MULTIPLE-SCALE APPROACHES TO THE RESTORATION OF DECIDUOUS FOREST IN SOUTHWESTERN ONTARIO, CANADA

STEPHANE MARC MCLACHLAN

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Declaration Regarding Contribution to Collaborative Research

The research in Chapter 2 was conducted in collaboration with Dr. C. M. Pearce at University of Western Ontario. S. M. McLachlan's contribution was to conduct ground-truthing on mainland areas in Essex county. All data interpretation and discussion of theory were carried out independently by S. M. Mclachlan. The research (experimental design and statistical analysis) in Chapters 3-7 was conducted by S. M. McLachlan with supervisory input and suggestions from Dr. D. R. Bazely.

Abstract

Intense agricultural and urban land-use has reduced forest cover to 3% in Essex county, southwestern Ontario, Canada. The remaining forest has been degraded by over-grazing, non-native species, recreational use, and, in some cases, poor management. From 1994 to 1996, field studies were conducted in and around Point Pelée National Park (PPNP) with the overall objective of assessing various approaches to habitat restoration.

A preliminary landscape-level analysis of three areas near to PPNP used satellite imagery and geographical information systems (GIS). Forest cover in the area directly north of PPNP (Pelée-north) was less than 3%, while that of nearby Cedar Creek and Pelée Island was 9% and 14%, respectively. The relatively large number of forest patches <10ha and great inter-patch distances in Pelée-north suggested that the management focus in this area should be on habitat protection. In contrast, restoration efforts might be more effective elsewhere, where land values are lower and possibilities of increasing the connectivity between the forest remnants are greater.

Since the 1960s, cottages and roads in PPNP have been removed and these sites allowed to regenerate (passive restoration). Since 1988, many sites have been actively restored. Although actively-restored sites were still dominated by ruderal non-natives, results suggested that passively restored sites increased in similarity to relatively undisturbed reference sites as time-since restoration increased. After 35 years, some mesic sites seemed to have recovered completely. In addition, there was no overall difference in native diversity between restored and reference sites. However, multivariate analyses showed significant differences in native species composition between reference and restored sites. Spring ephemerals with restricted seed dispersal were highly vulnerable and will likely have to be reintroduced. Non-native species diversity showed a significant decline over time, especially in wet/mesic sites. Ruderal non-natives declined most rapidly as time-since-restoration increased, while regeneration-inhibiting non-natives showed a less rapid decline. The non-native garlic mustard (*Alliaria petiolata*) had little longterm effect on the native understorey plant community.

The success of agroforestry and afforestation was examined in a post-agricultural field outside of PPNP. The effects of fertilisation, weed control, and corn shelter treatments on the growth of three native deciduous tree species was studied from 1994 to 1996. Fertiliser significantly increased tree growth, but only when weeds were adequately controlled. Trees in clover treatments had less growth than those in either full-weed or mown-weed treatments, while trees in weed-free and inter-weed treatments had the greatest growth. Silver maple (*Acer saccharinum*) and green ash (*Fraxinus pennsylvanica*) growth was greatest under the corn shelter when plots were fertilised and controlled for weeds. In contrast, growth of bur oak (*Quercus macrocarpa*) was adversely affected by the corn.

The restoration of deciduous forest holds great promise for this region. whether it create new natural habitat or accelerate the recovery of existing but degraded habitat. However, this region is so highly fragmented that restoration should be co-ordinated at the landscape level if generations of neglect are to be successfully reversed.

Acknowledgements

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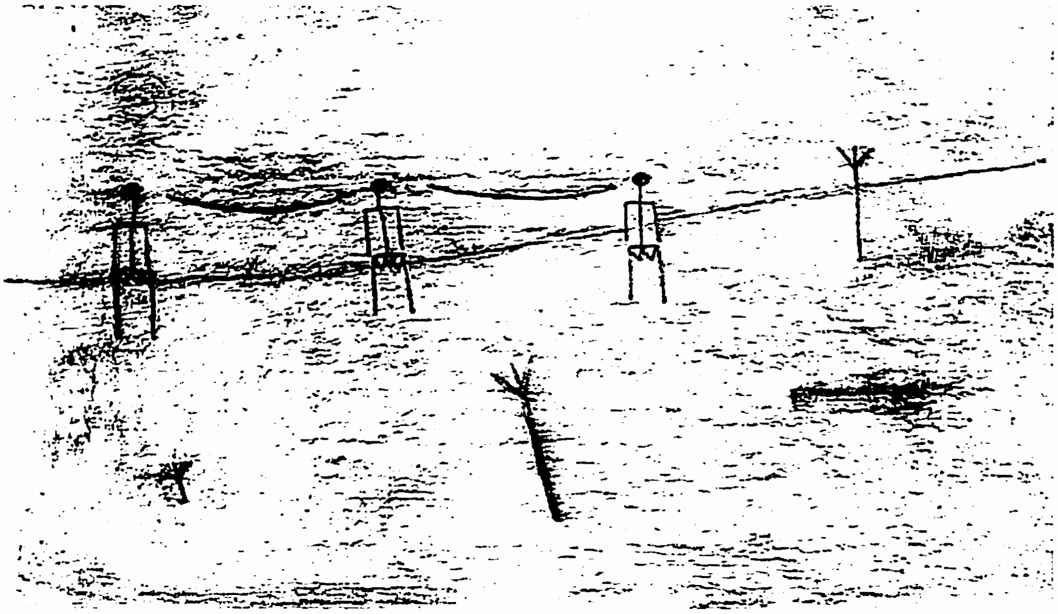


Idols and ambergris and rare inlays,
These are your riches, your great store; and yet
For all this sea-hoard of deciduous things,
Strange woods half sodden, and new brighter stuff:
In the slow float of differing light and deep.
No! there is nothing! In the whole and all,
Nothing that's quite your own.
Yet this is you.

E. Pound

CHAPTER 1

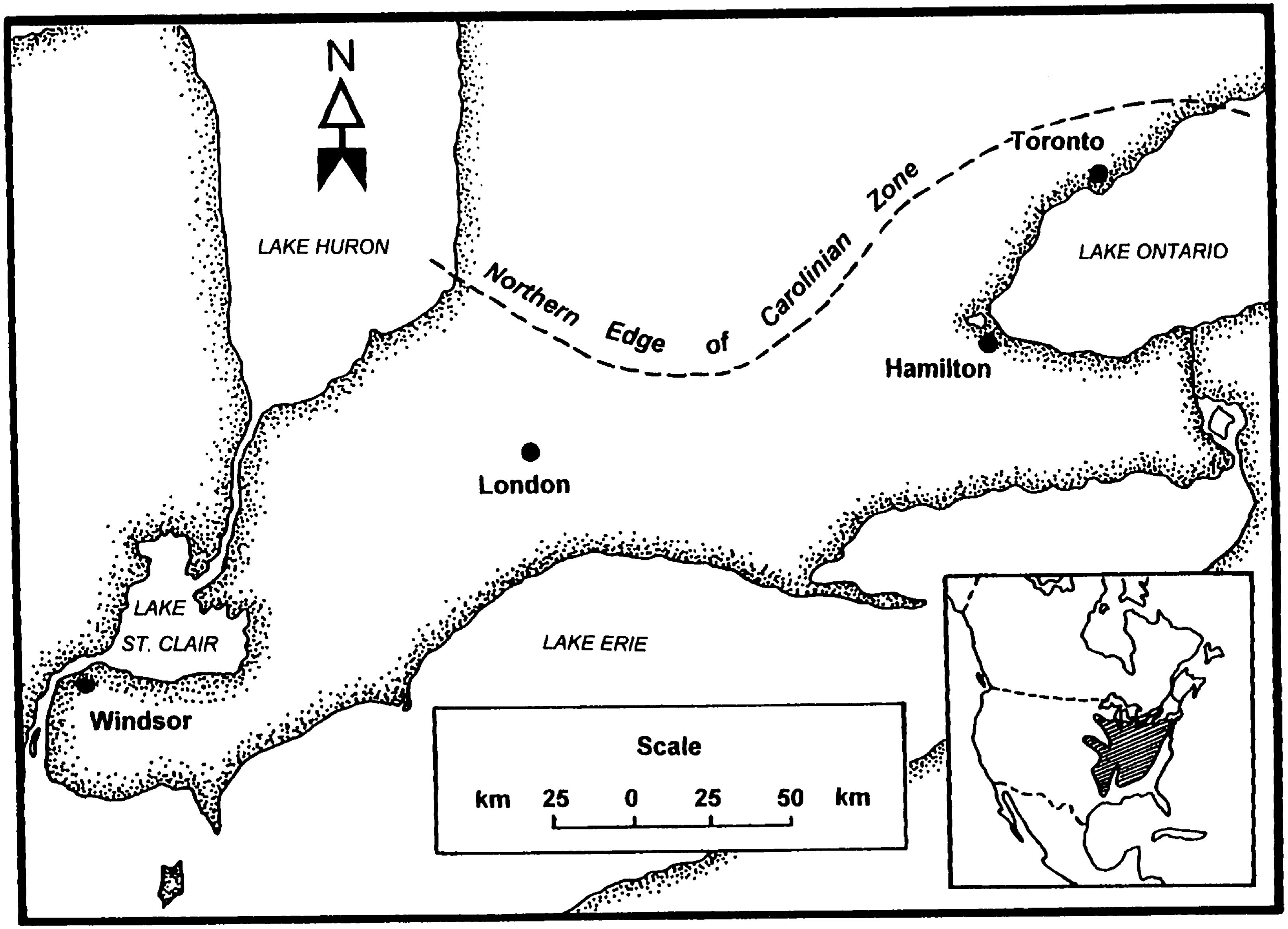
LITERATURE REVIEW

INTRODUCTION

The Carolinian or Deciduous Forest Zone of southwestern Ontario is the northern fringe of an expanse of deciduous forest that extends up into Canada from the northeastern United States (Reid, 1985). Its north-most boundary stretches from Grand Bend in the west to the eastern border of metropolitan Toronto (Figure 1.1). In Ontario, this zone represents a transition from the pure Carolinian forest in the south to the mixed deciduous/conifer forest in the north and contains a unique mixture of species and ecosystems that characterize both life zones. Prior to European settlement, the Carolinian region of Ontario was dominated by closed-canopy deciduous forest. However, it also contained extensive wetlands and marshes, as well as tall grass prairies, savannahs and alvars. The Carolinian has the highest species richness of any life zone in Canada, containing, for example, over 2,200 herbaceous and 400 bird species (Allen et al., 1990). However, intensive human development now threatens much of the natural habitat in the region.

Despite covering only 0.25% of Canada's land mass, the Carolinian supports over 25% of this country's human population (Allen et al., 1990) and is the most heavily urbanized and intensively farmed area of Canada. This intense landuse pressure has resulted in the extensive loss and degradation of natural habitat. Mean forest cover is less than 10% and reaches a low of 3% in Essex county, Ontario (Riley and Mohr, 1994).

Figure 1.1. Map of the Carolinian Zone or Deciduous Forest Zone for Ontario, Canada, showing major cities, and for North America (inset).


N
LAKE HURON
Northern Edge of Carolinian Zone
Toronto
LAKE ONTARIO
Hamilton
London
LAKE
ST. CLAIR
Windsor
LAKE ERIE
Scale
km 25 0 25 50 km

Similarly, savannahs and tall grass prairie have been reduced to 0.1% and wetlands to 42% of their former cover, respectively (Bakowsky and Riley, 1994). The resulting fragmentation of the remaining forest has been associated with an increase in edge habitat, invasion by exotics, overgrazing by white tailed deer and a decline in the diversity of native species (Sauer, 1994).

Currently, 65% of Ontario's rare plant species are found in the Carolinian and 40% are restricted to this zone (Allen et al., 1990). Thirty-seven plant species have no record of occurrence since 1937 and 101 other species exist in five or fewer locations (Oldham, 1990). Point Pelée National Park, Canada's best-known and largest Carolinian preserve is no exception to this degradation. There, this loss of integrity is shown by declines in native biodiversity (40 plant species in the park are nationally listed as rare) and encroachment by exotics (40% of the vascular flora is non-native) (Dunster, 1990). There has also been extensive deer overgrazing (Koh, 1995). These symptoms of habitat degradation are severe enough that habitat restoration, protection, and monitoring are necessary if Point Pelée National Park is to retain its status as a premier Carolinian preserve and if the Carolinian forest as a whole is to persist meaningfully in Canada (Stephenson, 1994). The overall objective of this study is to determine ways in which Carolinian forest in and around Point Pelée National Park can be effectively restored.

INDUSTRIAL FORESTRY AND AGRICULTURE

Southwestern Ontario is a "settled landscape" in which forestry and agricultural practices as well as urban expansion have expanded tremendously over the last 200 years.

Forests were cleared primarily for timber immediately after European settlement in the mid 18th century and the land used for agriculture (Wilcox, 1993). Over the last 50 years, the major form of land use change has been the continued conversion of natural habitat into farmland and, more recently, the conversion of both natural habitat and farmland into urban and industrial use (Lawrence and Beazley, 1994). Presently, 70% of the Carolinian lies within 50 km of a major urban centre and is subject to development pressures (B. McDonald, pers. comm.). Over 21 000 ha of farmland were developed in Ontario between 1981 and 1986, the majority of which was high quality and situated in the Carolinian (OMAF, 1992).

The majority of the remnant patches of forest are privately owned. Although some of these remnants have been cleared for agricultural production, most are not actively managed (Jones, 1994). Human activity adversely affecting these forest remnants includes selective harvesting, for the most part by local sawmill operators, harvesting for fuelwood, and grazing by livestock (G. Mouland, pers. comm.). Although some of this forest has been assessed by agency foresters, its composition and status are largely unknown (C. Jones, pers. comm.).

In this region, intensive cash-cropping and vegetable production comprise agriculture. At the turn of the century, southwestern Ontario was dominated by mixed (i.e. both crops and livestock) family farms that generally used manure for fertilizer and mechanical cultivation to control weeds. However, at this time, drought and excessive soil erosion resulted in much marginal land being taken out of production and some land being reforested (Wilcox, 1993). After WW II, the development of chemical fertilizers, pesticides, and new crop hybrids began changing agriculture into "industrial" or "high input" farming throughout North America. The use of chemical fertilizers freed producers from livestock production and allowed full time "cash cropping" which translated into continuous hybrid corn production in the early 1970s. These crop monocultures, in turn, allowed for the use of non-selective herbicides and large planters, cultivators, pesticide and fertilizer spreaders, and combine harvesters. This technology and capital-intensive production in turn contributed to greater crop specialization, increased farm size, and reduced numbers of farms. Many family farms went bankrupt, rural communities collapsed as residents migrated to the cities for work, and farms close to expanding urban centres were converted into suburbs or unproductive, "hobby farms" (Pimental et al., 1989).

The local impact of this industrial agriculture on the environment has been enormous. Pesticides are applied on 3 million ha in the Carolinian, mostly in the form of herbicides (Stats Canada, 1994), 50-year flooding is common (J. Robertson, pers.comm.), and public concerns over pesticide residues in food and contamination of ground water remain high. The adverse impact of pesticides such as DDT and organochlorines such as dieldrin and PCB on wildlife, especially top predators such as Bald Eagles and Ospreys, is well documented (McKeane and Weseloh, 1993). Recent studies have indicated the presence of herbicides such as metalochlor and atrazine in surface runoff, ground water (AAFC, 1994), well water (OMOE, 1992) and in the Great Lakes (Schotter and Eisenreich, 1994). Soil erosion is high on sandy, sloped land, often in excess of 100 tonnes/ha/yr, and is associated with wind and rain, cropping practices and excessive tillage (Kachanoski, 1992b). The resultant increases in sedimentation and turbidity of surrounding waterbodies have also adversely affected aquatic vegetation, fish habitats, recreation, and water availability (Richards and Baker, 1993). Nonpoint-source loading of phosphorous and nitrogen from agriculture has increased relative to that of localized industrial sources, due to difficulties in identifying sources (Sharpley et al., 1994) and growing fertilizer use (Richards and Baker, 1993).

IMPLICATIONS OF HABITAT FRAGMENTATION

The fragmentation of natural habitat has been identified as one of the most "serious threat(s) to biological diversity and...the primary cause of the extinction crisis" (Wilcox and Murphy, 1985). Fragmentation has been shown to have adverse effects on birds (Robbins et al., 1989; McCollin, 1993), mammals (Weddell, 1991; Celada et al., 1994), invertebrates (Davis, 1994; Webb, 1989; Klein, 1989), and plants (Weaver and Kellman, 1981; Simberloff and Gotelli, 1984; Soule et al., 1992). However, there is still extensive debate over the mechanisms underlying this decline (Simberloff and Cox, 1987; Bohning-Gaese et al., 1993; Rolstad, 1991; Paton, 1994).

The theoretical framework for explaining and predicting the effects of fragmentation on natural communities is primarily provided by theories of island biogeography (*sensu* McArthur and Wilson, 1967). The fragmentation of vegetation cover that accompanies intensive human use inevitably decreases the size and increases the isolation of the remnant habitat patches (Noss, 1987). Ecologically, these remnant patches are perceived as "terrestrial islands", surrounded by a hostile landscape matrix and connected by bridges or corridors of natural vegetation. The decline or "relaxation" of diversity that accompanies fragmentation is attributed to reductions in patch area as well as the reduced immigration associated with increases in isolation (Wilcox and Murphy, 1985). Consequently, many conservationists have advocated that natural preserves should be as large as possible (Noss, 1993) although others suggest that patterns in biodiversity are more likely related to changes in habitat heterogeneity (Simberloff and Gotelli, 1984; Quinn and Harrison, 1988; McCoy and Mushinsky, 1994). Thus, many small preserves should be spread throughout the landscape, at once maximizing habitat heterogeneity and preserving biodiversity.

In addition to changes in sizes and isolation of natural areas, fragmentation has been associated with an increase in the proportion of edge to interior habitat (PEIH) (Saunders et al., 1991). Relative to forest interiors, edge habitat shows increased radiation, ambient temperature, soil fertility, wind speed, and tree mortality (Esseen, 1994) as well as decreased soil moisture and relative humidity (Kapos, 1989; Matlack, 1993a), especially in south-facing slopes. As these properties generally extend 40-50m from the edge into mature, deciduous forest (Matlack, 1994b; Fraver, 1994), the minimum area for a habitat patch containing interior habitat is approximately 1ha. However, PEIH is also influenced by patch shape, thus a corridor which is only 100m in width, regardless of its length, will consist entirely of edge habitat (Bricker and Reader, 1990).

Edge habitat may also contribute to increases in grazing pressure, invasions by exotics, predation, tree mortality, disease and parasitism (Murcia, 1995). Whereas there is some evidence that nest parasitism (Brittingham and Temple. 1983) and predation (Yahner and Scott, 1988) contribute to a decline in animal diversity in edges. the evidence is. at best, equivocal for plants. Shade tolerant plants that are ostensibly restricted to interior habitat show little (Ranney et al., 1981; Palik and Murphy, 1990) or no (Brothers and Springarn; Fraver, 1994) decline in species number in patch edges. These so-called "interior" plants are frequently found in marginal. edge habitat such as fencerows, roadside verges, and railways (Fritz and Merriam. 1993. 1995). Conversely. shade intolerant species and/or exotics are generally restricted to the edge. Although commonly asserted, there is no evidence that this increase in exotics. even those that occur in "monodominant" stands, directly contributes to the decline of native species in natural habitat (Anderson, 1995). Consequently, although conservation efforts have traditionally emphasized the importance of large and/or contiguous patches. smaller remnants can play an important role, especially in highly developed landscapes (Saunders et al.. 1987) and may actually function as refugia for threatened species (Kellman. 1997).

MANAGEMENT RESPONSES

In settled landscapes such as southwestern Ontario, a variety of management approaches have been developed in response to decreasing agricultural yields. various environmental concerns. and habitat loss. These include mitigation, conservation. and restoration (Cairns. 1993; Hobbs and Norton, 1996).

Mitigation

Management approaches which attempt to reconcile production and environmental concerns by changing technology and management practices, without fundamentally changing the way humans interact with their environments are known as mitigative. "Ecosystem management" approaches have ostensibly revolutionized forestry practices in the Pacific northwest of North America (Slocombe, 1993; Rowe, 1994; Salwasser, 1991). However, these approaches have also been criticized (Lawrence and Murphy, 1992; Czech, 1995) and have not yet been applied to the privately owned, fragmented forests of northeastern North America (Sample, 1994; Jones, 1994). However, mitigation has influenced affected agronomic practices in southwestern Ontario (Swanton and Murphy, 1996).

The agriculture industry has successfully reduced the adverse impacts of pesticides, fertilizer runoff, and soil erosion on the environment in this region (Swanton and Murphy, 1996). The use of crop rotations (Gunsolus, 1990), intercropping (Francis et al., 1987), increased planting densities (Forcella et al., 1992), focused weed control (Hall et al., 1992; Van Acker et al., 1993) and increases in the efficacy of herbicides, have all reduced the need for pesticide use (Swanton and Weise, 1991). Furthermore, the development and adoption of alternative agronomic practices such as "conservation tillage" or "no-till" which leaves crop residue on at least 30% of the soil surface (Fawcett et al., 1994; Aspinall and Kachanoski,1993), the use of cover crops (Karlen and Doran, 1991; Sullivan et al., 1991), and the construction of artificial wetlands (Brix, 1993) have helped to reduce phosphorous runoff and soil erosion. Contrary to popular belief, modern breeding programs have generated stress-tolerant cultivars that out-produce old varieties in weedy, nutrient-poor environments (Tollenaar et al., 1994). Organic produce has become commonplace in most grocery stores and Community Supported Agriculture (CSA) groups have emerged as an opportunity for urban residents to buy organic food and to participate in their food production and rural environments. Over 300,000 trees were planted in Essex county in 1995 (ERCA, 1995), the majority in windbreaks that act to reduce soil erosion (Stats Can, 1994; van Hemessen, 1994). Farmers are being encouraged to maintain fence rows that are otherwise periodically removed to increase field areas and facilitate the use of machinery (C. Jones, pers. comm). Even the presumed antagonism between wildlife conservation and agricultural production is beginning to be questioned. For example, under the auspices of the Wetlands/Woodlands/Wildlife Program, corn management plans are being developed that will provide fodder for fall duck migrations (M. Williams, pers. comm.).

Conservation

The casual use of concepts such as "nature" and "natural" in conservation belies an underlying complexity and subjectivity which has polarized "environmental philosophers" into two opposing "biocentric" (Rolston 1994) and "anthropocentric" (Caldicott, 1991; Norton, 1986) camps. The biocentric view, which permeates conservation thinking, considers human-induced changes of natural habitat as "artificial", undesirable, and devaluing (Rolston, 1991). Katz (1993), for example, defined natural as being "independent of the actions of humanity" and "existing as far as possible from human manipulation and control." Similarly, Anderson (1991) identified three indices of naturalness: (1) the degree to which systems would change if human presence was removed; (2) the amount of cultural energy required to maintain the function of the present system; and (3) the ratio of native species present in the area compared to that present prior to settlement. Historically, natural or "wilderness" areas have been seen as inviolable and have not been actively managed. If left alone, nature was seen as being self-healing. At one point, this particular characteristic was described as an inherent, emergent property of all healthy ecosystems (*sensu* Odum, 1969). Human activity, no matter how well-intentioned (e.g. restoration, bio-remediation) is viewed as inevitably compromising natural habitat regardless of its level of degradation (Katz, 1993).

Some "anthropocentric" conservation biologists, however, are beginning to acknowledge that diverse natural systems can coexist with, and in some cases are actually dependent on, human use (Vandermeer and Perfecto, 1997; Gotmark, 1991, 1992), and that these cultural and semi-cultural ecosystems extend over most of the "temperate world" (Rackham, 1991). Human-dependent ecosystems include ancient farmland which contain 68% of the 419 threatened species of vascular plants in Sweden, grazing-maintained limestone grasslands and hay meadows in Western Europe, and tall grass prairies that were spring-burned by native Americans (Gotmark, 1991). It is this approach to conservation that will have to be applied to settled landscapes such as the Carolinian, if they are to be adequately protected.

Legislation has had little impact on conservation efforts in the Canadian portion of the Carolinian Zone. Canada, outside of International Agreements such as the Great Lakes Water Quality Agreement (1972), has only recently begun to legislate environmental protection and the Liberal federal government just finished tabling Endangered Species Legislation for the third time (Anon, 1997). This is in direct contrast to the U.S. The National Environmental Policy Act, passed in 1969, required the American federal government to perform cost-benefit analyses of all federally financed activities. Furthermore, the Endangered Species Act was passed in 1973 which established government policy stating that species and their associated habitats would be protected, while the National Forest Management Act passed in 1976 set high management standards for forests managed by the U.S. Forest Service (Thomas, 1994). In particular, the latter restricted where and under what conditions timber production could take place, inserted environmental protection requirements for management and began the shift in forest management away from production priorities (Thomas, 1994).

In southwestern Ontario, conservation efforts have traditionally focused on the creation of federal, provincial, and municipal preserves and have been government agency-driven (Gartshore, 1994). However, over the last decade, non-governmental organizations, special interest groups, and private stewardship initiatives have become more important in establishing management priorities (Skibicki, 1993). Although land purchase has traditionally been a conservation priority (e.g. Nature Conservancy, 1994), the majority of extant forest in the Carolinian Zone is privately owned and alternative arrangements such as trust-agreements are playing an increased role (Hilts, 1985). The

Carolinian Canada Trust has targeted inadequately protected, high quality sites using a three tiered approach:(i) identifying and ranking natural areas, (ii) identifying vulnerable species, and (iii) developing land agreements with private landowners. This process identified 38 public and high quality sites which are still inadequately protected (Allen et al., 1990). However, changes in legislation are required to ensure the perpetuity of these private agreements (D. Bazely, pers. comm.). A promising start is the reformulated *Provincial Planning Act* which explicitly includes the protection of natural heritage and prime agricultural land in a comprehensive set of policy statements and delegates greater planning responsibility to municipalities (MMA, 1994).

Historically, most of the existing preserves in this region have been managed in isolation, both of one another and of the surrounding landscape as a whole. However, land managers are realizing that these fragmented landscapes may be more effectively managed at a higher, landscape scale of organization rather than the species or the habitat level. The World Wildlife Fund has initiated an endangered spaces program that aims at linking protected areas across Canada although it currently places little emphasis on the Carolinian (K. Kavanagh, pers. comm.). Other, explicitly multiple-use management approaches include the metacore (Stephenson, 1994) and bioreserve (Francis, 1994) models. These recognize that the management of natural areas in developed landscapes must accommodate both human and nonhuman uses. Each identifies a high-quality, minimally disturbed, core natural habitat characteristic of the region, a surrounding "buffer zone" which accommodates both human use and conservation priorities, and a bordering "intensive use zone" where conservation priorities are de-emphasized. Ideally, networks or clusters of these complexes would be functionally interconnected (Francis. 1994). This approach can theoretically accommodate activities and partners that have historically been mutually antagonistic. Current examples of this approach include the Long Point Ecosystem Complex and Port Frank Area of Notable Scientific Interest (ANSI) and it has also been proposed for managing the landscape surrounding Point Pelée National Park (Stephenson, 1994).

Restoration

It is arguable that mitigation and conservation approaches are not likely to be sufficient in maintaining or improving the quality of natural habitat in settled landscapes such as the Carolinian. A third approach which covers a wide variety of management activities is habitat restoration.

Definition and objectives

A new subdiscipline of ecology, restoration ecology, has emerged as a response to habitat loss and degradation. It is being employed globally as a way of slowing, even reversing, the degradation of natural habitat, and has even been nominated as a new paradigm for biological conservation (Turner, 1994; Jordan et al., 1994). The concept of habitat restoration is not new, however and was viewed, for example, as a management priority throughout the early 1900s in North America (Clements, 1936). Over the last half-century, when resource extraction was complete or proved unprofitable, much of the land was allowed to regenerate naturally and in many cases, actively replanted. Industry representatives have often claimed that the regeneration of these disturbed sites is successful and that the structure and function of replacement habitat such as forests approximates the pre-existing natural habitat (Cairns, 1993), although accumulating evidence suggests exactly the opposite.

Forest plantations have been heavily criticized as not being representative of natural forests. Monocultures of even-aged, economically desirable trees are planted in geometric patterns that apparently facilitate invasion by exotic species and predation, and increase windspeed, alter nutrient cycling and hydrological regimes, and despite extensive habitat cover, support substantially fewer uncommon species (von Althen, 1991; Michelsen et al., 1996). Even naturally regenerating forests are likely to require centuries to recover following exploitation (Peterken and Game, 1988) if recovery occurs at all (Duffy and Meier, 1989). Furthermore, though large areas of habitat have been protected by legislation since the turn of the century, many of these are also showing signs of degradation (Merriam, 1993). Thus, past attempts at protection and restoration have often met with limited success.

Restoration ecology can be defined as a process by which human-caused damages to the diversity and dynamics of indigenous ecosystems is repaired (SER, 1994) by introducing indigenous diversity and transforming the site to some desirable and/or pre-existing state (Cairns, 1993). This change can be achieved in four ways: (1) *mitigation*, in which the former productivity and integrity of managed systems, such as agriculture and forestry, are recovered; (2) *reclamation*, in which new, more natural habitat is generated in areas previously having other forms of landuse; (3) *rehabilitation*, in which existing, but degraded, natural habitat is regenerated; and (4) *re-creation*, in which previously existing habitat is constructed using historical site descriptions. This first type of restoration is almost entirely ignored because these management-intensive systems tend to be disregarded by conservationists. In contrast, re-creation seems to hold the greatest appeal to most restoration practitioners as indicated by restoration journals such as Restoration Ecology and Restoration and Management Notes. This is so much so the case, that re-creation is frequently used synonymously with restoration (e.g. Cains, 1993). However, the restoration of ecological communities to their pre-degradation conditions might be impractical if, for example, information about their original states is inadequate, availability of the desirable species is restricted, factors contributing to degradation (e.g. acid precipitation, ground-level ozone) are outside the ecosystems and thus beyond control, or the ecosystems under study are largely unknown (Cairns, 1988).

Presently, much effort and resources are being expended on restoration activities world wide (Jordan, 1994). While the relative success is often assessed and reported, much is conducted on an *adhoc* basis, without adequate appraisal. Perhaps this reflects the belief that restoration is a defensible end in itself (Higgs, 1992). As such, habitat restoration can be seen as "self-aggrandized nature gardening", and has been criticized as "an expensive self-indulgence for the upper-classes, a New-Age substitute for psychiatry...(that) distracts intelligent and persuasive people from systemic initiatives" (Kirby, 1994).

In fact, it is possible that much ill-conceived and poorly conducted restoration activity is further degrading sites which will have to be "unrestored" in the future. One example is the planting of the now pervasive black locust (*Robinia pseudo-acacia*) at Point Pelée National Park (Reive et al., 1992). Possible results of restoration failures include: an exacerbation of disturbance, replacement of native by exotic species, detraction from a natural tendency toward regeneration, and failure and/or unnecessarily high maintenance costs (Bradshaw, 1991)

The requisite first step in habitat restoration, then, is to establish clearly defined and justifiable objectives which are tractable and attainable. Throughout the 1980s, a number of general and qualitative guidelines were used to guide projects, these included an increase of existing habitat values, maintenance of biological productivity and species diversity, and the protection and enhancement of threatened and endangered species (Berger, 1990). Another more "science-derived" approach results in properly designed, quantitative, and clearly defined studies, which some critics would claim are reductionistic and narrowly conceived. These differences in approach reflect an ongoing debate between "restoration ecologists" (the science) (e.g. Bradshaw, 1993) and "ecological restorationists" (the more qualitative, experience-based process) (e.g. Higgs, 1994). In both cases, adequate expertise tends to be "culturally defined" and is often unavailable. However, more accessible "evaluator" or "indicator" attributes (e.g. species) can be used by both approaches to focus subsequent planning and progress evaluation (McDonald, 1988).

Following a "top-down" process, once overall site restoration goals and then individual habitat restoration goals are defined, the appropriate "indicator species", the range of biological characteristics necessary for their success (e.g. vegetation cover and composition, territory size etc.), and the range of their associated abiotic environmental parameters (e.g. topography, nutrient and moisture status, aspect etc.) can be defined. Characteristics or "vital attributes" of natural systems which have been used in measuring ecosystem "health" and decline (Costanza et al.1992, Costanza, 1992) and which may be used meaningfully in restoration are: vegetation cover, species composition, species origin (i.e. native vs. exotic), structure (vertical arrangement), pattern (horizontal arrangement), habitat heterogeneity, ecological function (hydrology, nutrient cycling), scale (e.g. site-level vs. landscape-level processes), and successional-stage (Aronson et al., 1993; Hobbs and Norton, 1996). Although these attributes, individually or in combinations, can be easily manipulated, the challenge lies in assessing whether the change that inevitably accompanies restoration is, indeed, desirable. The success of restoration is generally assessed by comparing the restored habitat with relatively undisturbed comparison or "reference" sites (Aronson et al., 1995). Picket and Parker (1994), however, question whether the use of undisturbed sites as defining a desirable end state is useful or meaningful especially if this means perpetuating the restored systems in stasis.

There is still relatively little information available about the restoration of agricultural regions and most data are from the reclamation of mined areas (Hobbs, 1993). Similarly, most restoration efforts are site-based and little landscape-based information is available (Naveh, 1994). However, benefits arising from revegetation in agricultural landscapes could include: the development of buffer zones around existing habitat, which can reduce the impact of abiotic characteristics associated with edge habitat, the construction of corridors that connect existing patches, which theoretically can facilitate mobility across the landscape, and the development of additional, contiguous habitat which could extend the area of vegetation available to wildlife (Hobbs, 1993).

Ideally, restoration ecology is a meeting ground between theoretical and applied interests and has been described as "the litmus test of ecology" (Bradshaw, 1993). Most restoration activity is end-oriented and involves the one-time introduction of many species. However, restoration activity is most successful when it incorporates and facilitates natural mechanisms and is process-based. One approach is to identify and maximize underlying assembly rules (Lockwood, 1997). However, these are generally simulation-derived, difficult to apply to complex systems, and labor-intensive (Pritchet, 1997). Another important approach is to use mechanisms that underlie vegetational change over time (i.e. succession) (Luken, 1990) and space (i.e. landscape ecology).

The theoretical framework

Succession theory and restoration

The majority of restoration activity involves an attempt to change vegetation over time and is, thus, succession-based. However, succession theory itself, has a controversial past.

The first comprehensive theory of vegetation dynamics or succession was formulated by Clements in the early 1900s (Clements, 1916). Succession was described as a highly predictable process in which the plant community followed a predetermined or teleological, organism-like path from simple to climax community (Clements, 1936).

The steps that this process followed were: *nudation* (the break in vegetation cover by disturbance); *migration* (the dispersal of propagules); *ecesis* (the establishment of plants); *competition* (the interaction between plants); *reaction* (the modification of the site by established species to allow the introduction of new species); and *climax* (the creation of a climate-determined, stable end state) (Clements, 1916; Miles, 1979).

Thus defined, succession was "autogenic", directional, convergent, predictable, and stable in its final, climate-determined "climax" state (Clements, 1916). Old-field succession, for example, followed a regular series of stages or "seres". Immediately after cultivation, bare soil was colonized by annual crab grass (*Syntherisma sanguinale*), which, in turn, was replaced by tall broadleaf weeds (e.g. *Solidago* spp., *Aster* spp.), then *Andropogon* spp. and finally by *Pinus* spp. (Crafton and Wells, 1934).

This holistic, organismic view of succession dominated plant ecology until the late 1960s (e.g. Margalef, 1968; Odum, 1969) when it was replaced by an "allogenic" individualistic, non-deterministic view of succession (e.g. Glenn-Lewis and van der Maarel, 1992; Myster and Pickett, 1988). This alternate view was initially developed by Gleason (1936) in response to the perceived excesses of Clementsian succession. In Gleason's view, succession was a population-level phenomenon, characterized by multiple pathways of development, and was a fundamentally stochastic process (Pickett et al., 1987a). Climax systems were interpreted as partially stabilized systems adapted to the environment as a whole and situated along a continuous environmental gradient while community composition changed continuously (Whitaker, 1953). Indeed, plant ecologists increasingly question whether communities or ecosystems are functionally important at all (the continuum concept *cf.* Austin, 1985).

However, these latter approaches continued to emphasize that vegetational change was disturbance-initiated and mediated by both abiotic factors and competition. Although the concepts of determinism, climax community, and organismic views of nature are rejected by most academic plant ecologists, the Clementsian view continued to influence much research on succession into the 1980s (MacMahon, 1980) and is still presented in many undergraduate texts.

The Clementsian model was one of three models presented by Connell and Slatyer (1977) when describing the net effect of established plants on subsequent colonizing plants. As such, this *facilitation* model proposes that established species create the conditions for their eventual displacement by newly colonizing species (i.e. reaction *sensu* Clements). This situation is now regarded as being relatively rare, and most likely to occur during primary succession and in extreme environments. Examples include the action of nurse plants in deserts, the thinning of dense early successional vegetation by shrubs, and the creation of favorable microsites in litter (e.g. Yarrongton and Morrison, 1974). Facilitation has been used to accelerate successional change by using bird perches to increase seed dispersal by birds (McClanahan and Wolfe, 1993) as well as by the restoration of previous soil fertility and hydrology (Marrs and Gough, 1989).

The second, *inhibition* model (cf. Connell and Slatyer, 1977) is the most ubiquitous of the three models, and suggests that established species such as dense herbaceous vegetation and shrubs prevent the colonization of later occurring species

(Niering and Egler, 1955; Olson, 1958). It occurs under most closed canopies and results in reduced growth and seed germination (Peart, 1989). Plants are released from this inhibition in a number of ways: gap phase regeneration whereby randomly occurring treefalls temporarily provide resource-rich environments that release either established seedlings or propagules (Platt and Strong, 1989); the regeneration niche in which the resource availability during seedling phase of establishment dictates species composition (Grubb, 1979); and, finally transient populations of plant species that move through a forest without establishing stable populations (Hubbell and Foster, 1985). However, inhibition will only produce directional change if subsequent colonizing species have late successional characteristics. Inhibition is employed, in agriculture, through the use of cover crops and green mulches (Swanton and Weise, 1991) and, in the management of utility corridors, through the planting of shrubs (Niering, 1987).

The third, *tolerance*, model has two forms: *passive* and *active tolerance*. Passive tolerance proposes that succession is determined by initial conditions (initial floristics *cf.* Egler 1954). Uncommon species are largely unaffected by the dominant species and are eventually released by chance-mediated events (e.g. tree fall, disease, herbivory etc.) (Picket et al., 1987b). Late successional woody species often colonize old fields within the first 2-3 years (Houssard et al., 1980; Myster, 1993) and regeneration often occurs in safe sites under shrubs and logs (Morgan, 1991). Similarly, vegetational change can be dictated by initial field conditions (e.g. tillage, sterilization), management (mowing, mulching), and time of crop abandonment (Myster and Pickett, 1991) as well as the opportunistic colonization of species regardless of their successional status (Drury and

Nisbet, 1973). In contrast, *active tolerance* proposes that vegetational change is individualistic in nature (*sensu* Gleason), largely dictated by competition and underlying differences in stature, physiology, lifehistory, longevity, and/or resource availability (Bazzaz 1979; Peet and Christenson, 1980; Tilman, 1985). Examples of applications of the active tolerance models include the planting of late successional trees in afforestation (von Althen, 1991), as well as using differences in crop architecture, ecophysiology, and competitiveness in agriculture (Swanton and Weise, 1991; Swanton and Murphy, 1996).

Three mechanisms underlie the changes described by these succession models: differential site availability, species availability, and species performance (Pickett et al., 1987b). Site availability is largely determined by disturbance, which can be defined as any activity resulting in the destruction of plant biomass (*cf.* Grime, 1979). In turn, species availability is affected by the presence of the standing propagule pool and differential seed dispersal. In primary succession, by definition, there is no remnant seedbank and colonization is entirely dependent on immigration (Miles, 1979), whereas in secondary succession propagules can exist as seeds, rhizomes, stumps, and even seedlings. Seed dispersal distances range from long-distance wind (anemochores) and vertebrate (endo/epizoochores) dispersers to those of short distance ant (myrmecechores), gravity (autochores) and explosion (barochores) dispersers (van der Pilj, 1982). Generally-speaking, early and mid successional habitat is dominated by long distance dispersers, whereas late successional habitat is dominated by short-distance dispersers (Willson, 1993). Finally, species performance is influenced by ecophysiology (e.g. germination and growth rates (Grime, 1979; Bazazz, 1979); life history (e.g. reproductive allocation, phenology (e.g. ephemeral, summer, fall flowering), reproductive mode (e.g. annual, biennial, perennial), vital attributes (Noble and Slatyer, 1980), environmental stress, competition (Tilman, 1985; Tilman and Wedin, 1991), as well as allelopathy, herbivory, predation, and disease (Pickett et al., 1987a,b).

Succession-based management can be achieved through the adoption of the models described in Connell and Slatyer (1977) and the mechanisms described by Pickett et al. (1987b) as well as by manipulating the frequency and intensity of *disturbance* (Niering, 1987). Disturbance (e.g. grazing, recreation) can be reduced if late-successional communities are desired and increased if early successional communities (retrogression) are desired (Luken, 1990). Management models derived from ecological succession theory have been developed for use in range, agroecosystem, and protected area management (Niering, 1987; Rosenberg and Freedman, 1984; Luken, 1990; LaJeunesse et al., 1995) but have yet to be applied in habitat restoration.

Most restoration activity is end-oriented and involves the one-time introduction of many species and, thus, reflects an "allogenic" successional approach. If species composition is manipulated, it is through disturbance (e.g. fire) when "early successional" ecosystems are desired. In contrast, process-based approaches are relatively rare but much more interesting. An autogenic succession approach assumes that suites of organisms exist in relatively stable states through time and can affect groups of species that precede and follow them. These suites of organisms can be manipulated by restorationists to achieve different project-defined ends. For example, the establishment of an intermediate "mid-successional" suite of organisms may not be of immediate interest but may accelerate further vegetational change. Another example is the planting of grasses which will increase the burn-temperatures in prairie restoration resulting in declines in exotic species and proportional increases in the desired guilds of native forbs (Pritchett, 1997). In as much as this procedure is facilitative and involves a desired, largely management-determined but process-based end state, it is remarkably similar to Clements' initial formulation of succession.

Landscape ecology and restoration

When research is conducted at the site-level, the implication is that the landscape consists only of the site-level habitat. However, recent studies suggest that site-level species composition is heavily influenced by external factors (Schaeffer, 1996). Some of these landscape factors include: migration (Merriam, 1993), seed dispersal (Dzwonko, 1993), and, perhaps most importantly, surrounding land use (Matlack, 1993; Robinson et al., 1994). Fragmentation has been identified as a great threat to natural habitat and biodiversity (Wilcox and Murphy, 1985) and, thus, the connectivity of these patches become central issues in fragmented ecosystems and for isolated protected areas such as Point Pelée National Park. From a management perspective, these fragments should be spatially integrated within larger ecosystem preserves if long term habitat preservation is to be achieved (Saunders et al., 1991). As such, landscape ecology is beginning to provide the theoretical foundation for managing these fragmented landscapes.

The primary focus of landscape ecology is the study of spatially heterogeneous areas or landscapes. Most studies examine the impact of the size, shape, number, kind and configuration of the landscape elements on the distribution of species, energy and materials and how these change over time and are affected by disturbance (Risser, 1987). Different temporal and spatial scales are used and underlying ecological processes vary in importance and effect as scale changes (Risser et al., 1984). Landscapes can be divided into five types on a gradient of human-use. In increasing intensity this landscape modification gradient is: natural, managed, cultivated, suburban, and urban (Forman and Godron, 1986).

Studies of the effects of fragmentation on biodiversity have largely depended on "island biogeography" theory, which was initially used to explain diversity patterns on offshore islands (MacArthur and Wilson, 1967). This theory suggests that the number of species on the island represented a dynamic equilibrium (S) as local species extinctions are balanced by immigration by new species. S tends to increase as island size grows and as the distance between islands decreases. While, for island systems, the predictive value of this theory for islands is equivocal, for terrestrial systems, it is tenuous at best (Gilbert, 1980; Williamson, 1989). The use of this "oceanic island" analogy in conservation biology requires that the surrounding landscape matrix be viewed as isolated from and antagonistic to the islands of natural habitat. Furthermore, the research remains focused on the natural habitat. More recently, metapopulation theory has been increasingly developed and applied to fragmented landscapes (Verboom, 1993; Opdam, 1991). Populations in these remnant, largely self-contained, patches, are perceived as being functional parts of a larger metapopulation (Hanski and Gilpin, 1991). Local population extinction is commonplace and the probability of extinction increases as populations decline with patch size (Hanski and Gilpin, 1991). However, the migration necessary to replenish these populations, either from neighbouring small patches or much larger "source" patches, continues to be adversely affected by isolation (Opdam et al., 1993). As with island biogeography, connectivity between these patches remains of paramount importance and the surrounding landscape matrix is still perceived as hostile (Hansson, 1991). Thus, movement between patches is assumed to be largely restricted to corridors of natural vegetation cover that join the remnant habitat (Burel and Baudry, 1990).

In fragmented agricultural-urban landscapes, a prime management objective has been to increase the connectivity between isolated remnant patches of natural habitat (Riley and Mohr, 1994; Lindenmayer and Nix, 1993). Increased connectivity is assumed to occur through corridors of natural habitat, which act to facilitate dispersal across the landscape (e.g. Dmowski and Kozakiewicz, 1990; LaPolla and Barrett, 1993; Riley and Mohr, 1994). These landscape ecological networks, whether they be roadside verges, waterways or riparian habitat, have become an essential component of landscape planning (Thorne, 1993; Zonneveld, 1990; Noss, 1993). The corridors can, in of themselves, increase vegetation cover, increase foraging area, function as refuges from disturbance, and increase aesthetic appeal of the region (Forman and Godron, 1986). In agricultural landscapes, corridors frequently provide the only vegetative cover especially in the winter and spring (Burel, 1992) and can reduce soil erosion and nutrient runoff (Forman and Baudry, 1984). The problem with this type of corridor-dependent research, which dominates landscape-level studies, is that corridors are equated with connectivity and thus assumed to be desirable.

In large part, their perceived benefit stems largely from the assumption that there is little or no migration within the landscape matrix. However, I have yet to encounter any study showing that organisms *preferentially* use corridors over the surrounding matrix (Simberloff et al., 1992). Most of the literature ignores the likelihood of and fails to measure intra-matrix migration (e.g. MacClintock et al., 1977; Demeyers, 1993; Dmowski and Kozakiewicz, 1990; LaPolla and Barrett, 1993). However, preliminary research suggests that many species make extensive use of this matrix (Webb, 1989; Weddell, 1991; Klein, 1989; Merriam and Lanoue, 1990; Szacki and Liro, 1991; Jarvinen, 1982). In addition, corridors have been associated with increased disease and have functioned as sinks of predation (Simberloff et al., 1992) and routes for exotic species dispersal (Brothers and Springarn, 1992).

Another major limitation of landscape ecology is that it tends to reflect technology-driven research priorities and remain short both on ground data and tests of predictions arising from theory (e.g. Jensen et al., 1992; Remillard and Welch, 1992a,b). Similarly, land cover classification of satellite imagery is often conducted without training sites (i.e. unsupervised training), involves little ground truthing, and frequently fails to analyze the degree of erroneous classification (Thapa, 1992). Finally, many of the assumptions regarding habitat use by organisms are taken from the literature (e.g. Herr and Queen, 1993, Scott et al., 1993, Wallin et al., 1993) and almost certainly cannot be generalized among regions, much less among taxa. Consequently, studies that combine substantial ground data as well as the study of the spatial relationships of patches at the landscape-level of organization are in short supply. Such research is even rarer in restoration ecology (Naveh, 1994).

Restoration projects in the Carolinian

Habitat restoration is becoming increasingly important in regions such as the Carolinian Zone. Historically, restoration activity has focused on species-level reintroductions. Projects initiated in the Carolinian include: the Southern Flying Squirrel at Point Pelée (I. Adams, pers. comm.), the Bald Eagle at Long Point Ecosystem Complex (McKeane and Weseloh, 1992), and Wild Turkeys in Simcoe (Reid, 1990) as well as research on a number of species including the Karner Blue Butterfly (Packer, 1990) and the Cucumber Tree (*Magnolia acuminata*) (Ambrose and Kevan, 1990). Habitat-level rehabilitation has been conducted on forests, savannas, tall grass prairie ecosystems at Pinery Provincial Park (D. Bazely, pers. comm.), Long Point Ecosystem Complex (M. Gartshore, pers. comm.) and Point Pelée National Park (N. Falkenberg, pers. comm.; Sharp, 1992, 1993; Reive et al., 1992) and on area alvars and wetlands (A. Woodliffe, pers. comm.). Forest restoration has been almost entirely limited to Ontario Ministry of Natural Resources- subsidized afforestation efforts. However, this activity has shifted from the establishment of coniferous plantations to Tree Plan Canada-sponsored projects that use locally grown combinations of fast-growing native deciduous species such as green ash (*Fraxinus pennsylvanica*), red oak (*Quercus rubra*), and silver maple (*Acer saccharinum*) (van Hemessen, 1994; NHRP, 1994).

THE PRESENT STUDY

One major gap in both Carolinian restoration efforts and restoration as a whole is that few are approached from a landscape level, asking whether these newly created habitats are situated properly, in terms of a larger-scale perspective. Additionally, monitoring and evaluation of the success of this activity is generally limited. The overall objective of this study was to determine ways in which forest in and around Point Pelée National Park can be effectively restored. This was further divided into the following objectives:

(1) To determine the extent of fragmentation of natural habitat in the landscape surrounding Point Pelée National Park (PPNP) in order to test the potential for restoration efforts being coordinated at the landscape level.

Specific questions asked were:

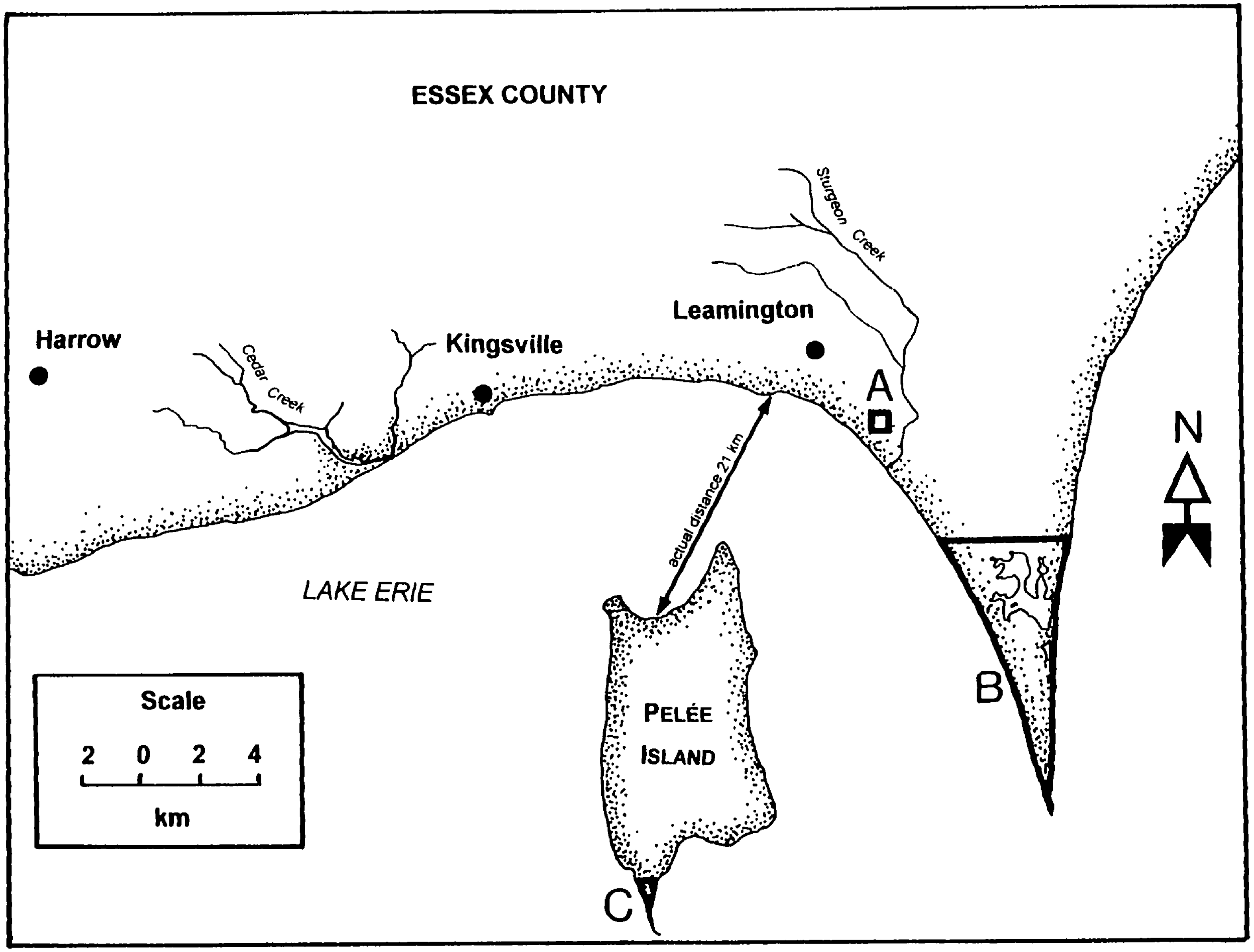
(i) How isolated is PPNP and how fragmented is the surrounding landscape?

(ii) What potential does PPNP have as a potential core area for landscape-based bioreserve management models?

The associated hypothesis examined was that PPNP, being a highly valued Carolinian preserve, would have a high degree of connectivity with the surrounding fragments of natural habitat.

This research was covered by a GIS study of Essex county (Figure 1.2), presented in Chapter 2.

Figure 1.2. Map of southwestern Ontario showing portion of Essex county, towns, and study areas in Sturgeon Creek (A), Point Pelée National Park (B), and, on Pelée Island, FishPoint Nature Preserve (C).


ESSEX COUNTY
Harrow
Cedar Creek
Kingsville
Leamington
Sturgeon Creek
A
B
C
N
LAKE ERIE
actual distance 21 km
PELÉE ISLAND
Scale
2 0 2 4
km

(2) To determine the success of ongoing restoration efforts conducted within PPNP over the last 35 years.

Specific questions asked were:

(i) How successful have restoration efforts aimed at promoting forest succession been on restoring native understorey plant communities?

(ii) What factors best indicate site recovery?

(iii) What effect has disturbance-associated invasions by non-native species had on native understorey plant communities?

The associated hypothesis examined was that a management approach which accelerated succession was an effective means of increasing the diversity of native plant species in restored sites.

This research was covered by a three year study of restored sites in PPNP and relatively undisturbed reference sites in PPNP and FishPoint Nature Preserve (Figure 1.2), presented in a series of papers in Chapters 3-6.

(3) (a) To determine methods of managing afforestation efforts aimed at increasing natural habitat cover and landscape connectivity in the region.

(b) To determine methods of maximizing tree growth and therefore of encouraging tree canopy closure.

Specific questions asked were:

(i) How can fertilization, weed control, and shelter crops be combined to maximize growth of three native tree species?

(ii) Can agricultural and conservation concerns be reconciled in afforestation efforts in a settled landscape?

The associated hypothesis examined was that native tree species in post-agricultural land will achieve maximum growth when competition is reduced.

This research was covered by a three year study of a tree plantation located adjacent to Sturgeon Creek (Figure 1.2), presented in Chapter 7.

CHAPTER 2

The Use Of Satellite Imagery And GIS to Describe the Landscape Surrounding Point Pelée National Park and to Guide Future Restoration Activity

STEPHANE M. McLACHLAN, CHERYL M. PEARCE, and DAWN R. BAZELY

Note: initial classification and GIS analysis was conducted by C.M. Pearce and is derived from Pearce (1996). In addition, guided by questions posed by S.M. McLachlan. C.M. Pearce conducted further analysis which is referenced as: Pearce (pers.comm.).

INTRODUCTION

Although only representing 0.25% of Canada's landmass, the Carolinian region supports 25% of this country's human population. In addition this region is the most intensely farmed area in Ontario. This combination of intense agricultural use and urban expansion has reduced forest cover to less than 10% (Riley and Mohr, 1994), while in Essex county, forest cover has dropped below 3%. Natural habitat continues to be cleared for urban expansion, increased field sizes, and field drainage and, in many cases, even fence-rows are being removed. At the same time, however, many areas are being removed from production and planted with trees.

In the Carolinian, afforestation has been conducted since the turn of the century, mostly as non-native conifer plantations, for economic gain and the control of soil erosion. However, most recent plantations are of combinations of native deciduous trees such as green ash (*Fraxinus pennsylvanica*), red oak (*Quercus rubra*), and silver maple (*Acer saccharinum*) grown from local seed sources (Crofts, 1994; NHRP, 1994).

Beginning in the early 1970s, this tree planting was conducted under the auspices of the provincially managed Woodlands Improvement Act (WIA), and tree-stock, planting, and subsequent management costs were almost entirely subsidized. Since 1990, afforestation has been largely run by the Essex Regional Conservation Authority using a fair-market pricing approach. Over three million trees have been planted in the Carolinian over the last decade (van Hemessen, 1994). In 1995, over 305,000 trees were planted on 428 sites in Essex county alone and afforestation accounted for 4.6% of Essex Regional Conservation Authority's annual expenditure (ERCA, 1995). Most of these trees were planted in windbreaks aimed at reducing soil erosion and nutrient runoff, although some were in plantations (van Hemessen, 1994).

These afforestation efforts represent, by far, the majority of the natural habitat restoration activity in the Carolinian. Although theory from the discipline of landscape ecology has strongly influenced how highly fragmented landscapes are managed, recent studies suggest that it has little effect on efforts to coordinate restoration activity (Naveh, 1994), even in settled landscapes such as the Carolinian. In fact, the landscape of Essex county was not classified using satellite imagery until 1996 (the present study). However, many management models that are being prescribed for highly fragmented landscapes incorporate multiple-use, multiple-partner and multiple-scale approaches and may be appropriate for guiding restoration activity in the Carolinian. For example, both the metacore (Stephenson, 1994) and bioreserve (Francis, 1994) models recognize that the management of natural areas in developed landscapes should accommodate both human and non-human uses. Each identifies a high-quality, minimally disturbed, core natural habitat which is characteristic of the region, a surrounding "buffer zone" which accommodates both human use and conservation priorities, and a bordering "intensive use zone" in which conservation priorities are de-emphasised.

