves. One must ask the following questions. Is the plant's entire physiology affected? Are reproduction, growth, survival and other important processes equally affected? At what scales of space and time are these processes affected? Therefore, one must first determine the processes being perturbed in this hierarchical association; then, it is necessary to study the limits of response for each process; and, finally, relevant spatial and temporal scales must be determined. For instance, some processes are linearly associated with their environmental controls, such as photosynthetic activity, which may be closely correlated with canopy light levels (to the point of saturation), which, in turn, may be markedly altered by defoliation. Other processes behave in a non-linear fashion. For example, the effects of growth regulators in animal saliva on plant growth are dose-dependent, but non-monotonic (Dyer 1980, unpublished). An example on another scale is the one cited earlier, where increased quantities of NO_3-N flowed out of a watershed as a result of moderate insect defoliation. As it is unlikely that the insects were directly responsible for releasing this amount of NO_3-N, an indirect amplification was involved. An unknown series of interacting processes in the hierarchy of physical and biotic associations in the watershed was apparently involved. This example shows the complex nature of direct and indirect interactions, and indicates that it is not always easy to determine which system responses should be judged appropriate for a series of natural events or experiments.

Allen *et al.* (1984) address this problem in detail. Once the processes are identified, they must then be organized according to their hierarchical positions within the problem to determine multi-level responses. If whole-system function is to be understood from studying the dynamics of the parts, the correct observations must be made for each level of the study. The lesson for studies of herbivory effects in communities lies in ensuring that, when a defoliator consumes a leaf, we can relate direct results to the plant's new physiological behaviour which develops as a function of the herbivorous event. Then, it is necessary to understand local events and to link them to higher-order processes in order to understand indirect events in the immediate vicinity, and so on through the watershed. If only a few leaves above nominal herbivory, or if even only a few trees on the affected watersheds at Coweeta, had been affected by cankerworms, or if there had been no mechanism to link the flow of nutrients to streamwater, the efflux of nitrogen at the weir would not have been observed.

2 Models and concepts

2.1 Herbivore function in forest succession models

Insects have a pronounced role in forest dynamics and succession (Schowalter 1981, 1985). Wood-boring species, such as *Dendroctonus frontalis* Zimmerman (southern pine beetle) (Schowalter *et al.* 1981a), oligophagous leaf-eating species, such as *Lymantria dispar* L. (gypsy moth), and other species which can have intense effects at both local and regional levels can affect patterns and processes of vegetation distribution over landscapes. Thus, it is of prime importance to include insect herbivores in forest succession studies. However, by definition, forest succession means long-term study or measurement. Shugart (1984) summarizes current information about forest succession, but little is provided about herbivores, mostly because much less is known about such biotic effects. Therefore, if one is to examine the influence of herbivory on forest succession, a long-term element is needed in the overall study, both for determining nominal or background levels of herbivory, as well as for outbreak conditions. Logically, this requirement produces a problem, as most studies have not been designed to detect long-term outcomes. One approach has been to turn to computer simulation studies. The JABOWA and FORET community-level simulation models have been developed and used extensively for studies on succession (Shugart 1984). However, in neither modelling paradigm are herbivores structured explicitly. How, then, can such models represent long-term successional conditions if, indeed, herbivores are so important? The answer can only lie in reformulating our approaches to studies of the effects of herbivory.

2.2 The watershed conceptual model

In abbreviated form, key state variables and their linking processes are shown in Figure 2 for plant/herbivore related events in a generalized temperate forest (after Seastedt & Crossley 1984).

A large variety of herbivores resides in the canopy throughout the growing season, and comprises the basis for a complex food web. The trees and herbivores provide litter, throughfall to surface water, frass and arthropod remains to the forest floor, all of which enter the below-ground components. Litter, frass and arthropod remains are decomposed by a detritivore food web, including a microbial population. As a result of this decomposition, CO_2 is evolved to the atmosphere and nutrients are made available to a soil pool for incorporation by plant roots and re-entry into the decomposition cycle. Alternatively, nutrients are solubilized in soil water and subsequently leach to streams, eventually flowing out of the watershed.

2.3 Processes linking state variables on watershed

Many processes link the state variables, and 22 of the more ecologically important ones are shown in Figure 2 and Table 1. As depicted, above-ground interception, transpiration, translocation and stemflow governing events in the tree canopy are driven, in part, by the defoliation and feedback from the herbivores. Materials entering the below-ground part of the system are regulated by throughfall, leaf-fall, and excretion or death of canopy arthropods. At various times, surface

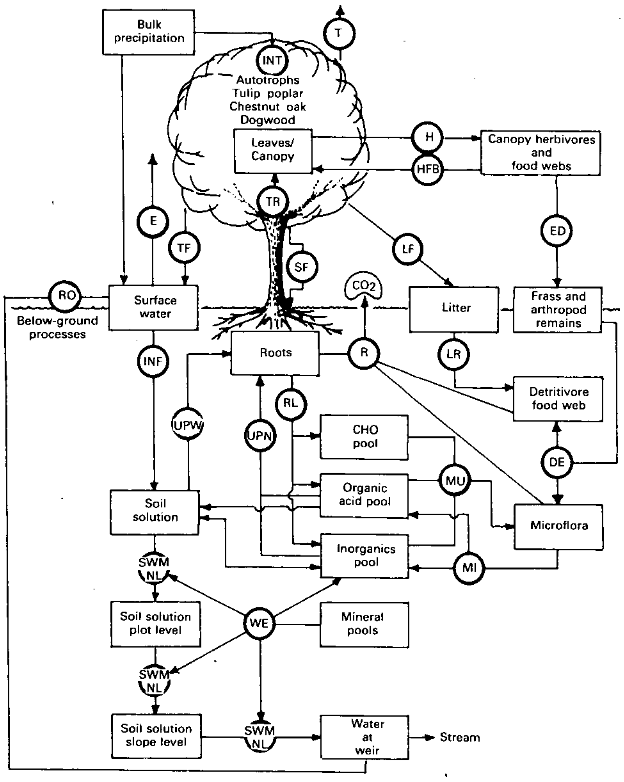

Figure 2. Conceptual model showing state variables and process linkages involved with the effects of herbivory in a forest ecosystem in the south-eastern USA (source: Seastedt & Crossley 1984). See Table 1 for list of processes

Table 1. Processes in the conceptual model of watershed associations involved in herbivory effects in a temperate forest of the south-eastern United States of America

Code	Process
DE	Decomposition
ED	Excretion, death of canopy insects
E	Evaporation
H	Herbivory
HFB	Herbivory feedback
INF	Infiltration
INT	Interception
LF	Litterfall
LR	Litter reduction
MI	Mineralization
MU	Mineral uptake by microbes
NL	Nutrient loss
R	Respiration (below-ground)
RL	Root loss of nutrients
RO	Surface runoff
SF	Stemflow
SWM	Soil water (solution) movement
T	Transpiration
TF	Throughfall
TR	Translocation
UPN	Uptake of nutrients by roots
WE	Weathering

runoff may contribute to water being measured at the watershed weir, but, for undisturbed watersheds, this is a rare event. Above-ground litter is reduced by a variety of detritivores and micro-organisms. They rapidly break down complex organic material into inorganic components which can be cycled by mineralization and mineral uptake processes. The organic and inorganic materials are also cycled through live roots. The combined metabolic activity of roots and organisms involved in decomposition produces relatively large levels of CO_2, which are released to the atmosphere. The combined action of infiltrating surface water and solubilizing of ions made available from biotic events and the weathering of geological and soil parent material produce soil solutions at different hierarchical levels in the watershed. Finally, all the material is integrated into solutions which pass from the watershed at the weir.

2.4 Herbivore composition and incidence

The Coweeta Basin has received considerable attention in respect of herbivores and their effects during the past 5 years. Much of this work has been prompted by the Mattson and Addy (1975) hypothesis that the impact of herbivores on forest ecosystems far exceeds their apparent position relative to numbers or biomass in the system. Schowalter *et al.* (1981b) and Seastedt *et al.* (1983) reported the dynamics of herbivore influence within the system, mostly from work tracing nutrient dynamics and determining some degree of impact on energetics. For instance, Schowalter *et al.* (1981) estimated that, in watersheds perturbed by clearcutting, regrowth vegetation was defoliated to a small degree, an estimate of less than 3% of all plant biomass. However, in these early successional communities, consumption by all chewing and sucking insects was estimated to amount to approximately 20% of NPP. The amount of leaf area removed (LAR) by defoliators, estimated by Seastedt *et al.* (1983) for *Robinia pseudoacacia* L. (black locust), ranged from 5.3% in June to 13.2% in July, whereas for *Acer rubrum* L. (red maple) it was 3.4% in June and 4.4% in August. Treatment with insecticide lowered rates by half. These authors could not determine that nominal herbivory had any short-term or proximate effects on biomass production, or whether there was nutrient accretion in these tree species (Seastedt *et al.* 1983). However, altering levels of herbivory with insecticide increased the cycling rate of potassium and other elements.

Risley (1982) summarized the arthropod guilds on 2 watersheds thought to encompass conditions within the entire Coweeta Basin. Twenty-four guilds based on foraging habits, size and life history were defined. According to L Risley (pers. comm.), the most apparent and currently active folivores in the system are geometrid caterpillars, even though they may be relatively rare at any given time. Several species of phytophagous beetles, as well as many sucking insects, are numerous in the ecosystem. To date, no systematic survey has been assembled for Coweeta, the functional or guild system (Crossley *et al.* 1976) being sufficient to categorize herbivory effects to this point.

A considerable amount of unpublished LAR study information has been collected for 4 species since the Seastedt *et al.* (1983) report (D A Crossley, unpublished data). The foliage of *Liriodendron tulipifera* L. (tulip tree), *Quercus castaneifolia* C. A. Mey (chestnut-leaved oak), *Cornus* spp. (dogwood) and *Robinia pseudoacacia* has been sampled extensively during the summer of 1983–85 in several watersheds. One of the primary reasons for this work is to determine the amount of leaf tissue removed by folivores, and in extreme conditions, where leaves are considerably deformed by herbivores, to reconstruct the leaf outline so that the amount eaten or not filled in can be estimated (W Hargrove, pers. comm.).

The numbers of insects in the canopy are difficult to quantify, but the best indication of their relative abundance comes from the studies emphasizing LAR estimates. When branches are bagged and clipped (Crossley 1985), folivores residing on the leaves or sucking insects on stems and leaves are also trapped. A relative density can be obtained by subsequently collecting and counting the numbers of insects after they have been classified in their guilds. Differences are known among the various watersheds, and a catalogue of LAR values is now being obtained from old-growth reference watersheds, as well as from the experimental watersheds which have been clearcut or otherwise heavily perturbed. This catalogue will provide an important background for both experimental process studies and biomonitoring in the future.

2.5 Herbivore impacts in other Biosphere Reserves: Changbai Mountain

No papers presented at the Symposium deal directly with effects of heterotrophs, or, more specifically, with defoliation as a process on Changbai Mountain. The reason is easy to understand in view of the goals and objectives presented about setting up a Biosphere Reserve data base for monitoring. Normally, it seems logical to consider other biotic and abiotic information needs before turning to the heterotroph function in an ecosystem. However, even though it has been standard practice, a note of caution is introduced. For instance, the watershed/canopy model discussed earlier focuses on many processes which are identical to those considered for problems of airborne contaminants, but sometimes with slightly different methods or emphases. Thus, in a Biosphere Reserve such as Changbai Mountain, which has been established primarily for its perceived pristine condition so that the effects of contaminants, for instance, can be determined in a landscape, it is highly likely that some causal effects may be incorrectly or incompletely identified. The point of caution stems from the fact that many physical processes involved in landscape perturbation may be linear or narrowly curvilinear, whereas the effects of herbivores may be strongly non-linear and non-monotonic. Therefore, interactions involving heterotrophs may be masked, or misunderstood, sometimes perhaps with disastrous implications. Results from monitoring studies could be interpreted as representing normal unperturbed background, or even as reactions to known perturbations. For example, in the case cited earlier, if there had not been a close examination of the Coweeta watersheds for defoliating insects, or if, in the Colorado case, it was not apparent that pine beetles had such an impact on the regional vegetation, major responses to changes in biogeochemical cycling parameters might well have been misread. The major reason for ensuring that several biological processes such as herbivory are included in system monitoring and study is because their non-linearity in interactions can contribute a large amount of variance to the other standard measures. In grasslands, this contribution to variance can be as high as 50–70% for many productivity measures (McNaughton *et al.* 1983). Such values are not known for temperate forest ecosystems, and studies should be launched in various regions to determine them. Otherwise, it is virtually impossible to determine cause and effect associations for anthropogenic activities, one of the major reasons that Biosphere Reserves such as Changbai Mountain have been created.

3 Recommendations

The major objective of this paper is to highlight the potential for examining the effects of a major biotic process in ecosystem function, eg herbivory in the forest canopy. The same can be said about heterotroph activity elsewhere in the system, eg below ground and in the woody matter and litter decomposition cycles. Therefore, I recommend that, as soon as it is reasonably feasible, research scientists at Biosphere Reserves, and specifically at Changbai Mountain for the purposes of this Symposium, undertake a well-organized series of process studies to determine the degree of nominal herbivory in the various systems, linking them to other processes and monitoring procedures. In this way, it is possible that such work will be allocated to the same routine operations in biomonitoring in the future as we currently consider for biophysical features, such as water quantity and quality, changes in site indices, or atmospheric inputs into the region.

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Studies on the composition and activity of microbial populations in the forest ecosystem of Changbai Mountain

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Abstract
The distribution and composition of the soil microbial population, soil enzyme activity, the soil oxidative metabolism, the rôle of sugars in soil organic matter, and seasonal dynamic variation under different conditions of altitude, vegetation and soil type were studied from 1979 on the northern slope of the Changbai Mountain Reserve. The results have demonstrated that the ecological distribution of the microbial population, the combination of dominant species and the biochemical properties of the soil micro-organisms are all closely correlated to water temperature conditions, the composition of plant material, and the decomposition of soil organic matter. They were highest in the mountain soddy forest soil which existed mainly under broadleaved trees and in the mountain dark brown forest soil under the mixed broadleaved and coniferous trees, lower in the mountain tundra soil with a cover of herbs and grasses, and lowest in the mountain brown forest soil under coniferous trees.

1 Introduction

The Nature Reserve on the northern slope of Changbai Mountain is now the largest Reserve in China, with typical ecological characteristics of a mountain ecosystem. Soil micro-organisms are one of the important constituents of the ecosystem and play an important role in transforming organic matter and energy. The distribution and activities of the micro-organisms in the soil provide essential evidence of the influence of each ecological factor in the ecosystem. The composition, biochemical properties and seasonal dynamic variation of microbial populations with different altitudes, vegetation and soil types on the northern slope of the Changbai Mountain Reserve were studied systematically from 1979 to 1983. The results are reported in this paper.

2 Materials and methods

2.1 Collection of soil samples

The soil samples were collected at varying depths in a standard area on the northern slope of the Reserve, at different altitudes and under different forest types (Table 1). The samples were taken to the laboratory and analysed as soon as possible after collection.

2.2 Methods

Analyses were undertaken to determine the following.

i. Total numbers of bacteria, microfungi and actinomycetes. The numbers of bacteria were subdivided into spore-forming bacteria, nitrogen-fixing bacteria, and nitrifying bacteria.

ii. Activities of soil enzymes, ie proteinase, invertase, catalase and polyphenol oxidase.

Table 1. Description of soil

Soil number	Altitude (m)	Forest type	Soil type	Soil horizon (cm)	Organic matter (%)	Depth of sampling (cm)
1	2615		Alpine tundra soil	0–7	3.5	0.13
				7–13	2.4	
2	2260		Alpine tundra soil	6–14	16.8	6–27
				14–27	3.3	
3	1900	*Betula ermanii/ Rhododendron aureum*	Mountain soddy forest soil	3–9	22.1	14–22
				9–18	12.5	
				45–55	7.5	
5	1200	*Picea jezoensis/ Abies nephrolepis*	Mountain dark brown coniferous forest soil	4–10	12.4	4–15
				10–16	1.8	
6	1380	*Larix olgensis/ Ledum palustre*	Mountain dark brown coniferous forest soil	3–8	21.4	3–23
				8–11	3.4	
				46–55	0.5	
7	740	Broadleaved/ *Pinus koraiensis*	Mountain dark brown forest soil	3–5	27.6	5–11
				5–11	6.7	
				40–50	0.6	
9	690	*Pinus sylvestriformis/ Lespedeza bicolor*	Mountain dark brown forest soil	8–11	—	3–12

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*Zheng Liandi, Yao Zhihong and Li Qi also contributed to the study

- iii. Processes of soil oxidative metabolism, including the intensity of soil respiration using glucose, pyruvic acid and pyrogallol as substrates.
- iv. The different varieties and quantities of carbohydrates in the soil organic matter.

The methods used in the analyses are described by the Institute of Forestry and Pedology (1960) and by Zheng and Zhang (1982).

3 Results and discussion

3.1 Ecological distribution of the microbial populations in soils under different vegetation types

The variation in abundance and composition of the population of micro-organisms was closely correlated with forest type. The numbers of soil bacteria under deciduous forest and under mixed broadleaved/coniferous forest were greater than under coniferous forest. Microfungi were more abundant in the soil under the subalpine mixed coniferous forest. The distribution of soil actinomycetes under different soil types decreased with increasing altitude.

While investigating the ecological distribution of soil micro-organisms under different forest types, the representative isolates of the different microbial populations were identified and analysed. The species and population composition of *Bacillus*, microfungi and actinomycetes differed markedly with different altitudes, vegetation and soil types. Almost one thousand isolates of spore-forming bacteria (*Bacillus*) were classified into 14 species. The dominant species was *Bacillus coagulans*, followed by *B. cereus*, *B. megaterium*, *B. firmus* and *B. cereus* var. *mycoides*. *B. subtilis* and *B. alvei* were only found in the soil under *Pinus sylvestriformis* T. Wang (Changbai pine)/*Lespedeza bicolor* Turcz. (bush clover) forest, and *B. macerans* only appeared in soil under tundra and *Betula ermanii* Cham. (Erman's birch)/*Rhododendron aureum* Georgi (golden rhododendron) forest. The composition of the dominant species of *Bacillus* varied significantly under different forest and soil types. In alpine tundra soil, the dominant species were *B. circulans* and *B. coagulans*, while, in soil under broadleaved/*Pinus koraiensis* Sieb. et Zucc. (Korean pine) forest, the dominant species were *B. megaterium* and *B. cereus*. In soil under *Betula ermanii/Rhododendron aureum* forest, the dominant species were *B. circulans* and *B. cereus*, and under subalpine coniferous forest (*Picea jezoensis* (Sieb. et Zucc.) Carr. (Yezo spruce)/*Abies nephrolepis* (Trautv.) Maxim. (East Siberian fir)), the dominant species were *B. circulans* and *B. firmus*. Under *Larix olgensis* A. Henry (Olga Bay larch)/*Ledum palustre* L. (white-leaved ledum) forest, the dominant species were *B. laterosporus* and *B. coagulans*, while in soil under *Pinus sylvestriformis/Lespedeza bicolor* forest, the dominant species were *B. sphaericus* and *B. brevis* (Table 2).

A total of 1953 isolates of microfungi from the different forest types were identified as belonging to 30 genera (Table 3). In alpine tundra, the dominant species were *Mortierella polycephala* and *Fusarium* spp. Under *Betula ermanii/Rhododendron aureum* forest, the dominant species were *Penicillium* spp. and *M. polycephala*. In soil under subalpine coniferous forest (*Picea jezoensis/Abies nephrolepis*), the dominant species were *M. vinacea* and *Trichoderma polysporum*. In soil under *Larix olgensis/Ledum palustre* forest, the dominant species were *M. vinacea*, *Penicillium* spp. and *T. polysporum*. Under broadleaved/*P. koraiensis* forest, the dominant species were *M. vinacea* and *Phialocephala* spp., and, under *Pinus sylvestriformis/Lespedeza bicolor* forest, the dominant species were *Penicillium* spp. and *T. köningi*.

It has been reported that *Mortierella* is more tolerant of lower temperatures (Latter & Heal 1971). *Mortierella*

Table 2. Distribution of *Bacillus* species in the soils of the northern slope of Changbai Mountain (nos × 10^3 g^{-1} dry soil)

				Soil number			
Species	1	2	3	5	6	7	9
B. coagulans	3.7	0.9	4.8	0.1	7.6	10.1	8.0
B. cereus	2.0		6.1	3.0	5.0	43.8	17.9
B. megaterium		0.2	1.9	2.8	1.2	47.4	23.3
B. firmus		0.1	1.0	4.8	0.3	12.6	19.1
B. cereus var. *mycoides*	0.7		1.0	0.3		5.0	4.5
B. sphaericus				2.1	4.2	17.8	68.5
B. brevis		3.3		0.1		13.2	8.5
B. circulans	4.1		6.9	7.4			29.7
B. laterosporus	0.8				20.1	1.2	
B. pumilus	0.1				3.3		53.0
B. polymyxa		1.5					12.9
B. macerans	0.3		1.8				
B. alvei							14.0
B. subtilis				0.74			1.1
Bacillus spp.		6.4	1.5	4.4		3.4	53.0
Total	11.7	12.4	24.9	25.7	41.6	154.5	313.5

Table 3. Relative density of fungal distribution in the soils under different forest types (% of total isolates)

	Soil number						
Fungi	1	2	3	5	6	7	9
Aspergillus niger group			1.8	0.4			
A. vesicolar	4.8	0.7	6.4	1.9	3.6	1.8	0.9
A. flavus		0.2					
A. ochraceus	1.6		0.9				
Absidia spp.							3.0
Acremonium spp.	6.5		4.6	0.4	0.4	1.4	0.4
Chrysosporium spp.	9.7		2.8	1.5		0.9	0.9
Epicoccum spp.						0.5	
Aureobasidium spp.		0.2	0.9	0.4	3.2	1.4	
Beauveria spp.	4.8	66.7	9.2				
Phialocephala spp.				3.5	6.5	10.0	
Mortierella polycephala	32.3	16.1	12.8	2.7		2.7	1.3
M. vinacea	1.6	0.7	0.9	47.4	26.0	42.1	0.4
Mucorales spp.			2.7	1.9	1.8	0.5	
Oidiodendron spp.	1.6		0.9	1.2	11.2	0.9	
Penicillium spp.		7.0	21.0	7.3	15.1	8.6	62.3
Trichoderma polysporum	1.6	2.9	8.3	24.7	11.2	7.7	
T. köningi		1.1	3.7	1.2	2.9	5.9	10.4
T. viride	4.8						
Thielaviopsis spp.					2.9		2.6
Zygorhynchus spp.						0.5	
Phialophora spp.				0.4		0.8	
Peyronellaea spp.		0.2		0.4			
Cladosporium spp.		0.5	0.9	0.4	0.7	0.5	
Chaetopsina spp.					1.1		
Gliomastix spp.						0.5	
Circinella spp.						0.8	
Fusarium spp.	21.0					0.5	
Spicaria spp.							0.9
Coniothyrium spp.						0.5	
Cylindrocarpon spp.	1.6		1.8			0.9	0.4
Gliocladium spp.							8.7
Monocillium spp.						0.5	
Phaeolisaria spp.						0.9	
Doratomyces spp.						0.5	
Dark hyphae	8.1	2.3	13.8	1.2	1.1	1.4	0.4
Hyaline hyphae		0.5	3.7	0.4	7.6	2.6	3.5
Others		0.9	2.8	2.7	4.7	4.5	3.9
Total	62	442	109	259	277	221	230

and *T. polysporum* were the dominant species in soil under coniferous forest where conditions were wet and cool (Söderström & Bååth 1978), and abundant in the soil under forests of *Picea jezoensis/Abies nephrolepis*, *Larix olgensis/Ledum palustre*, and broadleaved/*Pinus koraiensis*. Their abundance was related to the wet and cool condition of the soils under these forest types. On the upper part of the northern slope of the Mountain, *Mortierella* and *Trichoderma* were fewer in number in soils under *Betula ermanii/Rhododendron aureum* forest and under *Rhododendron*/moss shrub, where conditions were comparatively cool and wet. Therefore, in addition to water temperature condition, the distribution of microfungi is also affected by different vegetation and other ecological factors.

The distribution of actinomycetes also differed markedly under different forest types. A total of 364 isolates of *Streptomyces* were identified as belonging to 32 species (Table 4). Under broadleaved/*Pinus koraiensis* forest soils, the dominant species were *Streptomyces nigrogriseolus*, *S. chromogenes*, *S. lavendularectus* and *S. rutgersensis*. In soil under *P. sylvestriformis/Lespedeza bicolor* forest, the dominant species were *S. nigrogriseolus*, *S. lavendulae* and *S. microsporus*. Under *Larix olgensis/Ledum palustre* forest, the dominant species were *S. griseoloalbus* and *S. nigrogriseolus*. Under *Picea jezoensis/Abies nephrolepis* forest, the dominant species were *S. rutgersensis* and *S. prunicolor* var. *solubilis*. In soil under *Betula ermanii/Rhododendron aureum* forest, the dominant species was *S. griseoloalbus*, while under alpine tundra the dominant species was *S. roseofulvus*. Some species of *Streptomyces* appeared only in certain soil types. For example, *S. chromoflavus* was found only in soil under *Pinus sylvestriformis/Lespedeza bicolor* forest, *S. roseosporus* only appeared in soil under broadleaved/*Pinus koraiensis* forest, and *S. roseocastaneus* only in soil under *Betula ermanii/Rhododendron aureum* forest. The composition of the dominant micro-organisms seems to be closely related to the water temperature conditions of

Table 4. Composition of *Streptomyces* species in the soils under different forest types

	Soil number							
Streptomyces species	1	2	3	5	6	7	9	Total
S. longisporoflavus	1			3	6	1		11
S. alboflavus	2	1				2		5
S. flaveolus var. *rectus*						3		3
S. chromoflavus							1	1
S. roseofuscus							4	4
S. lilacinorectus							1	1
S. roseofulvus		6				2	6	14
S. fradiae			2					2
S. fumanus		2	2			2	2	8
S. roseocastaneus			1					1
S. lilacinofulvus						4		4
S. roseosporus						1		1
S. lavendulae	3			6	4	5	20	38
S. lavendularectus	4	3				13	7	27
S. prunicolor var. *solubilis*		1		12		3	5	21
S. violaceorectus						2		2
S. violaceoagglomeratus						1		1
S. violaceochromogenes						1		1
S. nigrogriseolus			4		11	25	27	67
S. castaneus			1			1		2
S. rutgersensis				12		13	2	27
S. aburaviensis var. *tuftformis*					1	4		5
S. microsporus						4	10	14
S. chromogenes						19	3	22
S. niger						2		2
S. griseoviridis							1	1
S. griseoloalbus		5	8		22	1	1	37
S. graminearus						2		2
S. graminearus var. *rectus*						2	5	7
S. aureochromogenes	3	1	1					5
S. aureus	3							3
Streptomyces spp.	13		2	3	1	2	4	25
Total	29	19	21	36	45	115	99	664

the soil, to the constituents of the plant residues, the decomposition processes of the soil organic matter, and to the variation in species' physiological properties. The distribution of each species is, therefore, influenced by the different ecological factors.

The results have proved that it is possible to define a particular ecological condition from the soil microbial population.

3.2 Variation in soil enzyme activities under different ecological conditions

The enzyme activities in soil may reflect the vertical variation of soil and the presence of certain plants (Table 5). Soil enzyme activities were greater in soil under *Betula ermanii/Rhododendron aureum* and under broadleaved/*Pinus koraiensis* because these forests were comprised mainly of broadleaved trees, than in soil with a cover of herbs and grasses.

Activities were lowest in soil under *Picea jezoensis/Abies nephrolepis* forest and under *Larix olgensis/Ledum* spp. forest, which consisted primarily of coniferous trees. Variation in soil enzyme activities under different forest types indicated the conversion ability of different organic residues. Thus, the intensity of activities of hydrolytic enzymes (proteinase, invertase) represents the intensity of the decomposition process of organic residues, while the intensity of oxido-reductive enzymes (catalase, polyphenolase) represents the intensity of the humification process.

Table 5. Variation in soil enzyme activities under different ecological conditions

Soil number	Activity of protease (Tyrosine mg g^{-1} dry soil 24 h^{-1})	Activity of invertase (Glucose mg g^{-1} dry soil 48 h^{-1}	Activity of catalase (0.1 $NKMnO_4$ ml g^{-1} dry soil)	Activity of polyphenol oxidase (O_2 µl g^{-1} dry soil h^{-1})
1	2.8	18.6	18.4	22.7
2	3.3	16.4	34.5	70.0
3	3.3	18.2	65.9	57.2
5	2.3	13.1	49.6	27.9
6	1.9	12.3	22.0	15.3
7	3.3	16.8	72.0	62.1
9	3.0	11.2	37.9	6.9

In the soil under *Betula ermanii/Rhododendron aureum* forest which comprised mainly broadleaved trees, and the broadleaved/*Pinus koraiensis* forest with a mixture of broadleaved and coniferous species, the activities of both hydrolytic enzymes and oxidative enzymes were highest. The conversion process of organic matter was intensive, so that the accumulation of humic carbon and humic nitrogen was considerably greater. However, in the soil under dark coniferous forest which contained a higher proportion of coniferous trees, the activities of hydrolytic enzymes were rather weak. In these soils, the conversion process of organic matter was markedly slow, so that the amount of humic carbon and humic nitrogen accumulated was also low.

3.3 Seasonal variation in ecological distribution of forest soil micro-organisms

Following on from the fundamental study of the vertical distribution of forest soil micro-organisms on the northern slope of Changbai Mountain, seasonal variation in microbial populations under the 3 main forest types (*Larix olgensis/Ledum* spp., *Pinus sylvestriformis/Lespedeza bicolor* and broadleaved/*P. koraiensis*) was investigated (Table 6).

Table 6. Seasonal variation in distribution of forest soil micro-organisms under 3 main forest types (nos × 10^4 g^{-1} dry soil)

	19 June							10 August							19 September						
Soil	Total	Bacteria		Actinomycetes		Fungi		Total	Bacteria		Actinomycetes		Fungi		Total	Bacteria		Actinomycetes		Fungi	
number	no.	no.	%	no.	%	no.	%	no.	no.	%	no.	%	no.	%	no.	no.	%	no.	%	no.	%
6	137.7	77.0	55.9	0.02	0.03	60.7	44.1	11.5	3.4	29.6	0.10	0.86	8.0	89.6	35.9	12.0	33.4	0.13	0.4	23.8	66.2
9	187.1	115.0	61.5	3.36	1.79	68.7	36.7	58.8	16.0	27.2	3.02	5.14	39.8	67.7	85.1	43.4	51.0	9.08	10.7	32.6	38.3
7	398.2	339.0	85.1	5.14	1.29	54.1	13.6	11.5	8.9	77.9	0.40	2.98	2.2	19.1	74.3	56.7	75.6	4.36	5.9	13.8	18.6

The general trend of seasonal variation in the main populations of soil micro-organisms under different forest types was higher in spring, lower in summer, and increased in autumn, but the proportion of each group varied with different types of forest. In soil under broadleaved/*P. koraiensis* forest, the percentages of bacteria in the microbial populations were all highest in spring, summer and autumn. Under *Larix olgensis/Ledum* spp. and *Pinus sylvestriformis/Lespedeza bicolor* forest, the number of bacteria was highest in spring, but the percentage of microfungi was highest in summer and autumn. It is evident that seasonal variation among the main groups of soil micro-organisms is closely related to the vegetation structure under the different forest types. Furthermore, seasonal variation in the distribution of soil micro-organisms in different forest soils was not only correlated with forest litter, but also with seasonal variation in the water temperature of the soil. In spring, the weather became warmer and air temperature increased gradually. In *Pinus sylvestriformis/Lespedeza bicolor* forest located at the lowest altitude, the ground temperature increased to 16°C, while in broadleaved/*P. koraiensis* forest it was 10°C. At this temperature, the soil micro-organisms become active and propagate abundantly, especially the bacteria, decomposing soil organic carbon and organic nitrogen. At the start of summer, the ground temperature increases to 13.8–20°C, and plants grow vigorously, using up considerable amounts of the soil nutrients. Of course, the plants compete with micro-organisms for such nutrients, and the propagation of the micro-organisms is restricted. In autumn, plant growth is not as vigorous, and the reservoir of nutrients increases by litterfall, promoting the activity and propagation of the soil micro-organisms.

In contrast, seasonal variation in the intensity of soil respiration and in soil enzyme activity generally corresponded with seasonal variation in abundance of soil micro-organisms. The increased soil respiration and soil enzyme activity demonstrated that, before summer, the main process affecting forest organic residues was decomposition, the nutrient elements re-

Table 7. Seasonal variation in endogenous respiration and soil enzyme activity under different forest types

	Soil number								
	6			9			7		
	Dates								
Activity	19.6	10.8	17.9	19.6	10.8	17.9	19.6	10.8	17.9
Endogenous respiration									
(CO_2 µl 4 g^{-1} soil h^{-1})	11.8	15.8	69.8	12.3		41.9	71.8	65.0	79.5
(O_2 µl 4 g^{-1})	16.0	14.2	52.2	7.6		34.7	61.4	55.3	69.2
Protase (Tyrosine mg g^{-1} dry soil 24 h^{-1})	2.54	2.02	4.14	4.55	3.49	4.84	7.34	3.65	6.13
Invertase (Glucose mg g^{-1} dry soil 48 h^{-1})	22.7	35.8	36.4	18.9	28.1	28.3	26.9	33.7	43.6
Polyphenol oxidase (O_2 µl g^{-1} dry soil h^{-1})	14.3	19.7	72.1	9.2	5.5	21.4	67.1	51.7	72.8

leased being taken up in tree growth. After summer, in addition to decomposition, the resynthesis process (humification) begins. This process is more intensive in the broadleaved/*P. koraiensis* forest than in the *P. sylvestriformis/Lespedeza bicolor* forest (Table 7).

3.4 Soil oxidation under different forest types

When studying the transformation of soil organic matter and the cycling of energy in an ecosystem, we use the words 'pool' to indicate microbial biomass and 'force' (kinetic) to indicate enzyme activity. Soil respiration is a result of soil metabolism, and may reflect the potential of soil biological activities when organic matter containing carbon or nitrogen as a source of energy and nutrient is added to soil. On the other hand, the rate and intensity of decomposition of the organic residues can be determined according to the amount of CO_2 released. In this way, we compared the capacity of the oxidative metabolism of glucose, pyruvic acid and pyrogallol in the soil under different forest types (Table 8).

used as an energy material to promote (stimulate) oxidation of the soil humus. Protein, polysaccharides, and glucose may play a part in the synthetic process of new humus, either in its original form or in the form of intermediate metabolites (Hodge 1953; Kononova 1966).

Pyruvic acid is the intermediate product in the metabolism of carbon and nitrogen in living organisms. Theoretically, the value of RQ is equal to 1.2 when pyruvic acid is oxidized completely, but the actual value in the oxidation of soil pyruvic acid is much higher, indicating that intermediate products accumulate when pyruvic acid is oxidized.

The polyphenol resource in soil is essentially formed during plant decomposition. When the polyphenols are oxidized completely, the theoretical value of RQ equals 1, but, when the polyphenol is oxidized in the soil, the value is less than 1, indicating that part of the polyphenol has been oxidized to quinone during the decomposition of organic matter (Kononova 1966).

Table 8. Capacity of soil respiration under different forest types (μl 4 g^{-1} soil h^{-1})

Soil	Endogenous			Glucose oxidation			Pyruvate oxidation			Polyphenol oxidation		
number	O_2	CO_2	RQ	O_2	CO_2	RQ	O_2	CO_2	RQ	O_2	CO_2	RQ
1	17.4± 9.6	25.3±11.7	1.45	48.4± 6.6	60.0±11.7	1.24	29.9± 2.6	54.6± 5.1	1.82	109.0±16.9	47.5± 9.7	0.44
2	28.8± 5.8	30.6± 6.3	1.06	47.2±11.2	53.3±11.9	1.13	34.5± 8.6	56.3±15.5	1.63	174.1±39.2	57.8±45.5	0.33
3	62.5±13.8	65.9±12.7	1.05	109.2±13.6	118.2± 2.2	1.08	103.5±25.4	152.9±14.9	1.48	290.2±39.7	125.3±44.8	0.43
5	16.3± 4.9	20.6± 4.1	1.26	24.8± 4.2	29.2± 5.8	1.18	23.0± 5.9	52.2± 1.9	2.26	136.7±17.2	70.3± 6.8	0.41
6	27.5±17.5	32.5±26.4	1.18	32.5±25.8	33.7±25.6	1.04	40.5±38.8	84.1±68.6	2.08	141.5±10.4	52.4±49.8	0.37
7	62.0± 5.7	72.1± 5.9	1.16	88.5± 3.5	96.0± 4.3	1.08	74.3± 7.3	134.3±13.5	1.81	255.5±35.7	149.3±36.4	0.58
9	21.2±13.6	27.1±14.8	1.27	30.0±26.2	35.8±32.6	1.15	25.8±22.6	54.3±32.0	2.10	48.2±27.2	34.4±14.7	0.71

The rates of endo-respiration, or of respiration with added substrates, were highest in *Betula ermanii/Rhododendron aureum* forest, consisting primarily of broadleaved trees, and in broadleaved/*P. koraiensis* forest with a mixture of broadleaved and coniferous trees. In forests consisting of coniferous trees, such as the *Picea jezoensis/Abies nephrolepis* and the *Larix olgensis/Ledum* spp. forests, the rate of endo-respiration was low. In soils under *Betula ermanii/Rhododendron aureum* and broadleaved/*P. koraiensis* forests, not only was the actual biological activity intensive, but the potential activity also. In soils under *Picea jezoensis/Abies nephrolepis* and *Larix olgensis/Ledum* spp. forests, the total biological activity was weak, as also was the potential activity. When the proportion of broadleaved trees in the coniferous forest increased, soil respiration also increased significantly.

When glucose is completely oxidized in biological systems, the respiratory quotient (RQ) is equal to 1, whereas in soil the RQ is greater than 1. This result confirms that glucose is not completely oxidized in soil, but may undergo some process to form alcohol or carboxylic acids. On the other hand, glucose can be

Sugar compounds in the soil are formed partly by the decomposition of plant remains and partly from the metabolic activities of the soil micro-organisms. Variation in the amounts of sugar in the soil under different forest types coincided with the ecological distribution of the micro-organisms (Table 9). It was greatest in the soil under broadleaved/*P. koraiensis* forest and *Betula ermanii/Rhododendron aureum* forest, and lowest under *Picea jezoensis/Abies nephrolepis* forest.

The levels of sugars in the different soils are mostly determined by the amount of organic matter present. Thus, every factor in the ecological environment which influences the organic matter input and the rate of decomposition may influence the level of sugar content in the soil.

4 Conclusions

4.1 The analytical results have demonstrated that a combination of dominant species of different soil micro-organisms reflected some difference in soil under different conditions of altitude, vegetation and soil type. Some species may be indicative of a particular soil type. Variation in composition at generic or species level was

Table 9. The amount of sugars in the soil organic matter under different forest types

Soil number	Depth sampling (cm)	Organic matter (%)	Neutral sugar		Uronic acids		Amino sugar		Total amount	
			(mg 100 g^{-1} soil)	(%)	(mg 100 g^{-1} soil)	(%)	(mg 100 g^{-1} soil)	(%)	(mg 100 g^{-1} soil)	(%)
1	0–13	2.9	145	5.2	15	0.5	40	1.4	200	7.1
2	6–27	10.0	1911	17.6	100	0.8	119	1.2	2130	18.65
3	3–18	17.3	2418	14.5	134	0.7	154	0.9	2706	16.10
5	4–15	7.1	896	10.5	35	0.4	66	0.9	997	11.80
6	3–11	12.4	1009	8.5	51	0.4	63	0.6	1123	9.50
7	3–11	17.1	2448	16.1	151	1.1	349	2.9	2948	20.10
9	—	—	—	—	—	—	—	—	—	—

correlated with water temperature, organic matter and the conversion process of the soil material.

4.2 The number of micro-organisms, soil enzyme activity, soil respiration intensity, soil oxidative metabolism, and the amount of sugar in the soil were determined in soils under different forest types on the northern slope of Changbai Mountain. They were highest in the soddy forest soil under broadleaved trees and in the dark brown forest earth under the mixed forests, as in the broadleaved/*P. koraiensis* forest, and less in the mountain tundra soil under a cover of herbs and grasses. They were lowest in the brown coniferous forest soil, which existed mainly under the *Picea jezoensis/Abies nephrolepis* forest and the *Larix olgensis/Ledum* spp. forest. In the mountain soddy forest soil and dark brown forest earth, the activities of hydrolytic and oxidation enzymes were both intensive, and, as a result, the accumulation of carbon and nitrogen in the soil was highest. In contrast, the hydrolytic enzyme activity in dark brown coniferous forest soils was very weak, indicating that, in these soils, the breakdown of organic matter takes place very slowly, and, therefore, the amount of carbon and nitrogen accumulated is low.

4.3 In soils under different forest types, the important groups of micro-organisms, the intensity of soil respiration, and soil enzyme activity all showed seasonal variation. The general trend was higher in spring, lower in summer, and increased in autumn, indicating that the decomposition of forest organic matter occurs mainly before summer and that the nutrients released are taken up in the growth and development of the trees. After summer, decomposition proceeds in conjunction with the resynthesis process (humification).

4.4 The variation in activities of the hydrolytic enzymes (proteinase, invertase) can be used to define the intensity of organic matter decomposition, and the variation in oxido-reductive enzymes (catalase, polyphenol oxidase) to define the intensity of the humification process. We can also use the variation in the intensity of soil respiration and respiratory quotient to explain the ability and direction of soil oxidation.

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Biological nutrient cycling in the broadleaved/*Pinus koraiensis* (Korean pine) forest of Changbai Mountain

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Abstract

Broadleaved/*Pinus koraiensis* Sieb. et Zucc. (Korean pine) is the main type of forest in north-east China. This paper describes a study of the nutrient distribution and cycling within the stand.

The total biomass of the above-ground vegetation was about 211 t ha^{-1}, and the annual production 7.1 t ha^{-1}. The amounts of nitrogen, phosphorus, potassium, calcium and magnesium in the above-ground parts of trees were 602.9, 54.3, 498.2, 1038.1 and 71.6 kg ha^{-1}, respectively. Litterfall plays an important role in the nutrient cycle, and this study shows that the amounts of N, P, K, Ca and Mg in the annual litter were 43.5, 3.7, 13.5, 56.3 and 10.9 kg ha^{-1}, respectively. The amounts taken up annually from soil by trees were about 112, 10, 47, 134 and 22 kg ha^{-1}.

Nutrient consumption is larger by broadleaved species than by coniferous trees, between 4 and 10 times as much, if expressed per unit of stem volume increment.

1 Introduction

The nutrient cycle consists of biological and geological elements. The biological cycle is mainly concerned with the transfer of nutrients between soil and vegetation, and the geological cycle with the transfer of nutrients from the sea and atmosphere to the ecosystem, their release by weathering, and their loss through leaching. In fact, the biological cycle represents merely one link in the geological cycle. Broadleaved/*Pinus koraiensis* forest is the main type of forest in NE China. The aim of this study was to determine the distribution of nutrients among different compartments of the stand, the nutrient requirements of annual primary production, and the composition of the annual nutrient balance.

The sample plot studied is situated in Erdaobeihe, Antu county, Jilin Province, 740 m above sea level. The mean annual temperature ranges from 0.9°C to 3.9°C, the mean annual precipitation is 632.8–782.4 mm, and the total annual radiation is 12178–12318 Cal cm^{-2}. The soil in the area is a dark brown forest earth (alfisol), with a pH of 5.3–5.6 and a silty clay texture.

The dominant tree species are *P. koraiensis*, *Tilia amurensis* Rupr. (Amur linden), *Acer mono* Maxim. (painted mono maple), *Fraxinus mandshurica* Rupr. (Manchurian ash), *Quercus mongolica* Fisch. ex Turcz. (Mongolian oak) and *Ulmus propinqua* Koidz. (white elm), with a mean age range of 120–245 years.

After a study plot was established in the forest, the diameters of all trees were measured and all vegetation present was recorded. After cutting the sample trees, the length and diameter of each branch were measured. The volume of a tree trunk was calculated by using stem analysis, and its weight was calculated by the volume method. In order to determine the quantity of litter in the sand, 10 wood litter collectors were placed in the plot.

2 Distribution of dry matter in the stand

2.1 Biomass and annual production

The biomass and annual production of the stand were estimated in 1983. In this study, the total biomass of the above-ground vegetation was estimated as 211 t ha^{-1}, of which trees comprised 81%, shrubs 0.9% and ground vegetation 0.12% (Table 1). Of the tree biomass, *Pinus* species made up 18% and broadleaved species 82%.

Table 1. Biomass and annual production (t ha^{-1})

Compartment	Biomass	Production
Trees	170.9	5.35
Leaves	3.4	2.62
Branches	42.2	1.45
Stems	110.2	1.12
Bark	15.0	0.16
Shrubs	1.9	0.16
Ground vegetation	0.2	0.24
Others	0.6	0.56
Above-ground vegetation	173.6	6.31
Below-ground vegetation	37.4	0.78
Total	210.9	7.09

Annual production of the stand (including roots) was 7.1 t ha^{-1}, of which *Pinus* accounted for 17% and broadleaved trees 64%.

The leaf biomass was 3.4 t ha^{-1}, and the annual production of leaves 2.6 t ha^{-1}. The ground vegetation biomass was 0.2 t ha^{-1}.

2.2 Annual litter production

Litterfall is the main source of soil humus and can be used to study the dynamics of a forest ecosystem.

According to this study, average litter production was 3838 kg ha^{-1} yr^{-1}. The proportion of leaf litter in total litterfall represents about 60%. It forms a soft layer on the ground surface, and is beneficial to soil biology and fertility.

2.3 Soil organic matter

The total amount of organic matter on the forest floor and in the humus layer (0–60 cm) is 95.4 t ha^{-1}. Soil ecological condition is generally considered to be more favourable in a mixed forest than in a coniferous stand, and litter decomposition is believed to be faster.

2.4 Annual balance of biomass

Within a period of one year, the stand biomass increases as a result of stand growth, but there is a loss of biomass as litter at the same time. The quantity of biomass at the time of measurement forms the basis for determining annual production. However, annual production and the amount removed as litterfall are more difficult to determine accurately than the quantity of biomass at any given time, because it is difficult to measure the amount lost during a given period.

The amount removed should include all dry matter lost from the stand. In this study, only the litter on the wood litter collector and ground vegetation were included, while bark litter, root removal and leaves destroyed by animals and insects were omitted because these losses were impossible to determine.

However, the annual amount removed was relatively small compared to the total annual production, and did not constitute a major source of error in estimating the annual biomass balance. The annual changes in biomass calculated from the data on dry matter distribution in the sample plot are shown in Table 2. The Table shows that the total annual production was nearly twice the amount removed. Possibly, the annual net production decreases gradually as the stand develops.

Table 2. Annual changes of biomass in the experimental stand

Biomass change	Biomass t ha^{-1}	%
Biomass at the beginning of measurement period	210.9	100
Annual total production	7.1	3.4
Annual amount lost	4.5	2.1
Annual net production	2.6	1.2
Biomass at the end of measurement period	213.6	101.2

3 Distribution of nutrients in the stand

In general, the biological nutrient cycle can be divided into several nutrient pools: (i) mineral soil, (ii) tree layer, (iii) ground vegetation, and (iv) forest floor.

3.1 Nutrients stored in soil

All nutrients in the soil are included in the biological nutrient cycle, even though they may be mobilized at very slow rates at greater soil depth. The nutrients available to plants in the soil can also be considered to be part of the nutrient cycle. Site productivity is closely related to nutrients in the soil, and particularly to those available to plants. Table 3 shows that 2.9% of nitrogen was available.

Table 3. The amounts of total and available nutrients in the surface soil (kg ha^{-1})

Soil layer	Total nitrogen	Available amounts N	K
0–6 cm	4403	30	135
6–27 cm	2293	147	177
27–60 cm	3604	123	578
Total	10311	300	890

3.2 Nutrients bound to vegetation

3.2.1 Nutrients in tree crops

Large amounts of nutrients are bound to tree crops in the nutrient pool of the forest ecosystem. The nutrient content of the different tree compartments varies both between trees and also within the same tree. The nutrient content in coniferous species is lower than in broadleaved trees. As a general rule, the highest nutrient content is found in leaves, and the lowest in stemwood, within the same tree species. Although the nutrient content of stemwood is relatively small, the nutrients are bound in the stemwood for a long time.

The amounts of nitrogen, phosphorus, potassium, calcium and magnesium in the above-ground parts of trees were 602.9, 54.3, 498.2, 1038.1, and 71.6 kg ha^{-1}, respectively (Table 4). The nitrogen content in leaves of broadleaved trees was about 1.5 times that in leaves of *Pinus* species. Within the same tree, the N, P and K contents in leaves were usually 10 times those in stemwood.

3.2.2 Nutrients in shrubs and ground vegetation

This stand was characterized by an abundance of shrubs and ground vegetation. Their growth was closely related to light, and their distribution was irregular. The amounts of N, P, K, Ca and Mg in the above-ground parts of shrubs and ground vegetation were 15.7, 2.2, 13.6, 19.8 and 4.2 kg ha^{-1}, respectively (Table 4). The nutrient contents of the ground vegetation is higher than that in shrubs, especially for potassium which is 3–4 times the level in shrubs.

3.2.3 Nutrients in litter

A considerable amount of the nutrients taken up by vegetation returns to soil in the form of litter. In this study, the amounts of N, P, K, Ca and Mg in litter were

Table 4. Nutrient distribution in the stand (kg ha^{-1})

Nutrient	Trees Foliage	 Branches	 Stems	 Bark	Total above-ground	Shrubs and ground vegetation
Nitrogen	66.9	323.0	147.3	65.6	602.9	15.7
Phosphorus	5.9	39.3	5.9	3.3	54.3	2.2
Potassium	31.1	136.0	249.6	81.6	498.2	13.6
Calcium	59.5	499.5	227.5	251.6	1038.1	19.8
Magnesium	10.2	32.3	20.4	8.7	71.6	4.2

43.5, 3.7, 13.5, 56.3 and 10.9 kg ha^{-1}, respectively (Table 5). The levels of nutrients were higher in leaf litter of broadleaved trees, particularly calcium which was 4–5 times that in coniferous trees.

Table 5. Amounts of nutrients returned to soil in litter (kg ha^{-1})

Compartment	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Broadleaves	21.0	1.94	9.45	43.45	6.29
Needles	4.69	0.35	1.44	2.45	0.81
Branches	6.58	0.52	1.76	9.60	0.54
Fruits and residual	11.23	0.89	0.80	0.80	3.27
Total	43.5	3.70	13.45	56.30	10.91

4 Nutrient cycling in the stand

4.1 Nutrient cycling in the biological cycle

The nutrients already present in the biological cycle or likely to be taken up into it form a reservoir of nutrients in the ecosystem. In a stand, all nutrients bound to the vegetation, forest floor and soil humus are included in the cycle, although the rate of mineralization of organic matter in humus may be very slow. In mineral soil, only exchangeable cations can be regarded as mobilized nutrients. Table 6 indicates that only about 7.3% of nitrogen in the sample plot was bound to the biomass, as most of it was present in a form unavailable to the plants.

Table 6. Distribution of nitrogen in the biological cycle of a stand

Stage of cycling	Nitrogen (kg ha^{-1})
Biomass	827
Forest floor	163
Mineral soil (0–60 cm)	10298
Total	11288
Bound into biomass (%)	7.3
Available N as % of total N in the mineral soil	2.9

The amount of available nutrients in the ecosystem may be subject to constant change. Losses through leaching and fire are compensated by the addition of nutrients entering from the atmosphere and released by weathering.

4.2 Annual nutrient balance in the stand

Estimating the annual nutrient requirement by the vegetation is a major problem which should be taken into account when studying the biological cycling of nutrients. Judging from the nutrient quantities bound annually to the biomass, it can be seen that the largest part of the nutrients taken up in a stand is utilized in annual leaf production. For example, the nitrogen taken up annually in leaf production represents about 78% of the tree's total consumption. Table 7 indicates that the broadleaved forest takes up significantly more nutrients than *Pinus* species – the nutrient consumption of the broadleaved forest is nearly 4–10 times that of *Pinus* trees, if the amounts are expressed per unit of stem volume increment.

Ground vegetation plays a greater role in the consumption of nutrients than tree production. The nutrients can be compared more easily if they are expressed per unit of dry matter produced, particularly potassium which is consumed by the ground vegetation 2–6 times more than by the tree.

The annual nutrient requirement of trees can be illustrated by the amounts taken up by trees from the soil, retained by them and returned in litter to the soil. In the present study, the trees' annual nutrient requirement was estimated as the sum of the nutrient quantities bound in the annual biomass production and of those returned to the soil in litter. However, nutrient quantities taken up from the soil are underestimated because they do not include the amounts leached from the canopy by precipitation.

Table 8 shows that the amounts of N, P, K, Ca and Mg taken up annually from soil by trees, or the annual requirement of nutrients by trees, were about 112, 10,

Table 7. Amounts of various nutrients bound to annual biomass production (kg ha^{-1})

Compartment	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Trees	68.7	6.2	33.5	77.5	10.7
Shrubs	1.0	0.1	0.4	1.5	0.3
Ground vegetation	8.8	1.4	11.8	5.5	3.0
Total	78.6	7.7	45.8	84.5	14.0
Nutrients as % of total annual nutrient requirement					
Tree	87.4	79.9	73.1	91.7	76.3
Shrubs	1.3	1.7	1.2	1.8	2.0
Ground vegetation	11.2	18.4	25.8	6.5	21.7
Nutrient consumption per unit of dry matter produced (kg 1000 kg^{-1} dry matter)					
Trees					
P. koraiensis	8.9	0.7	3.0	3.6	0.9
Broadleaved species	15.5	1.2	9.2	16.8	3.7
Shrubs	6.2	0.8	2.9	8.9	1.7
Ground vegetation	14.2	2.3	19.0	8.9	4.9
Nutrient consumption per unit of stem volume increment (kg m^{-3} stemwood)					
P. koraiensis	13.5	1.0	4.5	5.4	1.4
Broadleaved species	58.8	4.6	35.0	63.8	13.0

Table 8. Nutrients taken up annually by tree and returned in litter (kg ha^{-1})

Component of balance	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Taken up from soil by trees	112.2	9.9	46.9	133.8	21.6
Retained by trees	68.7	6.2	33.5	77.5	10.7
Returned in litter	43.5	3.7	13.4	56.3	10.9
Amount returned as % of amount taken up	39	38	29	42	51

47, 134 and 22 kg ha^{-1}, respectively. The Table also shows that 39% of nitrogen, 38% of phosphorus, 29% of potassium, 42% of calcium and 51% of magnesium are returned to the ground in litterfall. The percentage of calcium returned is larger than that of nitrogen, phosphorus and potassium, possibly because of the trees' internal nutrient cycle. Nitrogen, phosphorus and potassium are believed to be translocated to the growing parts, and are re-used in various biosynthetic processes, but calcium is considered to be less mobile.

Using the data from the annual changes in stand biomass (Table 2), we can extend our examination of the annual nutrient balance in the stand (Table 9). Interest is concentrated especially on the amount of nutrients available to the plants in soil (Table 3). It is obvious from the data that the soil in the stand is fertile, and the main nutrient elements in the stand, such as available nitrogen, are sufficient for the plants' requirements.

5 Conclusions

5.1 Broadleaved/*P. koraiensis* forest is the main type of forest in NE China, and can thrive for long periods of time. Its potential for survival is closely related to its nutrient cycle process.

5.2 In the broadleaved/*P. koraiensis* forest, more nutrients are returned to soil in litter than in coniferous forests.

Table 9. The annual nutrient balance in the stand (kg ha^{-1} yr^{-1})

Component of balance	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Bound into biomass at beginning of measurement period	827.1	87.9	662.9	1246.6	141.5
Bound to annual total production	78.6	7.7	45.8	84.5	14.0
Removal in litter	52.3	5.1	25.3	61.8	13.9
Bound to annual net production	26.2	2.6	20.5	22.7	0.0
Bound into biomass at end of measurement period	853.3	90.5	683.4	1268.7	141.5

5.3 Although the soil in the stand is fertile, the stand's annual production is not high compared with plantations, perhaps because of poor methods of management. Therefore, it is necessary to adopt sound forest management practices to increase forest productivity.

6 References

Mälkonen, E. 1974. Annual primary properties and nutrient cycle in some Scots pine stands. *Folia For.*, no. 210, 53–54.

Pritchett, W. L. 1979. *Properties and management of forest soils.* London: Wiley.

Nitrogen cycling in a *Quercus/Fraxinus* (oak/ash) woodland in northern England, examined using the computer model FORTNITE

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Abstract

Nitrogen cycling in a mixed deciduous woodland (Meathop Wood, a UK International Biological Programme research site) is considered in 2 ways: (i) through the presentation of a 'static' annual nitrogen cycle, and (ii) by dynamic modelling using the computer model FORTNITE. In the 'static' cycle, the nitrogen content of forest components and annual transfers are quantified in terms of kg N ha^{-1} and kg N ha^{-1} yr^{-1} respectively. Data required for the dynamic modelling are presented, as are predictions (model outputs) of changes in tree growth, forest floor and available nitrogen parameters over 100 years following the 1939 coppicing of the woodland. Predictions for the years 1962, 1967 and 1972 closely match estimates derived from field measurements. The modelling also suggests that the woodland is unlikely to change its species composition during the next 50 years, except that the *Betula* (birch) may die out. The effects of removing one tree species, *Acer pseudoplatanus* L. (sycamore), on the growth of the woodland, and the F+H layer and available nitrogen were also simulated using the dynamic model. Both approaches to the study of nitrogen cycling are discussed with respect to their value for integrating scientific research and for developing scenarios on the effects of environmental factors and management practices on forest structure and productivity.

1 *Introduction*

If both the short- and long-term changes in the forest as it develops, and the consequences of forest management practices on the environment and on forest site quality are to be predicted with any satisfactory degree of accuracy, the biological functioning of the forest ecosystem needs to be properly understood. The complexity and dynamic nature of forests make difficult any long-term predictions, particularly when they comprise several interacting tree species. Though many research studies can be usefully carried out on component parts of forests, it is only when the forest is viewed as an integrated unit that the complex interplay of environmental factors and the biological processes can be fully visualized. As part of the International Biological Programme of the late 1960s and early 1970s, a semi-natural woodland ecosystem, Meathop Wood, in northern England, was chosen for such a study, and many papers have been published describing aspects of the research (eg Bunce 1968; Frankland 1982; Gray *et al.* 1974; Harkness *et al.* 1986; Harrison 1979, 1985; Mosse 1978; Satchell 1971; Satchell *et al.* 1971; Spink 1975; Swift 1977; Swift *et al.* 1976; Sykes & Bunce 1970; White & Carlisle 1968; White & Harrison 1987).

2 *Study site*

The site is a mixed deciduous coppice-with-standards woodland, located on the northern edge of Morecambe Bay at 54°12'N and 2° 53.5'W, with an oceanic climate. The tree species comprise *Quercus petraea* Mattuschka (Liebl.) (sessile oak), *Fraxinus excelsior* L. (common ash), *Betula pubescens* Ehrh. (downy birch) and *B. pendula* Roth (silver birch), and *Acer pseudoplatanus*, with an understorey of *Corylus avellana* L. (hazel). The site was last fully coppiced in 1939, and its tree age structure partially reflects the effect of this management. The soil is an acid (pH 4.3–7.0) brown earth, averaging 13.5 cm in depth, derived from Silurian slates and shales, overlying Carboniferous limestone.

3 *Static model of nitrogen cycling*

Nutrient cycling processes were a central theme in the study of this woodland. In the nitrogen cycle of the woodland (Figure 1), all the values presented are derived from measurements made in the woodland, except for estimates of (i) direct assimilation of nitrogen as ammonia from the atmosphere by the tree canopy from Eriksson (1966), and (ii) N fixation, which has been calculated on the assumption that the nitrogen capital within the soil remains constant with time, by the formula used by Bormann *et al.* (1977):

$$\begin{aligned} N_{fix} = {} & \text{N in net annual tree production} \\ & + \text{N lost from the soil} - \text{N in rainfall and aerosols} \\ & + \text{gaseous uptake by tree canopy.} \end{aligned}$$

The value of such a budgetary cycle is that it provides information on the amounts and distribution of nitrogen capital within the forest ecosystem. It shows clearly that the trees' nitrogen requirements far exceed the amounts needed for annual increments in tree growth, for much of the nitrogen taken up each year is subsequently lost, being recycled to the soil in organic debris. It indicates, too, that the trees conserve nitrogen by withdrawing over 60% of the element from the leaves prior to leaf-fall; whether there is an equivalent conservation of nitrogen prior to root death is unknown. We can also obtain an estimate of the amounts of nitrogen gained (though the input

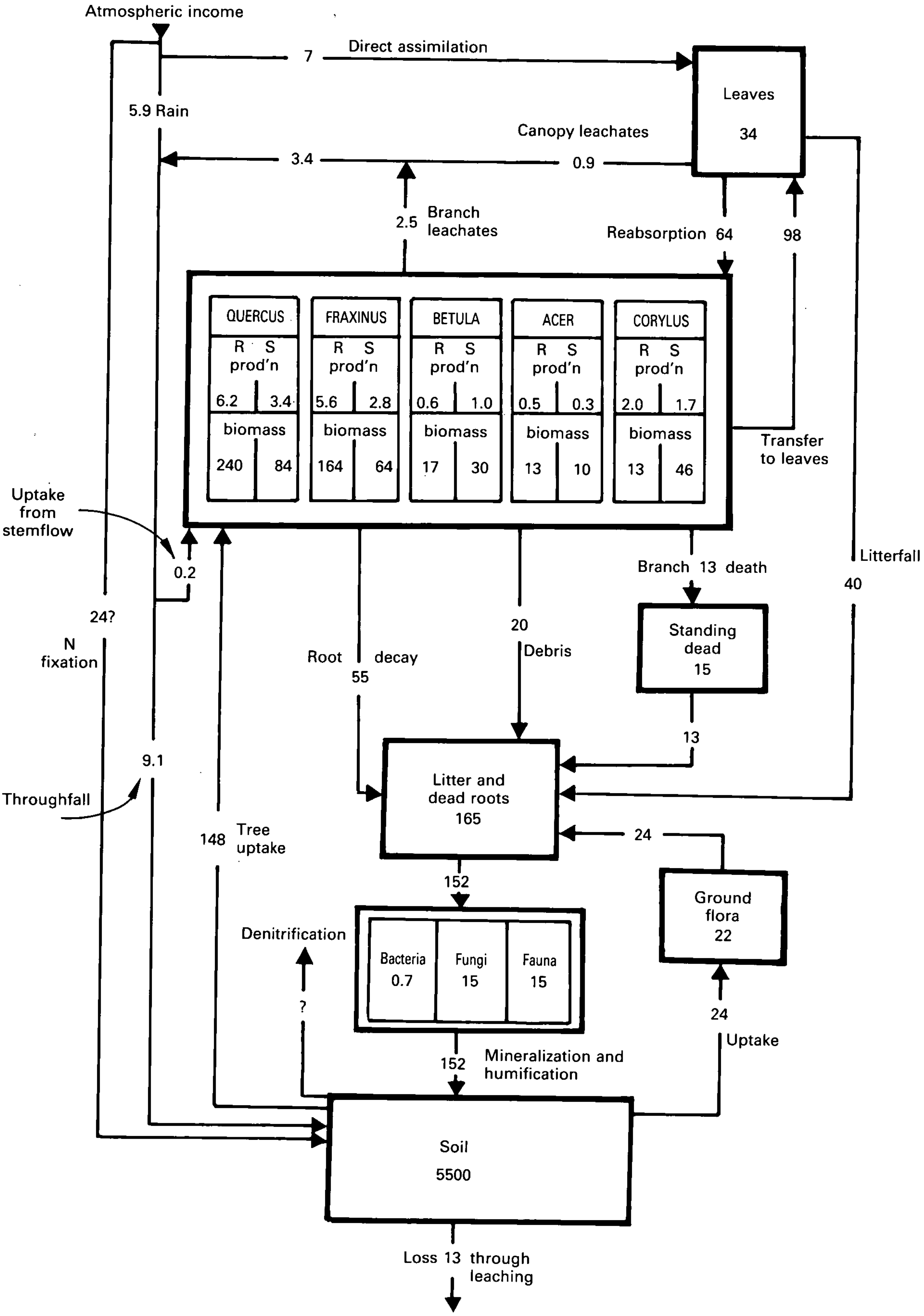

Figure 1. The nitrogen cycle of the mixed deciduous woodland in Meathop Wood, UK; nitrogen contents in kg ha^{-1} and annual net transfers in kg ha^{-1} yr^{-1}

from N fixation is uncertain) and lost from the ecosystem. The forester can ascertain the approximate amount of nitrogen which would be removed in timber, and this amount can be roughly equated with the known capital within, and inputs to and losses from, the ecosystem. Unfortunately, the research forester cannot use this type of 'model' to understand the consequences of the various management practices, how they may influence future forest productivity, and which of the practices are most important in this respect.

4 Dynamic model of nitrogen cycling

Full integration of research data, such that the influences of different environmental factors and the interactions of the various dynamic biological processes in the forest ecosystem, and possible outcomes of specific forest management strategies, can all be examined, is really only possible through the use of computer simulation models. The forest computer model called FORTNITE, published by Aber and Melillo (1983), is, to our knowledge, the most comprehensive model that is suitable for a multi-species, uneven-aged forest ecosystem, and which integrates tree growth parameters, environmental factors and nitrogen cycling elements. It also gives the potential to 'manipulate' the forest in a variety of ways, and to indicate the consequences in the outputs. Validation runs show that the model accurately predicts successional changes in tree growth, species composition, leaf production, forest floor biomass and dead wood biomass following clearfelling, for some North American forests.

Details of the data required to run the model are given by Aber and Melillo (1983). In summary, 4 classes of data are required: (i) environmental factors, (ii) tree growth parameters, (iii) tree nitrogen response data, and (iv) forest floor decomposition and nitrogen variables. The environmental factors are (i) the heat sum (degree days) for the global distribution limits (DMIN and DMAX) of each tree species, calculated by the formula given by Botkin *et al.* (1972), (ii) the actual evapotranspiration levels (WMIN and WMAX) for the same distribution limits, calculated by the method given by Thornthwaite and Mather (1957), and (iii) the responses of each species to varying light intensities—first, an estimate of the lowest percentage of full light intensity (LMAX) below which the species fails to grow and reproduce itself, and, second, regression constants (A1) and coefficients (A2 and A3) for the so-called light-demanding and shade-tolerant groups of species (Aber *et al.* 1979). The tree growth parameters are the constants and coefficients from equations relating the tree diameter at breast height or 1.3 m (dbh) to tree height (B2 and B3), stem dry weight (SA and SB), branch dry weight (BA and BB), root biomass dry weight (RA and RB), and the constant and coefficient for the regression relating crown width to stem dbh (SLTA and SLTB) for all species (see Whittaker *et al.* 1974). Maximum leaf dry weight (LFWT) produced 100 m^{-2} area canopy, the root/stem biomass ratio (RTST), the maximum likely stem dbh (DIMX) and age (AGMX) and the numbers of regenerating saplings 100 m^{-2} (SAPN) under optimum conditions in the site are also required for each tree species. The tree nitrogen response data are the constants and coefficients (N1–N5) from regressions of tree responses on available soil nitrogen based on fertilizer trials, for 3 groups of tree species classed according to their nitrogen requirement (Mitchell & Chandler 1939; Aber *et al.* 1979). For the decomposition module, the model requires information for up to 6 leaf litter types, 10 size classes of above-ground woody material, woody roots, fine roots, twigs and forest floor material. These data are (i) the fraction of the initial litter weight as nitrogen, (ii) the fractional weight loss per year, (iii) the amount of nitrogen immobilized per gram weight loss, (iv) the fraction of weight as nitrogen when litter cohort transfers to the

Table 1. Data file: tree variables required for FORTNITE model (data structured as input file)

```
MEATHOP RAW DATA   NO CLEARFELL
                NRVAR=        4
 KTMS=      25.  NYR=      100.  KPNT=       3.  FRPT=     1.
 NSPP=       5 NSVAR=       33
 SPNM   Q PE   F EX   B PE  A PS   C AV
 G          1.40    1.40    1.70    0.65    1.60
 B2        .0053   .0043   .0043   .0048   .0058
 B3        .0007   .0007   .0007   .0008   .0003
 LFWT      302.    209.    360.    237.    180.
 DMIN     1755.   1755.    735.   1755.   1251.
 DMAX     7375.   7375.   6590.   7375.   6590.
 WMIN      510.    510.    382.    510.    455.
 WMAX      682.    682.    682.    682.    682.
 RTST      0.75    0.67    0.23    0.57    0.33
 DIMX      170.    170.     50.     80.     25.
 AINC       .01     .01     .01     .01     .01
 AGMX      300.    200.     90.    120.     50.
 SAPN        4.      3.      1.      1.      8.
 LMAX       .20     .30     .20     .20     .05
 A1        1.00    1.00    1.00    1.00    1.00
 A2      -4.640  -4.640  -4.640  -4.640  -4.640
 A3         .05     .05     .05     .05     .05
 TC          1.      2.      3.      5.      4.
 SA        74.7    64.5    72.5   165.5    91.7
 SB        2.38    2.39   2.388   2.123   2.144
 BA        12.5    17.5   21.76    26.5    55.3
 BB        2.72    2.67   2.393   2.459   2.047
 RA        66.8    52.6   22.03   100.2   50.86
 RB        2.45    2.50   2.389   2.228   2.104
 SLTA      1.13    1.18    1.67    1.63    3.02
 SLTB      .219    .222    .106    .199    .081
 N1        2.79    2.99    2.94    2.94    2.94
 N2     -.00175 -.00175 -.00234 -.00234 -.00234
 N3      219.77  207.43  117.52  117.52  117.52
 N4        -0.6    -5.0    -1.2    -1.2    -1.2
 N5         1.0     2.9     1.3     1.3     1.3
 DGRO        1.      1.      1.      1.     .1.
NPLOT=        1 NTREE=      12
SPECIES       1. DBH        16.
              1.             1.
              2.             3.
              3.             3.
              4.             .2
              5.             1.
              5.             1.
              5.             2.
              5.             2.
              5.             2.
              5.             3.
              5.             3.
```

next compartment, (v) the destination compartment for the litter cohort, and (vi) the litter type.

To run the model, a simulated starting plot of 100 m^2 is described as the number of trees occurring, their species identity, and their dbh in cm. A further input file is required containing data for the study site, namely the accumulated degree days (°F), actual annual evapotranspiration rate, a relative solar energy input factor, the timing and degree of harvesting intensity required, and an estimate of the nitrogen available from precipitation, mineral soil and fertilization. The structure, development and functional rationale, together with a listing of the model program written in FORTRAN 66, are presented by Aber and Melillo (1983).

We have recently started to examine the research data for Meathop Wood, using this model. Our first objectives were to examine (i) the possible time-course of woodland development since the last full coppicing of the woodland, when the stems of *Fraxinus, Corylus, Acer, Betula* and all but the largest *Quercus* were removed, and (ii) the possible effects of a management practice in which the *Acer* trees were removed at 52 years after regrowth; this is an invasive species, and the timber is of little commercial value. We would have liked to investigate the influences of thinning and coppicing the woodland, but the computer program as written does not allow these aspects to be investigated.

To study the long-term development of the woodland, the model was run (using a VAX 8600 computer) for 100 years, with an initial plot of trees representative of the situation which would have been present a year or so after the coppicing. The sapling numbers (SAPN) were taken as the relative numbers of each species which grew up following the coppicing; these figures were derived from tree age distribution data for the woodland. The relationships between heights of trees and dbh (1.3 m) for the species studied do not follow the parabolic function described by Aber and Melillo (1983); instead, they were related linearly by an equation in the form:

$$\frac{1}{h(\mathrm{cm})} = f\left(\frac{1}{\mathrm{dbh}} + k\right)$$

so the program and B2 and B3 in Table 1 were adjusted accordingly. Values for LFWT for each species were calculated in grams of leaf material m^{-2} of tree crown area (incorrectly quoted as g 100 m^{-2} of crown area in the original document—J D Aber, pers. comm.), based on litterfall data. Because specific details on the sensitivity of growth and seed generation to light intensity and on the general growth responses to nitrogen fertilization, as determined by Mitchell and Chandler (1939), are not available for these tree species, the appropriate equations were selected (Aber *et al.* 1979) based on published information on generalized tree responses (Evans

Table 2. Data file: decomposition and nitrogen variables required by FORTNITE model (data structured as input file)

NCMPAR=	7	NFVAR=	20				
FNM1	F+H	FFLR	LRGE	ROOT	FINE	LEAF	TWIG
FNM2	LAYR	WOOD	WOOD	WOOD	ROOT		
0.	.013	.200	.000	.020	1.	6.	
0.	.019	.495	.000	.019	1.	6.	
0.	.013	.292	.000	.020	1.	6.	
0.	.019	.331	.000	.019	1.	6.	
0.	.013	.495	.000	.020	1.	6.	
0.	.007	.420	.000	.019	1.	6.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	.00	0.005	2.	3.	
0.	.003	.095	0.00	0.006	1.	4.	
0.	.008	.595	0.00	.020	1.	5.	
0.	.009	.120	0.00	.015	1.	7.	
0.	.005	.370	0.00	.010	1.	2.	
NCOHRT	7						
16.	.186	.310	−.025	5.	0.	1.	
2.14	.047	.363	.00	.02	1.	6.	
4.7	.014	.095	.00	0.005	2.	3.	
4.8	.017	.095	.00	0.006	1.	4.	
2.70	.015	.595	0.00	.020	1.	5.	
1.33	.007	.370	0.00	0.005	2.	2.	
2.70	.023	.120	0.00	.015	1.	7.	
DDEC1	1.00	DDEC2	1.00				
IHARV 1							
DLIM 0. 0. 0. 0. 0.							
REGEN 0. 0. 0. 0. 0.							

1984, 1986). The model was run with 7 classes of litter cohorts initially defined in terms of biomass, nitrogen content and decomposition rates (Table 2), a sophistication provided for, but not used, by Aber and Melillo (1983). The decomposition rates of organic matter in the F+H layer and of twig material on the soil surface were estimated by modelling the rate of incorporation of ^{14}C-bomb carbon from the atmosphere (Harkness *et al.* 1986). The turnover rate of the fine roots used is very similar to the initial k values found by experimentation elsewhere (McClaugherty *et al.* 1984). The woodland degree-day sum and actual evapotranspiration values, with net available N input from the mineral soil (10 kg N ha^{-1} yr^{-1}), are given in Table 3.

During the testing of the model, the decomposition rates of the fine roots and the F+H layer on the soil surface, and the tree responses to light and available nitrogen, were found to be very sensitive parameters, and hence these factors require particular attention in research studies.

Table 3. Data file: site variables required for the FORTNITE model (data structured as input file)

NPVAR= 5

YEAR	DEGD	AET	PHI	CUT	N IN
1	3350.00	595.00	1.00	0.00	0.1600
2	3350.00	595.00	1.00	0.00	0.0100
3	3350.00	595.00	1.00	0.00	0.0100
4	3350.00	595.00	1.00	0.00	0.0100
5	3350.00	595.00	1.00	0.00	0.0100
6	3350.00	595.00	1.00	0.00	0.0100
7	3350.00	595.00	1.00	0.00	0.0100
8	3350.00	595.00	1.00	0.00	0.0100
9	3350.00	595.00	1.00	0.00	0.0100
10	3350.00	595.00	1.00	0.00	0.0100
⋮					
50	3350.00	595.00	1.00	0.00	0.0100
⋮					
80	3350.00	595.00	1.00	0.00	0.0100
⋮					
90	3350.00	595.00	1.00	0.00	0.0100
⋮					
100	3350.00	595.00	1.00	0.00	0.0100

The computer simulation of the woodland resulted in a close match between the predicted biomass values for all the 5 species and the biomass estimates derived for the woodland during the period 1962–72 (Table 4). It also showed that the total biomass may increase to about 280 tonnes dry matter ha^{-1} (Figure 2), with *Quercus* and *Fraxinus* forming the majority of the biomass (Figure 3). Thereafter, there will be a short-term decline in the live biomass, due to a short-term increase in tree mortality. *Betula* will show a significant decline, and this genus may well die out (Figure 3); this is a realistic prediction in that *Betula* is a short-lived

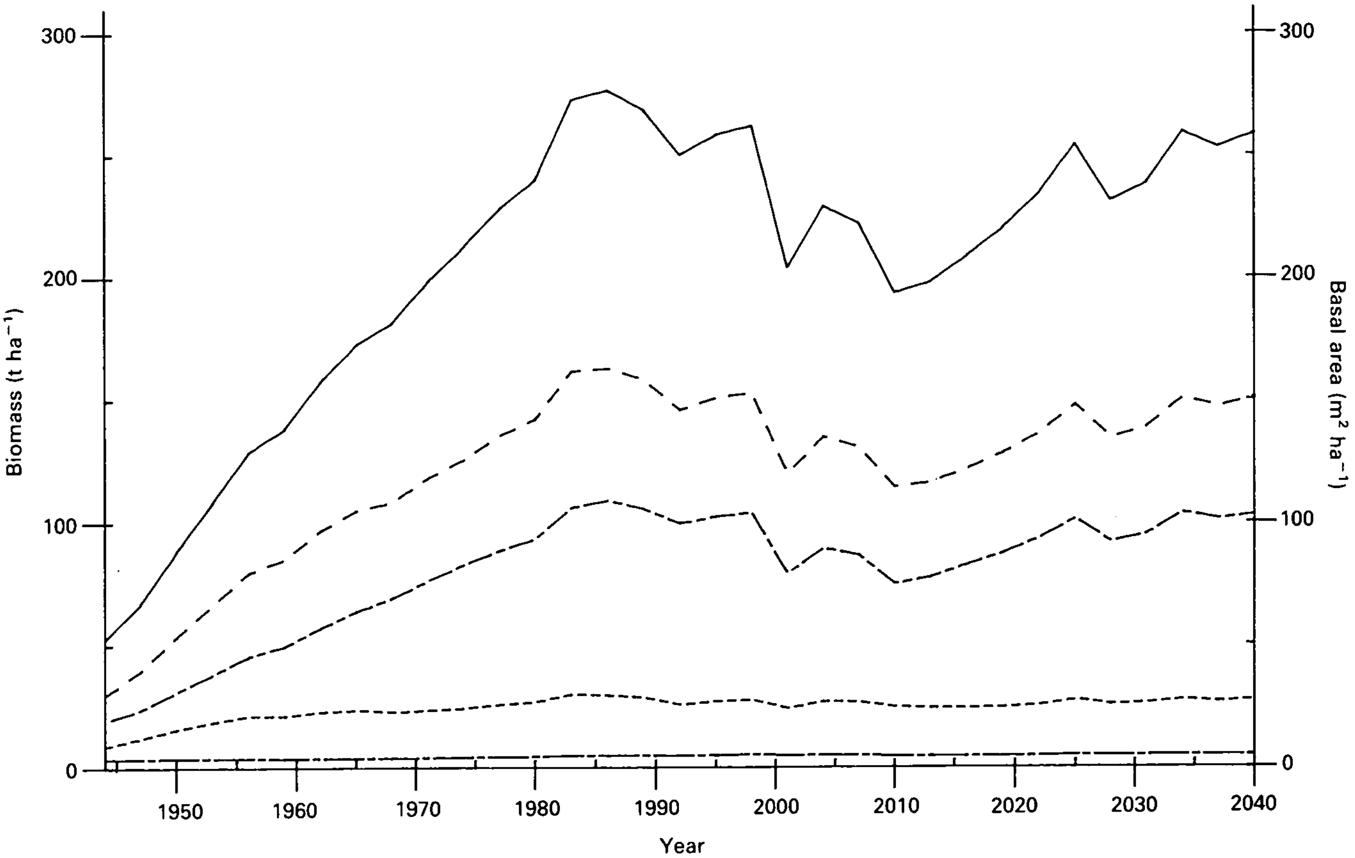

Figure 2. Trends in the biomass of all tree species combined and tree components in Meathop Wood, predicted using FORTNITE
(——— total; - - - basal area; — — — stems & branches; — - — roots; —— - —— leaves)

Table 4. Comparison of predicted (P) and measured (M) biomass values for Meathop Wood

	1962		1967		1972	
	P	M	P	M	P	M
Quercus	58	68	74	78	100	88
Fraxinus	56	46	61	53	69	63
Betula	20	16	16	18	13	20
Acer	8	5	12	6	15	7
Corylus	15	10	10	18	7	19
Total tree	158	146	173	173	204	198
Stem + branch	97	88	104	108	121	124
Roots	57	58	65	65	79	74
Basal area	23	18	22	23	24	25

Measured data provided by J M Sykes and R G H Bunce
Biomass is expressed as t ha^{-1} and basal area as m^2 ha^{-1}

tree and individuals can now be seen in the woodland to be rotting and falling over. *Corylus* may show some slight decline, but death in some coppice stools will probably be matched by new recruitment. *Acer*, the invasive species, may not become a major component of the woodland, and could even show a decline after 80 years. Apart from these minor changes, the model predicts that the woodland will probably remain in a similar state as at present.

The computer simulation also shows that the inputs of leaf, root and branch litters increase only slowly as the woodland ages, following the last coppicing (Figure 4). The predicted values, perhaps with the exception of the dead rootwood biomass, agree well with the estimates from field measurements. The dead wood remaining within the woodland canopy increases with time, as trees age; this result is as expected.

The model also predicts a slow increase in the F+H layer material on the soil surface; this prediction is consistent with the known tendency for organic matter to accumulate in soils under woodland (Van der Drift 1971). The so-called available nitrogen shows a significant increase, along with the organic matter in the F+H layer, as the woodland ages; again, this prediction is consistent with known accumulation of nitrogen in soils under woodland (Jenkinson 1971).

The computer simulation of the removal of all the *Acer* trees 52 years after coppicing suggests that this would result in significant increases in the growth of *Fraxinus* and *Quercus* (Figure 5), due partly to increases in the amount of available nitrogen (Figure 6). The prediction is in agreement with the well-known effects of thinning on the growth of trees in forest ecosystems (Evans 1984; Carey *et al.* 1982). It is all the more interesting, as conservationists often wish to remove *Acer* from British woodlands, because it is considered a non-native species. Its removal could result in larger

Figure 3. Trends in total biomass of each tree species in Meathop Wood, predicted using FORTNITE (---- Quercus; — — —Fraxinus; ——— Betula; — — — Acer; -·-·-·- Corylus)

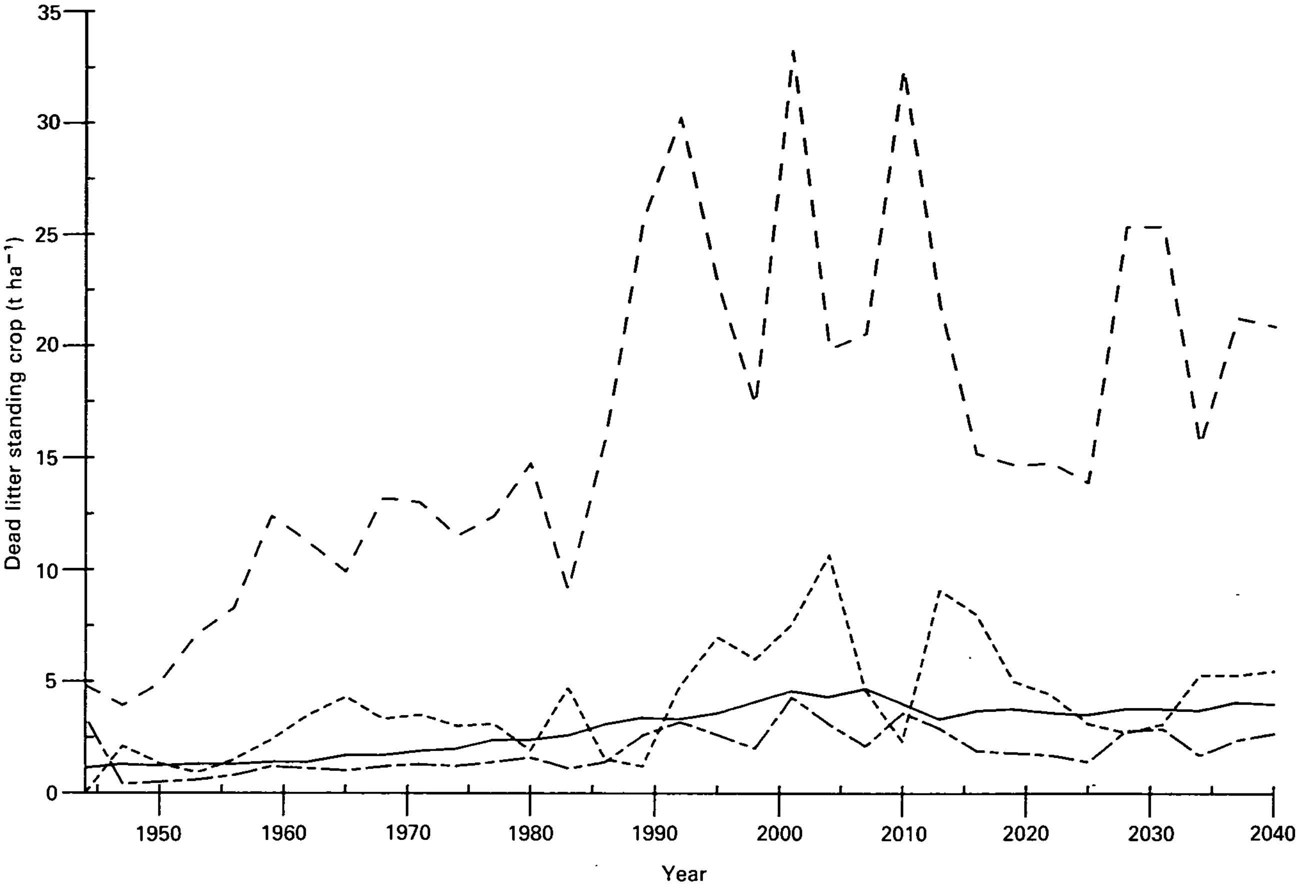

Figure 4. Trends in forest floor components and dead wood in the canopy of Meathop Wood, predicted using FORTNITE
(- - - wood on forest floor; — — — large wood in canopy; — - — rootwood; ——— fine roots)

Figure 5. Effects on the biomass of Quercus *and* Fraxinus*, predicted using FORTNITE, of the removal of* Acer *stems*
(——— Quercus*; — — —* Fraxinus*; — - —* Acer*; - - - - after removal of* Acer*)*

Figure 6. Effects on the amounts of F+H layer material and available nitrogen in the soil, predicted using FORTNITE, of the removal of Acer *stems*
(——— F+H layer; — — — available N; - - - after removal of Acer*)*

Fraxinus and *Quercus* trees, thus improving the potential yield of the more important timber.