While the main focus of this thesis is on site-level restoration, an additional goal was to place this activity in a regional context, in order to evaluate its effectiveness from a landscape perspective. We accomplished this by identifying three main areas in Essex county, each of which might function as a possible "core" habitat. The relationship between each of these core areas and the surrounding landscape was then assessed using GIS. The overall objective of this study was to assess the usefulness of satellite imagery for identifying high and low quality sites for protection and restoration in the Essex county region, as described in a Memorandum of Understanding (MOU) between Dr. Cheryl Pearce, Stephane McLachlan, and Parks Canada. My role (SM) in this part of the project was to help develop a vegetation classification scheme for the area and to identify and describe training sites for each class. Individually, my goal was to:

(1) compare the three main areas (Pelée-north, Cedar Creek, Pelée Island) from a landscape and restoration perspective;

(2) describe how they might function as cores in the bioreserve model;

(3) describe and contrast past restoration activity (i.e. Woodland Improvement Act plantings in each of the three principal areas) in each of the three main areas at the local and landscape level of organization; and

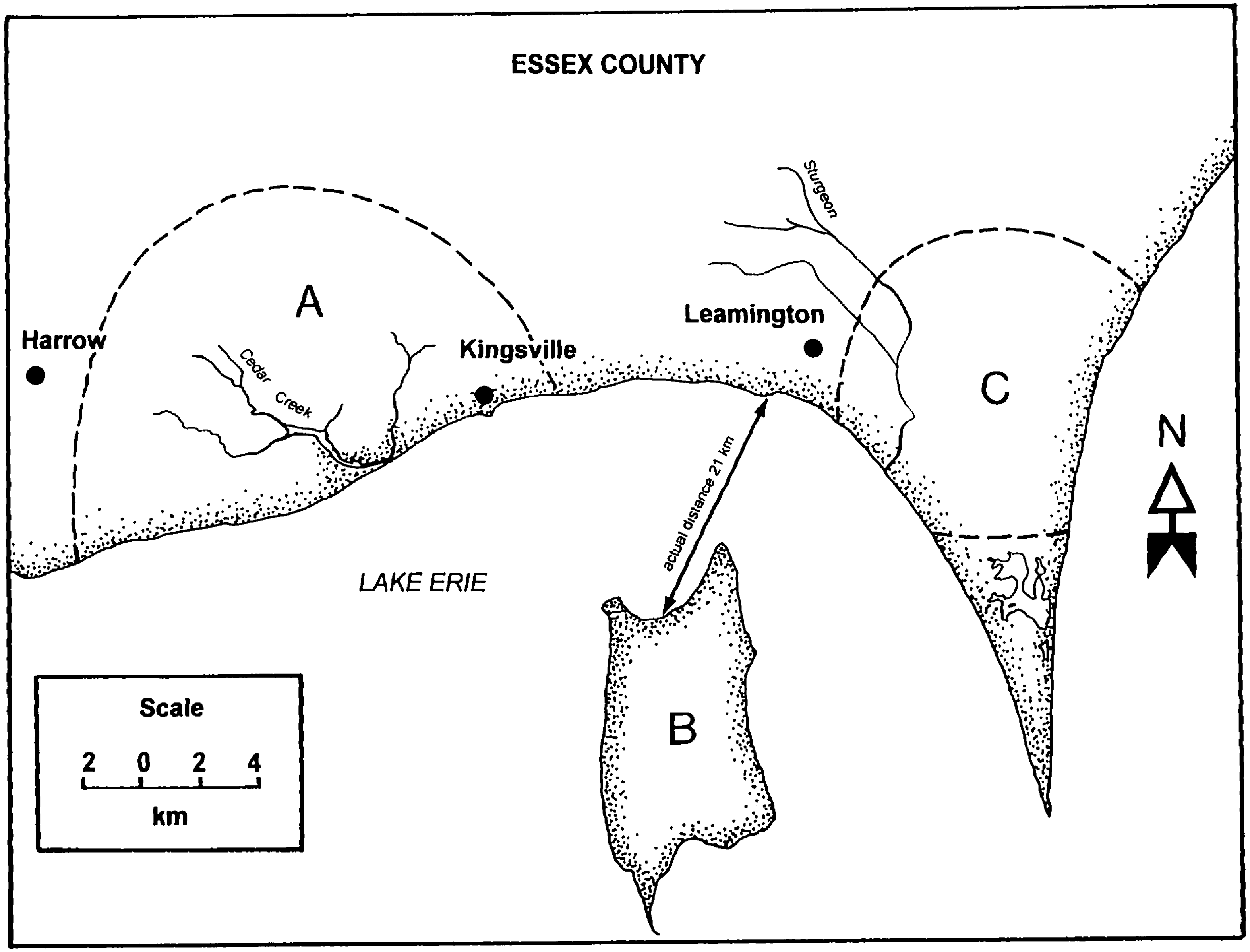
(4) use these data to begin developing landscape-informed restoration strategies.

Because of time constraints and inadequate technical support, here at York University, the analyses and satellite images used in this chapter are derived from Pearce (1996) and C. Pearce (pers. comm.).

Sites selected as potential "core" habitats were: Point Pelée National Park (PPNP), which is one of the premier protected Carolinian habitats in the region and is managed by Parks Canada; Cedar Creek (CC), which is an archipelago of natural habitats, owned and managed by ERCA, and FishPoint Nature Preserve (FFNP), which is a minimally disturbed protected area situated on the neighbouring Pelée Island and is managed by Ontario Ministry of Natural Resources (OMNR) (Stephenson, 1994) (Figure 2.1).

PPNP is a sandspit that extends southward in Lake Erie, of which the upland forest component is 1,100 ha in size, and contains at least 70 vascular plant species that are designated as rare in Ontario or Canada (Allen et al., 1990). Approximately one-third of the area consists of upland deciduous and mixed forest. The tree canopy is dominated by hackberry (*Celtis occidentalis*), white pine (*Pinus strobus*), white ash (F*raxinus americana*), and black walnut (*Juglans nigra*). Point Pelée was designated as a national park in 1918 but, over the next 50 years, was extensively used for agriculture, orchards, recreation, and human habitation. In 1963, the park began purchasing and demolishing cottages and removing roads in order to restore the natural habitat. Although many of these sites show signs of recovery, over 70% of the upland habitat of the park has been disturbed (Reive et al., 1992).

Figure 2.1. Map of Essex county, Ontario, indicating each of proposed bioreserves (Cedar Creek (A), Pelée Island (B), and Pelée-north (C)) and corresponding core areas (FishPoint Nature Preserve, Cedar Creek, and Point Pelée National Park).


ESSEX COUNTY
A
Harrow
Cedar Creek
Kingsville
Leamington
Sturgeon
C
N
actual distance 21 km
LAKE ERIE
B
Scale
2 0 2 4
km

Cedar Creek is also composed of both forest and wetland. It is quite large (715 ha) and extensively developed where it opens onto Lake Erie. However, approximately 1 km upstream, it is largely undisturbed and consists of mature Carolinian species such as swamp white oak (*Quercus bicolor*), black oak (*Quercus velutina*), shagbark hickory (*Carya ovata*), and sassafras (*Sassafras albidum*). It contains over 100 tree and shrub species, 148 rare vascular plants (79 and 74 that are designated as rare in Canada and Ontario, respectively) and contains one of the two nesting pairs of Bald Eagles in Essex county (Oldham, 1983).

FishPoint Nature Preserve is a sandspit that extends southward into Lake Erie from Pelée Island and the upland forest component is 400 ha in size. The southern two thirds of FPNP are "essentially undisturbed" although the northern portion has been selectively logged and was intermittently grazed by cattle until 1972. It is the largest forested area remaining on Pelée Island and is dominated by black maple (*Acer nigrum*), white ash (*Fraxinus americana*), hackberry (*Celtis occidentalis*) and silver maple (*Acer saccharinum*). Over 115 rare vascular plants have been recorded (77 and 63 are designated rare in Canada and Ontario, respectively).

The landscape-matrix surrounding all three potential core areas is highly fragmented by agricultural use and human habitation. However, the type of agriculture differs for each: around PPNP (Pelée-north) there are cashcrops (i.e. corn, soybean, winter wheat) and vegetables; around Cedar Creek, there is mixed farming (cash crops, perennial crops (e.g. clover), and livestock); and around FPNP (Pelée Island), there are both cashcrops and vineyards.

METHODOLOGY

Classification

The Landsat Thematic Mapper (TM) data were taken for May 24, 1994 and covered a region extending from Pelée Island to Rondeau Park and from Pelée Island to Lake St. Clair. Thematic mapper bands TM3 (red), TM4 (near-infrared), and TM5 (mid-infrared) were selected because they are of greatest use in measuring bare soil and vegetation cover. The data were corrected to 1:50,000 topographic maps using the cubic convolution resampling process (Pearce, 1996). An unsupervised classification, in which clustering algorithms objectively divide the data into spectral classes, was conducted using the EASI/PACE migrating means clustering process and a site-dependent request for 15-25 classes which were then merged into 10-15 classes by merging similar cover types (Pearce, 1996). For areas extending from PPNP to Rondeau Park and from PPNP to Harrow, supervised classification, in which the software is "trained" by known cover types, was conducted using sites that had been confirmed by ground truthing and with aerial photos and then assigned spectral values with the EASI/PACE maximum likelihood classifier (Pearce, 1996). Normally, because of the large area described in the Memorandum of Understanding (5400km^2), an unsupervised classification would normally have been used to classify the vegetation types. However, because of our particular emphasis on forest restoration, and perhaps more importantly, because of the difficulties in differentiating forest cover from green crops, a combined supervised

/unsupervised classification protocol was ultimately used to identify vegetation cover types of interest.

It is generally easiest to distinguish crops from trees in early spring. This is typically after tree canopy and winter crops have expanded but before the full expansion of the summer crop canopy. However, in 1994, a cold, wet spring delayed crop development and thus the spectral qualities of winter wheat cover were very similar to those of trees. Classification was further complicated by the cloud cover that typically forms in lake-edge regions such as our study sites; for example, three out of 16 satellite passes in 1993 and 1994 had higher-than-acceptable cloud cover. Additionally, part of the problem was that the Landsat provides 25 m x 25 m resolution which was probably too coarse to provide enough detail for results which might guide forest restoration efforts. However, many of the various vegetation types present in the region were eventually differentiated successfully using enhancement techniques (e.g. "histogram equalization enhancement" in which the cover types that occupy the greatest area are enhanced to a proportionately greater degree) (Pearce, 1996).

In both 1994 and 1995, sites that conformed to these vegetation classes were identified by "ground truthing" (ground-level confirmation of cover types) and were located on the preliminary unsupervised classed maps (see Appendix 1 for examples). This ground truthing was supplemented by information taken from aerial photo series owned by Essex Regional Conservation Authority and was completed in January, 1996. The results of this classification and preliminary analyses were included in the final report prepared for Parks Canada (Pearce, 1996). Since then, Dr. Pearce has further analyzed each of the three main areas that were of interest in my study (C. Pearce, pers. comm.).

We identified 21 vegetation types and 12 natural vegetation types. The latter represented plant communities of different successional age which were assumed to generate information of possible relevance for forest restoration (Table 2.1). However, once classification was completed, only 16 of the vegetation types and 11 of the natural vegetation types were deemed to be of practical use (Table 2.1) (Pearce, 1996). Even so, the resultant classification scheme still provided much more information of native vegetation cover than most studies which often only distinguish forest (deciduous, coniferous, and mixed) from non-forest cover (e.g. Ontario Hydro, OMNR classification schemes) (C. Pearce, pers. comm.).

No formal error analysis was conducted on the completed classification. This, in large part, was due to the lack of additional suitable sites available for each vegetation class, since most suitable sites had already been used as training data. This problem was aggravated by our difficulties in separating forest from green crops, which required a larger than anticipated number of sites for ground training. Furthermore, a lack of available funding prohibited further ground work, especially in the area extending from PPNP to Rondeau Park also hampered the identification of other sites. However, the relative spectral homogeneity of the sites revealed how consistently each vegetation class had been classified. Using this approach, Pearce (1996) suggested that water, bare soil, grassland, cropland, and roads were readily detectable while shrub, orchards, deciduous and coniferous plantations, shrubby and grassy pastures were not.

Table 2.1. Ideal and functional vegetation cover classes used for Essex county, Ontario (derived from Pearce, 1996)

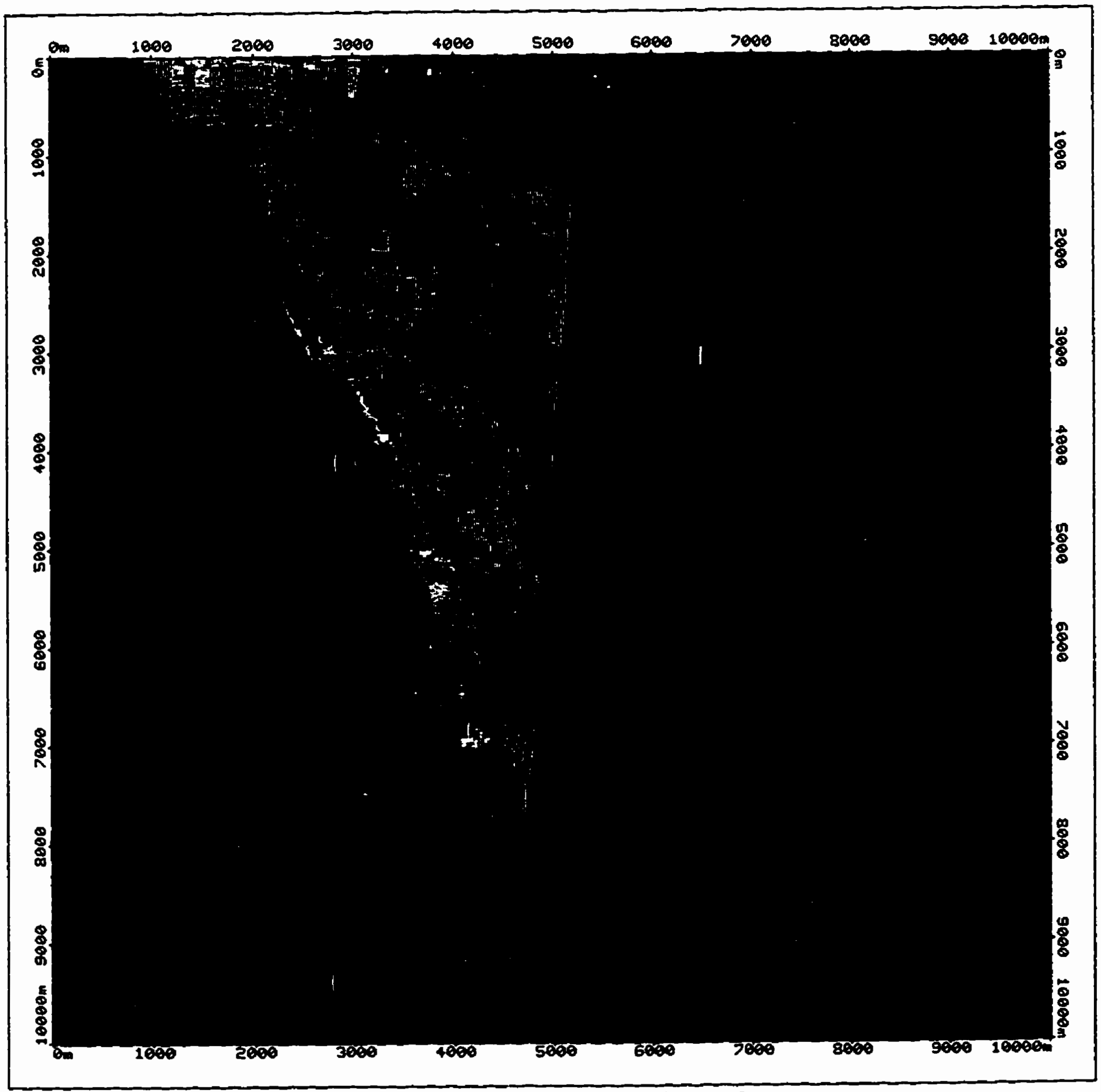
Vegetation cover classes	
Ideal	Realistic
1) *Forest*	
deciduous forest - upland	deciduous - upland
- wet	- wet
coniferous forest - upland	none
- wet	
degraded forest - grazed	
- early successional (forest + shrub)	
plantation - deciduous	
- coniferous	
2) *Shrubland*	
old field (hawthorne + grass)	old field (with shrubs or trees)
	savannah (PPNP)
scrub (shrub + trees)	shrubs (Pelee Island)
	willow (PPNP)
3) *Grassland*	
pasture	pasture
old-field (goldenrod)	pasture
4) *Agriculture*	
corn	
soybean	
wheat (winter)	green crops
hay	green hay
sunflower	
orchards	some orchards
vineyard	
lawn/golfcourse	pasture
5) *Hedgerows*	some hedge rows
6) *Bare soil*	bare soil

The success of classification also varied for each principal area. Pelée Island was most easily classified, in large part because there was more natural habitat and the island is relatively small. Cedar Creek was more difficult to classify but showed great enough forest cover that classification was relatively successful. In contrast, the area to the north (Pelée-north) and east of PPNP (Pelée-east) was more difficult to classify, in large part because non-crop vegetation cover is rare and, therefore, not enough data were available for adequate classification. Thus, with respect to our three potential core areas, unsupervised classification was used for Pelée Island, Cedar Creek, and PPNP, and a supervised classification was used for Pelée-north.

RESULTS OF ANALYSIS

When averaged across the entire region, which included all three main sites and their respective core areas, forest cover and inter-patch distance approached 7% and 300m, respectively (Pearce, 1996). Of the area included in the analysis, Point Pelée National Park contained the largest forest patch (153ha) (Figures 2.2 and 2.3). However, our primary interest was comparing the three main areas. Because of the site-dependent difficulties in classification, two comparative approaches were available: (1) to classify all main areas using the same methodology which would allow for inter-site comparison but would result in substantial loss of information and (2) to classify each main area separately which would result in more information on a per-site basis, but which would hamper the comparison among areas.

Figure 2.2. Unclassified image of Point Pelée National Park, from Landsat TM data taken on May 24, 1994 (C.M. Pearce, 1996).



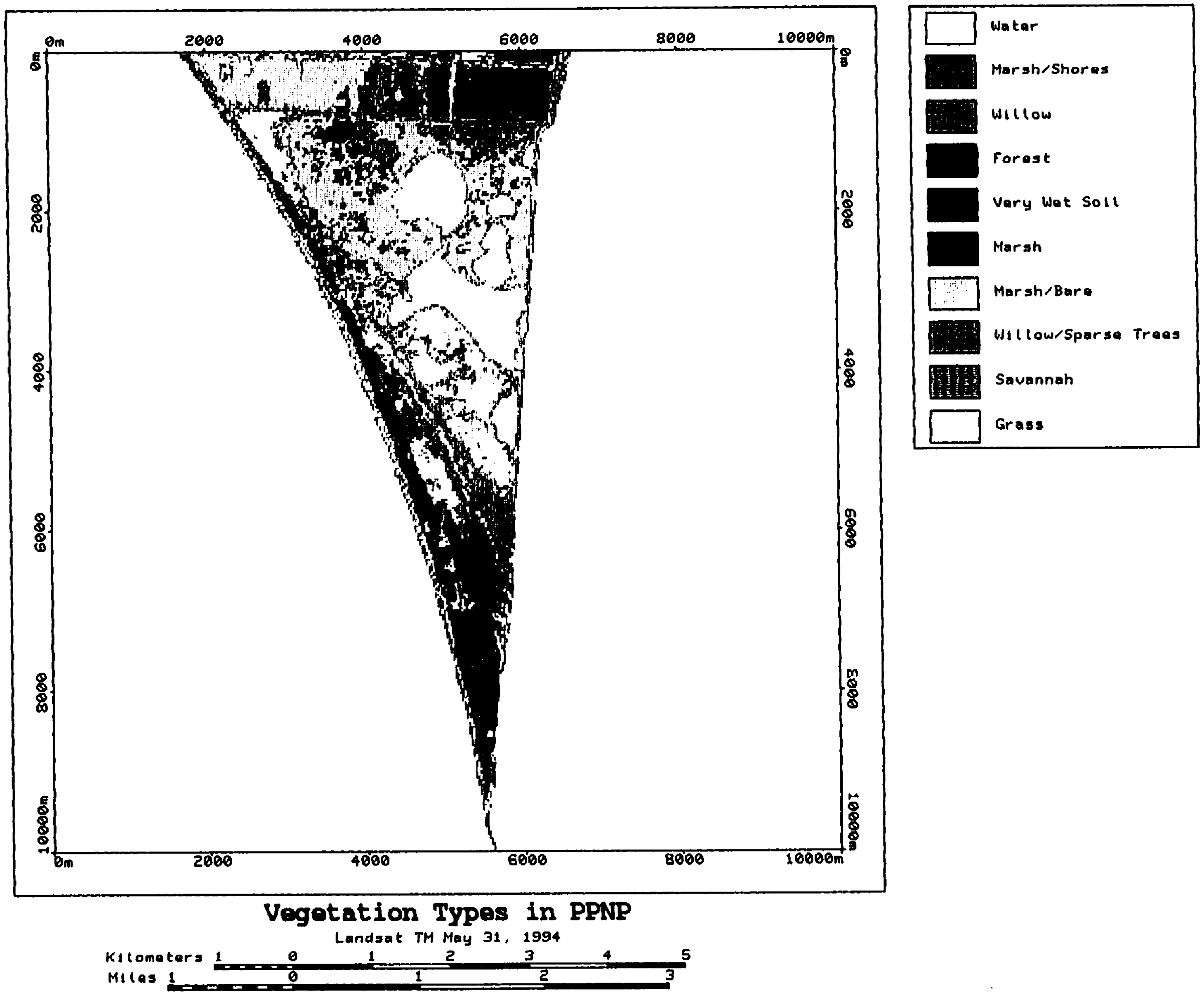
Point Pelee National Park

Landsat TM May 31, 1994

Kilometers 1 0 1 2 3 4

Miles 1 0 1 2

Figure 2.3. Image of Point Pelée National Park, Ontario, classified for forest cover, from Landsat TM data taken on May 24, 1994 (C.M. Pearce, 1996).



Vegetation Types in PPNP

Landsat TM May 31, 1994

Although the latter approach was used in Pearce (1996), some comparison among areas was still possible. Forest comprised 8% of the total land area on Pelée Island (Figures 2.4 and 2.5), compared to 6% for Cedar Creek (Figures 2.6 and 2.7), 8% for PPNP, and only 3% for Pelée-north (the area immediately north of PPNP) (Figures 2.8 and 2.9; Table 2.2). Furthermore, there was another 15% for additional natural habitat on Pelée Island. Thus, Pelée-north had very little forest cover compared with Cedar Creek and Pelée Island.

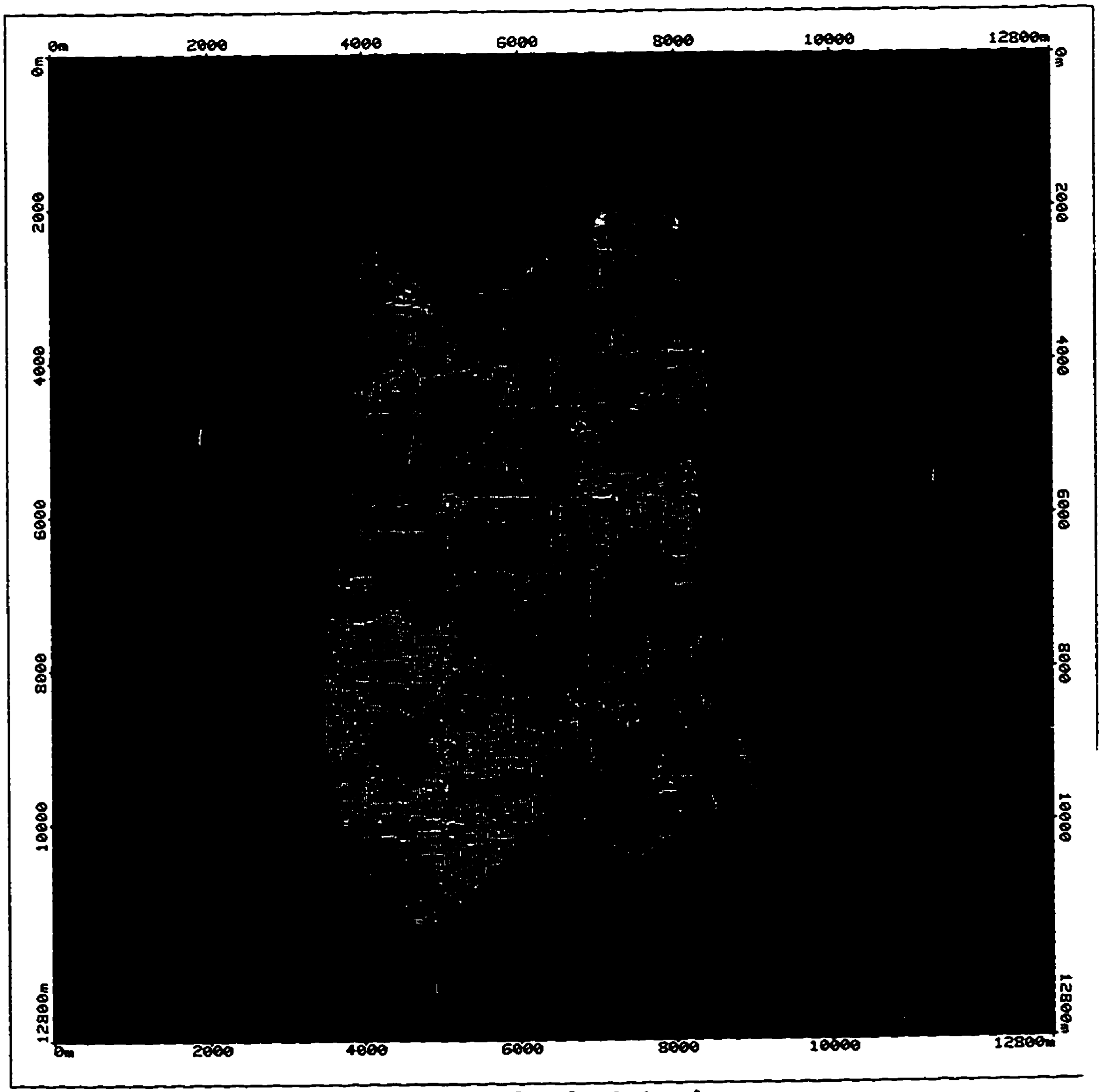
Spatial analysis of these areas revealed similar trends (Pearce, 1996). For this analysis, Pelée-north and Cedar Creek were combined into one area. In Cedar Creek/Pelée north, the only forest patch greater than 100ha was PPNP, while, on Pelée Island, only FPNP was greater than 100ha. A greater proportion of patches were less than 10 ha in the Cedar Creek/PPNP area (89%) than on Pelée Island (72%). Conversely, only 5% of the patches were greater than 20 ha in Cedar Creek/PPNP compared with 22% for Pelée Island (Pearce, 1996).

Average inter-patch distance was calculated using the equation

$$\text{(i)} \qquad \text{Distance}=1/(2\sqrt{n/A})$$

where n = total number of forest patches and A = total land area (Pearce, 1992). When patches under 1 ha were included, average inter-patch distances were calculated as 289m for Pelée Island and 314m for Cedar Creek, and the inter-patch distance for Pelée-north was only 219m (Pearce, pers. comm.). In part, this was attributable to the prevalence of evenly spread, small patches of forest in Pelée-north and that equation (i) does not take into account patch size. However, it should be noted that, when each main area was

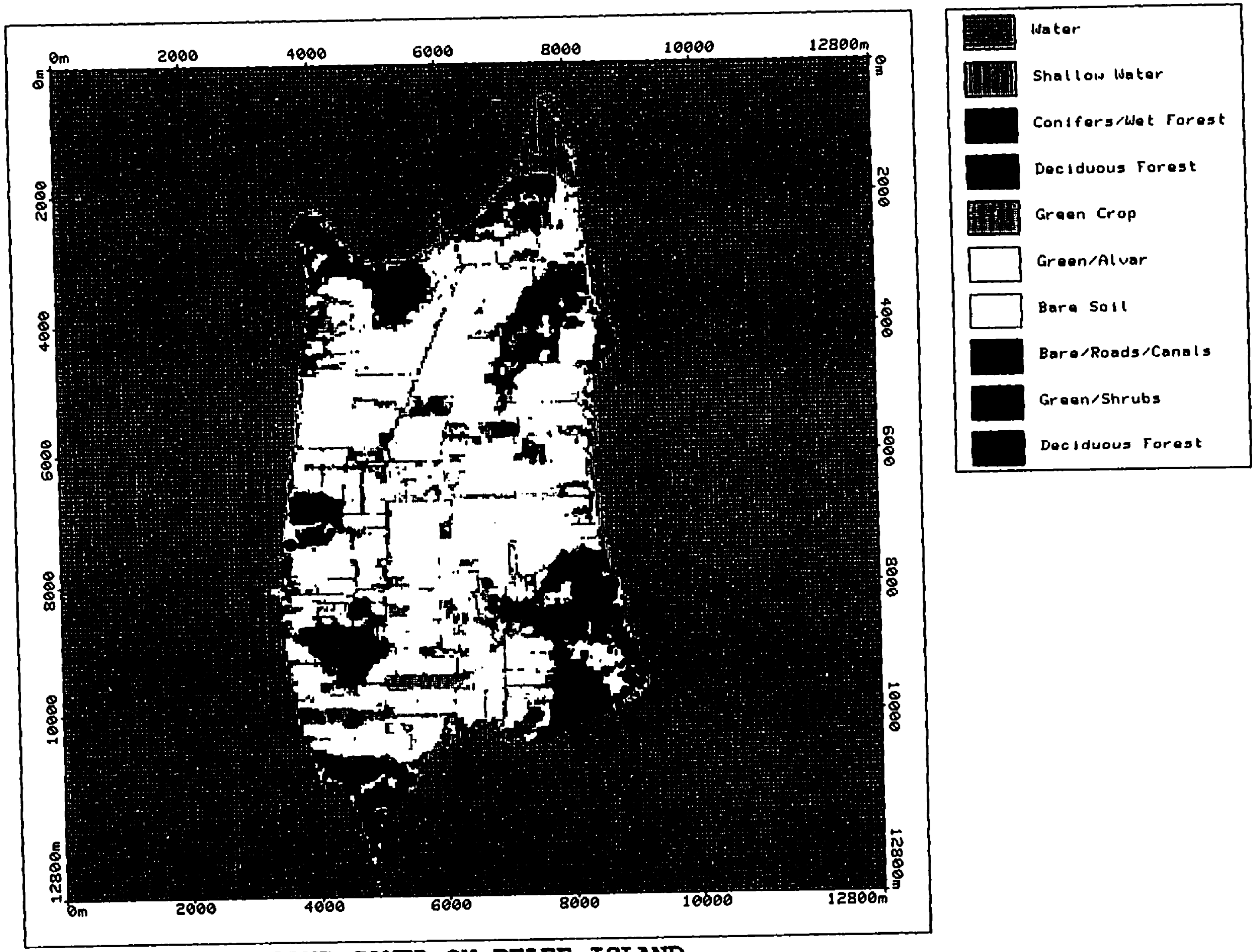
Figure 2.4. Unclassified image of Pelée Island, Ontario, from Landsat TM data taken on May 24, 1994 (C.M. Pearce, 1996).



Pelee Island, Ontario

Landsat TM May 31, 1994

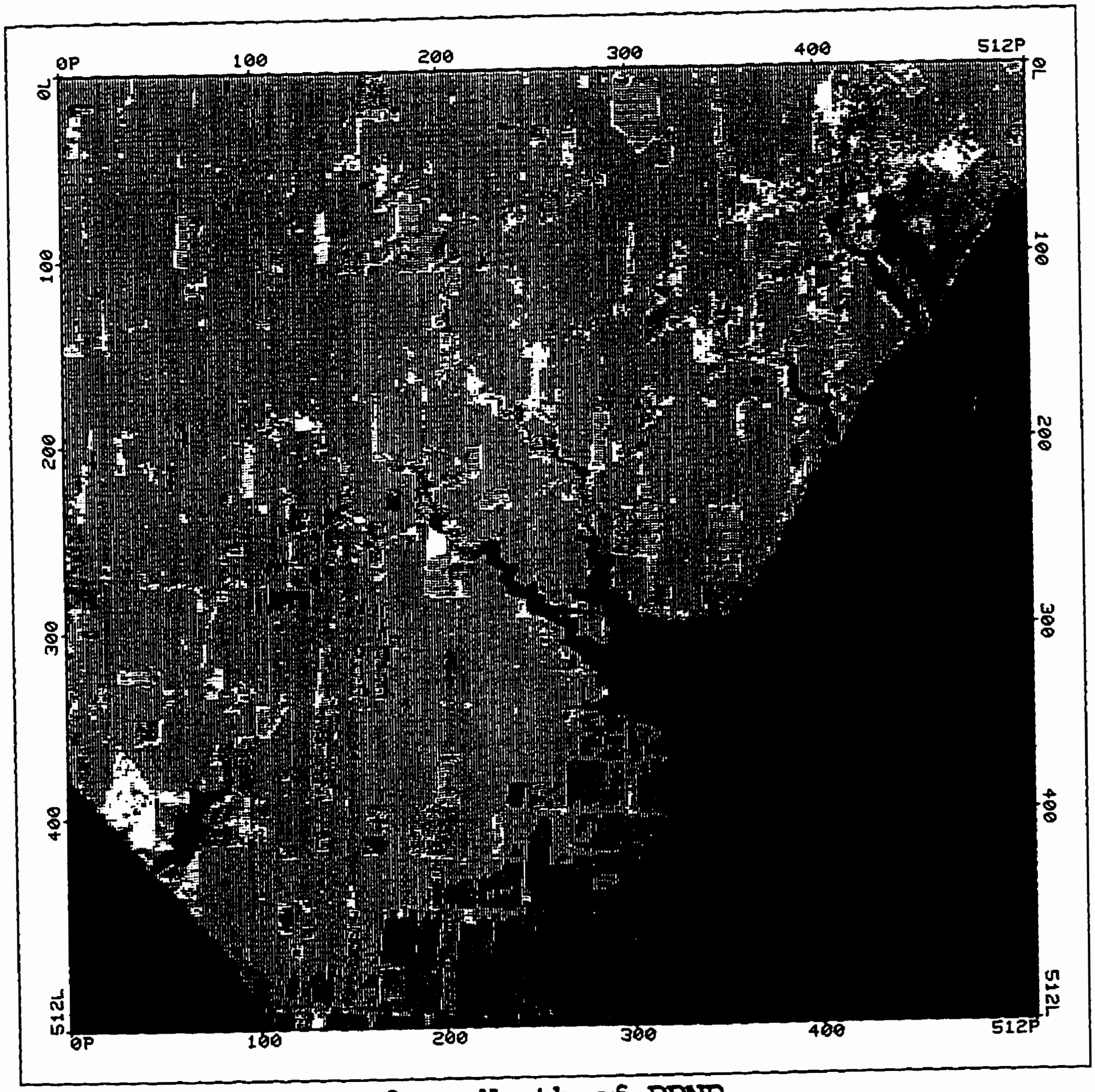
Figure 2.5. Classified image of Pelée Island, Ontario, from Landsat TM data taken on May 24, 1994 (C.M. Pearce, 1996).



LAND COVER ON PELEE ISLAND

Landsat TM May 31, 1994

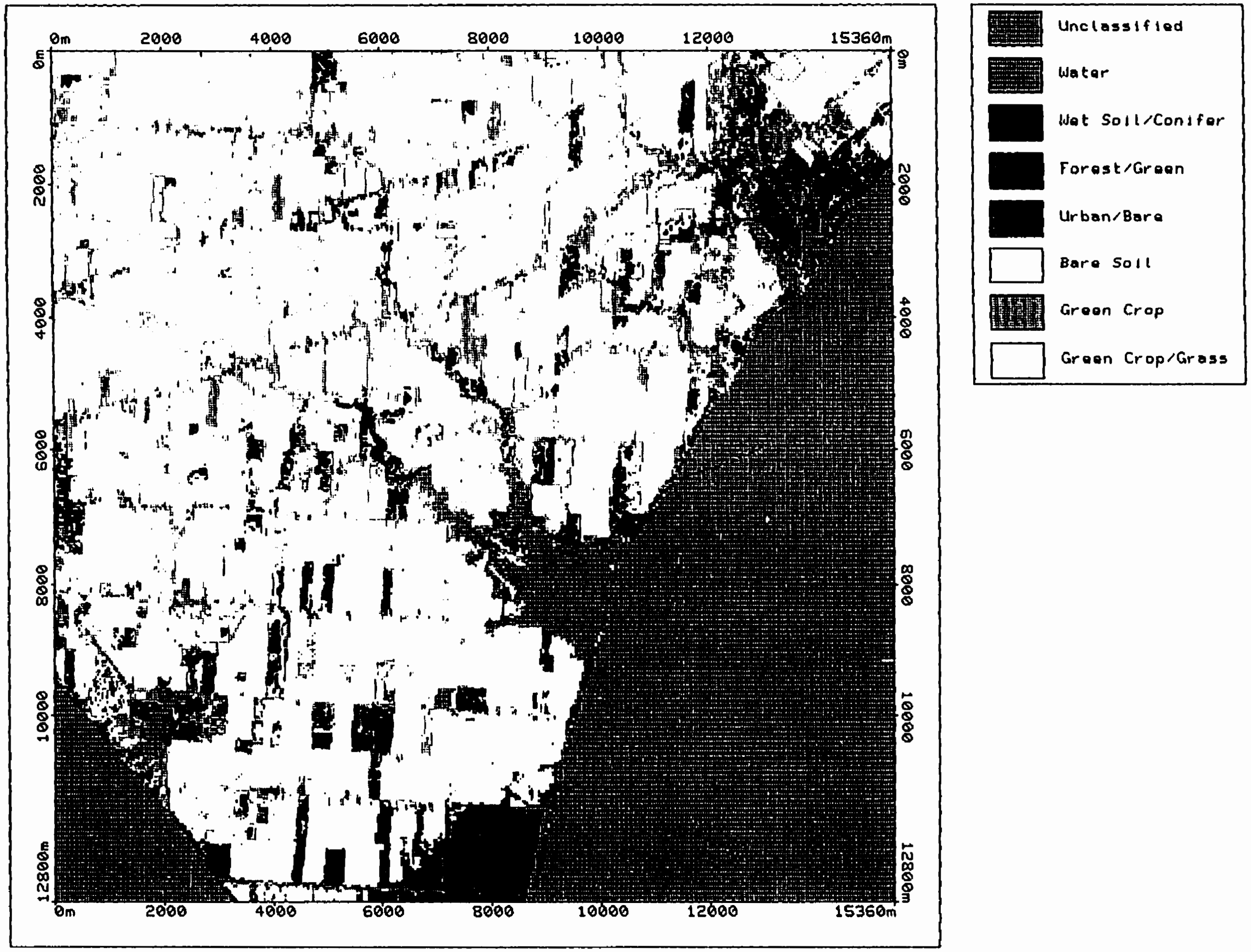
Figure 2.6. Unclassified image of Pelée-north, Ontario, from Landsat TM data taken on May 24, 1994 (C.M. Pearce, 1996).



Area North of PPNP

Landsat TM, May 31, 1994

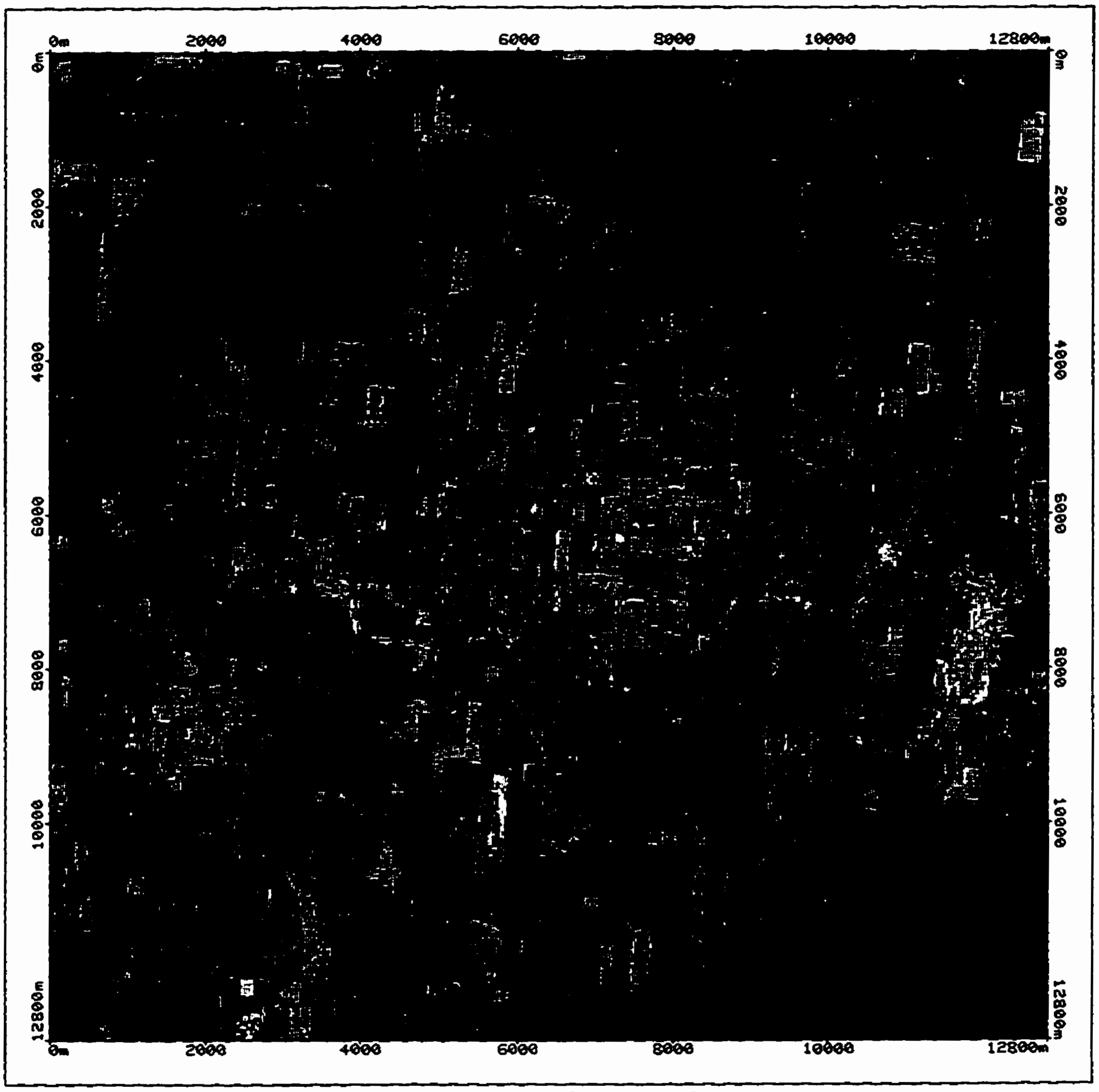
Figure 2.7. Classified image of Pelée-north, Ontario, from Landsat TM data, taken on May 24, 1994 (C.M. Pearce, 1996).



Land Cover North of PPNP

Unsupervised Classification

Figure 2.8. Unclassified image of Cedar Creek, Ontario, from Landsat TM, data, taken on May 24, 1994 (C.M. Pearce, 1996).



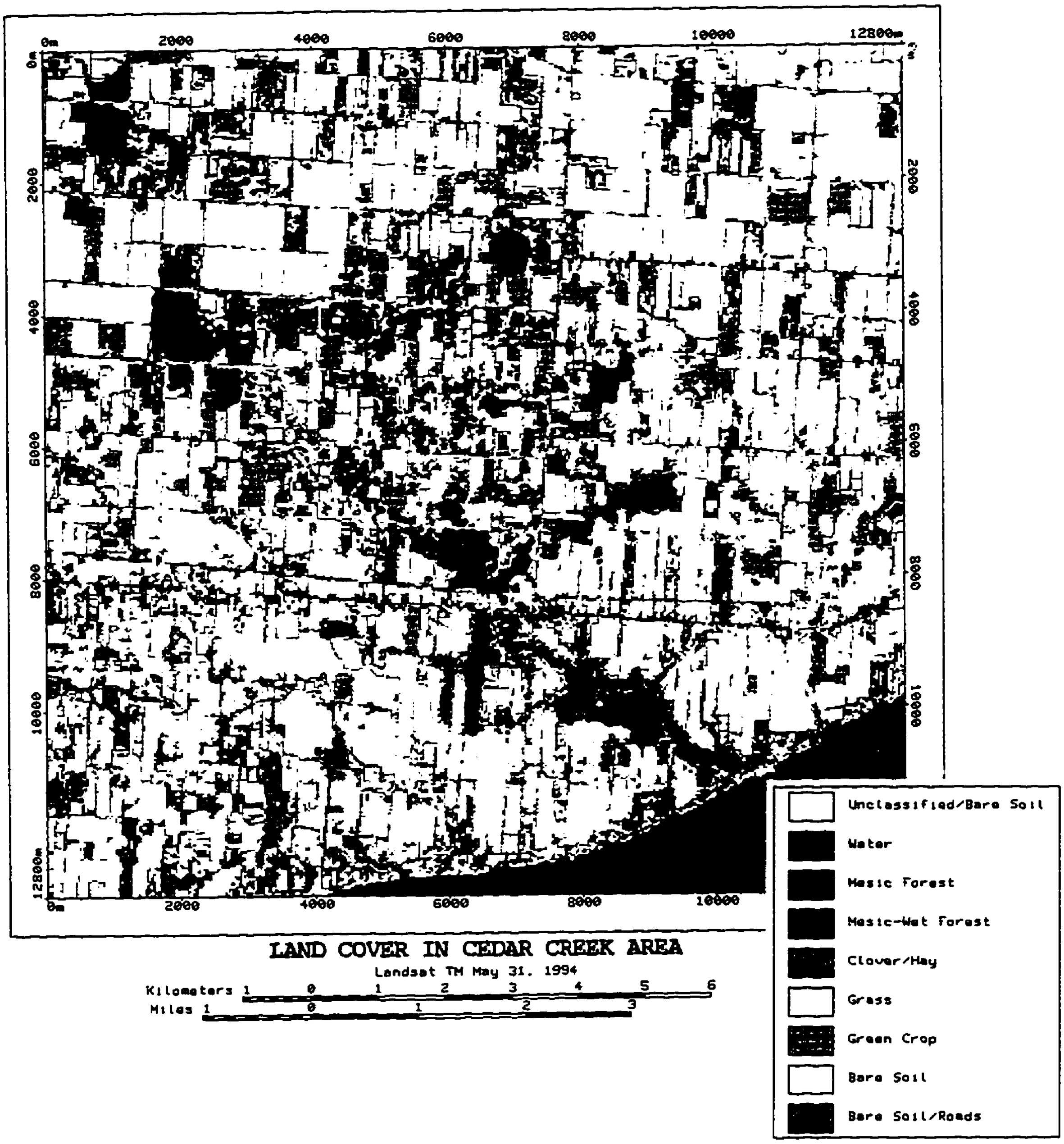
Land Cover in Cedar Creek Area

Landsat TM Data for May 31, 1994

Kilometers 1 0 1 2 3 4 5 6

Miles 1 0 1 2 3

Figure 2.9. Classified image of Cedar Creek, Ontario, from Landsat TM data, taken on May 24, 1994 (C.M. Pearce, 1996).



LAND COVER IN CEDAR CREEK AREA

Landsat TM May 31, 1994

Table 2.2. Percentage of land area lying within 0-100m, 101-500m, 501-800m, and 801-1000m buffer zones around forest as well as total percentage forest cover for each of three proposed bioreserves (Pelée Island, Cedar Creek, and Pelée-north) in Essex county, Ontario (Pearce, pers. comm.)

	Pelee Island	Cedar Creek	Pelee-north
		% land area	
Forest	8.1	6.3	3.4
0-100m	12.0	11.0	12.6
101-500m	44.6	58.7	61.9
501-800m	24.0	19.4	16.4
801-1000m	11.5	5.1	5.6

analyzed separately, there was a relatively large degree of misclassification in Pelée-north due to the low forest cover (50% misclassification of forest compared to roughly 5-10% for both Pelée Island and Cedar Creek). However, when, both Cedar Creek and Pelée-north were combined in the analysis, forest misclassification was lower due to the higher overall forest cover, and most patches in Pelée-north were assessed as being greater than 1500m apart (Pearce, 1996). Furthermore, 12% of the landscape matrix in Pelée Island was located 100m from forest cover and 57% within 500m of forest cover (Figures 2.10, 2.11, and 2.12) (C. Pearce, pers. comm.). Similarly, for Cedar Creek, 11% and 59% of the landscape matrix was located within 100m and 500m of forest, respectively (Figures 2.13, 2.14, and 2.15) while, in Pelée-north, 13% and 62% of the landscape matrix was located within 100m and 500m (Figures 2.16, 2.17, and 2.18) of forest, respectively (Table 2.2) (C. Pearce, pers. comm.). Because forest cover was more concentrated in Pelée Island and Cedar Creek, a greater percentage of the landscape was situated within 800-1000m of forest (12%) than for either Cedar Creek (5%) or Pelée-north (6%) (Table 2.2). Again, for Pelée-north, the percentage of the landscape in the 800-1000 zone was under-represented due to the misclassification of forest cover.

Woodland Improvement Act (WIA) planting constituted the great majority of the forest restoration efforts in Essex county. Of the 39 WIA sites located in the three main areas, seven were situated in Pelée-north, 31 in Cedar Creek, and one on Pelée Island.

The most frequently planted tree species in these sites were green ash (*Fraxinus pennsylvanica*), red oak (*Quercus rubra*), silver maple (*Acer saccharinum*), and white pine (*Pinus strobus*). None of these plantations were big or had developed enough to

Figure 2.10. Percentage of land area on Pelée Island covered by forest as well as by 0-100m, 101-500m, 501-800, and 801-1000m buffer zones around remnant forest (C.M. Pearce, pers. comm.).

distance classes for forests

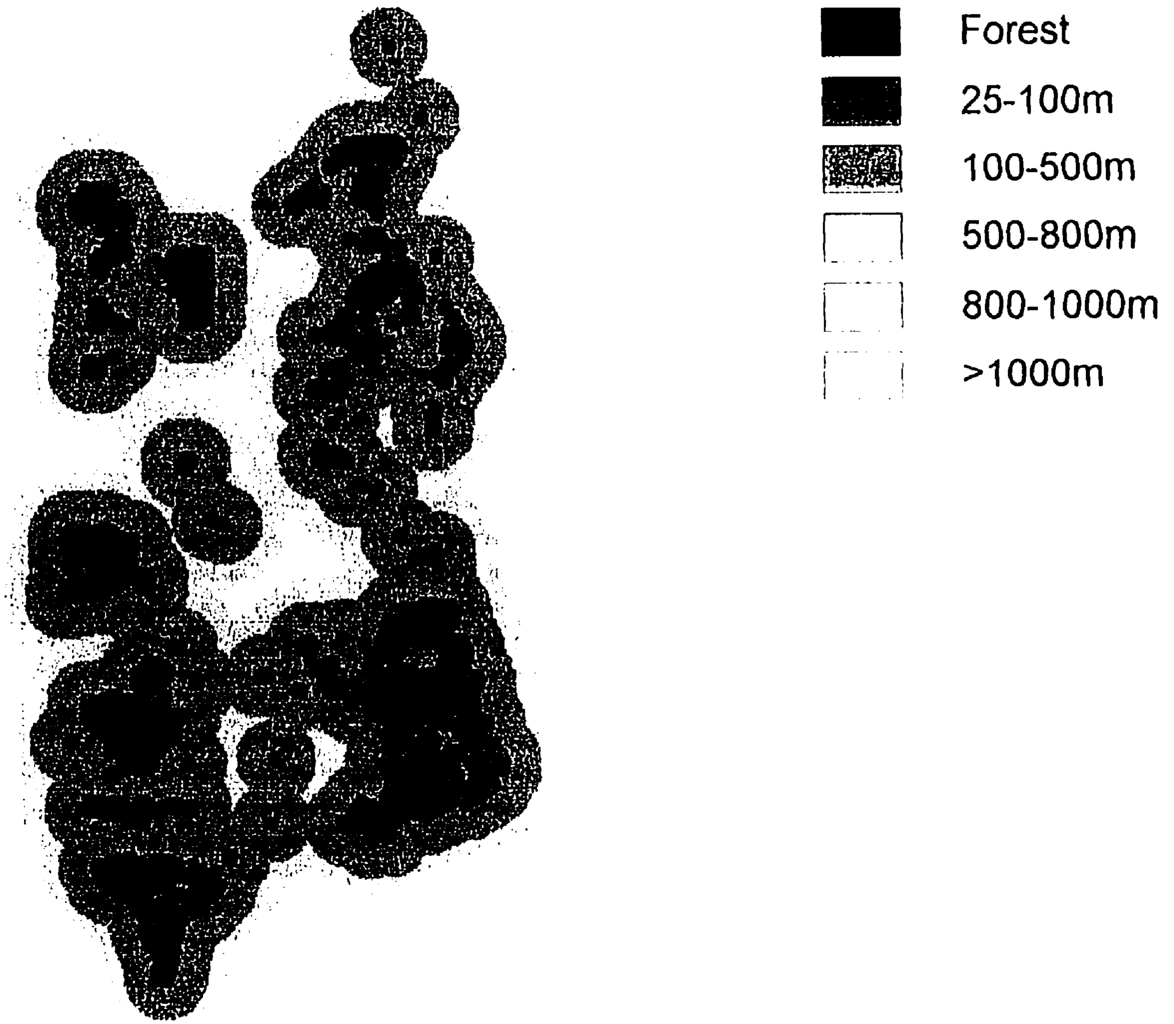


Figure 2.11. Percentage of land area on Pelée Island covered by forest and by 0-100m buffer zones around remnant forest (C.M. Pearce, pers. comm.).

Buffer zones within 100m of Forest

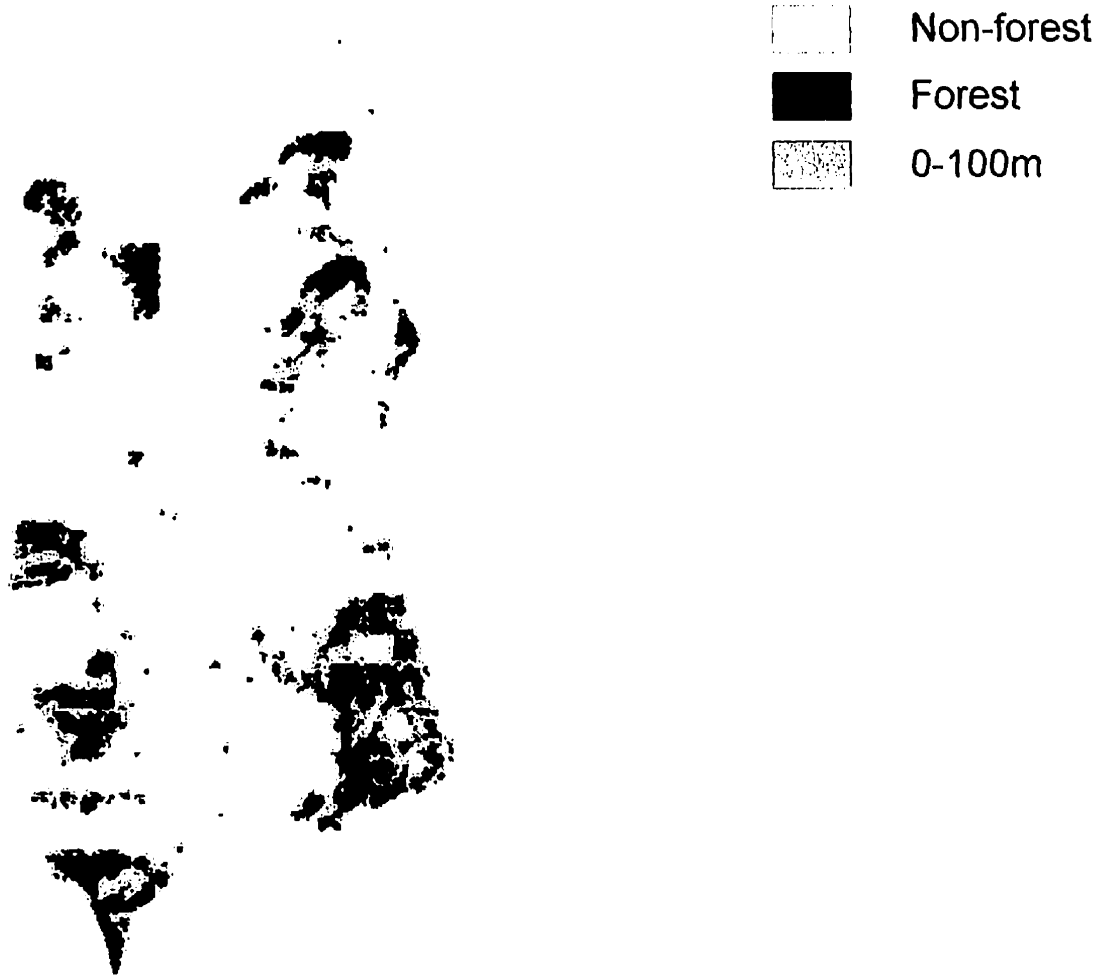


Figure 2.12. Percentage of land area on Pelée Island covered by forest and by 0-500m buffer zones around remnant forest (C.M. Pearce, pers. comm.).

Buffer zones within 500m of Forest

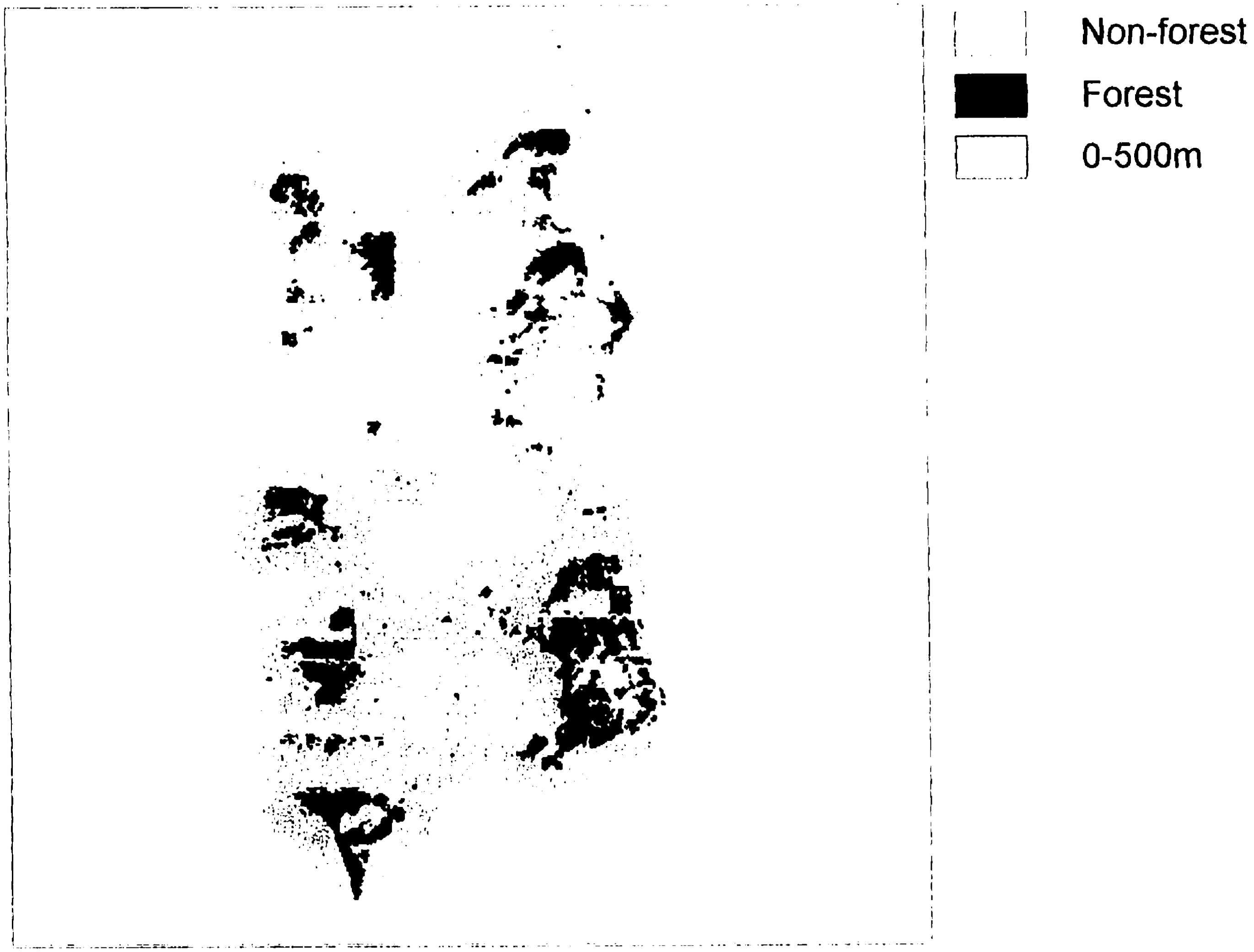


Figure 2.13. Percentage of land area on Cedar Creek covered by forest as well as by 0-100m, 101-500m, 501-800, and 801-1000m buffer zones around remnant forest (C.M. Pearce, pers. comm.).

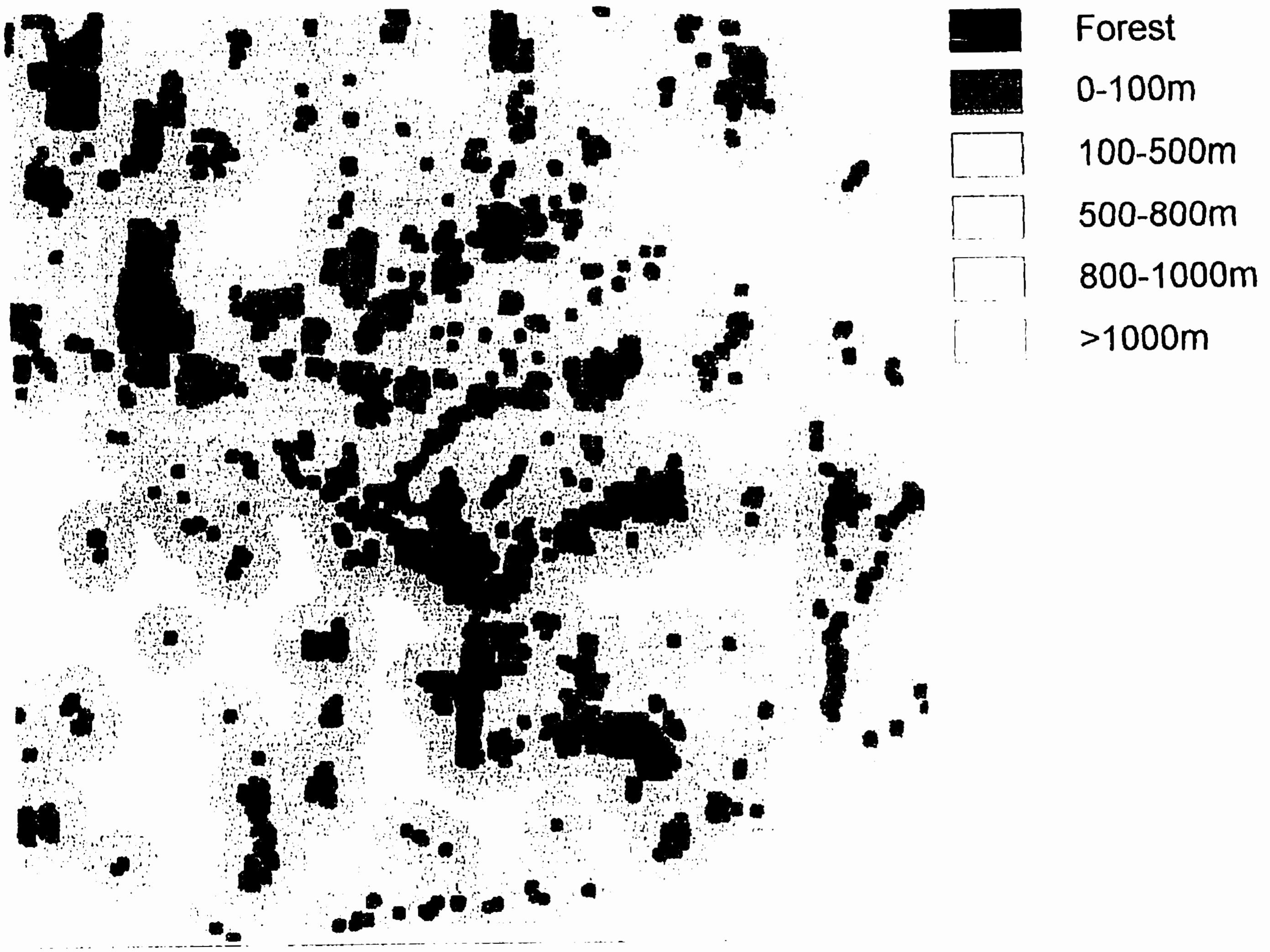

Distance Classes Between Forest Patches

Figure 2.14. Percentage of land area on Cedar Creek covered by forest and by 0-100m buffer zones around remnant forest (C.M. Pearce, pers. comm.).

100m Buffer Zones Around Forest Patches

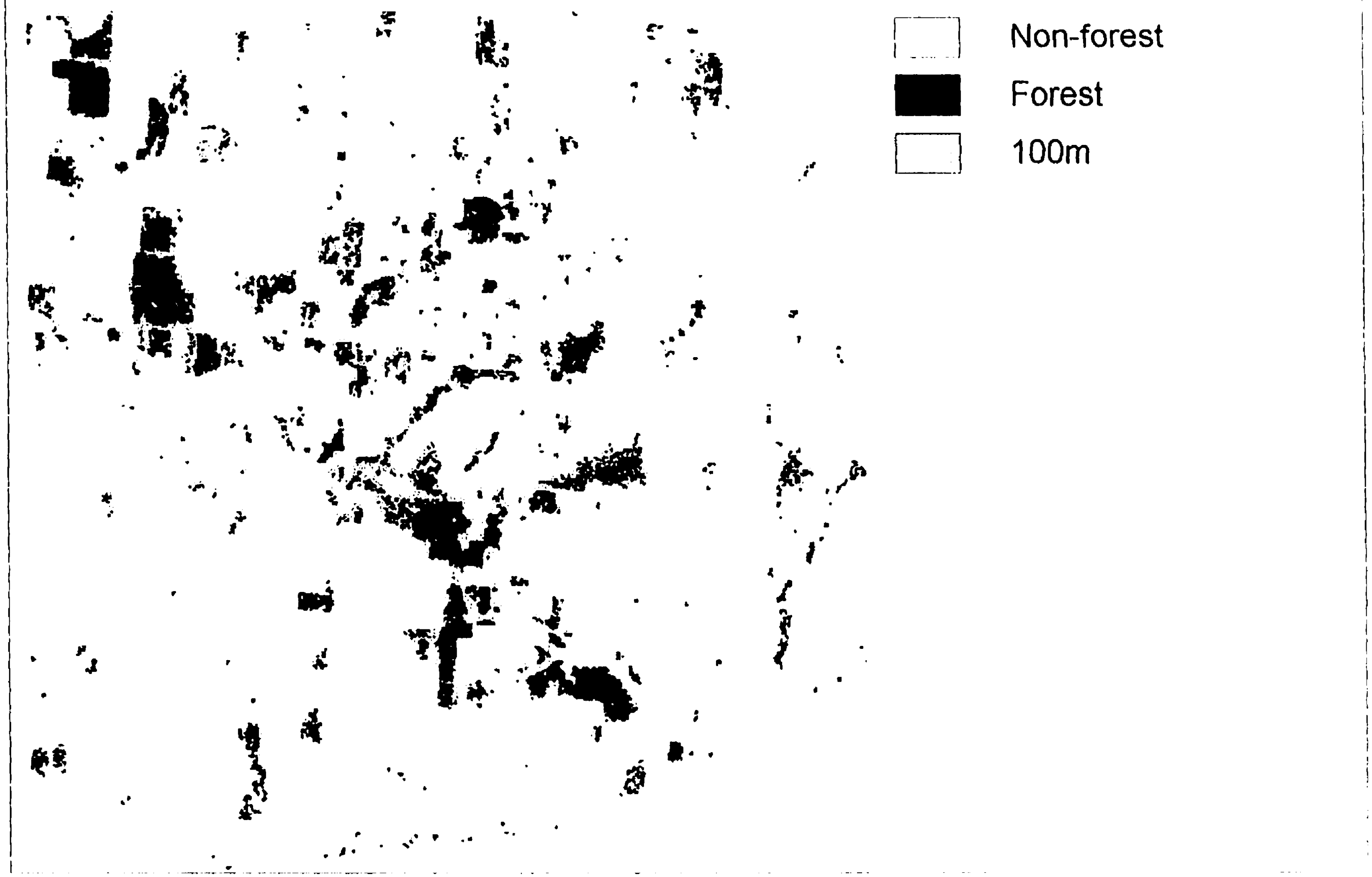


Figure 2.15. Percentage of land area on Cedar Creek covered by forest and by 0-500m buffer zones around remnant forest (C.M. Pearce, pers. comm.).

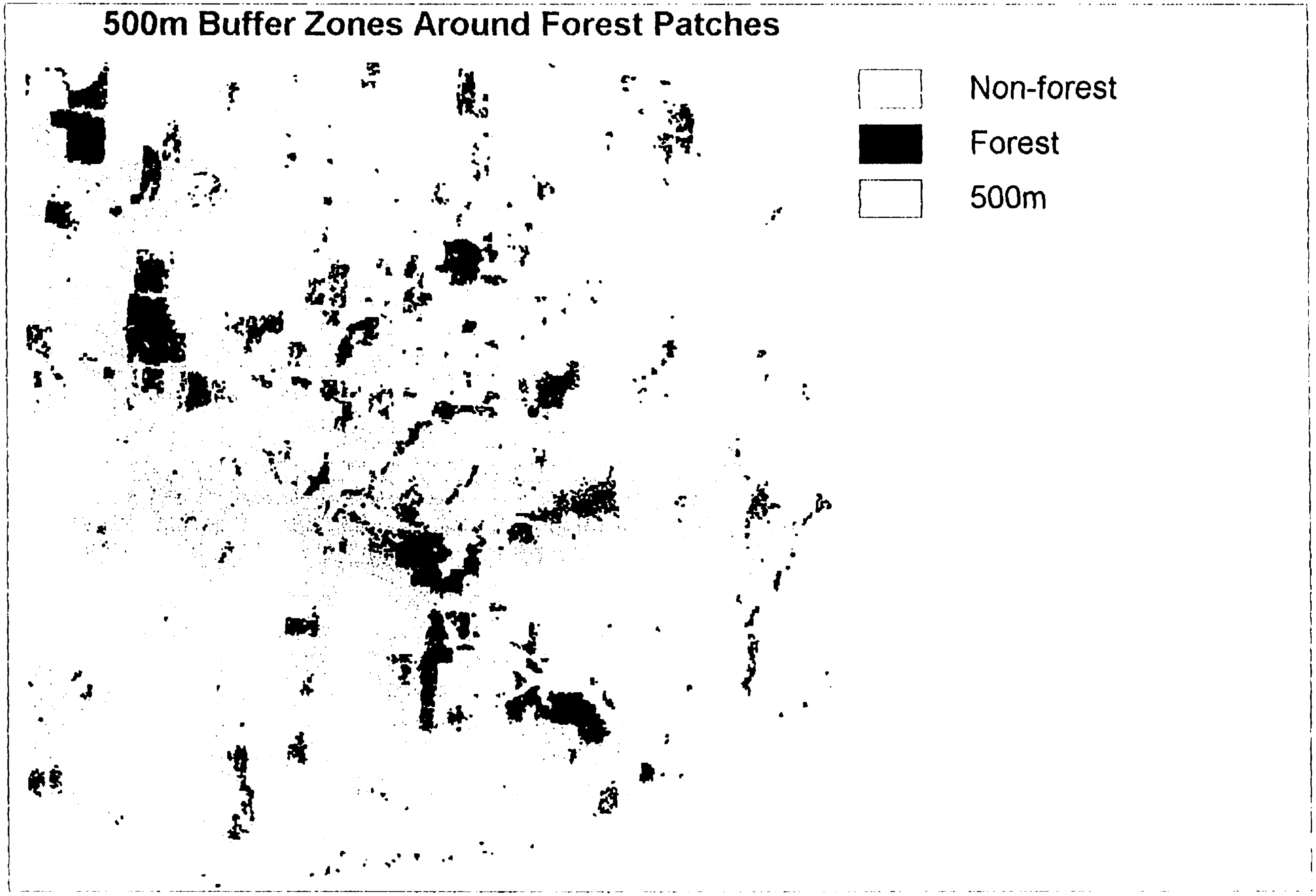

500m Buffer Zones Around Forest Patches
Non-forest
Forest
500m

Figure 2.16. Percentage of land area on Pelée-north covered by forest as well as by 0-100m, 101-500m, 501-800, and 801-1000m buffer zones around remnant forest (C.M. Pearce, pers. comm.).

Distance Classes Between Forest Patches

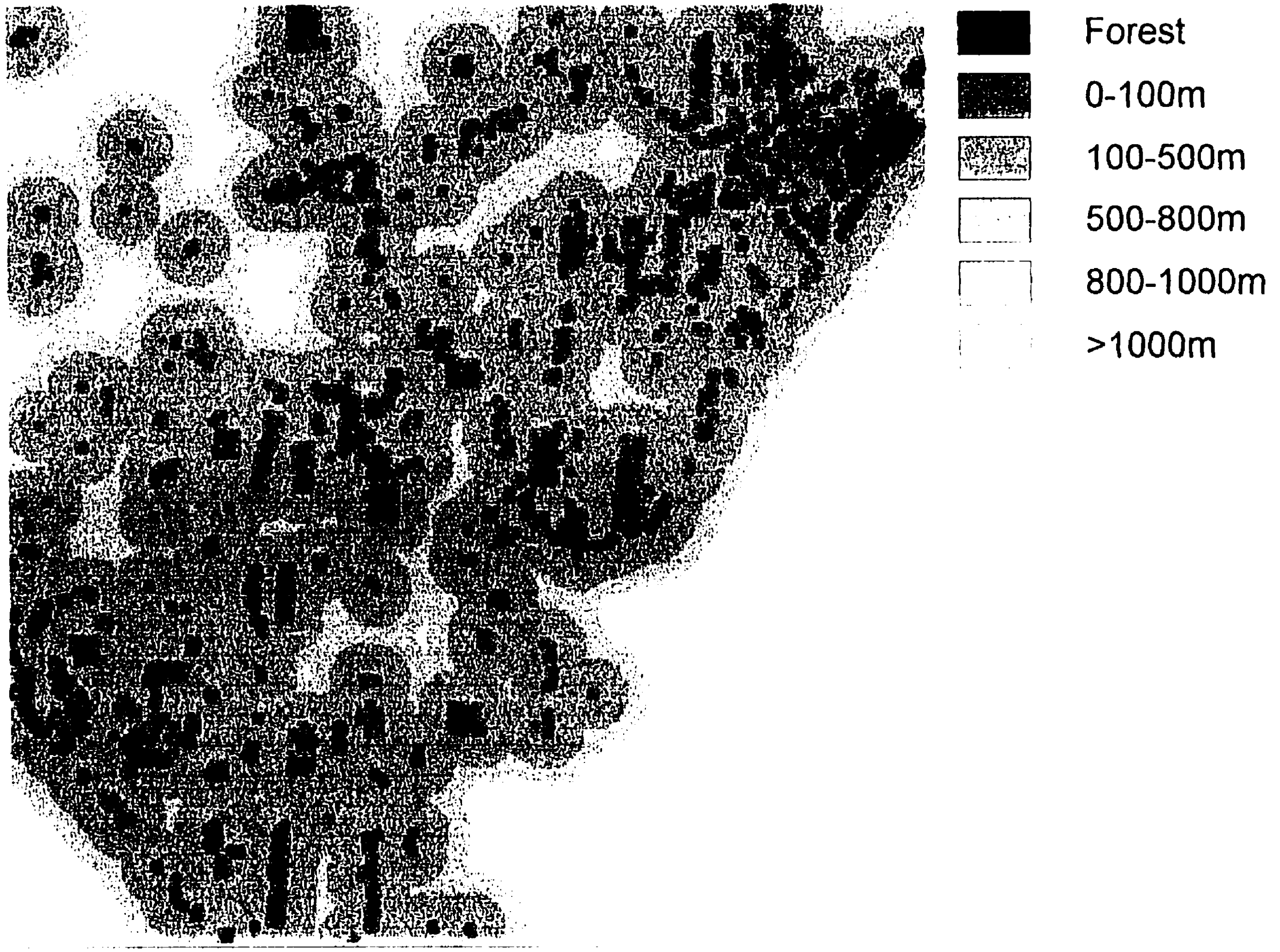


Figure 2.17. Percentage of land area on Pelée-north covered by forest and by 0-100m buffer zones around remnant forest (C.M. Pearce, pers. comm.).

100m Buffer Zones Around Forest Patches

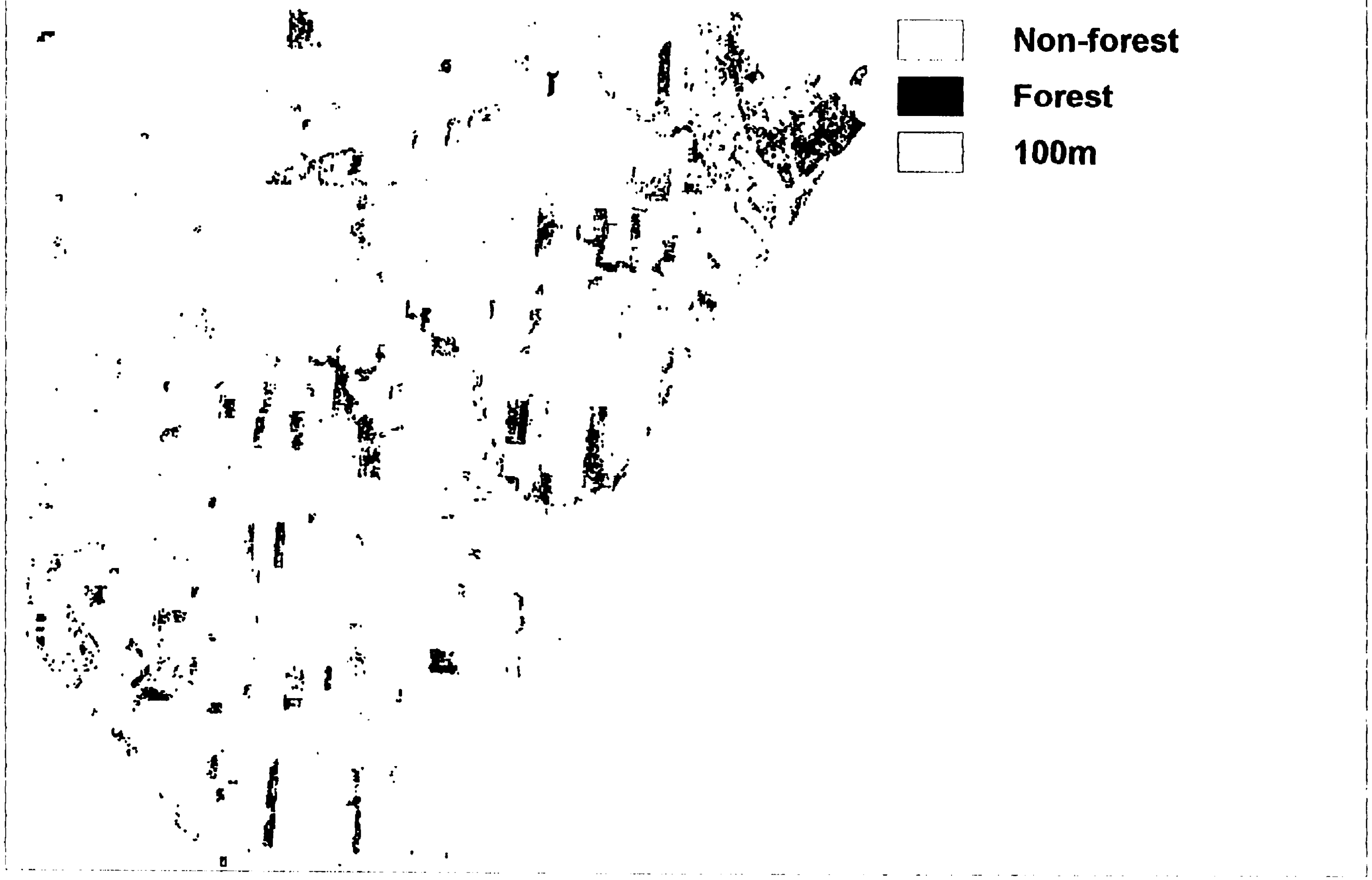
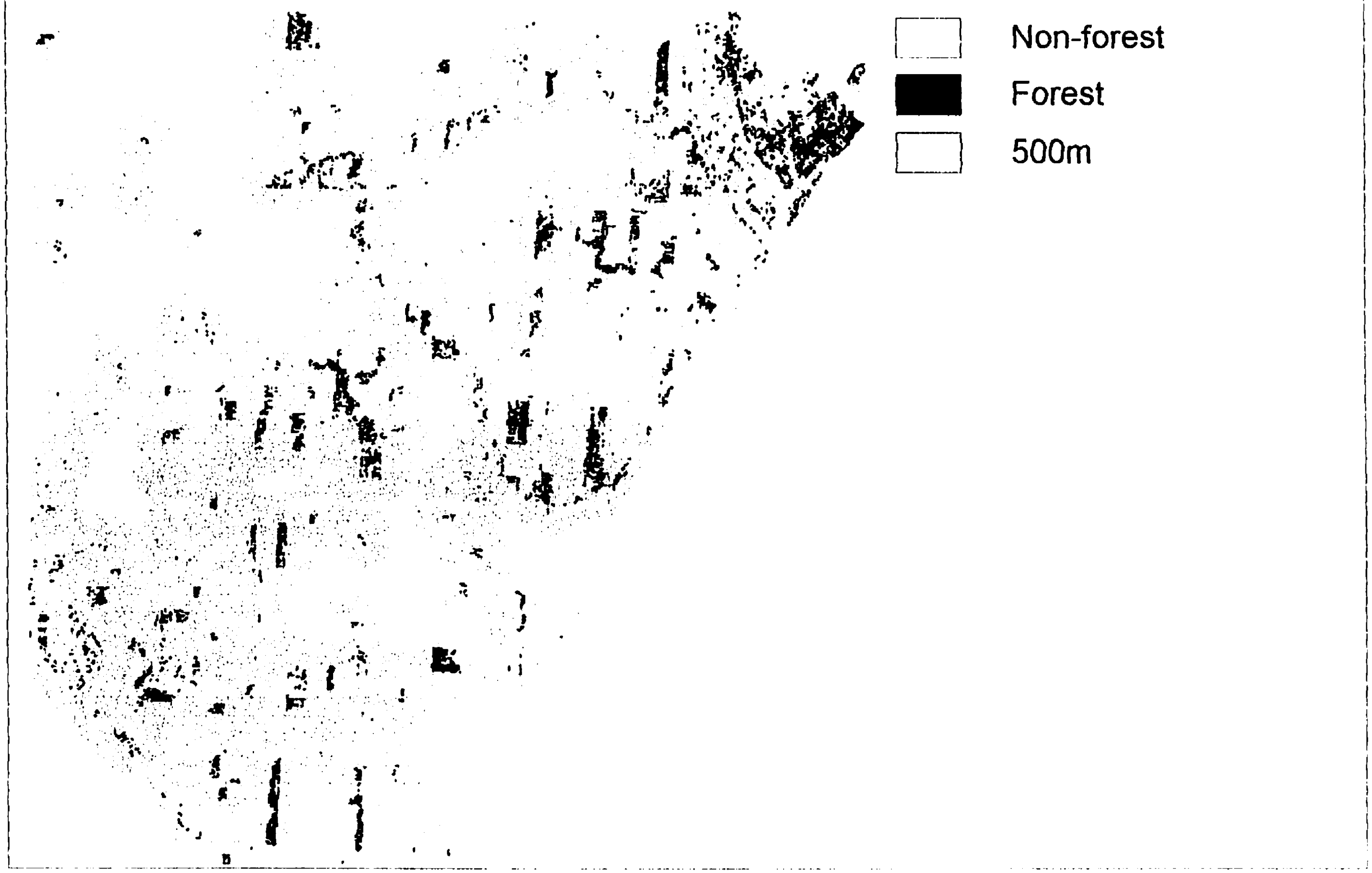


Figure 2.18. Percentage of land area on Pelée-north covered by forest and by 0-500m buffer zones around remnant forest (C.M. Pearce, pers. comm.).

500m Buffer Zone Around Forest Patches

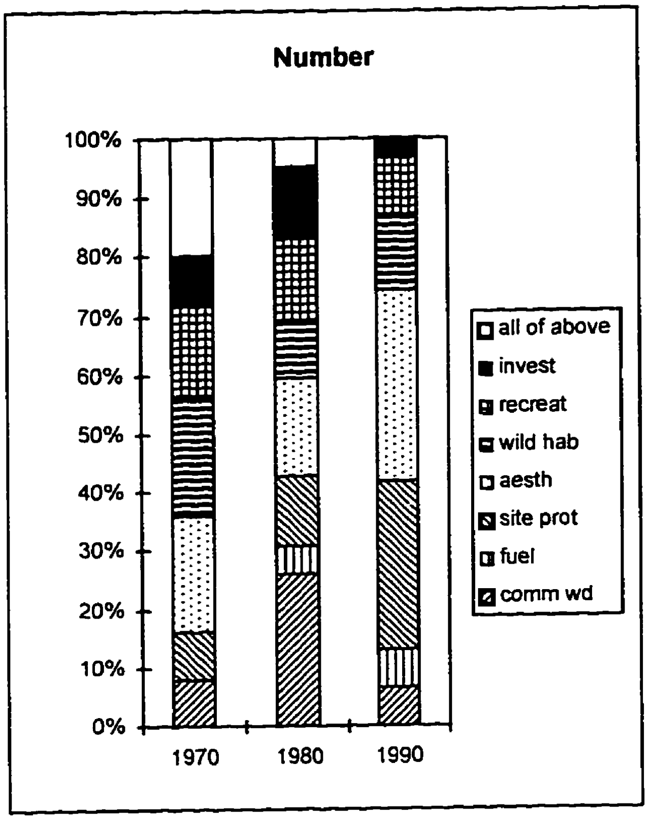


appear on the classified imagery, but they were subsequently located on the images using OMNR planting records. Not surprisingly, given that landscape information for the region was not available until 1997, these restored site seem to serve little landscape purpose (*sensu* Hobbs, 1993). They are spread throughout each of the main areas and thus fail to increase the connectivity between habitat patches. Furthermore, as only 4/ 25 were contiguous to pre-existing forest, they would neither protect nor increase the area of existing forest patches. Brief surveys were completed by clients prior to planting. Survey results suggested, when classified according to the decade of planting, that motivations for restoration were expected increases in commercial value, aesthetics and site protection (Figure 2.19) and that the latter has become more important in the last 10 years (Figure 2.20).

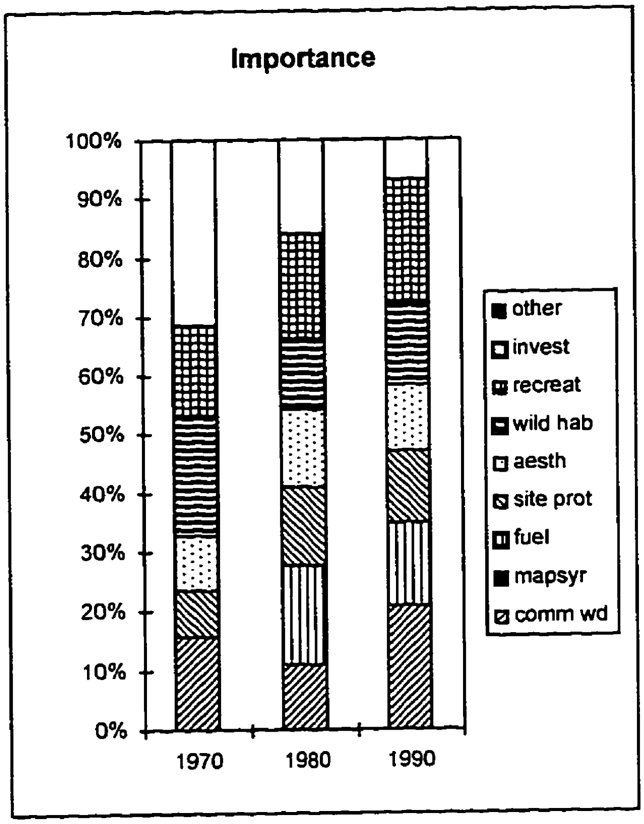
DISCUSSION

As expected, forest cover in Essex county was found to be highly fragmented. In fact, there was so little remaining natural vegetation cover, that more-detailed classification was difficult. This problem was aggravated when each of the three main areas was analyzed separately. Landsat TM imagery was of little use in areas with the least amount of natural vegetation cover (e.g. Pelée-north, Pelée-east), where even forest cover was routinely misclassified. In order to achieve more accurate results, the forest cover for these areas should be reclassified by hand. In contrast, for Cedar Creek, non-crop classes that were successfully identified included: pasture, shrubland, grasslands, wet deciduous forest, mesic/dry deciduous forest, green-crops (Pearce 1996). In addition,

Figure 2.19. Motivation (importance and number) behind clients of plantations created under Woodland Improvement Act according to decade of planting (i.e. 1970, 1980, 1990).

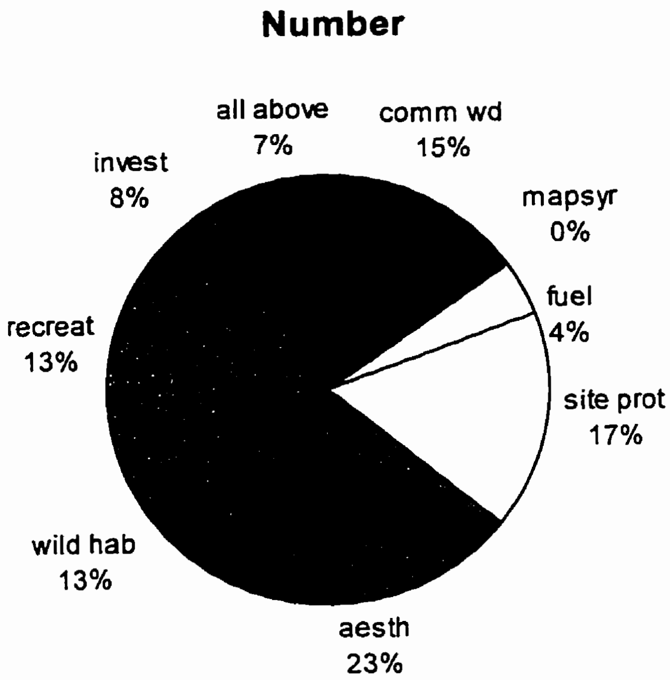

Number
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1970
1980
1990
all of above
invest
recreat
wild hab
aesth
site prot
fuel
comm wd

a)

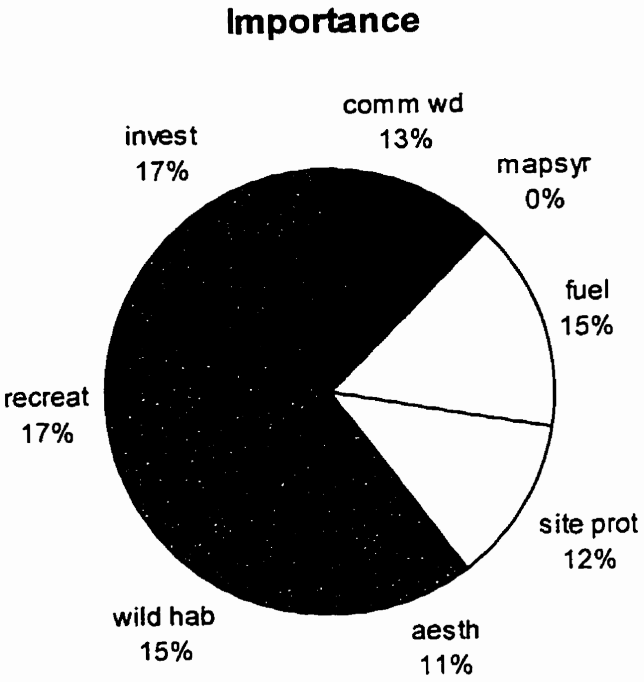

Importance
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
1970
1980
1990
other
invest
recreat
wild hab
aesth
site prot
fuel
mapsyr
comm wd

b)

Figure 2.20. Motivation (importance and number) behind clients of plantations created under Woodland Improvement Act (WIA) summed for period extending from 1970 to 1993.


Number
all above
7%
comm wd
15%
invest
8%
mapsyr
0%
fuel
4%
recreat
13%
site prot
17%
wild hab
13%
aesth
23%

a)


Importance
comm wd
13%
invest
17%
mapsyr
0%
fuel
15%
recreat
17%
site prot
12%
wild hab
15%
aesth
11%

b)

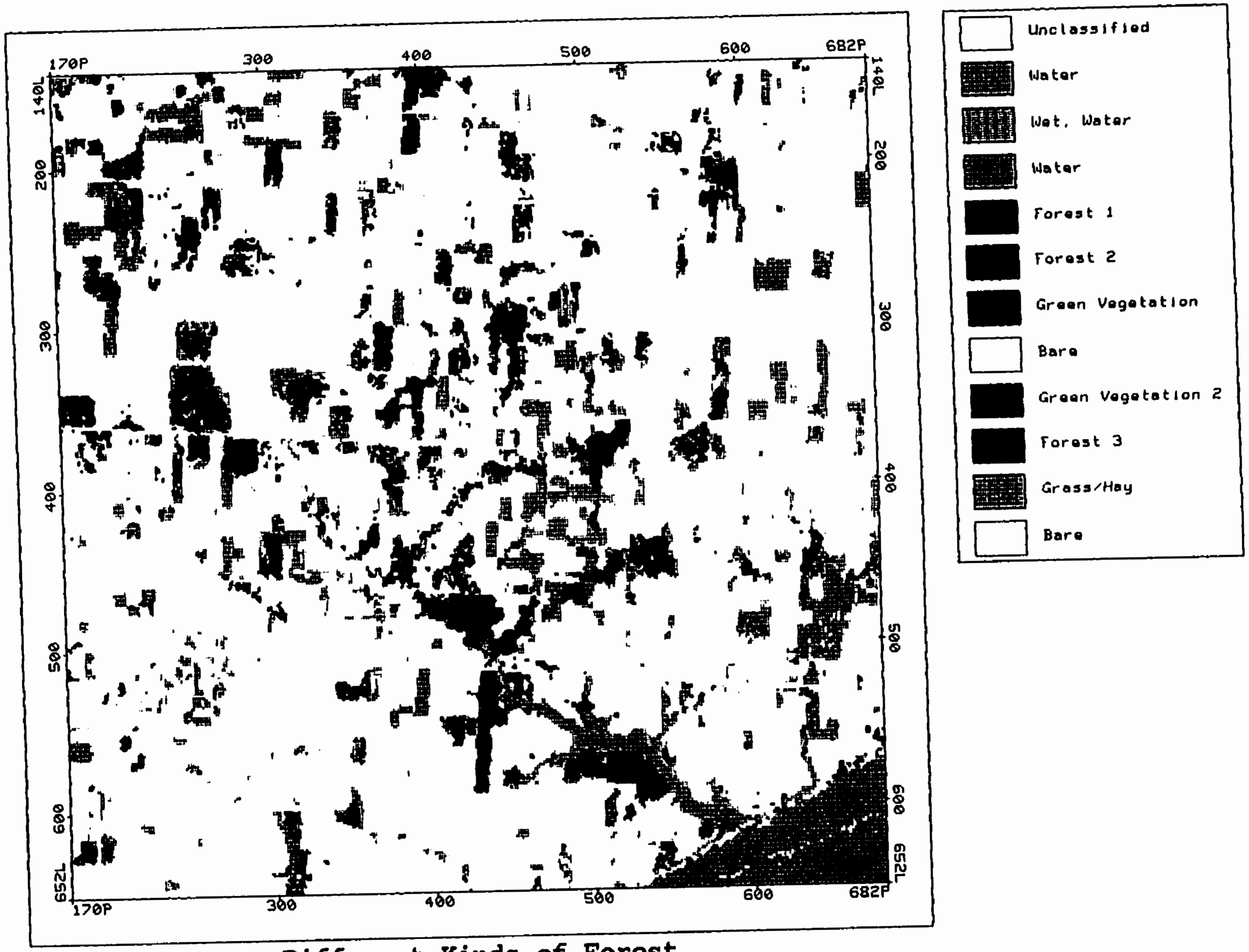
some fence-rows and orchards were identified. Chapman (1996) refined these vegetation classes by further identifying cover-classes through the use of 1:50.000 "NTS" maps (revised in 1994) and aerial photographs (taken in 1989). She created a multi-layer data base for the region that included roads, railways, major human uses (golf-courses, orchards, etc.) as well as the aforementioned vegetation classes. Furthermore, Chapman (1996) was able to further distinguish between high and low-integrity forest patches within Cedar Creek. In addition, three classes of forest were identified for Cedar Creek using unsupervised classification (C. Pearce, pers. comm.) (Figure 2.21). However, these classes seemed to correspond more closely with soil moisture than with the disturbed forest patches identified by Chapman (1996). These disturbed, marginal sites are of primary interest to restoration ecologists. A more detailed description of the existing forest patches could be easily achieved using aerial photos and maps, as so few fragments of natural habitat remain in this region.

The remnant forest patches were small and highly isolated. Although, not measured in this study, fence-rows were not readily detected by the classification. While they comprise a large amount of edge-dominated habitat, they appeared to be patchy in distribution and, thus, are unlikely to greatly facilitate inter-patch movement. These fence-rows could be further described using aerial photos.

Management implications

From a site-level perspective, of the three main areas studied, PPNP would seem to be the most reasonable choice for a core area. It is easily the largest area of natural

Figure 2.21. Classified satellite image of Cedar Creek derived from satellite image taken on May 24, 1994. Indicated are three classes of forest. (C.M. Pearce, pers. comm.)



Different Kinds of Forest

6=red;7=green;13=blue;4=gold

Pixels 100 0 100 200

habitat (50% larger than Cedar Creek and 300% larger than FishPoint Nature Preserve). is internationally known as a birding site, is visited by over 300,000 people per year. has an active collaborative research program, and is relatively highly funded (W. Stephenson. pers.comm.). However, compared with the other main areas, there were substantial differences in regional forest cover, patch area, and inter-patch distance. Pelée Island showed almost 30% natural habitat cover and had three times the total forest cover of Pelée-north. Similarly, Cedar Creek showed twice the forest cover of Pelée-north.

These differences, as discussed below, suggest: (1) that conservation (i.e. protection of remaining woodlots) should be the greatest priority in Pelée-north and (2) that restoration which increases connectivity could be of greater importance on Pelée Island, or if only mainland sites are being considered, at Cedar Creek. That two separate site-dependent strategies might exist, suggests, in turn, that restoration and conservation are not analogous activities. In fact, only one WIA was planted on Pelée Island while seven were planted in Pelée-north.

Conservation should be aimed at protecting and managing high-quality natural habitat and does not require any changes in landuse. The majority of remaining natural habitat in the Carolinian is privately owned (Hilts, 1985). Thus, conservation goals are mainly attained through land purchases (e.g. ERCA, Nature Conservancy) and trust agreements with land-owners (e.g. Carolinian Canada (Allen et al., 1990)). There are 38 Carolinian-Canada sites located in the Ontario region of the Carolinian (Allen et al., 1990). Ironically, none of these are located in Pelée-north (although three are located on

Pelée Island, and two are located in Cedar Creek). The satellite imagery might help co-ordinate the description and selection of these protected areas, particularly in Pelée-north.

Restoration activity, on the other hand, if focusing on the landscape-matrix, requires changes in landuse. There were substantial differences in land-use between the three main areas. Landuse in Pelée-north is dominated by cash-crop (corn, soybean, winter wheat) and vegetable production. In contrast, there was more marginal land at Cedar Creek and on Pelée Island. Correspondingly, land values in Pelée-north are 3-5 times that of land in Cedar Creek, and on Pelée Island (although the latter is appreciating due to the establishment of a more-efficient ferry transportation and a burgeoning wine industry) (C. Jones, pers. comm.). Thus, the cost of large-scale restoration in Pelée-north would be much higher than in the other two areas. Because of its relative low cost and the greater likelihood of owner participation in set-asides, and its greater likelihood of success (Marrs and Gough, 1989), it seems that restoration efforts could more effectively focus on marginal land particularly in Cedar Creek and on Pelée Island. In contrast, this kind of marginal land is relatively rare in Pelée-north.

Intensely managed agricultural landscapes are almost completely ignored in the conservation literature (Vandermeer and Perfecto, 1997). However, landscape connectivity between natural habitat in these landscapes might be facilitated by changes in agronomic practices. Currently, the "landscape-matrix" is dominated by bare-soil. However, additional habitat for, and movement between patches by, small mammals and birds might be promoted by the establishment of "permanent crops" and increases in vertical complexity of fields through intercropping (Francis et al., 1987) and agroforestry

(Williams and Gordon, 1987), as well as by increases in diversity through reductions in pesticide use (Swanton and Murphy, 1996). This is an area of study that has been long overlooked and differences in connectivity could be assessed using satellite imagery and information on regional farming practices.

Currently, however, the majority of landscape studies situated in agricultural landscapes assume that the matrix surrounding extant natural habitat is of no conservation value and focus on generating connections between existing natural habitat (Noss, 1993; Thorne, 1993; Zonneveld, 1990). Assuming that corridors actually work, the distances between patches are so great in Pelée-north, (approximately three times that of Pelée Island and the PPNP-to-Harrow region) that increases in connectivity may have little meaning. In contrast, increases in connectivity may have some functional meaning in Cedar Creek and on Pelée Island.

Much of the recent literature also suggests that corridors connecting patches of natural habitat are of limited value (Simberloff et al., 1992). In addition to increases in the levels of parasitism and predation (Simberloff and Cox, 1987), and the presence of non-native plant species (Brothers and Springarn, 1992) in corridors, it has yet to be shown that organisms preferentially use these habitat corridors compared with the rest of the landscape matrix (Simberloff et al., 1992). In fact, recent radio telemetry studies suggest that small mammals make extensive use of the landscape matrix (Merriam and Lanoue, 1990; Wegner and Merriam, 1996). Furthermore, corridors, by definition, require that all land designated as corridor be set aside. This is, at best, unlikely in a highly productive agricultural landscape. An alternative "opportunistic" approach to restoration, relies on functional rather than structural increases in connectivity (e.g. percolation theory). This approach predicts that "landscape resistance" will decrease with the density of these restored patches. Thus, it is not necessary that these patches be contiguous but that the grain size of the natural habitat be smaller than the ranges of the resident organisms (Rolstad, 1991). Once a certain landscape-level threshold of density is obtained, any patch, regardless of its location will contribute to increased connectivity. If these patches are situated in marginal land (e.g. low-lying or nutrient-poor portions of fields), it seems likely that farmers will be more open to setting aside land. The restoration of these "habitat grains" could then be co-ordinated at the landscape level using the satellite imagery and modelled using GIS.

As suggested earlier, from the site-level perspective, PPNP would seem to be an ideal "core" area. However, bioreserve models prescribe that these core areas be surrounded by a "buffer zone", in which both conservation and "production" concerns are met. The area surrounding PPNP is so highly fragmented that it would be unlikely to meet these conservation priorities without large-scale changes in land-use. In fact, PPNP is surrounded by water on all sides (because to the north there is a large water-filled drainage ditch and converted wetlands). As Pelée-north contains some of the premier farmland in Canada, major changes in landuse are highly unlikely to occur. In contrast, Cedar Creek is much less fragmented, and has much greater forest cover and lower inter-patch distances. Similarly, although smaller in area, it is less disturbed, supports similar numbers of rare species compared to PPNP (Oldham, 1983), is owned by multiple parties, shows much more marginal land, and property is lower in price. Thus, from a landscape perspective, it might serve better as a core area.

In conclusion, the satellite imagery showed that this region is indeed highly fragmented and forest cover ranged from less than 3 % in the area surrounding PPNP to 14% on Pelée Island. The distances between forest patches were great enough in Pelée-north that the conservation of the few remaining high-quality patches should be emphasized. In contrast, these distances are so great that afforestation, or any other restoration activity, will have little functional impact on landscape connectivity. Thus Cedar Creek and Pelée Island might be better candidate areas for restoration. However, only one of the WIAs planted over the last 25 years was located on Pelée Island. In fact, there is so little forest remaining and the cost of land so high in the region extending from Rondeau to Harrow that the idea of using PPNP as a core site might be questioned.

CHAPTER 3

EVALUATING THE SUCCESS OF DECIDUOUS FOREST RESTORATION IN SOUTHWESTERN ONTARIO, CANADA

Stéphane M. McLachlan[1]
Dawn R. Bazely[1]

[1]Department of Biology, York University, North York, ON, Canada M3J 1P3

Abstract

At present, forest cover in southwestern Ontario, Canada, remains at less than 5% due to intensive agricultural and urban land use. While remaining forest fragments are increasingly protected by legislation, they continue to be degraded by the spread of non-native plant species, deer overgrazing, and recreational use. Some parks in the region have therefore adopted management programs aimed at mitigating this degradation. Over the last 35 years, cottages and roads at Point Pelée National Park have been removed and sites both passively and actively restored. In 1994 and 1995, we assessed the effectiveness of restoration by comparing 28 former cottage and road sites with less disturbed reference sites. We analyzed the understorey plant community composition, while taking into account the effects of selected environmental and landscape variables. There was a significant increase in similarity between restored and reference sites as time-since-restoration (TSR) increased. However, dominant understorey herbs in reference sites, such as Viola pubescens, Allium tricoccum, Trillium grandiflorum, *and* Dicentra cucullaria, *were absent from all restored sites. Soil moisture, canopy cover,* *distance to continuous forest, and site-shape all significantly affected plant community composition. Former road sites recovered more rapidly than former cottage sites, while lawns in passively restored sites were the slowest to recover. After 5 years TSR, non-native ruderals continued to dominate actively restored sites. Non-native species also dominated the seedbanks of recently restored sites while native species richness in seedbanks increased with TSR. Seedbanks of newly restored sites were relatively species-poor. The observed recovery of plant communities in restored sites could be attributed to their proximity to natural vegetation which provided a seed source. In some sites, full recovery appeared to have occurred already and, assuming present trajectories of change are maintained, we predict that full recovery could occur in most mesic sites within 50 years. This rapid recovery suggests that policies aimed at balancing conservation and recreational use in deciduous forests can be successfully implemented.*

Keywords: restoration, conservation, regeneration, succession, disturbance, seed dispersal, multivariate analysis

INTRODUCTION

Agricultural and urban land-use dominate the landscape of southwestern Ontario, the most densely populated region of Canada (Allen *et al.*, 1990). Forest cover stands at less than 5% and remnants tend to be small, isolated, and privately owned (Riley & Mohr, 1994). Currently, 40% of Ontario's rare plant species are restricted to this ecoregion, known as the Deciduous or Carolinian Zone (Allen *et al.*, 1990). While conservation efforts have focused on habitat protection, either through the purchase of parks and conservation areas or, when privately owned, by trust and stewardship agreements (Hilts, 1985; Van Patter, 1990), these protected areas are frequently degraded (Sinclair et al., 1995). Causes of degradation include the spread of non-native species, such as *Alliaria petiolata* (McLachlan, 1997: Chapter 6), deer overgrazing (Alverson *et al.*, 1988; Anderson, 1994; Rooney, 1995; Pearl *et al.*, 1995), as well as recreational, historical, and adjacent land use (Cole & Landers, 1996; Taylor *et al.*, 1993; Matlack, 1993; Drayton & Primack, 1996). Interestingly, the low forest cover of southwestern Ontario contrasts with the trend of increasing forest cover in much of northeastern North America (Foster, 1992).

Since the turn of the century, forest restoration in southern Ontario has emphasized planting trees on marginal farmland. These plantations have the potential to generate additional forest habitat, provide buffer zones for pre-existing habitat, and increase connectivity between remnant patches of forest (Hobbs, 1993). However, in practice, they have tended to be management intensive (McLachlan, 1997: Chapter 5), remain largely isolated from surrounding natural or restored vegetation (McLachlan, 1997: Chapter 2), and bear little resemblance to adjacent pre-existing forest (Lugo, 1992; Larson, 1996). Historically, silviculture has been driven by commercial concerns (Jonasse, 1995) and when considered at all, the forest understorey has been perceived as compromising overstorey productivity and regeneration (Lorimer *et al.*, 1994; Bratton, 1994). In addition, recent studies indicate that understorey flora may take many decades

(MacLean & Wein, 1977; McLachlan, 1997: Chapter 4), if not centuries (Peterken & Game, 1984; Duffy & Meier, 1992; Meier *et al.*, 1995), to recover.

In contrast, more recent forest restoration efforts have tended to emphasize all components of the habitat as well as broader issues of research and education, recreation, and aesthetics (Howell, 1986; McLachlan, 1997: Chapter 6). These efforts have generally: increased in scale from the species to that of the community or ecosystem, involved multiple partners, incorporated multiple use objectives (Grumbine, 1994), and emphasised adaptive management strategies (Bradshaw, 1993). While, most forest restoration in North America, like silviculture, is climax or end-state driven (Lockwood, 1977), the understorey plant community has also become a major focus of forest restoration in Britain (Down & Morton, 1989; Helliwell *et al.*, 1996).

Factors which determine rates of vegetation change or succession associated with forest restoration include assembly rules (Drake, 1990) as well as site availability, species performance, and species availability (Pickett *et al.*, 1987). Changes in understorey plant communities can be accelerated by increasing the availability of colonizing species. Species availability can be promoted by increasing vertical complexity in vegetation (McDonnell & Stiles, 1983; McDonnell, 1986), constructing bird perches (McClanahan & Wolfe, 1993), planting dispersal-restricted species adjacent to their dispersers (Culver & Beattie, 1980), and introducing fruit bearing shrubs (Robinson & Handel, 1993). Succession-based management can be used to regulate these processes (Luken, 1990) and may be effective in controlling exotics (McLachlan, 1997: Chapter 3). It has also been used to arrest vegetational change in utility corridors (Niering, 1987), and to promote vegetational change in tropical (Brown & Lugo, 1994) and bottomland (Shear *et al.*, 1996) forests. An underlying assumption of this management approach is that management promoting succession and increasing vegetation complexity will have overall benefits for other, non-targeted components of the ecosystem.

This study was conducted at Point Pelée National Park (PPNP) in southwestern Ontario. The park has been subjected to extensive human use and disturbance in the past. Habitat restoration has become an important management objective at PPNP and programmes include reintroductions of native species and the control and removal of non-native plants (Dunster, 1990). In addition to these species-level efforts, restoration has been conducted at the ecosystem-level (Reive *et al.*, 1992). The present study evaluated the impact of management promoting forest succession on understorey plant communities. Prior to being designated a park in 1918, PPNP was cleared of white pine (*Pinus strobus*) and planted with the now-dominant hackberry (*Celtis occidentalis*). Agriculture peaked in the 1950s when 40% of the park was allocated to orchard, crop and vegetable production. By 1960, 600 cottages and numerous roads were situated in the park and there were 500,000 annual visitors. At this time, park managers initiated an intensive naturalization program (Reive *et al.*, 1994) and during the last 35 years, the majority of these cottages and roads have been removed. Passive ecosystem restoration consisting of cottage or road removal was conducted from 1960 until the present. In contrast, since 1988, active ecosystem restoration has incorporated the planting of shrubs and alterations of topography and hydrology. In addition to PPNP, we used a second study location, FishPoint Nature Preserve (FPNP), which is minimally disturbed and dominated by Black Maple (*Acer nigra*) and *Celtis occidentalis*, as a reference area.

The specific objectives of this study were: (1) To assess the impact of succession-based restoration on understorey plant communities; (2) To compare the composition of understorey communities of restored and relatively undisturbed, reference deciduous forest sites at PPNP and FPNP; (3) To relate changes in species composition to environmental variables expected to affect rates of recovery; and (4) To compare active with passive restoration. We hypothesised that succession-based management results in increased diversity of native species, and that active habitat restoration aimed at accelerating succession is more effective than passive restoration.

METHODS

Study areas

Point Pelée National Park (PPNP) (lat. 41°54'N, long. 82°22'E) is approximately 1650 ha, of which 1,100 ha is upland forest, while FishPoint Nature Preserve (FPNP), on Pelée Island, (lat. 41°44'N, long. 82°40'E) is 400 ha and dominated by upland forest. These protected areas are located in southwestern Ontario at the northern edge of the Carolinian or Deciduous Forest Zone. This zone represents only 0.25% of Canada's land base, but supports 25% of the country's human population (Allen *et al.*, 1990). Forest cover in the immediate area of the study sites is less than 3% and the remaining forest is highly fragmented. Over 95% of the remnant forest patches are less than 10ha and most are over 1.5km apart (Pearce, 1996). PPNP is the only mainland patch greater than

100ha. This region is the southernmost part of Canada and has the warmest mean temperatures, longest annual frost-free seasons and mildest winters in Ontario (Reid, 1985). Most of the region is a flat former lake bottom with poorly drained, fertile, silt and clay soils (Chapman and Putman, 1984). Both study areas are sandspit formations that extend southward into Lake Erie.

Selection of study sites

In 1994, 28 former road and cottage sites were identified throughout PPNP using aerial photographs, park blueprints and input from long-time park employees. Sites were categorized according to time-since-restoration (TSR) and visual assessment of soil moisture. Because of the long history of widespread disturbance in PPNP, three relatively undisturbed reference sites (10m x 80m) were located at FPNP. In 1995, three additional reference sites (10m x 80m) were identified in relatively undisturbed upland forest at PPNP, using park records.

The herbaceous plant community composition of the sites was measured in June and September, 1994 and May, 1995. The three additional sites in PPNP were also measured in May and September, 1995. Depending on site area and habitat heterogeneity, between 13 and 22 1m x 1m quadrats were randomly located in each site, approximately 10m apart. Pins were used to mark the SE corner of each quadrat. The percentage cover of all herbaceous species and woody species less than 40cm in height was recorded. Species nomenclature followed Morton & Venn (1990) and voucher specimens were deposited in the PPNP herbarium. Non-native species were defined as having been introduced to PPNP since European settlement (c.1700) and were classified according to Jellicoe & Rudkin (1984).

Environmental data collected at all sites in both PPNP and FPNP included: soil moisture, canopy cover, and topography (Table 3.1). Eight soil samples were taken from each site and analyzed for moisture content in September, 1994, and June, 1995. Samples were dried at 100°C for 24 hours before weighing. Percentage canopy cover was estimated at each quadrat corner for all quadrats in all sites. Surface topography was qualitatively assessed and sites were classified as 0 (flat), 1 (rolling), or 2 (hilly).

Historical forest data were collected only for restored sites at PPNP from aerial photos taken at roughly ten year intervals (1933, 1955, 1968 and 1973) using the set that most closely preceded the restoration date. Cottages and roads restored since 1983 were initially described using the most recent aerial photo and this was corroborated by ground truthing. Measurements taken from aerial photos were: the size of the forest gap in which the cottage or road had been situated, site area of the cottage or road, distance-to-continuous forest (DCF), proportion of the site boundary that was adjacent to forest (PAF), whether sites had been cottages or roads (previous use), and shape index (Table 3.1). Shape index was calculated from the forest gap using the formula $Is=P/(2\sqrt{A\pi})$, where P is the gap perimeter and A is the area (Faeth & Kane, 1978). The value of this index increases the more the shape departs from a circle; for a circle, $Is=1$. DCF was measured by dividing the longest axis of each site into three equal parts. From the two points at which the long axis intersected these divisions, 8 polar axes (N, NE, E, SE, S,

Table 3.1. Environmental variables measured in restored sites and from aerial photographs of sites at PPNP, 1994-1995.

Environmental variable	Abbreviation	Variable	Dimension
Physical			
Time-since-restoration	TSR	continuous	years
Soil moisture*	Soilm	continuous	dry weight %
Canopy cover*	Cancov	continuous	cover %
Landscape			
Distance to continuous forest	DCF	continuous	m
Proportion of adjacent forest	PAF	continuous	length %
Gap area	Gaparea	continuous	m^2
Site area	Sitarea	continuous	m^2
Shape index	Shapind	continuous	none (ratio)
Topography*	Surftop	continuous	1-3
Previous use	Prevuse	categorical	road/cottage
Restoration type	Restype	categorical	passive/active

* also measured at PPNP and FPNP reference sites

SW, W, NW) were drawn. The three shortest distances to continuous forest along these axes were measured and averaged for the entire site (Table 3.2).

Seedbank composition was assessed at each site from eight 20cm x 30 cm x 15 cm deep turves collected from restored sites at PPNP and reference sites at FPNP in June 1994. Each of these was sampled from 0.5 m south of eight randomly selected quadrats in each site. Turves were stored in a partially-shaded, protected nursery at PPNP, regularly watered, and periodically stirred. Seedlings were identified and removed at least five times each year for three years. Four pots containing sterilized soil were placed in the nursery as controls, in order to identify species seeding in from the nursery area.

Statistical analyses

Sorensen's coefficient of similarity (SCS) was used to compare restored and reference sites at PPNP with reference sites at FPNP over time (Kappelle et al., 1995) and can be written as:

$$SCS = 2c/(a + b + 2c)$$

where a is the number of species unique to plot A, b the number of species unique to plot B, and c the number of species shared by plots A and B. Each PPNP site was compared to each of the three sites at FPNP and values were averaged to generate a mean SCS value for each PPNP site.

Two-way indicator species analysis (TWINSPAN) (Hill, 1979) and canonical correspondence analysis (CCA) (ter Braak, 1988, 1990) were used to explore changes in species composition and their relationship with measured environmental variables.

Table 3.2. Summary of environmental properties and spatial characteristics of each site: previous use (prevuse), time-since-restoration (TSR), restoration type (restype), canopy cover (cancov), soil moisture (soilm), and distance to continuous forest (DCF).

Site	Prevuse[1]	TSR	Restype[2]	Cancov (total quadrat no. =553)		Soilm (n=8)		DCF (n=6)	
		(years)		$\bar{x}$ (%)	SE	$\bar{x}$ (%)	SE	$\bar{x}$ (m)	SE
MiddR	2	1	2	46	7.41	6.6	0.80	1.7	2.2
MiddC	1	1	2	43	8.30	8.1	0.41	24.5	0.6
DuneC	1	2	2	62	3.73	7.2	1.13	19.4	3.68
DuneR	2	2	2	49	6.53	7.0	0.93	2.4	0.73
EastB	2	4	2	37	10.35	10.6	3.20	3.3	0.13
Kraus	1	4	1	33	7.07	8.9	1.60	7.7	0.89
GaryC	1	6	2	34	8.65	7.9	0.88	9.5	0.34
GaryRN	2	6	2	37	7.95	8.5	2.10	3.7	0.22
TipR	1	7	1	13	6.87	5.9	0.14	6.8	1.62
MarsC	1	10	1	43	9.07	8.2	2.10	4.1	1.33
MarsR	2	10	1	77	2.55	8.7	1.31	3.5	0.01
Wpine	1	11	1	47	7.42	8.6	2.70	7.9	1.75
Stucc	1	17	1	70	5.82	12.0	3.12	9.3	0.97
Ogar	1	18	1	48	8.89	10.0	2.25	4.1	0.75
Ribb	1	18	1	22	7.02	7.5	0.92	20.1	1.08
Tav	1	18	1	74	3.44	16.3	2.22	86.6	7.26
GaryRS	2	19	1	60	6.89	9.4	1.76	1.4	0.15
BWBC	2	20	1	72	6.62	8.3	3.24	4.2	9.8
AndC	1	21	1	47	7.22	11.0	1.55	19.4	5.7
Brun	1	21	1	65	5.98	10.1	3.43	24.3	0.01
Indian	1	23	1	77	5.34	9.6	4.10	5.3	0.71
Tild	1	24	1	85	3.15	14.5	2.29	12.2	0.21
WardR	2	26	1	77	4.10	5.9	1.17	4.6	0
VC	1	28	1	76	2.51	8.8	0.93	27.2	8.57
AndR	2	29	1	65	5.59	7.9	1.34	3.5	0.04
Schl	1	30	1	30	7.32	7.1	0.24	42.1	3.43
PostH	1	31	1	81	1.53	9.1	1.37	20.3	5.14

Dust	1	32	1	39	7.33	6.8	2.43	24.0	0
FishA	4	*	*	74	2.99	9.2	1.11	*	*
FishB	4	*	*	83	1.83	11.6	2.59	*	*
FishC	4	*	*	82	3.60	6.3	1.41	*	*
Sanc	3	*	*	82	2.00	8.3	0.99	*	*
Sleep	3	*	*	74	4.79	9.1	2.14	*	*
WNT	3	*	*	77	3.17	9.3	2.00	*	*

[1] (1): cottage site; (2): road site; (3): PPNP reference site; (4): FPNP reference site.