5 Conclusions

From this limited application of the simulation model FORTNITE to the Meathop woodland data, our conclusions are that it has considerable potential. Not only can it be used to integrate data from various forest studies in a dynamic way, thus enabling a more thorough examination of the research information, but it can also be applied, as Aber and Melillo (1983) indicate, to predict the potential long-term effects of forest management practices on forest ecosystems.

We would recommend that this model is considered as a means for (i) integrating the research data, and (ii) developing scenarios on the effects of various management practices in the Changbai Mountain Reserve.

6 Acknowledgements

We are particularly grateful to J M Sykes and R G H Bunce of the Institute of Terrestrial Ecology, for providing basic data on the tree growth parameters from which the relationships with dbh were derived, and in addition the tree production data (Table 4) for comparison with the model outputs.

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Water retention and erodibility in natural and disturbed mountain forest soils

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Abstract
This paper first takes a close look at the composition of 'natural' soils and discusses the manipulation and related erosion catastrophes that forest ecological systems have undergone during centuries of management. Quantitative comparisons are made of several forest areas to show the effects of the various soil moisture parameters. Finally, the possibility of regenerating various forest areas is examined, and those forest types classified whose soils require absolute conservation because of their extremely low regenerative capacity.

1 Introduction

The forest, with its undisturbed soil, not only acts as a great reservoir but also controls the movement of water. Throughout the mountainous areas of Europe, forests have spread to high altitudes, following the last major glaciation in the Atlantic Climate Interval. Alpine forests are known to have reached altitudes of 2200 m. During this time, major soil formations 2200 m above sea level (asl) have occurred in the subalpine region, and act as regulators of water movement. In the course of the later climatic fluctuations and the beginning of human settlements in the mountain valleys, the woodlands have diminished and their soil has been converted. The consequences of the ever-increasing deforestation in high montane and subalpine regions have become particularly evident in the water regime: soil moisture is subject to strong seasonal fluctuations, with mudflows and avalanches becoming widespread events.

A series of such natural catastrophes occurred toward the end of the 19th century, following which date state agencies were founded to provide torrent and avalanche control services and to conduct forestry research (Strele 1936; Killian 1974). In the western Alps, afforestation was introduced in an exemplary manner (Mougin 1919).

The most recent avalanche catastrophes occurred in the Tyrol in 1950–51 and prompted an increased effort throughout the Austrian Alps to afforest the higher areas and to promote interdisciplinary research of specific problems.

During the course of this project, the study group investigated the water regime of different forest soils and the possibilities for regenerating water reservoir space.

2 Influence of soil parameters on the water regime of various forest ecosystems

Natural soil units are used to compare the influence of soil parameters on the characteristic values of the water regime.

Soil investigations in the subalpine region have revealed that natural soils have been reduced to an infinitely small area, and only survive in economically unprofitable sites. Soils that are almost natural are more common. These were utilized during more favourable climatic periods and then abandoned, whereupon the processes of natural regeneration encouraged their restoration to their natural state. Another group of forest soils was so strongly manipulated by management that their characteristics can only be discerned by precise comparative studies. The soils developed in a manner that weakens some functions of the water and bioelement regime, while strengthening others. In soil genetics, these units are often termed 'degenerate'. This paper refers to them as 'management units' or pastures.

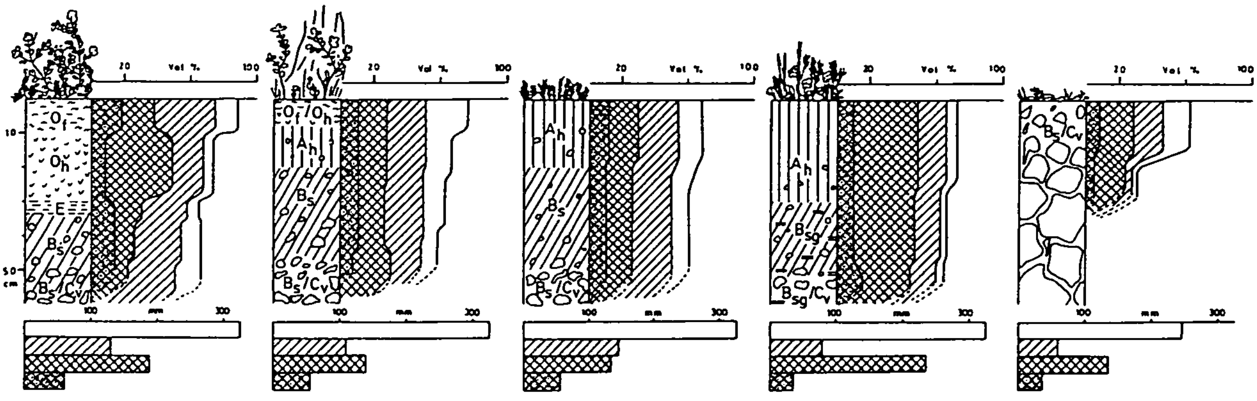
One last group of forest soils has been transformed beyond all recognition, as a result of exploitation by machinery. Soil denudation or aggradation has destroyed the natural water and bioelement storage areas, or at least severely reduced them. The following paragraphs compare the characteristic values of the water regime with the soil parameters of the above units.

2.1 Forest ecosystems on siliceous parent material in the Austrian Alps

In the subalpine and high montane areas of Austria's central Alps, the natural ecological unit is the forest of *Pinus cembra* L. (Arolla pine) and *Rhododendron ferrugineum* L. (alpine rose), growing on iron podzols on crystalline, acid-weathered siliceous parent material. From radioactive carbon dating, it has been confirmed that this forest type existed on both the north and south slopes of the Alps at altitudes of 1500–2200 m (2400 m) as long as 3000–4000 years ago (Neuwinger 1970). Today's timber-line is found at 1900 m asl, and the vegetation cover on the north slope between 1900 m and 2200 m (2400 m) is struggling for survival. It comprises forest in various stages of retreat, with stunted and young growth on slightly changed podzols of the former forest. These forms are transitional from iron podzols to iron-humus podzols often with very shallow profiles and embedded charcoal.

On the south slope of the Alps and in southern exposures on the north slope, management has cut back the forest to 1700 m, and grazing has caused severe changes in the soil. Podzol colluvia have developed, in which the remains of eluvial and illuvial horizons, as well as burnt horizons, can still be discovered by careful examination.

Figure 1 shows the soil profiles of this unit in a manipulation series (anthropogenic series), and the change in the most important characteristic values of the water regime. Figure 2 presents a similar comparison; however, the influence of the parent material has given it hydromorphic character. Both series are found frequently, with pastures comprising the greatest area in each case.



Natural iron podzol under undisturbed forest of *Pinus cembra* and *Rhododendron ferrugineum*

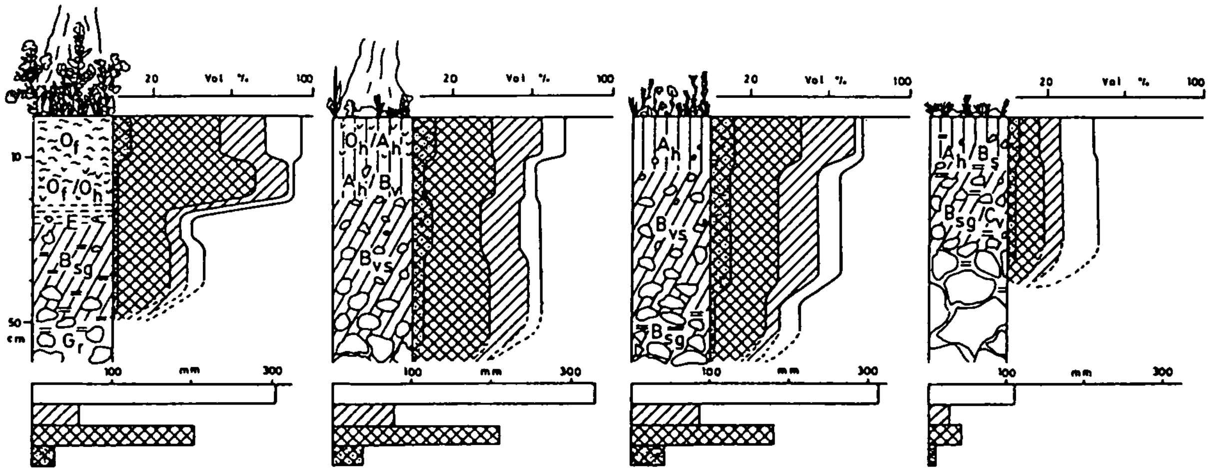
Almost natural podzol colluvium under forest of *Pinus cembra* and *Rhododendron ferrugineum* formerly used as pasture

Extensively used pasture soil (podzol colluvium) under dwarf shrub heath

Pseudogley podzol colluvium under intensively used, dunged pasture

Podzol remains under ski slopes

Figure 1. Anthropogenic change in the Pinus cembra/Rhododendron ferrugineum *forest ecosystem over iron podzol on siliceous rock on Austria's central Alps (source: Neuwinger 1987a)*
☐ *(air-)pore space;* ▨ *pore space for seepage water;* ▩ *pore space for retention water;* ▦ *minimum water retention (difference between field moisture capacity and maximum water saturation)*



Almost natural iron podzol under forest of *Pinus cembra/Rosa pendulina* formerly used as pasture

Almost natural podzol colluvium under forest of *Pinus cembra, Larix* and *Picea* with occasional use as pasture

Intensively used pasture soil (pseudogley podzol colluvium) under sparse grassland

Gley podzol remains under ski slope

Figure 2. Anthropogenic change in the Pinus cembra/Rhododendron ferrugineum *forest ecosystem over gley podzol on argillaceous slate (source: Cernusca 1986)*
☐ *(air-)pore space;* ▨ *pore space for seepage water;* ▩ *pore space for retention water;* ▦ *minimum water retention (difference between field moisture capacity and maximum water saturation)*

Disturbance to the humus horizons in the second series has had a detrimental influence on the water regime. Because pasture soils are very wet, mudflows are a frequent occurrence in steep terrain.

2.2 Forest ecosystems on calcareous shales in the Austrian central Alps

Soils on the calcareous shales of Austria's central Alps occupy a special position because, in warm sites, valuable fodder plants are favoured by the rich supply of nutrients in the parent soil. For this reason, these soils have long been used for intensive grazing and hay crops high up into alpine regions (2400 m).

However, as in the first example, forests have survived in those areas not worth managing. The moist subalpine climate gives rise to the formation of podzols with a good water-retention capacity and a high porosity for seepage water. The conversion of sunny exposed sites to pasture has led to significant changes in the soil. Exploitation has robbed the mature soil of its characteristic features and initial stages have appeared, such as para-rendzinas and moderately acidic brown soils. To a large extent, these soils are characterized by stagnant water.

Figure 3 shows the differences in the soil-dependent characteristic values of the water regime in the disturbed and undisturbed forest and pasture soils. Those soils on calcareous shales with their extremely fertile mountain pastures are more widespread in the western Alps than in the eastern Alps, and their exploitation had led to widespread forest devastation and erosion.

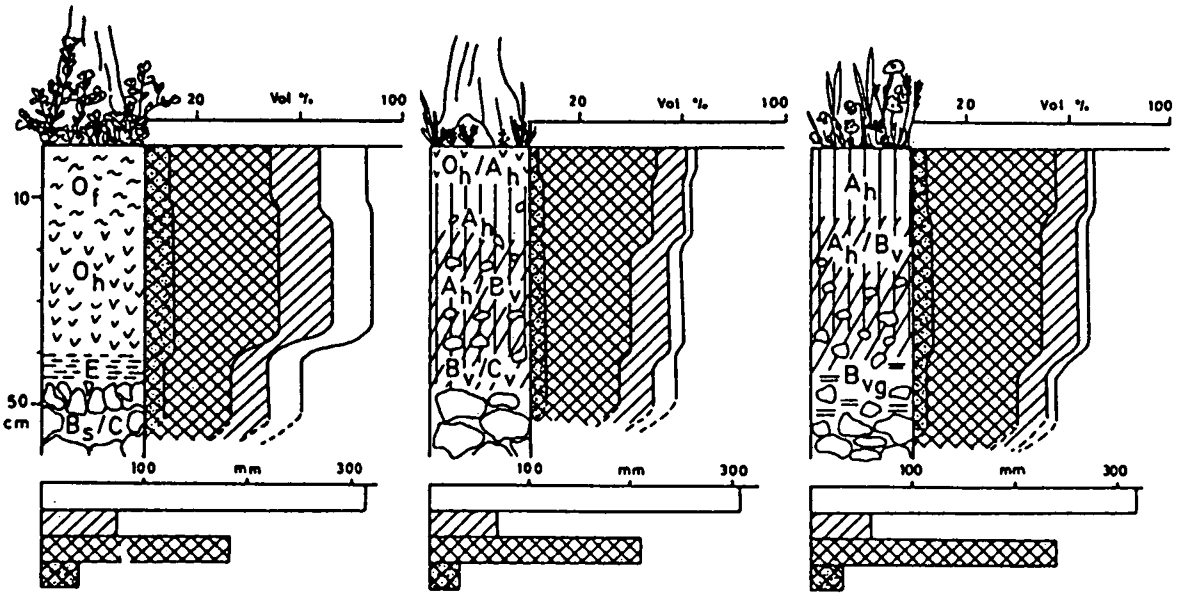
2.3 Forest ecosystems in Austria's calcareous Alps

Two types of forest ecosystems with different soil formations depending on the parent material are found. Coniferous forests with dwarf shrub undergrowth on shallow rendzinas are widespread on hard limestones and dolomites, while mixed deciduous/coniferous forests, with an understorey of grass and herb species, are found over loamy brown soils on weathered exposures of the soft, clayey limestones and on siliceous moraines.

For a long time, exploitation has influenced the differences in the nutrient- and water-retention capacity of the soils in these areas. Sites devoted to grazing and hay crops are concentrated around the areas with loamy soil that guarantee sufficient water and a balanced supply of bioelements throughout the entire growing season of the plants. Figure 4 shows the distribution of the characteristic values for water in the profile of natural and manipulated rendzinas, while Figure 5 illustrates an anthropogenic series of loamy brown soils,.

3 Potential of forest regeneration and rehabilitation of the water regime in disturbed ecosystems

In mountainous areas, the potential for regenerating disturbed ecosystems is closely linked to the soil's



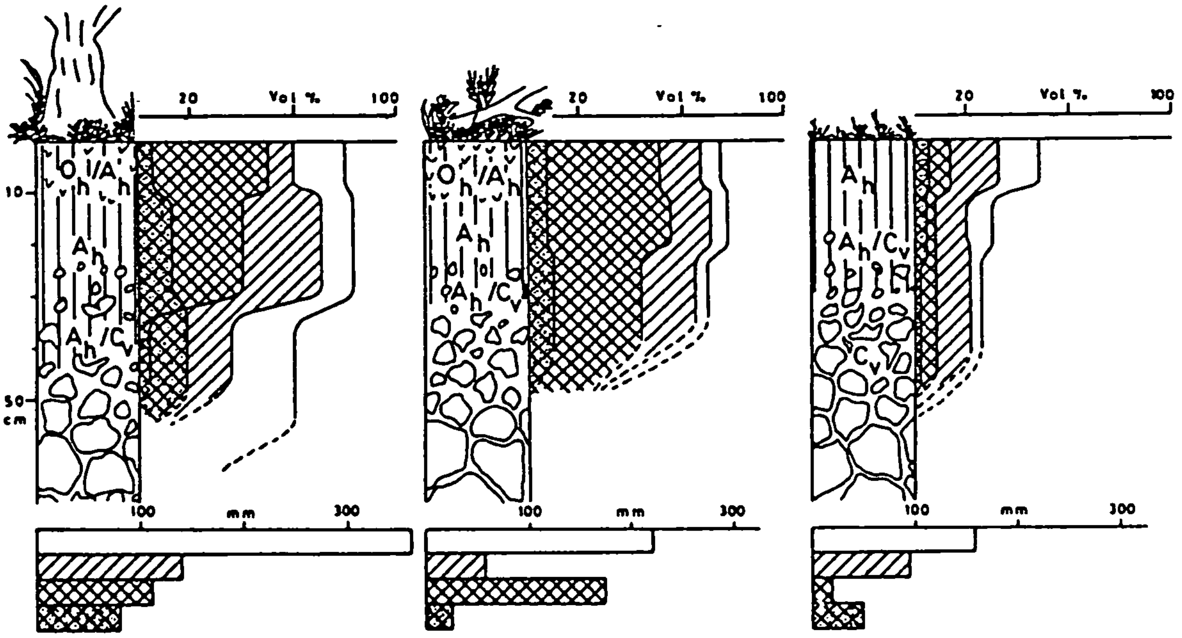
Natural iron podzol under forest of *Picea, Larix* (and *Pinus cembra*)

Podzol colluvium under extensively grazed *Larix* forest

Pseudogley brown soil colluvium under intensively used meadowland

Figure 3. Anthropogenic change in the Pinus cembra/Rhododendron ferrugineum *forest ecosystem over iron podzol on calcareous shale (source: Neuwinger 1987b)*

☐ *(air-)pore space;* ▨ *pore space for seepage water;* ⊠ *pore space for retention water;* ▩ *minimum water retention (difference between field moisture capacity and maximum water saturation)*

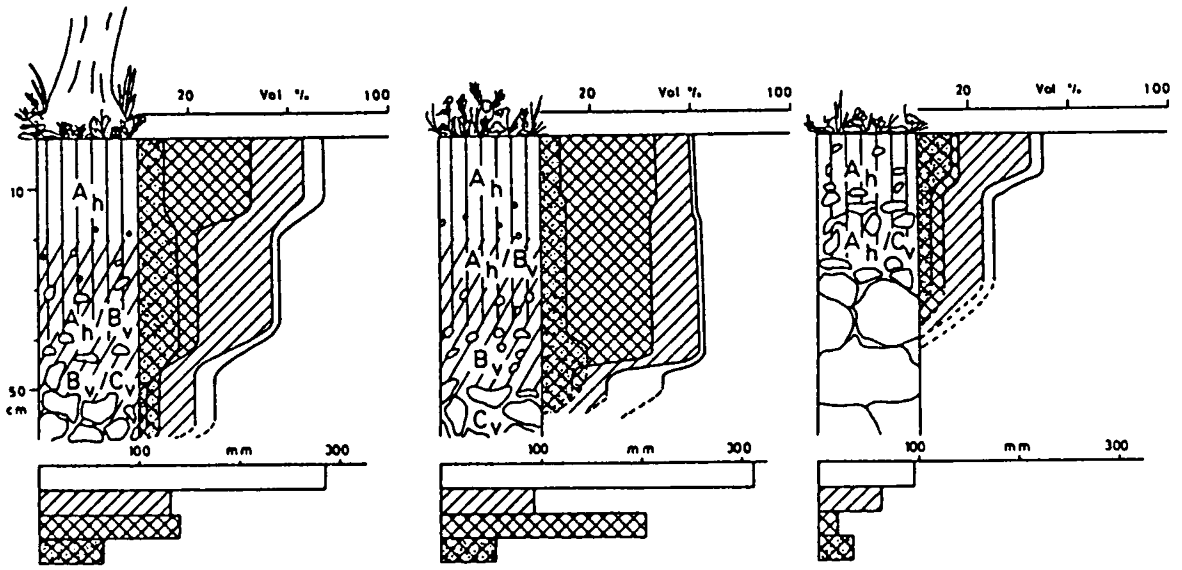


Natural moder rendzina under *Picea*, *Pinus* and *Larix* forest

Almost natural moder rendzina under somewhat changed brush of *Pinus mugo* (mountain pine)

Rendzina remains under ski slope

Figure 4. Anthropogenic change in the Picea *(spruce),* Pinus *(pine) and* Larix *(larch) forest ecosystem over moder rendzina on dolomite limestone (source: Neuwinger & Friedrich 1977; Guggenberger & Neuwinger 1977)*
☐ *(air-)pore space;* ▨ *pore space for seepage water;* ▩ *pore space for retention water;* ▦ *minimum water retention (difference between field moisture capacity and maximum water saturation)*



Natural brown soil under undisturbed *Fagus, Abies* and *Picea* forest

Almost natural brown pasture soil under *Sesleria* grassland

Brown soil remains under ski slope

Figure 5. Anthropogenic change in the Fagus *(beech),* Abies *(fir) and* Picea *forest ecosystem over loamy brown soil on clayey limestone breccia (source: Neuwinger & Friedrich 1977; Guggenberger & Neuwinger 1977)*
☐ *(air-)pore space;* ▨ *pore space for seepage water;* ▩ *pore space for retention water;* ▦ *minimum water retention (difference between field moisture capacity and maximum water saturation)*

NB In Figures 1–5, attention is called to the high proportion of pore space for seepage water in all natural, undisturbed forest soils and the increase in space for retention water in pasture soils, as well as the strong reduction in water retention capacity in the completely destroyed soils under ski slopes. The legends refer to volume percentage in the horizons and mm for the whole solum erodibility. Two types are differentiated here, depending on the type and composition of the soil parent material.

3.1 Regeneration potential in the crystalline central Alps

As already described, undisturbed forests have mainly survived in the climatically unfavourable areas in the mountain valleys, whereas warm, sunny exposures have attracted exploitation since early times, resulting in changes to the ecosystems. The steep valley sides undergo a natural erosion process, which is encouraged by land use. This erosion process is closely related to the entire climatic situation.

Along the loosely knit timber-line, snow shifts from the northern to the southern exposed sites in late winter, and, at snowbreak, forms a water surplus that initiates small, shallow soil erosion events, which generally repeat themselves at intervals of less than 50 years.

In northern exposed sites, erosion is mainly caused by less frequently occurring excesses of perched water at greater soil depth. These excesses recur at periods of over 100 years, and cause large block movements.

Such diversified erosion events generally result in complete denudation of the northern exposures and in colluvial soil formation mainly in the south, thereby creating various prerequisites for forest regeneration. The deep-reaching denudation results in a loss of the entire body of humus, including its water and bioelement storage space.

Only pioneer plants can be used for reafforestation and the process is tedious because of the poor climatic conditions. In contrast, the colluvia of the southern exposed sites are new types of soil formation; the raw humus of the previously mature forest soils has become *moder* and *mull-like moder*, favouring the regeneration of ecosystems with a wide variety of species. This abundance of species is also encouraged by the beneficial moisture and temperature conditions, as well as by the availability of bioelements in the colluvia. Therefore, the potential for afforestation in these areas is good, if extreme accumulations of snow can be prevented by structural measures.

The climatic conditions in treeless areas above the timber-line, about 1900–2200 m asl, are so extreme that it is difficult to afforest these former wooded regions. This zone has been the scene of large-scale afforestation attempts over the past 30 years.

Figure 6 shows a small but differentiated afforestation field in the Tyrolean central Alps.

The factors governing the success or failure of this project include the choice of provenance of the young plants and, particularly, the climate complex, with its many side-effects. Problems have been experienced with the podzols that survived in the wind-swept northern exposures, where they underwent only minor change. In late winter, the sparse snow cover causes frost damage in exposed sites (Tranquillini 1967), and the lack of snow in spring and early summer, at the beginning of the growing season, often induces water stress, which, together with the low temperature, restricts the growth and overall vitality of the plants.

In places with large amounts of transported snow, the plants have suffered damage from fungal diseases and have died (Donaubauer 1963). Most success has been achieved on soils with a mean snow cover in warm locations. It can, therefore, be concluded that, during the first 2 decades of growth, technical measures must be adopted to guarantee an even accumulation of snow.

3.2 Regeneration potential in calcareous areas

The effects described above exerted by climate on the erosion and regeneration of ecosystems are also evident in calcareous areas. However, the main causes of variation in regeneration potential are related to the diversity of soils.

As already mentioned, and as can be seen from Figures 4 and 5, in many cases the difference between brown soils and the rendzinas, which are often small in volume and in close proximity to one another, is not only evident in the composition of their profile, their thickness and humus form, but also in the differing parameters of the soil's water regime. An additional distinguishing feature, that will not be discussed further here, is the amount of calcium in the soil's adsorption complex.

The dissimilarity in the vegetation has already been noted in undisturbed soils: a few species of dwarf shrubs predominate in the rendzinas compared with a multitude of grasses and herbs in the forest understorey on the brown soils. An abundance of species is a commonly observed indication of good regenerative potential.

Experience with afforestation in calcareous areas has shown that most success is achieved on soils with a moderate calcium content and an average proportion of fine sand and clay. The shallow rendzinas on hard limestone and dolomites are endangered by dryness at the beginning of the growing season. Brown soils with a high clay content absorb so much water at snowbreak that their weight often results in large blocks sliding downhill.

Mean depths of sandy, loamy brown soils of morainal material and talus debris have a sufficiently large moisture reservoir during the summer, and also remain stable at snowbreak. Here, too, the best prerequisite for successful afforestation is an evenly accumulated snow cover.

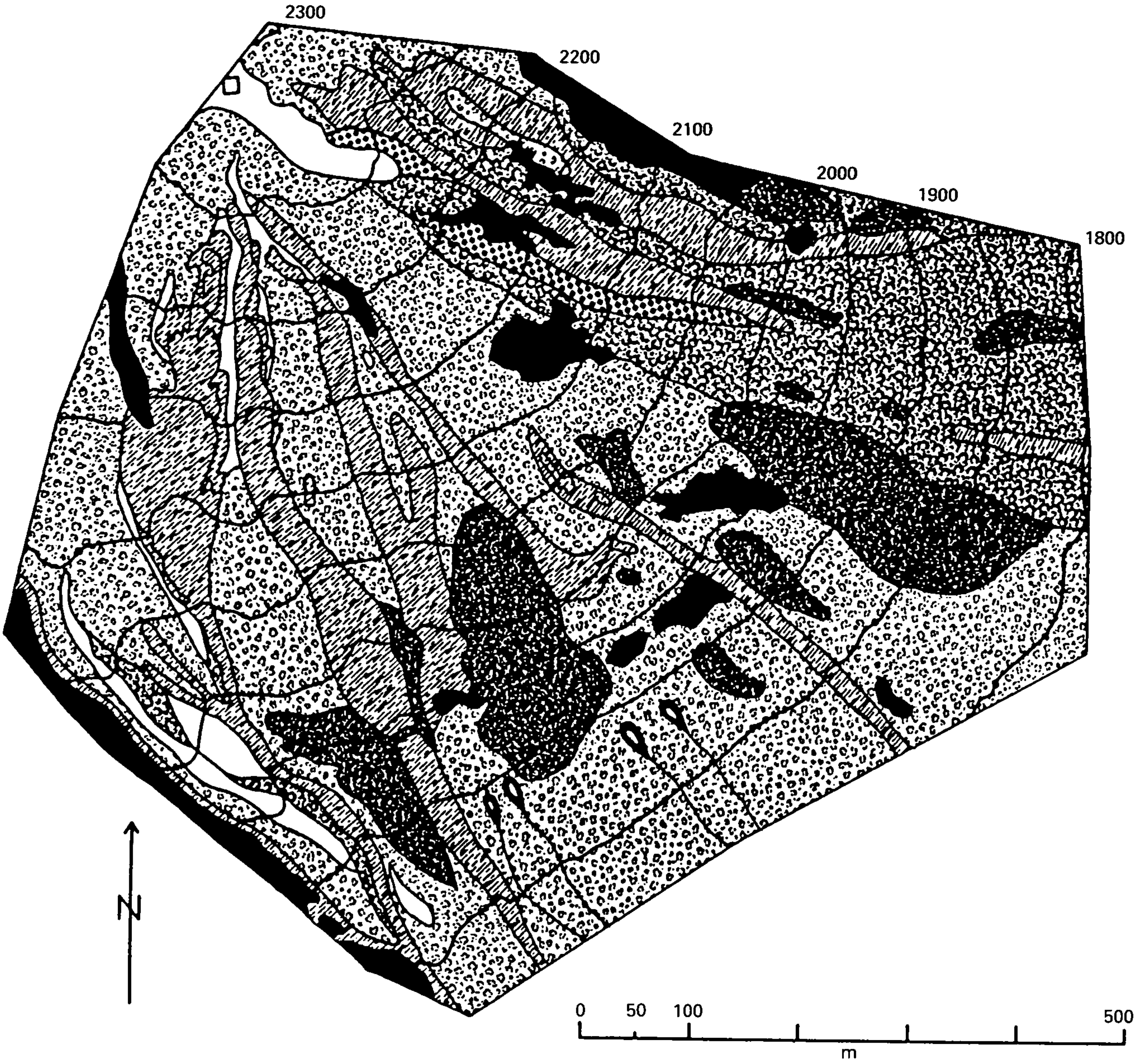


Figure 6. Example of afforestation at the timber-line and the deforested zone of the Austrian crystalline central Alps: Taschachalm, Pitztal, Tyrol (source: Hanke 1981)

▓	*Remains of anthropogenically changed* Picea/Larix *forest over almost natural podzol colluvia*
▒	*Dwarf shrub heath over shallow iron humus podzols*
▩	*Lichen heath over shallow iron humus podzols*
░	*Grassland over pasture soil of podzol colluvia*
▤	*Species-rich grassland over shallow colluvia of eroded podzols in avalanche gulleys*
☰	*Moist meadow*
⌁	*Spring field over slope gleys*
■	*Rock and debris*
□	*Wind-eroded stand*
□ □	*Refuges*

Afforestation with Larix, Pinus cembra *and* Picea *trees was started in 1960 and completed 15 years later. At present, distinct zones can be observed in the evenly planted material. Afforestation was successful up to 2100 m asl. However, plant growth was only sparse between this altitude and the upper limit of the terrain planted (2250 m). Areas with little snow cover show frost damage and those with long-lasting snow cover were characterized by numerous losses through fungal disease*

4 Conclusions

Studies of the water retention capacity and erodibility of soils in various forest ecosystems have shown that the combined influences of climate, parent material and management have created various soil types that must be considered when deciding on an appropriate regeneration method. In general, it is concluded that mature, very old soil formations in mountainous areas that are climatically unfavourable for management can only be regenerated with difficulty and over a long period of time.

Colluvia in crystalline siliceous and limestone areas, that have been formed by constant, small shallow slides, provide afforestation sites that are young and promising. They contain a rich assortment of fine-grained mineral components and a wide range of plant-available bioelements. Thus, the most rational procedure is to establish large-scale afforestation projects in favourable areas, setting aside the more difficult areas for technical preparation.

Development projects (eg highway construction, forest roads, recreational facilities) require the utmost precautions to preserve areas with a limited regeneration capacity and an unstable water regime.

To be able to plan such far-reaching measures, it is recommended that projects be prepared with the aid of ecological maps (Neuwinger 1984, 1987a).

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PHYSIOLOGICAL ECOLOGY OF THE FOREST ECOSYSTEM

Growth and water use in *Nothofagus truncata* (hard beech) in temperate hill country, Nelson, New Zealand

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Abstract

An uneven-aged beech stand, of predominantly *Nothofagus truncata* (Col.) Ckn (hard beech) forming an upper canopy at about 20 m, was selected for intensive gas exchange and biomass studies.

The seasonal behaviour of this wintergreen tree was determined for foliar photosynthesis, stomatal conductance, and respiration of above- and below-ground components. Photosynthesis occurred all year, with partial suppression during summer drought and during a brief period in winter. Stomatal responsiveness to atmospheric humidity declined during the summer. Respiration was a function of temperature (Q_{10} 2.3) and the seasonal pattern of growth activity.

Calculations using stand biomass distribution gave estimates of annual carbon fixation of 27.2 tonnes ha^{-1}, of which 24.7 t ha^{-1} were accounted for by tissue increment and respiratory losses. Fifty-nine per cent of the accountable annual carbon was lost to respiration, with 61% of total respiration required by the large root system. Water use, estimated from stomatal conductance, indicated that the beech stand used 423 mm, or 28% of annual incoming rainfall, for transpiration.

1 Introduction

Interest in forest growth is not confined to the importance of wood production as a sustainable and cheap form of harvesting sunlight energy. The bulk of terrestrial organic carbon exists in forests and their soils, which act as the major biological contact between the earth's atmosphere and the geological substrate. This photosynthetic interface has been of enormous importance in creating the biosphere as we find it today. It is estimated that the equivalent of the earth's entire atmospheric CO_2 passes through terrestrial biota in 7 seasons, and that about 70% passes through forest ecosystems (Waring & Schlesinger 1985). Development of wise forest management regimes will depend greatly on progress in understanding how forests accumulate and distribute carbon. A good starting point is the study of the fate of carbon in relation to water and nutrients in natural ecosystems. Such studies are essentially multidisciplinary.

Natural forests still cover extensive areas of New Zealand (23%). Of these about two-thirds, more than 4 Mha, contain *Nothofagus* species as a major component, and are classified as mixed or pure beech associations. The bulk of the beech forests occur on mountain slopes and associated valleys, where soil protection, wildlife and recreational functions are of prime importance. Less than 0.5% of these forests are managed silviculturally.

Because of their economic value as timber species, *Nothofagus fusca* (Hook. f.) Oerst. (red beech) and *N. menziesii* (Hook. f.) Oerst. (silver beech) are the *Nothofagus* species best understood silviculturally (Franklin 1981; Gleason 1982). There is much similarity in growth and regeneration between the deciduous *Fagus sylvatica* L. (European beech) and the wintergreen *N. fusca*. Both attain heights of 30 m and maximum mean annual stem increments of 10 m^3 ha^{-1} in 80–90 years on good sites (Teissier Du Cros 1981; Evans & Jackson 1972).

N. truncata is closely related to *N. fusca* but does not quite attain the same final size, being competitively confined to the drier and nutritionally poorer sites (Wardle 1984). However, *N. truncata* is the beech studied most intensively at the stand and catchment level in terms of nutrient cycling (Miller 1963a,b,c), biomass distribution (Beets 1980), and forest hydrology (O'Loughlin *et al.* 1978; Pearce *et al.* 1982).

This paper presents some results of recent research in mature *N. truncata* forest, which had the objective of determining canopy carbon fixation with its associated water use and the ensuing fate of the photosynthate. We confine ourselves to aspects of leaf and structural gas exchange and accurate stock-taking of component biomass distribution and its seasonal increment.

A stand carbon budget highlights the photosynthate requirements of different parts of the forest stand. If stem increment is taken as an indication of the energy surplus to immediate tree needs, this may allow speculation on how the health and resilience of the studied stand responds to physical and biological disturbance.

2 Study site

The study area in Big Bush, Nelson (41°31'S, 172°45'E), borders on extensive natural, unmanaged, indigenous forests of the north-west Nelson Forest Park (376 000 ha), with further large forested areas to the south. The evergreen forest communities are complex and are influenced primarily by temperature (eg altitude and distance from ocean) and rainfall gradients (increases from east to west). The Fagaceae dominate (all 4 New Zealand species are present), with a varying canopy component of conifers (Podocarpaceae) and a subcanopy or seral component of many evergreen broadleaved hardwood species (eg Cunoniaceae, Araliaceae, Elaeocarpaceae).

The regional climate is sunny and sheltered, with periodical high-intensity rainfall; summers are warm and winters mild, the annual rainfall of 1000–2000 mm showing a winter maximum (New Zealand Meteorological Service 1983). According to Thornthwaite's classification, the area is superhumid and microthermal, with moisture adequate in all seasons (Garnier 1950). Soil temperatures remain above 0°C and frosts are mild, rarely reaching tissue freezing level. The study site lies at 600 m above sea level on the upper slope (28°) of a westerly face on dissected hills carrying mature *N. truncata* stands typical of the region (Plate 11).

The closed canopy of the study stand reached more than 20 m above-ground, with 90% of the stem basal area occupied by *N. truncata*. Two other *Nothofagus* species, *N. menziesii* and *N. solandri* var. *solandri* (Hook. f.) Oerst. (black beech), and the podocarp *Dacrydium cupressinum* Lamb. (rimu) were minor components of the upper canopy, representing 10% of total stand basal area. Some salient features of stand composition and structure are presented in Figure 1. The upper canopy dominants (570 stems ha^{-1}) of >10 cm diameter at breast height (dbh) were uneven-aged, but tended to fall into 3 natural groups around 75, 150 and >200 years. Total number of stems >1.5 m in height amounted to 3400 ha^{-1}, but of this figure trees of >40 cm dbh made up 90 stems ha^{-1}.

The key climate parameters of the study site during the year of intensive investigations are presented in Figure 2. Mean annual air temperature was 10.7°C, with the coldest and warmest months at 4.6°C and 15.8°C respectively. Soil temperatures (15 cm depth) remained within this seasonal monthly air temperature range. In spite of a high annual rainfall (*ca* 1500 mm,

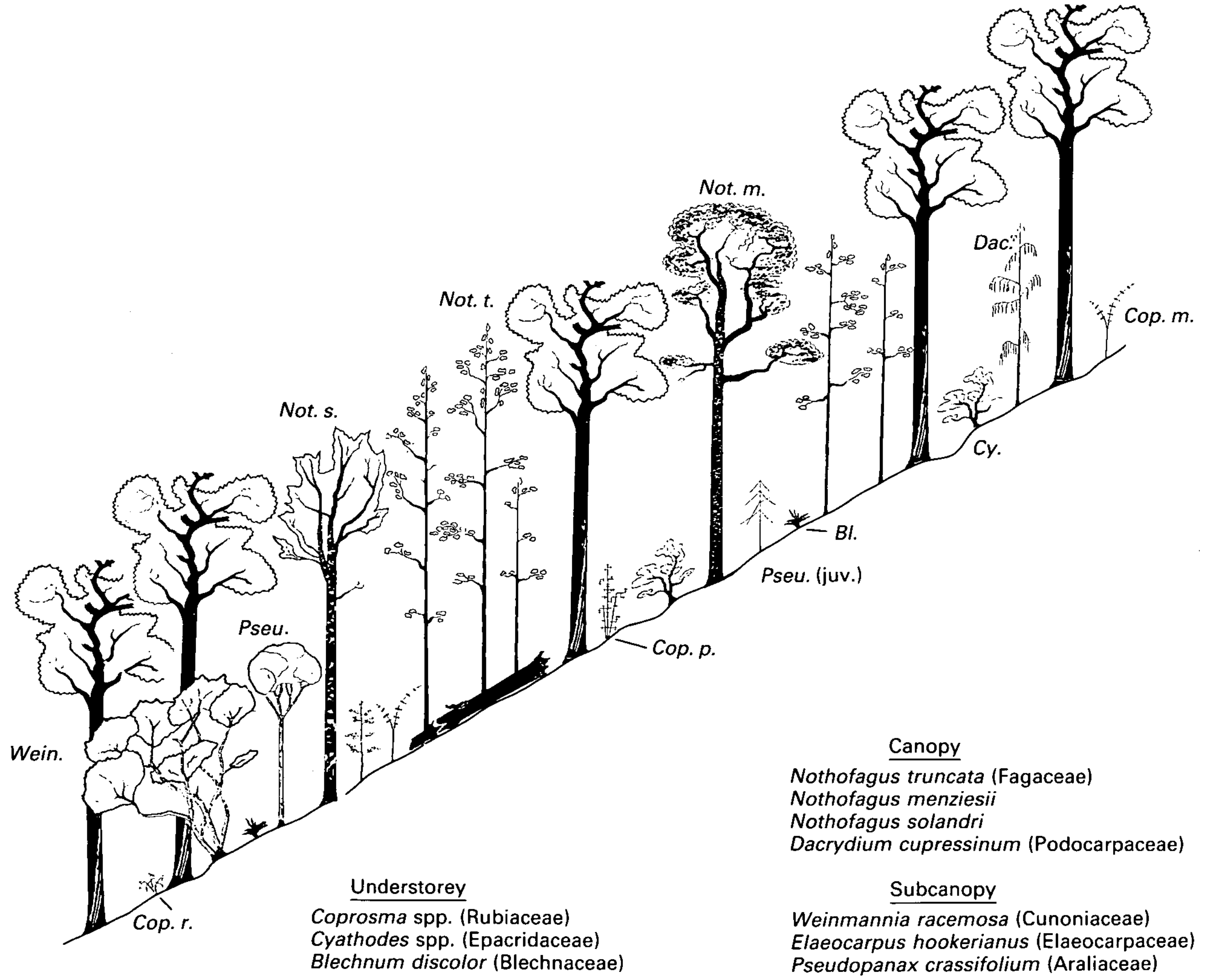


Figure 1. Stand representing typical N. truncata *forest, Big Bush, Nelson. Canopy dominants – mean height 21 m, diameter 34 cm (dbhob range 10–80 cm). Stand basal area 50 m^2 ha^{-1} ob (*N. truncata *45 m^2, other* Nothofagus *species 3 m^2, podocarps 2 m^2).* N. truncata *stem volume 353 m^3 ha^{-1} ub (490 m^3 ob), periodic (5 yr) mean annual volume increment of 4.6 m^3 ha^{-1} ub*

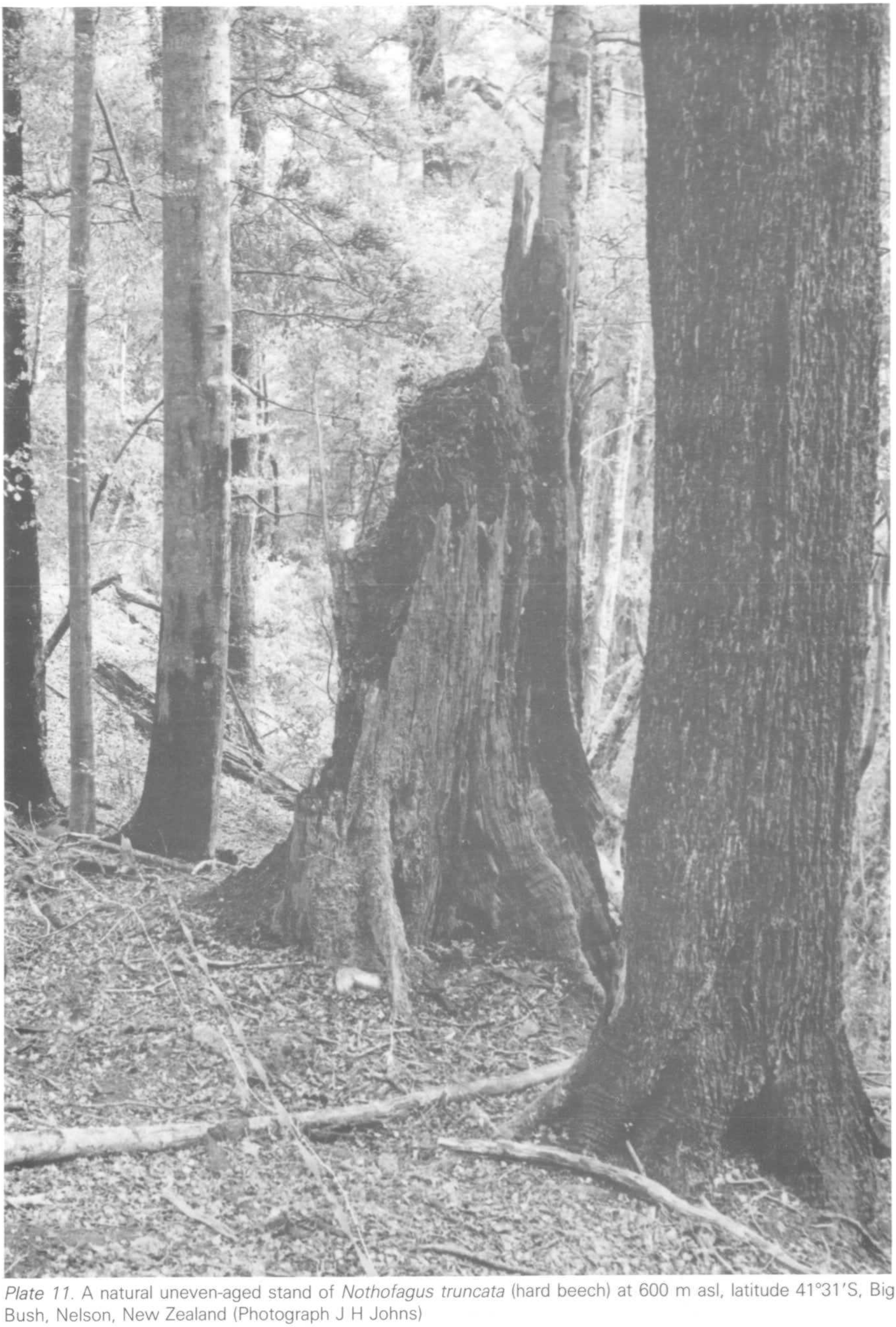


Plate 11. A natural uneven-aged stand of *Nothofagus truncata* (hard beech) at 600 m asl, latitude 41°31′S, Big Bush, Nelson, New Zealand (Photograph J H Johns)

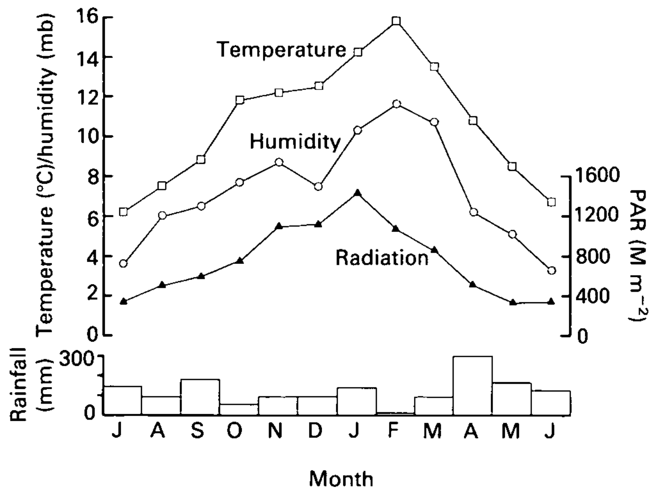


Figure 2. Seasonal monthly mean daily air temperature (°C), mean daily maximum atmospheric water vapour pressure deficit (mb vpd), photosynthetically active radiation (PAR M photon m^{-2}), and rainfall (mm) for Big Bush, Nelson, at time of study (1983 presented in standard growing season format). Mean annual temperature was 10.7°C (absolute max/min 28/ −0.5°C), mean daily max vpd 7.3 mb, total annual radiation 7970 M m^{-2} PAR (3905 MJ m^{-2}), and total rainfall 1493 mm with 125 rain days (>1 mm day^{-1})

125 rain days of >1 mm), relatively dry periods leading to some tree moisture stress can occur in late summer (February/March), as happened in 1983. The shallow and stony soils under the study stands are podzolized yellow-brown earths characteristic of the region. These soils are nutritionally poor, so that foliar nitrogen and phosphorus concentrations border on deficiencies (A H Nordmeyer, pers. comm.).