[2] (1): passively restored; (2): actively restored.

TWINSPAN is a classification technique in which sites are situated on detrended correspondence analysis (DCA) ordination axes and then polarized using indicator species. CCA is a multivariate technique which maximally separates species distribution in ordination space; stand and species placements are constrained to be linear combinations of environmental variables (ter Braak, 1988). TWINSPAN was conducted on a data set that included both restored and reference sites whereas CCA were conducted only on restored sites as well as on the subset of sites restored since 1983.

Default settings were used and species occurring less than twice were eliminated from the analysis. A minimal set of environmental variables that adequately explained the species data was selected using forward stepwise multiple regression as determined by a Monte Carlo simulation test set at 999 permutations.

As previously stated, diversity measures were calculated for each site, even though they were of different areas. However, no significant relationship was found between either exotic ($F_{1,27}$=0.35, p=0.5576) or native ($F_{1,27}$=2.36, p=0.1363) species richness and site area. In addition, quadrat number per site varied depending on the site area and habitat heterogeneity of each site. However, cumulative area/ species richness curves calculated for each site all showed an asymptote around the x-axis (McLachlan, 1997: Chapter 5), thus we were able to present diversity measures at the site level.

Univariate ANOVA and ANCOVA were conducted with SAS (1990). If necessary, log or square root transformations of data were conducted to achieve homogeneity of variance (Sokal & Rohlf, 1981). Only untransformed data were presented in the results.

RESULTS

Plant community composition and classification of the entire data set

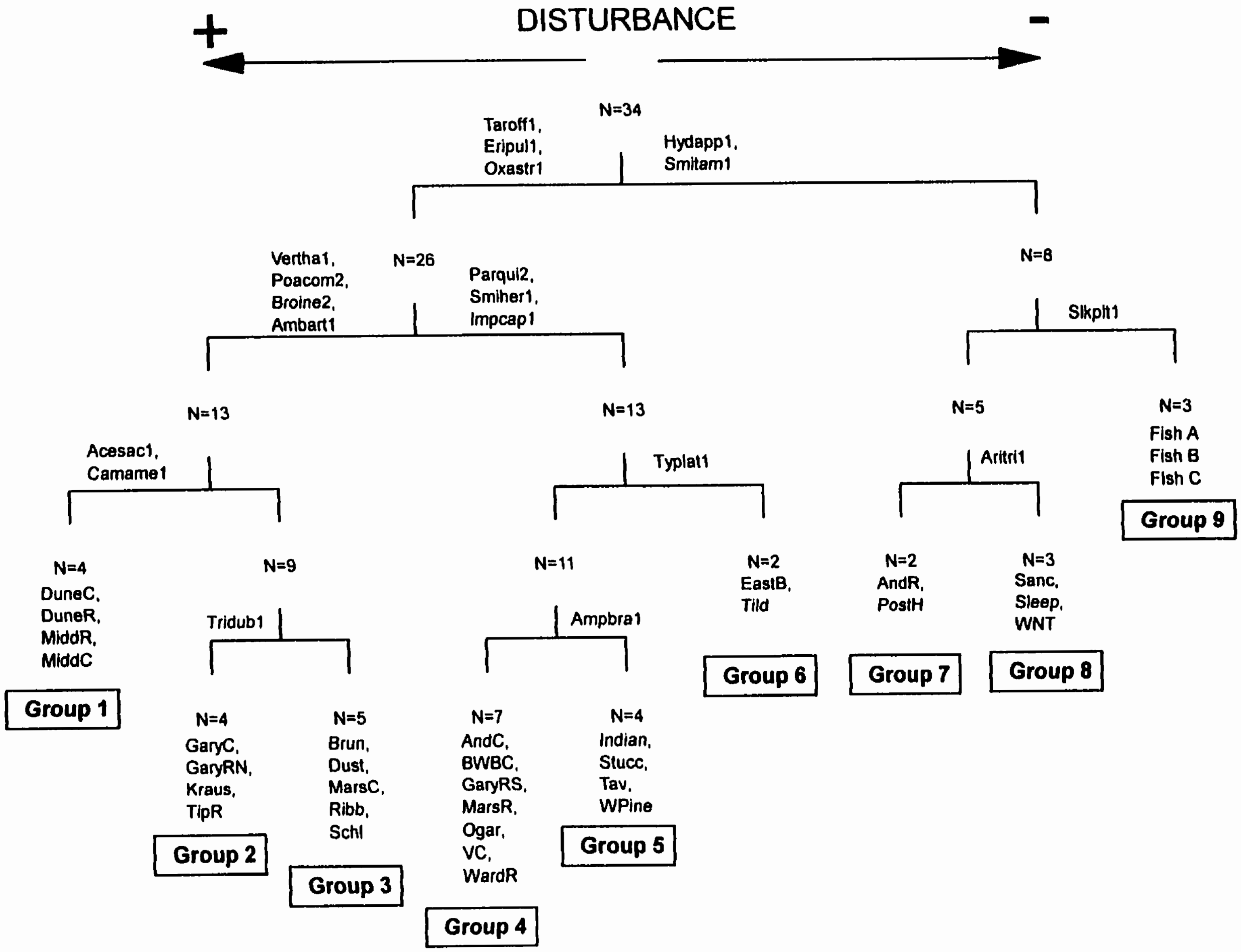
The first division of the TWINSPAN analysis of herbaceous plant community data distinguished recently restored sites from long-term restoration and reference sites (Figure 3.1). Species associated with more recently restored sites included *Oxalis stricta* and *Erigeron pulchellus* while older restored sites and reference sites included *Hydrophyllum appendiculatum* and *Smilax tamnoides*. Overall, the TWINSPAN classification distinguished nine groups (Figure 3.1). The grouping appeared to be largely determined by soil moisture, canopy cover, and time-since-restoration (TSR) with mesic sites of all ages exhibiting a relatively high degree of overlap (Table 3.2).

Group 1: Dry sites restored in 1994 and 1995 having intermediate canopy cover (Table 3.2). Species distinguishing these sites included *Acer saccharum* and *Campanula americana* and associated species included *Setaria viridis*, *Chenopodium album*, and *Digitaria sanguinalis*.

Group 2: Dry sites restored since 1990 exhibiting low to intermediate canopy cover (Table 3.2). Associated species included *Berteroa incana*, *Poa pratensis*, *Glechoma hederacea*, *Verbascum thapsus*, and *Potentilla recta*.

Group 3: Dry sites restored in the 1960s and 1970s with intermediate canopy cover (Table 3.2). They were distinguished from those restored in the 1980s and 1990s by *Trifolium dubium* and associated with *Phryma leptostachya*, *Bromus inermis*, *Prunus serotina* and *Osmorhiza longistylis*.

Figure 3.1. Results of the TWINSPAN classification of 34 sites (28 restored sites at Point Pelée National Park (PPNP), three reference sites at PPNP and three at FishPoint Nature Preserve). TWINSPAN resolved the sites into 9 groups based on herbaceous data. The indicator species and sites at each division are given. See Table 3.2 for site abbreviations and Appendix 1 for species abbreviations.


DISTURBANCE
+
-
N=34
Taroff1,
Eripul1,
Oxastr1
Hydapp1,
Smitam1
N=26
Vertha1,
Poacom2,
Broine2,
Ambart1
Parqui2,
Smiher1,
Impcap1
N=8
Slkplt1
N=13
Acesac1,
Camame1
N=13
Typlat1
N=5
Aritri1
N=3
Fish A
Fish B
Fish C
Group 9
N=4
DuneC,
DuneR,
MiddR,
MiddC
Group 1
N=9
Tridub1
N=11
Ampbra1
N=2
EastB,
Tild
Group 6
N=2
AndR,
PostH
Group 7
N=3
Sanc,
Sleep,
WNT
Group 8
N=4
GaryC,
GaryRN,
Kraus,
TipR
Group 2
N=5
Brun,
Dust,
MarsC,
Ribb,
Schl
Group 3
N=7
AndC,
BWBC,
GaryRS,
MarsR,
Ogar,
VC,
WardR
Group 4
N=4
Indian,
Stucc,
Tav,
WPine
Group 5

Groups 4&5: Mesic sites restored in the 1970s and 1980s with intermediate to high canopy cover (Table 3.2). They were associated with *Alliaria officinalis*, *Osmorhiza longistylis*, *Geranium robertianum* and *Smilax herbacea.* Group 5 was distinguished from Group 4 by *Amphicarpa bracteata.*

Group 6: Wet sites distinguished by *Typha latifolia* and associated with *Verbena urticifolia*, *Equisetum hyemale*, *Salix spp.*, and *Eupatorium album* (Table 3.2).

Group 7: Largely recovered mesic sites restored in the 1960s with high canopy cover (Table 3.2). They were associated with *Osmorhiza claytonii*, *Bromus inermis*, and *Solidago altissima.*

Group 8: Reference sites at PPNP with high canopy cover and intermediate soil moisture (Table 3.2). These were distinguished from mesic sites restored in the 1960s by *Arisaema triphyllum* and were associated with the presence of *Maianthemum canadense* and *Viola pubescens.*

Group 9: Reference sites at FPNP with intermediate soil moisture and high canopy cover (Table 3.2). They were distinguished from reference sites at PPNP by the presence of *Aralia nudicaulis* and were associated with *Trillium grandiflorum*, *Allium tricoccum*, *Urtica gracilis*, and *Hydrophyllum appendiculatum.*

The seedbanks of turves sampled from sites showed that newly restored sites had significantly lower non-native and native species richness than older restored sites and lower native species richness than reference sites (Table 3.3). When TWINSPAN was conducted on seedbanks from restored and reference sites, results were similar to those for herbaceous ground cover. Species that were associated with the seedbanks of newly

Table 3.3. The effect of time since restoration on species richness (total number of species per site) of the seedbank of restored sites at PPNP and reference sites at FPNP, 1994-1995. Age classes are: sites restored in 1994, from 1990 to 1993, from 1980 to 1990, from 1970 to 1980, from 1960 to 1970, and reference sites from FPNP. Data for non-native and total species richness were square-root transformed for ANOVA.

		Species richness		
Year of site restoration	no. of sites	Native	Non-native	Total
1994	2	4.5 (3.5) *a**	10.5 (7.5)ad	15.0 (11)a
1990	6	16.4 (2.5)b	20.0 (2.6)b	36.4 (3.0)b
1980	4	17.8 (2.8)bc	15.0 (3.0)bcd	32.8 (4.9)b
1970	8	23.9 (1.5)cd	16.6 (1.2)bc	40.4 (1.8)b
1960	7	25.9 (1.7)d	10.9 (0.7)cd	36.7 (2.2)b
Ref (FPNP)	3	16.0 (2.0)b	4.7 (0.3)a	20.7 (1.7)a

*each mean value followed by standard error in parenthesis

** values followed by different letters within each row significantly different at $p<0.05$

restored sites were generally non-native and included *Digitaria sanguinalis*, *Datura stramonium* and *Chenopodium album*. Recently restored sites from the 1980s were associated with non-native species such as *Agropyron repens*, *Poa compressa*, and *Alliaria officinalis* and native species which included *Solidago canadensis* and *Rubus occidentalis*. Finally seedbanks of reference sites were associated with native species including *Allium tricoccum*, *Viola pubescens*, *Urtica gracilis*, and *Hydrophyllum appendiculatum*.

Environmental variables associated with plant community composition in restored sites at PPNP

Canonical correlation analysis revealed that the understorey plant community composition was largely determined by soil moisture, time since restoration (TSR), distance to continuous forest (DCF), shape index, and canopy cover (Figure 3.2). Although environmental variables exhibited some degree of intercorrelation, none was greater than r=0.77 (Table 3.4). Predictably, canopy cover (r=0.48) and soil moisture (r=0.41) both increased with TSR. PAF (r=0.61) and previous use (r=0.55) were positively correlated with topography suggesting that roads were more hilly than cottage sites and more surrounded by forest. Thus, shape index was also positively correlated with proportion of adjacent forest (PAF) (r=0.77). TSR was positively associated with previous use (r=0.68) indicating that roads tended to be older than cottage sites, thus topography was positively associated with TSR (r=0.50). Predictably, TSR was negatively associated with restoration type (r=-0.72) as only new sites were actively

Table 3.4. Correlation coefficients among environmental and spatial variables from CCA of herbaceous plant community composition in restored sites (n=28) at PPNP, 1994 -1995. Selected environmental variables are: canopy cover (cancov), soil moisture (soilm), site area (sitarea), proportion of adjacent forest forest (PAF), distance to continuous forest (DCF), forest gap area (gap area), shape index (shapind), time-since-restoration (TSR), surface topography (surftop), restoration type (restype), and previous use (prevuse).

	Cancov	Soilm	Sitarea	PAF	DCF	Gaparea	Shapind	TSR	Surftop	Restype
Soilm	0.41*									
Sitarea	-0.37	-0.04								
PAF	-0.08	0.00	0.48*							
DCF	0.21	0.56*	-0.11	-0.40						
Gaparea	-0.14	-0.19	-0.09	-0.20	0.16					
Shapind	-0.08	-0.16	0.38	0.77*	-0.22	-0.06				
TSR	0.48*	0.11	-0.26	-0.19	0.28	0.41*	-0.06			
Surftop	-0.24	0.04	0.32	0.61*	-0.38	-0.15	0.37	-0.50*		
Restype	-0.32	-0.16	0.33	0.31	-0.23	-0.16	0.04	-0.72*	0.49*	
Prevuse	0.10	-0.18	0.17	0.77*	-0.45*	-0.19	0.68*	-0.21	0.55*	0.28

*p <0.05 according to Bonferonni adjusted Spearman's rank coefficients restored. In the CCA, 33.6% and 45.0% of the variance was explained by the first four vegetation-determined ordination axes and selected environmental variables, respectively (Table 3.5).

The first CCA axis was positively associated with DCF, soil moisture, and canopy cover (Table 3.6, Figure 3.2) and associated with *Amphicarpa bracteata*, *Hedera helix*, and *Hemerocallis fulva*. Axis 2 was positively associated with canopy cover, soil moisture, and TSR and associated with *Equisetum hyemale*, *Galium trifidum*, *Salix spp.*, and *Onoclea sensibilis*. Axis 3 was positively associated with TSR and canopy cover and negatively associated with restoration (Table 3.6). Correspondingly, species positively associated with this axis included *Rosa blanda*, *Tovara virginiana*, *Geranium robertianum*, *Smilacina stellaria*, *Rhus aromatica*, and *Prunus serotina* whereas negatively associated species included *Phalaris arundinacea*, *Eupatorium album*, *Lindera benzoin*, *Equisetum arvense*, *Lycopus uniflorus*, and *Typha latifolia*. Finally axis 4 was negatively associated with shape index, previous use, and PAF (Table 3.6). Associated species included *Phalaris arundinacea*, *Lindera benzoin*, *Eupatorium album*, *Menispermum canadense*, and *Polygonatum canaliculatum*.

Forward selection on the linear combinations of environmental variables for the first two CCA axes suggested that herbaceous species composition was most significantly affected by soil moisture, DCF, canopy cover, and, to a lesser degree, TSR.

Table 3.5. Summary diagnostic statistics from CCA on herbaceous plant community composition in: a) all restored sites (n=28) and b) sites restored since 1980 (n=12) at PPNP, 1994-1995.

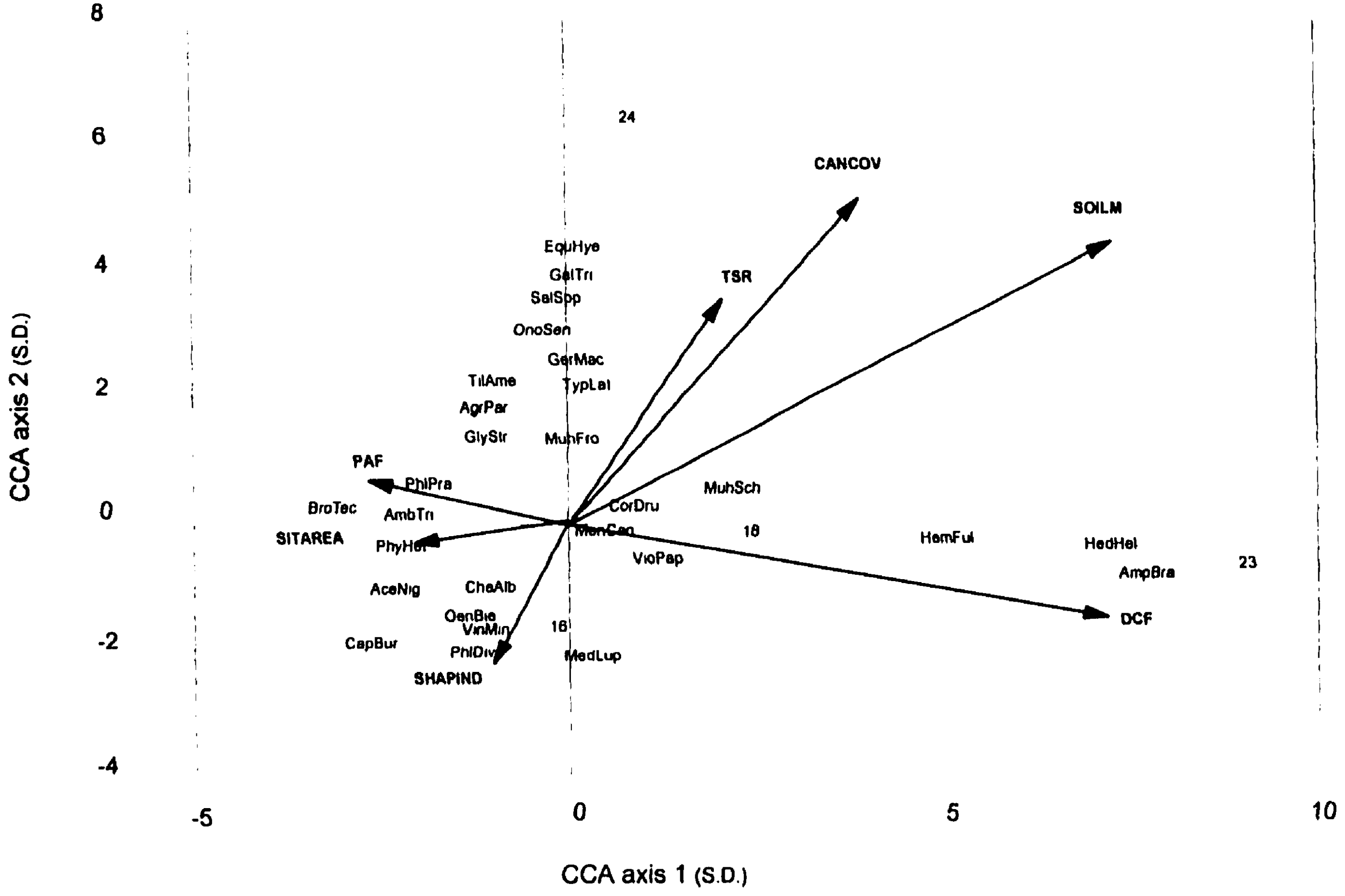
CCA axis	All restored sites			Sites restored since 1980		
	Eigenvalue	Species-env correlation	Cumulative % Variance	Eigenvalue	Species-env correlation	Cumulative % Variance
1	0.552	0.933	10.6	0.416	0.956	15.2
2	0.500	0.829	20.2	0.387	0.919	29.3
3	0.435	0.914	28.5	0.228	0.833	37.6
4	0.265	0.866	33.6	0.203	0.923	45.0

Table 3.6. Correlation coefficients between environmental variables and the first four ordination axes of the canonical correspondence analysis (CCA) on all restored sites (n=28) at PPNP, 1994-1995. Selected environmental variables are: canopy cover (cancov), soil moisture (soilm), site area (sitarea), proportion of adjacent forest forest (PAF), distance to continuous forest (DCF), forest gap area (gap area), shape index (shapind), time-since-restoration (TSR), surface topography (surftop), restoration type (restype), and previous use (prevuse).

Environmental Variable	CCA Axis 1	CCA Axis 2	CCA Axis 3	CCA Axis 4
Cancov	0.447*	0.543*	0.526*	-0.286
Soilm	0.761*	0.469*	-0.364*	-0.076
Sitarea	-0.276	-0.044	-0.432*	-0.139
PAF	-0.228	0.095	-0.202	-0.491*
DCF	0.883*	-0.165	-0.056	0.165
Gaparea	-0.021	-0.091	0.079	0.001
Shapind	-0.084	-0.270	0.083	-0.635*
TSR	0.243	0.389*	0.657*	0.069
Surftop	-0.202	-0.191	-0.366*	-0.268
Restype	-0.315*	-0.265	-0.569*	-0.362*
Prevuse	-0.183	-0.083	0.140	-0.512*

*$p < 0.05$ according to Bonferonni adjusted Spearman's rank coefficients

Figure 3.2. Canonical correspondence analysis (CCA) diagram of restored sites (axes 1 and 2) based on herbaceous data with environmental variables indicated by biplot arrows. herbaceous species with high scores. and sites with high scores. Species are listed by first three letters of genus and species and abbreviations are included in Appendix 1.



8
6
4
2
0
-2
-4
CCA axis 2 (S.D.)
-5
0
5
10
CCA axis 1 (S.D.)
24
CANCOV
SOILM
TSR
EquHye
GalTri
SalSpp
OnoSen
GerMac
TilAme
TypLat
AgrPar
GlySir
MuhFro
PAF
PhlPra
BroTec
AmbTri
SITAREA
PhyHet
CorDru
MuhSch
MenCan
18
HemFul
HedHel
23
AmpBra
VioPap
AceNig
CheAlb
OenBie
VinMin
16
CapBur
PhlDiv
MedLup
DCF
SHAPIND

Comparison of similarity indices between restored and reference sites

The similarity between restored sites (n=28) and reference sites (n=3) at FPNP was used as the primary indicator of habitat recovery. The Sorensen's coefficient of similarity (SCS) between restored and reference sites represented a value averaged for all three reference sites at FPNP. Predictably, FPNP sites were most similar to each other (SCS mean=1.94, SE=0.31, n=3). Overall, for all species, SCS increased linearly as TSR increased (y=0.0119x +0.306, $F_{1,27}$=25.3, p<0.0001) indicating that the plant community composition of restored sites was becoming more similar to the reference sites from PPNP. Thus, restored sites were recovering over time (Figure 3.3a).

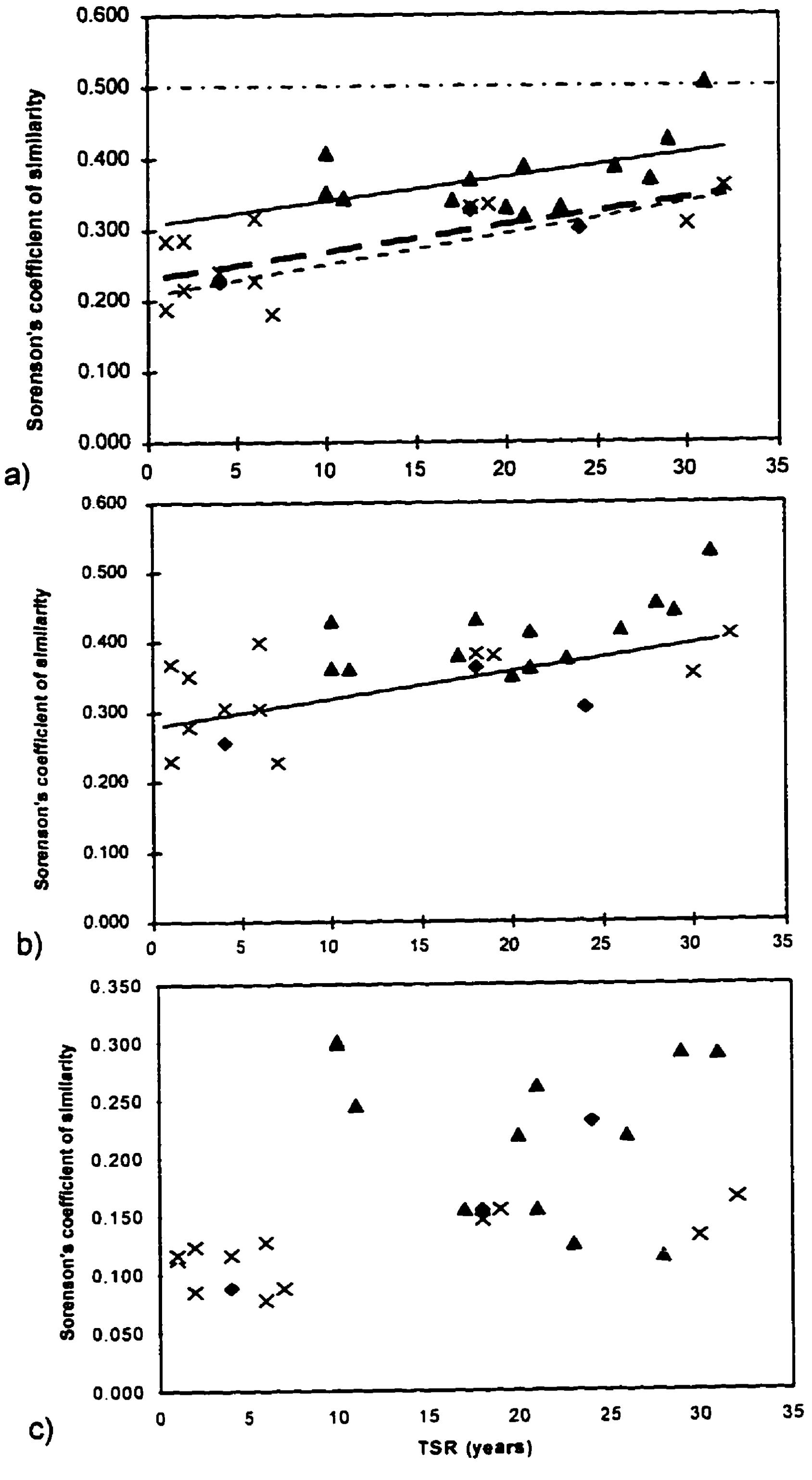
When sites at PPNP were compared to FPNP sites, the PPNP reference sites were the most similar to FPNP sites (SCS mean=1.02, SE=0.06, n=9). Most restored sites at PPNP were relatively different from FPNP reference sites. The exception was one mesic cottage site from the 1960s (PostH) that exhibited even greater similarity to reference sites from FPNP than those from PPNP (SCS mean=1.04, SE=0.13, n=3). When the soil moisture of restored sites was classified as dry (<8%), mesic (8-10%), or wet (>10%), and their SCS was regressed against TSR for each soil moisture class, the intercept of mesic sites was significantly greater than that of either dry or wet sites (ANCOVA=2.09, p<0.034) (Figure 3.3a). This suggested that overall differences in species composition among sites were due to differences in soil moisture but that regeneration rates were similar for all soil moisture classes, as reflected by similar slopes of regressions.

In contrast to the effect of soil moisture on SCS for herbaceous species as a whole, when native species were examined as a separate group, SCS increased with TSR.

Figure 3.3a. Relationship between Sorenson's coefficient of similarity (SCS) and time since restoration (TSR) for all herbaceous species in restored sites at PPNP. FPNP reference sites were used to generate all SCS values.. — dry sites, —— mesic sites, -- wet sites. Dry sites: $y=0.004x + 0.230$, $F_{1,10}=10.17$, $p=0.009$; mesic sites: $y=0.004x + 0.306$, $F_{1,12}=4.02$, $p=0.047$; wet sites:, $y = 0.004x + 0.2280$. $F_{1,10}=2.25$, $p=0.391$. SCS = 0.66 and 0.50 for FPNP and PPNP reference sites, respectively. Only the latter are indicated. x dry sites, ▲ mesic sites, ● wet sites.

Figure 3.3b. Relationship between Sorenson's coefficient of similarity (SCS) and time since restoration (TSR) for native herbaceous species in restored sites at PPNP. FPNP reference sites were used to generate all SCS values. When all sites combined, $y = 0.004x + 0.298$, $F_{1,27}=18.27$, $p=0.0002$. x dry sites, ▲ mesic sites, ● wet sites.

Figure 3.3c. Relationship between Sorenson's coefficient of similarity and TSD for non-native herbaceous species in restored sites at PPNP. FPNP reference sites were used to generate all SCS values. x dry sites, ▲ mesic sites, ● wet sites.


a)
Sorenson's coefficient of similarity
0.600
0.500
0.400
0.300
0.200
0.100
0.000
0
5
10
15
20
25
30
35
b)
Sorenson's coefficient of similarity
0.600
0.500
0.400
0.300
0.200
0.100
0.000
0
5
10
15
20
25
30
35
c)
Sorenson's coefficient of similarity
0.350
0.300
0.250
0.200
0.150
0.100
0.050
0.000
0
5
10
15
20
25
30
35
TSR (years)

but was unaffected by soil moisture (Figure 3.3b). There was no linear relationship between SCS and TSR when the non-native component of restored sites at PPNP was compared to FPNP reference sites (Figure 3.3c). This was because FPNP had very few non-native species unlike restored sites in PPNP, which were largely dominated by non-native species (Table 3.7). However, dry sites were significantly less similar to reference sites than either mesic or wet sites ($F_{1,29}$=3.37, $p<0.001$).

Impact of active restoration on species richness, community composition, and SCS

When all sites were included in the statistical analysis, different types of restoration activity were confounded with TSR, because active restoration was conducted only in the last eight years. Consequently, a subset of more recently restored sites, which excluded sites restored in the 1960s, was analyzed. In addition, each site was divided into lawn, cottage, and edge habitat types.

Species richness.

TSR significantly affected the species richness of both non-native and total species. In contrast, habitat type significantly affected only native species richness (Table 3.8). The species richness of both non-native and total species was higher in actively restored sites than in passively restored sites from the 1980s or 1970s (Table 3.9). Similarly, the species richness of actively restored sites was higher than that of passively restored sites of the same age but equivalent to that of sites restored in the 1970s (Table 3.9). With respect to habitat type, the species richness of both non-native and total species was significantly lower in lawn sites than either cottage or edge sites (Table 3.10).

Table 3.7. Herbaceous species associated with passively restored sites (since 1980), actively restored sites (since 1990), high quality restored sites (1960s) and reference sites as identified by canonical correspondence analysis (CCA) and TWINSPAN. Species for restored sites and reference sites were identified by CCA and TWINSPAN, respectively.

Passive (1980s) CCA1[1]	Active (1980s+) CCA3	Recovered (1960s) CCA3	Undisturbed TWIN[2]
Ambrosia trifida	*Phlox divaricata*	*Rosa blanda*	*Aralia nudicaulis*
Stellaria vulgatum[3]	***Medicago lupilina***	*Tovara virginiana*	*Trillium grandiflorum*
Veronica arvensis	***Capsella bursa-pastoralis***	*Geranium robertianum*	*Acer nigrum*
Erigeron canadensis	*Oenothera biennis*	*Smilacina stellaria*	*Hydrophyllum virginianum*
Capsella bursa-pastoralis	*Acer nigrum*	*Rhus aromatica*	*Allium tricoccum*
Lamium amplexicaule	***Chenopodium album***	*Prunus serotina*	*Dicentra cucullaria*
Urtica dioica	***Vinca minor***	*Ranunculus abortivus*	*Urtica gracilis*
Verbascum thapsus	***Plantago major***	*Onoclea spp.*	*Hydrophyllum appendiculatum*
Euphorbia maculata	*Asclepias syriaca*	***Lonicera japonica.***	*Smilacina stellaria*
Oenothera biennis	***Digitaria sanguinalis***	***Scilla spp.***	*Arisaema triphyllum*
Hesperis matronalis	***Portulaca oleracea***	*Osmorhiza claytoni*	*Viola pubensis*
	Lamium purpureum	*Osmorhiza longistylis*	*Maianthemum canadense*
		Ornithogalum umbellatum	

[1] CCA1 is the first ordinal axis, CCA3 is the third ordinal axis associated with these herbaceous species

[2] TWINSPAN groups 8 and 9

[3] Species in bold face are non-native in origin

Table 3.8. ANOVA for the effects of time-since-restoration (TSR) and habitat type on native, non-native, and total species richness at PPNP, 1994-1995. Time since restoration divided into three age classe: (1) passively restored since 1980 (n=7), (2) actively restored since 1980 (n=5), and (3) passively restored since 1970 (n=9). Habitat type classes were: lawn, cottage foundation, and edge.

		Species richness					
		Native		Non-native		Total	
Source	df	SS	F	SS	F	SS	F
Age (A)	2	98.24	2.97	324.76	20.47****	339.46	7.91***
Habitat (B)	2	150.46	5.94*	27.45	1.73	248.88	5.80*
A * B	4	50.70	0.77	18.18	0.57	69.02	0.80
error	72	1190.20		969.55		1545.71	

*p<0.05, **p<0.01,***p<0.001, ****p<0.0001

Table 3.9. Species richness per quadrat in each age of different age classes of restored sites at PPNP in 1994 and 1995. Age classes are: sites actively restored since 1980s (1980 -active), sites passively restored since 1980 (1980-passive), and sites passively restored between 1970 and 1980 (1970-passive).

Age	Species richness		
	Native	Non-native	Total
1970 - passive	8.7AB[1]	3.5A	12.2A
1980 - passive	6.5B	6.6B	13.0A
1980 - active	8.9A	8.8C	17.8B

[1] values followed by different letters within each column significantly different at $p<0.05$ according to Duncan's multiple means test

Table 3.10. Species richness per quadrat in habitat classes in restored sites at PPNP in 1994 and 1995.

Habitat	Species richness		
	Native	Non-native	Total
Cottage	9.6A[1]	5.4AB	15.0A
Edge	8.5A	6.9A	15.3A
Lawn	6.6A	5.0B	11.5B

[1] values followed by different letters within each column significantly different at $p<0.05$ according to Duncan's multiple means test

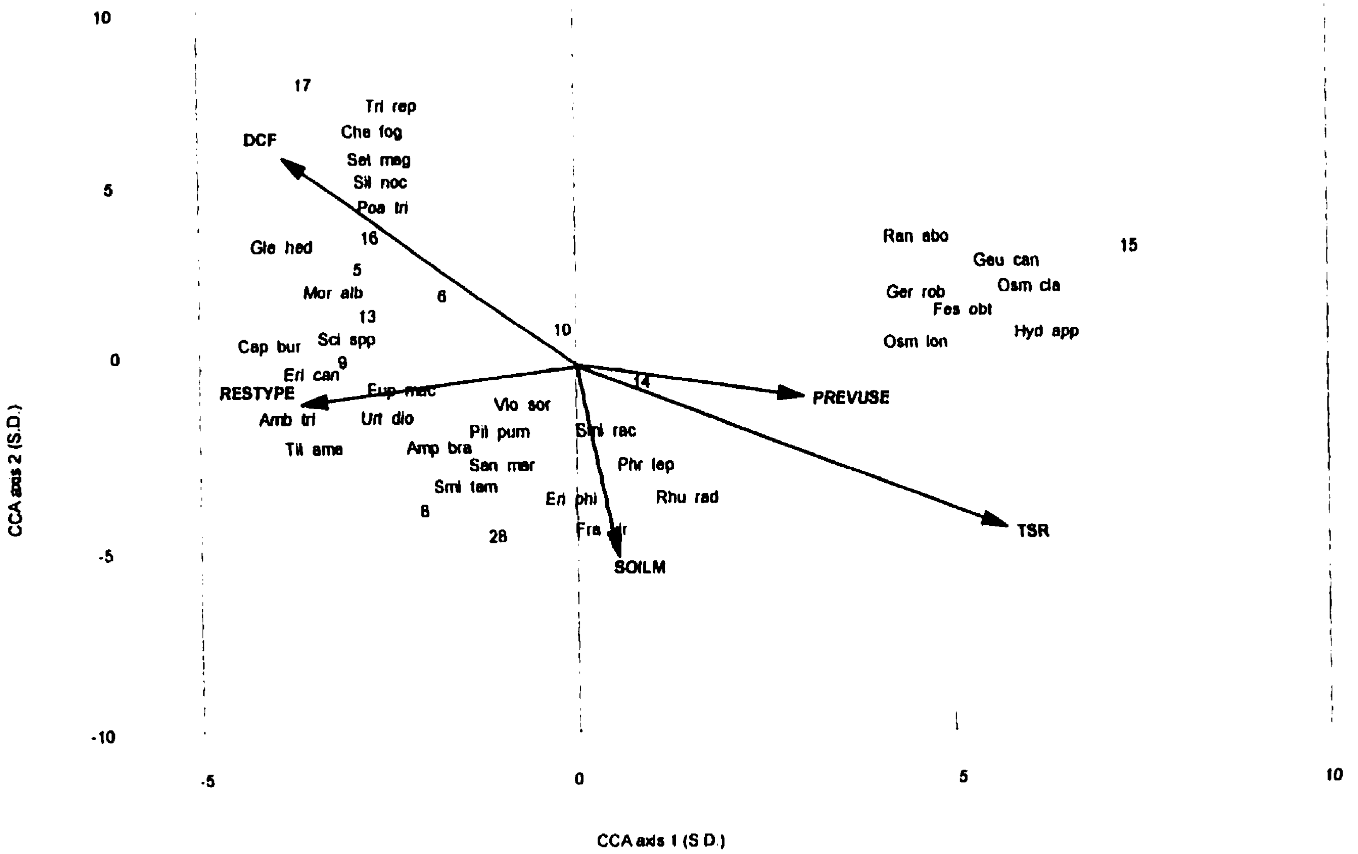
Similarly, the species richness of non-natives tended to be lower in the lawn than in the edge sites.

We compared the vegetation cover and species richness of the former lawn of an actively restored cottage site and a portion of a site that had inadvertently been left unchanged. When percentage cover per quadrat was examined, there were significant differences between the restored and control site for native and non-native classes of herbaceous plants (G=25.74, p<0.001). The control site was dominated by former lawn species that inhibit succession, and ruderals were largely absent, while the restored site was dominated by both inhibitors and ruderals. In contrast, native understorey species were relatively less important in the restored site (Figure 3.4). When species richness was examined there were no significant differences between the restored and control site for native and non-native classes of herbaceous plants (G=4.544,p=0.208) although non-native ruderals tended to be slightly more dominant in the restored site. Little difference was found for native species (Figure 3.4).

Species composition.

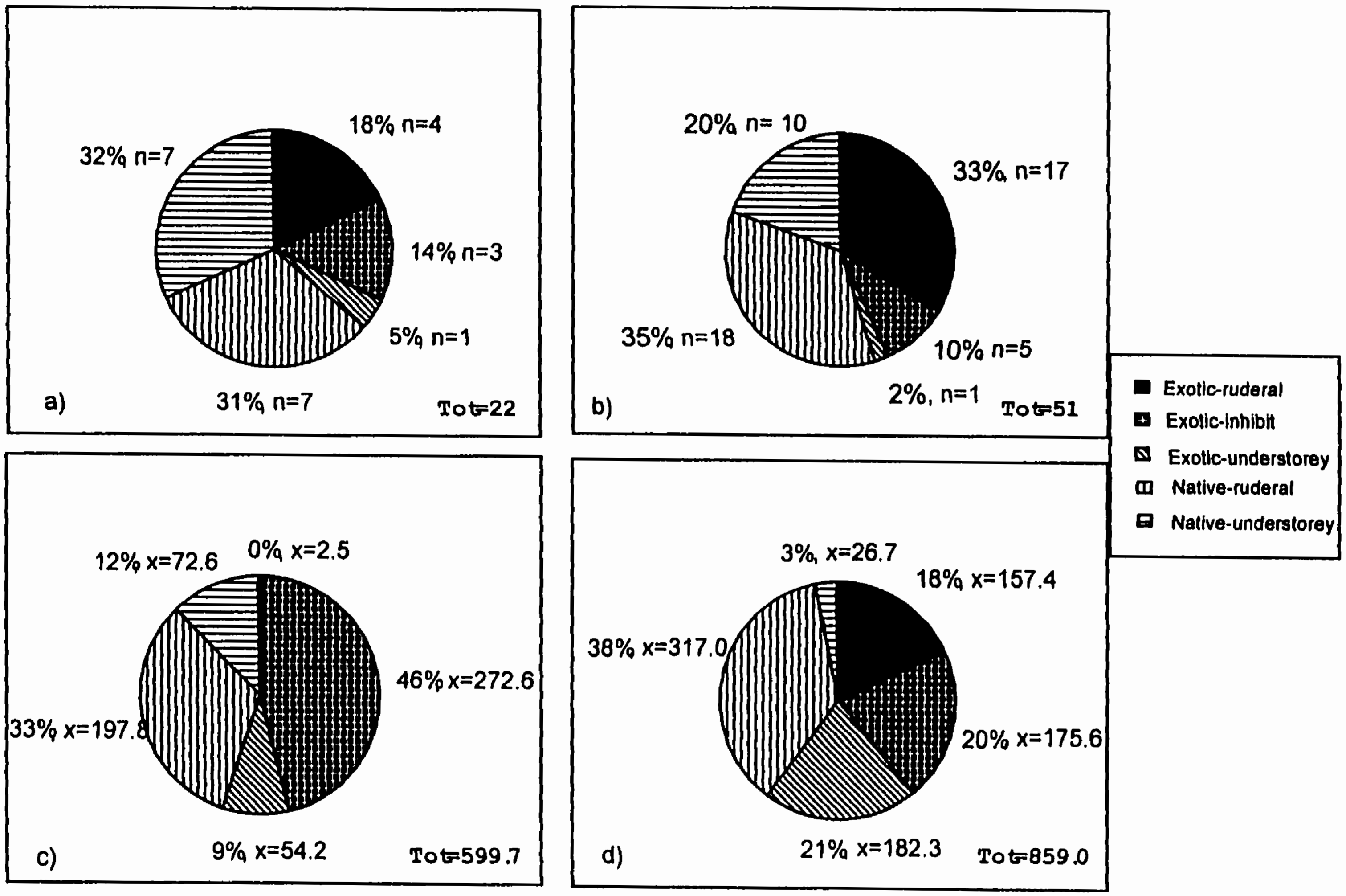
A subset of actively and passively restored sites from the last eight years was included in a CCA analysis (Figure 3.5, Table 3.5, 3.7). The first CCA axis was positively associated with TSR, however, and remained negatively associated with restoration type. Positively associated species included *Osmorhiza claytonii*, *Hydrophyllum appendiculatum*, *Festuca obtusa*, *Geum canadense*, *Osmorhiza longistylis*, *Geranium robertianum*, and *Ranunculus abortivus* while negatively associated species included *Capsella bursa-pastoralis*, *Ambrosia trifida*, *Glechoma hederacea*, *Morus alba*,

Figure 3.4. Canonical correspondence analysis (CCA) diagram of sites restored since 1980 (axes 1 and 2) based on herbaceous data with environmental variables indicated by biplot arrows, herbaceous species with high scores, and sites with high scores. Species are listed by first three letters of genus and species and abbreviations are included in Appendix 1.



CCA axis 2 (S.D.)
10
5
0
-5
-10
CCA axis 1 (S.D.)
-5
0
5
10
DCF
RESTYPE
PREVUSE
TSR
SOILM
17
Tri rep
Che fog
Set meg
Sil noc
Poa tri
16
Gle hed
5
Mor alb
6
13
10
Cap bur
Sci spp
9
Eri can
Eup mac
Amb tri
Urt dio
Vio sor
14
Til ame
Amp bra
Pil pum
Smi rac
Sen mar
Phr lep
Smi tam
Eri phi
Rhu rad
8
28
Fra vir
Ran abo
Geu can
15
Ger rob
Osm cla
Fes obt
Hyd app
Osm lon

Figure 3.5. Differences in percentage cover and species richness between an actively restored site and an adjacent, passively restored site. Values are categorized as exotic ruderal, exotic inhibitor, exotic understory, native ruderal, and native understory herbaceous species. a) percentage cover for actively restored site b) percentage cover for passively restored site c) species richness for actively restored site d) species richness for passively restored site.


a)
18% n=4
32% n=7
14% n=3
5% n=1
31% n=7
Tot=22
b)
20% n= 10
33% n=17
35% n=18
10% n=5
2%, n=1
Tot=51
c)
12% x=72.6
0% x=2.5
46% x=272.6
33% x=197.8
9% x=54.2
Tot=599.7
d)
3%, x=26.7
18% x=157.4
38% x=317.0
20% x=175.6
21% x=182.3
Tot=859.0
Exotic-ruderal
Exotic-inhibit
Exotic-understorey
Native-ruderal
Native-understorey

Tilia americana, and *Erigeron canadensis*. The second CCA axis was positively associated with DCF and negatively associated with soil moisture. Positively associated species included *Trifolium repens*, *Chenopodium foggii*, *Setaria magna*, *Silene noctiflora*, and *Poa trivialis* while negatively associated species included *Fragaria virginiana*, *Erigeron philadelphicus*, *Rhus radicans*, and *Smilax tamnoides*.

SCS

Road sites seemed to have more rapid regeneration than cottage sites especially in sites that had been recently restored. Most road sites had greater-than-predicted similarity to reference sites for native species (Figure 3.3b) and herbaceous species as a whole (Figure 3.3a). When a subset of adjacent pairs of roads and cottages that had been restored in the last 6 years were compared, roads had significantly higher similarity to the reference sites than their companion cottage sites ($F_{1,5}$= 29.74, $p<0.005$). Roads were positively with DCF ($r=0.45$).

DISCUSSION

Overall, this study suggests that highly disturbed deciduous forest sites can be restored successfully within 30-50 years. While we used the similarity between restored sites and reference sites as the primary gauge of recovery, the use of "reference" sites has been questioned recently (Pickett & Parker, 1994, but see Aronson *et al.*, 1995). However, in addition to quantifying the changes in species composition that accompany restoration, we wanted to assess whether they were occurring along a desirable, management-defined trajectory: in this case, a trajectory oriented by a defined deciduous-forest end point (Cairns, 1991). While some extreme approaches to restoration attempt to recreate previously existing ecosystems (SER, 1994), our objective was not to duplicate pre-existing site-conditions or even to define the reference sites at FPNP as an end objective (*sensu* Hobbs & Norton, 1996). Rather, it was to assess whether the observed changes indicated that recovery was occurring.

In using relatively undisturbed forest habitat at the nearby FPNP as the reference site, we found, as expected, that the three sites in FPNP were the most similar. Of the PPNP sites, those that were the least disturbed had the highest similarity to FPNP sites. However, the FPNP sites, with their low, historical levels of disturbance, represented a more conservative means of estimating recovery than the reference sites at PPNP.

One restored site at PPNP, PostH, was as similar to the FPNP reference sites as the PPNP reference sites were. PostH was a mesic site with extensive canopy development, containing few ruderals and persistent, ornamental species. However, along with all other restored sites, this site lacked typical understorey species such as *Viola pubescens*, *Allium tricoccum*, *Trillium grandiflorum*, *Arisaema triphyllum*, *Dicentra cucullaria*. Their absence from restored sites was likely associated with their early-season flowering phenology and restricted seed dispersal (McLachlan, 1997: Chapter 4). Species from this spring ephemeral group were present in only one restored site, MarsC. Their presence here was attributable to a number of contiguous, remnant populations of *Arisaema triphyllum* and *Hydrophyllum appendiculatum* that were present on the edges of that site. However, a large population of *Dicentra cucullaria* located across the road, less than 20m away, had not colonized that site.

Restoration and succession

Clearly, habitat restoration can be viewed as accelerated or facilitated successional change. The mechanisms underlying vegetational change include site availability as well as differential species availability and performance (Luken, 1990; Picket *et al.*, 1987).

Species availability was a major factor in this study. Long-standing disturbance at PPNP has contributed to the presence of a species-poor seedbank, suggesting that species availability in restored sites was dependent on seed immigration from surrounding natural habitat. Seedbanks of newly restored sites were dominated by exotics. As TSR increased and opportunities for seed immigration continued, native species richness increased. The most important landscape variable was distance-to-continuous-forest (DCF). Only one site, Tav, was greater than 80m from standing, continuous forest, and it was characterized by low diversity and associated with remnant ornamentals such as *Hemerocallis fulva* and *Hedera helix* and animal dispersed species such as *Amphicarpa bracteata* and *Muhlenbergia schreberi*. Regeneration also seemed to occur more quickly in road than in cottage sites, in contrast to other studies indicating that road-associated soil compaction tends to impede regeneration (Greacen & Sands, 1980; Corns, 1988). Although park roads in this study were smaller and subject to less traffic than most logging roads, most were asphalted and had been in use since at least 1933. DCF, shape index, and proportion-of-adjacent-forest were all significantly correlated with road use, suggesting that the greater proximity of seed sources and the greater proportion of edge habitat in restored road sites might have contributed to the relatively rapid recovery of these sites.

The slower regeneration in cottage sites was associated with the presence of former lawn species such as *Poa compressa* , *P. pratensis*, and *Festuca rubra* which appear to inhibit successional change (Hiebert, 1990; McLachlan, 1997: Chapter 5).

Other studies of disturbed natural habitat which have estimated recovery times of many decades, or even centuries, describe larger-scale disturbance, such as forest clearing (Brewer, 1980; Duffy & Meier, 1992; Meier *et al.*, 1995; Dzwonko 1993; Peterken & Game, 1984) and flooding (Bratton *et al.*, 1994)). In contrast, our and other studies indicating a relatively rapid site recovery (e.g. Shear *et al.*, 1995) involve smaller-scale disturbance. It seems likely that recovery rates would have been substantially slower if dispersal distance required for immigration and colonization had been greater. However, despite these short distances from continuous forest, we found that, even after 40 years, ant or gravity dispersed species were still almost completely absent from restored sites (McLachlan, 1997: Chapter 4). In contrast, restored sites were dominated by wind and vertebrate dispersed species (McLachlan, 1997: Chapter 4) with dispersal distances of two to three orders of magnitude higher than the dispersal-restricted species (Willson, 1993; Matlack, 1994).

In this study, species performance seemed to be less important than site availability or species dispersal. While native species composition in restored sites became increasingly similar to that of reference sites as TSR increased, late successional, shade tolerant species such as *Acer saccarum* and species that currently dominate the overstorey such as *Celtis occidentalis* colonized sites immediately after restoration. This suggested that successful establishment was less likely to be limited by species performance than by chance-mediated establishment opportunities (*sensu* Egler, 1954). While some studies have indicated that the introduction of mature understorey herbs is often unsuccessful (e.g. Primack & Miao, 1992), others have suggested that it can be a key and productive part of a conservation strategy in protected areas (Gordon, 1994; Reading *et al.*, 1997). If such reintroductions were combined with favourable site conditions, such as those in the 35-year old restored mesic sites, there would be favourable microsites for continued growth and prevent their subsequent displacement by ruderals (Maunder, 1992). The restoration of former topography and hydrology might further improve performance. Alternatively, reintroduction attempts that focus on the seedbank rather than mature plants by introducing soil (Helliwell *et al.*, 1996), divots, and seedlings (Down & Morton, 1989) may be more likely to succeed. Although regeneration should be substantially affected by the existing seedbank (Keddy *et al.*, 1989), few forest restoration projects actively harness this resource (van der Valk & Pederson, 1989).

Restoration practices at PPNP have changed substantially over the last 40 years. Initially, cottages and roads were removed and sites allowed to regenerate naturally. In the 1980s, a few, large tree species including *Populus deltoides* and *Fraxinus americana* were planted at each site whereas, currently, hundreds of park-grown, 3-5 year old shrubs and tree species including *Rubus occidentalis*, *Fraxinus americana*, and *Rhus typhina* are planted in restored sites. These early-to-mid successional species tend to be either wind or vertebrate dispersed and are already successful at colonizing restored sites by themselves (only 10% of the shrubs sampled had been planted). However, even planted shrubs can facilitate recovery. As they are light tolerant they are more likely to survive competition with, and eventually outshade, fast growing ruderal and inhibitive species (Debussche & Isenmann, 1994). In turn, they can act as seed sources or seeding nuclei by increasing the vertical complexity of sites (McDonnell & Stiles, 1983; McDonnell, 1986) and attracting frugivores (Handel & Robinson, 1993; Kollmann, 1994). However, the reintroduction of species that remain absent from restored sites, especially if they can be shown to be dispersal-restricted, may need to be given priority. Although some of these species require a decade of vegetative growth before they can flower (e.g. *Trillium grandiflorum*) (Koh, 1995), vigorous populations of some species can spread vegetatively. In addition, planting also generates public interest, provides opportunities to learn more about species for researchers, managers, and the public (Reinartz, 1995).

The higher species diversity at site edges and in the former cottage locations suggests that lawn grasses continue to inhibit the establishment of native species and successional change after 20 years. Although the removal of these grasses in active restoration is likely to facilitate vegetational change (Choi & Pavlovic, 1994; Hiebert, 1990), the benefits of this activity were still ambiguous six years after restoration. These actively restored sites were subjected to recent, relatively intense disturbance such as bulldozing and planting and were characterized by exotic ruderals. Older sites, and in particular MarsC, were associated with herbaceous species characteristic of recovered and reference sites such as *Hydrophyllum appendiculatum*, *Festuca obtusa*, *Geum canadense*, and *Ranunculus abortivus*. Thus, the variable "restoration type" became a measure of the immediate effect of disturbance. Even after six years, the impact of disturbance was great enough to mask the possible benefits of active restoration. At this point in time, the impact of active restoration, however well intentioned, is no different, in effect, from any other intense, localized disturbance.

Significance of the study

This study has important implications for vegetation management in protected areas. Most protected areas located in urban and agriculture dominated landscapes are subject to intensive human use. Although this use tends to degrade the natural habitat (Drayton & Primack, 1996; Cole & Landers, 1996; Taylor *et al.*, 1993; Sinclair *et al.*, 1995), these areas continue to have considerable conservation and educational value (Shafer, 1995). Managers of many protected areas are attempting to mitigate habitat degradation by adopting "naturalization" programmes similar to those at PPNP. However, there are associated costs. As parks become less amenable to recreational and residential use, visitor numbers often decrease. Visitation levels at PPNP are approximately half of those two decades ago when the park was primarily oriented towards residential and beach use (G. Mouland, pers.comm.). Current decreases in government funding and park services and increases in park entrance costs can force parks to chose between conservation and recreation priorities (Manning *et al.*, 1996; Morgan, 1996). However, our findings suggest that these choices are not necessarily incompatible. When use-associated degradation occurs, these areas are readily restored as long as seed sources remain available. Although there will always be some degradation associated with human use, it can be minimized, for example, by rotating and reducing the size of trails, isolating high quality or heavily degraded areas, and visitor education.

As disturbance decreases in intensity and scale, regeneration times should also decline. The relative ease of restoration can influence use patterns and adaptive management priorities. Perhaps most importantly, future development should ensure that proximate natural vegetation remains. Soil removed during construction should be translocated to degraded areas. As forest regeneration is relatively slow on dry sites, these should remain undeveloped. Planting of *Poa* and *Festuca* lawn species should be avoided. The degree to which restoration piggybacks natural, successional processes, should translate into reduced regeneration times, inputs, and costs, and should result in restoration sites that more closely resemble their natural counterparts.

While these results are of relevance for protected areas contiguous to extant natural habitat, their relevance for isolated patches of natural habitat in highly fragmented agricultural landscapes is less clear. In Essex county forest cover is less than 3%; all patches, with the exception of PPNP, are less than 10ha in size; and inter-patch distances average 3km (Pearce, 1996; McLachlan, 1997: Chapter 2). Our findings are applicable to these patches only if there is an adequate and available seed source. If local or adjacent seed sources are relatively depleted, estimated regeneration times will be much higher than those indicated here (Dzwonko, 1993). Similarly, our findings are applicable only to restoration that is conducted within these remnants. In small fragments, such activity can be combined with the creation of additional habitat such as afforestation. This new and relatively unnatural habitat might: function as buffers mitigating against invasion by exotics and changes in microclimate associated with fragmentation; increase connectivity thereby facilitating interpatch migration (Fritz & Merriam, 1993, 1994); and act either as nuclei for further dispersal or sources of seed. Landscape studies investigating the impact of fragmentation on the recovery of degraded habitat are urgently needed (Hobbs & Norton, 1996).

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CHAPTER 4

RELATIONSHIPS BETWEEN RECOVERY PATTERNS OF NATIVE UNDERSTOREY HERBS AND THEIR FLOWERING PHENOLOGY AND SEED DISPERSAL

STEPHANE M. McLACHLAN and DAWN R. BAZELY

Abstract:

Forest fragmentation has resulted in reduced richness of native species in northeastern North America. Despite recent large-scale increases in forest cover, studies indicate that understorey herbaceous plant communities may take decades to recover. We studied recovery patterns of vegetation following up to 35 years of forest regeneration in former cottage and roads sites at Point Pelée National Park, Ontario, Canada. Overall, there were no significant differences in the diversity of native species between restored and relatively undisturbed reference sites suggesting that recovery of restored sites may have been successful. However, there was still significant among-site variation in the composition of the native species component of these plant communities. When only restored sites were examined, variation in native species composition was associated with time since site restoration, soil moisture, canopy cover, and distance to continuous forest. Native species were assigned vulnerability rankings according to their relative occurrence in reference and restored sites. Spring-flowering herbs such as *Hepatica acutiloba*, *Dicentra cucullaria*, and *Allium tricoccum*, with ant or gravity dispersed seeds, were absent from restored sites and were defined as highly vulnerable. In contrast, summer and fall-flowering herbs, with vertebrate and wind dispersed seeds, dominated restored sites and were assigned lower vulnerability rankings. Species assigned low and intermediate vulnerability rankings had colonized restored sites successfully. These intermediately ranked species should function as indicators of recovery. In contrast, species with high vulnerability rankings had not recovered at all and, because of their limited dispersal ranges, may only recolonize restored sites if they are actively reintroduced.

INTRODUCTION

Much of the deciduous forest in northeastern America was cleared for lumber and converted to agricultural and urban use at the time of European settlement (Sauer, 1994). Over the last century there have been large-scale regional increases in forest cover and wildlife habitat resulting from heightened protection efforts, the abandonment of marginal farmland, and active habitat restoration (Foster, 1992). However, forest cover remains at 3% in some counties in southern Ontario, Canada (Riley and Mohr, 1994).

Despite these overall increases in forest cover, recent studies suggest that understorey plant communities may have suffered a greater decline and may take longer to recover (Robinson et al., 1994). For example, while the diversity of spring ephemeral plant species tends to increase as succession proceeds (Reiners, 1992; Bratton et al., 1994), there was little evidence of recovery of late successional herbaceous species after two decades of forest regeneration in New Brunswick (MacLean and Wein, 1977). Undisturbed old growth forests had a higher richness of herbaceous species than neighbouring 45 to 87 year-old stands in the Appalachians (Duffy and Meier, 1992). In Michigan, the herbaceous plant community has continued to change during 150 years of forest regeneration (Brewer, 1980), and, in England, the understorey community of forests that had been regenerating for 450 years had lower species richness than ancient woodlands (Peterken and Game, 1984). This decline in species richness is frequently attributed to habitat loss and is also associated with changes in disturbance accompanying fragmentation (Weaver and Kellman, 1981; Saunders et al., 1991). Disturbances include increased ungulate grazing (Mitchell and Kirby, 1990), invasion by exotics (Robinson et al., 1994), intense human use of the surrounding landscape (Bratton et al., 1994), and changes in the physical environment of the forest (Matlack, 1994). In addition, declines in native species richness have been associated with particular patterns of flowering phenology (Meier et al., 1995) and seed dispersal (Dzwonko and Loster, 1992).

Many understorey, ephemeral forest herbs emerge early in the growing season before the tree canopy is fully extended. Compared with later flowering, shade-tolerant understorey species, they have high saturation points and maximum photosynthetic rates (Sparling, 1967; Taylor and Pearcy, 1976), low rates of dry matter accumulation, and an inability to adapt to low-light environments (Hicks and Chabot, 1985). Despite being light-adapted, they may be displaced by fast growing annuals or ruderals in relatively disturbed, open environments (Meier et al., 1995). Once displaced, recolonization by spring ephemerals seems to be prevented by the dense vegetation cover associated with these early successional habitats (Dzwonko, 1993; McLachlan, 1997: Chapter 2). The resultant decline of spring ephemerals has been attributed to their perennial life history strategy and associated relatively low growth rates (Nault and Gagnon, 1993), low reproductive output (Bierzychudek, 1982), long pre-reproductive phase (Koh, 1995), and dependence on the moist, nutrient-rich, non-competitive conditions associated with early-spring growth (Eickmeier and Schussler, 1993).

Most plant species produce seeds with structures that facilitate dispersal (Ridley, 1930). Dispersal distances are greatest for wind dispersed seeds, intermediate for vertebrate dispersed, and shortest for ant, explosion, and gravity dispersed seeds (Willson, 1993). The herbaceous understorey of temperate mesic forests is often dominated by species with restricted dispersal ranges. For example, more than 50% of the herbaceous species in a mesic forest in New York (Handel et al., 1981) and 41% of those in West Virginia (Beattie et al., 1979) were ant-dispersed. Once eliminated from a habitat, these species will recolonize more slowly than those vertebrate and wind dispersed species (Dzwonko and Loster, 1992) that tend to dominate early stages of succession (Myster, 1993). Given their apparent vulnerability to disturbance, we hypothesized that the presence of both spring ephemeral and dispersal-restricted forest herbs in restored forest sites would be good indicators of recovery.

Herbs have long been recognized as indicators of habitat conditions (Clements, 1916). They may function as indicators of edaphic conditions (Pregitzer and Barnes, 1982) such as soil moisture (Winkler and Rothwell, 1983) and fertility (Gilliam, 1988); site structure such as stand height (Strong et al., 1991); and overstorey management (Gilliam et al., 1995). Recently, they have been used as indicators of such disturbance as intense deer grazing (Pear et al., 1995; Anderson, 1994) and gaps in the tree canopy (Moore and Vankat, 1986).

In order to test the usefulness of native spring flowering ephemeral and dispersal-restricted species as indicators of forest recovery, we conducted a study in Point Pelée National Park, southwestern Ontario, Canada. Over the last 35 years, park resource managers have been implementing a naturalization program in which roads and cottages have been removed and these converted sites allowed to regenerate to woodland. We asked the following questions:

(1) Are understorey native species with restricted seed dispersal patterns less common in restored sites than native species with longer distance seed dispersal?

(2) Are native spring ephemerals less common in restored sites than native species which flower in the summer and fall?

We predicted that the numbers of spring-ephemeral and dispersal-restricted species should increase as time since site restoration increases and thus act as indicators of forest recovery. However, we expected that these numbers would still be lower in 35 year-old restored sites than in relatively undisturbed, reference sites.

METHODS

Study Area

Our study examined two areas in southwestern Ontario, Canada: Point Pelée National Park (PPNP) lat. 41°54'N, long. 82°22'E and FishPoint Nature Preserve (FPNP), Pelée Island) lat. 41°44'N, long. 82°40'E. Both protected areas are sandspit land formations that extend southward into Lake Erie, and are situated on the northern edge of the Eastern Deciduous Forest or Carolinian Zone (Allen et al., 1990). Twenty-five percent of Canada's human population live in this region of Ontario and land-cover is currently dominated by agricultural and urban landuse (Allen et al., 1990). This region is the southernmost part of Canada and has the warmest mean temperatures, longest annual frost-free seasons and mildest winters in Ontario (Reid, 1985). Most of the region is a flat former lake bottom with poorly drained, fertile, silt and clay soils (Chapman and Putman, 1984). The landscape surrounding PPNP has 3% forest cover, 90% of which exists in patches less than 10ha in size (Pearce, 1996).

PPNP is approximately 12,000ha in size, one-third of which is upland and swamp forest, and is the only mainland patch of forest in Essex county that is greater than 100ha. PPNP was created in 1894, largely cleared of white pine (*Pinus strobus*), and planted in hackberry (*Celtis occidentalis*), which now dominates the tree canopy. In the park, agriculture peaked in the 1950s, when over 60 percent of the landcover was allocated to orchard, crop and vegetable production. At this time there were over 600 cottages and numerous roads. Recreational use was high and over 600,000 people visited the park each year. In the 1960s, park managers initiated a naturalization program. Cottages were purchased and demolished, roads removed, and these areas allowed to regenerate. Over the last 10 years, the active restoration of these cottage and road sites has included the planting of shrubs and trees, the alteration of topography and hydrology, and the control of exotics. In contrast to PPNP, FPNP is only 400 ha in area, 90% of which is upland forest dominated by black maple (*Acer nigra*) and *Celtis occidentalis*. It is situated on

Pelée Island which has about 14% forest cover and is the only patch of forest on the island greater than 100ha (Pearce, 1996). Except for minimal recreational use, it is largely undisturbed.

Identification and assessment of restored and reference sites

In 1994, 28 former road and cottage sites in PPNP were identified using aerial photographs, blueprints and conversations with long-time park employees. Sites were initially characterized according to age and soil moisture. Site age, or time-since restoration (TSR), was classified as 30 years, 20 years, 10 years, or recent, while soil-moisture regime was visually assessed on-site and classified as wet, mesic, or dry. Because of the history of widespread disturbance at PPNP, three relatively undisturbed reference sites were located in FPNP. In 1995, three additional relatively undisturbed reference sites were located in PPNP.

Plant community composition of sites was measured in spring and late-summer, 1994 and early-spring 1995, except for reference sites in PPNP which were measured only in early spring and late-summer, 1995. Between 15 to 22 1m x 1m quadrats were randomly located in each site depending on site area and within-site habitat diversity. Pins were used to mark the SE corner of each quadrat. Stratified sampling was carried out in the "edges" and "interiors" of all sites and, when identified, in former buildings, driveways, and lawns of cottage sites. For each quadrat, frequency of plants (number of individuals per quadrat) and percentage cover were recorded for all observed herbaceous species as well as woody species less than 40cm in height. Species nomenclature follows Morton and Venn (1990) and collected specimens are located at the PPNP herbarium.

Environmental data collected at all sites (n=34) included soil moisture and canopy cover. Eight soil samples were randomly collected from each site in September, 1994, and June, 1995, and analyzed for percentage soil moisture content. Samples were dried at 100°C for 24 hours before weighing and these values used in all subsequent analysis. Percentage canopy cover was qualitatively assessed at each quadrat corner for all quadrats in all sites.

The size and shape of former road and cottage sites were described using aerial photographs that were taken at roughly ten year intervals (1955, 1968 and 1973). The photograph used for each site was that which most closely preceded each restoration date. Measurements for cottages and roads that were removed since 1983 were initially described using the most recent aerial photo and then updated by ground truthing. Measurements calculated using aerial photographs included: actual site area, the area of the forest gap surrounding the site, the gap perimeter, the proportion of the gap as adjacent forest (PAF), gap shape, and the distance to continuous forest (DCF). The latter was measured by dividing the longest axis of the site into three equal parts. Distances to continuous forest were measured along 8 compass bearings (N, NE, E, SE, S, SW, W, NW), the three shortest distances taken for each of the two points and averaged for the entire site. Gap shape was calculated from the formula, $Is=P/(2\sqrt{A\pi})$, where P is the gap perimeter and A is the area (Faeth and Kane, 1978). The value of this index increases the more the shape departs from a circle; for a circle, Is=1. Finally, the dates of site-restoration were confirmed using park records.

Characterizing the Vulnerability, Flowering Phenology, and Seed Dispersal of Native, Understorey Plant Species

Each native plant species was given a vulnerability ranking. This was defined as the proportion of reference sites (n=6) within which a given species occurred divided by the proportion of restored sites (n=28) in which it occurred. Only species occurring in either more than one (>1) reference site or more than three (>3) restored sites were included in the ranking. The higher the ranking the less likely the species was to occur in restored sites and thus it was defined as being more vulnerable to disturbance. Species that had vulnerability rankings greater than 2 (i.e. those that were more than twice as likely to occur in reference sites than restored sites) were further subdivided into four VR groups: those that were restricted to reference sites, with vulnerability rankings of infinity (VR1); those with vulnerability rankings greater than 5 that were much more common in reference sites (VR2); those with vulnerability rankings between 2 and 5 that were more common in reference sites (VR3); and those species having vulnerability rankings between 1 and 2 that were only slightly more common in reference sites (VR4). Species in these four VR groups were combined into a summary group, VRTOT. Species occurring in reference sites but with vulnerability rankings 0>1 were designated as woodland species (WD), and those that species found only in restored sites (VR=0) were designated as nonwoodland species (NONWD).

Herbs were characterized according to development pattern or phenology and seed dispersal. Phenology types were: spring-flowering or ephemeral (April-June), summer flowering (June-August), and fall flowering (August-October). Spring ephemerals were further subdivided into three groups: E1 (flowering and senescing in April-May), E2 (flowering in April-June), and E3 (flowering in May-June). These three ephemeral groups largely coincided with groups that develop leaves before, during, as well as during and after canopy closure as described in Sparling (1967). Flowering dates were obtained from Jellicoe and Rudkin (1984). Seed dispersal types were categorized as gravity (barochores), explosion (autochores), ants (myrmecochores), wind (anemochores), and both vertebrate consumption (endozoochores) and vertebrate exteriors (epizoochores), following van der Pilj (1982). When species-specific data were not available, the following assumptions were made about seed dispersal: all plants bearing fruit were categorized as endozoochores, grasses with long awns were defined as anemochores and those with short awns as epizoochores. If no adaptations were present, herbs were defined as autochores. Only plants that flowered during the study were categorized and, thus tree and shrub seedlings were omitted. It should also be noted that many species had more than one mode of dispersal (e.g. *Viola* spp. are both barochores and myrmecochores) and only one salient dispersal type, as described in the literature, was chosen.

Statistical Analysis

Only native plant species were include in this analysis and all non-natives were excluded. Species richness, Shannon-Weaver Index of diversity (H) and Evenness (E) diversity measures (Magurran, 1988) were calculated at the site level as described in McLachlan (1997: Chapter 4). These were analyzed using one-way MANOVA (SAS, 1985). Detrended Correspondence Analysis (DCA) was used to compare sites with respect to overall species composition (DCA, Hill and Gauch, 1980; CANOCO, ter Braak, 1992). DCA positions samples along orthogonal axes that sequentially explain the greatest amount of inter-sample variation.

As previously stated, diversity measures were calculated on a per site basis, even though they were of different areas. This was because no significant relationship was found between native species richness and site area ($F_{1,27}$=2.36, p=0.1363). In addition, quadrat number per site varied depending on the site area and habitat heterogeneity of each site. However, cumulative area / species richness curves calculated for each site all rapidly reached asymptotes (McLachlan, 1997: Chapter 5), indicating that diversity measures presented for the site were appropriate.

For each site, the maximum percentage cover was recorded for each species over the sampling dates. Pearson correlation coefficient (using sequential Bonferonni adjustments) were used to assess the relationship between site scores for the first four ordination axes and the environmental parameters. Regression analysis was used to assess the relationship between VR species richness and TSR. MANOVA and Duncan post-hoc multiple means tests were used to assess the relationship between species richness and percentage cover for vulnerability, development, and seed dispersal types across TSR age groups (SAS, 1985). G tests were conducted to assess whether there was a relationship between vulnerability and seed dispersal or phenology. In order to increase sample size per cell in the contingency table, VR1 and VR2 groups were pooled and VR3 and VR4 groups pooled to provide higher and lower vulnerability categories, respectively. G-tests were also conducted to examine if there was a relationship between seed dispersal and phenology. Data were log- or square root-transformed to achieve assumptions of normality where necessary (Sokal and Rohlf, 1981). Means were considered statistically different when $P<0.05$.

RESULTS

Native Diversity Measures

When only native species were analyzed, there were no overall differences in species richness, H, or E between restored and reference sites (MANOVA: Wilks' lambda (WL) = 0.88, $F_{3,30}=1.38$; $p=0.2686$) (Table 4.1).

Native Species Composition

In contrast to community-level measures of diversity, native species composition was strongly affected by disturbance history and selected environmental factors. Detrended Correspondence Analysis (DCA) indicated that species composition varied among sites (Figure 4.1) and was significantly affected by various measured

Table 4.1. Diversity measures calculated for native components of plant communities in restored and relatively undisturbed sites at Point Pelee National Park and FishPoint Nature Preserve.

Diversity index	Restored sites (n=28)	Reference sites (n=6)
i) species richness[a]	38.7 (2.03)[b]	37.3 (4.06)
ii) Shannon Weaver	2.0 (0.09)	2.4 (0.10)
iii) Evenness	0.6 (0.03)	0.8 (0.03)

[a]species number per site

[b]each mean value followed by the standard error in parenthesis

Figure 4.1. Detrended correspondence analysis (DCA) diagram of all sites (axes 1 and 2) using native herbaceous data indicating placement of reference sites (n=6) at both Point Pelée National Park (PPNP) and FishPoint Nature Preserve (FPNP) and restored sites (n=28) at PPNP. Reference sites (PPNP) (0), reference sites (FPNP) (1), 26-35 years (2), 16-25 years (3), 5-15 years (4), and <5 years (5) TSR. Species are listed by first three letters of genus and species and abbreviations are included in Appendix 1.


5.0
4.0
3.0
2.0
1.0
0
-1.0
-2.0
DCA axis 2 (S.D.)
-2.0
0
2.0
4.0
6.0
DCA axis 1 (S.D.)
3
Ampbra
Muhsch
Viopap
Pilpum
Cordru
Lycuni
Impcap
Urtdio
Aqucan
Quevel
Phaaru
Viosor
Carcra
Gerrob
1
1
Aritri
Ribcyn
Pruvir
Rhutyp
Hepacu
4
2
Geulac
0
Smitam
Malcan
5
Eripur
2
Polbif
0
0
4
1
Galapa
Viopub
Smiher
2
2
Phrlep
Urtgra
Onosen
Polcan
2
Eupalb
Muhfro
3
Podpel
Elyvil
5
3
Equhye
Samcan
Viopen
3
Anecan
Cirqua
Parqui
4
3
Camame
Dessp
Germac
2
Boecyl
Chefog
4
4
4
4
Rudtri
Pancap
Solcan
Equarv
Cardou
Polsca
Tilame
Oxastr
Phyhet
Astvim
Agrpar
Acarho
Querub
Fraame
Urtpro
Fravir
Erican

environmental variables (Table 4.2). When both disturbed (restored) and undisturbed (reference) sites were included, DCA separated sites according to disturbance history (i.e. whether sites were restored or not) and soil moisture. Disturbance history was negatively correlated with DCA axis 1 and associated with *Hepatica acutiloba*, *Cerastium arvense*, *Dicentra cucullaria*, *Allium tricoccum*, and *Trillium grandiflorum*, while soil moisture was positively correlated with DCA axis 1 and associated with *Galium asprellum*, *Asclepias incarnata*, *Equisetum hyemale*, *Onoclea sensibilis*, *Geranium maculatum*, and *Muhlenbergia racemosa*. In turn, canopy cover and disturbance history were significantly correlated with axis 2 (Table 4.2). Herbaceous species positively associated with canopy cover included: *Amphicarpa bracteata*, *Muhlenbergia schreberi*, *Viola papilionacea*, *Cornus drummondii*, and *Lycopus americanus*, while those negatively associated with disturbance history included *Erigeron canadensis*, *Fragaria virginiana*, *Urtica procera*, *Quercus rubra*, and *Oxalis stricta*.

The effect of the disturbance-related environmental variables on native species composition was examined by including only restored sites in a second DCA (Table 4.3). Only soil moisture was significantly correlated with axis 1. Positively associated species included *Sambucus canadensis*, *Galium asprellum*, *Asclepias incarnata*, *Equisetum hyemale*, *Onoclea sensibilis*, *Geranium maculatum*, while negatively associated species included *Prunus serotina*, *Acer saccharum*, *Hydrophyllum appendiculatum*, *Rosa blanda*, *Rhus aromatica*, and *Ranunculus abortivus*. Canopy cover, time since restoration (TSR), and distance-to-continuous forest (DCF) were all positively correlated with axis 2. Positively associated species included *Amphicarpa bracteata*, *Mentha arvensis*,

Table 4.2. Eigenvalues associated with each of first four DCA axes and the correlation between each axis and environmental variables for all sites (n=34) at Point Pelee National Park and FishPoint Nature Preserve. Environmental variables are: canopy cover (cancov), soil moisture (soilm), and whether restored or reference site (disturb).

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.844	0.536	0.299	0.174
Cancov	-0.164	0.523*	-0.179	0.211
Soilm	0.423*	0.322	0.146	-0.060
Disturb	-0.400*	0.399*	0.029	0.173

*$p<0.05$ (Bonferroni adjusted)

Table 4.3. Eigenvalues associated with each of first four DCA axes and the correlation between each axis and environmental variables for restored sites only (n=28) at Point Pelee National Park. Environmental variables are: canopy cover (cancov), soil moisture (soilm), and time-since-restoration (TSR), proportion of site in adjacent forest (PAF), distance to continuous forest (DCF), forest gap area (gap area), shape index (shapind), and site area (sitarea).

	Axis 1	Axis 2	Axis 3	Axis4
Eigenvalue	0.846	0.515	0.341	0.178
Cancov	0.085	0.509*	0.251	-0.009
Soilm	0.496*	0.400*	0.149	-0.153
TSR	-0.012	0.152	0.644*	-0.235
PAF	0.067	0.015	-0.138	-0.009
DCF	0.046	0.494*	0.282	0.051
Gaparea	0.004	-0.147	0.145	-0.227
Shapind	-0.297	0.055	-0.229	0.072
Sitarea	0.152	-0.219	0.123	0.146

*$p<0.05$ (Bonferroni adjusted)

Muhlenbergia schreberi, *Viola papilionacea*, and *Monarda fistulosa*, while negatively associated species included *Aster pilosus*, *Acer negundo*, *Lactuca biennis*, *Achillea millefolium*, *Panicum capillare*, *Chenopodium hybridum*, *Panicum virgatum*. Finally, TSR was significantly correlated with axis 3 and positively associated with *Onoclea spp.*, *Acer saccharum*, *Prunus serotina*, *Smilax tamnoides*, *Phryma leptostachya*, and *Smilacina racemosa*.

Vulnerability Ranking

Native species restricted to relatively undisturbed, reference sites (VR1) were *Aquilegia canadensis*, *Hepatica acutiloba*, *Dicentra cucullaria*, and *Allium tricoccum* (Table 4.4). At the other end of the ranking continuum, there were 23 native species found only in restored sites (NONWD), the most common of which were: *Solidago canadensis*, *Solidago altissima*, *Oxalis montana*, *Fragaria virginiana*, *Rhus typhina*, *Erigeron pulchellus*, *Scrophularia lanceolata*, and *Acalypha rhomboidea*. When the relative percentage cover of each vulnerable species was calculated and then ranked from the most abundant to least abundant, VR1 and VR2 species were more dominant than either VR3 and VR4 groups for VRTOT (VR>1) and WD (0>1) groups ($F_{3,32}$ =5.77, p=0.003; $F_{3,32}$ =5.26, p=0.005, respectively). However, when the NONWD (VR=0) group was included, VR2 species were less dominant than VR4 species ($F_{3,32}$=4.75, p=0.018) (Table 4.4). Overall, however, only four vulnerable species were ranked among the ten most dominant WD species. Of these, only *Hydrophyllum appendiculatum* and *Dicentra cucullaria* had more than 10% cover per reference site (18.3% and 15.3% per

Table 4.4. Native species classified according to their vulnerability to disturbance. The vulnerability ranking (VR) for each species was defined as the proportion of reference sites (n=6) in which a species occurred divided by the proportion of restored sites (n=28) in which a species occurred.

Species	Common Name	VR	Rel. % cov[1]	Rank VR % cov[2]	Rank ref % cov[3]	Rank rest % cov[4]	Dispersal type[5]	Phenology type[6]
VR1 (infinity)								
Aquilegia canadensis	Columbine	-	0.91	13	31	-	ba	e3
Dicentra cucullaria	Dutchman's breeches	-	15.32	2	4	-	my	e1
Hepatica acutiloba	Sharplobed Hepatica	-	1.51	12	25	-	my	e2
Allium tricoccum	Wild Leek	-	6.70	4	7	-	ba	e2
VR2 (5<VR<14)								
Viola pubescens	Downy Yellow Violet	28.00	0.42	19	27	147	my	e2
Podophyllum pelatum	May Apple	14.00	6.91	3	8	135	en	e2
Trillium grandiflorum	White Trillium	14.00	1.98	7	20	146	my	e2
Acer nigrum	Black Maple	9.33	0.53	16	30	83	an	w
Viola pensylvanica	Smooth Yellow Violet	9.33	0.67	15	26	143	my	e2
Polygonatum canaliculatum	Great Solomon's Seal	6.22	2.56	5	14	75	en	e3
Hydrophyllum appendiculatum	Appendaged Waterleaf	5.83	18.27	1	1	13	ba	s
VR3 (2<VR<5);								
Arisaema triphyllum	Jack-in-the-Pulpit	4.67	0.35	21	38	101	en	e2
Ostrya virginiana	Hop-hornbeam	4.67	0.16	26	53	95	an	w
Menispermum canadense	Moonseed	4.67	0.15	27	55	114	en	w
Hydrophyllum virginianum	Virginia waterleaf	4.67	1.74	10	21	54	ba	e3
Smilacina racemosa	False Solomon's Seal	3.73	2.36	6	16	87	en	e3
Smilax tamnoides	Green Briar	3.50	0.41	20	28	70	en	w
Mainthemum canadense	Maianthemum	3.50	0.52	17	33	89	en	e3
Circaea quadrisulcata	Enchanter's Nightshade	3.11	0.21	23	45	77	en	s
Tilia americana	American Bass	2.80	0.08	32	56	102	an	w
Fraxinus pennsylvanica	Red Ash	2.33	0.20	25	48	80	an	w
Prunus serotina	Black Cherry	2.33	0.11	28	43	63	en	w
Physalis heterophylla	Clammy Ground Cherry	2.33	0.20	24	47	56	ba	s
Quercus rubra	Red Oak	2.33	0.03	33	70	60	ep	w
Smilax herbacea	Carrion Flower	2.15	1.94	9	11	32	en	e3

VR4 (1<VR<2).								
Elymus villosus	Hairy Wild Rye	1.75	0.11	30	54	44	ep	g
Polygonatum biflorum	Solomon's-Seal	1.75	1.63	11	15	36	en	e3
Ranunculus abortivus	Kidney Leaf Buttercup	1.56	0.11	29	52	91	an	s
Ribes cynosbati	Prickly Gooseberry	1.56	0.78	14	29	58	en	w
Amphicarpa bracteata	Hog peanut	1.33	1.98	8	23	10	au	f
Tovara virginiana	Jumpseed	1.33	0.22	22	44	40	au	f
Quercus velutina	Black Oak	1.17	0.09	31	58	105	ac	w
Campanula americana	Tall bell flower	1.17	0.44	18	34	37	an	s

[1] Summed percentage of species divided by total vegetation cover in reference sites. [2] Percentage cover of species ranked against other species having vulnerability rankings >1. [3] Percentage cover of species ranked against the percentage cover of all species occurring in reference sites. [4] Percentage cover species ranked against percentage cover of all species occurring in restored sites. [5] Flowering phenology types are: ephemeral herbs flowering from April to June (e); summer herbs flowering from June to August (s); and fall herbs flowering after August (f). Ephemerals are further divided into ephemeral 1 (e1) herbs that flower and senesce from April to May; ephemeral 2 (e2) herbs that flower from April-June; and ephemeral 3 (e3) herbs that flower from May to June. [6] Seed dispersal types are: vertebrate dispersal (fur) (epizoochores) (ep), vertebrate (consumption) (endozoochores) (en), ants (myrmecochores) (my), explosion (autochores) (au), wind (anemochores) (an) and gravity (barochores) (ba). Species only included in analysis if occur at least two times in reference sites or five times in restored sites.

site, respectively). As might be expected, no vulnerable species were found among the ten most dominant NONWD species. Of the NONWD species, only *Solidago canadensis* and *Solidago altissima* had more than 10% cover per site (26.1% and 15.4%, respectively).

Vulnerability ranking was significantly associated with flowering phenology (G= 45.8, p<0.001). Nine of the ten VR1 and VR2 herbaceous species were ephemerals (Table 4.4, Figure 4.2). Of these, seven were either E1 or E2. In comparison, VR3 species were dominated by E3 and summer flowering herbs whereas both VR4 species and non woodland herbs were dominated by plants which flower in the summer and fall (Table 4.4, Figure 4.2). Thus a high vulnerability ranking was positively associated with ephemeral flowering and negatively associated with fall flowering.

Vulnerability ranking was also significantly associated with seed dispersal (G= 53.3, p<0.001). Highly vulnerable VR1 species were all myrmecochores and barochores while VR2 species were dominated by these dispersal types (Table 4.4, Figure 4.3). Some VR2 species and most VR3 species were endozoochores. VR4 species were dominated by epizoochores, endozoochores and anemochores, and NONWD species by anemochores. Thus a high vulnerability ranking was positively associated with restricted dispersal (i.e. barochores and myrmecochores) and negatively associated with effective dispersal (i.e. epizoochores, endozoochores, and anemochores).

Flowering phenology was significantly associated with seed dispersal type (G=230.4, p<0.001). E1 species tended to have restricted dispersal whereas summer and fall-flowering species, in particular, were classified mainly as effective dispersers. Thus,

Figure 4.2. The relationship between vulnerability ranking of native herbaceous species and flowering phenology. Phenology types are: ephemeral herbs flowering from April to June; summer herbs flowering from June to August; and fall herbs flowering after August. Ephemerals are further divided into ephemeral 1 (e1) herbs that flower and senesce from April to May; ephemeral 2 (e2) herbs that flower from April-June; and ephemeral 3 (e3) herbs that flower from May to June. Native species are classified into: four vulnerable VR groups: VR1: infinity, VR2: VR>5,VR3: 2<VR<5, VR4: 1<VR<2.; the total of all VR species (VRTOT); nonranked woodland species occurring in both disturbed and undisturbed habitat (WD); and nonwoodland species occurring only in disturbed habitat (NONWD).

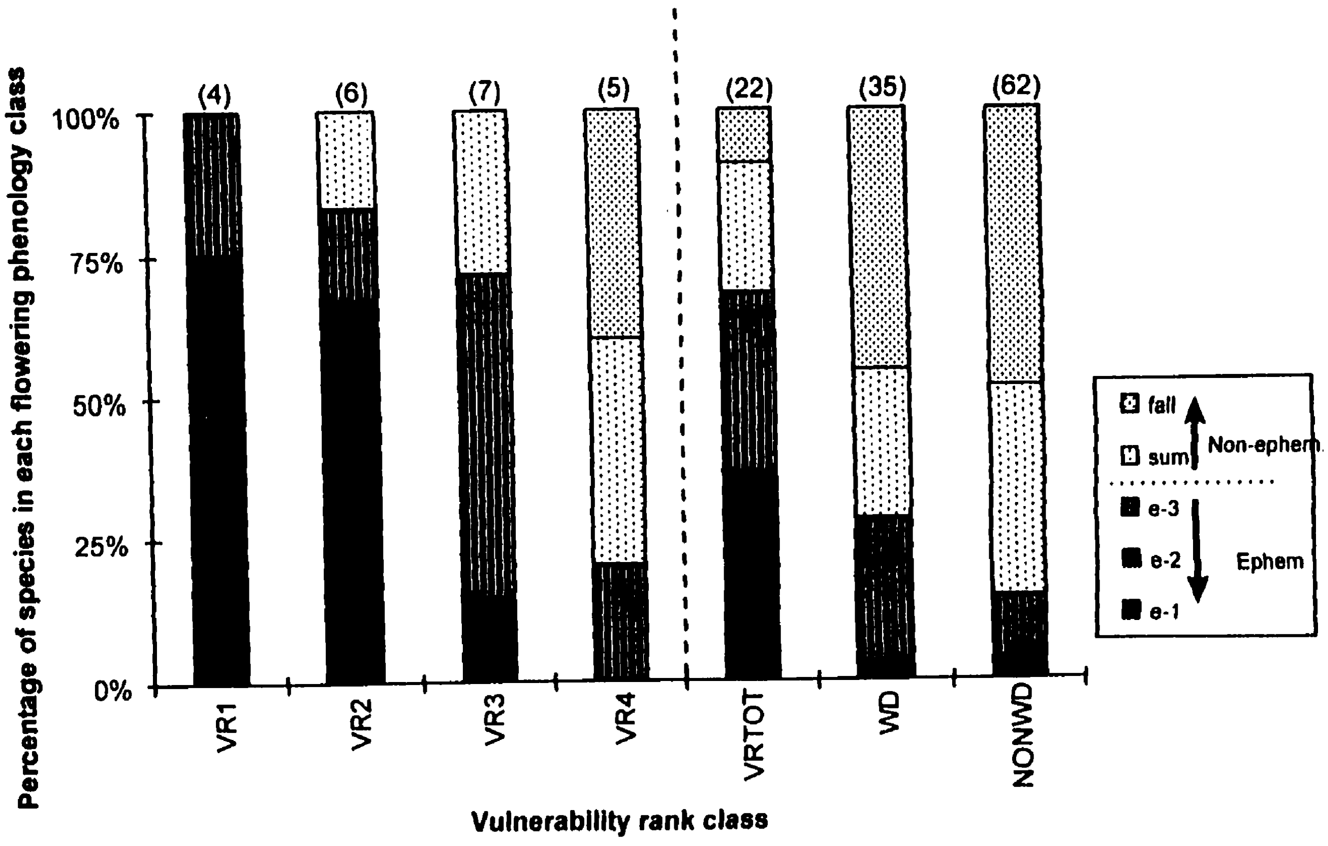
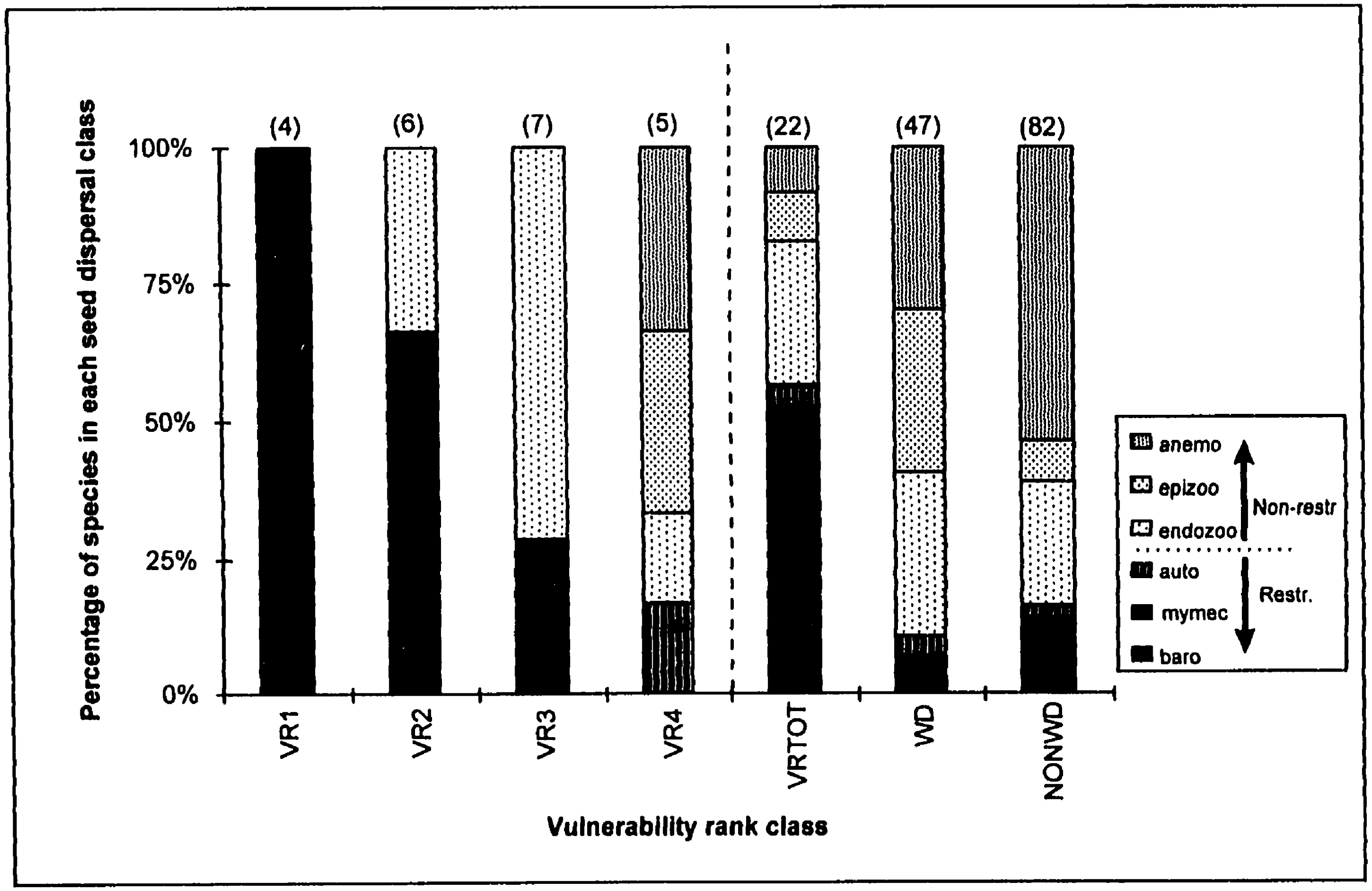

Percentage of species in each flowering phenology class
100%
75%
50%
25%
0%
(4)
(6)
(7)
(5)
(22)
(35)
(62)
VR1
VR2
VR3
VR4
VRTOT
WD
NONWD
Vulnerability rank class
fall
sum
Non-ephem.
e-3
e-2
e-1
Ephem

Figure 4.3. The relationship between vulnerability ranking of native herbaceous species and seed dispersal type. Dispersal types are: externally by animals (epizoochores); animal consumption (endozoochores), ants (myrmecochores), explosion (ballistic autochores), wind (anemochores) and gravity (barochores). Native species are classified into: four vulnerable VR groups: VR1: infinity, VR2: VR>5,VR3: 2<VR<5, VR4: 1<VR<2.; the total of all VR species (VRTOT); nonranked woodland species occurring in both disturbed and undisturbed habitat (WD); and nonwoodland species occurring only in disturbed habitat (NONWD).


Percentage of species in each seed dispersal class
100%
75%
50%
25%
0%
(4)
(6)
(7)
(5)
(22)
(47)
(82)
VR1
VR2
VR3
VR4
VRTOT
WD
NONWD
Vulnerability rank class
anemo
epizoo
endozoo
auto
mymec
baro
Non-restr
Restr.

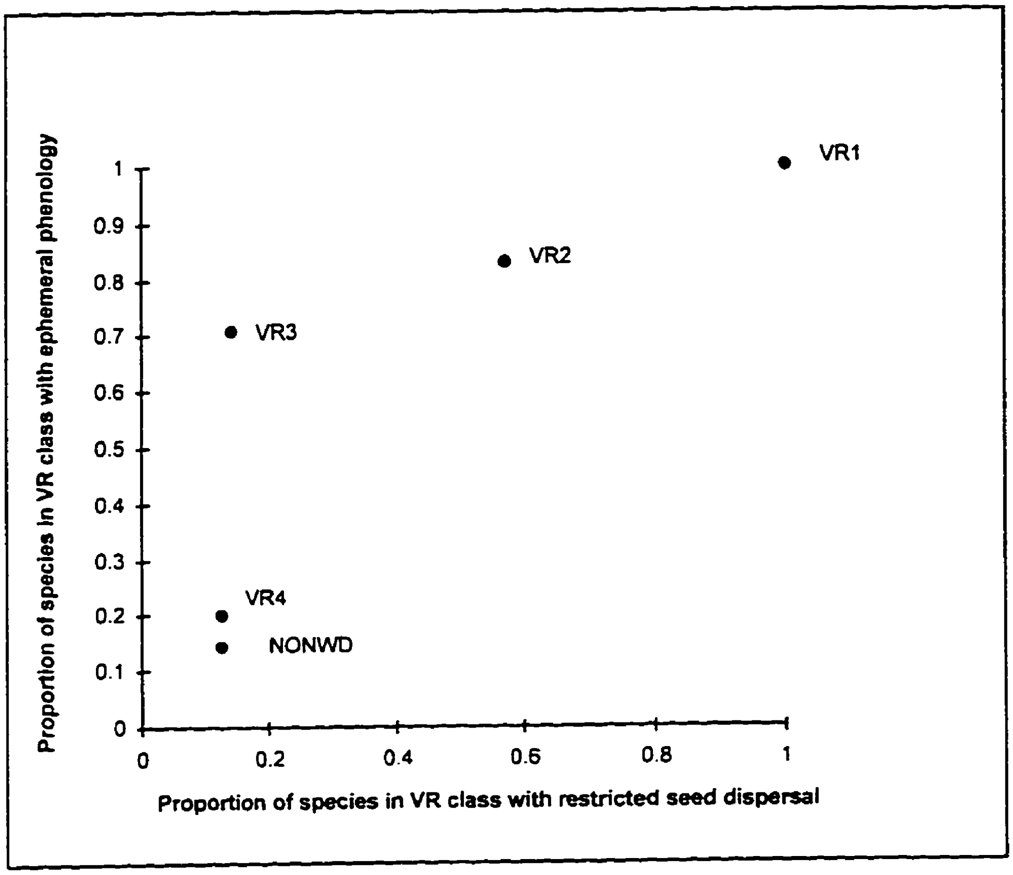
vulnerability ranking increased as the proportion of species exhibiting both restricted dispersal and ephemeral flowering increased (Figure 4.4).

The use of vulnerability rank as an indicator of site recovery

Our results indicated that community-level measures of diversity such as species richness and Shannon-Weaver index did not distinguish between restored and reference sites (Table 4.1). In contrast, the composition of the native component of understorey plant communities showed a strong association with disturbance history (Table 4.2) when both reference sites and restored sites were examined, as well as TSR, when only restored sites were examined (Table 4.4).

Similarly, classes of species grouped according to flowering phenology, seed dispersal, and vulnerability showed significant overall relationships with TSR. For flowering phenology this relationship was significant when all sites (n=34) were analyzed (WL=0.1290; $F_{24,85}$=2.83, p<0.0002), but this was not the case when only restored sites (n=28) were analyzed (WL=0.3326; $F_{18,54}$=1.43, p=0.1540). The mean percent cover and number of spring ephemeral species were highest in reference sites and the mean percent cover was lowest in the most recently restored sites (Table 4.5). In contrast, the mean percent cover and number of fall flowering species were lower in reference than in restored sites. With respect to seed dispersal, the relationship with TSR was significant when all sites (WL=0.0142; $F_{48,71}$=3.00, p<0.0001) and only restored sites (WL=0.8789;

Figure 4.4. Relationship between flowering phenology, seed dispersal. and vulnerability ranking of native herbaceous species. Native species are classified into five vulnerability groups: VR1: infinity, VR2: VR>5,VR3: 2<VR<5, VR4: 1<VR<2 and NONWD (nonwoodland species occurring only in restored sites). The proportion of species exhibiting ephemeral flowering phenology is calculated as: the number of species in each vulnerability group exhibiting ephemeral phenology (ephemeral herbs flowering and senesce from April to May (e1); ephemeral herbs flowering from April-June (e2); ephemeral herbs flowering from May to June (e3)) divided by the total number of species in each vulnerability group The proportion of species exhibiting restricted seed dispersal is: the number of species in each vulnerability group having restricted seed dispersal (ant dispersal (myrmecochores). explosion (ballistic autochores), and gravity (barochores)) divided by the total number of species in each vulnerability group.



Proportion of species in VR class with ephemeral phenology
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
VR1
VR2
VR3
VR4
NONWD
0
0.2
0.4
0.6
0.8
1
Proportion of species in VR class with restricted seed dispersal

Table 4.5. Relationship between disturbance history of sites and composition for the native plant communities of both restored and relatively undisturbed, reference sites at Point Pelee National Park and FishPoint Nature Preserve[1].

DOR	Site no.	Ephemeral		Summer		Fall	
	(n)	%cov[2,3]	spp.no.	%cov	spp.no.	%cov	spp.no.
1990	6	4.54 (1.27)[4] a[5]	8.00 (1.09)a	7.69 (3.69)a	8.89 (1.53)a	65.14 (23.21)a	12.89 (1.70)a
1980	7	28.25 (17.73)bc	9.67 (0.33)a	18.75 (10.57)a	10.00 (2.89)a	46.15 (29.40)ab	8.00 (3.61)bc
1970	8	12.93 (2.86)c	9.00 (0.37)a	16.18 (4.20)a	9.44 (0.73)a	44.16 (9.20)a	10.33 (0.96)ab
1960	7	31.95 (13.25)c	9.57 (1.04)a	21.39 (4.21)a	9.71 (1.04)a	20.69 (5.07)ab	11.29 (1.32)ab
Ref. site	6	69.27 (16.09)b	14.83 (0.65)b	16.29 (4.55)a	8.17 (0.75)a	7.29 (1.61)b	5.83 (1.17)c

[1] DOR: decade of restoration; ref. site: reference sites; site no.: site number; phenology types: ephemeral herbs flowering from April to June (ephemeral); summer herbs flowering from June to August (summer); and fall herbs flowering after August (fall).

[2] data square root transformed; untransformed means presented

[3] % cover is the mean percentage cover per site for each age class; spp. no. is the mean species richness per site for each age class

[4] each mean value followed by the standard error in parenthesis

[5] means followed by different letters significantly different at $p<0.05$ according to Duncan's multiple means test.

$F_{36,39}$=2.10, p=0.0123.) were examined. Thus, the mean percent cover and number of myrmecochore, barochore, epizoochore, and endozoochore species were highest in reference sites, and the mean percent cover for endozoochores was greater in old than in new sites. In contrast, the number of anemochore and autochore species was lowest in reference sites (Table 4.6). Finally, with respect to vulnerability ranking, there was a trend towards a significant relationship between vulnerability ranking and TSR when only restored sites were examined (WL=0.2793; $F_{18,54}$=1.72, p=0.0647). Although the species number of intermediately vulnerable species (VR3) seemed to be lower in newly restored sites, this relationship was hidden by the effective absence of VR1 and VR2 species from restored sites as well as the ubiquitous presence of VR4 species in all restored sites (Table 4.7).

Although vulnerability ranking showed a clear relationship with TSR, this relationship interacted with soil moisture. Both VR3 (Figure 4.5) and VRTOT (Figure 4.6) species richness showed a significant increase as TSR increased for wet/mesic sites whereas no significant relationship was shown for either VR3 or VRTOT species in dry sites.

DISCUSSION

Overall, our results showed no differences in diversity between restored and relatively undisturbed, reference sites. This suggests that the recovery of herbaceous plant communities in sites from which buildings and roads were removed has been largely successful in deciduous forests at PPNP. While these results are in agreement

Table 4.6. Relationship between disturbance history and seed dispersal types for the native plant communities of both restored and relatively undisturbed sites at Point Pelee National Park and FishPoint Nature Preserve[1].

DOR	Site no.	Epizoochores		Endozoochores		Anemochores	
	(n)	% cov[2,3]	spp. no.	% cov	spp. no.	% cov	spp. no.
1990	6	9.31 (1.75)a	5.89 (0.86)a	6.19(3.69)c	12.22 (1.65)a	67.67 (23.72)a	14.22 (1.39)a
1980	7	27.83 (11.29)a	6.00 (1.00)a	15.47(3.87)bc	11.67 (4.26)a	45.17 (30.77)a	11.33 (6.01)ab
1970	8	20.39 (3.38)a	7.22 (0.70)a	21.81 (5.72)ab	14.22 (0.97)a	38.16 (9.99)a	9.89 (0.77)ab
1960	7	37.93 (12.11)a	7.29 (0.57)a	19.83 (5.59)ab	16.86 (0.60)a	36.44 (13.70)a	11.29 (1.78)a
Ref.site	6	35.07 (5.39)b	6.83 (0.95)a	26.67 (4.68)a	15.83 (2.06)a	4.48 (1.40)b	4.48 (1.40)b*

DOR	Site no.	Myrmecochores		Barochores		Autochores	
	(n)	% cov[2,3]	spp. no.	% cov	spp. no.	% cov	spp. no.
1990	6	1.17 (0.84)[4]a[5]	1.22 (0.32)a	2.72 (0.88)bc	3.00 (0.50)ab	1.00 (0.25)a	2.56 (0.24)a
1980	7	2.03 (0.30)a	1.33 (0.33)a	8.37 (6.37)ab	2.33 (0.33)ab	3.09 (1.46)a	3.33 (0.88)a
1970	8	1.28 (0.44)a	1.44 (0.18)a	0.72 (0.28)c	1.67 (0.24)b	1.25 (0.34)a	3.00 (0.41)a
1960	7	0.60 (0.22)a	1.57 (0.61)a	0.97 (0.59)b	2.29 (0.36)ab	4.74 (2.56)a	1.86 (0.26)ab
Ref.site	6	11.97 (4.54)b	3.00 (0.26)b	20.97 (10.40)a	3.17 (0.31)a	2.62 (0.93)a	1.50 (0.43)b

[1] DOR: decade of restoration; ref. site: reference sites; site no.: site number; seed dispersal types are: epizoochores (vertebrate (fur)), endozoochores (vertebrate (consumption)), myrmecochores (ants), autochores (explosion), anemochores (wind), and barochores (gravity).

[2] data log transformed; untransformed means presented

[3] % cover is the mean percentage cover per site for each age class; spp. no. is the mean species richness per site for each age class

[4] each mean value followed by the standard error in parenthesis

[5] means followed by different letters significantly different at $p<0.05$ according to Duncan's multiple means test.

Table 4.7. Relationship between disturbance history and vulnerability ranking for the native plant communities of restored sites at Point Pelée National Park[1].

DOR	Site no.	VR1		VR2		VR3		VR4	
	(n)	%cov[2,3]	spp.no.	%cov	spp.no.	%cov	spp.no.	%cov	spp.no.
1990	6	0.00 (0.00)[4]a[5]	0.00 (0.00)a	0.58 (0.48)a	0.44 (0.24)a	0.30 (0.28)a	1.33 (0.37)a	0.56 (0.31)a	1.56 (0.38)a
1980	7	0.00 (0.00)a	0.00 (0.00)a	7.05 (5.70)a	0.67 (0.33)a	1.58 (1.06)a	3.67 (2.19)ab	2.54 (0.69)a	4.00 (1.53)a
1970	8	0.00 (0.00)a	0.00 (0.00)a	0.13 (0.11)a	0.44 (0.18)a	0.80 (0.27)a	2.78 (0.64)ab	5.93 (5.09)a	2.89 (0.51)a
1960	7	0.00 (0.00)a	0.00 (0.00)a	0.62 (0.61)a	0.57 (0.30)a	1.36 (0.40)a	5.00 (0.65)bc	1.42 (0.61)a	2.86 (0.63)a

[1] DOR: decade of restoration; ref. site: reference sites; site no.: site number; vulnerability rankings for each species defined as the proportion of reference sites (n=6) in which a species occurs / proportion of restored sites (n=28) in which a species occurs. Vulnerable native species are classified into four VR groups: VR1: infinity, VR2: VR>5; VR3: 2<VR<5; VR4: 1<VR<2.

[2] data log transformed; untransformed means presented

[3] % cover is the mean percentage cover per site for each age class; spp. no. is the mean species richness per site for each age class

[4] each mean value followed by the standard error in parenthesis

[5] means followed by different letters significantly different at $p<0.05$ according to Duncan's multiple means test.

Figure 4.5. Relationship between number of native herbaceous species of intermediate vulnerability (VR3) per site and time-since-restoration (TSR). Regression for wet/mesic sites is logy=0.019x + 0.245; $F_{1,19}$=10.94, p=0.0042. For dry sites it is logy=0.010x + 0.292; $F_{1,7}$=3.55, p=0.1016. ○ - wet/mesic sites; ● -dry sites

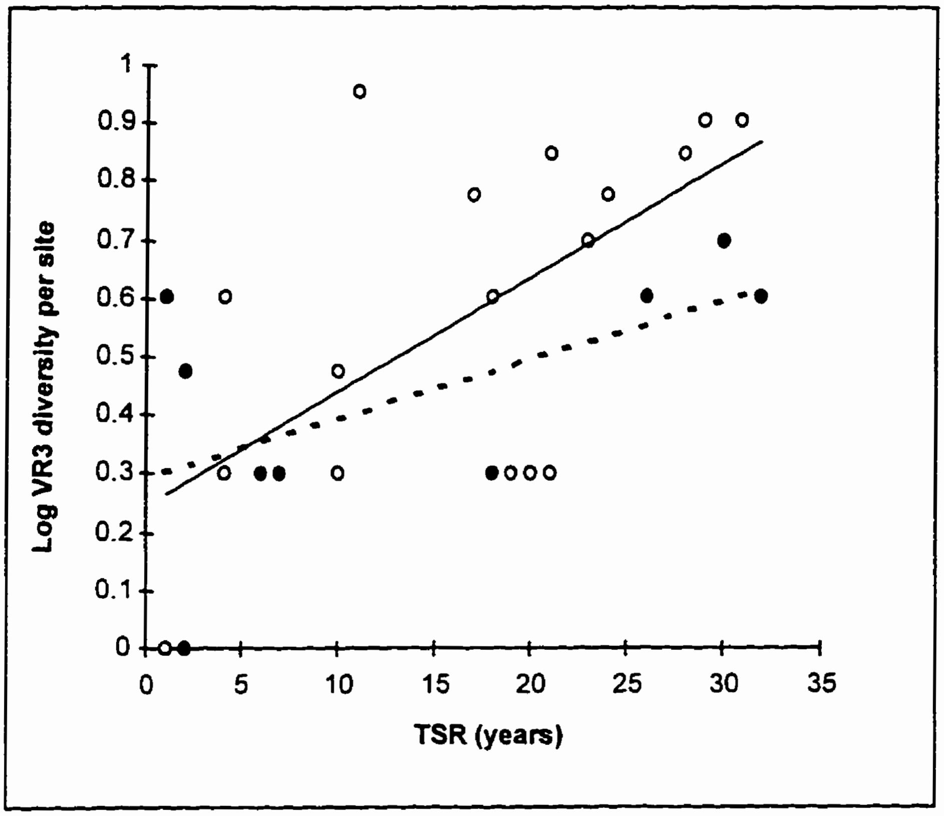
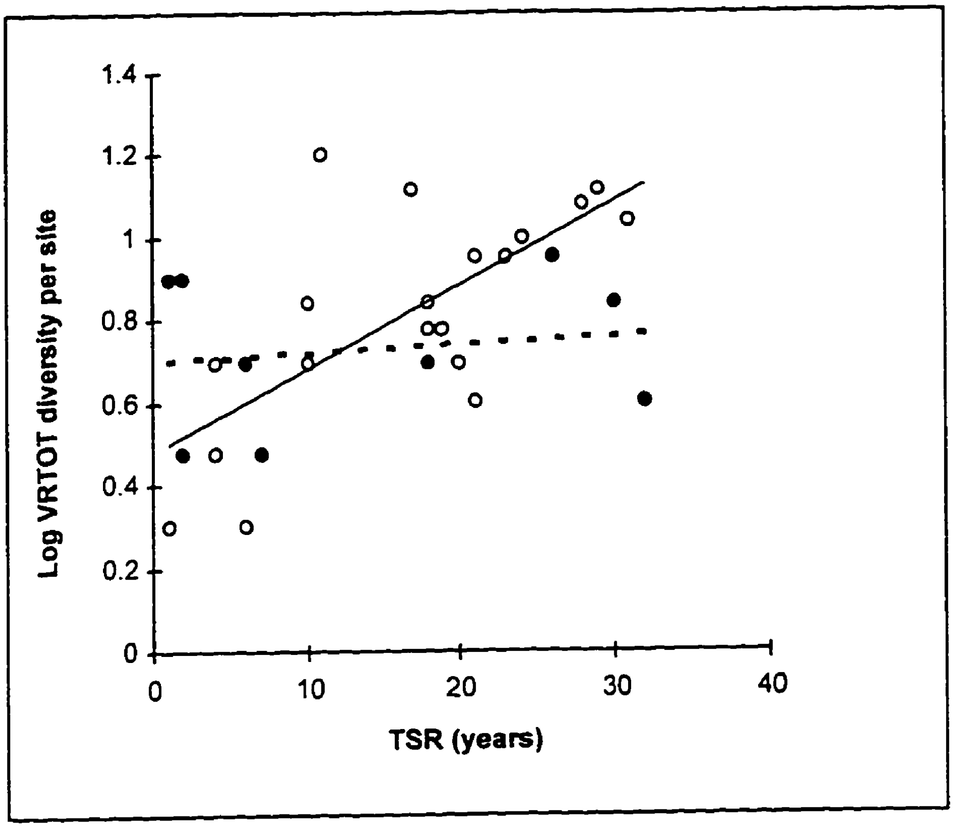

Log VR3 diversity per site
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
25
30
35
TSR (years)

Figure 4.6. Relationship between all vulnerable native herbaceous species (VRTOT) per site and time since restoration (TSR). Regression for wet/mesic sites is logy=0.020x + 0.480; $F_{1,19}$=15.00, p=0.0012. For dry sites it is logy=0.002x + 0.699; $F_{1,7}$=0.16, p=0.6991. ○ - wet/mesic sites; ● -dry sites



Log VRTOT diversity per site
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
10
20
30
40
TSR (years)

with those from some studies (e.g. Albert and Barnes, 1987; Gilliam and Turrill, 1993; Gilliam et al., 1995), in many other studies, native diversity remained lower in disturbed sites for extended periods of time (Duffy and Meiers, 1992; MacIntyre et al., 1994, Bratton et al., 1994; Meiers et al., 1995). The apparent success of recolonization by native species in PPNP might be associated with the relative proximity of the remnant natural habitat. However, while distance to continuous forest (DCF) did affect species composition, the proportion to adjacent forest (PAF), gap area, and shape index had no significant effect. Unlike other studies that examine the recovery of the understorey from large-scale disturbance such as deforestation (Meier et al., 1995), fragmentation (Dzwonko, 1993), and river flooding (Bratton et al., 1994), all of our sites, but one, were within 20m of natural habitat. Consequently, distance to standing forest, gap area, and shape index might have been below a critical threshold which has impeded recovery elsewhere (Dzwonko and Gawronski, 1994).

A reliance on community-level measures of diversity as indicators of habitat disturbance and recovery has been criticized (Taylor et al., 1993). Some understorey species may disappear from disturbed sites, but may be replaced by new species, so that no overall change in diversity is shown. Furthermore, differences in the successional or native/exotic status of the species associated with disturbance might not be reflected in overall changes in diversity. Consequently, some researchers have emphasized the importance of examining changes in species composition as well as overall diversity measures (e.g. Nicholson and Monk, 1974; Johnson et al., 1993). Our results strongly support this emphasis, since species such as *Hepatica acutiloba*, *Dicentra cucullaria*, *Allium tricoccum*, and *Trillium grandiflorum* remained absent from most restored sites. These species, all characterized by ephemeral phenology and restricted seed dispersal, show vulnerability to disturbance (Bratton, 1994; Nault and Gagnon, 1994; Drayton and Primack, 1996).

In general, native species found to be vulnerable to disturbance and associated with reference sites were strongly associated with specific phenology and dispersal functional types. Elsewhere, functional types such as physiology (Bazzaz, 1979), growth form (Grime, 1979), life history (McIntyre and Lavorel, 1994), and vital attributes (Noble and Slatyer, 1980) have been successfully used to examine plant response to disturbance. Highly vulnerable VR1 species such as *Hepatica acutiloba*, *Dicentra cucullaria*, and *Allium tricoccum* and VR2 species such as *Viola pubescens*, *Podophyllum pelatum*, and *Trillium grandiflorum* were characterized by spring development in which flowering and, often senescence, occurred before the overstorey canopy fully closed. In contrast, less vulnerable groups and nonwoodland species tended to be summer and fall flowering species, respectively. Other studies have suggested that ephemeral species tend to disappear from disturbed habitat (Bratton et al., 1994; Duffy and Meier, 1992) and conversely that summer flowering species increase with canopy disturbance (Moore and Vankat, 1986). Vulnerable species also tended to be ant and gravity dispersed whereas less vulnerable groups were dominated by endozoochores and epizoochores and nonwoodland species by anemochores. Our results are supported by other studies showing that early successional habitat is dominated by wind dispersed species (Myster, 1993; Kollmann, 1994, Dzwonko, 1993); mid successional habitat by vertebrate and in particular bird dispersed species (Howe and Smallwood, 1982); and that these long-distance dispersers seem to be the most effective colonizers of newly disturbed habitat (Nip-van der Voort et al., 1979; Willson, 1992). Interestingly, ballistic dispersers were unaffected by disturbance and equally prevalent in all habitats (see Stamp and Lucas, 1994). However, as they exhibit greater mean dispersal distances than mymecochores (Culver and Beattie, 1978), seed dispersal may be adequate enough to allow recolonization. Importantly, species that combined both restricted dispersal and ephemeral development seemed to exhibit the greatest vulnerability: there were no highly vulnerable species that did *not* combine both traits.

Despite the clear relationship between vulnerability and both restricted dispersal and ephemeral development, other factors may affect recovery. Slightly vulnerable species richness appeared to recover more rapidly in mesic/wet sites than in dry sites and vulnerable species, as a whole, did not increase at all in dry sites. Additionally, the continued absence of the many vulnerable species in older, mesic/wet sites might also be associated with the dense and early-developing canopy provided by the early-successional shrub thickets (Kollmann, 1994). Furthermore, changes in soil fertility, pH, and compactness that accompany long-term human use have been shown to hinder and even prevent recolonization (Peterken and Game, 1984).

It should also be recognized that species-level differences in response to disturbance, soil moisture and light might underlie changes in species composition. For example, while the ant-dispersed, ephemeral *V. pubescens* was largely restricted to undisturbed sites (VR=28.00), its congener *V. sororia* seemed to favor disturbed sites

(VR=.56), despite having similar dispersal and development patterns. *V. sororia* is a transitional species occupying both moist meadows and wet woods (Solbrig et al., 1980) and like the closely related, open meadow, ant-dispersed *V. fimbriatula*, it seems to have traits characteristic of many ruderal species. These include recruitment from buried dormant seed, rapid growth, and early seed production (Cook and Lyons,1983). Similarly, *V. sororia* exhibits higher light saturation values and later development than *V. pubescens* (Sparling, 1967) and seems to be more tolerant of dry soil conditions (McLachlan, unpubl.).