3 Methods

3.1 Biomass

Stand dimensions and stocking data were obtained from a 70 m × 30 m plot in a representative stand on a uniform slope. Nine *N. truncata* trees, spanning the canopy diameter range (10–80 cm dbh), were felled and systematically taken apart to obtain weight, surface area, and seasonal increment of all above-ground components, ie leaves, twigs, branches, and stem. The sizes of 7 root plots centred on stumps of felled sample trees were determined according to stump basal area as the proportion of total stand beech basal area (m^2 ha^{-1} dbh). These root plots, totalling 82 m^2 ground surface, were excavated to a depth of 20 cm below humus layer for a harvest of all roots, ranging from mycorrhizal fine roots to massive stumps and surface buttress roots. Seven subplots were excavated to a depth of 60 cm.

Branch systems of crowns were measured and foliage samples taken to determine specific leaf areas (cm^2 g^{-1}). These data were used to reconstruct crown dimensions and the spatial distribution of foliage according to leaf type, ie specific leaf area class.

The surface area of all branch, stem and coarse root material was measured according to diameter class (1 cm steps for diameters <5 cm, 5 cm steps for diameters >5 cm; roots were divided into 2 additional classes for diameters <1 cm). Bark was separated from wood, and wood increment was estimated from annual ring measurement, using the mean of the 5 outer rings to give a 5-year mean periodic annual increment. Subsamples of fine roots (<2 mm) were separated from soil and organic detritus, and classified into living and dead components.

The tree data were transferred to per hectare stand data, using logarithmic regressions of component parts on stem diameter. Weight and area of leaf-fall were estimated from the 4-weekly catch in 15 litter trays placed under the canopy. The seasonal pattern of shoot, stem, and coarse root growth was obtained from concurrent phenological studies (I J McCracken, pers. comm.).

3.2 Tree gas exchange

Steel towers were built in the forest to provide crown access. A 17 m *N. truncata* tree (age 55, 26 cm dbh) was intensively instrumented for various measurements taken over 10–12 days each month for 15 months during December 1982–April 1984. Stand climatic parameters were monitored continuously.

Thermo-electrically controlled cuvettes (H Walz, Effeltrich) were used to measure photosynthesis, transpiration and respiration of foliage shoots using standard procedures (Koch *et al.* 1971; Benecke *et al.* 1981). Leaf gas exchange was logged diurnally while tracking natural conditions. Response functions were also developed for the climatic parameters in single factor experiments. Sampling of foliage was concentrated on the upper sun crown and the deep shade crown to span the full spectrum of physiological leaf differentiation.

Respiration of branch, stem, and coarse roots was also measured continuously over extensive periods, using 6 unclimatized perspex chambers. Respiratory CO_2 was monitored by infra-red gas analysis while logging cambial temperature. The annual respiration rate of tree components for *N. truncata* has been published (Benecke 1985).

Tree internal moisture status was estimated regularly by measuring pre-dawn xylem water potential in shoots, using a Scholander pressure chamber.

4 Results

4.1 Leaf photosynthesis

Potential photosynthesis (A_{max}) measured periodically under non-limiting conditions of light, temperature, and humidity quickly attained seasonal maximum rates in newly expanding leaves (Figure 3). Photosynthesis was potentially high all year, with a slow ontogenetic decline and a more marked relatively brief suppression in winter (July–August). For fully expanded sun leaves, A_{max} ranged between 5.0 and 2.4 (mean 3.9 μM CO_2

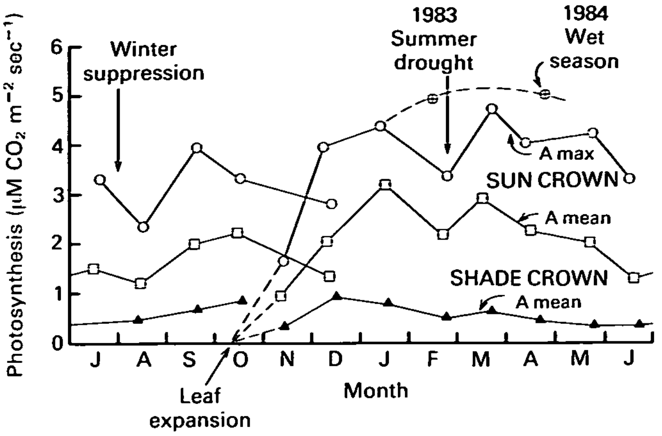


Figure 3. Rate of net photosynthesis (A $\mu M\ CO_2\ m^{-2}\ sec^{-1}$ total leaf surface) in sun and shade leaves of N. truncata, *Big Bush, Nelson. Seasonal patterns are presented for maximum photosynthesis (A_{max}) measured for sun leaves (with light, temperature, and humidity non-limiting), and for mean monthly photosynthesis (A_{mean}) measured under natural conditions for sun and shade leaves (n=90 days)*

$m^{-2}\ sec^{-1}$). Prevailing climate dictated lower mean rates of natural sun crown photosynthesis (mean 2.0 $\mu M\ CO_2\ m^{-2}\ sec^{-1}$, with a mean stomatal conductance (g) of 51 mM $H_2O\ m^{-2}\ sec^{-1}$), but the seasonal pattern followed that for potential photosynthesis (A_{max}).

As expected, mean photosynthesis in the shade of the crown was low (mean 0.6 $\mu M\ CO_2\ m^{-2}\ sec^{-1}$, with conductance at 27 mM $H_2O\ m^{-2}\ sec^{-1}$), primarily the result of limited sunlight. In addition, however, *Nothofagus* leaves showed considerable physiological adaptation to the light climate in which they grew. Thus, shade leaves had lower light compensation points and attained photosynthetic saturation at light levels less than half that for sun leaves (Figure 4).

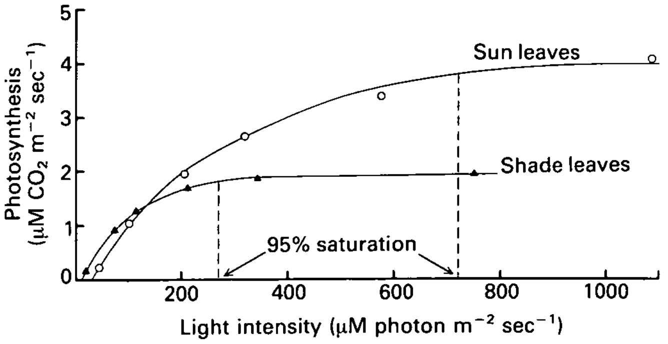


Figure 4. Example of the photosynthetic light response of N. truncata *leaves from sun and shade crown measured during May 1983 in a forest stand, Big Bush, Nelson. Maximum rate of photosynthesis for shade leaves was 50% of that for sun leaves. 95% light saturation in this field experiment occurred at 270 and 720 μM photon $m^{-2}\ sec^{-1}$ for foliage from deep shade and sun crown, respectively*

The dry period in late summer 1983 (Figure 2) was sufficient to cause some xylem water stress (predawn water potentials (ψwe) of −6 bar). This stress caused stomatal conductance to decline by 42%, compared to the same period in the following wet summer of 1984 when no xylem water stress (ψwe−1.5) was detected. Potential photosynthesis during the dry period was reduced by 32% by this stomatal closure (Figure 3).

The indirect effect on photosynthesis of stomatal response to atmospheric humidity was unexpectedly modest (Figure 5). New leaves showed a marked linear decline in stomatal conductance to 24 mb b^{-1} leaf/air water vapour gradient. Higher gradients, ie drier air, are uncommon in tree crowns at the study site. This stomatal response declined rapidly during summer and became insignificant in shade leaves. Surprisingly, however, a stronger humidity sensitivity was retained into mid-summer during the wet summer of 1984.

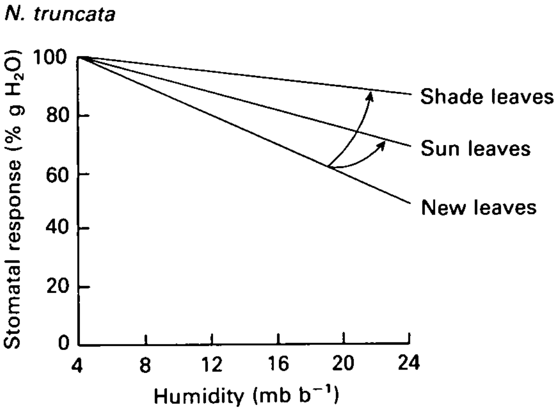


Figure 5. Stomatal response in N. truncata *leaves to atmospheric humidity (ie dw, leaf to air water vapour gradient in mb b^{-1}). Response was greatest in spring (November) for new leaves at −2.6% mb^{-1} (r^2=0.9), declining with leaf maturation in early summer to −1.6% mb^{-1} (r^2=0.7) for leaves in the upper sun crown and to −0.6% mb^{-1} (r^2=0.1) for leaves in deep shade*

In spite of cooler temperatures and much shorter daylight hours in winter than summer, diurnal photosynthetic carbon gains on sunny winter days can be substantial (Figure 6). Daylength was often the major factor restricting photosynthesis, whereas winter stomatal conductances were high, except in August.

Temperature was not an important constraint on photosynthesis because of the mild climate and the adaptive shift in optimum photosynthetic temperature between approximately 19°C in summer and 12°C in winter.

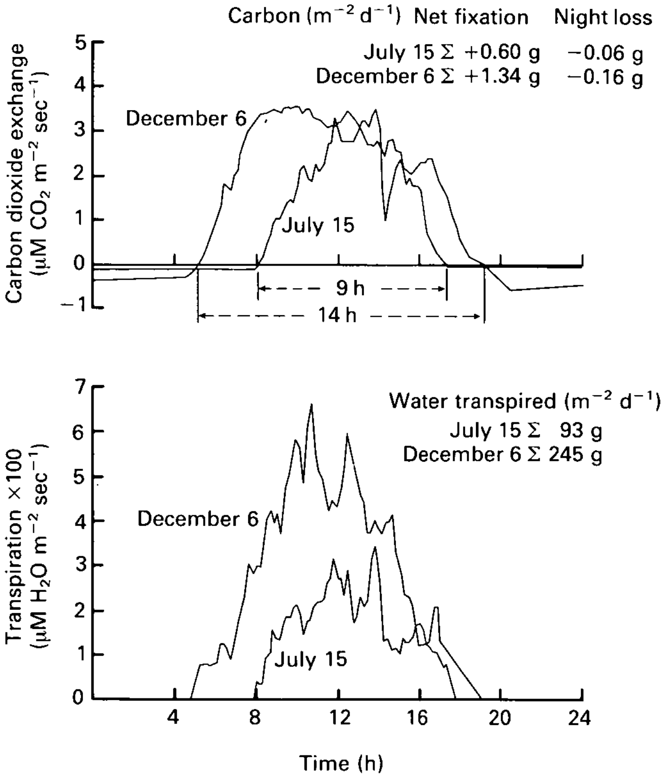


Figure 6. Example of N. truncata *diurnal gas exchange in winter (15 July) and summer (6 December) 1983 measured for foliage at 10.5 m height in the sun crown. Day-length between net photosynthetic compensation points for the winter and summer day was respectively 9 and 14 hours. Net photosynthetic carbon gain during daylight and respiratory carbon loss at night, as well as day-time transpirational water loss, are plotted as molar rates and stated as diurnal gravimetric sums, all per unit leaf area (total surface)*

4.2 Respiration

Day-time foliar measurements by infra-red gas analysis yield net photosynthetic data, with leaf and shoot respiration automatically taken into account. Dark respiration, leading to a nightly loss of foliar carbon (Figure 6), was monitored extensively at natural temperatures, and at a standard reference temperature (15°C) was found to vary seasonally due to growth and ageing processes. Highest leaf rates were measured in newly expanding sun shoots at 0.6 μM CO_2 m^{-2} sec^{-1}, declining slowly in fully expanded leaves from 0.24 to 0.18 μM CO_2 m^{-2} sec^{-1} during their first year, followed by a further decline in leaves retained into the second year. Shade leaves had considerably lower rates and declined from 0.17 to 0.07 μM CO_2 m^{-2} sec^{-1} in their first year.

Temperature-step experiments on sun and shade shoots carried out during the night in all seasons enabled determination of the respiratory temperature coefficient (Q_{10}). The Q_{10} of 2.3 showed no sign of seasonal variation. Allowing for daylength, the seasonal respiratory loss rates could then be calculated from temperature data (Figure 7). Annual rates of respiration were 2.6 and 1.3 M CO_2 m^{-2} yr^{-1} for sun and shade leaves respectively.

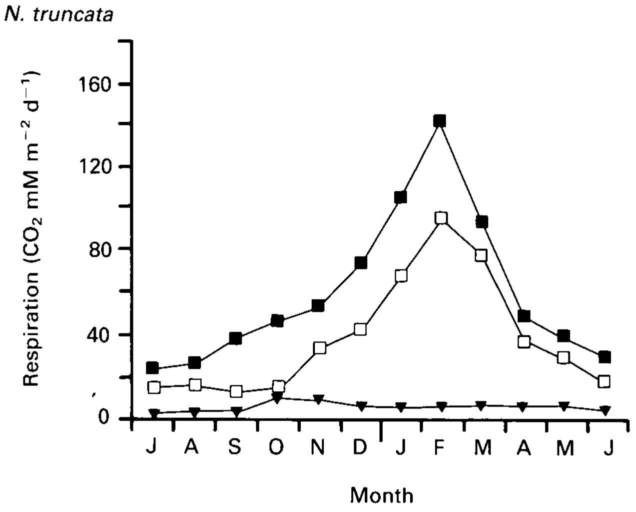


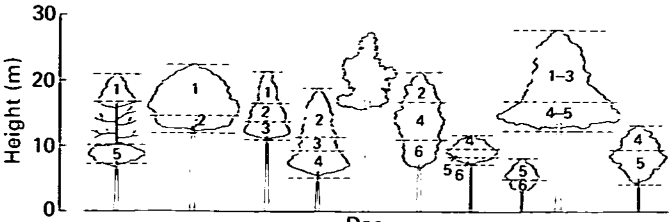
Figure 7. Seasonal variation in mean daily respiration losses for leaves, stem, and coarse root of N. truncata*. Annual respiration rate (R M CO_2 m^{-2} yr^{-1}) for structural components (branch, stem, and coarse roots) was correlated linearly with diameter ob (d cm) as $R=0.82\ d + 7.49$ ($r^2=0.84$) (Benecke 1985)*
(▼ sun leaves at 11 m; ■ stem at 7 m; □ root 4)

The 6 chambers placed on structural parts of the tree provided information on respiratory rates. Using the Q_{10} of 2.3 and temperature data, it was possible to estimate seasonal respiration of branch, stem, and roots of different diameters. Maximum annual rates of 23 M CO_2 m^{-2} yr^{-1} occurred in the stem. This yearly respiration rate at Big Bush correlated linearly with diameter, and one function was determined for branch, stem and coarse roots. However, present data seem to indicate little increase in rate of respiration of the main trunk from the bottom of the green crown to the base of the tree. This constraint has been applied in subsequent use of the diameter function (ie $R = 0.82\ d + 7.49$ M CO_2 m^{-2} yr^{-1}). Smooth bark in *Nothofagus* possesses chlorophyll close to the outer surface, and photosynthetic refixation of respiratory CO_2 was estimated (Benecke 1985). Annual refixation ranged from 5% of total respiration in the upper main stem to 23% in the branches. Relative refixation was greatest at cool temperatures.

For fine root respiration, a figure of 6.5 μM CO_2 g^{-1} h^{-1} at 10°C, with a Q_{10} of 2.9, was used from the closely related *N. fusca* (Hollinger, unpublished). This was a winter rate for excised fine roots in a water-saturated through-flow system.

4.3 Stand leaf area

Crowns of the 9 harvested *N. truncata* trees were spatially reconstructed from leaf and branch data, and zoned according to leaf type by specific leaf area classes (Figure 8). Specific leaf areas ranged from 120 cm^2 g^{-1} for sun leaves to 250 cm^2 g^{-1} for deep-shade leaves. Classes 1 and 5 corresponded to the sun and shade foliage shoots of gas exchange measurements



	Stand foliage cm^2 g^{-1}	ha ha^{-1}
1	120–140	2.7
2	140–160	1.9
3	160–180	2.3
4	180–200	4.3
5	200–220	2.9
6	>220	0.7

Total
Σ Leaf area ha^{-1} = 14.8 ha
LAI = 7.4

Figure 8. Diagrammatic representation of spatial crown foliage distribution for 9 harvested N. truncata *trees representative of sample plot tree diameter range (10–80 cm dbhob) in a forest stand, Big Bush, Nelson. Total leaf area (all surfaces) of 14.8 ha ha^{-1} is presented in subtotals for 6 specific leaf area classes, ranging from sun (<140 cm^2 g^{-1}) to deep shade (>200 cm g^{-1}) crown positions. Total tree harvests were completed 30 January–3 February 1984. Dac = podocarp (*Dacrydium cupressinum*) co-dominant*

in climatized cuvettes. The physiological performance of all leaves could then be assigned by specific leaf area, assuming a linear relationship between sun and shade foliage. Leaf areas were scaled up to stand level, using logarithmic regressions on stem diameter. Total stand leaf area at time of harvest (end of January/early February) was 14.8 ha ha^{-1}, equivalent to a leaf area index of 7.4.

Tree harvests in 1984 were made shortly after completion of new seasonal leaf growth. The current season's foliage area was assigned incrementally (4-weekly), according to phenological measurements. Together with the 4-weekly litterfall leaf area, it was possible to estimate seasonal change in total stand leaf area (Figure 9). Leaf area index thus fluctuated between about 4 in winter and 8 in early summer.

Canopy defoliation losses from agents such as leaf-spot fungi and insects were noted in tree crowns from the gas exchange towers. The difference in stand leaf area between annual litterfall and seasonal new leaf increment was assumed to be equivalent to this defoliation.

The largest shifts in seasonal leaf area were partly the result of peak leaf increment (November–December) occurring ahead of peak leaf-fall (December–January). At the time of tree harvest (January–February), approximately 25% of leaves were from the previous season and were therefore more than one year old. A large proportion of the old leaves fell during and immediately after new leaf growth in early summer.

4.4 Growth and carbon balance

The living biomass of *N. truncata* amounted to about 410 t ha^{-1} (Table 1), and probably constituted 90% of total stand biomass. No more than 2% of the *Nothofagus* biomass was found in leaves, whereas the below-ground root biomass of *ca* 83 t ha^{-1} made up 20% of the total.

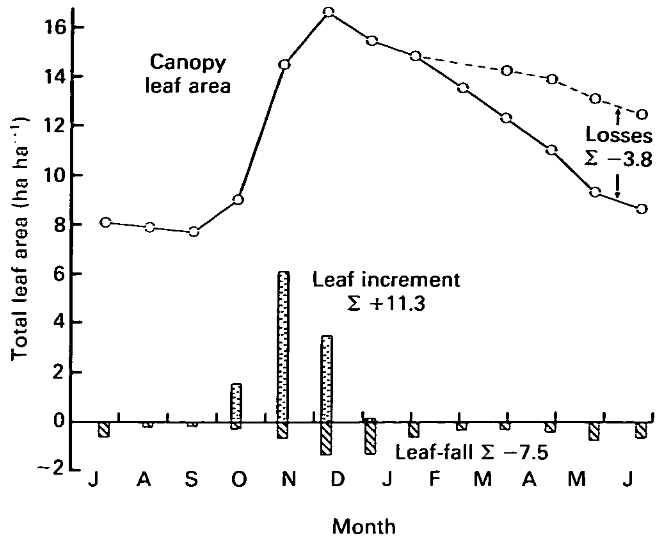


Figure 9. Seasonal variation in leaf area (all surfaces) of N. truncata *stand, Big Bush, Nelson. Leaf area gain estimated from phenological measurements (I J McCracken, pers. comm.) and total harvest of 9 sample trees 30 January–3 February 1984. Leaf area loss estimated from monthly sampling of litterfall during June 1983–May 1984. Leaf areas equate with LAI (plane area) by using a divisor of 2, giving an LAI range from 3.9 (September) to 8.3 (December). Canopy losses which did not appear in the litter catch are an estimate of consumption primarily by insects and fungi*

Total annual stand dry matter increment (ie net primary production) for *N. truncata* was 20 t ha^{-1}, of which 32% was in leaf production and 32% in root growth. The work of Clinton (1986) on fine root growth of *N. truncata* in Big Bush indicated that mycorrhizae live for at least one year. For calculation, we assumed that annual turnover rates in the fine root network constituted 0.5 of the very fine mycorrhizae and 0.33 of the <2 mm rootlets subtending them.

Carbon increment was derived from dry matter increment, using the approximation of 50% carbon content for all tissues. Stand respiratory losses were scaled up from annual rates published previously (Benecke 1985) and the actual surface areas. Foliage respiration was adjusted according to specific leaf area class (Figure 8), monthly changes in canopy leaf area, duration of darkness, and night temperature. Stand respiration losses of all other woody tissues were calculated from the diameter class surface area totals and the annual rates obtained from the regression of respiration on diameter.

In total, 59% of the accountable annual carbon was lost in stand respiration. Of this amount, the respiratory carbon losses were highest for fine roots (45% of

Table 1. Stand biomass dry weight (DM) and surface areas at time of tree harvests (January–February 1984); annual increments, carbon fixation and respiratory losses for *N. truncata*, at Big Bush, Nelson. A=net photosynthetic carbon gain. R=respiratory losses: branch, stem, coarse root respiration and leaf dark respiration based on measured surface areas; fine root respiration calculated from respiratory rate and measured root weight

	DM ($t\ ha^{-1}$)	Surface area ($ha\ ha^{-1}$)	Increment DM ($t\ ha^{-1}\ yr^{-1}$)	Increment carbon ($t\ ha^{-1}\ yr^{-1}$)	R carbon ($t\ ha^{-1}\ yr^{-1}$)	A carbon ($t\ ha^{-1}\ yr^{-1}$)
Leaves	8.5	14.8 (7.7–16.5)†	6.4	3.2	2.1*	27.2
Branches	55.4*	1.6	4.0*	2.0*	1.9	
Stems	263.3	0.6	3.3	1.7	1.8	
Coarse roots	72.8	9.7	2.4	1.2	2.3	
Fine roots (<2 mm)	9.9	–	3.9	2.0	6.5	
Total	409.9		20.0	10.1	14.6	27.2

* includes foliage shoots
† seasonal range of stand leaf area

the respiration total). For the whole below-ground system, losses amounted to 61% of the total respiration, thus constituting the major carbon sink for the forest ecosystem.

The stand's total incoming carbon fixed photosynthetically was estimated to be 27.2 t ha^{-1}. This figure was obtained from summation of monthly carbon uptake rates derived from leaf areas (Figures 8 & 9), mean photosynthetic rates (Figure 2), and daylength (ie sunlight hours between photosynthetic compensation points). Daily carbon uptake of the *Nothofagus* stand (Figure 10) peaked at 149 kg C ha^{-1} in early summer, when daylength and leaf area reached their seasonal maximum, and temperature and moisture conditions were closest to optimum. The dry summer period had a marked effect, shown by the reduction in carbon uptake accentuated by the seasonal pattern of leaf-fall. Substantial carbon was gained all year. Even during June (the month with the shortest day), cool temperatures ensured low foliar respiration losses, so that 21 kg C of the 24 kg C ha^{-1} day^{-1} fixed was a net diurnal gain.

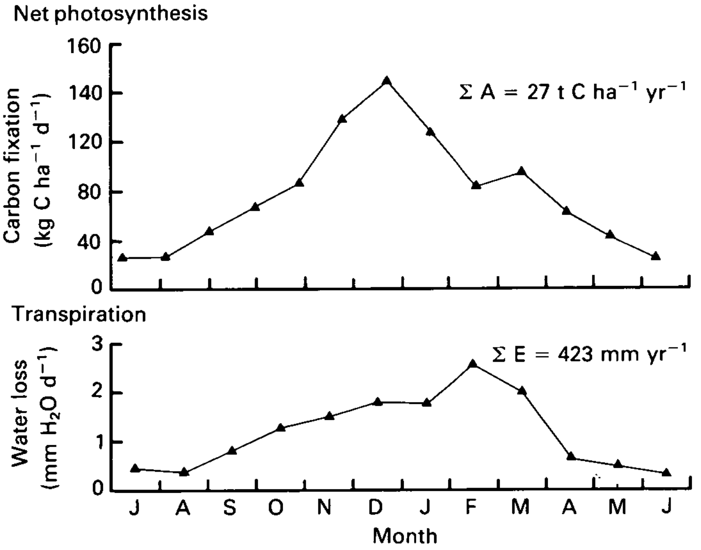


Figure 10. Carbon fixation and water loss in the canopy of N. truncata *forest, Big Bush, Nelson. Daily stand rates were estimated from seasonal foliar rates and total crown leaf areas. Sun to shade leaf categories were apportioned according to the crown areas in 6 specific leaf area classes, measured at time of tree harvests (cf Figure 9). Total annual carbon fixation by* N. truncata *in the forest stand was 27 t ha*$^{-1}$*. Annual transpirational water loss was estimated to be equivalent to 423 mm precipitation, ie 28% of annual precipitation*

The annual sum of carbon incremented in new tissues plus the respiratory losses balanced within 10% of the estimated annual canopy net photosynthetic fixation (Table 1). The 2.5 t C ha^{-1} of photosynthate not accounted for are believed to be within the error limits. All calculations are based on data information, and no major stand component (eg roots) has been estimated as a residual. Some underestimate of accountable carbon might have been expected because of uncertainties in exact seasonal fine root activity and turnover, and the need to use a periodic mean annual increment (pmai) instead of actual current annual increment (cai) for structural parts.

4.5 Canopy transpiration

Monthly canopy transpiration was computed from mean leaf conductances, leaf areas (Figure 9), rainless days, daylength, and mean day-time leaf/air water vapour gradient. Canopy foliage was weighted according to specific leaf area categories.

Transpiration, expressed in mm precipitation equivalent, yielded the highest monthly rate of 2.7 mm day^{-1} for February (Figure 10). Counting only rain-free days (<1 mm pptn), the 4 summer months, December–March, all averaged 3.0–3.2 mm day^{-1}. Transpiration occurred even in winter (Figure 6), with the lowest seasonal rates in June, averaging 0.3 mm day^{-1}. Again, taking only rain-free days, transpiration rates for the 3 winter months of June–August averaged 0.5–0.6 mm day^{-1}.

During the dry summer spell (February), canopy conductance was restricted to 60% of early summer

(December) conductance, thereby conserving water but at the expense of carbon uptake (Figure 10). In terms of overall water economy for carbon fixation, the *Nothofagus* stand in Big Bush transpired *ca* 16 mm of water per tonne of photosynthetically fixed carbon, ie 212 tonnes of water per tonne of dry matter increment, or 1282 tonnes of water per tonne of stem wood production.

5 Discussion

The maximum photosynthetic rates of *N. truncata* were the same as rates published for *N. solandri* var. *cliffortioides* (Hook. f.) Poole (mountain beech) at montane and subalpine sites (Benecke & Nordmeyer 1982). The cooler climates at the higher-altitude sites for *N. solandri,* however, resulted in stronger winter suppression, including a short period of complete photosynthetic dormancy after regular frosts and when soil temperatures approached 0°C (Benecke & Havranek 1980). No such dormancy was recorded in the mild climate of the *N. truncata* habitat.

The weakened response of stomata to humidity in summer, especially in shade foliage, was also very similar in *N. truncata* and *N. solandri,* suggesting that this may be a common feature of *Nothofagus* species. The exception could be the only truly evergreen New Zealand species, *N. menziesii,* particularly in genotypes from high-rainfall areas (Körner & Bannister 1985).

The lack of a well-developed feed-forward response mechanism of stomata to atmospheric humidity appears to be compensated for in *N. truncata* by marked stomatal sensitivity to xylem moisture stress induced by soil moisture deficits. Observations suggested that *N. truncata,* in addition to stomatal response, reduces canopy leaf area through increased leaf-fall when night-time equilibration with soil moisture no longer allows high pre-dawn xylem potentials to be attained.

Shade leaves of *N. truncata* were well adapted to their low light environment, as in *N. solandri* (Benecke & Nordmeyer 1982) and *Fagus* (Schulze 1970). They showed low respiratory losses and contributed significantly to canopy carbon uptake. Though photosynthesis was restricted in winter by duration of sunlight (eg Figure 6), a most important factor for canopy photosynthesis was the seasonal change in total leaf area (Figure 9), which fell in late winter to 50% of the early summer maximum. In spite of seasonal leaf area patterns, stand carbon fixation for the half year centred on winter amounted to 30% of the annual total.

Canopy carbon gain or gross primary production (GPP) was substantial at 27 t C ha^{-1} (≡54 t DM) because of the large leaf area duration (6.4 mean LAI × 12 months) of 77.

The *N. truncata* stand studied was at an advanced stage of development, but not yet senescent, with some standing dead stems (9 m^{-2} ha^{-1}) of suppressed trees or trees of the previous generation. With advancing succession, forests become less productive because of the respiratory demands (R_A) of increasing quantities of non-photosynthetic structural tissue. Total stand increment of *N. truncata* was, however, considerable at 20 t DM ha^{-1}, suggesting a production ratio (GPP/R_A) of 1.9. Undoubtedly, the mild temperature climate with relatively cool nights keeps respiration losses down to levels where surplus carbon for growth is abundant.

More than 61% of respiratory carbon was required for the root systems, and investment in root growth and leaf production both amounted to 32% of stand increment (NPP). This suggests that the *N. truncata* stand could be bordering on nutritional stress (cf Linder & Axelsson 1982). Only 17% NPP was available for wood production, compared with 26% stemwood allocation in a pole stand of *N. solandri* aged 55 years (Benecke & Nordmeyer 1982). The *N. truncata* stand may well be reaching dimensions (age and structure) where carbon reserves for stand response to stress become limiting, at least for the larger individuals. Stand resilience to maintain its present form is thus in question, with stemwood production at only 51 g m^{-2} of projected foliage (growth efficiency index).

Although the *N. truncata* stand was a relatively simple stand in terms of botanical composition, its function was complex because of the mixed ages and dimensions of the trees. Thus, the annual loss of one large tree ha^{-1} can account for the whole current stem increment of 3.3 t ha^{-1}. The stand is, therefore, not necessarily increasing in total biomass, in spite of the 27 t ha^{-1} of carbon being fixed annually.

There is much interest in use of catchment water by forests. Estimates of daily and seasonal transpirational losses for the *N. truncata* stand presented in this paper fall within the range published for various types of forest (O'Loughlin *et al.* 1985; Waring & Schlesinger 1985). From studies of soil water storage (Jackson 1985) in an adjoining *Nothofagus* subcatchment, it has been possible to estimate stand transpiration of 420±50 mm by an independent technique (R J Jackson, pers. comm.). This estimate for the same season reported here is identical to our calculation from stomatal conductance and canopy leaf areas of *N. truncata.* There was also broad agreement in winter (May–August) transpiration, which was estimated at 50 mm (0.41 mm day^{-1}) from stomatal conductance.

Soils in the study region are rarely cool enough to restrict transpiration, so that radiation and atmospheric water saturation deficit are the driving variables for transpiration via leaf stomata. In summer, soil moisture deficits can occur, as in February 1983, but extended periods of drought are rare. Stomata restricted conductance by −9.3% per bar of decline in pre-dawn water potential. When coupled with leaf area reduction, this provides *N. truncata* with an effective means of limiting canopy transpiration losses.

This multidisciplinary study of a forest stand has given us some understanding of forest function. The important steps were: (i) the measurement of carbon gain and water loss by foliage; (ii) the measurement of respiratory losses from all living tree components; (iii) the measurement of leaf and wood increments, and estimation of annual root growth; and (iv) the matching of biomass, surface area, increment and gas exchange data to estimate stand carbon change and water use. Such information can form a valuable baseline for developing predictions about the future health and growth of forests, as well as catchment hydrology and land surface stability.

6 Acknowledgements

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An ecological study on nitrogen-fixing tree species in the forest ecosystem of Changbai Mountain

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Abstract
Two species of *Alnus*, *A. mandshurica* (Call.) Hand.-Mazz (Manchurian alder) and *A. sibirica* var. *hirsuta* (Turcz.) Koidz. (Siberian alder), are non-leguminous tree species with nitrogen-fixing ability that are widely distributed in the Changbai Mountain forest ecosystem, in north-east China. Field and laboratory measurements were carried out in a study of nitrogen-fixing activity in *Alnus* nodules in relation to the main environmental factors, using acetylene reduction and an infra-red gas analyser. Results indicate that an adequate light supply is important for nodule formation and nitrogen fixation in the forest stand, while soil temperature affects nodule reduction activity directly. The optimum temperature for nitrogen fixation was 20°C for *A. mandshurica* and 25°C for *A. sibirica* var. *hirsuta*. In the temperature range tested, the reduction ability of *A. sibirica* var. *hirsuta* was 1–3 times higher than that of *A. mandshurica*.

1 Introduction

The presence of tree species with nitrogen fixation ability is one of the important factors for nitrogen input to the forest ecosystem, accounting for 87% of the total input to the terrestrial ecosystem (Larcher 1975). Twelve higher plant species with nitrogen-fixing ability are found in the Changbai Mountain forest ecosystem, mostly of the leguminous family. According to recent investigations, only 2 species of *Alnus* are non-leguminous species with nodulation and nitrogen fixation ability (Yang *et al.* 1984). This paper reports on a study of nodulation and nitrogen-fixing activity in *Alnus*, in relation to the main environmental factors. Data from field and laboratory experiments can be used to gain further understanding of the ecological characteristics of the 2 species and to improve management practices in mixed forest stands.

2 Materials and methods

The 2 species of *Alnus*, *A. mandshurica* and *A. sibirica* var. *hirsuta*, of approximately similar age growing in different sites in the Changbai Mountain area, were selected for determining nitrogen fixation in nodules and for measuring leaf photosynthesis. *A. mandshurica* occurs in the subalpine *Betula ermanii* Cham. (Erman's birch) forest, at an altitude of 1700–2000 m, where the main soil type is a soddy forest earth (Cheng *et al.* 1981). Together with a few other tree species, *Alnus* plays an important role in maintaining the ecological environment of the subalpine zone. A. *hirsuta* mainly occurs in the secondary forest stands below 1500 m. *Alnus* trees are usually scattered throughout the stand, among species of *Larix* (larch) and *Betula*. The main type of soil is a brown forest earth.

Root sections with nodules were cut from the sample trees. The nodules were detached and placed in serum bottles for incubation under required conditions, and acetylene reduction was used to determine nitrogen fixation (Hardy *et al.* 1968). To improve the method of incubation, 10% of acetylene was injected into the bottle, and, after one hour's incubation, a saturated NaCl solution was added to prevent reduction. Sample bottles were transferred to the laboratory for measuring ethylene (Shen & Yang 1983). In order to investigate the effects of the plants' internal factors on nitrogen fixation by the nodules, the photosynthetic rates of the attached leaves were tested *in situ*, using an infra-red gas analyser (Lin & Yang 1984).

3 Results and discussion

Alnus species are known to affect the nitrogen supply in forest stands, but further experiments are required with this particular species to determine the extent of the effect. To investigate the effect of symbiotic nitrogen fixation on forest ecosystems, an analysis was carried out of the nitrogen content in soil and in tree leaves. Results revealed that total nitrogen content in soil around the root system in the subalpine zone was 0.32%, 0.22% in the samples taken from the site under a *Betula* canopy, and only 0.09% in sites with poor vegetation. A higher content of nitrogen is found in nitrogen-fixing species than in other plants. Through the processes of litterfall and turnover of the root system, nitrogen is accumulated in soil. Analysis of leaf samples from the stands shows that *Alnus* species have a positive effect on the uptake of nitrogen by trees growing nearby.

In Table 1 (from Yang *et al.* 1984), it can be seen that nitrogen content in leaves of trees adjacent to *Alnus* species increased by 18% for *Betula ermanii*, 50% for *Larix olgensis* A. Henry (Olga Bay larch) and by 25% for *Betula platyphylla* Suk. (Manchurian birch).

Nodule formation on the 2 *Alnus* species under different site conditions was investigated. In *B. ermanii* forest in the subalpine zone, 8 *Alnus mandshurica* trees were sampled to estimate the quantity of nodules on their roots. The light condition in the stand was found to affect nodule formation significantly. On sites with sufficient irradiation, the fresh weight of nodules on a single tree averaged 8.6 g, while nodules weighed only 3.2 g under the shade of a *Betula*

Table 1. Nitrogen content in different tree species

Stands	Species	associated with *Alnus*	% dry weight	without *Alnus* association
Subalpine *B. ermanii* forest	*A. mandshurica*		2.17	
	B. ermanii	1.86		1.57
Secondary *Betula* forest	*A. sibirica* var. *hirsuta*		2.20	
	L. olgensis	1.59		1.06
	A. sibirica var. *hirsuta*		2.24	
	B. platyphylla	2.09		1.67

canopy. A similar tendency was found in *B. platyphylla* forest, where nodules on *Alnus hirsuta* were more numerous and bigger in sufficient light conditions than under *Betula* shade. Tests of nitrogen-fixing activity in nodules were conducted under different light conditions. The results in Table 2 show that the acetylene reduction rates were several times lower in shady conditions.

We were concerned to measure the effect of temperature in nodules on N_2-fixing activity of the 2 *Alnus* species. To clarify the effects of temperature and carbohydrate accumulation, 2 parallel experiments were set up in field and laboratory conditions. Nodules were collected every 2–3 hours from the same tree and samples were incubated *in situ*. The change in reduction rates at different temperatures during the day is presented in Figure 1. In the other parallel treatment, incubation was arranged in the laboratory at a controlled temperature of 20°C. Figure 1 shows that, at a constant temperature of 20°C, the reduction rate, which depends on carbohydrate supply, does not vary greatly. In the field incubation experiment, the reduction rate changes with soil temperature.

Table 2. Activity of N_2 fixation by nodules at different sites

		Full light condition		Under canopy	
Species	Time (h)	Reduction (μM C_2H_4 g^{-1} h^{-1})	Light (Lux)	Reduction (μM C_2H_4 g^{-1} h^{-1})	Light (Lux)
A. sibirica	0930	6.2	21 000	1.1	8800
var. *hirsuta*	1500	5.5	18 000	2.3	7500
A. mandshurica	1100	1.2	27 000	0.6	9600

To understand the effect of internal and external factors on N_2 fixation, measurements of photosynthesis, acetylene reduction and soil temperature were made on the same trees at the same time of day.

Table 3 shows that changes in reduction rate do not coincide with changes in photosynthesis, perhaps because carbon assimilation does not affect nodule activity directly, although photosynthate supplied to nodules is the basic source of energy limiting nitrogen fixation (Quebedeaux *et al.* 1975). It is more reasonable to suppose that changes in reduction rate during the day follow changes in soil temperature.

Table 3. Daily rates of photosynthesis and acetylene reduction in *A. sibirica* var. *hirsuta*

Time (h)	Reduction rate (μM C_2H_4 g^{-1} h^{-1})	Photosynthetic rate (mg CO_2 h^{-1} dm^{-2})	Soil temperature (°C)
0700	1.7	4.0	10.0
0900	5.4	4.3	13.5
1100	6.8	3.9	18.0
1300	6.9	3.7	21.0
1500	5.6	3.7	20.0
1700	3.0	1.1	16.5
1900	1.9	—	14.0

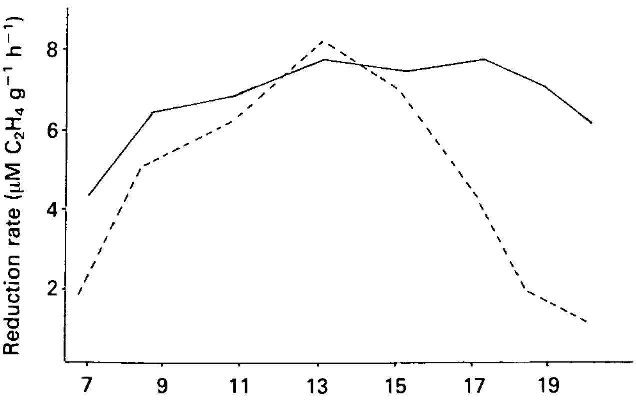

Figure 1. Daily rate of acetylene reduction. Nodule of A. sibirica *var.* hirsuta *incubated at 20°C (——), and under field conditions (----)*

A range of temperatures was tested in the laboratory for nodule incubation, and the determined reduction rates are shown in Table 4. At lower temperatures, reduction rate increased with increasing temperature, reaching a maximum value at 20°C for *A. mandshurica* and at 25°C for *A. hirsuta*. Furthermore, at all temperatures, the reduction activities of *A. hirsuta* were 1–3 times higher than those of *A. mandshurica*, presumably as a result of the different ecological characteristics between the 2 species.

Table 4. Effect of temperature on acetylene reduction in nodules on 2 *Alnus* species

Temperature (°C)	Reduction rate (μM C_2H_4 g^{-1} h^{-1}) *A. sibirica* var. *hirsuta*	*A. mandshurica*
5	0.18 ± 0.02	0.12 ± 0.04
10	0.45 ± 0.01	0.76 ± 0.14
15	3.04 ± 0.15	1.64 ± 0.21
20	5.11 ± 0.36	3.09 ± 0.39
25	8.18 ± 0.88	2.26 ± 0.24
30	6.11 ± 0.61	1.22 ± 0.11
35	3.34 ± 0.13	0.83 ± 0.08

4 *Conclusions*

As associate and pioneer species in the forest ecosystem of Changbai Mountain, the 2 *Alnus* species play an important role in nitrogen input and are beneficial to the other tree species. In the forest stands, adequate light conditions facilitate nodule formation and nitrogen fixation in *Alnus*. Soil temperature has a direct effect on the nitrogen-fixing activity of the nodule, with *Alnus hirsuta* being more adaptable to a larger range of temperatures than *Alnus mandshurica*.

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Discoveries in tree ecophysiology studies on Changbai Mountain

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Abstract

Unexpected discoveries which depart from the traditional concepts of ecophysiology are reported, a tentative explanation is offered, and the implications are discussed. Our findings include the following: (i) *Pinus koraiensis* Sieb. et Zucc. (Korean pine) seedlings grown for a period under shade have a higher potential for photosynthesis; (ii) overwintering *P. koraiensis* seedlings release CO_2 rather than absorb it under intense light; (iii) tree species growing at higher altitudes have a greater potential for transpiration and photosynthesis than their genetic counterparts at lower altitudes; (iv) a minor decrease occurs during the course of increasing transpiration in the morning, and a minor increase during the evening decline in transpiration; (v) transpiration reduces after leaf excision.

1 Introduction

The development of science, including ecology, relies not only on traditional methods of data collection, but also on the breakthrough of new discoveries. New discoveries in tree ecophysiology may modify traditional concepts of forest ecology and tree physiology. This paper discusses some recent discoveries in tree ecophysiology and their implications.

2 Pinus koraiensis *seedlings grown for a period under shade have a greater potential for photosynthesis*

Some potted 3-year-old *P. koraiensis* seedings were exposed to full sunlight, while others were placed in 75% shade from July. In September, the seedlings were taken into the laboratory, and photosynthesis was measured against varying levels of light at a constant temperature of 20°C by a CO_2 infra-red (IR) analyser. The results are shown in Figure 1. Photosynthesis in the shaded seedlings was double that of the fully exposed seedlings, a result which contradicts the traditional belief that shaded leaves should have a lower potential photosynthesis rate than those under full sunlight (Nichiporovich 1982). According to data collected in 1985, after 18 days in shade, the saturated photosynthesis rate increased by 30%. The increased potential for photosynthesis may be related to the increase in chlorophyll content.

It is known that *P. Koraiensis* seedlings are shade tolerant and regenerate naturally under a deciduous forest canopy. Our results indicate that the seedlings may make efficient use of light spots filtering through the canopy for their photosynthesis. Therefore, the seedlings are shade tolerant, but are also able to make use of stronger illumination.

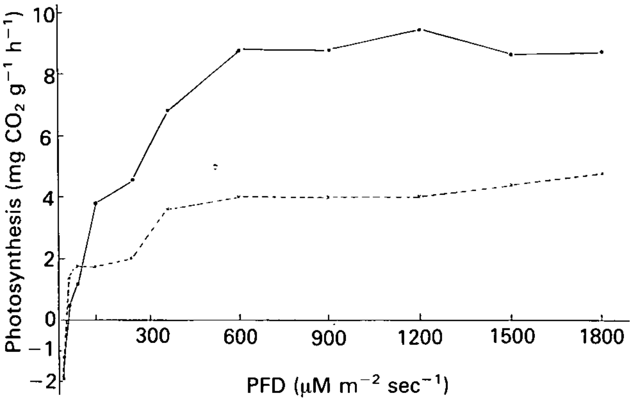

Figure 1. Photosynthesis/light curve of P. koraiensis *seedlings, measured in September 1984*
(———— shaded seedling; ---- seedling exposed to full sunlight)

3 'Negative' photosynthesis?

The photosynthesis/light curve of the *P. koraiensis* seedlings described above was measured each month from July to May. During winter, the potted seedlings were removed from the pots by thawing the soil overnight at room temperature and were then taken to Shenyang in an ice-filled thermos flask. Measurements were made after the seedlings had adapted to the temperature and light conditions of the laboratory. Figure 2 shows that the exposed seedlings (those which showed irreversible winter injury in the spring) release CO_2 instead of absorbing it under illumination, and the stronger the light, the more CO_2 is released.

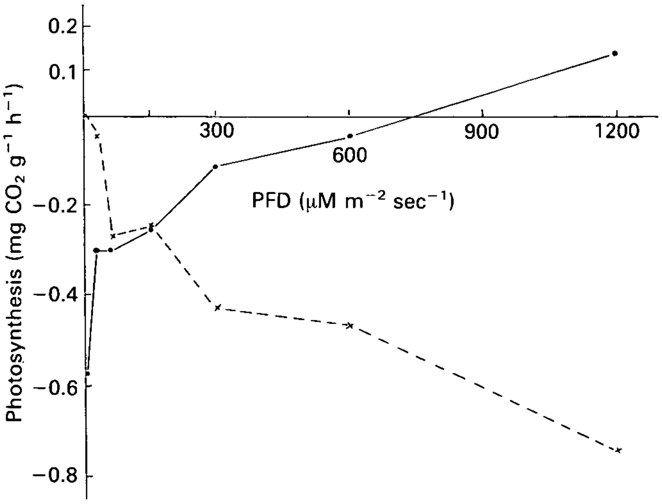

Figure 2. Photosynthesis/light curve of P. koraiensis *seedlings, measured in March 1985*
(———— shaded seedling; ---- seedling exposed to full sunlight)

Kramer and Kozlowski (1979) reviewed the winter inhibition of photosynthesis in conifers, but no 'negative' photosynthesis has been reported in the literature.

In our study, the 'negative' photosynthesis lasted from November to March. Shaded seedlings also released CO_2 from December to February, but the rate of release always decreased with increasing illumination. Measurements in the winter of 1984–85 and 1985–86 gave similar results. The implication is that photosynthesis in exposed seedlings is more inhibited. During the inhibition period, the chloroplasts sustained severe injury by photo-oxidation, resulting in the death of needles, or even of the whole seedling. Part of the released CO_2 is believed to be a direct product of photo-oxidation, or at least closely related to photo-oxidation activity. Shading alleviates the photoinhibition and the resulting photo-oxidation injury. A further implication is that light levels in the growing season only are insufficient, and the effect of winter solar radiation should also be considered when discussing shade tolerance. The problem of survival of *P. koraiensis* seedlings on open sites may be related more to winter solar radiation than to light levels in the growing season.

4 Tree species at higher altitudes have a greater potential for transpiration and photosynthesis than their genetic counterparts at lower altitudes

The forest on Changbai Mountain shows clear altitudinal patterns of distribution. *Betula ermanii* Cham. (Erman's birch) is the dominant species in the alpine forest zone at 1700–2000 m. *Alnus mandshurica* (Call.) Hand.-Mazz. (Manchurian alder) is distributed at similar altitudes. Their low-altitude counterparts, *B. platyphylla* Suk. (Manchurian birch) and *A. sibirica* var. *hirsuta* (Turcz.) Koidz. (Siberian alder), are distributed mainly in the broadleaved/*P. koraiensis* forest zone below 1300 m. How do these species adapt to their environment at different altitudes? The following experiments may provide some answers.

In spring 1985, 3-year-old natural seedlings were transplanted into pots and grown in the yard of the Research Station at 700 m. Daily rates of transpiration were monitored by a LI-1600 steady-state porometer during July. The alpine species, *B. ermanii* and *A. mandshurica*, displayed a low stomatal resistance, with no apparent daily fluctuation, and a high rate of transpiration. Their low-altitude counterparts, *B. platyphylla* and *A. sibirica* var. *hirsuta*, showed a quick adjustment of their stomatal resistance in response to the irradiance and a much lower transpiration rate. The results for *Alnus* are shown in Figure 3. A few days after the transpiration measurements, a CO_2 IR analyser was used to measure the photosynthesis/light curve for the same seedlings. Figure 4 shows that the photosynthesis rate of *A. mandshurica* was twice that of *A. sibirica* var. *hirsuta*. If the greater potential for photosynthesis in the shaded *P. koraiensis* seedlings is related to their higher chlorophyll content, then the higher potential for photosynthesis in the high-altitude species may be dependent on their lower stomatal resistance. This characteristic can be regarded as a physiological adaptation by alpine trees to the short, rainy and foggy growing season. The trees keep their stomata open all day for a high rate of photosynthesis, irrespective of the resulting water loss, because water is not a limiting factor. In contrast, their low-altitude counterparts must adjust their stomatal resistance in accordance with the light conditions to achieve a balance between photosynthesis and transpiration in a drier and warmer environment.

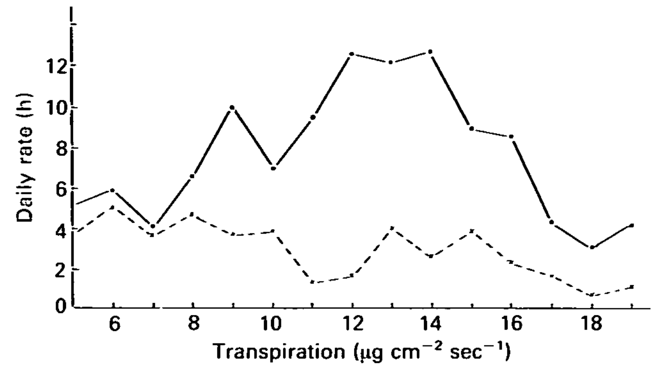

Figure 3. Diurnal transpiration rate of Alnus, *measured on a clear day in August*
(——— Alnus mandshurica*; ---- *A. hirsuta*)*

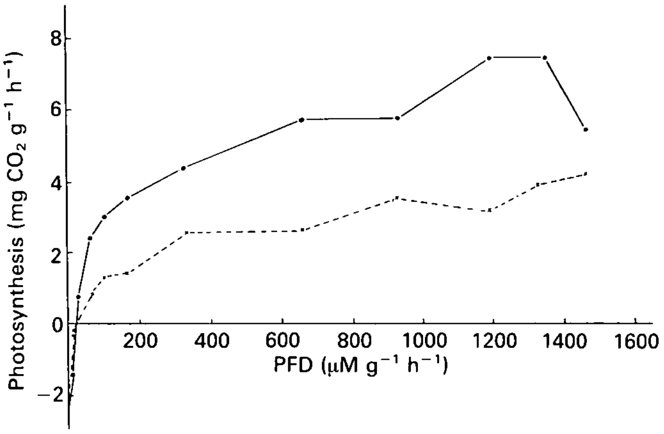

Figure 4. Photosynthesis/light curve of Alnus, *measured at 25°C in August*
(——— Alnus mandshurica*; ---- *A. hirsuta*)*

5 'Bounce-back' reaction in the daily rate of transpiration

Measurements of daily transpiration rates in late July and early August 1985 revealed that many tree species, including *Tilia amurensis* Rupr. (Amur linden), *Acer mono* Maxim. (painted mono maple), *Populus davidiana* Dode (Chinese aspen), *B. ermanii, B. platyphylla, A. mandshurica, A. sibirica* var. *hirsuta*, etc, display a special 'bounce-back' reaction. There is a minor decrease at 0600–0700 hours during the course of increasing transpiration in the morning and a minor increase at 1800–1900 hours during the evening decrease in transpiration (see Figure 3). This is another discovery that has not yet been described in the literature. The minor morning decrease was accompanied by a normal increase in stomatal resistance, while the minor evening increase was accompanied by an abnormal decrease in stomatal resistance. The controlling physiological mechanism and its implications are not known. We believe it may be related to the fine tuning in the feedback adjustment of leaf water potential. However, the tiny fluctuations are difficult to detect with the instruments currently available, such as the osmometer or pressure bomb.

6 Reduction in transpiration following leaf excision

Before the 1980s, 'fast-weighing' – a method introduced by Ivanov *et al.* (1950) – was used extensively in China to measure transpiration. The method is based on the theory that, when a shoot is cut off from its maternal plant, its leaf water potential will increase abruptly, resulting in an increase in transpiration as tension in the water-conducting tissue is released. Transpiration will then gradually reduce, as more and more water is lost from the excised shoot, and will eventually become lower than the rate before shoot excision. If we allow the shoot to transpire for a reasonable length of time, a similar rate will be obtained to the *in situ* transpiration rate. The theory is quite sound, but has not been tested by modern instruments in China. The L1-1600 steady-state porometer is a suitable instrument for measuring and recording transpiration and related parameters instantaneously and simultaneously. Transpiration rate was monitored at the same position on a leaf 5 minutes before and 10 minutes after leaf excision, while the leaf was kept in the same measuring position (Figure 5). Several different tree species have been tested. Most showed decreasing transpiration rates with increasing stomatal resistance after leaf excision in a steady environment. Five minutes after excision, the transpiration rates reduced to between 66% and 50% of the value before leaf excision. The predicted transpiration increase was not seen even seconds after excision in any species. The implication of this finding is clear: the 'fast weighing' method undervalues the transpiration rate *in situ* to such an extent that it should not be overlooked in any evaluation of the water balance in a forest. We suggest that the increased stomatal resistance is more important in controlling transpiration than leaf water potential after leaf excision.

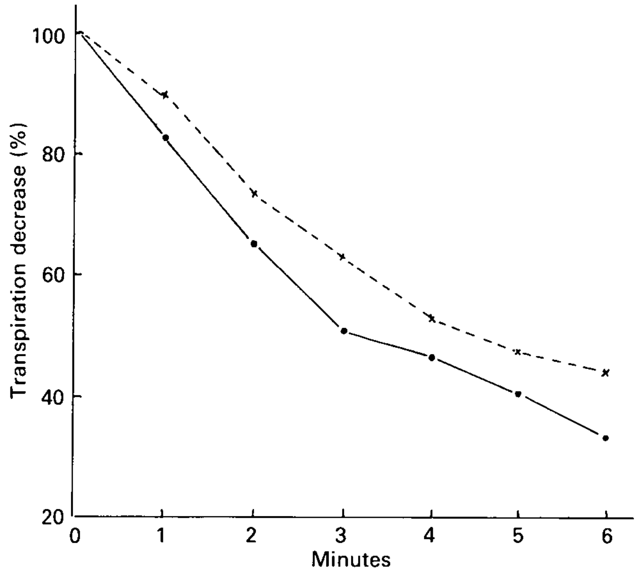

Figure 5. Decrease in transpiration rate after leaf excision. The lower curve is the average value for 8 species, 12 measurements under PFD 1000 $\mu M\ m^{-2}\ sec^{-1}$. The upper curve is the average value for 4 species, 8 measurements under PFD 600 $\mu M\ m^{-2}\ sec^{-1}$

There are many more traditional concepts in tree ecophysiology that have not been tested, at least in China. The foregoing are just some examples which challenge the traditionally held views. It is believed that, with the development of experimental technology, more discoveries will be made and more questions will be raised to stimulate ecologists' thinking and to advance the development of forest ecology.

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Nutrient control of growth in temperate forests

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Abstract
Forests are able to grow on soils from which arable agriculture is excluded because of poor nutrient availability. This is due to the ability of the trees both to obtain soil nutrients and to conserve and recycle them. The perennial roots and associated mycorrhizas of trees can exploit all the rootable volume of the soil, and it is often this volume, rather than the concentration of soil nutrients, which is the limiting factor. Once a nutrient ion has been taken up, there are very effective mechanisms for retaining it in the cycle, with the recovery of nutrients from dying tissues being an important feature. It is shown that, as a consequence, trees are more likely to suffer nutrient deficiency before canopy closure than afterwards. Examination of the accumulation and cycling of nutrients between tree species suggests that broadleaved species are no more nutrient demanding than coniferous species, so observed differences in site requirements must relate to the trees' ability to obtain nutrients from intractable soil sources. Deficiencies can be corrected by suitable cultural measures, including the application of fertilizers. Such measures are discussed and possible adverse environmental effects are indicated.

1 Nutrient supply in temperate forests

Generally, the soils of the temperate region, with the exception of the worst peats, are all capable of producing some form of natural forest cover. Where the activity of man, however, has led to deforestation, the resultant wetting of the soil and possible development of iron pans have so reduced the volume of soil available to roots that attempts at afforestation are often hampered by an inability to obtain sufficient nutrients. Thus, the heaths of some parts of northern Europe are extremely slow to revert to full forest canopy, although a 'pygmy forest' of severely stunted trees may develop, if there is an adequate seed source. The importance of an adequate rootable volume of soil cannot be over-stressed, and there are many examples of better tree growth on deep friable podzols than on neighbouring brown forest soils, if these latter are shallow or are heavily diluted by boulders.

Tree growth, therefore, is not a function of the concentration (in mg g^{-1}) of nutrients in the soil. Rather, it is a function of the total reserve of such nutrients that can be exploited by a perennial root system capable eventually of fully exploring the volume of potentially rootable soil. In this respect, forestry differs markedly from annual agricultural crops where, because of the short production cycle involved, roots are unlikely to exploit much more than the shallow layer of ploughed soil prepared for them. (There are, however, interesting parallels with permanent grassland.) It follows that the soil analytical techniques developed for diagnosing potential nutrient deficiencies in arable systems have little relevance to forest conditions, unless volume of soil is not limiting. Such conditions may exist over restricted areas; for example, soil analysis has proved quite useful in identifying phosphate-deficient sites in both North Island, New Zealand, and for the sands of south-eastern USA. However, there seems to be little general utility in this approach.

There is the further factor that trees may thrive even where the total quantity of available nutrients in the entire rootable soil volume (by whatever measure of 'availability' may be favoured by agriculturalists) is insufficient to support arable crops. In part, this is a result of the trees' ability to conserve and re-use nutrients, as discussed in the next section. In addition, however, the endo- and ecto-mycorrhizal associations of the perennial tree roots appear to enable trees to draw on sources of nutrients not normally considered available to annual plants. Thus, trees can obtain appreciable quantities of potassium from unweathered micas and microcline (H G Miller, unpublished), and the recent demonstration that the mycorrhizas of perennial heath plants can make direct use of low molecular weight organic compounds, without these having to be first mineralized to NH_4^+ or NO_3^- (Reid & Bajwa 1985), suggests that at least some tree species may share this ability. Taken alone, however, this factor, although important, is insufficient to explain the ability of trees to make high production on impoverished soils incapable of supplying large amounts of nutrients. Further explanation, therefore, has to be sought in the ability of trees to use and conserve nutrients once obtained.

2 Nutrient cycling

Nutrients taken up by a tree (Figure 1) may be recycled through the fall and decomposition of litter (biogeochemical cycle) or by internal retranslocation (biochemical cycle). Prior to a leaf being dropped, a large proportion of many of the nutrients it contains are withdrawn into the tree, and so become available for the formation of new tissues. About two-thirds of the leaf nitrogen may be so recovered and rather more of potassium. As a result, a fully formed forest places fairly small demands on the soil, being able to supply much of the nutrient requirements for the formation of new leaves from the amounts withdrawn from old leaves. High rates of growth can then be achieved on depauperate soils that otherwise are only capable of

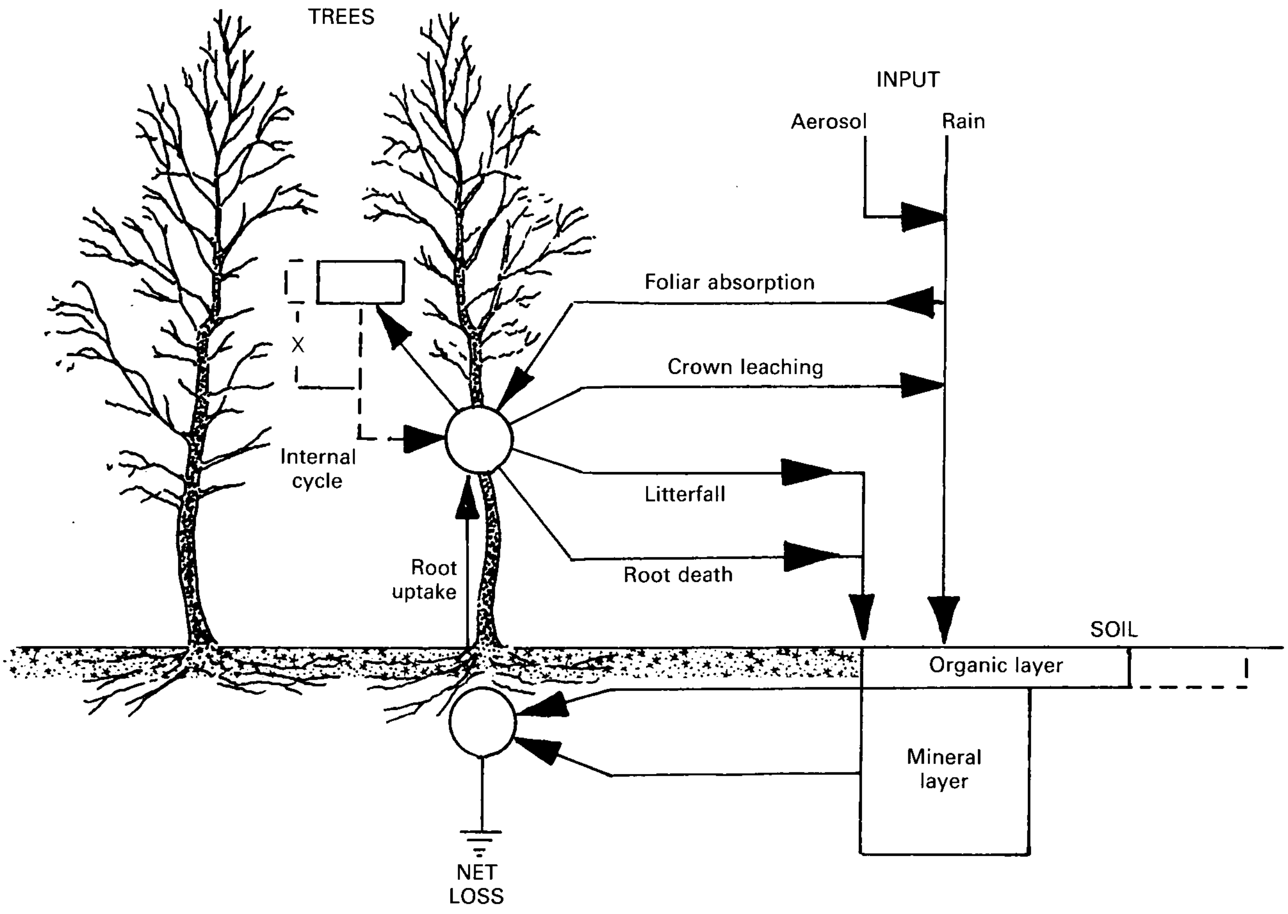

Figure 1. Illustration of the nutrient cycle in forests; zones of accumulation are represented by rectangles and mobile pools by circles

sustaining low production systems. There is the further factor that the cycle through the litter and humus is 'tight', ie virtually all of the nutrients mineralized are either taken up by the trees or become immobilized in the microbial biomass. In this respect, the efficiency of uptake by the trees has much to do with the mycorrhizal net that is supported by the well-developed root system. Tight cycling is well understood in relation to tropical forests on poor soils, but it is important to appreciate that this is a characteristic of all forests, including those of the temperate region.

A proportion of each nutrient released by a tree in litterfall is mineralized so slowly that essentially it may be considered as having been removed from the cycle. Most mineral elements are released relatively rapidly, but phosphorus and, to a greater extent, nitrogen are released somewhat slowly, the rate of nitrogen mineralization tending to decrease with increasing latitude, and generally being lower in coniferous litter than in the litter of broadleaved species.

The net result of the trees' ability to recover nutrients both from foliage prior to death and abscission and from decomposing leaves in the litter layer is that there is a pronounced decline in the demands placed on soil nutrient supplies once the canopy has closed. Subsequent to canopy closure, more or less every leaf formed can tap nutrients from a leaf being shed. Prior to this stage, however, 3 or even 4 times as many leaves are being formed as are being shed. The importance of this for a temperate pine crop is outlined in Table 1. In this example, although the total nitrogen requirement of the young stand is less than half that of the older trees, the greater ability of the latter stand to recover nitrogen both through internal retranslocation and, to a lesser extent, from decaying litter means that the younger stand places a 3-fold greater demand on the nitrogen capital of the site. It follows that the younger stand is the more likely to show nitrogen deficiency and respond to remedial applications of fertilizer nitrogen. Indeed, it is during this early stage that any nutrient deficiency is most likely to be manifest, as confirmed by recent observations in the field, where it is becoming increasingly clear that deficiencies are very much less likely in pole-stage crops than at the establishment stage (eg McIntosh 1984). Miller (1981) gave the term Stage I to the pre-canopy closure period when nutrient demands are high. The period thereafter is then Stage II. These stages are identical to those suggested independently

Table 1. Comparison of rates of transfer between units and sources of nitrogen modelled for 10-year-old (2 m tall) and 40-year-old (11 m tall) stands of *Pinus nigra* var. *maritima* (source: Miller 1986)

	kg N ha^{-1} yr^{-1}	
	10-year-old	40-year-old
1 Recovery from dying tissues	11	69
2 Uptake from soil	55	69
3 Total requirements (1 + 2)	66	138
4 Released by mineralization of litter	10	51
5 Immobilized in humus	3	12
6 Available for uptake (4–5)	7	39
7 Input in rainwater	5	5
8 Net change in tree accumulation (2–4)	+45	+18
9 Net change in soil capital (4 + 7 − 2)	−40	−13

by Attiwill (1979, 1981), who pointed out that, while young, a forest must 'gain perenniality' and devote a major proportion of its net primary production to the build-up of nutrients. The second stage is then characterized in his system by heartwood formation; the rate of increase of photosynthetic display slows and, although net primary production is increasing, it is largely as physiologically dead heartwood. This scheme was developed in relation to the growth sequence of *Eucalyptus obliqua* (L'Herit.) (messmate), and in many other species heartwood formation does not set in so early. Nevertheless, the basic premise remains because even the continued accumulation of sapwood involves a very much smaller quantity of nutrients per unit net production than does the expansion of the leafy crown.

In the particular case of nitrogen (and, perhaps rarely, phosphorus), deficiency conditions can develop in old age. Indeed, nitrogen deficiencies were first diagnosed at this stage despite the reduction in the demands made by the tree, as illustrated in Table 1. This problem appears to be restricted to coniferous forests and is the result of the continued and effective removal of nitrogen from the cycle, not only as incorporation in the living biomass but also, and most importantly, through immobilization in the humus layer. It is now well established that such continued removal of nitrogen from the cycle can lead, on sites of low nitrogen capital, to late-rotation nitrogen deficiency and progressive site deterioration (eg Tamm *et al.* 1960; Turner 1977). Miller termed this event Stage III and emphasized that it is by no means inevitable, being limited to those coniferous stands on poor soils where a pronounced humus layer develops. As such, the problem is far more common in the boreal than in the temperate zone, but yet may still occur in the latter.

3 Comparison of nutrition of broadleaved and coniferous species

In general terms, broadleaved species are often described as being 'nutrient demanding' or 'site demanding'. Although these terms seem synonymous, an important distinction should be drawn. It is necessary to ask whether broadleaved species actually need more nutrients than do conifers for a given growth rate. The alternative is that they may be slightly less effective at obtaining nutrients from the soil, so requiring soils of higher fertility for adequate nutrition. For a tree to be genuinely nutrient demanding, either it must have a higher concentration of nutrients in the various component parts of the tree, or there should be an unusually high loss of nutrients from the plant through litterfall or crown leaching.

Nutrient levels in tree foliage vary with age of tree (Miller *et al.* 1981) and season of sampling, and may show an accumulation in excess of absolute requirements under conditions of generous soil supply. As a result, comparison between species, or even between groups of species, becomes difficult. Reports of large

Table 2. Generalized critical and optimum levels of macronutrients in tree foliage at 3 growth stages

		% oven dry weight*			
		Evergreen conifers		Broadleaved species & deciduous conifers	
Tree height (m)	Nutrient	Critical	Optimum	Critical	Optimum
0.05–0.25	N	2.0	2.5	2.4	3.2
	P	0.2	0.3	0.24	0.34
	K	0.5	1.0	0.5	1.0
	Mg	0.07	0.17	0.07	0.17
1.5–3.0	N	1.2	1.5	1.4	1.9
	P	0.12	0.18	0.14	0.2
	K	0.3	0.6	0.3	0.6
	Mg	0.04	0.1	0.04	0.1
7.0	N	1.6	2.0	1.8	2.5
	P	0.16	0.23	0.18	0.26
	K	0.4	0.8	0.4	0.8
	Mg	0.05	0.13	0.05	0.13

*end of season concentrations

differences between conifers and broadleaves are often a reflection of differences in sampling time. Miller (1983), from a detailed survey of the literature, concluded that it did seem likely that deciduous broadleaved species require slightly higher levels of foliar nutrients than evergreen conifers, although it was clear that the deciduous *Larix* (larch) should be grouped with the broadleaves. A general guide to the levels that might be expected at 3 stages of growth is given in Table 2, and some information for micronutrients in Table 3. There is some distinction between the 2 groups of species, a distinction that is most pronounced for nitrogen. However, individual crops vary greatly around these values, a variation that appears to reflect availability in the soil rather than any necessary requirements of the tree (Miller 1984a). It should be borne in mind that, because trees can retranslocate nutrients from foliage, this acts as an important storage organ for nutrients, and excess amounts will be accumulated if generous soil supplies are available. Miller found that, although nitrogen levels appear to be higher in foliage of deciduous species, including broadleaved genera, than in that of conifers, the distinction for other elements is fairly minor. Indeed, the reports of phosphorus levels in *Pinus sylvestris* L. (Scots pine) showed a greater variation than was found between conifers and broadleaves. Furthermore, there was no clear distinction between these groups of species in nutrient levels in other component parts of the tree, including wood, bark and roots. The determining factor for levels of many nutrients seemed to be soil type rather than tree type. He concluded that, with the probable exception of nitrogen in foliage, there is little or no necessary specific variation in nutrient levels between those species for which suitable comparison was available. Therefore, differences in the nutritional behaviour of broadleaved and coniferous species seem unlikely to stem from necessary differences in nutrient concentrations.

Table 3. Generalized critical and optimum levels of micronutrients in foliage of trees of both coniferous and broadleaved species (there is insufficient information to suggest that levels alter with tree size)

Nutrient	ppm dry weight	
	Critical	Optimum
Copper	2	5+
Boron	5*	25
Manganese	20	50+

*critical B levels may be as high as 15 ppm under drought conditions (J Turner, pers. comm.)

As many broadleaved species of the temperate region are deciduous, it might be argued that the loss of the entire foliage biomass every year is expensive in nutrients. However, examination of the available literature (Miller 1986) reveals that the regression of weight of leaf litterfall on growth rate is common for both broadleaved and coniferous species. In other words, rate of litterfall per unit growth rate is the same for both groups of species.

There is insufficient confirmation of rates of crown leaching to be able to make useful comparisons of the significance of this pathway. It is likely that potassium is lost readily from all species and, although there is some indication of variations in the loss of nitrogen and phosphorus (H G Miller & J D Miller, unpublished), crown leaching is proportionally a very minor pathway for the movement of these elements.

Indeed, it seems that once canopy has closed there is remarkable similarity in nutrient uptake between crops of similar growth rates. Thus, the calculated uptake of N, P and K for *Betula* (birch) at this stage is, respectively, 43, 4.5 and 14 kg ha^{-1} yr^{-1} (Miller 1984b), compared with 45, 4.4 and 14 kg ha^{-1} yr^{-1} respectively for *Pinus nigra* var. *maritima* (Ait.) Melville (Corsican pine).

When values for nitrogen uptake reported in the literature are correlated with growth rate, a close relation ($r=0.90$) is found across forests ranging from Alaska to equatorial Africa, with both coniferous and broadleaved species lying along the same line (Miller 1984a).

On this basis, and from the prior discussion, there seems inadequate reason to argue that broadleaved species are more nutrient demanding, in the strict sense, than coniferous species. However, it should be borne in mind that the rapid early growth and canopy formation shown by pioneer broadleaved species will mean that they may place unusually heavy demands on the soil during Stage I. Even these peak demands are unlikely to be greater than the maximum demands, made by the much faster-growing conifers, excepting the very fast-growing broadleaved species such as *Populus* (poplar) (Bernier 1984).

The nutrient requirements of broadleaved species, therefore, are not significantly different per unit growth rate than are those of the conifers. Yet many broadleaved species will not thrive, or even survive, on those poor soils capable of carrying high-yielding crops of coniferous species. The reason would seem to lie in the relative inability of many broadleaved species to obtain nutrients from intractable soil sources. The nutrients demanded per unit growth rate are approximately the same, but the broadleaves are less able to find these nutrients in poor soils – the difference lies not in 'nutrient demands' but in 'site demands'.

4 Fertilizers in the amelioration of nutrient deficiencies

Nutrient deficiencies are usually corrected by the application of an appropriate artificial fertilizer, or very rarely the application of organic manures. Before considering the appropriate rates and times of fertilizers, it should be mentioned that deficiencies during Stage I can often be avoided by using appropriate cultural techniques. Thus, ploughing to increase rooting volume, particularly where this entails the breaking of an ironpan or other physical barrier in the soil, can greatly reduce the chances of developing deficiency conditions. It is now becoming increasingly clear that effective and thorough weeding can also improve nutrition. Indeed, it is likely that in the past fertilizers have frequently been used to overcome the problems associated with inadequate weed control.

These points notwithstanding, there are a number of soils on which tree growth would be impossible, or very poor, without the application of a suitable fertilizer. Throughout the temperate forests of the world, there is little doubt that phosphorus is the nutrient that is most frequently limiting early growth. Application of phosphorus can be in a variety of forms, including single and triple superphosphates or, in combination with nitrogen or potassium, as a phosphate salt. As long as careful application techniques are used, there seems no reason to believe that the more soluble forms would lead to root damage. Because most forest soils are fairly acid, untreated ground rock phosphate can also be used to great effect and need not necessarily be finely ground (Binns *et al.* 1980). Rates of between 40 and 80 kg P ha^{-1} are most commonly used and, although responses can be obtained with higher quantities, the gain is rather small.

Potassium is usually applied as potassium chloride, or as potassium salts also including one or both of ammonium and phosphate. Potassium sulphate is seldom used but, in forest nurseries, magnesium ammonium phosphate has found some favour. Rates are generally in the range 80–100 kg K ha^{-1}, there being few reports of any advantages of heavier rates. In young forests, phosphate, or phosphate and potassium, may have to be applied 2 or more times at intervals of 3–5 years.

Effective response to nitrogen can be obtained when applied as ammonium nitrate, as urea or as ammonium sulphate. The latter salt, however, is now seldom available. Salts containing only nitrate can provoke nutrient imbalances and growth disturbances, and should be avoided unless previously shown to be safe. Ammonium nitrate, however, is to be recommended and usually results in the greatest nitrogen uptake per kg of nitrogen applied. Urea is somewhat less efficient, and there is always a risk of appreciable losses through volatilization of ammonia in dry warm weather. Despite this, urea is often the preferred nitrogen fertilizer because of its cheapness and high concentrations. Bulky organics, such as manure, are very effective but are rarely used because of the difficulties of application over extensive areas. Some waste products, such as formalized casein, have been tried, but with little or no success. A large number of nitrogen fertilizer trials have been carried out and, although they suggest that increased responses can be obtained up to about 250 kg N ha^{-1}, and rarely beyond, when applied as a single dressing, once allowance is made for the decreasing additional response at higher rates, commercial applications in the region of 150–200 kg N ha^{-1} are to be recommended.

It is rarely necessary to apply any other nutrient to temperate forests, although both copper deficiency and boron deficiency have been confirmed in an increasing number of locations, particularly when growth has been boosted by nitrogen fertilizer, and magnesium deficiency is well established on very sandy soils. Magnesium is also causing concern in relation to acid rain pollution, but the exact nature of the link has still to be explained.

5 Nutrient management in relation to the environment

Several management techniques, and in particular the application of fertilizer, may have environmental consequences. Fertilizers are very unlikely to have an adverse effect on the area to which they are applied; indeed, the object is to induce beneficial effects. However, if not properly controlled, the application of fertilizers can lead to pollution of neighbouring waterways. Nitrogen is not readily lost, particularly if applied as ammonium or urea, unless fertilizer granules or prills enter streams and rivers directly. Heavy application of nitrate fertilizers, however, may cause problems, and Kreutzer and Weiger (1974) have pointed out that care should be taken to ensure that drainage water from such areas must be well diluted by non-contaminated streams before it is put to human use. Timing of the application may also have to be considered, although most reports suggest that there is little variation in amount lost, unless the fertilizer is applied to snow-pack. Phosphorus is usually tenaciously retained by mineral soil but can be slowly leached from organic peat. Potassium is lost to streams in fairly large amounts following fertilizer application but, unlike nitrogen and phosphorus, does not appear to stimulate algal blooms in streams and reservoirs.

Some management operations, other than the direct application of fertilizer, may stimulate loss of nutrients to streams. Ploughing is perhaps the most significant in this respect for it can lead to the oxidation and loss of nitrate and sulphate compounds from previously waterlogged organic soils. The quantities of nutrients involved are unlikely to be important, but the process can lead to pronounced, if short-lived, acidification of drainage water. It has been suggested that clearfelling may lead, as a result of stimulated organic matter breakdown, to loss of injurious substances, in particular nitrate, perhaps accompanied by acid-soluble metals such as aluminium. This potential problem has attracted considerable attention in recent years and, while the basic premise is usually confirmed, the levels of nitrate, although elevated, remain very low.

The most damaging aspect of many management operations is the risk of soil erosion, against which all other factors pale into insignificance. Fortunately, soil erosion should not occur when forests are under skilled management.

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Research objectives in US National Park Service Biosphere Reserves, with special reference to Great Smoky Mountains National Park

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Introduction

The Biosphere Reserve concept embraces several management philosophies, ranging from strict preservation in core conservation areas to direct manipulation in experimental research areas (Gregg & McGean 1985). In Biosphere Reserves that are managed by the US National Park Service (NPS), most management is of strict preservation type. Thus, US National Park Biosphere Reserves are core conservation areas devoted to the preservation of natural ecosystems and the biological diversity that these ecosystems contain.

In the United States, the National Park movement is over 100 years old. For nearly all of this history, the implicit premise of managers has been that legal protection would itself guarantee the survival of species and ecosystems in natural areas. Protected resources were viewed as either static museum objects or self-regulating systems that were best left alone. Such an attitude has promoted management that is passive and reactive. Today, we recognize that a variety of human threats, such as air pollution and exotic species, permeates the boundaries of Nature Reserves. We have also learned that some ecosystems are naturally dynamic (eg those dependent on fire) and that some species (eg migrating birds and large mammals) cannot be fully protected within even our largest ($>10^6$ ha) Parks because of seasonal movements or large home ranges. With the increasing realization that legal protection alone does not guarantee the survival of ecosystems and species has come the recognition that active research programmes are essential to conservation management. With the recognition that the success of preserves depends in part on the surroundings of the protected areas has come the realization that conservation strategies must extend beyond the legal boundaries of any one preserve. The Biosphere Reserve concept deals with these new realizations, and thus represents an important evolution in our conservation strategy.

In this paper, I will use the recent history of resource threats in Great Smoky Mountains (GRSM) National Park Biosphere Reserve, North Carolina and Tennessee, USA, to illustrate research that is appropriate to US National Park Biosphere Reserves. Before I discuss our experience in GRSM, I will present a short introduction to conservation agencies in the United States and a brief overview of the philosophy that has guided the National Park Service science programme. In the final section, I will outline a research strategy for US National Park Service Biosphere Reserves.

2 Protection of natural areas in the United States

In the United States, protection of natural areas on a national scale began with the creation of the first National Park in 1872 (Yellowstone National Park). The National Park Service of the Department of the Interior was created in 1916 to administer the growing National Park system. Today, the National Park Service manages a total of 320 natural and historical areas, divided into a diverse set of categories (Butowski 1979). Important natural areas are found in such categories as National Parks, National Preserves, National Monuments, National Natural Landmarks, National Lakeshores, National Seashores, National Rivers, National Wild and Scenic Riverways, and even in a number of historical parks. The most significant natural area parks of the National Park system include 39 units greater than 100 000 ha in size and 35 units 10 000–100 000 ha in size (these totals do not include National Recreation Areas, National Scenic Rivers, and related categories). In addition to these 74 units, 16 other units play a significant role in natural area protection on the continental scale, including 4 parks 5000–10 000 ha in size, and 12 National Seashores and Lakeshores. Of the 41 US Biosphere Reserves, 19 Reserves contain units managed by the National Park Service.