Management implications

The major management implication of our study is that highly vulnerable (VR1) herbaceous species may need to be actively reintroduced to restored sites. The re/introduction of native plants is now routinely employed in many restoration projects and has been suggested as a way of supplementing declining natural populations (Reinartz, 1995). This can be achieved, actively, by actual planting and/or passively, by changing habitat conditions in order to facilitate natural introduction. With respect to the latter, fruit-bearing shrubs and trees (Robinson and Handel, 1993) or bird-perches (McClanahan and Wolffe, 1993) can be established in order to attract frugivores. The resultant increases in structural complexity and perch height in old fields are associated with increases in bird-dispersed seed rain (McDonnell and Stiles, 1983; McDonnell, 1986; Debussche and Isenmann, 1994) and might counteract the dense herbaceous cover that inhibits succession on most old-field sites (McLachlan, 1977: Chapter 3: McLachlan, 1997: Chapter 5). While passive reintroduction will facilitate recolonization by vertebrate-dispersed species, it will contribute little to recolonization by dispersal-restricted species. Reintroduction seems to be especially warranted if, as in this study, vulnerability can be linked to restrictions in dispersal (Hansson, 1991; Primack and Miao, 1992; Quinn et al., 1994). However, integration with habitat management and restoration is necessary for reintroduction to be successful (Maunder, 1992). In our study, for example, new populations of vulnerable ephemerals might be outcompeted by ruderals in the absence of an adequate canopy cover or active maintenance.

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CHAPTER 5

EFFECT OF MANAGED SUCCESSION ON NON-NATIVE SPECIES IN FORMER COTTAGE AND ROAD SITES IN SOUTHWESTERN ONTARIO

STEPHANE M. McLACHLAN AND DAWN R. BAZELY

Abstract. Intensive agricultural and urban land-use has reduced the cover of natural habitat to less than 3% in Essex county, southwestern Ontario, Canada. Approximately 30% of plant species in the largest forest remnant, Point Pelée National Park, are non-native and the control of these species has become a park-management priority. In addition, most cottages and roads within the park have been removed over the last 35 years. These sites have been allowed to regenerate to forest naturally, and since 1990, have been actively restored. In 1994 and 1995, we studied the impact of this regeneration on the non-native component of the herbaceous plant communities in 28 restored sites and compared this with six relatively undisturbed, reference sites.

Over 75% of the non-native species were ruderals and restored sites had higher non-native diversity than reference sites. Non-native diversity decreased and species composition changed as time-since-restoration (TSR) increased and as canopy cover, soil moisture, and shape index of sites increased. When non-native species were classified according to their perceived management threat, habitat of origin and life history, ruderal forbs were found to decline the most as TSR increased. Former lawn species, which were annual and perennial grasses, declined only in older restored sites. Only woody perennials and escaped garden ornamentals did not decline significantly as TSR increased. However, the latter were associated with all restored sites. In contrast, native species diversity was unaffected by disturbance history and TSR. Of the three most widespread non-native species and genera (*Bromus inermis*, *Poa* spp. and *Alliaria petiolata*), only an increase in *Bromus inermis* was associated with a decline in the richness of native species.

Ecosystem management techniques that promoted succession resulted in an overall decline in non-native species as regeneration proceeded. Any restorative activity that accelerates this regeneration is expected, in turn, to further contribute to the decline of non-natives. If regeneration is successful, species-level control of non-natives may be unnecessary for many deciduous forests in north-eastern North America.

Key words: exotic, invasive, control, ecosystem management, restoration, succession, deciduous forest, disturbance

INTRODUCTION

From a global perspective, the introduction and spread of non-native species poses a serious threat to natural habitat (Hobbs and Humphries 1995). North American studies indicate that at least 25% of terrestrial plant species are nonindigenous (Deferrari and Naiman 1994, Robinson et al. 1994; Yost et al. 1991). Similarly, in Ontario, Canada, 700 of the 2600 vascular plant species are non-native (Anonymous 1995).

In general, non-native plant species are perceived to be undesirable components of natural habitat (Lugo 1991) since they can: displace native species (Sauer 1994, Tyser and Worley 1992, White et al. 1993), alter ecosystem structure (Humphreys 1993), affect nutrient cycling (Stock and Allsopp 1992) and biomass production (Vitousek 1986), increase landscape homogeneity, compromise aesthetic value, and reduce profitability in forestry and agriculture (Angenmeir 1994). Invaded habitats are perceived as having reduced ecological integrity (Karr and Dudley 1981, Noss 1990, Woodslee 1993, Angenmeir and Karr 1994). The control of non-native species is generally reactive, species-based, and mechanical, chemical, and/or biological in form (Nuzzo 1991, Hobbs and Huenneke 1992). In contrast to the prevailing approach, Hobbs and Humphries (1995) recently advocated a proactive, ecosystem-level management approach that incorporates prevention and detection of invasion, in addition to post-invasion control. Some of the desirable ecosystem-level changes in vegetation structure and composition which adversely affect non-native plant species are, by definition, successional processes. Therefore the extensive literature regarding plant succession (reviewed in McCook 1994, Miles 1979) should be of use in defining and achieving these process-based vegetation management goals.

Connell and Slatyer (1977) summarized succession in three, mutually-exclusive models that describe the net effect of established plant species on those that subsequently colonize a habitat. The effect is either positive (facilitation), neutral (tolerance), or negative (inhibition). The mechanisms that mediate these effects are: differential site availability as mediated by disturbance; differential species availability as affected by the existing propagule pool and migration; and differential species performance as affected by life history, ecophysiology, dispersal, lifespan, and vulnerability to predation and disease (Pickett et al. 1987, Connell et al. 1987). These models have been used to develop succession-based ecosystem-based management plans for pastures, agroecosystems, prairies and protected areas (Niering 1987, Rosenberg and Freedman 1984, Luken 1990, Packard 1994, LaJeunesse et al. 1995). For example, prescribed burns are frequently used to prevent succession and control weed escapes in prairies and forests, respectively (Brennan and Hermann, 1994). Thus, the net-effect models may have the potential for forming the basis for the ecosystem-based management of non-native plant species.

We conducted this study in two protected areas in southwestern Ontario: Point Pelée National Park (PPNP) and FishPoint Natural Preserve (FPNP). PPNP has been degraded by past intensive human use. PPNP is approximately 1650ha in size, 1100ha of which are upland forest. Prior to being designated a park in 1918, it was cleared of white pine (*Pinus strobus*) and planted with the now-dominant hackberry (*Celtis occidentalis*).

In-park agriculture peaked in the 1950s when 40% of the park was allocated to orchard. crop and vegetable production. By 1960. 600 cottages and numerous roads were situated in the park and over 600,000 people visited annually. In contrast. FPNP is only 400ha in area. 90% of which is upland forest dominated by black maple (*Acer nigra*) and *Celtis occidentalis* and, except for minimal recreational use, is largely undisturbed and was used as a reference site.

In 1962, park managers initiated an intensive naturalization program (Reive et al.. 1994). The majority of the in-park houses and roads were subsequently removed and sites restored so that succession would eventually result in a closed-canopy forest. Currently, 30% of the park flora is composed of non-native species, integrity of the flora is recognized as compromised, and the control of these species has become a primary management concern (Reive et al. 1992, Dunster 1990). While park managers have adopted extensive removal programs of non-native species, the concurrent restoration activity allowed us to assess the effectiveness of an ecosystem-based management approach in controlling non-native species. In particular, we hypothesized that, over time, site-level restoration would contribute to a significant decline in non-native species present in the restored habitat. In this study we asked: (1) Does site-level restoration reduce the diversity and change the composition of the non-native component of understorey plant communities? (2) Is there a variable effect of restoration on non-native species with different life-histories, habitats of origin, and levels of management-perceived threat? (3) What, if any, is the relationship between non-native species and selected environmental variables? For example, do dry sites tend to have more non-native species?

METHODS

Study areas

The study was conducted at Point Pelée National Park (PPNP), lat. 41°54'N, long. 82°22'E, and FishPoint Nature Preserve (FPNP), lat. 41°44'N, long. 82°40'E. Both protected areas are sandspits extending into Lake Erie, with PPNP on the mainland and FPNP on Pelée Island. They are located in southwestern Ontario, at the northern edge of the Carolinian or Deciduous Forest Zone (Allen et al. 1990). This region is the most urbanized and intensively farmed area of Canada; although it only represents 0.25% of Canada's land base, it supports 25% of the country's population (Allen et al. 1990). Forest cover in the immediate vicinity of both study areas is less than 3% and the fragmentation of the remaining cover is extreme. Over 95% of the remnant patches are less than 10 ha. PPNP is the only patch greater than 100ha, and most patches are over 1.5km apart (Pearce 1996). This region has the highest mean temperatures, longest annual frost-free seasons and mildest winters in Ontario. Mean temperatures and annual precipitation are 9.4°C and 86.4cm, respectively, and PPNP averages 170 frost-free days per year (Reid 1985).

Comparison of restored and reference sites

Sites that had been restored in the past were compared to relatively undisturbed, reference sites. Twenty-eight former road and cottage sites in PPNP were identified using aerial photographs, blueprints and the help of long-time park employees. Sites were initially classified according to time-since-restoration (TSR) (30 years-old, 20 years-old, 10 years-old, or recent) and visually-based inspections of soil moisture (wet, mesic, or dry). Because of the long history of widespread disturbance in PPNP, three relatively undisturbed, reference sites (10m x 80m) were located at FPNP. In 1995, three additional reference sites (10m x 80m) were identified in relatively undisturbed upland forest at PPNP, using park records.

The plant community composition of sites was measured in spring and summer, 1994 and early-spring 1995, except for the additional reference sites in PPNP that were measured in spring and fall, 1995. From 13 to 22 1m x 1m quadrats were randomly located at each restored site depending on site area and within-site habitat diversity (e.g. if there was an old lawn it was specifically sampled). In each reference site, 15 1m x 1m quadrats were located using a line transect oriented along the long axis of the forest patch. Pins were used to mark the SE corner of each quadrat. The percentage cover of all herbaceous species and woody species less than 40cm in height present was recorded and the maximum percentage cover measured for each quadrat was used in subsequent analyses. Species nomenclature follows Morton and Venn (1990) and collected specimens were deposited in the PPNP herbarium.

Soil moisture and canopy cover were measured at each site. Eight soil samples were randomly collected from each site and analyzed for moisture content in September, 1994, and June, 1995. Samples were dried at 100°C for 24 hours before weighing. Percentage canopy cover was qualitatively assessed at each quadrat corner for all quadrats in all sites.

Historical forest data were collected only for restored sites at PPNP from aerial photos taken at roughly ten year intervals (1933, 1955, 1968, and 1973) using the set that most closely preceded the restoration date. Only restored sites were described since reference sites were located in continuous forest. Cottages and roads restored since 1983 were initially described using the most recent photo and confirmed by ground truthing. Measurements taken from aerial photos were: forest gap surrounding the cottage or road, site area, distance-to-continuous forest (DCF), proportion of the site boundary that was adjacent to forest (PAF), whether sites had been cottages or roads (previous use), and shape index. Shape index was calculated from the formula, $Is=P/(2\sqrt{A\pi})$, where P is the gap perimeter and A is the area (Faeth and Kane 1978). The value of this index increases the more the shape departs from a circle; for a circle, $Is=1$. DCF was measured by dividing the longest axis of each site into three equal parts. From the two points at which the long axis intersected these divisions, 8 polar axes (N, NE, E, SE, S, SW, W, NW) were drawn. The three shortest distances to continuous forest along these axes were measured and averaged for the entire site. Finally, the dates of site-restoration were confirmed using park records.

Non-native species were defined as having been introduced to PPNP since European settlement (c.1700), according to Jellicoe and Rudkin (1984). Non-native species richness, Shannon Weaver diversity (H), and Evenness (E) (see Magurran 1988) were calculated at the quadrat and site level for native and non-native species at each site. These values are presented as a diversity measure for each site. Each non-native species was classified according to its life history, habitat of origin, and management-defined threat. Life history classes were: annual forb, biennial forb, perennial forb, annual grass, perennial grass, and perennial woody species. Classes for habitat of origin were: disturbed ground (i.e. ruderal), waste ground, garden, and lawn. Threat classes were defined by park managers and taken from Dunster (1990). These included: non-native species that are known to hybridize with native species (class 1); non-native species that are perceived as actively displacing native species (class 2); non-native species that are associated with disturbed habitat and whose ecological impact is unknown (class 3). An additional class was created for species which impede succession (class 4).

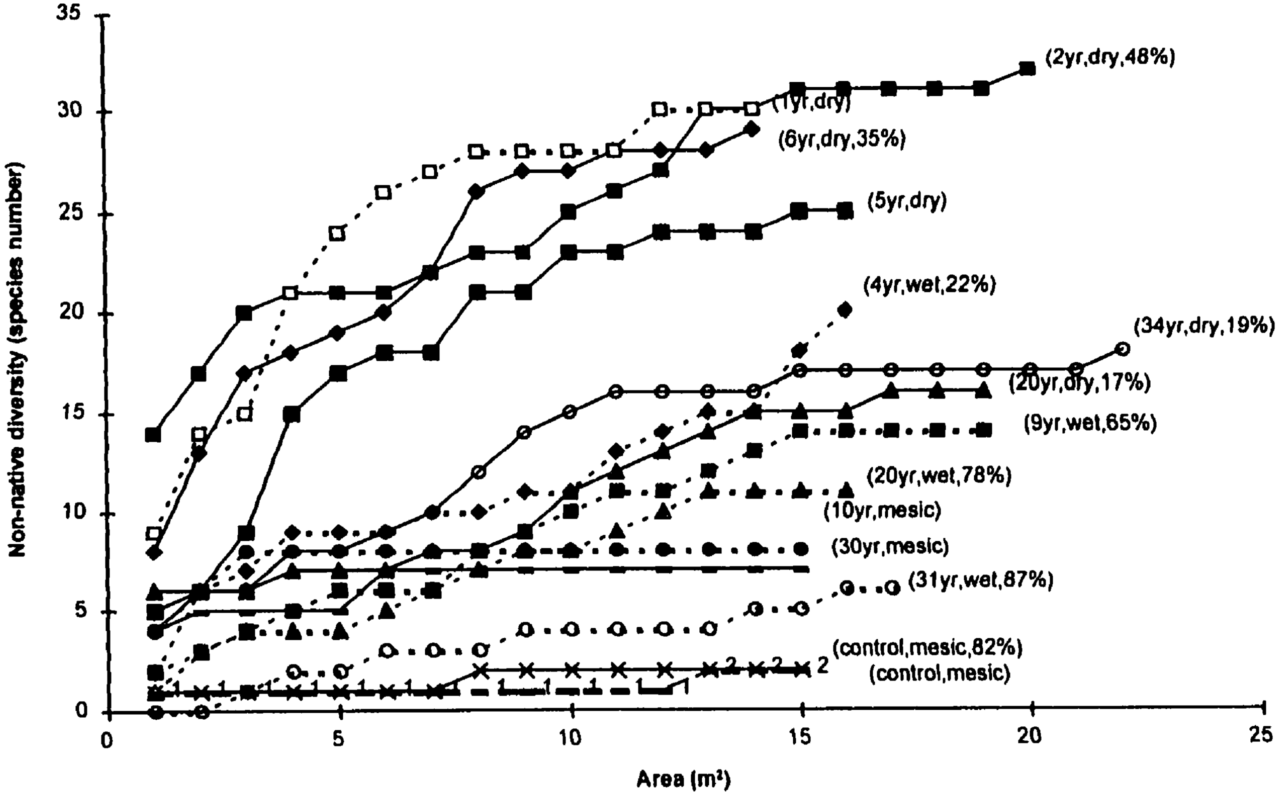
Several non-native species and genera, *Poa* spp, *Bromus inermis* and *Alliaria petiolata*, were relatively widespread and abundant. Their impact on the species richness of native species was assessed by selecting those sites in which they occurred in at least 50% of the quadrats. Quadrats with less than 5% cover for each of these species were eliminated from the analysis. The remaining quadrats were then separated into the following categories: 5-30%, 31-55%, 56-80%, 81-105%, and >105% cover of the non-native species. The native species richness was then recorded for each quadrat.

Statistical analysis

Detrended Correspondence Analysis (DCA) was used to compare changes in species composition among all 34 sites because of the limited environmental information regarding the reference sites. It is a multivariate technique that separates sites on a series of orthogonal axes that sequentially explain the greatest amount of inter-site variation (Hill and Gauch 1980, ter Braak 1992). The relationship between site scores for the first three ordination axes and environmental parameters was assessed using Pearson correlation coefficients (using Bonferroni adjustments to correct for multiple testing) (e.g. Stromberg et al. 1996). Environmental variables used for reference sites were: soil moisture, canopy cover, and disturbance. We used canonical correspondence analysis (CCA) (ter Braak 1988, 1990) to investigate changes in species composition and their relationship with measured environmental variables for disturbed sites where more historical data were available. CCA is a multivariate technique which maximally separates species distribution in ordination space; stand and species placements are constrained to be linear combinations of environmental variables (ter Braak 1988). For each site, the maximum percentage cover recorded for each species was used. Environmental variables used for restored sites were: TSR, soil moisture, canopy cover, forest gap area, site area, DCF, PAF, shape index, previous use, topography, and restoration type. Default settings were used and species occurring less than twice were eliminated from the analysis. A minimal set of environmental variables that adequately explained the species data was selected using forward stepwise multiple regression as determined by Monte Carlo simulation tests set at 999 permutations.

As previously stated, diversity measures were calculated on a per site basis, even though they were of different areas. This was because no significant relationship was found between non-native species richness and site area ($F_{1,27}$=0.35, p=0.5576). In addition, quadrat number per site varied depending on the site area and habitat heterogeneity of each site. However, cumulative area / species richness curves calculated for each site all rapidly reached asymptotes (Figure 5.1), indicating that diversity measures presented for the site were appropriate.

Figure 5.1. The relationship between non-native species richness and cumulative area for 15 sites from PPNP.



Non-native diversity (species number)
35
30
25
20
15
10
5
0
0
5
10
15
20
25
Area (m²)
(2yr,dry,48%)
(1yr,dry)
(6yr,dry,35%)
(5yr,dry)
(4yr,wet,22%)
(34yr,dry,19%)
(20yr,dry,17%)
(9yr,wet,65%)
(20yr,wet,78%)
(10yr,mesic)
(30yr,mesic)
(31yr,wet,87%)
(control,mesic,82%)
(control,mesic)
1
2

Univariate ANOVAs were calculated for differences in diversity between disturbed and reference sites and for the relationship between non-native percentage cover and native species richness using PROC GLM (SAS, 1990). Where necessary, diversity measures were transformed to achieve homogeneity of variance (Sokal and Rohlf 1981). In all cases, untransformed data are presented. Where necessary Bonferroni adjustments were applied to compensate for multiple comparisons. Pearson correlation coefficients were calculated between environmental variables to ensure they were mutually independent and as perimeter had $r>0.90$, it was eliminated from further analysis.

The relationship between measured environmental variables and species diversity was tested using both multiple regressions and ANOVA (Sokal and Rohlf 1981). Multiple regressions related dependent diversity measures to independent environmental variables. The relationship between species richness for each life history, habitat origin, or perceived threat of non-natives and significant environmental variables was analyzed using MANOVA on species richness for each combination of class and level of environmental variable. If a significant multivariate effect (Wilk's lambda) was observed, univariate ANOVA was conducted and protected LSD multiple range testing was used to separate means. Pearson correlation coefficients were calculated to examine the relationship between these non-native variables.

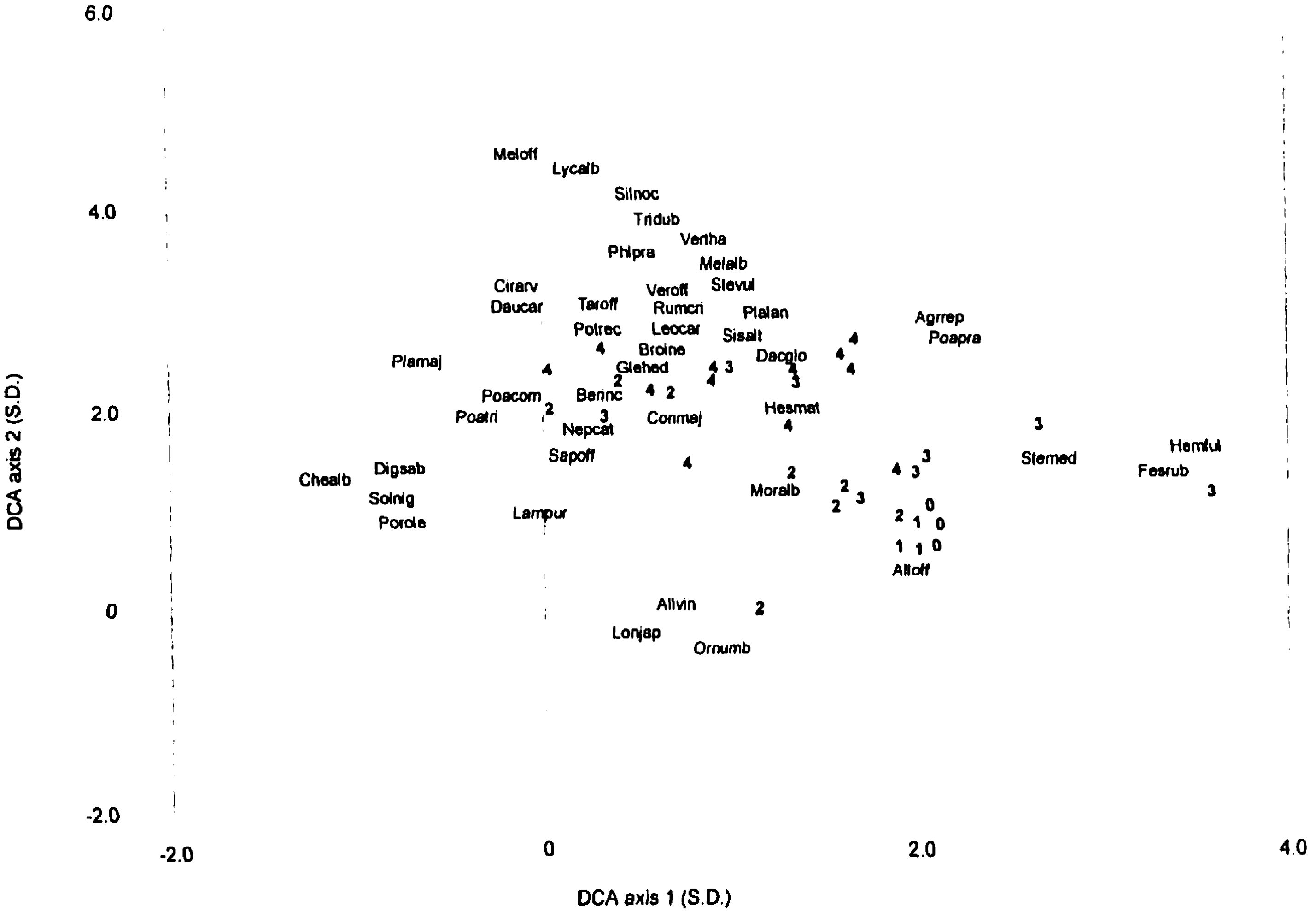
RESULTS

The composition of the non-native component of plant communities in restored and reference sites

Alliaria petiolata was the most widespread non-native species in this study. It occurred in both study areas, in all reference sites, and in all but two of the restored sites. It represented 31% of the total cover for all non-native species and 12% of the total cover for both native and non-native species. *Bromus inermis*, *Poa pratensis* and *P. canadensis*, were the next most common non-native species, representing 7-17% of the total cover for all non-native species, and 3-5% of the total cover for both native and non-native species. Other than *Alliaria petiolata*, the only non-native species occurring in more than one reference site were *Leonurus cardiaca* and *Morus alba*.

The DCA on all sites (n=34) indicated that species composition of the non-native plant community varied according to whether sites were restored or undisturbed (Figure 5.2). Reference sites were a distinct group of overlapping points compared with restored sites, and were associated with *Alliaria petiolata* (Figure 5.2). Most sites from the 1960s and 1970s were situated nearer to reference sites than more recently restored sites from the 1980s and 1990s although four older restored sites were classified with these sites. Site scores on each of the first four DCA ordinal axes were correlated with site values for disturbance history, soil moisture, and canopy cover. Axis 1 was positively correlated with disturbance history (i.e. whether the site was restored or not) (r=0.36) and canopy cover (r=0.38). It was negatively associated with *Hemerocallis fulva*, *Festuca rubra*, and *Stellaria media*, and positively associated with *Chenopodium album*, *Digitaria*

Figure 5.2. Detrended correspondence analysis (DCA) diagram of all sites (axes 1 and 2) using non-native herbaceous data indicating positions of reference (n=6) sites at Point Pelée National Park (PPNP) and FishPoint Nature Preserve (FPNP) and restored sites (n=28) at PPNP. Reference sites (PPNP) (0), reference sites (FPNP) (1), 26-35 years TSR (2) 16-25 years TSR (3), <15 years TSR (4). Species are listed by first three letters of genus and species and abbreviations are included in Appendix 1.


DCA axis 2 (S.D.)
6.0
4.0
2.0
0
-2.0
DCA axis 1 (S.D.)
-2.0
0
2.0
4.0
Meloff
Lycalb
Silnoc
Tridub
Vertha
Phlpra
Melalb
Cirarv
Daucar
Taroff
Veroff
Stevul
Rumcri
Plalan
Potrec
Leocar
Sisalt
Agrrep
Poapra
Broine
Dacglo
Plamaj
Glehed
Poacom
Bennc
Hesmat
Poatri
Nepcat
Conmaj
Sapoff
Stemed
Hemful
Fesrub
Chealb
Digsab
Solnig
Porole
Moralb
Lampur
Alloff
Allvin
Lonjap
Ornumb
4
4
2
2
3
4
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4 3
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4
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1
1
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3

sanguinalis, and *Solanum nigrum*. Axis 2 was positively correlated with disturbance history (r=0.53) and canopy cover (r=0.57). It was negatively associated with *Lonicera japonica*, *Allium vineale*, and *Ornithogalum umbellatum*, and positively associated with *Melilotus officinalis*, *Lychnis alba*, and *Silene noctiflora* (Figure 5.2).

Canonical correspondence analysis (CCA) was conducted on non-native species data from restored sites only (n=28). One third, 33.8%, of the variance was explained by the first four vegetation-determined ordination axes and 74.6% by the first four environmentally constrained ordination axes. Overall, composition of the non-native component of the community was significantly determined by soil moisture, TSR, DCF, and canopy cover (Table 5.1). The first CCA axis was positively correlated with DCF, soil moisture, and canopy cover (Table 5.2, Figure 5.3) and positively associated with *Hemerocallis fulva*. Axis 2 was positively correlated with TSR, shape index, canopy cover, and PAF and negatively correlated with restoration type (i.e. whether sites were passively or actively restored). Positively associated species included *Lonicera japonica*, *Lamium purpureum*, *Ornithogalum umbellatum*, *Allium vineale*, and *Glechoma hederacea*, while negatively associated species included *Stellaria vulgatum*, *Melilotus alba*, *Veronica officinale*, *Digitaria sanguinalis*, *and Solanum nigrum*. Axis 3 was positively correlated with restoration type and associated with *Chenopodium album*, *Lychnis alba*, *Plantago major*, *Portulaca oleracea*, and *Digitaria sanguinalis*. Finally, axis 4 was positively correlated with surface topography and previous use and negatively correlated with soil moisture. Positively associated species included *Melilotus officinalis*,

Table 5.1. Variance explained by each environmental factors retained after forward selection in the canonical correspondence analysis (CCA). Selected environmental variables are: soil moisture (soilm), time-since-restoration (TSR), distance to continuous forest (DCF), canopy cover (cancov), surface topography (surftop), shape index (shapind), restoration type (restype), proportion of adjacent forest forest (PAF), site area (sitarea), previous use (prevuse), and forest gap area (gap area).

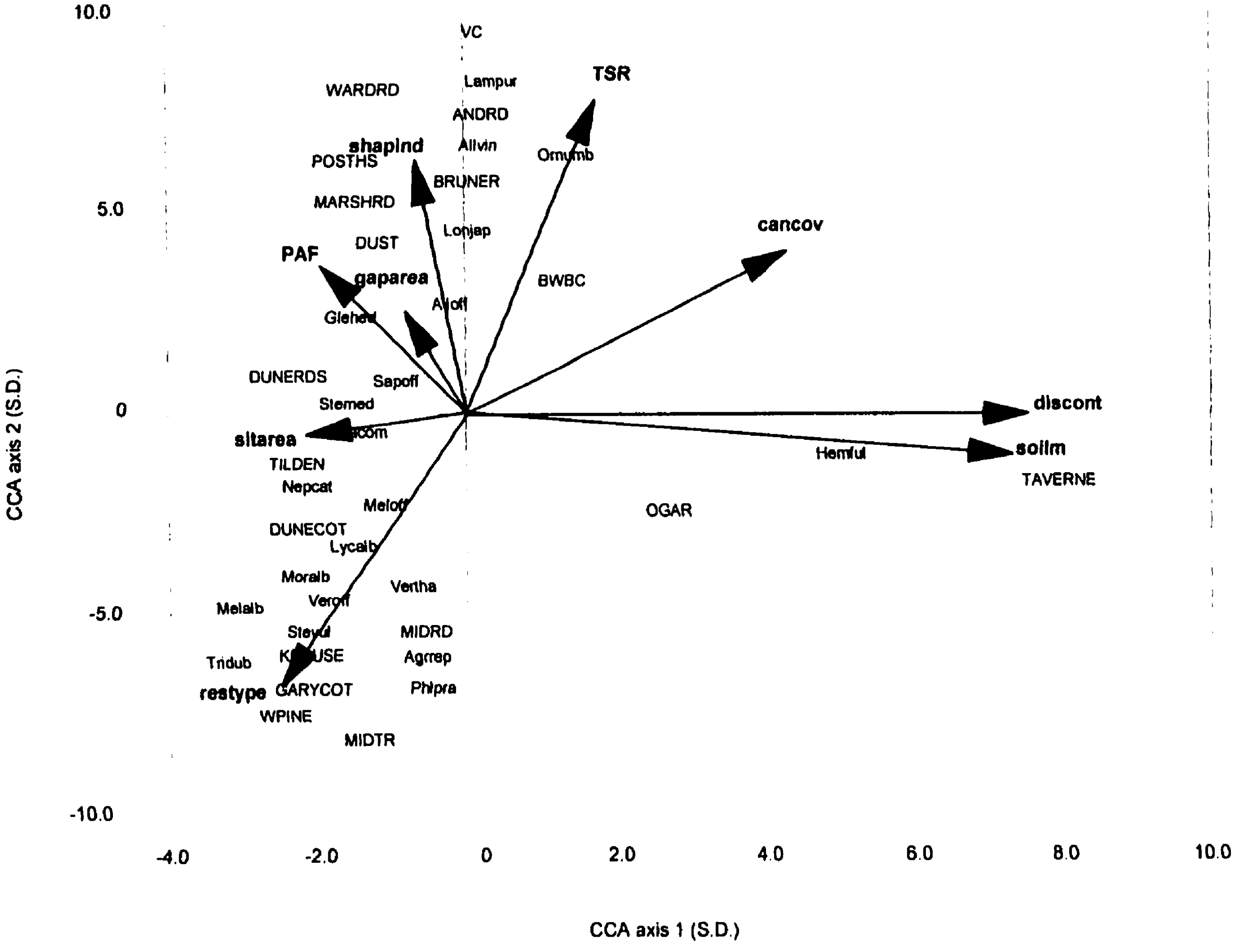
Environmental Variable	All restored sites	
	Variance explained (%)	Significance P-value
Soilm	19.5	0.002
TSR	14.4	0.005
DCF	9.3	0.053
Cancov	14.8	0.038
Surtop	5.5	NS
Shapind	3.5	NS
Restype	3.1	NS
PAF	2.8	NS
Sitarea	2.1	NS
Prevuse	1.8	NS
Gaparea	1.8	NS

Table 5.2. Correlation coefficients between environmental variables and first four ordination axes of the canonical correspondence analysis CCA). Selected environmental variables are: soil moisture (soilm), time-since-restoration (TSR), distance to continuous forest (DCF), canopy cover (cancov), surface topography (surftop), shape index (shapind), restoration type (restype), proportion of adjacent forest forest (PAF), site area (sitarea), previous use (prevuse), and forest gap area (gap area).

	CCA axis 1	CCA axis 2	CCA axis 3	CCA axis 4
Cancov	0.471*	0.434*	0.310*	-0.230
Soilm	0.828*	-0.107	-0.184	-0.350*
Sitarea	-0.253	-0.088	-0.256	0.286
PAF	-0.188	0.417*	-0.036	0.161
DCF	0.844*	-0.005	0.063	0.050
Gaparea	-0.057	0.284	0.084	-0.077
Shapind	0.003	0.625*	0.119	0.048
TSR	0.215	0.814*	-0.269	-0.116
Surtop	-0.094	-0.221	-0.026	0.554*
Restype	-0.294	-0.571*	0.630*	0.277
Prevuse	-0.156	0.271	0.286	0.321*

* indicate significance at $p < 0.05$ according to Bonferonni-adjusted Spearman's rank coefficient

Figure 5.3. Canonical correspondence analysis (CCA) diagram of restored sites (axes 1 and 2) using non-native herbaceous data with environmental variables (bold) indicated by biplot arrows, herbaceous species (lower case) with high scores, and sites (uppercase) with high scores. Species are listed by first three letters of genus and species and abbreviations are included in Appendix 1.


10.0
5.0
0
-5.0
-10.0
CCA axis 2 (S.D.)
-4.0
-2.0
0
2.0
4.0
6.0
8.0
10.0
CCA axis 1 (S.D.)
VC
Lampur
WARDRD
ANDRD
TSR
shapind
Allvin
POSTHS
Ornumb
BRUNER
MARSHRD
cancov
Lonjap
PAF
DUST
gaparea
BWBC
Alloff
Glehed
DUNERDS
Sapoff
Stemed
discont
sitarea
com
soilm
Hemful
TILDEN
TAVERNE
Nepcat
Meloff
OGAR
DUNECOT
Lycalb
Moralb
Vertha
Melalb
Veroff
Steyul
MIDRD
K USE
Tridub
Agrrep
restype
GARYCOT
Phlpra
WPINE
MIDTR

Lychnis alba, *Cirsium arvensis*, and *Cirsium arvensis*, while negatively associated species included *Plantago lanceolata*, *Morus alba*, and *Stellaria vulgatum*.

Relationship between diversity and site disturbance history

The overall species richness and diversity of the relatively undisturbed reference sites and restored sites varied greatly (Table 5.3). There was a significant overall effect of disturbance history on the various measures of diversity. Overall, species richness (total number of species per site) was significantly greater in restored sites than in reference sites and this was attributable to significantly higher non-native species richness in restored sites (Table 5.3). In contrast, native species richness showed no relationship with the disturbance history of sites. Similarly, Shannon Weaver diversity index and Evenness calculated only for non-native species, were both greater in restored sites for non-native species. As with native species richness, neither native Shannon Weaver diversity index nor native Evenness showed any relationship with disturbance history, although both tended to be lower in restored sites (Table 5.3).

Relationship between native and non-native diversity measures and environmental variables

A multiple regression was carried out for each of the site-level diversity measures using the environmental variables associated with each site as independent variables. None of the measures of diversity which were calculated for the native component of the plant community were significantly related to environmental variables (Table 5.4). In contrast, the non-native component showed a significant overall relationship between each diversity measure and environmental variables. Species richness of non-natives

Table 5.3. Effect of disturbance on diversity measures calculated for both non-native and native components of plant communities in restored sites at Point Pelée National Park and FishPoint Nature Preserve. MANOVA for overall effect of disturbance used Wilks Lambda. WL=0.1843; F=16.442, p<0.0001.

Component of plant community	Diversity measure	Restored sites (n=28)	Reference sites (n=6)
All species	species richness	56.5 a*	39.4 b
Non-native	species richness	17.8 a	2.0 b
	Shannon Weaver	1.5 a	0.1 b
	Evenness	0.5 a	0.1 b
Native	species richness	38.7 a	37.3 a
	Shannon Weaver	2.0 a	2.4 a
	Evenness	0.6 a	0.8 a

* means followed by different letters are significantly different at p<0.05 according to Duncan's multiple means test

Table 5.4. Summary of the multiple regression analyses in which different measures of diversity measured at the site-level were regressed on environmental variables. Both non-native and native components of restored sites (n=28) at Point Pelée National Park were analyzed. Data are partial regression coefficients and associated probabilities of significance [a].

Diversity measure	TSR	Soilm	Cancov	PAF	DCF	Shapind	Surftop	Prevuse	Restype	Sitarea	Gaparea	R2[b]	F value	P value
Non-native component														
i) species richness	0.593**[c]	1.397*	-	-	-	-	-	-	-		-	0.72	7.46	P<0.0002
ii) Shannon Weaver	0.044***	-	-	-	-	0.267*	-	-	-		-	0.76	9.01	P<0.0001
iii) Evenness	0.009**	-	-	-	0.004**	0.069*	-	-	-		-	0.72	8.23	P<0.0001
Native component														
i) species richness	-	-	-	-	-	-	-	-	-		-	0.40	1.88	P=0.1259
ii) Shannon Weaver	-	-	-	-	-	-	-	-	-		-	0.46	1.32	P=0.2924
iii) Evenness	-	-	-	-	-	-	-	-	-		-	0.51	1.07	P=0.4240

[a] Site-level independent variables are time-since-restoration (TSR), soil moisture (soilm), canopy cover (cancov), proportion of adjacent forest forest (PAF), distance to continupus forest (DCF), shape index, and forest gap area (gap area). Whether the sites was used as a cottage or road (Prevuse), whether it was actively or passively restored (restype), and whether it whether it was flat or not (surftop) were introduced as dummy variables.

[b] R^2_{adj} is the fraction of variance accounted for by the model, F value and P value are the F ratio associated with the model and the probability that it is significantly different from zero, respectively

[c] Significance level of each partial regression coefficient: *p<0.05, **p<0.01, ***p<0.001.

decreased as TSR and soil moisture increased (Figure 5.4, Table 5.5). For non-native species, Shannon Weaver diversity index also decreased as TSR and soil moisture increased and as shape index decreased (i.e. closer to a circle). Non-native species Evenness decreased as TSR, DCF, and shape index all increased (Table 5.5). Furthermore, when non-native species richness was regressed against TSR, non-native species richness showed a significant interaction between TSR and soil moisture. At any given time, dry sites had higher non-native species richness than wet sites (ANCOVA, p=0.04661; difference in y-intercept = 8.793) (Figure 5.5).

Life history, habitat origin, and perceived threat

While we observed that non-native species richness was significantly affected by TSR, soil moisture, DCF, and gap area (Table 5.4), the CCA showed that non-native species did not all respond equally to these variables. Consequently, we examined the relationship between these four environmental variables and particular life histories, habitat of origin, and perceived threat of non-natives in order to determine which classes of non-native species are most likely to persist in restored sites. A series of MANOVAs was conducted in which species richness per site classified according to different life history, origin of habitat, and perceived-threat, was compared among classes of different TSR, soil moisture, DCF, and gap area groups for restored sites. Results indicated that perceived threat barely differed significantly according to TSR age groups (Wilk's lambda (WL) = 0.044, $F_{12,14}$=2.539, p=0.052). Non-native species richness was higher in recently restored sites than in older sites for perceived-threat classes 1, 3, and 4 (Table 5.5). However, no significant relationship was found between Class 2 and TSR. In

Figure 5.4. Relationship between time since restoration (TSR) and non-native species richness. Regression is $y=27.666-0.628x$; $F_{1,26}=35.89$, $p<0.0001$.

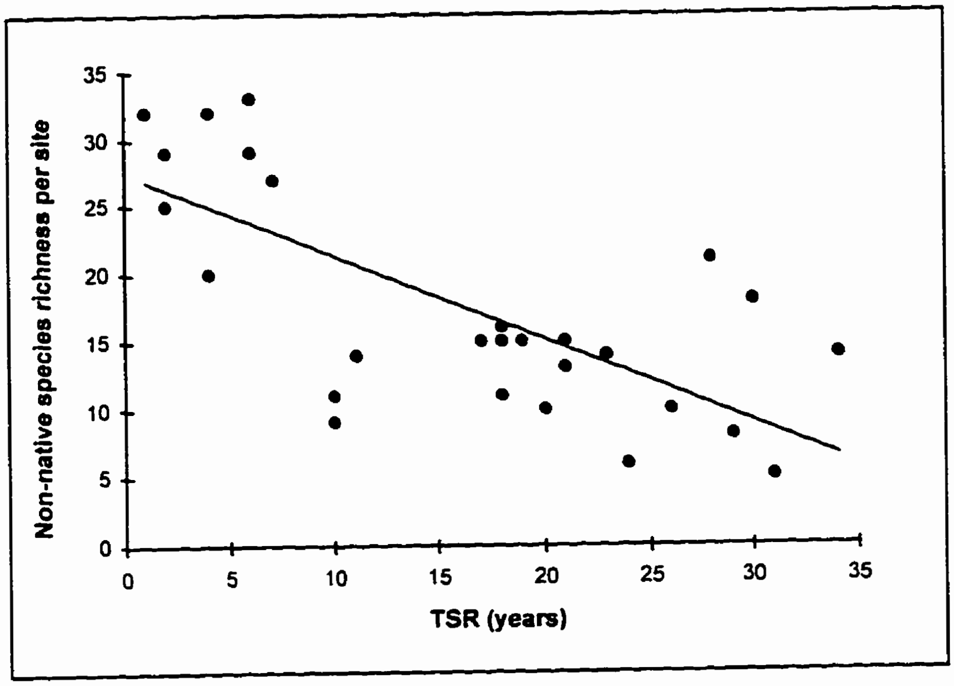
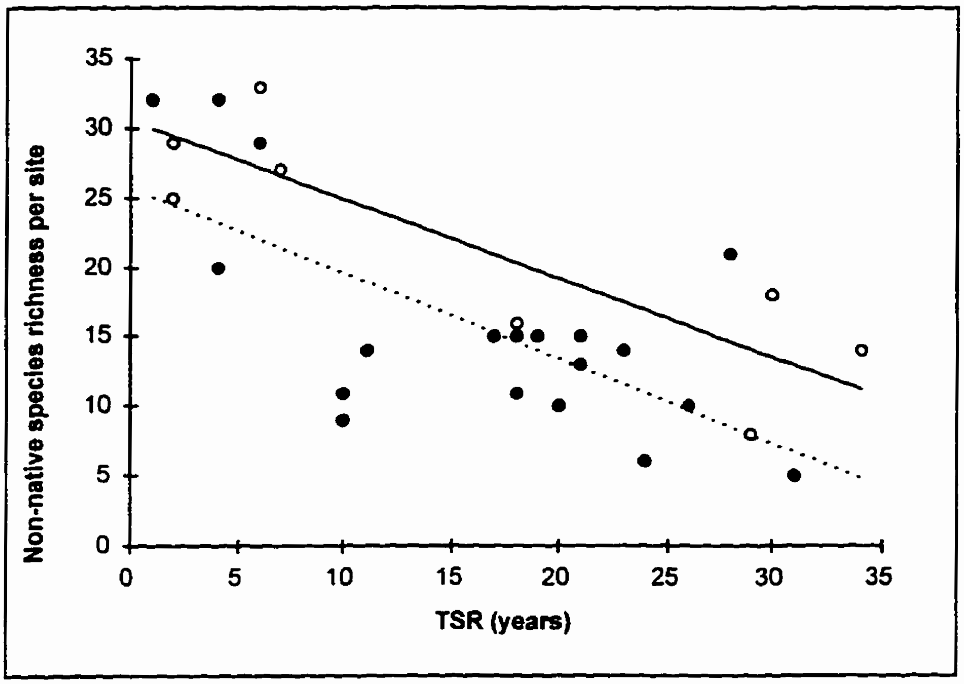

Non-native species richness per site
0
5
10
15
20
25
30
35
TSR (years)

Table 5.5. Effect of time-since-restoration (TSR) on the species richness of non-natives in each threat class. Threat classes defined according to Dunster (1990) are: non-native species that hybridize with natives (Class 1), non-native species that competitively displace native species (Class 2), non-native species whose ecological effects are unknown (Class 3), and non-native species that impede successional change (Class 4); Time since restoration (TSR) classes are: <5 years (1), 6-15 years (2), 16-25 years (3), and 26-35 years (4) since restoration. MANOVA for overall effect of disturbance using Wilks Lambda. WL=0.044, $F_{12,14}$=2.539, p=0.052.

TSR class	Perceived threat class			
	Class 1	Class 2	Class 3	Class 4
	(mean species richness per site)			
1	0.67 (0.17)a*	2.44 (0.41)a	21.78 (0.94)a	4.56 (0.24)a
2	1.00 (0.00)a	1.33 (0.33)a	5.33 (1.45)b	3.67 (0.33)a
3	0.11 (0.11)b	3.56 (0.38)a	6.89 (0.66)b	3.22 (0.32)ab
4	0.14 (0.14)b	2.43 (0.65)a	6.57 (1.54)a	2.57 (0.53)b

* means within each column followed by different letters significantly different at p<0.05 according to Duncan's multiple means test

Figure 5.5. Relationship between time-since-restoration (TSR) and non-native species richness for dry and wet/mesic sites. Soil moisture classes: <8% soil moisture (dry) and >8% soil moisture (mesic/wet).Regression for dry sites is y= 30.582-0.568x. $F_{1,7}$=23.10. p=0.0019: for mesic/wet sites y=25.729-0.615x, $F_{1,17}$=14.38. p=0.0015). ○ - dry sites: ● - wet/mesic sites



Non-native species richness per site
35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
35
TSR (years)

another MANOVA, habitat of origin differed significantly among different TSR age groups (WL=0.0215, $F_{12,14}$=3.683, p<0.012). Recently restored sites showed higher non-native species richness for species associated with waste ground, disturbed ground, and lawns (Table 5.6). No significant relationship was shown between non-native species escaping from gardens and TSR. Life history was significantly affected by three of the environmental variables: TSR (WL=0.0035, $F_{18,9}$=3.187, p=0.043), soil moisture (Wl=0.0061, $F_{12,6}$=5.89, p=0.0199), and DCF (WL=0.00145, $F_{24,13}$=2.683, p=0.041). The numbers of species with different life histories differed significantly among sites grouped according to TSR. Recently restored sites had significantly higher non-native species richness than older sites for annual forbs, biennial forbs, perennial forbs, annual grasses, and perennial grasses whereas perennial woody species showed no relationship (Table 5.7). With respect to soil moisture, dry sites had significantly higher non-native species richness than moist sites, but only for biennial forbs (Table 5.8). However, no biologically meaningful relationship between non-natives with different life histories and DCF was evident (data not presented).

Many of the categories in each of these three classifications applied to non-native species responded similarly to environmental variables. For example, when each category was correlated with all environmental variables, class 2 species were correlated with escaped garden species (r=0.80), while class 3 species were highly correlated with disturbed (r=0.95) and waste ground (r=0.95) species. The latter were also correlated with all life history classes especially annual (r=0.95), biennial (r=0.81), and perennial

Table 5.6. Effect of time-since-restoration (TSR) on the species richness of non-natives classified according to habitat of origin. Habitat of origin classes are: species associated with marginal or waste land (W); ruderal species associated with routinely disturbed habitat (R); former garden and ornamental species (O); and former lawn species (L). Time since restoration (TSR) classes are: <5 years (1), 6-15 years (2), 16-25 years (3), and 26-35 years (4) since restoration. MANOVA for overall effect of time since restoration used Wilks Lambda. WL= 0.0215, $F_{12,14}=3.683$, $p<0.012$.

TSR class	Habitat origin class			
	Waste	Disturbed	Ornamental	Lawn
	(mean species richness per site)			
1	13.56 (0.58)a*	12.67 (1.04)a	1.00 (0.29)a	2.26 (0.15)a
2	5.00 (1.73)b	3.67 (0.67)b	0.33 (0.33)a	2.33 (0.33)a
3	5.44 (0.63)b	4.56 (0.50)b	2.22 (0.40)a	1.56 (0.24)b
4	5.00 (1.02)b	3.71 (0.84)b	1.86 (1.08)a	1.14 (0.14)b

* means within each column followed by different letters significantly different at $p<0.05$ according to Duncan's multiple means test

Table 5.7. Effect of time-since-restoration (TSR) on the species richness of non-natives classified according to life history . Life history classes are: annual forb (AF), biennial forb (BF), perennial forb (PF), annual grass (AG), perennial grass (PG), and perennial woody (PW) species. Time since restoration (TSR) classes are: <5 years (1), 6-15 years (2), 16-25 years (3), and 26-35 years (4) since restoration. MANOVA for overall effect of time since restoration used Wilks Lambda. WL0.0035, $F_{18,9}$=3.187, p=0.043.

TSR			Life history			
class	AF	BF	PF	AG	PG	PW
			(mean species richness per site)			
1	8.67 (0.73)a*	3.33 (0.44)a	9.44 (0.84)a	1.78 (0.52)a	5.56 (0.38)a	0.67 (0.17)a
2	1.33 (0.67)b	1.33 (0.33)b	2.67 (1.20)b	0.00 (0.00)b	5.00 (0.58)ab	1.00 (0.00)a
3	2.22 (0.49)b	1.67 (0.24)b	5.44 (0.48)b	0.22 (0.22)b	3.56 (0.44)bc	0.67 (0.29)a
4	2.43 (0.75)b	1.43 (0.30)b	4.71 (1.02)b	0.00 (0.00)b	2.57 (0.53)c	0.57 (0.43)a

*means within each column followed by different letters significantly different at p<0.05 according to Duncan's multiple means test

Table 5.8. Effect of soil moisture (soilm) on the species richness of non-natives classified according to life-history. Life history classes are: annual forb (AF), biennial forb (BF), perennial forb (PF), annual grass (AG), perennial grass (PG), and perennial woody (PW) species. Soil moisture classes are: <8% (dry); 8-10% (mesic) and >10% (wet). MANOVA for overall effect of soil moisture used Wilks Lambda. WL= 0.0061, $F_{12,6}$=5.89, p=0.0199.

Soil moisture	Life history					
class	AF	BF	PF	AG	PG	PW
(%)	(mean species richness per site)					
dry	6.00 (1.02)a[*]	3.00 (0.54)a	7.00 (0.85)a	1.13 (0.61)a	4.63 (0.71)a	0.38 (0.18)a
mesic	4.06 (0.90)a	1.82 (0.25)a	6.23 (0.87)a	0.41 (0.23)a	4.12 (0.35)ab	0.77 (0.20)a
wet	0.67 (0.33)b	1.33 (0.33)b	4.33 (1.20)b	0.67 (0.67)a	2.67 (1.20)b	1.00 (0.58)a

[*] means within each column followed by different letters significantly different at p<0.05 according to Duncan's multiple means test

forbs (r=.85). Class 4 species were most strongly correlated with ruderal (r=0.82), former lawn (r=0.80), and perennial grass (r=0.95) species.

Although class 2 and garden non-native species richness showed no significant relationship with TSR, a MANOVA showed that both class 2 ($F_{1,27}$=8.23, p<0.0072) and garden ($F_{1,27}$=9.74, p<0.0038) species richness were significantly higher in restored than in reference sites. In contrast, perennial woody species richness was not significantly different between restored and reference sites ($F_{1,27}$=.75, p=0.6342).

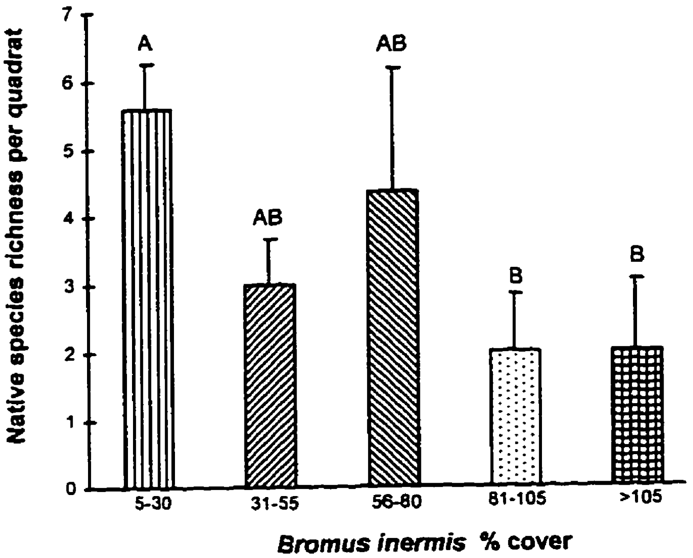
The relationship between the percentage cover of three non-native species and native diversity

Three prevalent non-native species that occurred in "monodominant" stands were selected to examine the relationship between non-native percentage cover and native species richness. There was a slightly significant decrease in native diversity as *Bromus inermis* percentage cover increased ($F_{4,14}$=3.23, p=0.0412) (Figure 5.6). However, no relationship between native diversity and either *Poa* spp. or *Alliaria petiolata* percentage cover was found.

DISCUSSION

Although PPNP is an internationally recognized preserve, approximately 40% of the upland area is recovering from some form of severe disturbance, such as agriculture (orchard, vegetable production), settlement, infrastructure (roads, parking), overgrazing

Figure 5.6. Effect of *Bromus inermis* percentage cover per quadrat on native species richness on restored sites at Point Pelée National Park (n=20). Different letters indicate significant differences among means at $p<0.05$ according to protected LSD.


Native species richness per quadrat
7
6
5
4
3
2
1
0
A
AB
AB
B
B
5-30
31-55
56-80
81-105
>105
Bromus inermis % cover

by deer, or intensive recreational use (W. Stephenson, pers. comm.). Over 30% of the park's flora is nonindigenous and the control of non-natives has been identified as a primary vegetation management goal (Dunster 1990; Reive et al. 1992). Consequently, PPNP was an ideal location in which to examine the effects of habitat regeneration and succession-based management on non-native species.

Non-native diversity

The presence of non-native plant species was strongly associated with habitat disturbance, with recently restored sites having ten times the diversity of non natives compared with reference sites. Most, (78%), of these species were associated with frequently disturbed or marginal habitats. Thus, disturbance seems to open a "window" for non-natives that, given a viable propagule bank and/or adequate migration, permits successful establishment (Johnstone 1986).

Non-native species richness decreased substantially as time-since-disturbance, soil moisture and canopy cover increased and gap area decreased. In dry sites, where canopy development was relatively slow, non-native species richness was higher at any given time than in wet/mesic sites of similar age. These findings support those of studies comparing non-native diversity in edge and interior habitats in which most non-natives decline sharply away from the edge (Brothers and Springarn 1992; Fraver 1994; Matlack 1994; Maas 1994). This decline is most strongly associated with decreases in radiation from edge to interior which are accompanied by changes in soil and air temperature, wind speed, soil moisture, and relative humidity. Most studies indicate that few non-native species penetrate more than 10m into the forest (Fraver 1994, Matlack 1994). This distance is reduced to 2m in "old-growth" patches which have developed some degree of "self-armoring" (Brothers and Springarn 1992). Interestingly. in PPNP. the strong association of non-natives with open, dry sites, increases their visibility to park visitors. who assume that non-natives are as common in less-accessible. canopy-enclosed areas.

Despite the regeneration-associated decline in non-natives. not all non-natives respond similarly to regeneration. Existing park management criteria. life history strategies. and habitat origin were used to identify functional groups of non-native species which might show differential responses to regeneration (Gitay and Noble. 1995). Class 3 species were widespread. due to the extent of in-park disturbance. and accounted for 73% of the non-natives. These annual, biennial and perennial forbs were generally associated with disturbed and marginal habitats. and were prevalent in recently restored sites, but declined rapidly in response to site regeneration. Class 4 species. which were frequently escaped lawn and perennial grasses. functioned as inhibitors of succession and decreased rates of regeneration (Figure 5.6). However. once their dense vegetation cover was penetrated, regeneration proceeded, and they too declined. Class 2 species tended to be escaped ornamentals. Even after 35 years, they persisted in restored sites. However. they were largely absent from reference sites, indicating that they are not "invasive". In older. highly shaded. restored sites they generally persisted in small, localized populations that only reproduced vegetatively. Finally, the only Class 1 species, *Morus alba*, did not decline with increasing TSR and also occurred in reference sites at FPNP, where the record of disturbance history is less well-known. However, *M. alba* was absent from reference sites as well as grass-dominated sites at PPNP, suggesting that some degree of disturbance might be necessary for its establishment.

Thus it appeared that, regardless of perceived threat, the great majority of these non-native species at PPNP were intolerant of shade and amenable to succession-based management. The exception was the shade-tolerant *Alliaria petiolata* (Nuzzo 1991) which has spread throughout both disturbed and undisturbed areas of the park since it was introduced in the late 1960s, and was only absent in the wettest sites. Similar shade tolerant non-natives have been identified elsewhere (e.g. *Lonicera japonica* (Japanese honeysuckle) (Williams 1980), *Acer platanoides* (Norway maple) (Webb and Kalafus-Kaunzinger 1993)) and shade tolerance is clearly a characteristic that facilitates forest invasion.

Native diversity

In sharp contrast to non-native species, native diversity showed little response either to habitat disturbance and restoration. Thus, there was no indication that native species were being adversely affected by the presence of non-natives in disturbed sites. The only decline in native diversity associated with the presence of an non-native was with *Bromus inermis*. This was attributed to the development of thick root mats and the resultant inhibition of subsequent seedling establishment rather than displacement *per se*. These findings agree with other studies, in which few, if any, native "interior" plant species show significant declines when forest edges are approached (Fraver 1994. Brothers and Springarn 1992, Ranney et al. 1981, Palik and Murphy 1990). Similarly, many "interior" plant species persist in small, entirely edge-dominated habitat patches.

while interior species are frequently found in patches under 2ha (Bricker and Reader 1989) as well as in marginal habitats such as fence rows, railroad tracks and roadside verges (Middleton 1982, Fritz and Merriam 1993, 1995). Although, some classes of vulnerable native species were identified in our disturbed sites, this had more to do with restricted dispersal and phenology, rather than displacement (McLachlan 1997: Chapter 4). Thus, it seems that native species can persist in both edge and interior habitats whereas only non-natives show a differential response to an edge-to-interior gradient. In fact, the concept of "interior habitats" may not be especially useful for native plant species in northeastern deciduous forests.

Overall, our findings are consistent with theories that associate disturbance with increases in diversity (e.g. Huston 1979, Connell 1978). Intermediate levels of disturbance reduce population growth and competitive displacement thereby resulting in an overall increase in species number. The resultant "species packing" seems to allow the establishment of non-natives without an adverse impact on native diversity, although, it seems likely that that there would be a proportional decrease in natives at relatively high levels of disturbance. In our study, disturbance was relatively small in scale compared to large-scale disturbances such as clear cutting and forest fires. All but one site were within 50m of standing, natural vegetation. Thus, despite the absence of native species from the seedbank at the time of disturbance (McLachlan, 1997: Chapter 3), the standing forest was close enough to allow for rapid migration.

Succession and non-natives management

Currently, the management of non-natives is generally conducted at the (single) species level of organization. Although this may be effective at early stages of invasion when populations are small, it is frequently inappropriate at later stages (Hobbs and Humphries 1995). Our results suggest that successional change will inevitably result in a decline of most non-natives. Consequently, any management activity that accelerates succession will, in turn, accelerate the decline of non-natives.

The dominant non-native grasses conformed to the *inhibition* model and effectively arrested vegetation change by inhibiting native species germination and establishment (Niering 1987). Establishment can be promoted by mechanical cultivation, herbicide application, scarification, controlled burning (Choi and Pavolvic 1994), and nutrient or seedbank impoverishment (Morgan 1994). Although this activity is associated with an initial increase in both non-native and native diversity, the consequent vegetational change will favor late-successional native species and select against shade-intolerant non-natives. Conversely, if succession is undesirable, further regeneration can be prevented by increasing vegetation cover, fertilization, and seeding. Likewise, inhibition can be used to maintain the structure of early successional ecosystems such as oak savannahs and prairies, if species composition is not the primary management concern. Inhibition is currently being used to supplement, and perhaps even replace, herbicide use in the management of utility corridors, roadside verges (Niering 1987), agroecosystems (NRC 1989, Swanton and Weise 1991) and afforestation (Williamson 1993, UK, VMAP; McLachlan, 1997: Chapter 7).

The rapid colonization of later-successional, shade tolerant woody and herbaceous species regardless of TSR conformed to the predictions of the tolerance model (*sensu* Egler 1954). Similarly, while early successional, annual forbs and grasses showed the most rapid decline, later-successional woody perennials showed little response to regeneration (MacIntyre et al. 1995). The *tolerance* model is relatively rare (Connell and Slatyer 1977) and, because of the absence of interaction between earlier and later colonizing species, is less amenable to manipulation. However, regeneration can be accelerated by supplementing species colonization through the planting of late successional species, as demonstrated by most afforestation and reforestation projects. Regardless of effectiveness of weed control, these species will tend to persist because of advantages associated with their perennial life histories, life span, biomass (Keddy 1992), and relative shade tolerance (Bazzaz 1979).

The thinning of non-native grasses by shrubs such as *Rhus* spp. and *Rubus* spp. and the consequent establishment of a shade tolerant understory conformed to the *facilitation* model (Connell et al. 1987). The migration of native species can also be facilitated by the planting of fast-growing, mid-successional shrubs (Robinson and Handel 1993) and the construction of bird perches (McClanahan and Wolfe 1993). These activities will increase vertical structure in open, disturbed sites and, by functioning as "dispersal nuclei", will attract seed dispersers and accelerate regeneration. Native species establishment and performance can be increased through the re-creation of pre-disturbance topography and hydrology and the creation of favorable microsites for subsequent understory herb reintroduction through the planting of trees and shrubs (Fu and Buckley 1993, Primack and Miao 1993). However, apart from decreasing the cover of former lawn species, these restorative activities have had little effect on the decline of non-natives at PPNP after five years but have reduced non-native grass cover (McLachlan, 1997: Chapter 3).

The final component of any succession-based control of non-natives is disturbance management. It forms the basis of most population-based forms of control and generally involves the destruction of weed biomass (Grime 1977) by mechanical cultivation, herbicides, and hand-pulling. If later-successional ecosystems are desired, the mitigation of disturbance is required and will result in a decline of non-natives. Alternatively, if early-successional ecosystems such as alvars, prairies, and savannas, are being managed, disturbance should be enhanced (Vogl 1980). Although isolated and/or intense disturbance will select for non-natives, if properly managed, recurrent disturbance can contribute to the decline of non-natives and the recovery of early successional native species (Howe 1994a). Prescribed disturbance techniques include grazing by sheep, scarification, cultivation and controlled burns (Brennan and Hermann 1994). Although some pervasive non-natives seem resistant to burning (Bock and Bock 1992), most decline relative to fire-adapted native species and prescribed burning has become an essential component of non-native management and/or restoration in early successional systems (Vogl 1974, Anderson 1990, Waldrop 1993, Howe 1994b).

Management implications

A succession-based approach to the management of non-natives is focused at levels of organization higher than the population. Although ecosystem-level approaches to control have been advocated elsewhere (Hobbs and Humphries 1995), non-natives are generally perceived as reducing system integrity (Karr and Dudley 1981, Noss 1990, Woodslee 1993, Angenmeir and Karr 1994) and health (Rapport 1991). Consequently, their control and elimination will remain a primary management objective whether or not system function and structure have been compromised. A succession-based approach recognizes that any increase in non-native diversity is generally associated with disturbance and is temporary. Properly viewed, non-natives are symptoms of disturbance rather than causes of degradation in of themselves. As ecosystems recover from disturbance, non-native diversity will also decline and can be used as an indicator of recovery. Succession-based approaches are process-driven and aim at accelerating the broader-scale recovery of these degraded systems rather than reducing non-native diversity *per se*. Furthermore, they recognize that native species can also contribute to natural habitat degradation. For example, at PPNP, the cedar savanna is being invaded by later-successional native species as well as by non-natives. This degradation threatens most of the remaining savanna and tall grass prairie in southern Ontario, has contributed to the decline of dependent animal species such as the Karner Blue butterfly (Packer 1990), and is attributable to improperly managed disturbance (Bakowsky and Riley 1994).

ACKNOWLEDGEMENTS

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CHAPTER 6

THE EFFECT OF GARLIC MUSTARD ON THE UNDERSTOREY OF DEGRADED DECIDUOUS FOREST IN SOUTHWESTERN ONTARIO.

STEPHANE M. McLACHLAN and DAWN R. BAZELY

Abstract. The introduction of non-native species has been identified as a global threat to natural habitat. *Alliaria petiolata* (garlic mustard) is a European biennial that is currently invading forests throughout northeastern North America. In 1994 and 1995, we assessed the effect of time-since-invasion (TSI), cover, and lifestage of *A. petiolata* on the understorey plant community in Point Pelée National Park, southwestern Ontario. Sites were classified according to TSI (5, 15, and 25 years) and quadrats according to *A. petiolata* cover (0-30%, 31-80%, and >81 percentage cover) and lifestage (rosette, adult). We found that the diversity of native species in both the plant community and seedbank declined significantly as *A. petiolata* cover increased, but only when 100 percentage cover of *A. petiolata* was approached. In contrast, the diversity of non-native species showed no relationship with *A. petiolata* cover but was significantly lower in quadrats with adult *A. petiolata* plants. However, there was no overall relationship between TSI and understorey diversity. Native species that showed a decline as *A. petiolata* cover increased included *Aster shortii*, *Geum laciniatum*, *Geranium robertianum*, and *Osmorhiza claytonii*. Only *Geranium robertianum* and *Viola sororia* were significantly affected by *A. petiolata* lifestage. Although TSI had no overall impact on species composition, sites of intermediate age showed the strongest effect of *A. petiolata*. With respect to the seedbank, *A. petiolata* was affected by cover and both *Leonurus cardiaca* and *Urtica gracilis* by lifestage. Understorey species affected by *A. petiolata* appeared to compensate for decreases in frequency by increasing percentage cover. The *A. petiolata* rosette and adult lifestages excluded one other in high-cover quadrats and, thus, alternated lifestages from year to year. The associated boom and bust cycles may have mitigated the long-term effects of *A. petiolata*. While *A. petiolata* can have a substantial impact on the understorey plant community, this was only true for more recently invaded sites, and these adverse effects seem to decline over time.

Keywords. Exotic, invasion, garlic mustard, disturbance, recovery, native, diversity.

INTRODUCTION

The human-mediated spread of non-native species is a global occurrence which has been identified as a major threat to both flora and fauna (Lodge, 1993). Currently, over 40% of the flora in Ontario is non-native (Anonymous, 1995). Although invasions by non-natives have long been associated with disturbance (Elton, 1958; Orians, 1986; Baker, 1986; Nuzzo, 1991; McLachlan,1997: Chapter 5; Dean et al., 1994), some studies suggest that true invasives are those species which can colonize intact, "undisturbed" habitat (Bazzaz, 1986). Once present, these invasives may establish "monodominant" stands with "irreversible" (DeFerrari and Naiman, 1994) "measurable (and) devastating"(Berman et al., 1991) effects on the native flora.

Adverse impacts on native plants communities which have been attributed to non-native species include changes in ecosystem structure, nutrient, and biomass production (Vitousek, 1986); increases in landscape homogeneity; compromises in aesthetic value; reductions in profitability for forestry and agriculture (Angermeier, 1994), and decreases in both ecological integrity (Karr and Dudley, 1981; Noss, 1990; Angermeier and Karr, 1994) and ecosystem health (Rapport, 1992). However, the most widely cited adverse effect is the displacement and eventual elimination of vulnerable native species (Malecki et al., 1993; Sauer, 1994; Tyser and Worley, 1992; White et al., 1993).

Mature forests are generally resistant to invasion, in part, because of their extensive canopy cover (Crawley, 1986). As most non-native plants are shade intolerant, they tend to be restricted to the forest edges (Brothers and Springarn, 1992; Matlack, 1994). However, some non-native species (e.g. *Lonicera japonica* (Japanese honeysuckle) (Williams, 1980) and *Acer platanoides* (Norway maple) (Webb and Kalafus-Kaunzinger, 1993)) invade mature forests. One of these, *Alliaria petiolata* (garlic mustard), has been identified as a grave threat to upland temperate forests (White et al., 1993).

Alliaria petiolata is an aggressive naturalized European herb that has invaded woodlands throughout northeastern North America since its introduction in the late 1800s (Nuzzo, 1993). It is an obligate biennial, existing in rosette and adult form in its first and second year of growth, respectively. Adults are capable of producing upwards of 800 seeds/plant and 100,000 seeds/m^2 (Cavers et al., 1979). It is most dominant in partially shaded, mesic environments, although it can also occur in open fields (Byers and Quinn. 1987). Invasion is strongly associated with disturbance and may be facilitated by deer grazing and human traffic (Anderson et al., 1996).

Alliaria petiolata is generally perceived as a major threat to understorey plant communities. Much of the literature has focused on aspects of its life history (Byers and Quinn, 1987), germination (Lhotska, 1975; Baskin and Baskin, 1992), mortality (Nuzzo. 1993), reproductive output (Byers and Quinn, 1988), and general ecology (Cavers et al.. 1979; Anderson and Dhillion, 1991; Anderson et al., 1996), whereas other research has focused on control measures (Nuzzo, 1991; Nuzzo et al., 1991, Nuzzo, 1994). All these studies assume that invasion by *A. petiolata* results in population declines and the displacement of native species (e.g. Cavers, 1979; Dunster, 1990; Nuzzo, 1991, Nuzzo et al., 1991; White et al., 1993), although, to our knowledge, this has yet to be shown. This assumption characterizes the exotics literature as a whole (e.g. Woods, 1993; Walker and Vitousek, 1991; Smallwood, 1994; Ruesink et al., 1995), even the most vigorously studied invasives such as *Lythrum salicaria* (purple loosestrife) (Anderson, 1995). Thus, the overall objective of this study was to quantify the effect of colonization by *A. petiolata* on understorey plant communities.

This study was conducted in Point Pelée National Park, in southwestern Ontario. The park has been subjected to intense agricultural, residential, and recreational use over the last century. *Alliaria petiolata* was first introduced there in 1969, has since spread throughout the park, and now represents one of the most dominant understorey species

(McLachlan, 1997: Chapter 5). Specific questions we asked were: (1) What effect does *A. petiolata* abundance and lifestage have on understorey plant diversity and community composition, and the seedbank? (2) What is the longterm effect of *A. petiolata* on native plant diversity and species composition? We predicted that increases in *A. petiolata* would be associated with declines in native species richness and changes in species composition, but only in high-cover quadrats, and, as observed by park vegetation managers, that this effect would decrease as time-since-invasion increased.

METHOD

Study site

Point Pelée National Park (PPNP), is located in southwestern Ontario, 41°54'N and 82°22'E, and is a sandspit formation that extends southward into Lake Erie. It is located at the northern edge of the Carolinian or Deciduous Forest Zone (Allen et al., 1990). This region is the most urbanized and intensively farmed area in Canada and, although only representing 0.25% of Canada's land base, it supports 25% of the country's human population. Forest cover in the immediate area is less than 3% and the fragmentation of the remaining cover is extreme. Over 95% of the remnant patches are less than 10ha, PPNP is the only patch greater than 100ha, and most patches are more than 1.5km apart (Pearce, 1996). This region has the warmest average temperatures, longest annual frost-free seasons and mildest winters in Ontario. Mean temperatures and annual precipitation are 9.4°C and 86.4cm, respectively, and PPNP averages 170 frost-free days per year (Reid 1985).

PPNP is approximately 1650ha in size, 1100ha of which is upland forest. As a naval reserve, it was cleared of white pine (*Pinus strobus*), planted with the now-dominant hackberry (*Celtis occidentalis*), and designated a park in 1918. Agriculture peaked in the 1950s when 40% of the park was allocated to orchard, crop and vegetable production. By 1960, 600 houses and numerous roads had been established and over 600,000 people visited the park each year. At this time, PPNP initiated a naturalization program (Reive et al., 1994). In the last 40 years, most houses and roads have been restored, and former orchards and fields allowed to regenerate.

Sampling design and protocol

Six sites were selected and classified according to time-since-invasion (TSI): 25 years (TipN, TipS); 15 years (Brun, Ogar); and 5 years (Sput, Sanct), based on the observations of longterm park employees. In each site, transects were laid out on the long axes of the *A. petiolata* patches and quadrats were located every 3m. Quadrats were categorized according to *A. petiolata* lifestage (adult or rosette) and cover (low (0-30% cover), medium (31-80% cover), and high (>81% cover)). Quadrats were added until five quadrats were included in each class. In 1995, from June 12 to June 15, stem frequency and percentage cover of all herbaceous species, as well as woody species less than 40cm in height, were measured.

In order to determine the relationship between disturbance and *A. petiolata*, results collected from low- and medium-cover quadrats in Sanct were compared to those from an adjacent site. The latter had been used as a high-quality reference site elsewhere

(McLachlan, 1997: Chapter 3) and showed less invasion by *A. petiolata*. The data from this reference site were collected from June 5-6, 1995 using similar protocols. these described fully in McLachlan (1997). Fifteen quadrats were classified as either low (<31% cover) and 15 as medium (31-80% cover) *A. petiolata* cover.

In order to assess between-year changes in *A. petiolata* populations, we used data from permanent quadrats that were collected in June,1994 and June. 1995 from three sites (WardRd. Brun, and Dust) as described in McLachlan (1997: Chapter 3). Sites were classified as having no (0%); low (1-30% cover); medium (31-80% cover), and high (>81% cover) cover of *A. petiolata* rosettes, the first year lifestage in 1994.

Seedbank composition was assessed at each site using 20cm x 30cm x 15cm deep turves collected in July 1995. Turves were located 0.5m south of the south-east corner of three out of the five herbaceous community quadrats, and removed. These were stored in a partially-shaded, protected nursery at PPNP, regularly watered, and periodically stirred. Seedlings were identified and removed in 1995, 1996, and the spring of 1997. Four pots containing sterilized soil were placed in the nursery as controls, in order to identify species seeding in from the nursery area.

Species nomenclature followed Morton and Venn (1990) and collected specimens were deposited in the PPNP herbarium. Non-native species were defined as having been introduced to PPNP since European settlement (c.1700), according to Jellicoe and Rudkin (1984).

Experimental design and statistics

Results were analyzed as a nested randomized block design with two replicates. TSI was the main plot effect (three levels), while lifestage (two levels) and cover (three levels) were treated as subplots. As the sample size of each treatment combination was n=5 for herbaceous communities and n=3 for the seedbank, this yielded a total of 180 and 108 plots, respectively.

Data were examined for homogeneity of variance and normality. Residual plots revealed high heteroscedasticity, thus ANOVA was conducted on ranked data (Conover and Iman, 1981). When overall significance was detected, ($p<0.05$), Duncan's multiple range tests on ranked data were used to indicate differences between treatments. Means for untransformed data are given. Spearman's correlation coefficents were used to examine the relationship between *A. petiolata* rosette and adult lifestages. All statistical differences were at the $p<0.05$ level unless otherwise indicated. In cases of multiple ANOVA, results were Bonferonni adjusted as to reduce chances of Type I errors. All analyses were conducted using SAS (1990).

We used two-way indicator species analysis (TWINSPAN) (Hill, 1979) to investigate differences in species composition. TWINSPAN is a classification technique whereby sites are situated on detrended correspondence analysis (DCA) ordination axes and then polarized using indicator species. In turn, DCA is an eigenanalysis technique that maximally separates species distribution in ordination space using species data (ter Braak, 1988, 1990)

RESULTS

Effect of A. petiolata on species richness

Understorey plant communities

In 1995, *A. petiolata* cover had a significant effect on native, non-native, and, therefore, total species richness per quadrat. Both total (Table 6.1a) and native species richness (Table 6.1b) declined as *A. petiolata* cover increased. However, this decrease only seemed to occur when *A. petiolata* cover was greater than 100% (Figure 6.1a,b). Both native and total species richness were greatest in low-cover and lowest in high-cover quadrats (Figure 6.1, Table 6.2). In contrast, there was a significant effect of *A. petiolata* lifestage on non-native species richness and a significant interaction between TSI and lifestage (Table 6.1c). While non-native species richness was lower in the adult stage, these differences were only significant in sites of intermediate age.

Although TSI had no overall effect on either native or non-native species richness (Table 6.1b,c), when TSI classes were analyzed separately, only sites of intermediate age showed a significant relationship between *A. petiolata* and non-native ($F_{11,48}$=3.10, p=0.0032), native ($F_{11,48}$=2.23, p=0.013), and total ($F_{11,48}$=3.33, p=0.0018) species richness. As before, native ($F_{2,48}$=6.08, p<0.0004) and total ($F_{2,48}$=8.24, p<0.0008) species richness were determined by cover, and non-native ($F_{1,48}$=20.44, p<0.0001) species richness was determined by lifestage. However, native and non-native species richness were unaffected by *A. petiolata* percentage cover both in old sites ($F_{11,48}$=1.44,

Table 6.1. Results of ANOVA for relationship between *Alliaria petiolata* and a) total species richness, b) native species richness and, c) non-native species richness. Rep: repetition; TSI: time since- invasion class (5, 15, 25 years); cov: *A. petiolata* cover class (low, medium, high); ls: lifestage class (rosette, adult).

a)

Factor	df	MS	F	p
Model	35	5696.0	2.92	0.0001
Rep	1	1090.3	0.56	ns
TSI	2	16558.2	1.67	ns
Error a	2	9916.2		
Ls	1	2149.4	1.10	ns
Cov	2	32600.3	16.69	0.0001
TSI*ls	2	5648.5	2.89	ns
Cov*ls	2	5226.3	2.68	ns
TSI*cov	4	3454.9	1.77	ns
TSI*ls*cov	4	1471.5	0.75	ns
Error b	144	1952.9		

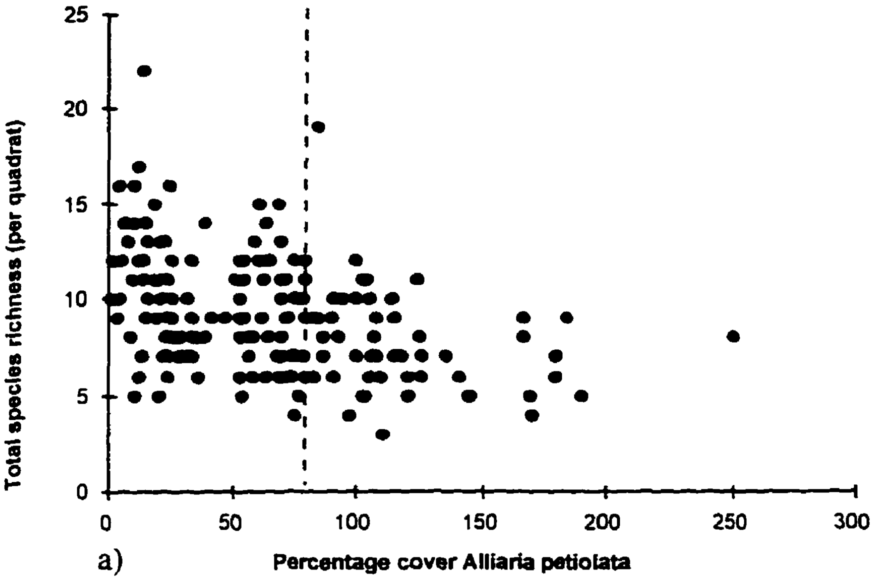
b)

Factor	df	MS	F	p
Model	35	5405.5	2.68	0.0001
Rep	1	1253.5	0.62	ns
TSI	2	25894.4	3.30	ns
Error a	2	7855.8		
Ls	1	66.0	0.03	ns
Cov	2	29073.3	14.42	0.0001
TSI*ls	2	2099.4	1.04	ns
Cov*ls	2	3467.5	1.72	ns
TSI*cov	4	3225.9	1.60	ns
TSI*ls*cov	4	1816.9	0.90	ns
Error b	144	2016.6		

c)

Factor	df	MS	F	p
Model	35	4881.4	3.11	0.0001
Rep	1	3050.5	1.95	ns
TSI	2	31476.6	3.55	ns
Error a	2	8869.2		
Ls	1	15290.5	9.76	0.0022
Cov	2	2804.6	1.79	ns
TSI*ls	2	11203.9	7.15	0.0011
Cov*ls	2	2503.2	1.60	ns
TSI*cov	4	296.7	0.19	ns
TSI*ls*cov	4	745.5	0.48	ns
Error b	144	1567.1		

Figure 6.1. Relationship between *Alliaria petiolata* percentage cover and a) total species richness and b) native species richness. Dotted line indicates point at which species richness seems to decline.


25
20
15
10
5
0
Total species richness (per quadrat)
0
50
100
150
200
250
300
a)
Percentage cover Alliaria petiolata

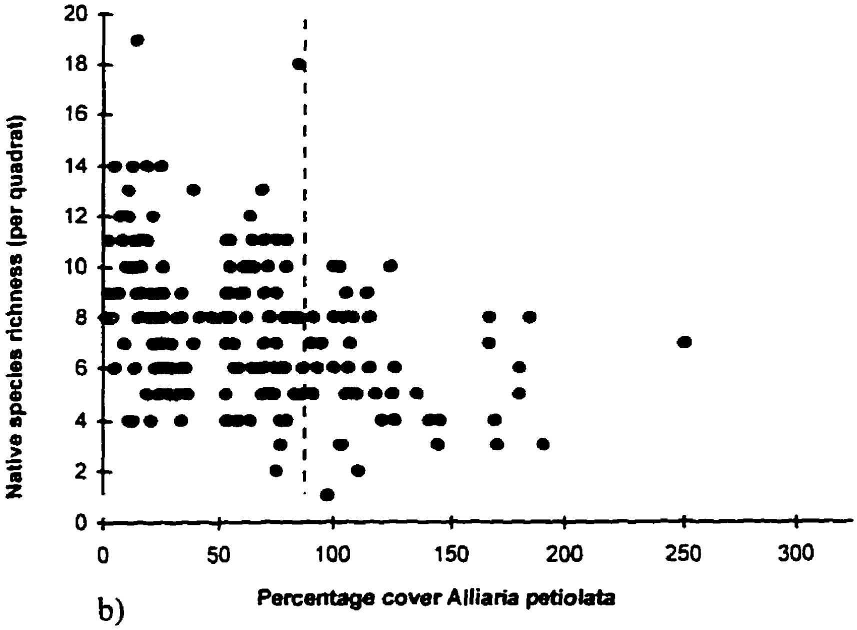

20
18
16
14
12
10
8
6
4
2
0
Native species richness (per quadrat)
0
50
100
150
200
250
300
b)
Percentage cover Alliaria petiolata

Table 6.2. Relationship between percentage cover and frequency per site of seven native species and *Alliaria petiolata*. Totals for rosette and adult lifestages for *A. petiolata* and total, native, and non-native diversity in each site also presented.

Site	Age	All pet[1] Total	All. pet Adult	All pet Rosette	Ast sho	Geu lac	Cel occ	Ger rob	Smi ste	Osm cla	Vio sor	Diversity site-total	Diversity site-native	Diversity site-exotic
% cover														
Sanctuary	5	1703.1	1023.0	680.1	121.2	460.3	2.7	221.3	96.9	66.3	349.6	37	32	5
Sputnik	2	1989.4	1239.3	750.1	16.6	150.9	9.7	36.8	3.3	58	29.1	51	39	12
Ogar	13	1871.4	1304.3	567.1	7.9	574.6	7.6	143.8	10.7	29	43.2	47	35	12
Brunner	15	1966.4	1242.3	724.1	452.3	85.5	10.3	14.3	10.6	102.3	7.5	49	36	13
Tip N.	25	1845.4	1162.0	683.4	50.3	289.9	14.9	132.6	16.0	108	10.3	35	33	2
Tip S.	20	2038.8	1424.0	614.8	322.2	172.6	17.3	66.6	134.3	103	38.9	37	30	7
Frequency														
Sanctuary	5	5511	1055	4456	103	278	14	257	102	47	334			
Sputnik	2	7153	2006	5147	32	162	65	98	8	34	69			
Ogar	13	23140	1549	21591	19	284	33	248	62	24	64			
Brunner	15	9617	1411	8206	324	75	60	52	19	51	21			
Tip N.	25	7136	1488	5648	19	275	143	138	10	22	22			
Tip S.	20	18303	1997	16306	568	126	121	103	137	35	30			

[1] All pet: *Alliaria petiolata*; Ast sho: *Aster shortii;* Geu lac: *Geum lacinatum*; Cel occ: *Celtis occidentalis*; Ger rob: *Geranium robertianum*; Smi ste: *Smilacina stellata*; Osm cla: *Osmorhiza claytonii*; Vio sol: *Viola sororia.*

p=ns; $F_{11,48}$=1.28, p=ns, respectively) and new sites ($F_{11,48}$=1.53, p=ns; $F_{11,48}$=2.25, p=ns, respectively).

Seedbank

Native species richness showed a significant overall relationship with *A. petiolata* ($F_{35,72}$=2.05p<0.0052) and tended to be lower species richness in high-cover quadrats ($F_{2,72}$=3.39; p<0.032). In contrast, for the seedbank, neither non-native ($F_{35,72}$=1.46; p=ns) nor total ($F_{35,72}$=1.62, p=ns) species richness was affected by *A. petiolata*.

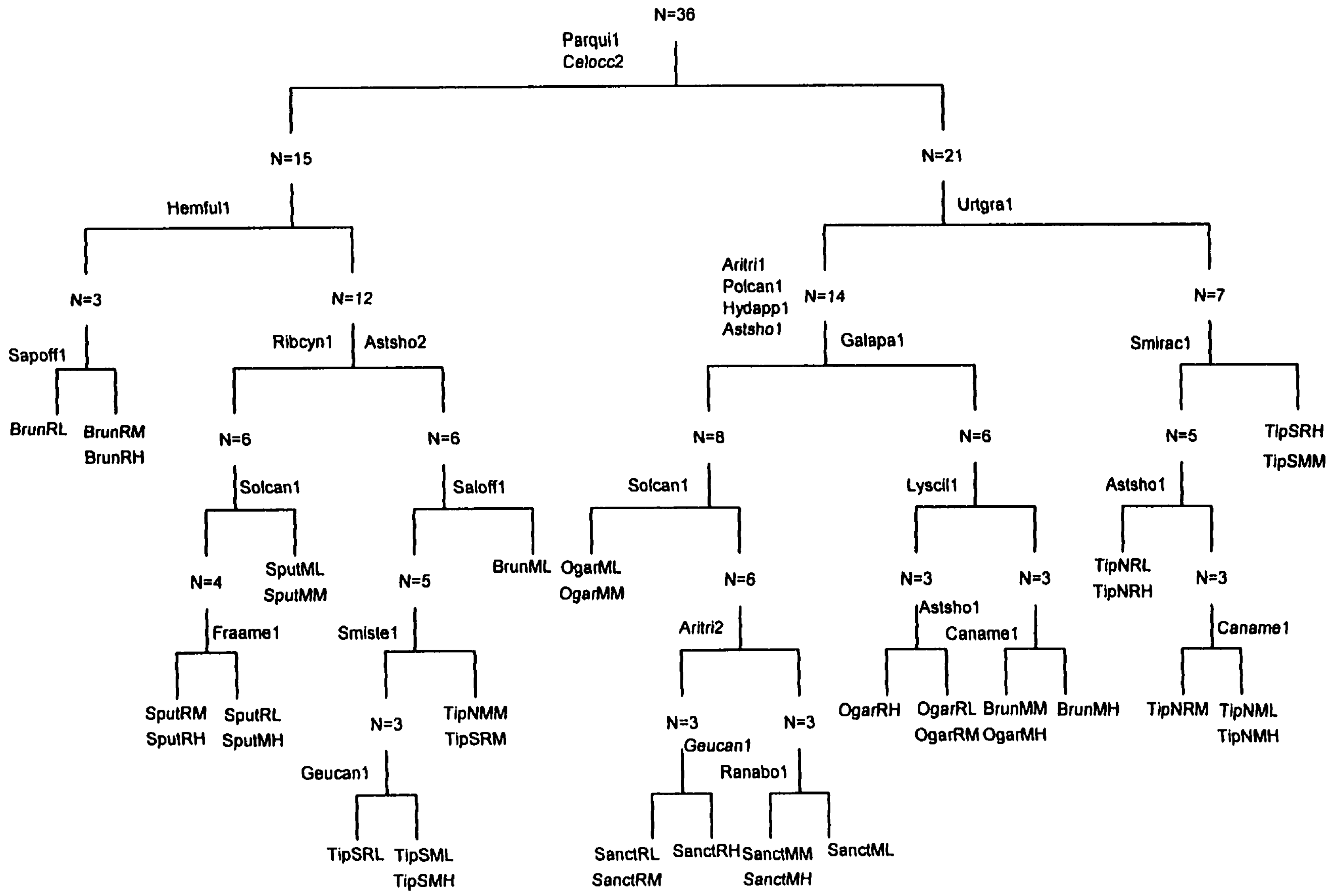
Changes in species composition in response to A. petiolata

Results from TWINSPAN suggested that both cover and lifestage strongly influenced species composition (Figure 6.2). As most quadrats showed high site fidelity, the effects of *A. petiolata* on species composition were interpreted on a site-by-site basis.

Sanct. Rosette quadrats were differentiated from adult quadrats by the presence of *Arisaema triphyllum*. Both low- and medium-cover rosette quadrats were distinguished from high-cover rosette quadrats by the presence of *Geum laciniatum*. Similarly, medium- and high-cover adult quadrats were differentiated from low-cover adult quadrats by the presence of *Ranunculus abortivus* (Figure 6.2).

Sput. Low- and medium-cover quadrats were differentiated from high-cover adult and all rosette quadrats by the presence of *Solidago canadensis*. Low-cover rosette quadrats were differentiated from both medium- and high-cover rosette quadrats by the presence of *Fraxinus americana* (Figure 6.2).

Figure 6.2. TWINSPAN for frequency data indicating relationship between *Alliaria petiolata* age, lifestage and species composition. Listed species are "indicator species" used to distinguish clusters.


N=36
Parqui1
Celocc2
N=15
Hemful1
N=21
Urtgra1
N=3
Sapoff1
BrunRL
BrunRM
BrunRH
N=12
Ribcyn1
Astsho2
N=6
Solcan1
N=4
Fraame1
SputRM
SputRH
SputRL
SputMH
SputML
SputMM
N=6
Saloff1
N=5
Smiste1
N=3
Geucan1
TipSRL
TipSML
TipSMH
TipNMM
TipSRM
BrunML
Aritri1
Polcan1
Hydapp1
Astsho1
N=14
Galapa1
N=8
Solcan1
OgarML
OgarMM
N=6
Aritri2
N=3
Geucan1
SanctRL
SanctRM
SanctRH
N=3
Ranabo1
SanctMM
SanctMH
SanctML
N=6
Lyscil1
N=3
Astsho1
OgarRH
OgarRL
OgarRM
N=3
Caname1
BrunMM
OgarMH
BrunMH
N=7
Smirac1
N=5
Astsho1
TipNRL
TipNRH
N=3
Caname1
TipNRM
TipNML
TipNMH
TipSRH
TipSMM

Brun. Rosette quadrats were distinguished from adult quadrats by the presence of *Hemerocallis fulva*. Low-cover rosette quadrats were differentiated from both medium- and high-cover quadrats by the presence of *Saponaria officinalis*. For adult lifestages, low-cover quadrats were differentiated from medium- and high-cover quadrats by the presence of *Parthenocissus quinquefolia* and *Celtis occidentalis*, whereas medium-cover quadrats were differentiated from high-cover quadrats by the presence of *Campanula americana* (Figure 6.2).

Ogar. Low- and medium-cover adult quadrats were distinguished from high-cover adult quadrats as well as all rosette quadrats by the presence of *Arisaema triphyllum*, *Polygonatum canaliculatum*, *Hydrophyllum appendiculatum*, and *Aster shortii*. High-cover adult quadrats were distinguished from rosette quadrats by the absence of *Lysimachia ciliata*. Similarly, high-cover rosette quadrats were differentiated from both low- and medium-cover rosette sites by the absence of *Aster shortii* (Figure 6.2).

TipsS, TipN. Neither TipS nor TipN showed any discernible relationship with either *A. petiolata* cover or lifestage (Figure 6.2).

Effect of A. petiolata on individual species

Understorey plant communities

The effect of *A. petiolata* on individual native species was examined using the ten most dominant native species. *Alliaria petiolata* cover significantly affected *Aster shortii*, *Geum laciniatum*, *Geranium robertianum*, and *Osmorhiza claytonii*. All four species showed the highest frequencies in low-cover quadrats (Table 6.3). However, for the latter

Table 6.3. ANOVA of relationship between *Alliaria petiolata* lifestage and cover versus both % cover and frequency of ten most dominant native species in understorey. TSI was not included as not significant for any of the species.

Species	Class	Cover			Lifestage		ANOVA P					
		Low	*Medium*	*High*	*Rosette*	*Adult*	*Overall P*	*Cover*	*LS*[d]	*Cover* TSI*	*LS * TSI*	*LS* cover*
Ast sho[c]	cover	78.1B[a]	89.6B	103.7A	84.4	96.6	0.0001	0.0002	ns	ns	0.0021	ns
	freq.	104.2A	89.7B	77.6C	95.5	85.5	0.0001	0.0001	ns	ns	0.0014	ns
Geu lac	cover	105.0A	95.4A	71.2B	89.9	91.2	0.0006	0.0003	ns	ns	ns	ns
	freq.	108.6A	94.6A	68.3B	87.0	94.0	0.0001	0.0001	ns	ns	ns	ns
Cel occ	cover	83.5	96.6	91.5	87.4	93.6	0.0010	ns	ns	ns	ns	ns
	freq.	95.9	84.4	91.2	94.8	86.2	0.0001	ns	ns	ns	ns	ns
Ger rob	cover	74.1A	97.0B	100.4B	99.7A	81.3B	0.0001	0.0011	0.0033	ns	ns	ns
	freq.	108.4A	82.3B	80.8B	85.3	95.7	0.0001	0.0006	ns	ns	ns	ns
Smi ste	cover	90.6	93.6	87.3	*96.1*	*84.9*	*0.0001*	*ns*	*ns*	*ns*	*0.0031*	*ns*
	freq.	89.9	88.2	93.4	85.0	96.0	0.0001	ns	ns	ns	0.0028	ns
Osm lon	cover	86.6	86.9	98.0	89.2	91.8	0.0051	ns	ns	ns	0.0006	ns
	freq.	94.5	93.8	83.2	92.9	88.1	0.0027	ns	ns	ns	0.0004	ns
Osm cla	cover	73.0A	96.3B	102.3B	86.1	94.9	0.0043	0.0005	ns	ns	ns	ns
	freq.	108.1A	84.8B	78.4B	95.4	85.6	0.0008	0.0003	ns	ns	ns	ns
Pol bi	cover	85.1	92.7	93.7	86.6	94.4	0.0020	ns	ns	ns	ns	ns
	freq.	95.4	88.5	87.6	94.3	86.7	0.0007	ns	ns	ns	ns	ns
Par qui	cover	83.6	93.3	94.6	87.7	93.3	0.0001	ns	ns	ns	ns	ns
	freq.	97.3	87.7	86.5	93.4	87.6	0.0001	ns	ns	ns	ns	ns
Vio sor	cover	97.9A	92.7AB	80.9B	80.1	100.9	0.0001	ns	0.0002	ns	0.0011	ns
	freq.	97.8	92.7	81.1	79.5	101.5	0.0001	ns	0.0001	ns	0.0004	ns

[a] means followed by different letters are significantly different at $p<0.005$ according to Duncan's Multiple Means Test (bonferonni adjusted)

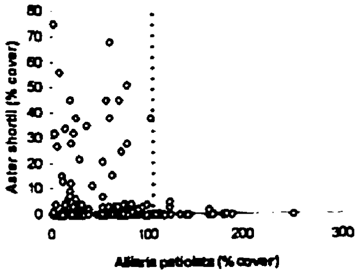
[b] Ast sho: Aster shortii; Geu lac: Geum lacinatum; Cel occ: Celtis occidentalis; Ger rob: Geranium robertianum; Smi ste: Smilacina stellata; Osm lon: Osmorhiza longistylis; Osm cla: Osmorhiza claytonii; Pol bi: Polygonatum biflorum; Par qui: Parthenocissus quinquefolia; Vio sol: Viola sororia.

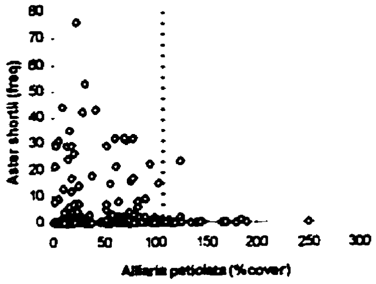
[c] LS: lifestage; TSI: time since invasion (years)

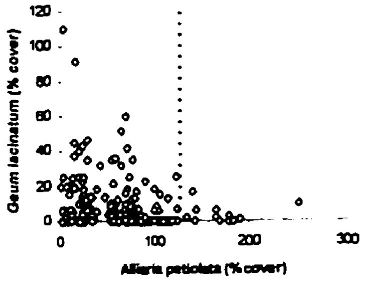
three species, percentage cover showed the opposite trend, and was greatest in the high-cover quadrats. In general, it seemed that the decreases in both frequency and percentage cover of each species only occurred as 100 percent cover of *A. petiolata* was approached (Figure 6.3).

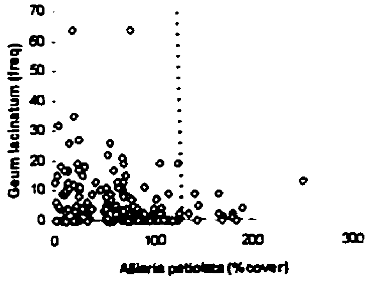
With respect to lifestage, *Geranium robertianum* percentage cover was higher in rosette quadrats (Table 6.3). Interactions between TSI and lifestage were significant for *Aster shortii*, *Smilacina stellaria*, *Osmorhiza longistylis*, and *Viola sororia* percentage cover and frequency (Table 6.3). *Aster shortii*, *Osmorhiza longistylis* and *Viola sororia* all showed higher percentage cover and lower frequency in adult quadrats, but for sites of intermediate age only. In contrast, *Smilacina stellaria* showed lower percentage cover and greater frequency in adult quadrats from old sites only. Again, TSI had no overall effect on any of the species. However, when each TSI class was analyzed separately, *Aster shortii* and *Osmorhiza claytonii* showed significantly greater frequency in low-cover quadrats ($F_{2,48}=7.55$, $p<0.0014$; $F_{2,48}=14.13$, $p<0.0001$, respectively) but greater percentage cover in high-cover quadrats ($F_{2,48}=8.05$, $p<0.0010$; $F_{2,48}=17.51$, $p<0.0001$, respectively), but only in sites of intermediate age. With respect to lifestage, *Aster shortii* and *Osmorhiza longistylis* showed greater frequency in the rosette quadrats ($F_{1,48}=27.76$, $p<0.0001$; $F_{1,48}=18.71$, $p<0.0001$, respectively), greater percentage cover in adult quadrats ($F_{1,48}=25.86$, $p<0.0001$; $F_{1,48}=17.51$, $p<0.0001$, respectively), but only in sites of intermediate age. *Viola sororia* showed greater frequency and percentage cover in adult quadrats ($F_{1,48}=14.76$, $p<0.0004$; $F_{1,48}=15.27$, $p<0.0003$, respectively), but only in sites of intermediate age. In contrast, the only species that responded to *A. petiolata* in

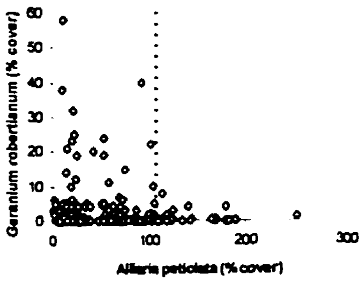
Figure 6.3. Relationship between *Alliaria petiolata* percentage cover and both frequency and percentage cover of a) *Aster shortii*, b) *Geum lacinatum*, c) *Geranium robertianum*, and d) *Osmorhiza claytonii*. Dotted line indicates point at which percentage cover of native species begins to decline.

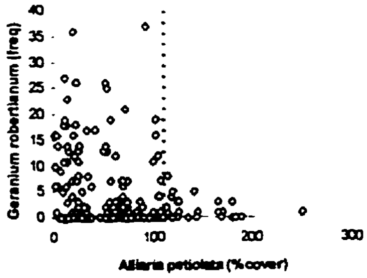

Aster shortii (% cover)
80
70
60
50
40
30
20
10
0
0
100
200
300
Alliaria petiolata (% cover)

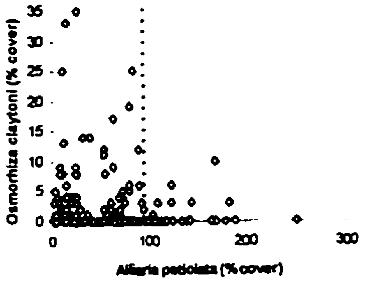

Aster shortii (freq)
80
70
60
50
40
30
20
10
0
0
50
100
150
200
250
300
Alliaria petiolata (% cover)

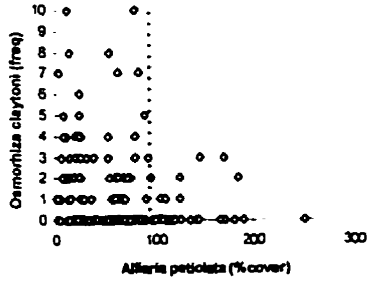

Geum laciniatum (% cover)
120
100
80
60
40
20
0
0
100
200
300
Alliaria petiolata (% cover)


Geum laciniatum (freq)
70
60
50
40
30
20
10
0
0
100
200
300
Alliaria petiolata (% cover)


Geranium robertianum (% cover)
60
50
40
30
20
10
0
0
100
200
300
Alliaria petiolata (% cover)


Geranium robertianum (freq)
40
35
30
25
20
15
10
5
0
0
100
200
300
Alliaria petiolata (% cover)


Osmorhiza claytoni (% cover)
35
30
25
20
15
10
5
0
0
100
200
300
Alliaria petiolata (% cover)


Osmorhiza claytoni (freq)
10
9
8
7
6
5
4
3
2
1
0
0
100
200
300
Alliaria petiolata (% cover)

old sites was *Geum laciniatum* ($F_{1,48}$=10.86, p=0.0019), which was higher in the rosette quadrats. As might be expected, species in new sites showed no significant responses to *A. petiolata*.

Although none of the non-native species, apart from *A. petiolata*, were important compared to native species, we examined them in greater detail because of the significant response of non-native species richness to *A. petiolata* lifestage. Of the ten most dominant non-native species examined, *Hemerocallis fulva*, *Glechoma hederacea*, *Vinca minor*, and *Poa pratensis* showed a significant response to lifestage (Table 6.4). All four species showed higher percentage cover and frequency in the *A. petiolata* rosette lifestage and all, except for *Vinca minor*, showed these differences in sites of intermediate age only (Table 6.4).

Seedbank

The impact of *A. petiolata* on individual species in the seedbank was examined using the ten most dominant species. Only *A. petiolata* was affected by cover, which was significantly lower in low-cover quadrats. *Hesperis matronalis*, *Leonurus cardiaca*, and *Urtica gracilis*, showed significant interactions between TSI and cover and were absent from low-cover quadrats, and present in old sites, only. *Hesperis matronalis* and *Leonurus cardiaca* were also significantly affected by *A. petiolata* lifestage and, with. *Geranium robertianum* showed a significant interaction between TSI and lifestage (Table 6.5). *Geranium robertianum* was lower in adult quadrats from sites of intermediate TSI. *Leonurus cardiaca* was present only in adult quadrats in old sites and those of

Table 6.4. ANOVA of relationship between *Alliaria petiolata* lifestage and density vs. both % cover and frequency of ten most dominant non-native species in understorey data. TSI was not included as not significant for any of the species. Only species having significant relationship with *A. petiolata* are presented.

Species	Class	Overall	TSI[1]	Cover	Lifestage	TSI*Lifestage	TSI*cover	Cover*lifestage
Hemful[2]	% cover	p<0.0001	ns	ns	p<0.0020	p<0.0001	ns	ns
	frequency	p<0.0001	ns	ns	p<0.0020	p<0.0001	ns	ns
Glehed	% cover	p<0.0001	ns	ns	p<0.0001	p<0.0001	ns	ns
	frequency	-	-	-	-	-	-	-
Vinmin	% cover	p<0.0001	ns	ns	p<0.0040	ns	ns	ns
	frequency	p<0.0001	ns	ns	p<0.0043	ns	ns	ns
Poapra	% cover	p<0.0001	ns	ns	p<0.0032	p<0.0002	ns	ns
	frequency	-	-	-	-	-	-	-

[1] TSI: Time since Alliaria petiolata invasion of site (5, 15, 25 years); cover (low, medium, high); lifestage (rosette, adult)

[2] Hemful: *Hemerocallis fulva;* Glehed: *Glechoma hederacea*; Vinmin: *Vinca minor*; Poapra: *Poa pratensis*;

Table 6.5. ANOVA for relationship between *Alliaria petiolata* lifestage and cover versus the frequency of ten most dominant species in seedbank data. TSI was not included as not significant for any of the species[1].

Species[2]	Cover			Lifestage[3]		ANOVA P					
	Low	*Medium*	*High*	*Rosette*	*Adult*	*Overall P*	*Cover*	*Lifestage*	*Cover* TSI*	*LS[d] * TSI*	*LS*cover*
All pet	42.8A	66.3B	54.4AB	58.6	50.4	0.0021	0.0029	ns	ns	ns	ns
Geu spp	52.4	57.6	53.5	53.4	55.6	ns	ns	ns	ns	ns	ns
Ast sho	54.6	55.8	53.1	57.6	51.4	0.0001	ns	ns	ns	ns	ns
Vio sor	56.8	53.3	53.4	53.4	55.6	0.0013	ns	ns	ns	ns	ns
Sol nig	50.0	58.1	55.4	52.0	57.0	ns	ns	ns	ns	ns	ns
Ger rob	55.9	56.4	51.2	56.6	52.4	0.0001	ns	ns	ns	0.0002	ns
Leo car	56.2	55.6	51.8	49.7	59.4	0.0074	ns	0.0079	ns	0.0048	ns
Ste med	56.0	53.0	54.5	55.7	53.3	0.0001	ns	ns	ns	ns	ns
Urt gra	53.0	57.5	53.0	54.0	55.0	0.0001	ns	ns	0.0036	ns	ns
Hes mat	57.6	53.0	52.9	57.5	51.5	0.0001	ns	0.0007	ns	0.0001	ns

[1] means followed by different letters are significantly different at $p<0.005$ according to Duncan's Multiple Means Test (bonferonni adjusted)

[2] All pet: Alliaria petiolata; Geu spp: Geum spp.; Ast sho: Aster shortii; Vio sol: Viola sororia; Sol nig: Solanum nigrum; Ger rob: Geranium robertianum; Leo car: Leonurus cardiaca; Ste med: Stellaria media; Urt gra: Urtica gracilis; Hes mat: Hesperis matronalis.

[3] LS: lifestage

intermediate age. Finally, *Hesperis matronalis* was higher in rosette quadrats, but present only in young sites.

Relationship between disturbance and invasion by A. petiolata

The successional status of the overall plant community was used as an indicator of disturbance. For this, results from the Sanct site in this study, which showed relatively high invasion by *A. petiolata*, were compared to those from Sanct in an adjacent reference site for both herbaceous community and seedbank data.

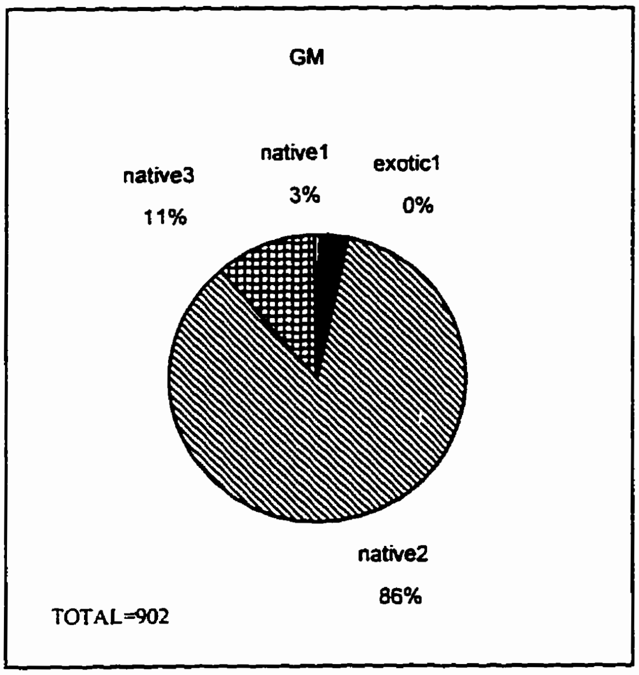
Herbaceous plant community

When classified according to origin and lifehistory, the proportions of each class were different for the two sites ($G=666.0$, $p<0.001$). Early and mid successional species were more dominant in the *A. petiolata*-dominated site (89 vs. 68%) whereas late successional species dominated the reference site (32% vs.11%) (Figure 6.4).

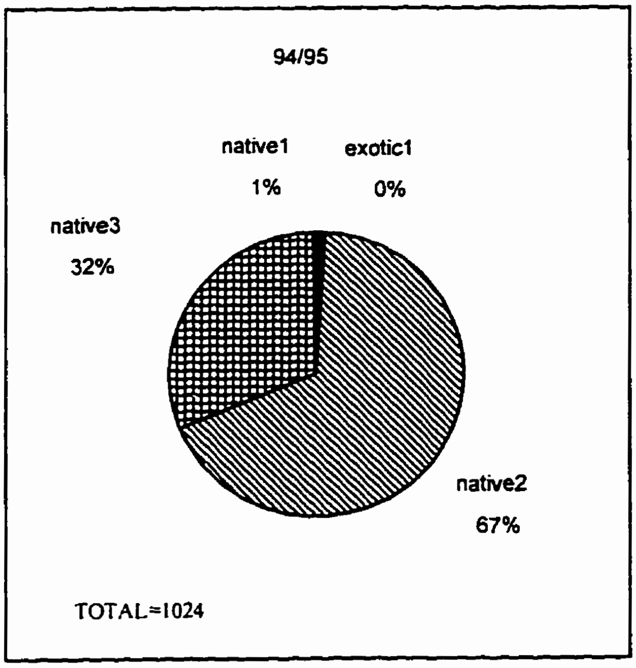
Seedbank

Overall, early successional species were much more dominant in the seedbank than in the herbaceous community (43% vs. 3%). When classified according to origin and lifehistory, the proportions of each class were different between the *A. petiolata*-dominated site and the reference site ($G=123.6$, $p<0.001$). In particular, the proportion of early successional species in the *A. petiolata*-dominated sites was slightly higher than in the reference site (43% vs. 37%). The former site was also dominated by early successional non-natives (36% vs. 16%). In contrast, early successional natives dominated the reference site (21% vs. 7%). As with the herbaceous community, late

Figure 6.4. Comparison of early (1), mid (2) and late (3) successional classes of non-native and native understorey species for (a) highly invaded *Alliaria petiolata* site and (b) neighbouring, less-invaded reference site.


GM
native3
11%
native1
3%
exotic1
0%
native2
86%
TOTAL=902

a)


94/95
native1
1%
exotic1
0%
native3
32%
native2
67%
TOTAL=1024

b)

successional native species were more prominent in the reference site (32% vs. 14%) (Figure 6.5).

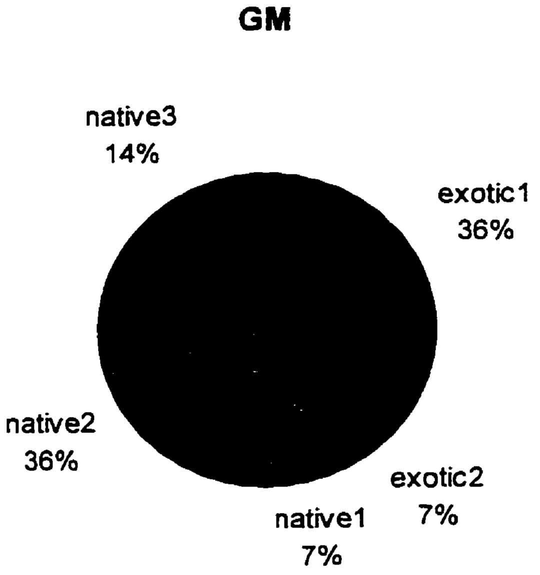
Intra-specific lifestage effect in A. petiolata

Alliaria petiolata adult percentage cover ($r = -0.45$, $p<0.001$) and frequency ($r = -0.31$, $p<0.01$) decreased as rosette percentage cover and frequency increased (Figure 6.6). When changes in *A. petiolata* percentage cover and frequency were compared between years, frequency and percentage cover showed a significant interaction between year and cover for both adult (Table 6.6a,c) and rosette (Table 6.6b,d) quadrats (Table 6.6). The *A. petiolata* rosette lifestage alternated with the adult lifestage in the medium- and high-cover quadrats (Figure 6.7). However, neither native nor non-native species richness showed a significant interaction between year and cover ($F_{3,82}=1.12$, p=ns; $F_{3,82}=0.85$, p=ns, respectively). Reductions in rosette cover seemed to occur at 50 percent cover of adult *A. petiolata* (Figure 6.6a), in contrast to other species which only seemed to decline at 100 percent cover of *Alliaria petiolata* (Figure 6.3).

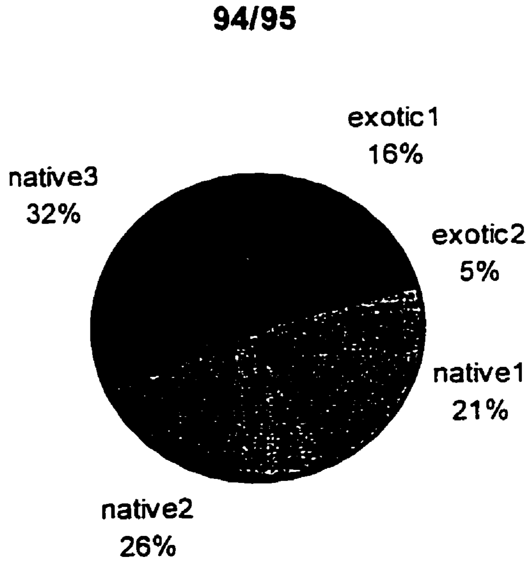
DISCUSSION

In this study, species richness and species composition were substantially affected by both *A. petiolata* cover and lifestage. While these effects were greatest for sites of intermediate age, contrary to the predictions of most of the literature, they seemed to decline as time-since-invasion increased. Other studies also show that native communities can recover from invasion by non-natives. Both *Phalaris arundinacea* (reed

Figure 6.5. Comparison of early (1), mid (2) and late (3) successional classes of non-native and native species from seedbank data for (a) highly invaded *Alliaria petiolata* site and (b) neighbouring, less-invaded reference site.

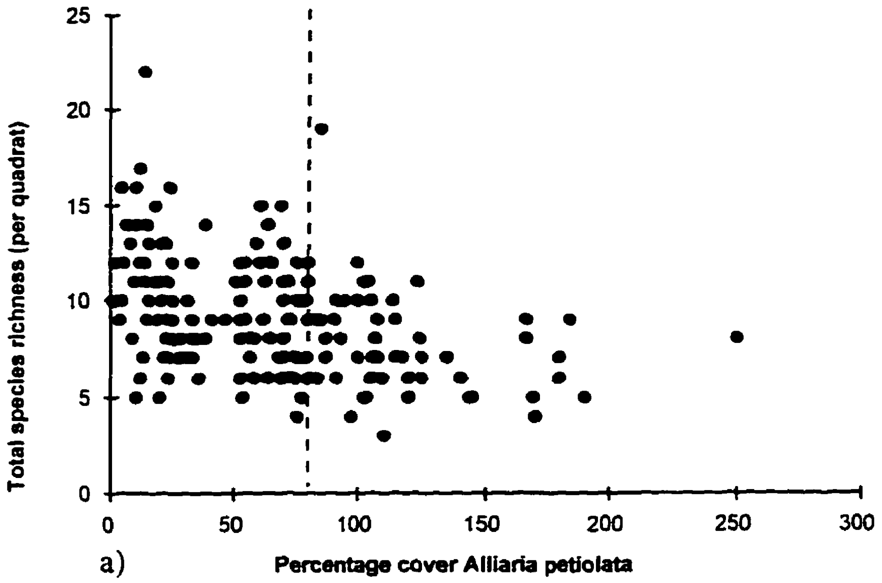

GM
native3
14%
exotic1
36%
native2
36%
exotic2
7%
native1
7%

a)


94/95
exotic1
16%
native3
32%
exotic2
5%
native1
21%
native2
26%

b)

Figure 6.6. Relationship between *Alliaria petiolata* rosette and adult a) percentage cover (r = -0.45) and b) frequency (r= - 0.31). Dotted line indicates point at which percentage cover or frequency of *A. petiolata* declines.