In addition to lands managed by the National Park Service, protection of natural areas is carried out by a wide range of other public and private agencies in the United States. For example, the US Forest Service manages 16 Biosphere Reserves. The US Fish and Wildlife Service and US Army Corps of Engineers play roles in the protection of wetlands. The Wilderness Act provided for the protection of wildlands independent of management agency, and these areas are managed by NPS, the Forest Service, the Bureau of Land Management, and others. Similarly, the Endangered Species Act provided for protection of critical habitat for rare species on lands managed by a variety of agencies. State governments manage natural areas in state parks, some of which are important to nature conservation on a national scale. Many private groups also protect and manage important natural areas, including the Audubon Society and the Nature Conservancy. At present, there is no easy way to grasp the national significance of this network of natural areas; indeed, the agencies involved do not share common management objectives and have not communicated readily with one another. The co-ordination of these efforts for some larger purpose (eg addressing the overall goal of protection of biological diversity at the continental scale) is desirable, but has not yet been attempted.

3 Research in US National Parks

The role of research in the National Park Service has been controversial because National Park Service legislation lacks an explicit research mandate (Dennis 1985). This lack has resulted in a number of attempts to define National Park Service management philosophy and the role of science in National Parks (Bonnicksen & Stone 1982; Bratton 1985; Dennis 1985; Graber 1983; Sumner 1983; White & Bratton 1980). Basic National Park Service legislation simply describes the purpose of the agency as 'to conserve the scenery and natural . . . objects and wildlife therein, and to provide for the enjoyment of same . . . by such means as will leave them unimpaired for . . . future generations' (the National Park Service Organic Act of 1916).

The overall purpose of the National Park Service supports 2 general categories of research. First, the goal of preserving resources in perpetuity implies the need to know the nature and trajectory of these resources (this knowledge is required if management success is to be evaluated). The second research objective derives from the fact that the US National Parks were established not only to protect natural resources, but also to provide for their enjoyment in a manner that does not cause lasting impacts. Thus, the mission of the National Park Service implies a need to monitor visitor impacts to natural resources. The early legislation strongly implies that recreational and aesthetic values are related to ecosystem and landscape integrity. For example, in Great Smoky Mountains National Park these human values can be identified with vistas of the large, man-free, wilderness, landscape; the abundance and diversity of flowering plants (eg spring floral displays); and the presence of virgin forests with trees that surpass 300–500 years in age and 2.5 m in diameter.

The omission of an explicit research mandate in early NPS legislation derives, at least in part, from the assumption that establishing National Parks would ensure success of the preservation mission. This concept is, in turn, based on the assumption that large natural areas are stable or are recovering from past human influence. Since the establishment of the National Park system, however, resource change in protected areas has become a universal conservation issue (White & Bratton 1980). Some human influences permeate Park boundaries in ways not envisaged by early planners (eg air pollution and exotic species invasions), while other changes result from the interaction of Park management decisions with natural processes (eg fire suppression results in failed reproduction in some tree species). The realization that natural disturbances are intrinsic to ecosystems has implications for National Park Service management. This concern is exemplified by coastal areas, whose shorelines and dunes are shaped by dynamic processes (Dolan *et al.* 1978) and by fire-dependent ecosystems such as prairies and some coniferous forests, where fire suppression has resulted in resource change (Heinselman 1973).

The question of stability in natural systems is tied to spatial scale. Ecosystem dynamics on a local scale may define a broader-scale equilibrium. For example, fire causes dramatic local change, but from a larger perspective there may be a relatively stable distribution of land in various history states (further, native species may depend on the landscape array of different successional states). This is the 'shifting mosaic' of Heinselman (1973). Such dynamic equilibria are to be expected only when patch size is small relative to landscape scale, when there is feedback between community state and disturbance vulnerability (ie when disturbance vulnerability increases with time since disturbance), and if climate is relatively stable (White & Pickett 1985). These conditions may hold for some ecosystem types and some species in a particular Park, but not for others.

In research that was particularly applicable to the National Park Service, Romme and Knight (1982) showed that a 7300 ha watershed in Yellowstone National Park was too small to be in equilibrium with the fire regime, and predicted that the entire National Park was just large enough to be described by equilibrium dynamics. Within their study watershed, they predicted that wildlife populations, water quality, and fish populations would fluctuate in cycles of several 100 years, even within large watersheds, because of the non-equilibrium patch structure of the landscape. This observation has 2 interesting corollaries. First, the study of external threats, such as air pollution, will often be carried out in systems that are patchy, each patch following a dynamic trajectory that may interact with the influence of the external threat. Second, there will sometimes be conflicts between National Park Service goals: within the Romme and Knight study watershed, a natural process (fire) was hypothesized to have caused local fluctuations in native populations (wildlife populations).

The question of Park size and resource stability is especially important for the protection of large and/or migratory animals. For example, large mammals may have large home ranges, occur at low population densities, require large areas for protection of minimum viable population sizes, and migrate seasonally beyond Park boundaries. If Parks were universally large enough to contain equilibrium dynamics of ecosystems and to contain seasonal habitat for the species they protect, National Park Service research could conceivably be devoted entirely to the issue of visitor impacts. However, even the largest National

Parks (eg Yellowstone) do not contain the entire home range necessary for some large mammals (Leopold *et al.* 1963; Stone 1965).

We can conclude from this discussion that external threats to Park resources will often interact with non-equilibrium Park systems (Bonnicksen & Stone 1982); that, even in the absence of external threats, basic ecosystem research and active management will usually be required to meet NPS goals; that external threats and varying climates further support the idea that Park resources will rarely be influenced solely by internal processes; and that the conservation of at least some protected resources will require regional and international action (eg migratory birds).

The Man and the Biosphere Programme of UNESCO further helps to define the role of science in National Parks. The goals of the Biosphere Reserve Programme are to provide an international network of areas representative of the world's biogeographic provinces for ecological and environmental research, including long-term and baseline studies, and for the protection of biological diversity. There are 4 major areas of concern for research programmes (Table 1; Franklin 1985a): research management (eg a strong research presence, adequate facilities, and quality-assured data management), research strategy (eg long-term interdisciplinary and holistic studies), networking and comparative studies (eg regional and international projects, participation in environmental monitoring networks), and specific research areas for the conservation of resources (eg protection of genetic diversity, conservation strategy, and sustained use of natural resources).

Table 1. Programme elements for Biosphere Reserve research (adapted from Franklin 1985a)

RESEARCH MANAGEMENT
Develop an information system
Compile comprehensive research history
Develop a strong research archive and reference collections
Develop a data management strategy
Provide field and logistic support for research
RESEARCH STRATEGY
Perform holistic studies
Initiate a long-term monitoring and research programme
Encourage interdisciplinary studies
Complete resource inventories and design baseline studies
NETWORKS AND COMPARATIVE STUDIES
Co-ordinate research in core and experimental areas
Perform comparative studies on a regional, national, and international scale
Participate in monitoring networks
RESEARCH AREAS FOR EMPHASIS
Study protection of genetic resources
Study conservation strategy and preserve design
Study theoretical and practical aspects of wise resource use

Corresponding to the evolution of the role of research in National Parks, we can recognize 3 broad phases of research in the National Park Service: an early period of resource inventory and baseline studies, sometimes including the definition of critical, usually wildlife-related, management issues (1916–40); a period of decreased research effort (eg 1940–63); and a period in which there has been an effort to establish research as an integral part of NPS operations (1963–present) (Dennis 1985; Sumner 1983). In the last 10 years, there has been an increased emphasis on recognizing threats to our National Parks, and thus on the need to understand the risk of resource loss and strategies to decrease this risk (USDI 1980). Thus, sustained and purposeful research is very much a new activity in the National Park Service.

4 Great Smoky Mountains National Park and Biosphere Reserve

Great Smoky Mountains National Park, Tennessee and North Carolina, is a 208 000 ha preserve in the Unaka Range of the southern Blue Ridge physiographic province of eastern North America (35°37′N; Figure 1). Elevation ranges from 260 to 2021 m. Climate varies from mesothermal–humid at low elevations (mean July temperature = 22°C; mean January temperature = 4°C; mean annual precipitation = 150 cm) to microthermal–perhumid at high elevations (mean July temperature = 13°C; mean January temperature = −2°C; mean annual precipitation = 250 cm) (Shanks 1954; Stephens 1969). Drainage is steep, and natural ponds and wetlands are rare. Pre-Cambrian sandstones and phyllites dominate the bedrock geology, with 4 younger limestone fensters present in the western part of the Park (King *et al.* 1968). Continental glaciation did not reach the vicinity of GRSM.

Great Smoky Mountains National Park was created in 1934. Because of its size and rugged scenery, and because it is located relatively close to large centres of population, it is the most visited of the US National Parks, with about 8–10 million visits annually.

4.1 The vegetation

The vegetation pattern of Great Smoky Mountains National Park is one of the most complex in North America (Whittaker 1956). The vegetation is a mix of evergreen, needle-leaved, and deciduous, broadleaved forests, with 2 major types of non-forest vegetation, heath and grassy balds (Figure 2). The 2 dominant environmental gradients controlling vegetation composition in the old-growth areas of the Great Smoky Mountains are elevation and site moisture class (Whittaker 1956; Golden 1974). Although these gradients explain much of the variance in vegetation distribution, other factors modify the vegetation pattern predicted from these 2 gradients. Disturbance forms an overlay to the general environmental control of vegetation and interacts with those environmental gradients (Harmon *et al.* 1983; Pyle 1985).

The mountains are not high enough for a climatic tree-line (Cogbill & White 1987). The highest summits

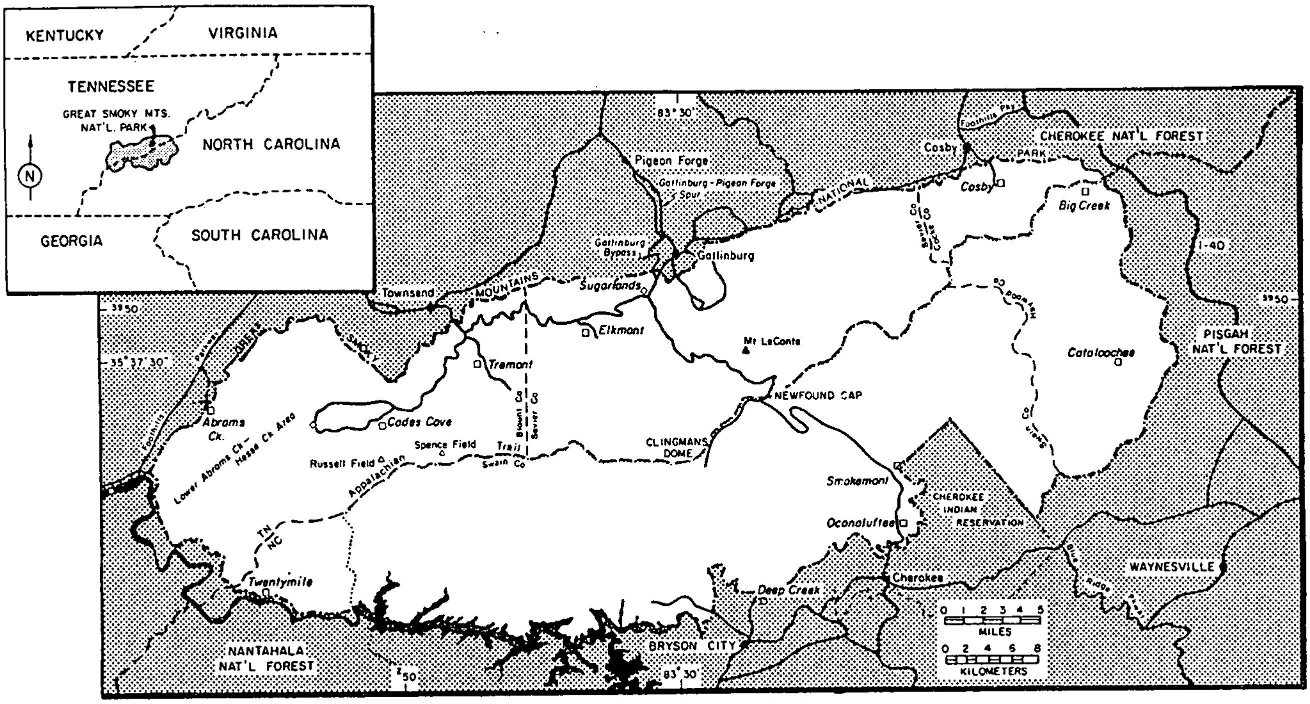

Figure 1. Location of Great Smoky Mountains National Park

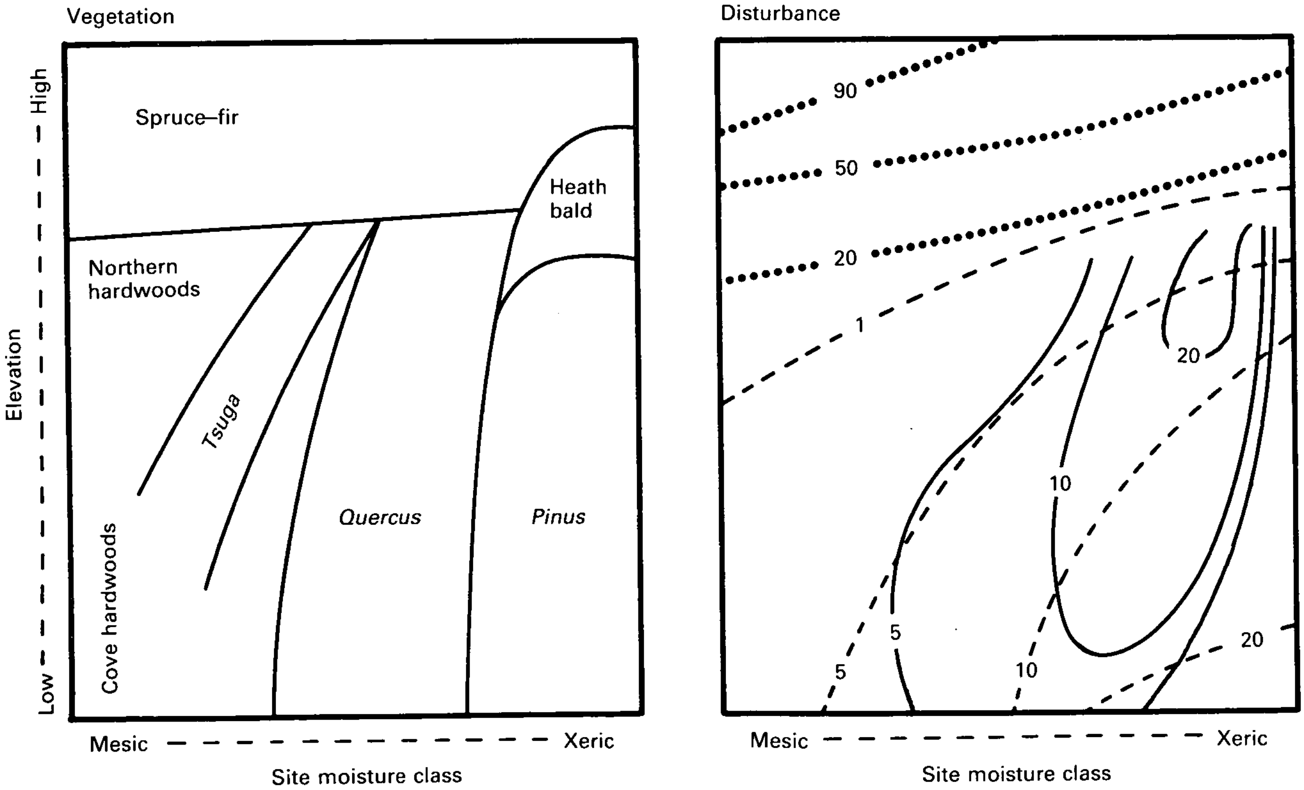

Figure 2. Vegetation and disturbance patterns in Great Smoky Mountains National Park (source: Whittaker 1956; Harmon et al. *1983). Numbers refer to percentage of canopy stems removed*
(••••••• Adelges piceae; – – – – Endothia parasitica; ——— *number of lightening ignitions 1940–79)*

are dominated by *Picea rubens* Sarg. (red spruce) and *Abies fraseri* (Pursh) Poir. (Fraser fir). The spruce–fir forests are a distinctive variant of boreal conifer forests found below the tree-line in northern latitudes (White 1984b). The hardwood/spruce–fir interface represents an important ecotone because it marks the boundary of 2 contrasting physiognomic vegetation types. This boundary has fluctuated during at least the last 18 000 years, in response to changing climate (Delcourt & Delcourt 1984).

At the time of its establishment (1934), 20% of the Park was free from major human disturbance (if the pervading influence of *Endothia parasitica* Murr. (chestnut blight) is excluded) and an additional 8% had suffered only from diffuse disturbance (Pyle 1985). Thus, about 60 000 ha of the Park is relatively free of direct human disturbance. Big tree stands in these areas include trees which reach 2.5 m in diameter (*Liriodendron tulipifera* L. (tulip tree) and *Tsuga canadensis* Carr. (eastern hemlock)). The rest of the Park had been subject to farming (predominantly at lower elevations) and logging. Post-logging fires were particularly severe in several watersheds (eg during the 1925 drought), with effects quite evident on aerial imagery today.

Bedrock geology is not, generally speaking, a major influence on vegetation distribution within the Park. The exceptions to this statement are found in the 4 limestone windows in the western part of the Park and in the comparison between the Anakeesta and Thunderhead Formations at high elevations. Debris avalanches and narrow ridgetops are more prominent on Anakeesta; heath balds tend to be somewhat more frequent on Anakeesta bedrock as well, all else being equal.

4.2 Flora

Despite being only the twelfth largest US National Park, GRSM has the richest vascular plant flora (1200 native vascular plants within the National Park, about 2000 native vascular plants in the southern Appalachian biotic province) (White 1982). This is because within-community floristic diversity generally reaches its highest values in the humid, warm, temperate forests of the eastern United States.

Within the flora of eastern North America are approximately 150 genera which are strictly disjunct from east Asia or are strongly discontinuous in their range and best developed in east Asia and eastern North America (Li 1952). Fully 25% of the vascular plant genera of GRSM fall into this category (White 1983). Within the temperate humid-climate groups which show this pattern of distribution, almost all are more diverse in east Asia than in eastern North America; although the data are not fully developed to confirm this pattern, it is likely that the forests of eastern China were the most diverse temperate forests on earth (White 1983). In the protection of the biological diversity of the temperate zone, conservation activities in China have a truly global significance.

5 Fifty years of conservation, 50 years of change

In the southern Appalachians, the peak in agricultural activity occurred about 1850–80. This activity was mostly restricted to lower-gradient, warmer, and more fertile sites at lower elevations (one exception was the creation of upland summer grazing pastures – see discussion of grassy bald succession below). By the late 1800s, agriculture was waning and logging was becoming the main economic force. The early 1900s were a time of heavy resource exploitation in the southern Appalachian Mountains. Clearfelling of large areas was often followed by severe fire on the logging slash, and by subsequent erosion. If unchecked, such exploitation threatened to permanently reduce the productivity of this landscape, to say nothing of the loss of biological diversity and aesthetics. Concern over this danger led to the establishment of several conservation and research institutions, including the Great Smoky Mountains National Park, several National Forests (managed for diverse purposes, including wildlife, recreation, and sustained timber yield by the US Forest Service), Coweeta Hydrologic Laboratory (a US Forest Service research laboratory that possesses the longest continuing hydrologic record in the world; this site is also an experimental area for forest management, a long-term ecological research site, and a Biosphere Reserve), Highlands Biological Station (a research and teaching facility at the University of North Carolina), and the Tennessee Valley Authority (a multi-purpose agency which has erected dams for power and erosion control and addressed soil conservation problems in the southern Appalachians).

The National Park movement was successful in saving old-growth vegetation over about one third (60 000 ha) of the Great Smoky Mountains, including several large watersheds. The information we can learn from these areas in an otherwise disturbed mountain landscape is invaluable. These lands constitute the largest block of intact wilderness in the region – thus, the scientific merit of the lands extends beyond the study of individual old-growth stands. The wilderness also supports unique recreational and aesthetic values. Despite the overall success of this conservation effort, however, a number of resource losses, changes, and threats have occurred during the 50-year period of protection, and have constituted the major management challenges facing the National Park Service. I will discuss below those threats which have major direct impacts on dominant plant communities.

The most important threats to natural resources have been the invasion of 3 exotic species (*Endothia parasitica*, *Adelges piceae* Ratz. (balsam woolly adelgid), and *Sus scrofa* L. (European wild boar)), deposition of air pollutants, changes in Park fire regime, and the impacts of visitors (White & Bratton 1980; Harmon *et al.* 1983).

Endothia parasitica, an Asian fungus, invaded the southern Appalachians shortly before the National Park was established and caused nearly complete mortality of mature trees of *Castanea dentata* (Marsh.) Borkh. (American chestnut) by 1940. *C. dentata* was a large and dominant tree in GRSM and had a wide environmental range. This tree was also a consistent and important producer of hard mast, and thus was important to wildlife populations. While mature stems have suffered nearly complete mortality, root systems have remained alive and have continued to produce suckers which occasionally survive to flowering and fruiting. Fertile seeds are rare, however, because of a requirement for cross-fertilization. The suckers usually do not survive past 4–10 cm in diameter. In any case, while the root systems and suckers remain alive, the potential to preserve some portion of the original gene pool through propagation continues. It is likely that the next several decades will see the gradual loss of this remnant of the gene pool. At an ecosystem level, the loss of a dominant tree over such a wide area was significant; however, *Castanea* occurred in species-rich communities and a variety of species have replaced it, depending on site factors (Woods & Shanks 1959).

The second exotic, *Adelges piceae*, arrived in the southern Appalachians by 1960. The narrow southern endemic *Abies fraseri* has proved to be highly vulnerable to this pest, with mature trees suffering nearly complete mortality (Hay *et al.* 1978). However, seedlings and saplings are less affected; it is unclear, at this time, if the adelgid will become locally extirpated with the death of mature trees, thus allowing seedlings and saplings to survive until seed production. Further, there is an outlying population of *Abies* in south-west Virginia that may possess some genetic resistance to the adelgid. Unfortunately, we currently lack an ability to predict the future of the *A. fraseri* gene pool. Unlike *Castanea dentata*, however, the root systems do not survive and sucker; thus, the species is dependent on new seed-origin plants for the ultimate survival of its gene pool. The adelgid is producing more dramatic ecosystem change than *E. parasitica*, in that *A. fraseri* is a codominant of species-poor stands; further, it may be replaced by deciduous species, rather than evergreen coniferous trees, with concomitant changes in within-stand environment and soil organic layers.

The third exotic is *Sus scrofa*. While the 2 pests described above have caused widespread mortality in dominant tree species, the European wild boar causes impacts to forest understoreys (Bratton 1975). These effects are most severe in high-elevation *Fagus grandifolia* Ehrh. (American beech) forest and in springs, seepage areas, streamsides, and swamps. It reduces understorey herbaceous plant cover and drastically reduces the density and cover of species that are preferred food items. The animal may influence nutrient availability in stands, the pattern of tree and shrub reproduction, and downstream water quality. Effects on animal populations also occur (Singer *et al.* 1984).

The second general kind of resource threat is air pollution. Like exotic species invasions, the contemporary spread of potentially toxic substances does not respect political boundaries. Great Smoky Mountains National Park lies in a region of North America that has pollutant deposition levels second only to the north-eastern United States. Of particular concern is the deposition of oxides of sulphur and nitrogen, ozone, and trace elements. Many research projects were initiated on air pollutant effects in GRSM in the last 5 years. The most detailed and complex projects are now only 2 years old. Hence, there is little to report at this time about pollutant effects. We do know that ozone and trace elements reach levels which are potentially toxic to plants, that there are unexplained trends of reduced growth in some species on some sites, that sensitive species show ozone damage symptoms, that storm events result in downstream pulses of reduced pH, and that deposition chemistry has changed over the last several decades, pollutant exposures increasing with elevation.

A third kind of resource threat is that of a changed fire regime (Harmon 1981, 1982). Three major species of *Pinus* dominate dry ridges at low- and mid-elevations in GRSM: *P. virginiana* Mill. (Virginia pine), *P. rigida* Mill. (northern pitch pine), and *P. pungens* Michx. f. (table mountain pine). These 3 species reproduce well only after fires hot enough to destroy the organic mat on the forest floor. *Pinus pungens* has a serotinous cone as well. Fire suppression has been practised since Park establishment in 1934. As a result, very few new *Pinus* stands have been initiated (those that have been initiated were on sites of severe fires that were not successfully suppressed), and existing stands are slowly succeeding to dominance by *Quercus* (oak) species. The situation is more complex than the interaction between fire and *Pinus*. A native insect, *Dendroctonus fontalis* Zimm. (the southern pine beetle), periodically infests *Pinus* stands, producing heavy mortality (Kuykendall 1978) and increasing local fuel loads (Nicholas & White 1984). The infestations occur first in trees stressed by drought, competition, fire or other factors, and are terminated within several years by periodic occurrence of severe winter temperatures. As decomposition is relatively fast in this humid landscape, there is probably a narrow window (about 20 years) for the successful initiation of hot fires on these heavy fuel loads. If no fire occurs, the beetle merely hastens succession to *Quercus* by selectively removing overstorey *Pinus*, causing minimal soil disturbance, and releasing understorey *Quercus*. Fire suppression has also allowed understorey hardwoods to survive into size classes that are more resistant to subsequent fires (Harmon 1984), thus changing the effects of fires of a given intensity.

A management dilemma is introduced by the fact that we do not have good data on 'natural' fire frequencies (the restoration of which would theoretically be the goal of management), and by the fact that fires occurring with this natural frequency would no longer have the same effects as earlier in the successional history of these stands. The pre-Park fire regime was dominated by human-set fires (first fires set by Indians, later by white settlers; Harmon 1982). As yet, we do not have a good predictive model of fire behaviour in these stands. The net result has been management resistance to the re-introduction of fire, although there is a draft fire management plan that calls for prescribed natural fire and direct use of management-set fire. We do know that change is occurring in a native ecosystem and that native species (in all strata and including some animal species) are declining as a result. However, we do not yet have quantitative data on the rate of loss of *Pinus*-dominated stands.

The grassy balds management issue is related to that of the *Pinus* stands because natural succession is resulting in community change and in the decline of species populations (Lindsay & Bratton 1979). However, in this situation, we have a better idea of history: the grassy balds are remnants of high-elevation summer pastures created by white settlers in the 1820–80 period (the Smokies are not high enough for a climatic tree-line; the grassy balds are small areas of open grass-dominated plant communities that occur sporadically around the Park). Of the approximately 30 grassy balds originally in the Park, 2 are being managed by the National Park Service as open areas and the others are being allowed to succeed naturally to forest. Interestingly, some rare plant species are found in the Park only on the grassy balds (White 1984a; Stratton & White 1982). This phenomenon, plus their aesthetic value in an otherwise forested landscape, has resulted in management protection for 2 balds. The rare plants have probably spread to the balds in historic times from naturally open sites, like cliff faces and seepage zones.

A final kind of resource threat is the direct impact of visitors. The most important example is that of the high-elevation cliffs which are valued for their open vistas and which often support rare plant populations. For example, Cliff Tops on Mount LeConte has the single most important concentration of rare plants in the Park, and receives about 30 000 visits per year, causing erosion of plant cover from along the top of the cliffs. Although illegal, some direct gathering of plants occurs in the park, as with the valuable medicinal herb *Panax quinquefolius* L. (ginseng), for export to the orient.

In summary, despite legal protection, threats have occurred to resources in nearly all parts of the GRSM landscape (Harmon *et al.* 1983; White & Bratton 1980), and are likely to continue. For example, climatic warming due to elevated carbon dioxide levels and invasion by the exotic *Lymantria dispar* L. (gypsy moth) have been suggested to be imminent.

The threats discussed above are those which cause the most important impacts to the vegetation of GRSM. Other typical kinds of resource change in protected areas include the loss of large predators (in the Smokies, these included the *Felis concolor* L. (mountain lion) and *Canis lupus* L. (timber wolf), which were eliminated by about 1920), overgrazing by native mammals (important only in small areas in the Smokies), changes in hydrology (the dominant issue in the Everglades National Park Biosphere Reserve), and water pollution (White & Bratton 1980).

6 Discussion: a research strategy for Great Smoky Mountains National Park and Biosphere Reserve

Faced with the kinds of threats to resources discussed above, what should be the goals of conservation-oriented research in Great Smoky Mountains National Park? I will first describe the need for the development of understanding at 3 basic levels of inquiry; I will then present a list of 15 research-related management goals.

Stated simply, conservation-oriented research requires an understanding of the state and trajectory of protected resources, predicting their survival (over years to decades or more) and designing management strategies to promote the survival of these resources. Resources include diverse elements, ranging, in particular circumstances, from gene pools and species to ecosystems and landscapes. Recently, the term 'conservation biology' has been applied to conservation-oriented research in the United States, particularly by scientists with a population, island biogeographical, and zoological point of view (Soule & Wilcox 1984). However, the field has older and more diverse roots than these kinds of studies (Franklin 1985b).

The following 3 levels of investigation represent basic elements in a conservation research plan: (i) we must understand ecosystem pattern and dynamics at the stand scale (0.01–10 ha), (ii) we must understand ecosystem pattern and dynamics at the landscape scale (100–10 000 ha), and (iii) we must understand the distribution and survival of biological diversity (species and genetic diversity). The processes of tree mortality, growth, and successional replacement must be studied on a plot scale; the pattern of these processes on broader spatial scales is important in such areas as wildlife studies, assessments of pollutant impacts, and their effect on terrestrial and aquatic ecosystems. I have described resources primarily in terms of state variables. However, understanding the state and trajectory of vegetation will depend on understanding key processes as well (eg nutrient dynamics as it relates to the deposition of pollutants). The third organizational theme is based on the need to protect biological diversity. Despite our best management efforts, sensitive species and gene pools will probably be threatened (eg by such highly specific pathogens as *Endothia parasitica* and *Adelges piceae*). We must identify and monitor populations, assess genetic resources, and design strategies to rescue or protect threatened gene pools.

6.1 The stand scale

Sudden increases in tree mortality have been a key concern in studies of human impacts in the Park. Tree mortality is also central to vegetation pattern and dynamics: it causes the release of regeneration during successional change; it controls the internal heterogeneity and patchiness of communities and, because the tree stratum dominates total ecosystem biomass, it influences site environment and ecosystem processes.

Several management problems in GRSM were first recognized because of rapid increases in tree mortality. Research projects to determine the effects of this mortality have usually been initiated after the event (eg in the case of *Endothia parasitica, Dendroctonus fontalis*, fire effects, *Adelges piceae*, and air pollution effects). Without planning, this situation is likely to recur (eg for *Lymantria dispar* establishment and potential climatic warming). Even in the case of acute threats, 2–5 year research projects have shown that forest mortality develops over a >5–20 year timespan (*E. parasitica, A. piceae*) and that predictions of future ecosystem state are subject to much uncertainty. Thus, short-term (<3–5 yr) answers are likely to be dissatisfying, particularly if no pre-impact data are available. The permanent reference plots used to develop an understanding of vegetation dynamics should also be used as the focus of ecosystem research (eg on such processes as litter- and woody debris-fall, decomposition, nutrient pools and transformations, and soil biology).

6.2 The landscape scale

GRSM possesses one of North America's most complex vegetation patterns. Diversity – of microclimate, vegetation, and species – characterizes this landscape. Stand level investigations will not, by themselves, supply us with a straightforward means of extrapolation to broader scales because of landscape heterogeneity and the variance in those processes that require spatially explicit information for extrapolation (eg the rate of spread of an insect pest across the GRSM landscape). Only within a broader context can we understand the significance of stand level mortality and compositional change. Examples of the need for this broader perspective are seen in the *Adelges piceae* infestation and successional processes in *Pinus* stands. In the case of *A. piceae*, we have good stand level data, but we have no clear picture of the rate of spread of the adelgid in space. After the first wave of mortality of mature *Abies*, we do not know whether the adelgid will become locally less common or whether the existing seedlings and saplings will reach cone-bearing age before the adelgid is able to re-invade. Predicting extinction risk in *Abies fraseri* requires working out the patch dynamics of this situation. In the case of successional processes in *Pinus* stands, we have good stand level data on succession from *Pinus* to *Quercus*, but we have no understanding of the overall net trajectory of the landscape; we do not know the rate of loss in *Pinus*-dominated areas per year or how this varies with site.

6.3 Biological diversity

Within the temperate zone, only the East Asian flora is more diverse than that of the southern Appalachians. Great Smoky Mountains National Park ranks at or near the top of all National Parks in floristic diversity, despite the fact that it ranks below the top 10 in size (uncertainty is caused by poor floristic data bases at several large western Parks). Among the Park's 1500 vascular plant species are 3 strict endemics, as well as a number of other regional endemics for which GRSM protects the most important populations. The high mountains support many northern species, including disjunct species and species at their southern range limits. High-elevation cliffs support a flora that is the remnant of a southern Appalachian alpine zone (last important in the south 12 000 years previously). Despite the Park's legal protection, highly specific threats to particular gene pools have occurred (eg *Adelges piceae* and *Endothia parasitica*). Management for the survival of these gene pools might consist of, for example, seed storage, intense local management against the threats (as with *Adelges piceae*), and cultivation of a representation of the genetic diversity in botanical gardens.

A general approach to these 3 levels of inquiry is shown in Figure 3. This approach is seen as an interactive process, including the collection of stand level data, the extrapolation of these data to the landscape level, the verification of this extrapolation with the collection of additional data at key points in the landscape, and the use of models at all levels of prediction.

6.4 Fifteen research-related management goals for National Park Service Biosphere Reserves

The 3 levels of inquiry discussed above are general, and might apply to the misunderstanding of any natural area. To make the research mandate of Biosphere Reserve National Parks more specific, I have constructed a list of 15 research-related management goals (Table 2). These goals are phrased in terms of management in order to underscore the specific connection between research and management in nature preservation. Further, resource management plans are necessary to show where the information needs are and how the results of research will be applied. In the National Park Service, every Park is intended to have a resource management plan, plus specific action plans for subareas of management (eg

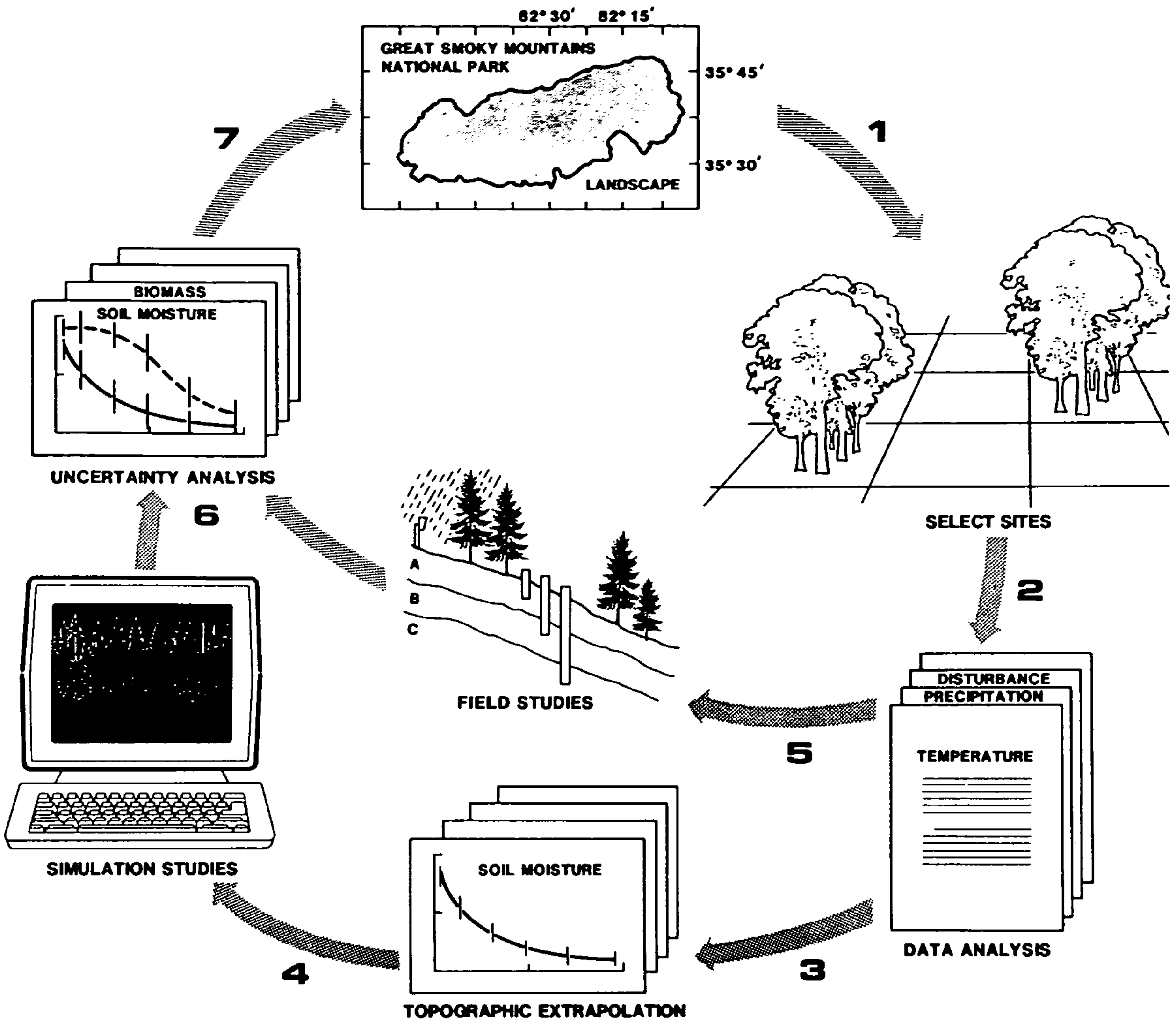

Figure 3. An illustration of a research approach integrating field studies, data summary, modelling, prediction, and verification (source: Dale et al.*, in review). The 7 steps indicated in the Figure are: (1) identify landscape and study sites; (2) analyze existing data sets; (3) interpolate variables across site gradients; (4) perform simulation studies and sensitivity analysis; (5) implement field studies to verify predictions and supply additional ground truth; (6) evaluate the need for additional variables in data set; and (7) assimilate information via spatially explicit maps*

fire management). There should also be periodic review and assessment of the management plans. Ideally, this process will allow us to determine quantitatively the success or failure of a conservation effort.

The first three of the goals are derived from basic National Park Service legislation (inventory resources; understand ecosystem and landscape structure, function, and dynamics; minimize visitor impacts). The next 4 concern specific kinds of threats to natural resources (restore natural processes; minimize exotic species impacts; understand and minimize the effects of atmospheric deposition; prevent adverse impacts of Park management). Goals 8 and 9 concern particularly vulnerable resources (protect unique areas; protect rare species). Goals 10 to 15 are derived from special emphasis of the Biosphere Reserve Programme (develop strong research management; develop long-term and holistic studies; participate in comparative research; participate in monitoring networks; carry out research in conservation biology; protect genetic diversity). Under 'develop strong research management' is meant the need for research permit systems and the importance of data archiving and documentation.

Specific action plans based on these management goals will vary from Park to Park. This list is long and ambitious; while Parks are unlikely to be able to initiate research on all 15 of the goals, the list can be used to begin a research strategy that will eventually grow to encompass this breadth. Further, tracking the 3 levels of stand, landscape, and biological diversity can begin with the institution of permanent plots that will be useful to address a variety of management goals.

Table 2. Fifteen general categories of National Park Service management objectives that determine research objectives

OBJECTIVES RELATED TO BASIC NATIONAL PARK SERVICE LEGISLATION
1. Inventory resources
2. Understand ecosystem and landscape structure, function, and dynamics
3. Minimize visitor impacts

OBJECTIVES RELATED TO SPECIFIC THREATS
4. Restore natural processes
5. Minimize exotic species impacts
6. Understand and minimize the effects of atmospheric deposition
7. Prevent adverse impacts of Park management

OBJECTIVES RELATED TO VULNERABLE RESOURCES
8. Protect unique areas (special protection areas)
9. Protect rare species

OBJECTIVES RELATED TO THE BIOSPHERE RESERVE PROGRAMME
10. Develop strong research management
11. Develop a long-term and holistic research strategy
12. Participate in comparative studies
13. Participate in monitoring networks
14. Perform research in conservation biology
15. Protect genetic diversity

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SYSTEMS ANALYSIS AND MODELLING

A study of spatial pattern in mixed broadleaved/*Pinus koraiensis* (Korean pine) forest on Changbai Mountain

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Abstract

The mixed broadleaved/*Pinus koraiensis* Sieb. et Zucc. (Korean pine) forest is a zonal vegetation type on Changbai Mountain. *P. koraiensis* and *Tilia amurensis* Rupr. (Amur linden) are the most widely distributed species, followed by *Quercus mongolica* Fisch. ex Turcz. (Mongolian oak) and *Acer mono* Maxim. (painted mono maple), etc, at an altitude of 600–1150 m.

In order to examine the spatial distribution of tree species, several separate stands were studied in this area, using 'grid analysis', and the 'Morisita index'. The results confirmed that individual trees occur at random, most species growing in random groups, while others are intermingled. This pattern probably confirms that the broadleaved/*P. koraiensis* forest is in a steady state. Inter- and intraspecific competition does not prevent species establishment or the growth of individual trees.

1 Introduction

Each individual plant species occupies a position in space. As a result of the influences of internal biological characters and a complex variety of external environmental factors, individual plants are dispersed in space to form a certain 'pattern'. This spatial pattern of plant distribution reflects the relationship between individual plants and their response to local site conditions, and has important implications for vegetation sampling (Goodall 1974). As a result, a great variety of methods has been developed to identify and study such patterns.

The sampling methods available for examining spatial distribution fall into 2 classes: line samples (one-dimensional, nearest neighbour and run, etc) and area samples (2-dimensional, quadrat and quadrat grids, etc).

This paper describes and analyses the distributional pattern of several major tree species in the broadleaved/*P. koraiensis* forest on Changbai Mountain. Table 1 shows the tree species occurring in this area. The commonest species are *P. koraiensis*, *A. mono*, *T. amurensis* and *Q. mongolica*. Some of them, eg *Ulmus* (elm) spp., only appear in certain parts of the forest.

The questions addressed are as follows. Do individual trees occur at random? Does a particular tree species grow randomly mixed with other species? Do various species intermingle at random with each other?

Table 1. Species occurring in the broadleaved/*Pinus koraiensis* forest on Changbai Mountain

Number	Species name	Number	Species name
1	*Pinus koraiensis*	10	*Abies holophylla*
2	*Acer mono*	11	*Betula costata*
3	*Tilia amurensis*	12	*Populus ussuriensis*
4	*Fraxinus mandshurica*	13	*Acer triflorum*
5	*Acer* spp.	14	*Maackia amurensis*
6	*Quercus mongolica*	15	*Abies nephrolepis*
7	*Tilia mandshurica*	16	*Picea jezoensis*
8	*Ulmus* spp.	17	*Ulmus propinqua*
9	*Acer mandshurica*	18	*Ulmus laciniata*

2 Study area

Five separate stands were studied, and the site characteristics are shown in Table 2. At each stand, a 0.64 ha plot was marked into 8 × 8 = 64 contiguous subplots, each 10 m^2 (a grid of contiguous quadrats), and the diameter of all species was measured at 1.3 m above ground level. Figure 1 shows the pattern of occurrence of 6 tree species in the 64 quadrats. *P. koraiensis* and *T. amurensis* were the most widely distributed species, occurring on all 5 plots, followed by *Q. mongolica*, *Acer mono*, etc. Figure 1 confirms the hypothesis that all tree species are distributed at random.

Table 2. Site characteristics of the 5 stands

Number	Locality	Altitude (m)	Slope (°)	Slope aspect	Number of species
A	Baihe	780	5	NW	8
B	Baihe	750	3	N	9
C	Lushuihe	910	3	N	7
D	Lushuihe	750	5	N	7
E	Wuitong	1150	5	N	5

3 Results

3.1 Morisita index

The Morisita index of information theory is defined as

$$I_\delta = q\frac{\Sigma n(n-1)}{N(N-1)}$$

where n is the number of individuals in a particular quadrat, q is the number of quadrats, and N (= Σn) is the total number of individuals observed. In the case of a random distribution, the expected value is unity.

Figure 1. Pattern of occurrence of 6 tree species in contiguous quadrats of 10 m × 10 m, 64 quadrats in total (░ only one individual; ▨ only two individuals; ■ at least 3 individuals)

In order to test the null hypothesis H_0, Morisita (1959) proposed that the distribution of the formula

$$F_0 = \frac{I_\delta (N - 1) + q - N}{q - 1}$$

is approximately equal to the variance ratio F, with $q-1$ and ∞ degrees of freedom (Goodall & West 1979). $F_0 = 1$ indicates a random distribution, $F_0<1$ indicates a regular distribution, and $F_0>1$ an aggregated or clumped distribution.

For all 5 grids of contiguous quadrats and some of the most abundant species, the Morisita index and the F_0 value are calculated for successively larger-sized blocks of contiguous samples, ie with 1, 2, 4, etc, quadrats in each sample. The larger-sized block was formed by combining 2 smaller ones.

The calculations, Morisita index and F_0 value are plotted against block size; as shown in Figure 2 from the F-test, there is strong evidence that, almost irrespective of scale, all species show a random distribution in this area. In fact, the F_0 value is quite low everywhere.

Some F_0 values exceeded the critical value of $P=0.05$ (marked with an asterisk in Figure 2), ie *P. koraiensis* at a scale of 10×10, 20×10, 20×20 m^2 in plot B; 10×10, 20×10, 40×20 m^2 in plot C; 20×10, 20×20, 40×20 m^2 in plot D; and *Q. mongolica* at a scale of 10×10, 20×10 m^2 in plot C; 10×10, 20×10, 20×20, 40×20 m^2 in plot D; 10×10 and 20×10 m^2 in plot E. However, no species exceeded the critical value of $P=0.01$. We can, therefore, say that *P. koraiensis* and *Q. mongolica* showed a slight clumping at certain scales in some areas, while most species showed a random distribution (Table 3).

3.2 Mean square/block analysis

A method that has been widely used for studying pattern, especially on a large scale, was introduced by Greig-Smith (1952), ie the so-called 'grid analysis'.

For the 5 (A–E) contiguous quadrats, variance is plotted against size. From Figure 2, it is clear that the results of the grid analysis are the same as those produced by the Morisita index or F-test. In fact, the peak values of all the 3 broken lines arise from the same scales. In other words, the 3 curves display the same trend, up or down.

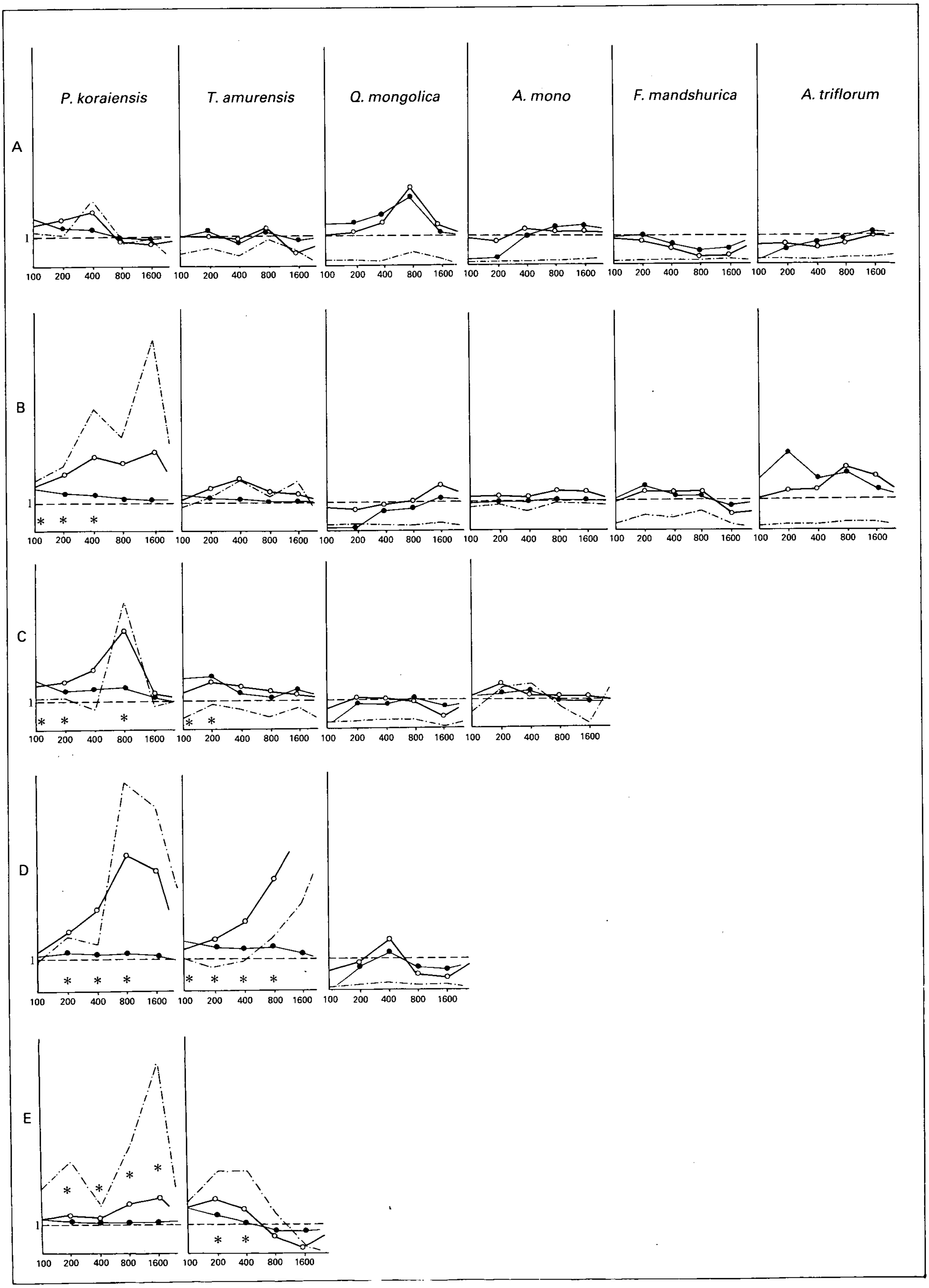

*Figure 2. Morisita's index of dispersal, I_δ and variance ratio F_0 deduced by I_δ as a function of quadrat size for 6 tree species. $I_\delta = 1$ indicates the expected value for random dispersal as well as $F = 1$. *indicates where the H_0 random dispersal hypothesis has been rejected*
(o—o F-test; •—• Morisita index; —·—·—mean per block)

Locality	Species	Clump size (m) 5%	1%	Nature of intraclump distribution
A	*P. koraiensis*	No	No	Random
	Q. mongolica	No	No	Random
B	*P. koraiensis*	100,200,400	No	Random
	Q. mongolica	No	No	Random
C	*P. koraiensis*	100,200,800	No	Random
	Q. mongolica	100,200	No	Random
D	*P. koraiensis*	No	No	Random
	Q. mongolica	100,200,400,800	No	Random
E	*P. koraiensis*	No	No	Random
	Q. mongolica	100,200	No	Random

3.3 Run method

The method of runs is a method of line sampling, and was used to find answers to the following questions:

i. Does one tree species tend to grow in clumps with other species?

ii. Are all species randomly intermingled with each other?

This method is easy to use, and the data required are easy to collect in the field. It can be likened to having a bag with lots of different coloured balls inside. Each time we take a ball out at random, we record its colour, thus obtaining a series of marks. In a similar way, someone walks through the forest in a fixed direction, and each time he meets a tree he records the species, thus also obtaining a series of marks which can then be used in the analysis to find solutions to the 2 questions.

3.3.1 Two species Mann–Whitney test

Originally, this test was used to compare the effects of 2 medical treatments. To adapt this method to solve the first pattern problem, we mark one species with '1' and the others with '0', so that the observations become a '0–1' series. Suppose that n_0 is the number of 0s and n_1 the number of 1s in this series, so that (n_0+n_1) individual trees are observed. S then denotes the sum of the ranks of 0, and

$$U = S - \frac{n_0\,(n_0 - 1)}{2}$$

is the test statistic (Eason *et al.* 1980).

For the mixed broadleaved/*P. koraiensis* forest, 5 sites were investigated, so that 5 series of data were obtained. The results of the Mann–Whitney test for the 5 series are shown in Table 4.

To determine whether the null hypothesis should be rejected or accepted, using the Mann–Whitney test, depends on whether or not U falls in the critical region. However, if n_0 or n_1 (or both) exceed 20, the test cannot be applied, and, in this case, we must seek another statistic. Let

$$T = n_0\,n_1 + \frac{n_1\,(n_1 + 1)}{2} - S$$

It is then easy to calculate that

$$E(T) = \frac{n_0\,n_1}{2} \text{ and } D(T) = \frac{1}{12}\,[n_0\,n_1\,(n_0 + n_1 + 1)]$$

If the null hypothesis is correct, then the distribution of

$$U_n = \frac{T - E(T)}{D(T)^{1/2}}$$

will be a standard normal distribution, N(0, 1).

The results for the 5 series are shown in Table 4, in the last row, and we use this statistic for the test.

From Table 4, we find that the critical regions for a 5% significance level will be 2-tailed, commencing at −1.64 and 1.64. In most cases, the test statistic falls into the critical region and the null hypothesis is accepted. Therefore, most species in this area are randomly clumped together with the others.

There are 2 or 3 exceptions which are rejected (marked by '–' in Table 4), but they are not important because the individuals of the species are rather few in number, only 2 or 3 (except *P. koraiensis* in series 4). If we had chosen a 1% significance level, the critical regions would commence at −2.57 and 2.57, and there would be no rejections.

3.3.2 Kruskal–Wallis test

This test, which is an extension of the previous method, allows several marks or species tests simultaneously. We have used this method to solve the second question.

Suppose there are c species, ie c different marks, in the series $S_1, S_2, \ldots, S_c$, and n_1 individuals observed of species 1, n_2 of species 2, and so on. The total number of observations will be $N = n_1 + n_2 + \ldots + n_c$. To produce an appropriate test statistic, $c_1, c_2, \ldots, c_c$ denote the totals of the ranks for each species in the series. As a measure of closeness, the test statistic

$$v = \frac{12}{N(N + 1)}\left(\frac{C_1^2}{n_1} + \frac{C_2^2}{n_2} + \cdots + \frac{C_c^2}{n_c}\right) - 3(N + 1)$$

can be used (Eason *et al.* 1980), and the hypothesis H_0 is that all species are randomly intermingled with each other.

If the null hypothesis was correct, the probability distribution of the statistic is an approximate χ^2 distribution, with c − 1 degrees of freedom.

Calculating values of v for the 5 series, the results are shown in Table 4. As the v values are less than the critical value at the 5% significance level, there is no

Table 4. Mann–Whitney test and Kruskal–Wallis test at 5% significance level

Null hypothesis H_0: the tree species are randomly clumped together with other species
+ H_0 accepted/− H_0 rejected

Series 1. (located on Changbai Mountain about 3000 km behind the Research Station)
Number of species = 7; number of trees observed = 30; run distance = 200 m

Mann–Whitney test

Number	Species	n_0	n_1	U	H_0	U_n	H_0
1	*P. koraiensis*	12	18	102	+	0.254	+
2	*A. mono*	2	28	14		1.164	+
3	*T. amurensis*	7	23	67		0.662	+
4	*F. mandshurica*	3	27	41		−0.346	+
5	*Acer* spp.	2	28	16		0.998	+
6	*Q. mongolica*	1	29				
7	*T. mandshurica*	3	27	76		−2.454	−

Kruskal–Wallis test

Chi-square	Freedom	Critical value	H_0
9.154	6	10.64	+

Series 2. (same location as above)
Number of species = 7; number of trees observed = 24; run distance = 200 m

Mann–Whitney test

Number	Species	n_0	n_1	U	H_0	U_n	H_0
1	*P. koraiensis*	10	14	86	+	−0.937	+
2	*A. mono*	7	17	61	+	−0.095	+
3	*T. amurensis*	2	22	30		−0.836	+
4	*F. mandshurica*	1	23	10		0.217	+
5	*Acer* spp.	2	22	8		1.462	+
6	*Q. mongolica*	1	23				
7	*T. mandshurica*	1	23				

Kruskal–Wallis test

Chi-square	Freedom	Critical value	H_0
4.253	6	10.64	+

Null hypothesis H_0: the tree species are randomly clumped together with other species
+ H_0 accepted/− H_0 rejected

Series 3. (located as series 1 and 2)
Number of species = 8; number of trees observed = 54; run distance = 200 m

Mann–Whitney test

Number	Species	n_0	n_1	U	H_0	U_n	H_0
1	*P. koraiensis*	18	36	377	+	−0.973	+
2	*A. mono*	11	43	239		−0.054	+
3	*T. amurensis*	12	42	188		1.332	+
4	*F. mandshurica*	6	48	129		0.413	+
6	*Q. mongolica*	3	51	119		−1.605	+
7	*T. mandshurica*	1	53				
8	*Ulmus* spp.	2	52	43		0.412	+
9	*A. mandshurica*	1	53				

Kruskal–Wallis test

Chi-square	Freedom	Critical value	H_0
6.903	7	12.02	+

Table 4 (continued)

Series 4. (located in Jin-Song stand)
Number of species = 10; number of trees observed = 28; run distance = 200 m

Mann–Whitney test

Number	Species	n_0	n_1	U	H_0	U_n	H_0
1	*P. koraiensis*	7	21	106		−1.723	–
2	*A. mono*	2	26	20		0.535	+
4	*F. mandshurica*	2	26	6		1.784	–
5	*Acer* spp.	2	26	20		0.535	+
6	*Q. mongolica*	1	27				
8	*Ulmus* spp.	5	23	51		0.390	+
9	*A. mandshurica*	2	26	24		0.178	+
10	*P. holophylla*	3	25	25		0.928	+
12	*P. ussuriensis*	2	26	46		−1.784	–
13	*A. triflorum*	2	26	23		0.267	+

Kruskal–Wallis test

Chi-square	Freedom	Critical value	H_0
9.845	9	14.64	+

Null hypothesis H_0: the tree species are randomly clumped together with other species
+ H_0 accepted/– H_0 rejected

Series 5. (same location as above)
Number of species = 7; number of trees observed = 22; run distance = 200 m

Mann–Whitney test

Number	Species	n_0	n_1	U	H_0	U_n	H_0
1	*P. koraiensis*	3	19	26	+	0.239	+
2	*A. mono*	4	18	58	–	−1.872	–
3	*T. amurensis*	6	16	53	+	−0.369	+
8	*Ulmus* spp.	2	20	11	+	1.028	+
10	*P. holophylla*	3	19	9	–	1.866	–
11	*B. costata*	2	20	18	+	0.228	+
12	*P. ussuriensis*	2	20	26	+	−0.685	+

Kruskal–Wallis test

Chi-square	Freedom	Critical value	H_0
7.458	6	10.64	+

evidence for rejecting the null hypothesis. In other words, the tree species are mixed at random with each other.

4 Discussion

Patterns of species distribution have relevance for many disciplines, and a great variety of different methods have been used by plant ecologists for their study. Over the past 40 years, the major concern has been to identify whether the individual tree species are dispersed at random in an area. When the dispersion is non-random, it may be a result of aggregation (overdispersion) or a trend toward regularity (underdispersion).

Our study has focused not only on the spatial dispersion of one species but also on how the many species intermingle with each other in a mixed forest. It is probably important to discuss this question because the pattern of many species intermingling with each other reflects interspecific relationships, such as competition, repulsion and reciprocal symbiosis, etc, as well as species response to site conditions and establishment and growth success.

In our study, there is strong evidence that, almost irrespective of scale, all species display a random distribution, with many species intermingling randomly in the mixed broadleaved/*P. koraiensis* forest. This pattern probably reflects that the forest is in a steady state, and that inter- and intraspecific competition is not preventing species establishment or the growth of individual trees.

The simplest method available for examining pattern is the run method, although the Mann–Whitney and Kruskal–Wallis tests are also useful.

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The role of Expert Systems in temperate forest research

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Abstract
In the management of temperate forests, there is a need, as in many other kinds of resource management, to make use of the latest information available from scientific research, and from the field experience of practical foresters. Some of this information can be gained from books and training courses, but the number of experts and teachers is insufficient to provide the advice and information where it is required. This paper emphasizes the need to take account of recent advances in ecological research in the management of biological resources, as in a forest, and suggests that Expert Systems provide one possible way in which such advice can be made available quickly and cheaply.

1 *Introduction*

During the last few years, a new development has taken place through the combination of computer programming, mathematical theories of artificial intelligence, and the knowledge and skill acquired by human beings in the management of practical affairs. We call the products of this new development 'Expert Systems', and it might be helpful for me to define precisely what we mean by the use of those 2 words.

'An Expert System is a computer program that embodies some fraction of the knowledge characteristic of an expert in a specialized area and which can use that knowledge to suggest the same types of conclusions as the expert would reach if confronted with the same information, and can justify those conclusions.'

The emphasis in this definition is on the incorporation of specialist knowledge which would not otherwise be generally available, and on the use of this knowledge to solve particular classes of problems from the same information that would be available to a human expert, or which would be requested by the human expert from whom advice was sought. However, an important additional property of Expert Systems is that they are able to provide the reasons for the use of the solution of the problem, and it is this property which sets Expert Systems apart from other types of computer programs.

The emphasis on the solution of particular kinds of problems is also quite deliberate. The academic community has long been accustomed to the importance of allowing scientists to develop theoretical approaches to their fields of interest without too much regard for the practical value of those approaches. If the theory has a practical 'spin-off', so much the better, but the need to solve practical problems must not be allowed to inhibit the development of research and theory. In contrast, today's principal requirement is for the application of what we know now to problems which we can already perceive and anticipate. Access to the required information is restricted by the formats which have been adopted by scientists for the publication of their results, aimed inevitably at other scientists, and, in general, intelligible only to other scientists. Simplified accounts of scientific results are almost always incomplete or inaccurate in essential details, so that resource managers, decision-makers and administrators have little access to the scientific information which they need to solve their problems. In-house advisors who may have been trained as scientists can provide some help, but themselves quickly fall behind current developments by the simple fact that they are no longer doing research themselves.

2 *The role of ecology in temperate forest management*

A proper understanding of the complex interrelationships between organisms, including man, and their environment is essential if we are to manage temperate and tropical forests rationally. There are 3 essential criteria for the ecological management of forests:

i. maintaining essential ecological processes and life-support systems;
ii. preserving genetic diversity;
iii. utilizing species and the forest ecosystem sustainably.

These criteria can only be achieved by knowledge and by the application of that knowledge in practical decision-making.

However, ecological research is greatly complicated by the fact that the interactions between individual organisms and between organisms and their environment are dynamic, in the sense that they are time-dependent and constantly changing. Furthermore, the interactions frequently contain feedback, ie the carrying back of some of the effects of a process to its source or to a preceding stage so as to strengthen or modify it. Such feedback will sometimes be positive, in the sense that the effect is increased, and sometimes negative, in the sense that the effect is decreased. The feedback itself may be complex, involving a series of positive and negative effects, with various results depending on a series of environmental factors. In addition, living organisms are themselves variable – variability being one of their essential characteristics. This variability may be expressed in terms of effects on other organisms, for example by competition or predation, or it may be expressed in the response of organisms, either collectively or singly, to environmental factors. Such response will be reflected in variable rates of growth and of reproduction, and even in variable ability to exist under strongly adverse conditions. When this characteristic is added to independent variations in environmental factors such as climate and habitat, changes in ecological processes and systems are not easy to predict from simple 'common-sense' rules.

Nevertheless, ecologists have been successful in developing a body of ecosystem theory which can be used to predict how ecological systems will behave under certain conditions. This theory depends on a set of concepts which are themselves relatively complex and frequently counter-intuitive in their prediction of changes in organisms and communities. As a result, the only effective way that ecologists have found for managing the complexity is through the use of mathematical models. The abstract language of mathematics provides a representational symbolic logic which simplifies, but does not markedly distort, the underlying physical and biological relationships. These representations, in turn, enable us to make comparisons between our model systems and the real systems which decision-makers have to manage, and, in this way, to test the adequacy of the model against observations and data derived from the real world – the appeal to nature which is a necessary component of the scientific method.

3 Models and decision-makers

While the use of mathematical models may be convenient, even essential, for those of us engaged in ecosystem research, such models do not solve the problems of communicating the results of scientific research. Few of the resource managers, decision-makers and administrators who need to understand the consequences of their proposed policies and management practices on temperate and tropical forests are likely to be able to find sufficient time to understand the models which are used to describe such ecosystems. Today, we use computers to make the calculations necessary to show the effects of changes on the forest, and the unfamiliarity of forest managers with these computers adds to the difficulties of understanding.

The effective use of mathematical models for the solution of practical problems also depends on the correct estimation of key parameters in the model, and the knowledge of these values lies with the decision-maker. Identification of the correct values depends on the ability of the scientist to communicate the precise meaning of the parameters, and the role which those parameters play in the model. For example, in many situations in which it is necessary to control the population of one or more species of animals in, say, a National Forest Park, it is essential to have some measure of the rates at which animals are harvested or culled, but quite difficult to identify the basis of the calculation of rates as used by game wardens, etc. The degree of genuine agreement between what is assumed by the scientist and what is understood by the decision-maker needs constantly to be checked if the model is to be useful.

4 Role of Expert Systems

The role of Expert Systems is 2-fold. First, they act as an intelligent interface between the models built by ecologists and the users of those models. The interface guides the user by structuring questions to which answers are required, in the correct order, and by leading the user through a complicated series of procedures so as to enable him to make effective use of the knowledge which has been gained through scientific research. The answers to key questions can be checked by asking the questions in several different ways so as to ensure that the responses are consistent. In more complicated situations, it may be especially important to devote time to establishing the correct background to the problem, before choosing the most appropriate solution.

Second, Expert Systems can be used to provide more detailed explanations of why particular solutions are obtained from the use of the models that have been developed by the scientists. Such explanations often require the systematic display of fairly simple relationships between the key variables in a temperate forest system, perhaps related to equally important variables in the associated economic or social systems. The variables can then be grouped in combinations controlled by the user so as to build up an understanding of the non-linear or feedback mechanisms which so often dictate outcomes that are unexpected or unwelcome. By placing the whole of the explanation phase under the control of the user, he does not feel threatened in the same way that a decision-maker may when confronted by a scientist telling him that some proposed policy or project simply will not work.

As more and more specialists become involved in the preparation of the interface, the Expert System builds up a body of knowledge which is greater than that which would be provided by a single specialist, or even a small team of specialists. Contradictions and inconsistencies are gradually eliminated as the System is tested and improved. Weaknesses can be remedied as they are pointed out by the users, and omissions repaired. Every Expert System used as an interface in this way should, therefore, contain a section which reports on the pathways taken through the system during its practical use, and on any points at which the System failed. Such a tracing facility provides the specialists who are attempting to co-ordinate their expertise with a 'map' of where difficulties occurred in the interpretation of their advice.

5 Expert System applications in temperate forests

Although Expert Systems will almost certainly play a major role in most practical applications of ecological theory to forest management, there are 4 principal areas which will be described briefly in this paper, as illustrations of what is currently being developed. Expert Systems do not have to be either extensive or expensive to be useful. Indeed, it is usually better to start 'small' and grow by collaboration between the specialists and the decision-makers.

5.1 Vegetation succession

One of the critical areas of forest research is that of vegetation dynamics and succession. The classical theory of succession in forestry assumes a gradual development towards a climax vegetation from the first colonization of bare ground.

This climax vegetation may then be disturbed by some natural occurrence, like a fire, flood or earthquake, or by some man-made intervention, such as the felling of a forest, ploughing of grassland, or the elimination of herds of grazing animals. The vegetation then goes back to some earlier stage in the succession, before gradually returning to the climax vegetation, in the absence of any further intervention. The system may actually be very much more complicated, with the existence of truncated successions resulting from invasions by species of plants which do not allow further invasions, and hence prevent the full development of the successional states.

One especially important problem in many countries is concerned with the development of forest vegetation after the occurrence of fire. Overprotection of many forest systems against small brush fires may lead to the build-up of so much inflammable material that a subsequent 'hot' fire does more damage to the system than regular small fires. The effect of fire on vegetation succession is especially important in arid zones and in the Mediterranean region. Other examples of the value of a knowledge of succession include the management of shifting cultivations, land reclamation, and the protection of ecologically fragile areas against overexploitation.

Dr I R Noble of the Australian National University has developed an Expert System to predict the successional changes in ecosystems from a knowledge of the species which are known to exist in the communities of the various successional states. The Expert System is based on a theory of 'vital attributes' of plant species, which determines the ability of a species to survive various kinds of 'intervention' and to reproduce. The characteristics of each plant species are determined by the Expert System through a dialogue with users of the System who are assumed to have at least some basic knowledge of the plants in their vegetation communities, although the answers to the questions are checked by the System itself for inconsistencies and inaccuracies. Repeated use of the Expert System for the same communities draws on the knowledge which has already been provided about individual species. This Expert System has been tested extensively in Australia and was recently tried out in the temperate forest region in China. The results are certainly promising, both in indicating solutions to practical problems and in stimulating further research.

5.2 Identification of plant and animal species

A continuing problem in the management of forests is the correct identification of species of plants and animals. The expertise necessary for correct identification is highly fragmented, any one individual usuall being a specialist in one group of organisms and having only a very general knowledge of other organisms. Where the numbers of species in a group are small, as for the mammals, reptiles or birds, the problems of identification are not particularly severe, but identification of insects, mosses and microbes, for example, poses especially difficult problems because of the large numbers of closely related species and the small size of the differentiating characteristics. The traditional method of identification is through the use of taxonomic keys, but where attributes are difficult to determine on an individual specimen, or are perhaps missing from the specimen, such keys quickly become useless. It is interesting to note that the specialists in particular groups seldom use taxonomic keys but have their own, often unwritten, ways of recognizing species, helped by their knowledge of the likelihood of finding a particular species in that location and of the degree of variation which species exhibit in certain attributes.

Expert Systems are ideally suited to this kind of problem, being able to hold the taxonomic keys themselves, and to combine them with the knowledge used by human experts to take short-cuts in the use of the keys. Bayesian inference techniques can direct the user's attention to the species most likely to be found in a given location, and can help to make a guess at the most probable identification, even when some of the important information is missing. The estimated probability of the identification being correct provides a measure of the confidence which the user can place on his consultation with the Expert System. Use of modern computer graphics can supply the user with a picture of his identified organism for comparison with the actual specimen, and can illustrate the technical terms used in the taxonomic descriptions. Taxonomic Expert Systems are currently being developed by ecologists and seem likely to play an increasingly important role in both research and management.

5.3 Ecosystem management

The management of the extensive forest systems of the world has always presented man with problems to which he has failed to find satisfactory solutions. Time and again, apparently common-sense policies and practices have led to the destruction of forest systems we have been trying to preserve. The recognition that many ecosystems are fragile and vulnerable to unexpected influences has stimulated concern and interest in wildlife and habitat conservation. In almost every country of the world, National Parks and Reserves have been set up in an attempt to halt the destruction of wildlife, as well as to provide opportunities for recreation, observation and research. The management of these Reserves, however, depends on our understanding of ecosystem processes, and Expert Systems offer one important source of practical advice to National Park and Forest Reserve managers. Sound management depends in part on the correct identification of objectives, and Expert Systems can play a valuable role in making sure that the managers themselves ask the right questions when setting objectives within international, national and regional perspectives. How should the objectives for particular areas be related to the wider problems of land use and conservation policies? What are the relative priorities in the conservation of organisms and habitats? Should we continue to allow most attention to be directed towards organisms which are conspicuous and obviously attractive, like large animals, birds and butterflies, or to organisms which play an essential role in forest ecosystem dynamics, for example the micro-organisms mainly responsible for the essential processes of decomposition in the nutrient cycle?

Having decided on the objectives, management of vegetation by cutting, fire, or the use of herbicides, and management of animal populations by harvesting, culling, or the use of predators offer many possible combinations of options to the manager. Many widely differing types of scientific expertise are required, and the practical manager is unlikely to have access to all of them, or even to more than one or 2 of them. If they can be combined into an Expert System specifically designed to enable the manager to monitor the changes taking place in the ecosystem he is seeking to manage, and to select appropriate forms of management to achieve the desired objectives, the results of ecological research will be made available in the most practical way possible. Some preliminary trials of such Expert Systems are currently being made, initially concentrating on particular kinds of ecosystems, for example lowland heaths, wetlands and woodlands. The combination of many different types of system into the kind of mosaic likely to be found in, say, a National Park poses problems of spatial and dynamic heterogeneity which still have to be solved. Nevertheless, we expect to have workable Expert Systems for the management of forest ecosystems within 5 years.

5.4 Environmental impact assessment (EIA)

So far, EIA methods have been largely based on confrontation between those who wish to develop some industry or project, and those who oppose the development on the grounds of a predicted environmental impact. Very little of what is asserted by either side in this confrontation has much basis in hard science, or in any deep understanding of the ecological theory that underlies the arguments, principally because of the inaccessibility of that theory. Expert Systems offer one possible solution to making the results of ecological theory available to those who will have to assess the likely effects of any proposed project on the environment. Attempts to build such Expert Systems have only just begun, but, in their overall effect on practical decisions affecting the environment on which we all depend for our natural resources, they may be the most important of all applications of such Systems.

6 Conclusions

This paper does no more than sketch out the beginnings of the use of Expert Systems to provide ecological advice to forest managers, administrators and politicians. Clearly, there is much still to be done before such Expert Systems are accepted as an alternative to the present-day reliance on advice from human experts, reports and scientific publications. Nevertheless, even the limited experience we now have of such Systems has shown the exceptional promise they offer of being able to make ecosystem theory accessible to decision-makers in practical and understandable ways.

Propagation of light through an arbitrary inhomogeneous forest canopy

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Abstract

In terms of a parametric equation for a straight line and the concept of directional derivatives, the Ross equation of light propagation in a forest canopy is converted into a general formula in arbitrary inhomogeneous models. An example is given.

1 Introduction

Ross and others have presented equations for the propagation of light through forest canopies (see Ross 1981):

$$\nabla i(\bar{p}, \bar{r}) \cdot \bar{r} = -u_L(\bar{p})\, G(\bar{p}, \bar{r})\, i(\bar{p}, \bar{r}) + u_L(\bar{p})\eta_L(\bar{p}, \bar{r}) + \frac{1}{\pi} u_L(\bar{p}) \int_{4\pi} \Gamma_L(\bar{p}, \bar{r}', \bar{r})\, i(\bar{p}, \bar{r}')\, d\Omega' \qquad (1)$$

where ∇ is the Hamiltonian operator; $i(\bar{p}, \bar{r})$ radiant intensity in the direction of $\bar{r}$ at point $\bar{p}$ in the canopy; $u_L(\bar{p})$ the leaf area density around $\bar{p}$; $G(\bar{p}, \bar{r})$ the projection ratio of leaves in the direction of $\bar{r}$ and around point $\bar{p}$; η_L the emission coefficient; and

$$\frac{1}{\pi}\Gamma_L(\bar{p}, \bar{r}, \bar{r})$$

the area scattering phase function.

Although equation (1) can be used for any inhomogeneous forest canopy, only approximate solutions have been given for horizontal homogeneous models of forest canopies.

For real forest canopies, however, horizontal homogeneous models are first approximations. In fact, there may be some periodic variation of the parameters in a particular direction in the stand planted in rows, and other forests may have varying symmetries. Natural woodlands present more complex statistical characteristics. It is evident that further efforts to describe the true forest must consider inhomogeneous models of forest canopies.

In this paper, parameter equations for a straight line and the concept of directional derivatives in the field theory are used to transform equation (1) into a pure integral equation, eliminating all the boundary conditions.

2 Background

Let the z-axis of the Cartesian co-ordinates run vertically downwards, so that $z=0$ is the top of the forest canopy, and the $x-y$ axes represent the upper surface of the stand canopy. Suppose the direction cosines of $\bar{r}$ in equation (1) are $(\cos\alpha, \cos\beta, \cos\gamma)$, then a straight line in the direction of $\bar{r}$ and through the point $(x=a, y=b, z=0)$ can be expressed as follows:

$$\begin{aligned} x &= S.\cos\alpha + a \\ y &= S.\cos\beta + b \\ z &= S.\cos\gamma \end{aligned} \qquad (2)$$

S can be regarded as the 'distance' between the points $(x=a, y=b, z=0)$ and (x, y, z). (As a parameter, S can be positive or negative.) Because $\bar{p}$ in equation (1) can be represented by (x, y, z), taking account of equation (2), every term on the right-hand side should be shown by s, a and b, instead of $\bar{p}$ or (x, y, z). On the other hand, according to the concept of directional derivatives in the field theory, we have

$$\nabla i(\bar{p}, \bar{r}).\bar{r} = \frac{di}{ds} \qquad (3)$$

Equation (1) can, therefore, be transformed into equations in which s is a variable and a, b are parameters.

$$\frac{di}{ds} = -A(s)\, i + B(s) + \int_{4\pi} C(s)\, i(s, \bar{r}')\, d\Omega' \qquad (4)$$

with $A(s) \equiv u_L G$, $B(s) \equiv u_L \eta_L$, $C(s) = \frac{u_L}{\pi}\Gamma_L$.

Here, a and b are omitted, and the symbol $i(s, \bar{r}')$ is used to represent radiant intensity at the position (s, a, b) in the direction of $\bar{r}$, provided there is no confusion.

Although the integral on the right-hand side of equation (4) is a function of $i(s, \bar{r}')$, it is an unknown function of s and $\bar{r}$. Therefore, the constant variation method can be used to obtain:

$$i = e^{-\int_{s_0}^{s} Ads'} \cdot \int_{s_0}^{s} \left(B + \int_{4\pi} Ci d\Omega' \right) e^{\int_{s_0}^{s'} Ads''} ds'$$

$$+ De^{-\int_{s_0}^{s} Ads'} \qquad (5)$$

where D is an integral constant. Combining the 2 integrals on the exponent of the first term on the right-hand side, then

$$i = \int_{s_0}^{s} \left(B + \int_{4\pi} Ci d\Omega' \right) e^{\int_{s_0}^{s} Ads''} ds' + De^{-\int_{s_0}^{s} Ads'} \qquad (6)$$

For downward radiation $(0 \leqslant \gamma < \pi/2)$,

let $S_0 = 0$. Equation (6) can, then, be written as:

$$i(s, \bar{r}) = \int_{0}^{s} B + \int_{4\pi} Ci d\Omega' \, e^{\int_{s}^{s'} Ads''} ds'$$

$$+ i^0 (s = 0, \bar{r}) \, e^{-\int_{0}^{s} Ads'} \qquad (7)$$

where $i^0(s = 0, \bar{r})$ indicates radiant intensity in the direction of $\bar{r}$, which reaches the upper forest canopy from the sun or sky.

For upward radiation $(\frac{\pi}{2} < \gamma \leqslant \pi)$, let $S_0 = H \sec\gamma$, where H is the thickness of the forest canopy. Equation (6) then becomes:

$$i(s, \bar{r}) = \int_{H \sec\gamma}^{s} \left(B + \int_{4\pi} Ci d\Omega' \right) e^{\int_{s}^{s'} Ads''} ds'$$

$$+ i^H (s = H \sec\gamma, \bar{r}) \, e^{-\int_{H \sec\gamma}^{s} Ads'} \qquad (8)$$

and

$$i^H (s = H \sec\gamma, \bar{r}) \equiv \int_{\Omega_1} b(\bar{r}', \bar{r}) \, i (s = H \sec\gamma, \bar{r}') \, d\Omega' \qquad (9)$$

represents reflected radiation from the forest.

Ω_1 represents the solid angle which satisfies

$0 \leqslant \gamma < \pi/2$

, and $b(\bar{r}, \bar{r}')$ is the reflectance density.

Equations (7) and (8) are integral equations and a formal solution to equation (1).

3 Direct and scattering radiation

Let $i \equiv i_0 + i_s$, where

$$i_0 = \begin{cases} i^0 (s = 0, \bar{r}) \, e^{-\int_{0}^{s} Ads'} & (0 \leqslant \gamma < \pi/2) \\ e^{-\int_{H \sec\gamma}^{s} Ads'} \cdot \int_{\Omega 1} b(\bar{r}, \bar{r}) \, i_0 (s = H \sec\gamma, \bar{r}') \, d\Omega' & (\pi/2 \leqslant \gamma < \pi) \end{cases} \qquad (10)$$

and

$$i_s = \begin{cases} \int_{0}^{s} \left[B + \int_{4\pi} C(i_0 + i_s) \, d\Omega' \right] e^{\int_{s}^{s'} Ads''} ds' & (0 \leqslant \gamma < \pi/2) \\ \int_{H \sec\gamma}^{s} \left[B + \int_{4\pi} C(i_0 + i_s) \, d\Omega' \right] e^{\int_{s}^{s'} Ads''} ds' & \\ + e^{-\int_{H \sec\gamma}^{s} Ads'} \cdot \int_{\Omega 1} b(\bar{r}', r) \, i_s (s = H \sec\gamma, \bar{r}') d\Omega' & (\pi/2 < \gamma \leqslant \pi) \end{cases} \qquad (11)$$

indicate both direct radiation and scattering radiation respectively. The formulae in equation (10) are direct expressions, the first indicating direct radiation from the sun or sky through the forest canopy. If the radiation is reflected by the land, its intensity will be described by the second formula in equation (10), where i_0 can be calculated from the known quantities.

The formulae in equation (11) are integral equations, where scattering radiation is calculated either by various approximations (Ross 1981), or by numerical solution using concrete computer models. Rigorous expressions of other relative physical quantities can also be obtained.

If all the parameters in equation (4) are independent of both x and y, it is evident that the whole problem reverts to the situation of horizontal homogeneity (Liu 1987a).

4 A useful example

Although it is difficult to obtain complete and accurate solutions to equations (10) and (11), the first expression in equation (10) can be used to create a typical model of direct radiation. As a useful example, let us consider a forest canopy which has a periodic change of parameters – we call it a 'periodic forest canopy' (Liu 1987b).

Suppose A is the simplest periodic function,

$$A = A_0\left(1 + \cos\frac{2\pi}{l}x\right) \tag{12}$$

where A_0 is a constant determined by the parameters of the forest canopy and l is periodic length in the direction of x. If we introduce equation (12) into the first formula of equation (10), we have

$$i_0 = i^0\, e^{\frac{lA_0}{2\pi\cos\alpha}\sin\frac{2\pi}{l}(x - z\sec\gamma\cos\alpha)}$$

$$e^{-A_0 z\sec\gamma - \frac{lA_0}{2\pi\cos\alpha}\sin\frac{2\pi}{l}x} \qquad (\alpha \neq 90°) \tag{13}$$

and

$$i_0 = i^0\, e^{-A_0(1+\cos\frac{2\pi}{l}x)z\sec\gamma} \qquad (\alpha = 90°) \tag{14}$$

According to equation (13), if $\alpha \neq 90°$, i_0 has a periodic cyclic factor of $1/\sec\gamma\cos\alpha$, and an exponential attenuation factor in the direction of z, as a result of the tilted radiation acting on the periodic forest canopies. Here, i_0 changes cyclically with periodic length, l, in the direction of x, but the periodic changes have different 'phase shifts' for different values of z.

If $\alpha = 90°$, in equation (14), i_0 changes with periodic length, l, independent of z in the direction of x, and takes an exponential attenuation in the direction of z.

Finally, in both cases, when $z \rightarrow \infty$ and $z \rightarrow 0$, there must be $i_0(\bar{r}) \rightarrow 0$ and $i_0(\bar{r}) \rightarrow i_0(\bar{r})$, respectively, and there is no longer any periodic change.

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An experimental system of forest hydrology modelling laboratory (FHML)

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Abstract
The first simulation laboratory in forest hydrology (FHML) in China was built between 1983 and 1985 to study hydrological effects on the forest ecosystem. The laboratory consists of 5 parts: water supply, rainfall, underlying model, measuring system, and a microcomputer control system. Artificial rain falls on the underlying model which represents a simulated forest and soil, and water then flows from the outlet section. The measurement system is controlled by a microcomputer and records rainfall intensity, flow, soil moisture and temperature; the results are output by the printer or plotter.

1 The experimental system of FHML

The laboratory includes 5 systems: water supply, rainfall, underlying model, measuring system and a microcomputer control system.

1.1 Water supply system

The water supply system includes a cistern, a driving pump, a water tower, an automatic device for controlling the water level, a filter cleaner, water transportation pipe, and a sewage sink, as shown in Figure 1.

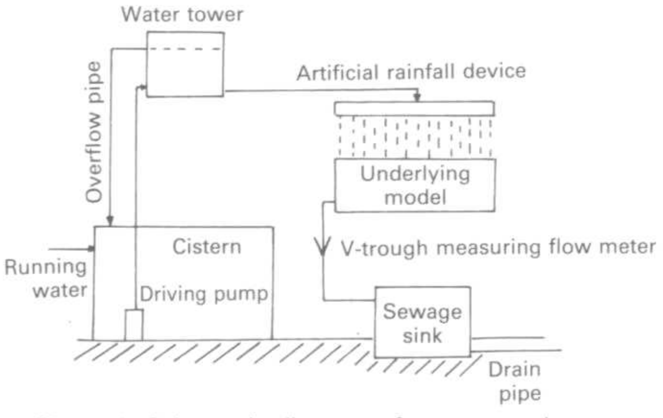


Figure 1. Schematic diagram of water supply system

1.2 The rainfall system

The rainfall system includes an artificial rainfall device (Plate 12), a driving device and guide tracks. The rainfall device has 11 outlet pipes that are installed in a rectangular frame, on 4 pairs of wheels. It is driven by a motor with retarder, and moves backwards and forwards along the guide tracks. Raindrops from the outlet pipes fall evenly on to the underlying model.

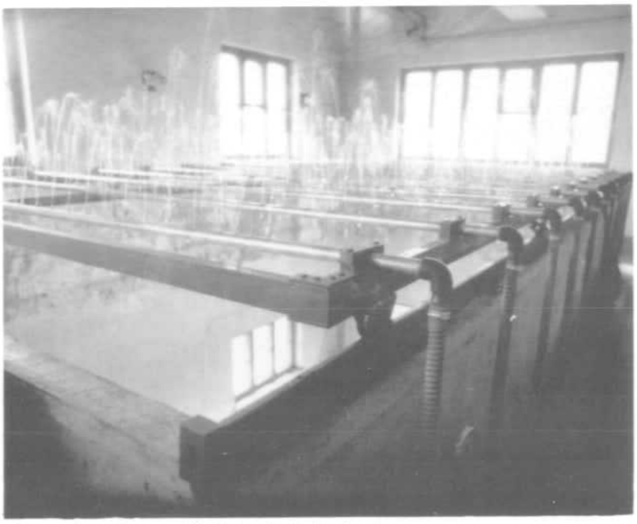


Plate 12. An artificial rainfall device
(Photograph Pei Tiefan)

The pipes are constructed of aluminium alloy, and have an internal diameter of 2.5 cm and a length of 3.6 m. There are 33 holes on each pipe, each 5 mm in diameter, and the distance between the nearest 2 holes is 100 mm. In order to reduce the boundary effect of rainfall and to introduce some regulation, the distance between the 2 nearest holes in the last 4 holes at the end of a pipe is 50 mm. The base for the spray nozzle is made of nylon, and can be installed on the taper hole on the outlet pipes. The spray nozzle can be installed to this base. Syringe needle seats, which have 4 different numbers, 4½, 9, 7 and 5½, are used instead of the spray nozzles. Their hole diameters are 1.4 mm, 1.0 mm, 0.75 mm and 0.55 mm respectively. Four kinds of spray nozzle, with 4 hand-operated valves, can simulate up to 60 levels of rainfall intensity in theory; in practice, because of the height of the lower waterhead, 40 levels are used, varying from 1 mm to 3 mm per minute.

The frame measures 5.3 m in length by 4.3 m in width, and the outlet rain pipes are installed evenly along the frame. The driving vehicle device comprises a type JZT 3-22-4 variable speed motor, a ZJT control box, JZQ-250-III-II-Z retarder, rocking arm and pull rod. The motor drives the retarder which is attached to the frame by the rocking arm and the pull rod. The reciprocation velocity of the rainfall device is from 2.6 to 38.7 times per minute.

The process of natural rainfall is complex. We have considered 4 factors in our model, ie rainfall intensity, raindrop size and distribution, falling speed, and the rainfall process which affects the rainfall–runoff relationships and soil erosion.

Rainfall intensity depends on the intensity of the water supply. It is regulated by 4 electromagnetic valves, and is measured by an electromagnetic flow meter. The height of the water head is 3.5 m. Rainfall intensity is measured at constant and varying speeds. Modelling constant rain intensity is only possible so long as the intensity is constant. It is also possible to measure varying intensity, which can be changed according to the designed rainfall column-line.

The size of raindrop in natural rainfall is distributed almost normally, but mean raindrop diameter increases with increasing rainfall intensity (Figure 2). Therefore, we have 2 different modelling methods.

The first method uses different spray nozzles according to raindrop distribution with a constant rain intensity. At a specified hole diameter, the more intense the rainfall, the less the raindrop diameter, which is in complete contrast to natural conditions. Therefore, the method is seeking an appropriate spray nozzle which will simulate the natural condition of rainfall. However, the distribution of raindrops is very complex and cannot be expressed easily by any analytical formula. Also, rainfall intensity changes continuously with time, and it is too troublesome to keep altering the spray nozzles. The present method of simulating natural rainfall is not satisfactory.

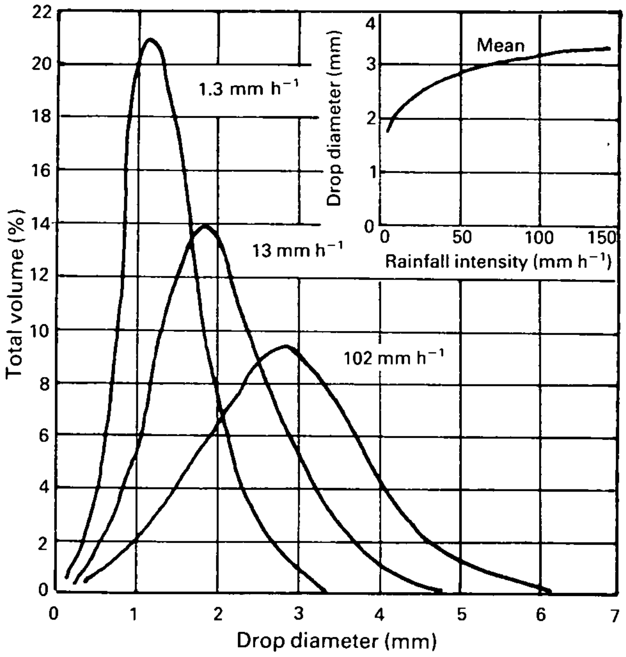


Figure 2. Effects of rainfall intensity on raindrop size and their contribution to total rainfall (source: Lows & Parsons 1943; Wischmeier & Smith 1958)

The second method uses an appropriate fixed spray nozzle, according to the mean raindrop diameter at a specified intensity. Therefore, modelling variable rainfall intensity is dependent on a designed rainfall process with a known mean intensity.

$$I = \frac{\sum_{i=1}^{n} I_i t_i}{T} = \frac{P}{T}$$

where I_i is rainfall intensity, t_i is duration, and T is total time of rainfall. The process is not continuous, depending on the mean raindrop diameter of mean intensity, and the spray nozzle is fixed.

In 1941, Laws found that the velocity of fall depended on the size of the particle, and that large drops fell more rapidly. As the height of fall was increased, the velocity increased only to a height of about 11 m; the drops then approached a terminal velocity, which varied from about 5 m sec^{-1} for a 1 mm drop to about 9 m sec^{-1} for a 5 mm drop. It has been suggested that the steady height of fall is 7 m for a 3–4 mm drop, and 9.5 m for a 6 mm drop. According to these figures, and considering the height of a tree crown and engineering conditions, we have designed the equipment so that the height of fall is 8.5 m. The specification meets most of the requirements caused by raindrops.

The natural rainfall process can be simulated by controlling the intensity, according to demand or the typical rain pattern in different areas. The uniformity of rainfall can be realized by regulating the velocity of the rainfall device and the distance between the outlet pipes. The results have shown that rainfall is uniform when the rotational speed of the motor is 750 rpm and the distance between outlet pipes is 45 cm.

Modelling rainfall on the forest floor was concerned mostly with total precipitation and total kinetic energy falling on the forest floor. Total precipitation can be determined from tree crown interception and stem runoff data. Total kinetic energy is modelled according to experimental formula for mean raindrop diameter and kinetic energy. As litter is present on the forest floor, even if the kinetic energy of raindrops differs significantly, the rain will not affect soil erosion or water infiltration. Therefore, we did not include the value of kinetic energy.

Artificial methods of rainfall calibration were tested. The results have shown that the velocity of the rainfall device is the main factor, with rain intensity and precipitation having a less significant effect. When the underlying model is level, the rainfall calibration results are as shown in Figure 3.

The simulation of rainfall is complex and our study requires further research.

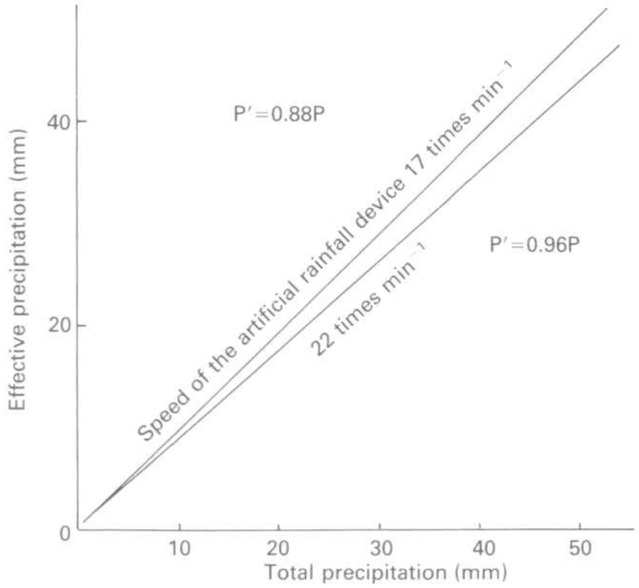


Figure 3. Calibrated curves of artificial rainfall

1.3 The underlying model

The underlying model is based on a non-scale concept, which includes a trough, dynamic devices and an operating mechanism (Plate 13).

Plate 13. The underlying model
(Photograph Pei Tiefan)

The trough is 5.0 m long and 2.8 m wide with a depth of 1.04 m. If the depth of earth in the trough is 1 m, the earth volume will be 14.0 m^3, and the total weight about 30 t. The floor base is made of a 10 mm thick steel plate, with 6 reinforcements under it in a crosswise direction, and 3 reinforcements lengthwise. Three bearing seats, fixed to the base, are welded at the junction of the third crosswise reinforcement and 2 sides of the model basic board, and at the central lengthwise reinforcement. Three axles are installed on the bearing. The steel boards are welded at the junctions of the central reinforcement on the lengthwise direction, and the fourth and fifth reinforcements on the crosswise direction. An oil cylinder turning model is fixed to the steel boards. The bearings and the oil cylinders have 5 point supporters in order to prevent fracture and deformation. To ensure rigidity lengthwise, 2 beams are installed under the reinforcements by the 2 sides of the oil cylinder. The trough is welded with 3 fenders on the left and right of it and at the back, and 8 mm thick plexiglass is installed on the fender so that the infiltrating water can be observed easily. To reduce errors in measuring precipitation, a galvanizing plate is fixed at right angles to the trough.

There is an outlet section in the front of the trough, with 3 fenders positioned according to the thickness of the soil layer. Four flow collecting troughs are fixed on the outlet section, and a V-trough measuring flow meter is suspended under each. Surface runoff, 2 layers of interflow and groundwater runoff are measured respectively. The flow collecting trough and V-trough turn at the same angle as the model trough. The flow collecting trough has an outlet, under which there is a V-trough measuring flow meter. The surface flow collecting trough has a cover fixed to it to prevent rainfall falling into it. Water from the outlet section then flows through the flow collecting trough and V-trough, finally running off through the drain.

The kinetic device includes a motor, oil pump and 2 oil cylinders. The operating mechanism comprises an operating table, with a starting switch for the motor and distributing equipment. The distributing equipment has 4 positions, ie rising, ceasing, dropping and following. When the handle is in an upright position, the piston rod of the oil cylinder supports the model (Plate 14).

The model trough can turn at any angle between 0 and 30 degrees around the axis. The turning angle can be read from an indicator board on the right of the model trough. To reduce the working loading pressure on the oil cylinder, after reaching a specified angle, the model trough is secured by a sustaining bolt.

Different artificial soils are placed in the model trough to simulate various natural conditions. The soil is divided into 3 layers according to its physical properties, and the surface runoff, interflows and groundwater flow are measured. The underlying trough has the 2 following functions.

First, we can study hydrological behaviour under 2 specified conditions: including (i) various types of vegetation, some of which is simulated, and (ii) various conditions such as soil type, mechanical composition, bulk density, root quantity and soil moisture. From this research into the hydrological behaviour under different underlying conditions, production flow is expressed in mathematical terms.

The second function simulates a basin. Topography, geomorphology, mountains and rivers can be reduced

Plate 14. The oil cylinders supporting the model (Photograph Pei Tiefan)

in size to simulate a basin, so that the hydrology of the basin can be studied comprehensively, including the mechanism of producing flow, together with processes of flow and hydrological forecasting. We can also study the effects of forest on flood, the effects of soil vegetation in purifying polluted water, the removal of elements, the leaching state, and the effect of acid rain on soil, etc.

1.4 Measuring system

The measuring system includes a flow measure in the water supply pipe, an outflow measure, a measure of soil moisture and soil temperature, and a sediment measure. Rainfall intensity is measured by a type LD-25 electromagnetic flow meter (Plate 15).

The maximum rate of flow is 4 m^3 h^{-1} through the type LD-25 electromagnetic flow meter, with a total accuracy of grade 2. The calibration curve is shown in Figure 4. Because it is necessary to change rainfall intensity during the experiment, 2 flow distributing boxes are connected to the water supply pipes. Two valves are connected with the same pipe, one of which is a hand valve, and the other an electromagnetic valve. Fifteen kinds of water supply flow can be achieved, ie 15 levels of rain intensity. Because the water head is lower when rain intensity is less, the spray nozzles cannot work. Eleven measures of non-equal distance can be achieved by spray nozzles nos 9 and 4½. Four types of spray nozzle can produce 40 levels of rain intensity, regulated by microcomputer-controlled electromagnetic valves.

Plate 15. Electromagnetic flow meter (Photograph Pei Tiefan)

Outflow is measured by the V-trough measuring flow meter, developed by Fang Xiang (1982) at the Institute of Geography, Academia Sinica, but the circuit has been changed slightly. After passing through a square-wave generator emitter, a follower output is added. When several V-trough measuring flow meters and resistance humidometers are run simultaneously, they

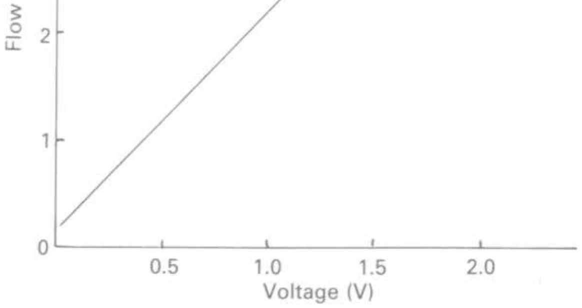


Figure 4. Calibrated curve of electromagnetic flow meter

cause interference. Therefore, each set is fitted to an independent power source. After smooth filtration, the photo-electric isolator is installed (circuit figure and humidometer of soil are plotted together). Four sets of V-trough measuring flow meter, which are displayed at the same time, measure one layer of surface flow, 2 layers of interflow and one layer of groundwater flow (Plate 16). Four sets of V-trough measuring flow meter, controlled by a type PS-85 microcomputer, are calibrated (Figure 5) to an accuracy of 2–3%.

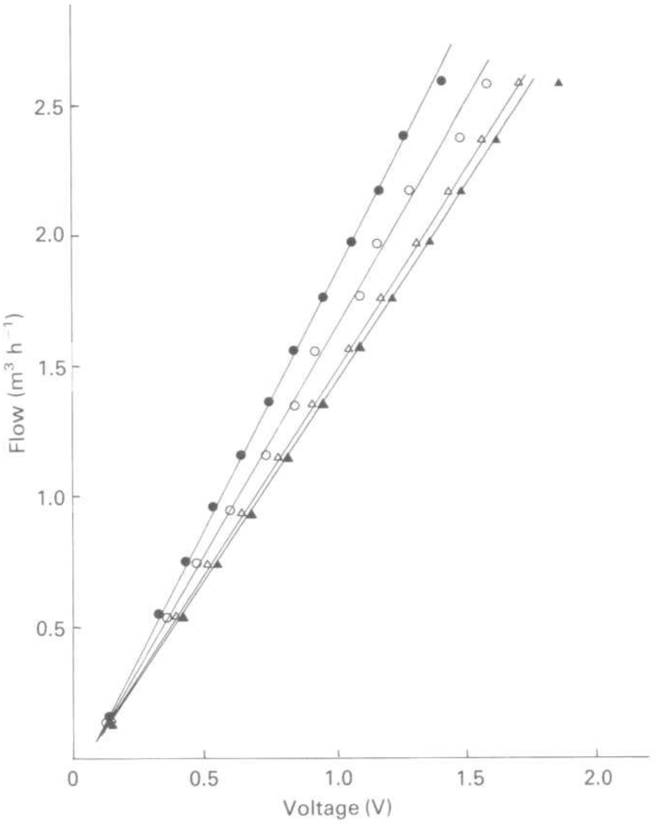


Figure 5. Calibrated curve of V-trough measuring flow meter (O = no. O; ▲ = no. 1; ● = no. 2; △ = no. 3)

Plate 16. V-trough measuring flow meter on outlet section of the underlying model
(Photograph Pei Tiefan)

Soil moisture at various underlying depths is measured on the same vertical line by the resistance soil humidometer (Plate 17). The humidometer is designed so that soil moisture is related to its resistance (Figure 6).

The square-wave generator and wave filter in the circuit consist of a high-operation amplifier. The square-wave generator in the circuit is a regulated wide generator. According to the different pH values of soil, frequency is regulated to eliminate electrode polarization in measuring soil moisture. The electrode is made of graphite in a steady state so that the soil humidometer will be steady and reliable. Five sets of

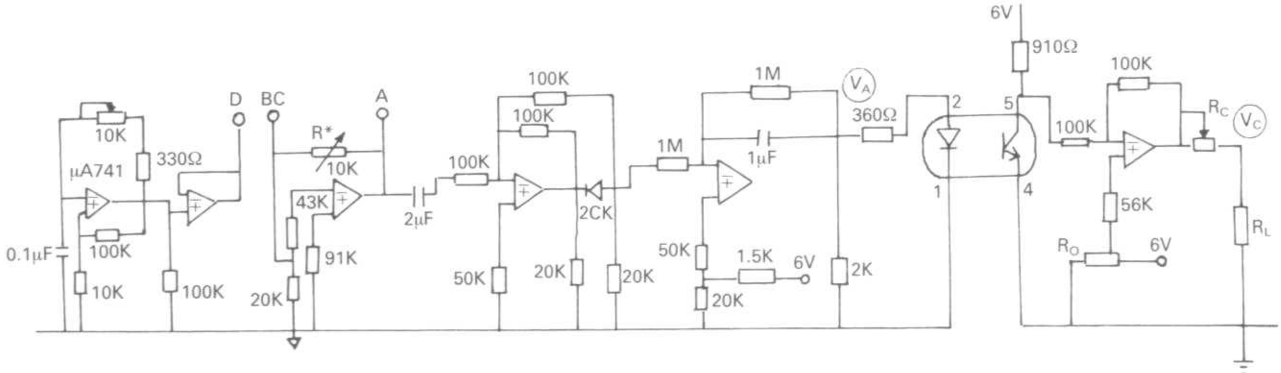


Figure 6. Circuit of V-trough measuring flow meter and resistance soil humidometer. Resistance $f_0 = 9.7k_c$; current $f_0 = 5.82k_c$

ABD 3 points connect with one meter at measuring points, 3 points are connected when flow is measured. B connects with D, but AB is replaced with R when moisture is measured. When BD opens, V_A is about 1.5V, then R_c is regulated for the sake of $V_c = 0$. When the soil is saturated, R* is regulated so that $V_A \leqslant 2.6V$, and then R_c is regulated so that $V_c = 2V$. The various circuits of power supply are all ± 6VDC respectively.*

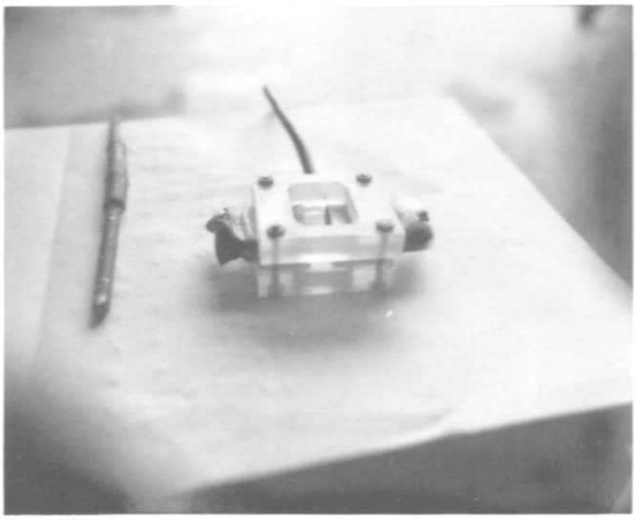
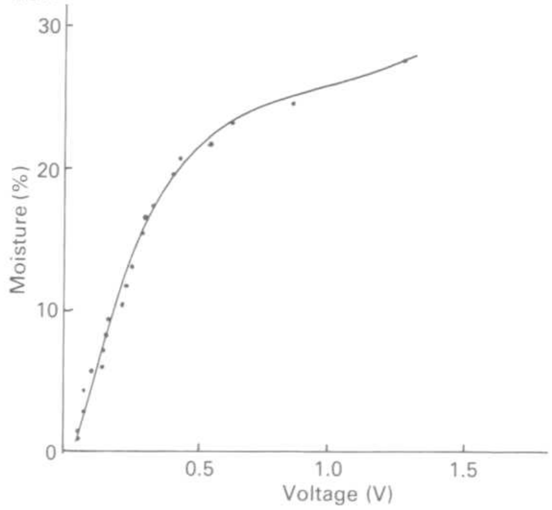


Plate 17. Resistance soil humidometer (left) and soil thermograph (right) (Photograph Pei Tiefan)

soil humidometers have been calibrated as an example using volcanic ash. The soil was collected from the grounds of the Changbai Mountain Research Station. The calibrated curve is shown in Figure 7.

The relationship between soil moisture and output voltage is non-linear. Its accuracy is related to soil structure, calibrating methods (which are difficult) and the stability of the sensing elements and circuit. Temperature drift has a greater effect on accuracy.

No. 1



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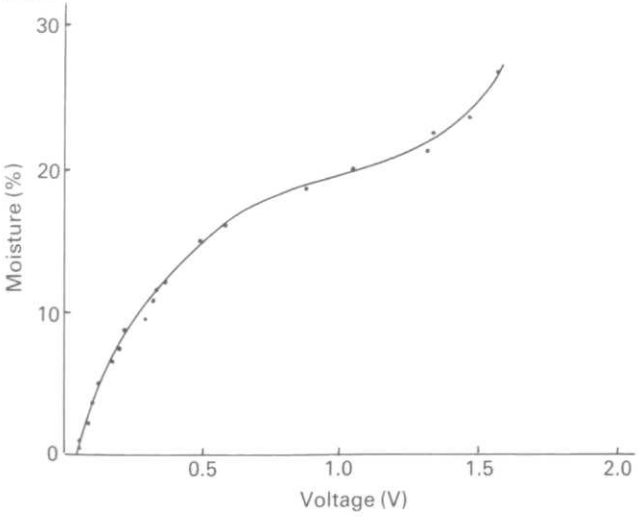

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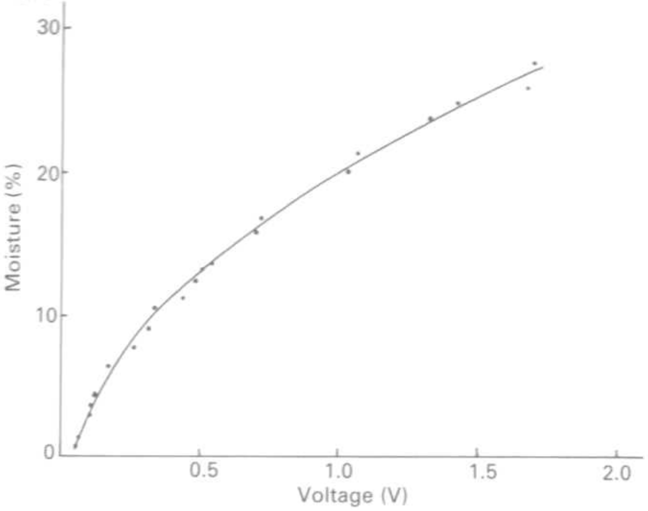

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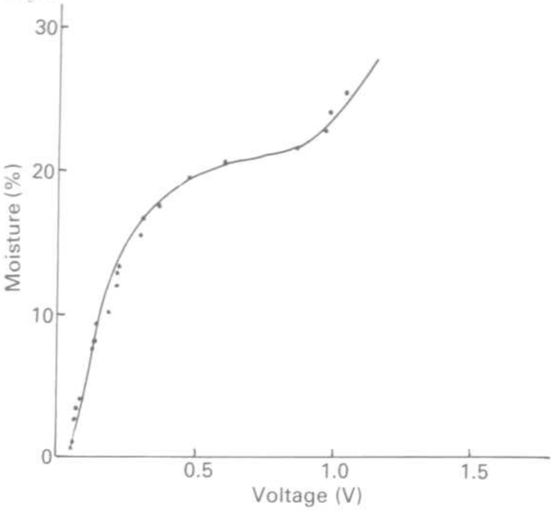

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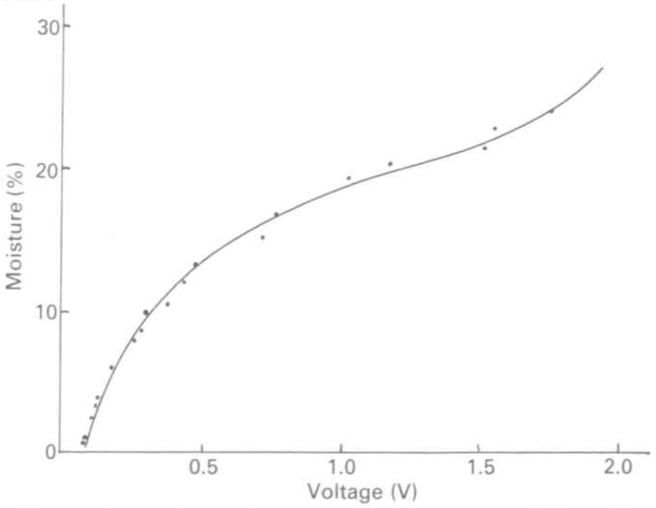
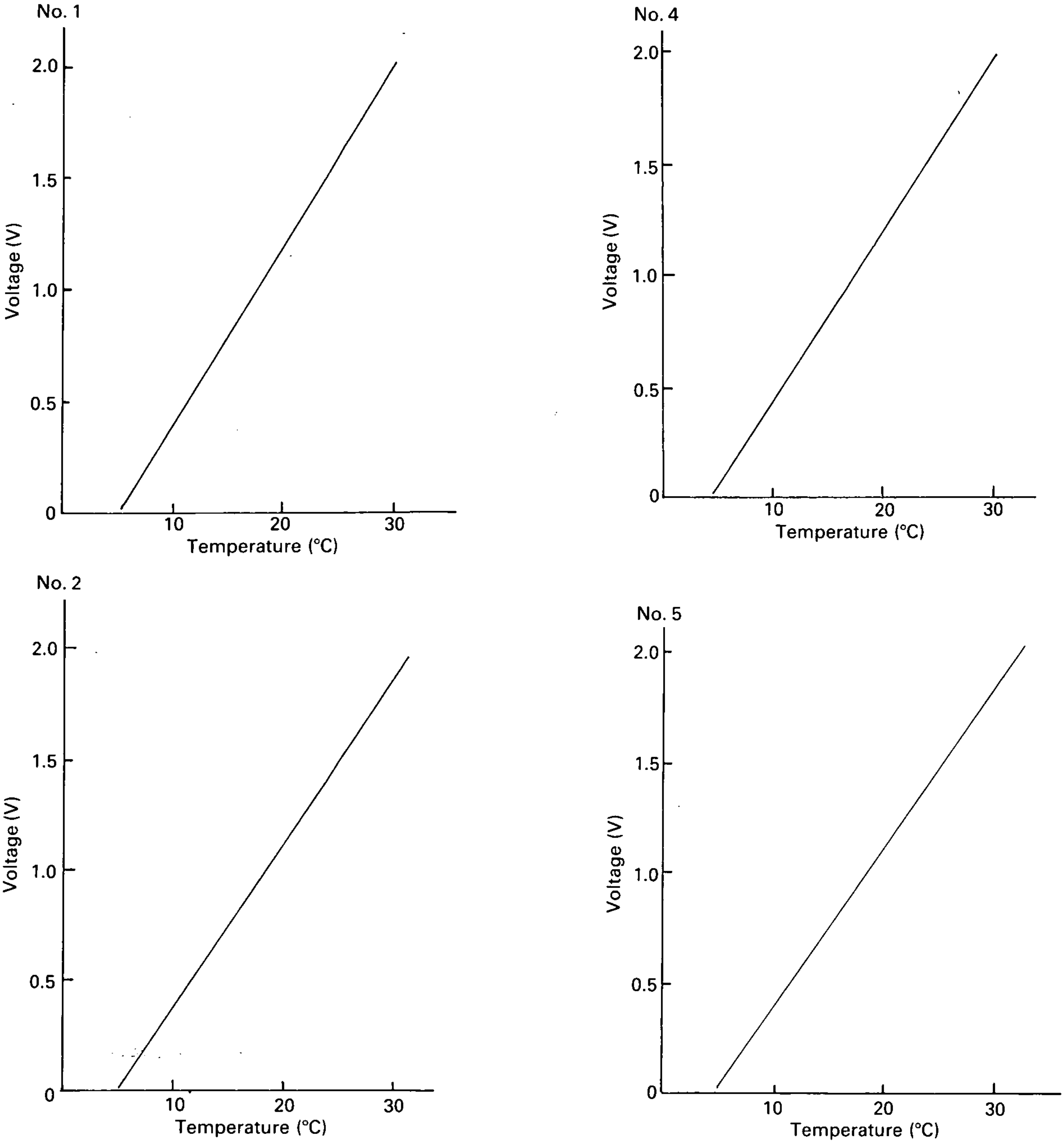


Figure 7. Calibrated curve of resistance soil humidometer (nos 1–5)

Five sensors (nos 1–5) for the soil humidometer when soil moisture is less than 20% achieve errors of 4%



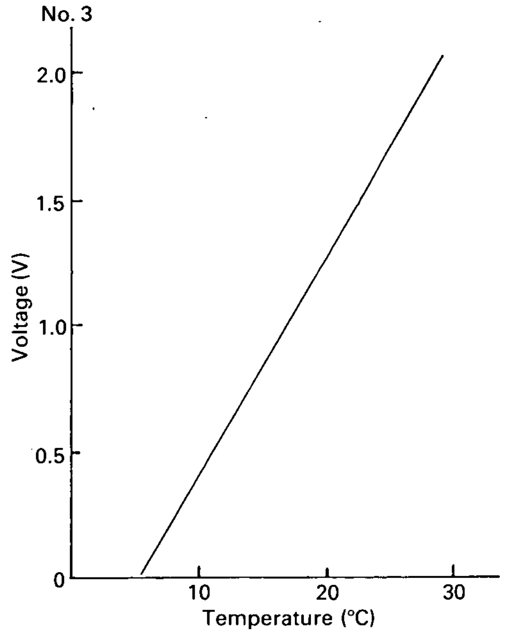


Figure 8. Calibrated curve of soil temperature sensors (nos 1–5)

(no. 1), 4% (no. 2), 3% (no. 3), 5% (no. 4), and 5% (no. 5). Accuracy is further reduced when moisture is greater than 20%. The problems require further study.

Because the accuracy of the humidity sensor is related to temperature, the soil temperature must be measured, and a copper resistance temperature sensor of WZGK53-2 is used. Soil temperature in the underlying model is measured at various depths from the surface.

The 5 sensors can measure temperature at the 5 depths simultaneously, and the values range from 5°C to 30°C. The sensitivity is 80 mv/°C and the accuracy is ± 0.5°C (± 2%). The calibration curve is shown in Figure 8. Sediment will be measured in the future.

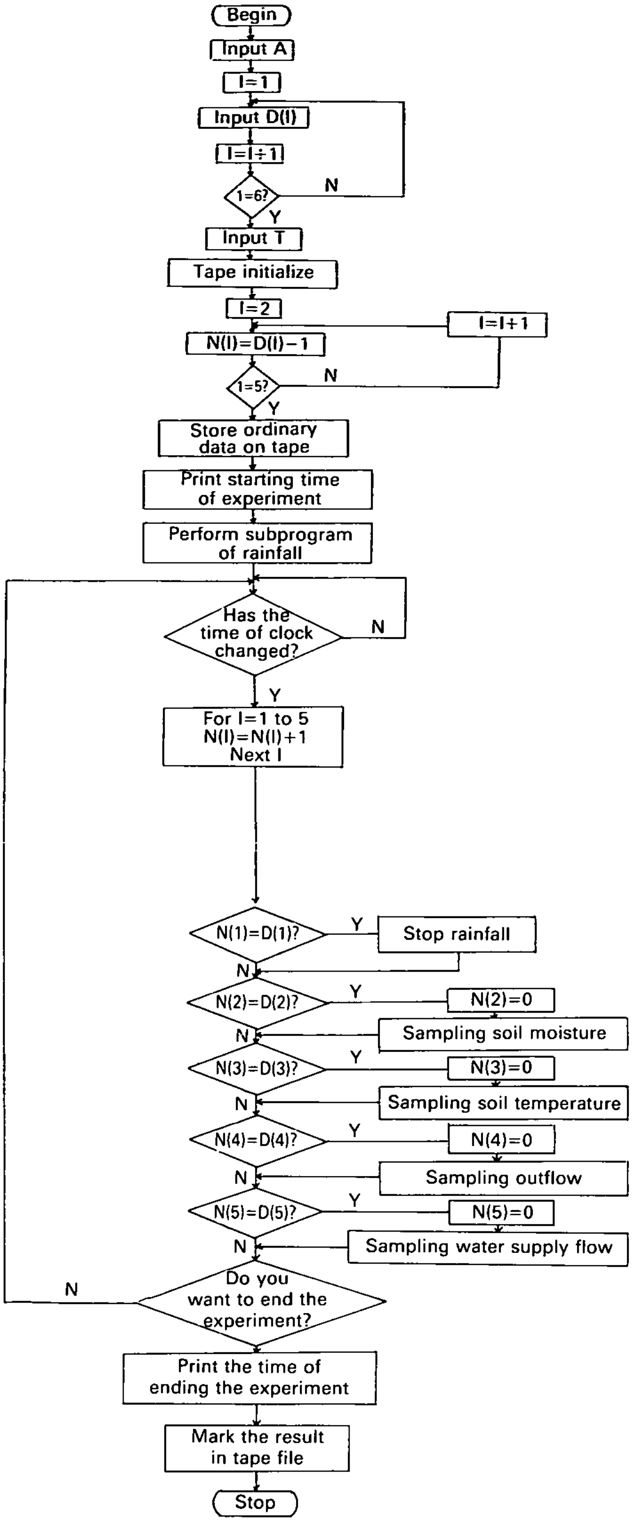


Figure 9. Flow diagram of computer program

1.5 Microcomputer control system

Hydrological elements such as rainfall intensity, flow, soil moisture and temperature are determined by meters controlled by a type PS-85 microcomputer in 30 channels. There are 4 channels to control rain intensity; one channel to measure rain intensity; 4 channels to measure outflow, with one reserved; 5 channels to measure soil moisture, with 10 reserved; and 5 channels to determine soil temperature.

The CPU of the main part of the PS-85 microcomputer is Z80A. The clock frequency is 4 MHZ, and the internal capacity is 48KB. There are 2 sets of 12.7 cm magnetic disk drives, and 16 channels in an extended interface board, which has a single end input, and a simulating input signal voltage of ± 2V. There are 2 pieces of A/D conversion board, which has the largest collection frequency of 10KHZ, and 32 channels. The DI/DO interface board of 64 bits is side by side, and consists of an interface chip Z-80APIO. The printer and magnetic tape driver are fitted for data output and storage.

Rain intensity is regulated by 4 DTF electromagnetic valves and 4 handle valves. The TTL level is maintained by the DI/DO of the microcomputer. By magnifying the triode and through 3-stage relay, 220V in AC is transformed by electromagnetic switches to control the stationary spray nozzle. Fifteen levels of rain intensity can be achieved by 4 electromagnetic valves and 4 handle valves.

Surface runoff, interflow and groundwater flow in the underlying model are measured by the V-trough measuring flow meter. Soil moisture is measured by the resistance humidometer, and soil temperature by WZGK53 copper resistance. Rainfall intensity is measured by the LD-25 electromagnetic flow meter. A standard electric current of 0–10mA flows from the measuring meters. To prevent electric signals transmitted over a distance being distorted when the microcomputer receives signals, the voltage can be changed between 0 and 2V by the transformer. The signals are transformed into a digital signal which is input by the A/D board. The frequency of collection is 10K, the accuracy is 12 bit, and signal voltage ranges from −2V to +2V.

Experimental time, rainfall time, control of rain intensity change and collecting frequency are all monitored by the computer clock. The maximum collecting frequency is once per second.

The collected data are stored on magnetic disk, and compared with the calibrated curves. The true values are determined and stored simultaneously on magnetic tape. The printer outputs data in tabulated form.

2 Acknowledgement

We wish to thank the Institute of Geography, Institute of Shenyang Automation, Academia Sinica, Shenyang Tractor Factory, and Engineer Chai Yingyu of the White River Forestry Service for their guidance. Professors Wang Zhan and Cui Qiwu have contributed to this research and Fan Shixiang and Xu Jun were involved in the writing up of the rainfall, underlying and control systems respectively. Assistant Professor Sun Jizheng and Engineer Wang Weihua also assisted in the work.

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Appendix I
LIST OF PAPERS PREPARED FOR PARTICIPANTS BUT NOT PRESENTED AT THE SYMPOSIUM

COPIES ARE AVAILABLE FROM THE INSTITUTE OF FORESTRY AND SOIL SCIENCE, ACADEMIA SINICA, PO BOX 417, SHENYANG, PEOPLE'S REPUBLIC OF CHINA

Chen Dako, Zhu Ning et al. Research on natural secondary forest in Heilongjiang Province – the way of Korean pine–deciduous forest recovery.

Chen Fudong & Du Guisen. The community composition and seasonal changes of phytoplankton in adult fish ponds.

Chen Fudong & Du Guisen. Phytoplankton in the Huairou reservoir.

Chen Peng & Zhang Yi. The relationship of soil animals to soil moisture and soil temperature in broadleaved/Korean pine forest on Changbai Mountain.

Chi Zhenwen, Zhang Fengshan & Li Xiaoyan. A preliminary approach to water and heat conditions of forest ecosystems on the northern slope of Changbai Mountain.

Cui Qiwu & Lawson, G. J. A new model of single populations with 3 parameters.

Cui Qiwu & Lu Fengyong. The nutrition structure of predator populations and its functional response on prey density.

Feng Baoxing. New results from comprehensive investigations in the forest on Changbai Mountain.

Fu Tongsheng, Gao Wei & Song Yujun. Birds on Changbai Mountain.

Gao Qian & Bai Enzhong. A primary study on water-storing bryophytes in Changbai Mountain nature reserve.

Gao Wei. The forest avian community changes of the last 15 years on the north slope of Changbai Mountain.

Gao Wei. The structure of the bird community in the main forest types on the north slope of Changbai Mountain.

Gao Wei. The winter richness and syngenesis (succession of community) of the bird community on the north slope of Changbai Mountain.

He Jingjie. Studies of birds' habitat structure and feeding habits in the forests of Changbai Mountain.

Kang Xuegeng. A preliminary study on Bryophyta of Zengfeng Mountain.

Li Junqing & Chen Dawo. Population size oscillation of Korean pine in the natural forest.

Li Shichun, Zhang Xinglu, Zhang Langji, Gao Wei, Song Yujun & Wang Bairan. Bird community structure and productivity in broadleaved/Korean pine forest during the breeding season.

Liu Jiagang. Propagation of light through forest canopies – an integral equation system.

Ou Yanghui. Vertical characteristics of ecological and economic factors in mountain and development direction.

Pan Weichou, Tian Dalan, Shen Xiaoyong, Wen Shizhi, Lei Zhixing, Kang Wenxing, Wei Xianming & Zhou Guoyi. Nutrient dynamics and balance of the hydrologic process of a subtropic Chinese fir plantation ecosystem.

Peng Yongshan, Xu Zhenbang, Dai Hongcai, Zhang Fengshan & Zheng Guizhi. The ecological effect of ground cover on afforestation.

Qiu Xuezhong, Xie Shouchang & Wei Tianhao. Preliminary studies on the forest ecosystem of Ailao Mountain nature reserve.

Song Daquan. On the genesis and characteristics of dark brown and brown forest soils in East Asia.

Tao Dali, Jin Yuehua & Yang Bifang. Freezing tolerance of woody plants on Changbai Mountain.

Tao Jinchuan, Song Shixian & Yang Zhibin. The geographical distribution of *Magnolia sieboldii* in relation to the climatic conditions.

Wang Bennan. An explanation of Cui–Lawson's single population growth model.

Wang Fengyou & Wang Yeju. Numerical classification of virgin Korean pine forest mixed with deciduous trees on the south slope of Lesser Xingan Mountains, north-east China.

Wang Gang & Zhao Songling. The niche model of secondary succession in *Picea wilsonii* forests.

Wang Guizhen, Pei Minghao & Yuan Zhiwen. Studies on species richness and composition of tree pathogenic fungi on Changbai Mountain.

Wang Hanjie. The instability of atmospheric waves and the precipitation distribution in forest regions.

Wang Hanjie. A numerical simulation model for radiation in the forest canopy.

Wang Zhan, Rosenberg, V. A. & Zhang Shiju. Mixed coniferous/broadleaved forests on the northern slope of the Changbaishan plateau and on the western spurs of the Inoling range.

Wang Zhengfei, Chen Dawo & Liu Ziqiang. Discussion on ecological balance and forest fire severity.

Xie Pingruo. Preliminary approach to mineralogy of volcanic ash soil on the northern slope of Changbai Mountain.

Xu Guangshan, Harrison, A. F. & Grimshaw, H. M. Development and application of a resin-bag method to determine available nitrogen in forest soils.

Xu Zhenbang, Li Xin, Dai Hongcai, Chang Yiping, Tao Zhengxiang, Peng Yongshan, Dai Limin & Guo Xingfen. A study on biomass of broadleaved/Korean pine forest on Changbai Mountain.

Yang Jinkuan. A preliminary study on *Hypera* species on *Ulmus*.

Yang Jinkuan & Qu Shipeng. Preliminary study of population dynamics of moths on Changbai Mountain.

Yang Jinkuan, Qu Shipeng & Ji Lanzhu. Morphology, bionomics and population dynamics of *Caligula boisduvali* Fallax Jordan.

Yang Mingxian & Ma Shucai. A survey and qualitative analysis of the soil mites on the northern slope of Changbai Mountain.

Yang Yiping, Wang Shuli, Yin Ruexue & Zhang Junli. Genetic variation of esterase isoenzyme in populations of Korean pine (*Pinus koraiensis*).

Zhang Fengshan, Chi Zhenwen, Pei Tiefan & Li Xiaoyan. The summer microclimate of the alpine tundra on Changbai Mountain.

Zhang Songyun. The study of fast-growing and disease-resistant genetic breeding of larch.

Zhao Songling & Zhang Dayong. The Lotka-Volterra competitive model – an approach to study the recovery succession of the forest vegetation in the Maxion Mountains.

Zhao Zhengjie. Protection and management of natural resources of Changbai Mountain.

Zhao Zhengjie. The composition and distribution of terrestrial vertebrates on Changbai Mountain.

Zhao Zhengjie. The analysis of bird fauna on Mount Changbai.

Zhu Tingchen & Rowe, J. S. A comparison of alpine tundra floras: NE China and NW North America.

Appendix II
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