25
20
15
10
5
0
0
50
100
150
200
250
300
Total species richness (per quadrat)
a)
Percentage cover Alliaria petiolata

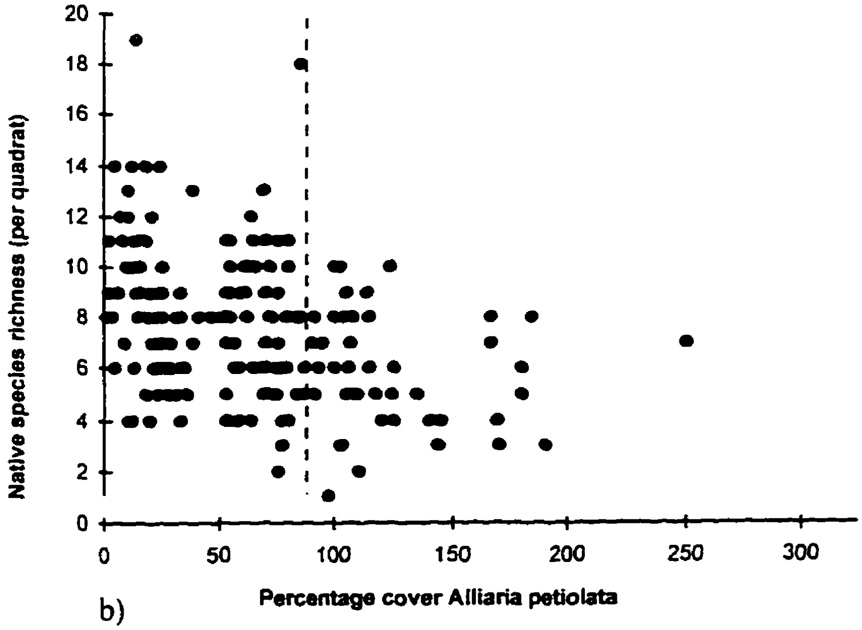

20
18
16
14
12
10
8
6
4
2
0
0
50
100
150
200
250
300
Native species richness (per quadrat)
Percentage cover Alliaria petiolata
b)

Table 6.6. Results of ANOVA for change in *Alliaria petiolata* cover and frequency between years. *A. petiolata* frequency of a) adult and b) rosette as well as percentage cover of c) adult and d) rosette in both 1994 and 1995. Rep: repetition; time: 1994 vs 1995; covR: cover class of *A. petiolata* rosette in 1994 (none: 0%; low: 1-30%; medium: 31-80%; and high: >81% cover).

a)

Variable	df	MS	F	p
Model	23	2419.7	4.81	0.0001
Rep	2	458.5	0.91	ns
Year	1	2828.0	5.62	ns
Error a	2	125.4		
CovR	3	20485.1	13.58	0.0001
Year*covR	3	3945.6	7.85	0.0001
Error b	80	41230.2		

b)

Factor	df	MS	F	p
Model	23	1995.3	3.49	0.0001
Rep	2	1823.5	3.19	ns
Year	1	14684.3	9.25	ns
Error a	2	1587.7		
CovR	3	336.9	0.59	ns
Year*covR	3	3672.4	6.43	0.0006
Error b	80	571.2		

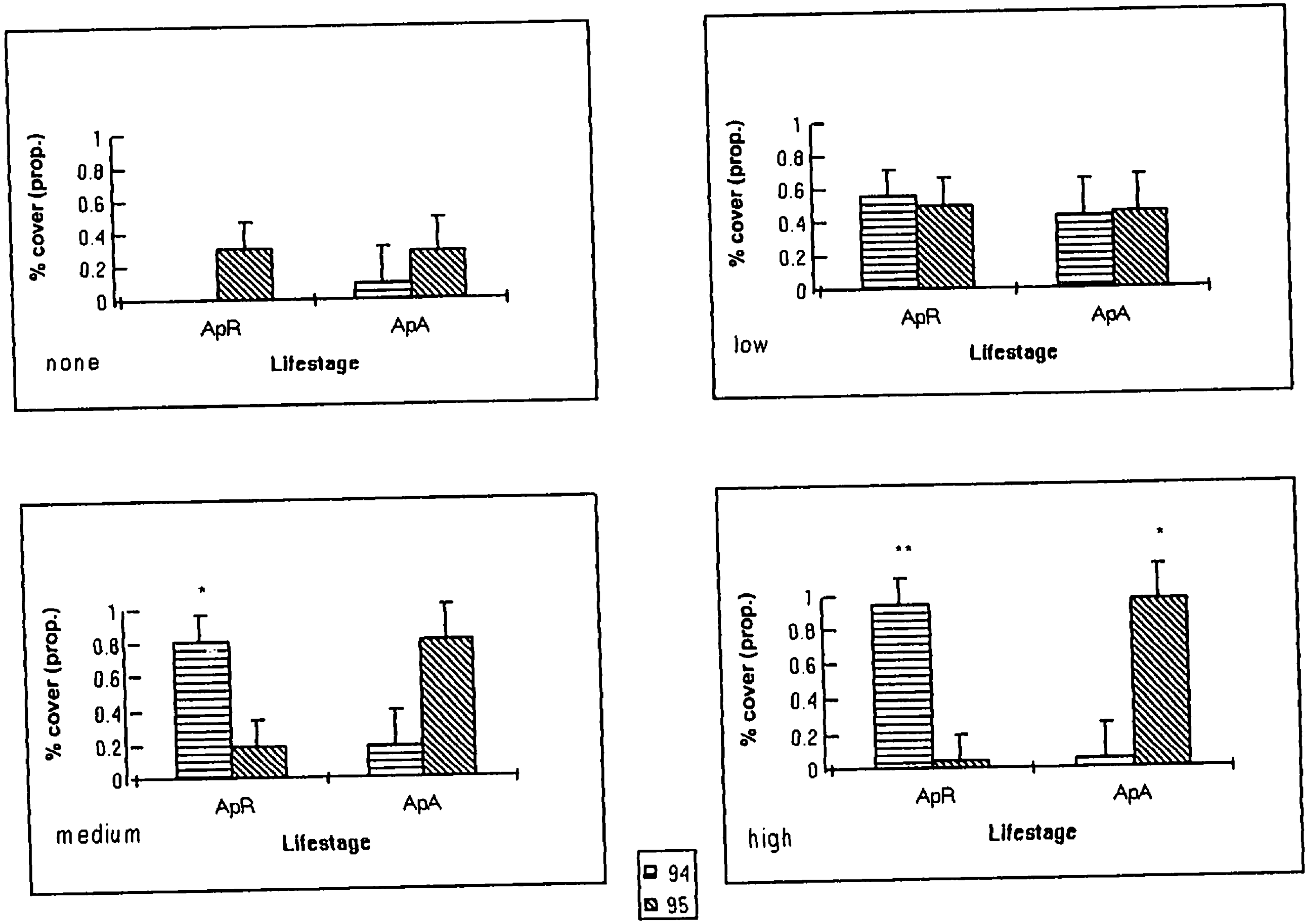
c)

Factor	df	MS	F	p
Model	23	2346.3	4.42	0.0001
Rep	2	4.8	0.01	ns
Year	1	1774.9	5.05	ns
Error a	2	351.5		
CovR	3	4527.2	8.53	0.0001
Year*covR	3	5015.7	9.45	0.0001
Error b	80	530.8		

d)

Factor	df	MS	F	p
Model	23	2036.4	3.43	0.0001
Rep	2	1470.5	2.48	ns
Year	1	11136.7	5.06	ns
Error a	2	2200.6		
CovR	3	1400.3	2.36	ns
Year*covR	3	2682.7	4.52	0.0055
Error b	80	593.7		

Figure 6.7. Relationship between *Alliaria petiolata* lifestage and year at four cover classes (none, low, medium, and high). Year either 1994 or 1995. ApA: adult; ApR: rosette. LSD test between years for both rosette and adult lifestages. *p<0.05; **p<0.01.


% cover (prop.)
1
0.8
0.6
0.4
0.2
0
ApR
ApA
Lifestage
none
low
medium
high
*
**
*
▢ 94
▨ 95

canary grass) (DeWitt, 1989) and *Myriophyllum spicatum* (Eurasian watermilfoil) (Creed and Sheldon, 1995) populations are declining, and the surrounding native communities are resembling their pre-invasion states, 45 and 30 years after introduction, respectively. Nevertheless, both native and non-native species richness showed a substantial response to *A. petiolata*, although for very different reasons. Native species richness decreased as *A. petiolata* cover increased. However, this decline seems important only when *A. petiolata* percentage cover approaches 100%. In part, this may be associated with the compensatory responses between frequency and percent cover shown by native species in response to *A. petiolata*, whereby decreases in one variable are offset by increases in the other. Similarly, in the seedbank, we found that native species richness tended to be lowest in high-cover quadrats. In contrast to native species, non-native species richness was affected by *A. petiolata* and associated with its biennial lifehistory.

A. petiolata can produce upwards of 800,000 seeds per plant (Cavers et al., 1979). Rosettes in our study showed densities of over 4,500/m^2, while adults were limited to 300 plants/m^2. Consequently, rosettes can suffer over 99% mortality between years (Nuzzo, 1993). The displacement of one lifestage by the other tended to increase as the cover of *A. petiolata* increased and, in dense stands, resulted in alternating adult and rosette years. Non-native species, in turn, were largely associated with the rosette lifestage of *A. petiolata*.

That only non-natives species responded to *A. petiolata* lifestage might be associated with differences in flowering phenology between non-natives plant species and most of the native understorey. Thirteen of the 15 non-native forbs in this study flowered in the summer or fall, as did all the non-native species that were affected by *A. petiolata* lifestage. Unable to germinate and grow under the dense cover of adult *A. petiolata*, non-natives seem to be restricted to "overtopping" the *A. petiolata* during rosette phases. Furthermore, three of the four native herbs showing a significant response to *A. petiolata* cover were also summer flowering, fall flowering, or evergreen. Three of the four native species failing to respond to *A. petiolata* cover were ephemeral and, presumably, were established before *A. petiolata* bolted in the spring. Thus, late-developing plants may be relatively vulnerable to *A. petiolata*.

Time since invasion, in contrast to *A. petiolata* cover and lifestage, had no overall effect on either species richness or species composition. However, in sites of intermediate age, both species richness and species composition showed a relatively large effect of both cover and lifestage. This effect was predictably less evident in newly invaded sites. Surprisingly, however, in old sites, species richness and species composition were largely unaffected by *A. petiolata*. As discussed, potential displacement of native species by *A. petiolata* might be reduced by compensatory responses of native frequency and cover in response to *A. petiolata*, and by the high degree of incompatibility between lifestages of *A. petiolata* when it occurs in dense stands. Over the last 15 years, populations of *A. petiolata* have shown repeated boom and bust cycles in the park (G. Mouland, pers. comm.). In some years, densities are high and native species displaced, whereas, in other years, *A. petiolata* is in decline and the native community resembles the pre-invasion understorey plant community. Thus, the continually changing densities and alternating lifestages observed over time in the old sites seems to mitigate the strong relationships shown between the understorey plant community and both *A. petiolata* lifestage and cover that are observed in more recently invaded sites. This longterm "boom and bust" cycle has also been observed for other non-native species (Williams and Fitter, 1996) and may prevent a permanent decline of natives from occurring. These results contradict the inevitable and irreversible post-invasion declines of native understorey plant communities predicted by most of the literature on exotics. However, longterm studies are needed to further quantify these relationships.

Management implications

Control measures are being developed to mitigate the effects of *A. petiolata*. as well as other non-natives. on understorey communities. These studies tend to focus on the target species and generally fail to measure the impact of control on the surrounding native plant community (e.g. Stensones and Garnett. 1994; Nuzzo. 1991. 1993). However, most of these control measures are intrusive (e.g. handpulling. biological) and/or non-selective (e.g. chemical, fire) and likely adversely affect the native understorey plant community, while, in turn, facilitating further colonization by non-natives species (Anderson et al.. 1996). If non-natives are managed as parts of the larger ecosystem by manipulating the natural processes that underlie vegetational change, it may be possible to devise relatively effective, low-input control protocols (McLachlan. 1997: Chapter 5). For example, we have shown that displacement (short-term) seems to occur only when *A. petiolata* cover approaches 100%. Ecosystem-level methods of management that lower *A. petiolata* cover below this threshold without severely disrupting the native understorey plant community might accelerate the decline in adverse impacts that seems occur over time. It may also be possible to exploit differences in propagule longevity and life history between *A. petiolata* and the native understorey. For example, unlike understorey native species which are largely perennial, *A. petiolata* is a biennial and its seeds generally persist in the soil for less than two seasons of growth (Cavers et al., 1979). It may, thus, be vulnerable to seedbank manipulation through the use of mulches or lifestage-specific herbicides. Although the native plant community is strongly affected by *A. petiolata*, our results suggest that the native understorey seems to recover over time, and that more intrusive species-level control measures may be unnecessary.

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CHAPTER 7

EFFECT OF FERTILISATION, WEED CONTROL, AND SHELTER CROP ON GROWTH OF THREE DECIDUOUS TREE SPECIES ON POST-AGRICULTURAL LAND IN SOUTHWESTERN ONTARIO, CANADA

S.M. McLachlan

Summary

1. Forest cover in intensely farmed regions of northeastern North America can be as low as 3 % and forest remnants are generally small and isolated. Afforestation has become an important means of increasing the cover of and the connectivity between natural habitat in agricultural landscapes.

2. We studied the effect of fertiliser, weed control, and shelter-cropping on a newly established (1993) deciduous tree plantation between 1994 and 1996 in southwestern Ontario, Canada. Native tree species planted were: silver maple (*Acer saccharinum*), green ash (*Fraxinus pennsylvanica*), and bur oak (*Quercus macrocarpa*). Weed treatments were: full-weed, clover (*Trifolium repens*) cover crop, mown-weed, inter-weed, and no-weed control. Shelter crop treatments were: none, low-corn (*Zea mays*) density, and high-corn density.

3. Overall, maple and ash responded similarly to treatments with maple having consistently better growth. The relatively poor growth and high mortality of oak

could be attributed to selective deer grazing, as oaks were grazed up to 75 times more frequently.

4. The heights and diameters of the three tree species increased the least in clover and the full-weed. Clover is the generally recommended cover crop for tree plantations in this region. Maple and ash in mown-weed treatments grew better than in either clover or full weed treatments although not as well as in inter-weed or no-weed treatments. There was no difference in oak growth between mown-weed, inter-weed, and no-weed treatments.

5. There was an interaction between fertiliser and weed treatments. Fertilisation increased maple and ash heights but only in no-weed and inter-weed treatments. In contrast, fertilisation resulted in decreased tree heights and diameters in full-weed and clover treatments.

6. The use of corn as a shelter crop resulted in increased maple and ash growth when plots were fertilised and weeds controlled. The shelter crop adversely affected oak growth. There was no difference between low and high corn density treatments.

7. When ground cover composition was assessed, clover treatments had the lowest species richness and lowest grass biomass. Furthermore, when clover was classified as a broadleaf weed, there was no difference between clover and full weed treatments in broadleaf or total weed biomass.

8. Corn growth was greatest in fertilised treatments, particularly when weeds were adequately controlled, and but there was no significant effect of any treatment on corn yield.

9. Corn-shelter systems could be used to accelerate the growth of maple and ash saplings if plantations were fertilised and weeds adequately controlled. This shelter-system may also be effective for slower-growing, shade-tolerant tree species that are currently excluded from most afforestation efforts. In contrast, the clover cover crop, which is currently promoted in this region to control weeds in tree plantations, is not recommended.

Keywords: afforestation, habitat restoration, native tree species, agroforestry, plantations.

Introduction

At the time of European settlement, forests across much of northeastern North America were cleared for timber and the land converted to agriculture. Over the last century there has been large-scale forest regeneration throughout most of this region (Foster, 1992) except in landscapes dominated by agricultural and urban use. Currently, parts of southwestern Ontario, Canada, show less than 3% forest cover (Riley and Mohr, 1993). In many of these sparsely forested areas, marginal land is being taken out of agricultural production and is either being allowed to regenerate naturally or planted with trees (van Hemmesen, 1994).

At the beginning of the twentieth century, afforestation efforts were largely motivated by economic gain and generated many high-value, monospecific coniferous plantations. These plantations have been frequently criticised for being even-aged, single-storied;, and highly susceptible to pests and disease (von Althen, 1991). Compared with natural forests, they contained weedy species and had low soil N and P (Michelsen et al., 1996). Since the 1980s, afforestation efforts have been motivated by additional factors including aesthetics, subsidised management programs, wildlife, recreation, fuelwood, and concerns over soil erosion and nutrient runoff, especially in riparian zones (Schultz et al., 1995; Williams et al., 1995). This has resulted in many multi-species plantations of fast-growing, native deciduous trees (Schlesinger and Williams, 1984; Friedrich and Dawson, 1984). The benefits of these plantations include the protection of existing, high-quality forest (Hobbs, 1993), their function as nurse crops for the subsequent growth of shade-tolerant native woody and herbaceous species (Way, 1989; Parotta, 1992; Otsamo et al., 1996), and increased connectivity between existing forests (Llewellyn et al., 1996), especially in areas with minimal natural cover (Frielinghaus, 1996). Various models suggest that other benefits may include: reduced water yield (Sahin and Hall, 1996) and methane loss from organic soils (Chapman and Thurlow, 1996), and increased sequestering of carbon (Lee and Dodson, 1996; Schroeder, 1994).

A major objective in all afforestation efforts is to maximize early growth of saplings. If adequate weed control is not achieved during tree establishment, intense below-ground competition for soil moisture and nutrients can decrease tree growth and result in high tree mortality (Gerry and Wilson, 1995). However, after three to four years, shading by the tree canopy is usually great enough to eliminate the need for weed control (Buckley and Knight, 1989). Traditionally, weeds have been eliminated by planting grass-turf, but grass, which is highly competitive, often results in poor tree growth (Calkins and Swanson, 1996). Similarly, mowing of the weeds may not reduce competition between weeds and trees and may stimulate weed root growth (von Althen, 1984). Complete weed eradication, either by mechanical cultivation or herbicide use, produces significantly higher tree growth (von Althen, 1993) but is high in cost, often results in excessive loss of soil moisture, and can aggravate soil erosion and nutrient runoff. Selective herbicide application, banded within the row of trees, can also be successful. Research into the effectiveness of mulches has yielded equivocal results (Bowersox and Ward, 1970; Siipilehto and Lyly, 1995; Cogliastro et al.,1993).

Cover crops planted between rows of trees have been widely used to control weeds (van Sambeek and Rietveld, 1982). The use of nitrogen-fixing legumes has been promoted because of the potentially beneficial nitrogen inputs (Peoples et al., 1995). Furthermore, if these crops have economic value, they may help to subsidise the costs of plantation management. Such intercropping is still relatively rarely in North America and is largely restricted to high-value systems such as pecan (*Carya illinoinensis*) orchards (Bugg et al., 1991) and black walnut (*Juglans nigra*) plantations (Ponder, 1991). Additional benefits of intercropping include improved tree stem form (Johnston, 1979) and stand structure consistent with park and recreational use (Williams and Gordon, 1991). Furthermore, if fast-growing nurse crops were interseeded they could act as windbreaks (Schneider et al., 1970; Sun and Dickinson, 1995), help to control weeds, and provide shade for late-successional, slow-growing trees.

In contrast to most agricultural crops, the use of fertilisers in afforestation has little effect and can even reduce tree growth while faster growing weeds benefit (Remphrey and Davidson, 1996). In fact, many post-agricultural nutrient levels are high enough that nutrient exhaustion, through continuous cropping (Bruns, 1988) and the direct removal of soil (Marrs and Gough, 1989) is often recommended. However, fertiliser can increase tree growth in highly degraded, nutrient-deficient areas (Hunter and Smith, 1996).

Clearly, there are both economic and ecological trade-offs to be made during the early stages of plantation management. In this study, we had the opportunity to assess different management approaches in a post-agricultural field planted with native deciduous trees. Our overall objective was to determine which approaches maximised tree growth. In a multi-year experiment, we assessed the impact of fertilisation, weed control, and shelter crops on the growth of three tree species: silver maple (*Acer saccharinum*), green ash (*Fraxinus pennsylvanica*), and bur oak (*Quercus macrocarpa*). We hypothesised that those treatments which reduced interspecific competition would maximise tree growth. Specific predictions were:

(1) that fertilisation should increase tree growth except in full-weed treatments where competition from weeds would reduce tree growth.

(2) that tree growth should be greatest in the no-weed treatments. followed by inter-weed and mown-weed treatments compared to full-weed treatments. while clover. an aggressive but commonly prescribed cover crop, should also reduce tree growth.
(3) that the use of corn (*Zea mays*) as a shelter crop should increase tree growth by providing shade and protection from the wind.

Materials and Methods

Study site and plantation history

The experiment was conducted on a post-agricultural field at Sturgeon Creek. approximately two kilometres southeast of Leamington, Ontario. Canada (41°54'N and 82°22'W). Because of its proximity to Lake Erie, the study site is routinely exposed to high winds. Mean temperatures and annual precipitation are 9.4°C and 86.4 cm, respectively, and this region averages 170 frost-free days per year. The site has a rating of 3100 Ontario Corn Heat Units (OCHU) where OCHUs measure the number of degree-days required to grow a cultivar of *Zea mays* in Ontario (see Brown 1978). The soil type in the field is a Brookston clay (Richards et al., 1949) and the field is tile drained.

The field was 25 ha and was previously used to grow corn and soybean. In the spring of 1993, the southern half of the field was cultivated and planted with two year old trees. The distance between rows was 8 feet and trees were spaced at 4 feet within each row. The preemergent herbicide simazine was banded within each tree row. Silver maple, green ash, bur oak, and shagbark hickory (*Carya ovata*) were randomly planted within each row at a 20:20:1:1 stocking ratio. *Trifolium repens* (white clover) was interseeded between tree rows and not within tree rows.

In May 1994, glyphosate was banded within the tree row (intra-row) and. in weed-free areas. supplemented by hand hoeing if needed. The regions between trees (inter-row) were disked and rototilled prior to corn planting, except for areas designated as clover-control treatments in which the standing cover crop was allowed to remain.

Experimental Design

The experiment was conducted as a split-strip-split-split block design with four replications. The whole plot factor was a fertiliser treatment which had two levels. Each of the four replicate plots was 20 tree rows wide and measured 53m x 60m feet. No fertiliser was applied in the low-fertiliser areas. In the high fertiliser areas. 60N. 120P. and 40K kg/ha were broadcast on May 12 in 1994 and May 16 1995 after rototilling and prior to corn planting.

The sub-plot factor was the weed-control treatment which had five levels. randomly applied within each fertiliser treatment plot. Each sub-plot was four tree rows wide and measured 10m x 60m. The five weed control levels were: (1) sub-plots in which naturally occurring weeds were allowed, after rototilling, to grow undisturbed for the remainder of the growing season (full-weed); (2) sub-plots that remained in clover between tree rows for the entire season. Glyphosate was banded within the tree row or intra-row. in May 1994 (clover); (3) sub-plots in which simazine was applied in June 1994 and then kept weed free by periodic hoeing within the intra row area, so that weeds grew in the inter-row (inter-weed); (4) sub-plots in which weeds occurring within the inter-row were mown twice a year but allowed to grow within the intra-row (mown); and (5) sub-plots that were kept entirely weed free, both by applying simazine in June 1994 and by repeated hand hoeing thereafter (no-weed).

The sub-strip-plot factor was the shelter crop treatment which consisted of three levels of corn density: no-corn, low-density, and high-density. Corn densities were randomised within each fertilised treatment plot, and randomized across weed treatment sub-plots. Each sub-strip-plot was 20 tree rows wide and measured 53m x 20m. Inter-row areas were rototilled and then planted with corn except for sub-plots designated as clover and mown-weed treatments because (i) corn could not be hand-planted in clover and (ii) mowers could not fit between corn rows. Low and high corn density treatment were hand planted with 'Northrup King 5202' (OCHU=3200) corn. Each inter-row consisted of two rows of corn planted approximately 1m apart. In the low density treatment, corn plants were spaced 20cm apart within the corn row and in the high density treatment, plants were 10cm apart yielding approximately 20,000 and 40,000 corn plants/ha, respectively. These were thinned to one plant per hole at the 3-4 leaf stage of corn development. Corn was planted late on June 2 in 1994 and though planted on May 21 in 1995, germination was delayed until the second week of June due to a lack of rainfall. In 1995, despite triple planting, germination failure resulted in gaps in the corn which were then filled by subsequent planting. In both 1994 and 1995, corn plants were left to stand over winter, harvested the following spring and cobs were donated to a neighbouring bird sanctuary.

The sub-split-sub-plot factor was tree species and referred to the four species. maple. ash. oak. and hickory which were randomly planted within each tree row in 1993.

Tree sampling

Trees selected for measurement were located in the first two of the three tree rows in each sub-strip plot and if additional trees were needed (usually oak) these were selected from the third row of trees. Trees located in the fourth row lay at the interface between different weed treatments and were not sampled. Tree selection was initiated 2m from the southwest corner of each sub-strip plot and the first 5 individuals of each species were selected in the first row. Measurements were continued 2m from the north edge of the sub-strip plot southward on the second row and the first five individuals from each species selected comprising a total of 10 individuals from both rows. If additional trees were needed. selection was initiated 2m from the southern edge of the sub-sub plot on the third row. The first tree measured in each harvest row was marked. In this way. repeated measures were conducted without having to mark each individual tree. Measurements were conducted on three dates (August 1994, August 1995. and May 1996). The point at which bark was formed and green growth commenced was judged as representing the maximum height achieved by the end of the previous growing season and thus representing growth achieved by November 1994 and 1995. when it was assumed that seasonal growth had stopped. Measurements consisted of height (from ground-level to apical meristem of the longest leader) and diameter (at 15cm from ground level). Thus. for height. five measurements were taken (corresponding to 0 (August. 1994). 3

(November, 1994), 8 (August, 1995), 11 (November, 1995), and 13 (May, 1996) growing months) and for diameter three measurements were recorded (corresponding to 0, 8, and 13 growing months, starting at August, 1994). Mortality was calculated for each species by using tree counts from each sub-strip plot and made in August 1994 and May 1996. The numbers of measured trees grazed by deer was recorded for each species in May 1995.

Soil samples were taken in May 1994 and 1995 from weed free, full weed, and clover treatments in both fertilisation levels.

Weed sampling

Four 1.0m x 0.5m quadrats were located in each sub-strip plot containing weeds in August 1994 and September 1995. One pair of quadrats was located 10m from the northern edge of the sub-sub plot and one 10m from the southern edge. Each pair of quadrats contained a quadrat located within the tree row (intra) and an adjacent one within the corn rows (inter). The stem frequency and percentage cover of each species present were recorded. All plants within each quadrat were clipped at ground level and separated into broadleaf forbs and grasses and dried at 60 °C until constant weight was achieved. *Trifolium repens* was classified as a broadleaf weed.

Corn sampling

Quadrats were located within each sub-strip plot containing corn when 100% tasselling was observed (i.e. full canopy closure) on July 14, 1994 and July 23, 1995. A

1m row of corn was harvested 13m from the southern most sub-strip plot edge and another, 13m from the northern-most edge. The total number of corn plants in each 1m row was recorded. These plants were then cut at ground level and weighed. On November 23, 1994 and November 2, 1995, two more 1m lengths of corn were located 7m from both the northern and southern-most edges of the sub-sub plot. Any cobs present were counted and dried at 40°C for 24 hours. All samples were dried at 80°C until constant weight was achieved. Ears were shelled and yield recorded. Grazing on corn was divided into two classes: small-mammal grazing (individual kernel eaten, gnawing marks) and bird/large mammal (multiple kernel or entire cob eaten).

Statistical analysis

The effects of fertilisation, weed-control, shelter, and time on tree were analysed with a repeated-measures multivariate analysis of variance (MANOVA) of a split-strip-split plot design (SAS 1990). However, a number of weed and shelter crop treatments were not viable (i.e. corn treatments in both clover and mown-weed treatments). Therefore, the 15 potential weed and shelter crop treatments were collapsed into 11 combined weed-shelter (WS) treatments (Table 7.1). The model was therefore analysed as a split-split-plot model with fertiliser as the main factor, weed-shade (WS) as the split factor, and species as the split-split factor. A mixed model was used with fertiliser, and WS taken as fixed effects and species and time as random effects. We used analysis of variance (ANOVA) to test the effect of fertiliser, weed-control, and shelter crop on weed

Table 7.1. Relationship between the original weed and shelter treatments and combined weed-shelter (WS) treatments used in the statistical analysis.

Weed treatment	**Shelter treatment**	**Weed-shelter treatment**
no-weed	no-corn	WS1
no-weed	low density	WS2
no-weed	high density	WS3
inter-weed	no-corn	WS4
inter-weed	low density	WS5
inter-weed	high density	WS6
full-weed	no-corn	WS7
full-weed	low density	WS8
full-weed	high density	WS9
clover	no-corn	WS10
clover	low density	not viable
clover	high density	not viable
mown-weed	no-corn	WS11
mown-weed	low density	not viable
mown-weed	high density	not viable

data collected from quadrats (grass biomass, forb biomass. total weed biomass. species richness. and percentage cover) and corn data (plant biomass, plant number per 1m row, biomass per plant, cob number, kernel weight, kernel weight per cob) (Table 7.2). The numbers of trees and corn cobs grazed as well as tree mortality were analysed using G tests. Data were log or square root transformed when necessary to achieve homogeneity of variance, however, with the exception of tree growth over time, only untransformed data are presented. Single degree of freedom contrasts were used to quantify treatment effects. Contrasts were identified before-hand and were not mutually orthogonal. Probability values from these tests were Bonferonni adjusted when appropriate.

Principal Components Analysis (PCA) was used to compare differences in species composition between quadrats. PCA is an ordination technique which maximally separates samples on a series of ordination axes according to differences in species composition (Hill, 1979). PCA was used because most species were present in all samples and thus did not have the unimodal distribution assumed by other ordination techniques. Quadrats examined with PCA were classified according to fertilisation, weed-control, and shelter treatments, and whether quadrats had been rototilled (inter) or not (intra).

Results

Tree growth

Overall, there were significant block, weed-shelter (WS), and species effects on tree

Table 7.2. Error terms used in calculation of F-ratios for repeated measures multiple analysis of variance (MANOVA).

Treatment		F ratio
Factor	d.f.	Factor
block	3	block / error c
fertiliser	1	fertiliser / block x fertiliser
WS	10	WS / error b
species	?	error c
time	?	error d

height and diameter while the effect of fertiliser approached significance (Tables 7.3 and 7.4). Fertilizer increased heights of ash and maple. In general, trees had the greatest heights and diameters in weed-free treatments (WS7, WS8, and WS9) and the least in clover (WS10) and full-weed treatments (WS1, WS2, and WS3). Maple had the greatest growth and oak the poorest growth across all treatments (Table 7.6). Hickory was dropped from the analysis because of its high mortality. There were also significant interactions between fertiliser and WS for both tree diameters and heights. All other higher-order interactions were also significant. Because of the highly significant effect of species, species were examined separately.

Silver maple

Fertiliser significantly increased maple height (Table 7.5). When averaged across all WS treatments, fertilisation increased tree heights and diameters by 17% and 13%, respectively (Table 7.6). The trees in weed-free treatments showed the best growth but fertilisation only increased heights by 5% and diameters by 4% compared with unfertilised trees in weed-free treatments. In contrast, fertilisation actually decreased heights and diameters of trees in clover treatments by 5% and 15%, respectively (Table 7.6).

Maples in clover treatments had the lowest heights and diameters, followed by those in no-corn, mown-weed (Figures 7.1 and 7.2; Tables 7.5 and 7.7: contrast 3), inter-weed (contrast 8), and no-weed (contrast 9) treatments. Trees in clover treatments had

Table 7.3. Repeated measures MANOVA for the effect of fertilization, weed-shade treatments, tree species and time on tree height.[1]

Factor	DF	Type III SS	Mean Square	F Value	Pr > F
Block	3	1389858.83	463286.28	159.16	**0.0001**
Fert[2]	1	384703.23	384703.23	9.45	0.0544
Error a	3	122172.36	40724.12		
Wslevel	10	2481898.16	248189.82	5.13	**0.0001**
Fert*wslevel	10	454134.43	45413.44	0.94	
Error b	60	2901747.60	48362.46		
Species	2	25798906.69	12899453.35	4431.54	**0.0001**
Fert*species	2	394889.01	197444.50	67.83	**0.0001**
Wslevel*species	20	1665558.15	83277.91	28.61	**0.0001**
Fert*wslevel*species	20	442901.15	22145.06	7.61	**0.0001**
Error c	9573	27865332.84	2910.83		
Time	4	27436612.76	6859153.19	13866.00	**0.0001**
Time*block	12	450236.69	37519.72	75.85	**0.0001**
Time*fert	4	195606.89	48901.72	4.01	**0.0273**
Time*block*fert	12	146417.22	12201.44	24.67	**0.0001**
Time*wslevel	40	1021721.25	25543.03	4.55	**0.0001**
Time*block*wslevel	120	535218.20	4460.15	9.02	**0.0001**
Time*block*fert*wslevel	120	811491.34	6762.43	13.67	**0.0001**
Time*fert*wslevel	40	308081.26	7702.03	15.57	**0.0001**
Time*species	8	4950862.59	618857.82	1251.04	**0.0001**
Time*fert*species	8	133582.32	16697.79	33.76	**0.0001**
Time*wslevel*species	80	510633.02	6382.91	12.9	**0.0001**
Time*fert*wslevel*species	80	295744.66	3696.81	7.47	**0.0001**
Error d	38292	18942067.62	494.67		

[1] log-transformed .

[2] Fert: fertilizer, wslevel (weed-shade treatment combinations).

Table 7.4. Repeated measures MANOVA for the effect of fertilization, weed-shade treatments, tree species and time on tree diameter.[1]

Factor	DF	Type III SS	Mean Square	F Value	Pr > F
Block		141.40	47.13	105.83	**0.0001**
Fert[2]	1	16.59	16.59	2.30	0.2266
Error a	3	21.63	7.21		
Wslevel	10	276.48	27.65	4.64	**0.0001**
Fert*wslevel	10	41.34	4.13	0.69	
Error b	60	357.22	5.90		
Species	2	1023.38	511.69	1148.90	**0.0001**
Fert*species	2	14.66	7.33	16.46	**0.0001**
Wslevel*species	20	202.75	10.14	22.76	**0.0001**
Fert*wslevel*species	20	56.25	2.81	6.31	**0.0001**
Error c	9573	4263.57	0.45		
Time	2	2568.44	1284.22	6959.83	**0.0001**
Time*block	6	73.79	12.30	66.65	**0.0001**
Time*fert	2	9.11	4.55	1.22	0.3587
Time*block*fert	6	22.35	3.73	20.19	**0.0001**
Time*wslevel	20	159.90	8.00	2.96	**0.0001**
Time*block*wslevel	20	26.11	1.31	7.07	**0.0001**
Time*block*fert*wslevel	60	100.51	1.68	9.08	**0.0001**
Time*fert*wslevel	60	96.90	1.62	8.75	**0.0001**
Time*species	4	495.69	123.92	671.60	**0.0001**
Time*fert*species	4	12.38	3.09	16.77	**0.0001**
Time*wslevel*species	40	99.83	2.50	13.53	**0.0001**
Time*fert*wslevel*species	40	35.56	0.89	4.82	**0.0001**
Error d			0.18		

[a] log-transformed.

[b] Fert: fertilizer, wslevel (weed-shade treatment combinations).

Table 7.5. ANOVA for effect of fertilization and weed-shade treatments on height of silver maple.[1]

Factor	DF	SS	Mean Square	F Value	Pr > F
Model	27		196191.39	119.89	**0.0001**
Block	3	683435.53	227811.84	139.21	**0.0001**
Fert[2]	1	788507.53	788507.53	76.13	**0.0032**
Error a	3	31070.33	10356.78		
Wslevel	10	3237911.56	323791.16	197.86	**0.0001**
Fert*wslevel	10	519468.96	51946.90	31.74	**0.0001**
Error b	4332		1636.46		

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1)cn vs nocn (noweed)	1	88.67	88.67	0.05	0.8159
2)cn vs nocn (inter)	1	35.84	35.84	0.02	0.8824
3)mow vs clov	1	192055.76	192055.76	117.36	**0.0001**
4)mow vs fullweed, (nocn)	1	731.53	731.53	0.45	0.5038
5)mow vs noweed, (nocn)	1	591380.02	591380.02	361.38	**0.0001**
6)mow vs inter, (nocn)	1	182305.33	182305.33	111.40	**0.0001**
7)clov vs fullweed, (nocn)	1	169152.65	169152.65	103.36	**0.0001**
8)clov vs inter, (nocn)	1	746223.69	746223.69	456.00	**0.0001**
9)clov vs noweed, (nocn)	1	1436789.66	1436789.66	877.98	**0.0001**
10)full vs inter, (nocn)	1	206133.36	206133.36	125.96	**0.0001**
11)Fert*(cn1 vs cn2),(noweed, inter)	1	22187.86	22187.86	13.56	**0.0002**
12)Fert*(cn vs nocn), (noweed)	1	101031.51	101031.51	61.74	**0.0001**
13)Fert*(cn vs nocn), (inter)	1	16173.60	16173.60	9.88	**0.0017**
14)Fert*(mow vs. clov)	1	6602.74	6602.74	4.03	0.0446
15)Fert*(mow vs noweed), (nocn)	1	1463.63	1463.63	0.89	0.3443
16)Fert*(mow vs inter), (nocn)	1	16394.98	16394.98	10.02	**0.0016**
17)Fert*(mow vs fullweed), (nocn)	1	915.92	915.92	0.56	0.4544
18)Fert*(clov vs noweed), (nocn)	1	13984.06	13984.06	8.55	**0.0035**
19)Fert*(clov vs inter), (nocn)	1	43634.53	43634.53	26.66	**0.0001**
20)Fert*(clov vs fullweed), (nocn)	1	12415.35	12415.35	7.59	**0.0059**

[1] log-transformed

[2] Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn); low corn density (cn1); high corn density (cn2). Weed contrast: no-weed (noweed); inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

Table 7.6. Effect of fertilizer and weed-shade (WS) treatments on a) diameter and b) height of silver maple, green ash, and bur oak. The final (H5) tree heights and diameters are given. Fertilizer treatments were: unfertilised (UF) and fertilised (F). WS treatments were: full-weed, no-corn (WS1); full-weed, low density corn (WS2); full-weed, high density corn (WS3); inter-weed, no-corn (WS4); inter-weed, low density corn (WS5); inter-weed, high density corn (WS6); no-weed, no-corn (WS7); no-weed, low density corn (WS8); no-weed, high density corn (WS9); clover cover crop, no-corn (WS10); mown-weed, no-corn (WS11). Means for each WS across both fertilization levels and means for each fertilisation level across all WS levels were calculated for each tree species . Overall means given for fertilizer across all WS levels, diameter across all species and fertilizer levels, and heights across all species and fertilizer levels.

a)

		Weed-shade treatment combination (WS)											
Species	**Fertiliser**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**Overall mean**
		Tree diameter (cm)											
Silver maple	**UF**	1.7	1.6	1.6	2.2	2.0	2.1	2.9	2.1	2.3	1.4	1.7	2.0
	F	1.5	1.9	2.1	2.3	2.3	2.4	2.8	3.1	3.0	1.4	1.8	2.2
	Mean	1.6	1.7	1.8	2.2	2.1	2.2	2.8	2.6	2.7	1.4	1.8	2.1
Green ash	**UF**	1.3	1.3	1.2	1.7	1.6	1.6	1.6	1.5	1.7	1.3	1.6	1.5
	F	1.1	1.3	1.4	1.5	1.7	1.7	2.0	2.0	2.0	1.2	1.6	1.6
	Mean	1.2	1.3	1.3	1.6	1.6	1.7	1.8	1.8	1.8	1.3	1.6	1.5
Bur oak	**UF**	0.9	1.0	0.9	1.2	1.2	1.1	1.1	1.2	1.3	0.9	1.0	1.1
	F	0.7	0.9	0.7	1.5	0.9	1.2	1.3	1.2	1.0	0.7	1.3	1.1
	Mean	0.8	1.0	0.8	1.3	1.1	1.1	1.2	1.2	1.1	0.8	1.2	1.1
	Overall mean	1.2	1.3	1.3	1.7	1.6	1.7	2.0	1.9	1.9	1.2	1.5	1.6

b)

		Weed-shade treatment combination (WS)											
Species	**Fertiliser**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**Overall mean**
		Tree height (cm)											
Silver maple	**UF**	145.2	136.8	123.5	170.4	159.4	166.5	201.1	177.7	186.6	124.3	149.2	158.2
	F	152.6	170.5	183.1	191.7	195.5	204.1	210.3	242.2	219.3	115.6	152.4	185.2
	Mean	148.9	153.7	153.3	181.0	177.5	185.3	205.7	209.9	203.0	119.9	150.8	171.7
Green ash	**UF**	99.0	101.2	92.0	108.3	114.2	115.3	121.8	109.7	126.7	93.0	99.0	107.3
	F	91.7	103.5	114.0	107.6	126.5	138.8	133.7	142.1	140.8	83.4	110.4	117.5
	Mean	95.3	102.4	103.0	108.0	120.4	127.0	127.7	125.9	133.7	88.2	104.7	112.4
Bur oak	**UF**	79.9	89.5	59.2	78.4	84.9	78.2	75.4	91.2	122.3	74.4	68.8	82.0
	F	67.8	85.4	84.1	100.1	81.9	117.8	98.3	100.7	75.8	61.2	107.1	89.1
	Mean	73.8	87.5	71.7	89.3	83.4	98.0	86.8	96.0	99.0	67.8	87.9	85.6
	Overall mean	106.0	114.5	109.3	126.1	127.1	136.8	140.1	143.9	145.3	92.0	114.5	123.2

Table 7.7. ANOVA for effect of fertilization and weed-shade treatments on diameter of silver maple.[1]

Factor	DF	SS	Mean Square	F Value	Pr > F
Model	27	1310.33	48.53	49.32	**0.0001**
Block	3	209.94	69.98	71.12	**0.0001**
Fert[2]	1	66.09	66.09	5.73	0.0964
Error a	3	34.61	11.54		
Wslevel	10	875.21	87.52	88.95	**0.0001**
Fert*wslevel	10	120.10	12.01	12.21	**0.0001**
Error b	4332	4262.51	0.98		

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1)cn vs nocn (noweed)	1	8.71	8.71	8.86	**0.0029**
2)cn vs nocn (inter)	1	0.18	0.18	0.19	0.6657
3)mow vs clov	1	26.76	26.76	27.20	**0.0001**
4)mow vs fullweed, (nocn)	1	3.00	3.00	3.05	0.0808
5)mow vs noweed, (nocn)	1	228.19	228.19	231.91	**0.0001**
6)mow vs inter, (nocn)	1	43.71	43.71	44.42	**0.0001**
7)clov vs fullweed, (nocn)	1	11.88	11.88	12.07	**0.0005**
8)clov vs inter, (nocn)	1	138.37	138.37	140.63	**0.0001**
9)clov vs noweed, (nocn)	1	406.35	406.35	412.98	**0.0001**
10)full vs inter, (nocn)	1	69.62	69.62	70.76	**0.0001**
11)Fert*(cn1 vs cn2),(noweed, inter)	1	2.16	2.16	2.20	0.1384
12)Fert*(cn vs nocn), (noweed)	1	53.38	53.38	54.26	**0.0001**
13)Fert*(cn vs nocn), (inter)	1	1.26	1.26	1.28	0.2578
14)Fert*(mow vs. clov)	1	1.54	1.54	1.57	0.2110
15)Fert*(mow vs noweed), (nocn)	1	2.28	2.28	2.32	0.1278
16)Fert*(mow vs inter), (nocn)	1	0.10	0.10	0.10	0.7484
17)Fert*(mow vs fullweed), (nocn)	1	6.48	6.48	6.59	0.0103
18)Fert*(clov vs noweed), (nocn)	1	0.08	0.08	0.08	0.7760
19)Fert*(clov vs inter), (nocn)	1	0.85	0.85	0.87	0.3517
20)Fert*(clov vs fullweed), (nocn)	1	1.68	1.68	1.71	0.1913

[1] log-transformed

[2] Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn); low corn density (cn1); high corn density (cn2). Weed contrast: no-weed (noweed); inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

lower heights and diameters than those in full-weed treatments (contrast 7). There were no significant differences between mown-weed and full-weed treatments (contrast 4) although trees in inter-weed treatments had relatively greater heights and diameters (contrast 6) and those in weed-free treatments had the greatest heights (contrast 5) (Table 7.6).

Maple growth was affected by interactions between fertiliser and weed-control (Tables 7.5 and 7.7). When fertilised, maple height increased in inter-weed treatments but not in mown-weed treatments (contrast 16). In contrast, when fertilised, trees growing in clover treatments decreased in height, while those in inter-weed (contrast 19) and no-weed (contrast 18) treatments, increased (Table 7.6).

The corn shelter crop affected tree growth (Tables 7.5 and 7.7). When fertilised, maples growing in corn had greater heights than those without corn for both no-weed (contrast 12) and inter-weed (contrast 13) treatments. However, maples had lower diameters in corn treatments under no-weed conditions (contrast 1). When fertilised, the diameters of maples also seemed to decrease in full-weed, no-corn plots but increased in both low and high density corn treatments. Maples also had increased heights in high density compared with low-density corn treatments but only when plots were fertilised (contrast 11) (Table 7.6).

There was an interaction between time and WS, in that maple heights in clover treatments seemed to decline in growth rate at the end of the second and third year relative to other treatments (Figures 7.1 and 7.2).

Figure 7.1. The effect of fertiliser and weed-shade treatments on silver maple height from 1994 to 1996. Bars indicate the least significant difference ($p<0.05$) between treatments on each sample date. Twenty-two weed shade treatments were combined into 13 categories to allow for more effective rendering in figures. F: Fertilised. UF: unfertilised

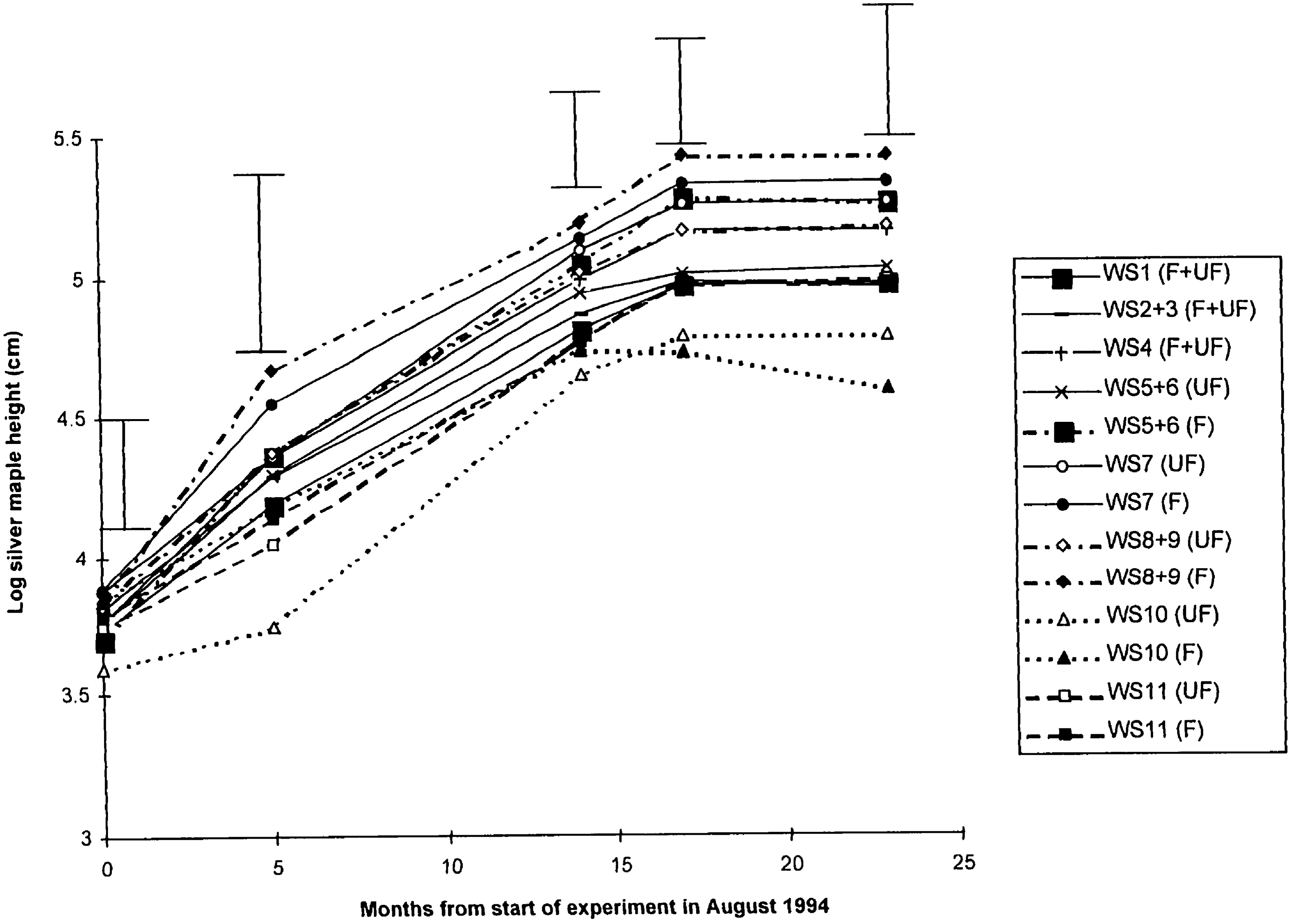
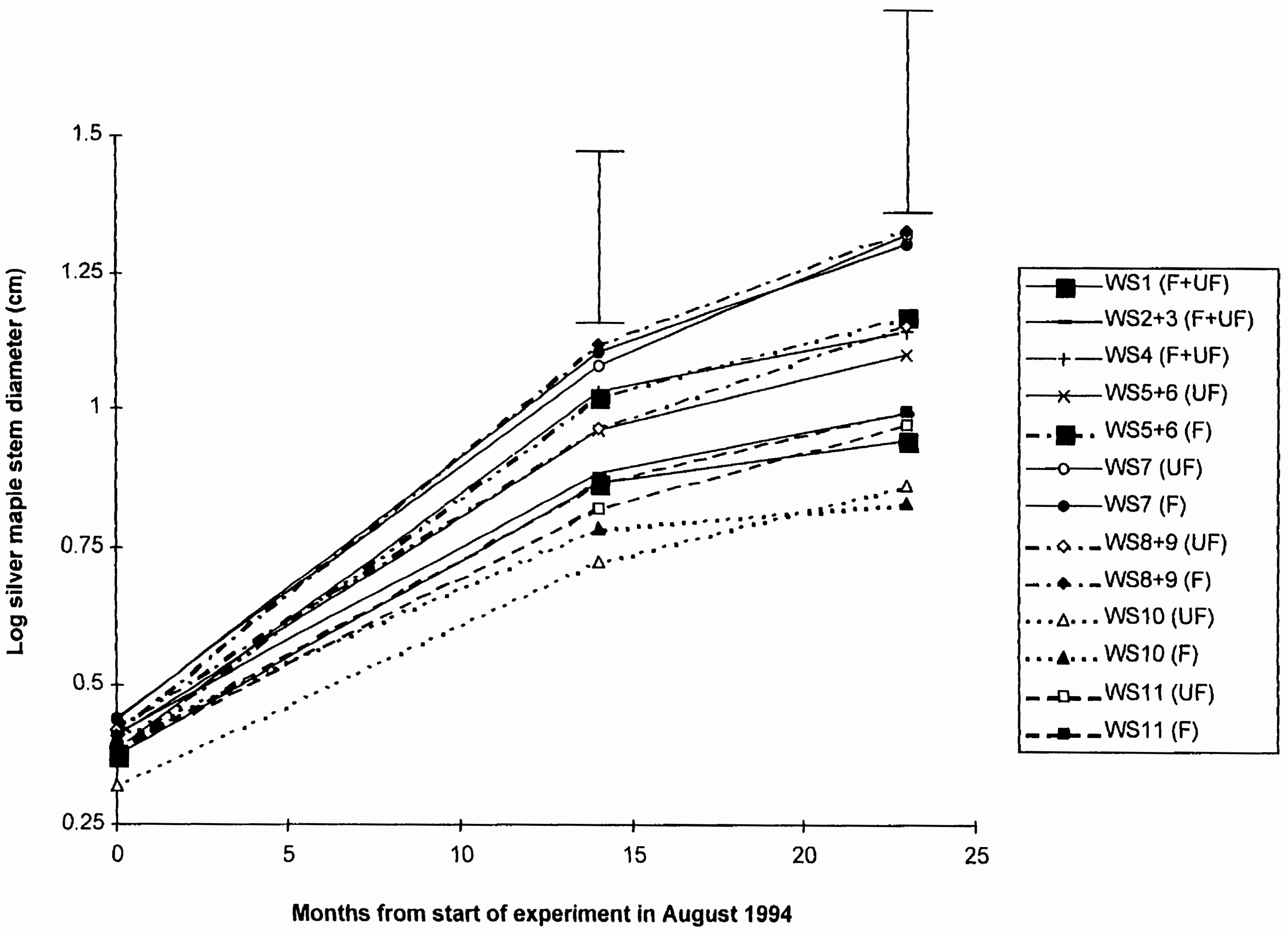

Log silver maple height (cm)
5.5
5
4.5
4
3.5
3
0
5
10
15
20
25
Months from start of experiment in August 1994
WS1 (F+UF)
WS2+3 (F+UF)
WS4 (F+UF)
WS5+6 (UF)
WS5+6 (F)
WS7 (UF)
WS7 (F)
WS8+9 (UF)
WS8+9 (F)
WS10 (UF)
WS10 (F)
WS11 (UF)
WS11 (F)

Figure 7.2. The effect of fertiliser and weed-shade treatments on silver maple diameter from 1994 to 1996. Bars indicate the least significant difference ($p<0.05$) between treatments on each sample date. Twenty-two weed shade treatments were combined into 13 categories to allow for more effective rendering in figures. F: Fertilised. UF: unfertilised.


1.5
1.25
1
0.75
0.5
0.25
Log silver maple stem diameter (cm)
0
5
10
15
20
25
Months from start of experiment in August 1994
WS1 (F+UF)
WS2+3 (F+UF)
WS4 (F+UF)
WS5+6 (UF)
WS5+6 (F)
WS7 (UF)
WS7 (F)
WS8+9 (UF)
WS8+9 (F)
WS10 (UF)
WS10 (F)
WS11 (UF)
WS11 (F)

Green ash

The heights and diameters of ash trees responded significantly to fertilisation (Tables 7.8 and 7.9). Tree heights and diameters were lower in clover than in mown-weed (Figures 7.3 and 7.4; Tables 7.8 and 7.9: contrast 3), inter-weed (contrast 8), and no-weed (contrast 9) treatments. However, ash heights and diameters in clover were similar to those in full-weed treatments (contrast 7) and less than tree heights and diameters in the mown-weed treatment (contrast 4). In turn, ash tree heights and diameters in mown-weed treatments were similar to those in inter-weed (contrast 6) treatments and less than those in the no-weed treatments (contrast 5) (Table 7.6).

There were significant interactions between fertiliser and weed control treatments (Tables 7.8 and 7.9). Trees in the mown-weed treatment increased in height and diameter when fertilised, while tree heights and diameters in clover (contrast 14) and full-weed, no-corn treatments (contrast 17) decreased. This was also the case for tree heights and diameters in fertilised, weed-free treatments compared with clover treatments (contrast 18) (Table 7.6).

The corn shelter crop significantly affected ash growth (Tables 7.8 and 7.9). Ash height increased when grown with corn in inter-weed (contrast 2), but both height and diameter only increased in with-corn, inter-weed treatments when they were fertilised. In contrast, tree growth in no-corn, inter-weed treatments was unaffected by fertilisation (contrast 13). There was no interaction between corn density and fertiliser (contrast 11) (Table 7.6).

Table 7.8. ANOVA for effect of fertilizer and weed-shade treatments on height of green ash.[1]

Factor	DF	SS	Mean Square	F Value	Pr > F
Model	27	1138575.61	42169.47	24.25	**0.0001**
Block	3	34954.05	11651.35	6.70	**0.0002**
Fert[2]	1	102887.84	102887.84	19.42	**0.0217**
Error a	3	15897.75	5299.25		
Wslevel	10	853251.47	85325.15	49.06	**0.0001**
Fert*wslevel	10	163101.72	16310.17	9.38	**0.0001**
Error b	4132	7186269.47	1739.17		

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1)cn vs nocn (noweed)	1	1641.67	1641.67	0.94	0.3313
2)cn vs nocn (inter)	1	58481.83	58481.83	33.63	**0.0001**
3)mow vs clov	1	49211.53	49211.53	28.30	**0.0001**
4)mow vs fullweed, (nocn)	1	15406.05	15406.05	8.86	**0.0029**
5)mow vs noweed, (nocn)	1	88047.58	88047.58	50.63	**0.0001**
6)mow vs inter, (nocn)	1	2200.36	2200.36	1.27	0.2607
7)clov vs fullweed, (nocn)	1	10188.78	10188.78	5.86	0.0155
8)clov vs inter, (nocn)	1	74807.98	74807.98	43.01	**0.0001**
9)clov vs noweed, (nocn)	1	273360.41	273360.41	157.18	**0.0001**
10)full vs inter, (nocn)	1	30399.26	30399.26	17.48	**0.0001**
11)Fert*(cn1 vs cn2),(noweed, inter)	1	1313.70	1313.70	0.76	0.3848
12)Fert*(cn vs nocn), (noweed)	1	8995.60	8995.60	5.17	0.0230
13)Fert*(cn vs nocn), (inter)	1	19872.44	19872.44	11.43	**0.0007**
14)Fert*(mow vs. clov)	1	21917.37	21917.37	12.60	**0.0004**
15)Fert*(mow vs noweed), (nocn)	1	73.39	73.39	0.04	0.8373
16)Fert*(mow vs inter), (nocn)	1	7595.91	7595.91	4.37	0.0367
17)Fert*(mow vs fullweed), (nocn)	1	17539.84	17539.84	10.09	**0.0015**
18)Fert*(clov vs noweed), (nocn)	1	18548.27	18548.27	10.66	**0.0011**
19)Fert*(clov vs inter), (nocn)	1	3635.80	3635.80	2.09	0.1483
20)Fert*(clov vs fullweed), (nocn)	1	259.92	259.92	0.15	0.6991

[1] log-transformed

[2] Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn); low corn density (cn1); high corn density (cn2). Weed contrast: no-weed (noweed); inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

Table 7.9. ANOVA for effect of fertilizer and weed-shade treatments on diameter of green ash.[1]

Factor	DF	SS	Mean Square	F Value	Pr > F
Model	27	254.55	9.43	42.36	**0.0001**
Block	3	8.08	2.69	12.11	**0.0001**
Fert[2]	1	11.65	11.65	10.19	0.0496
Error a	3	3.43	1.14		
Wslevel	10	197.73	19.77	88.84	**0.0001**
Fert*wslevel	10	48.84	4.88	21.94	**0.0001**
Error b	4132	919.67	0.22		

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
1)cn vs nocn (noweed)	1	0.02	0.02	0.07	0.7898
2)cn vs nocn (inter)	1	0.11	0.11	0.51	0.4751
3)mow vs clov	1	19.30	19.30	86.71	**0.0001**
4)mow vs fullweed, (nocn)	1	23.74	23.74	106.66	**0.0001**
5)mow vs noweed, (nocn)	1	9.40	9.40	42.24	**0.0001**
6)mow vs inter, (nocn)	1	0.20	0.20	0.91	0.3412
7)clov vs fullweed, (nocn)	1	0.25	0.25	1.10	0.2942
8)clov vs inter, (nocn)	1	24.22	24.22	108.81	**0.0001**
9)clov vs noweed, (nocn)	1	55.66	55.66	250.06	**0.0001**
10)full vs inter, (nocn)	1	29.24	29.24	131.38	**0.0001**
11)Fert*(cn1 vs cn2),(noweed, inter)	1	1.04	1.04	4.67	0.0307
12)Fert*(cn vs nocn), (noweed)	1	0.09	0.09	0.38	0.5361
13)Fert*(cn vs nocn), (inter)	1	3.26	3.26	14.66	**0.0001**
14)Fert*(mow vs. clov)	1	2.23	2.23	10.03	**0.0016**
15)Fert*(mow vs noweed), (nocn)	1	5.94	5.94	26.71	**0.0001**
16)Fert*(mow vs inter), (nocn)	1	1.46	1.46	6.58	0.0104
17)Fert*(mow vs fullweed), (nocn)	1	2.13	2.13	9.57	**0.0020**
18)Fert*(clov vs noweed), (nocn)	1	15.79	15.79	70.94	**0.0001**
19)Fert*(clov vs inter), (nocn)	1	0.07	0.07	0.32	0.5709
20)Fert*(clov vs fullweed), (nocn)	1	0.00	0.00	0.01	0.9403

[1] log-transformed

[2] Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn); low corn density (cn1); high corn density (cn2). Weed contrast: no-weed (noweed); inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

Figure 7.3. The effect of fertiliser and weed-shade treatments on green ash height from 1994 to 1996. Bars indicate the least significant difference ($p<0.05$) between treatments on each sample date. Twenty-two weed shade treatments were combined into 13 categories to allow for more effective rendering in figures. F: Fertilised, UF: unfertilised.

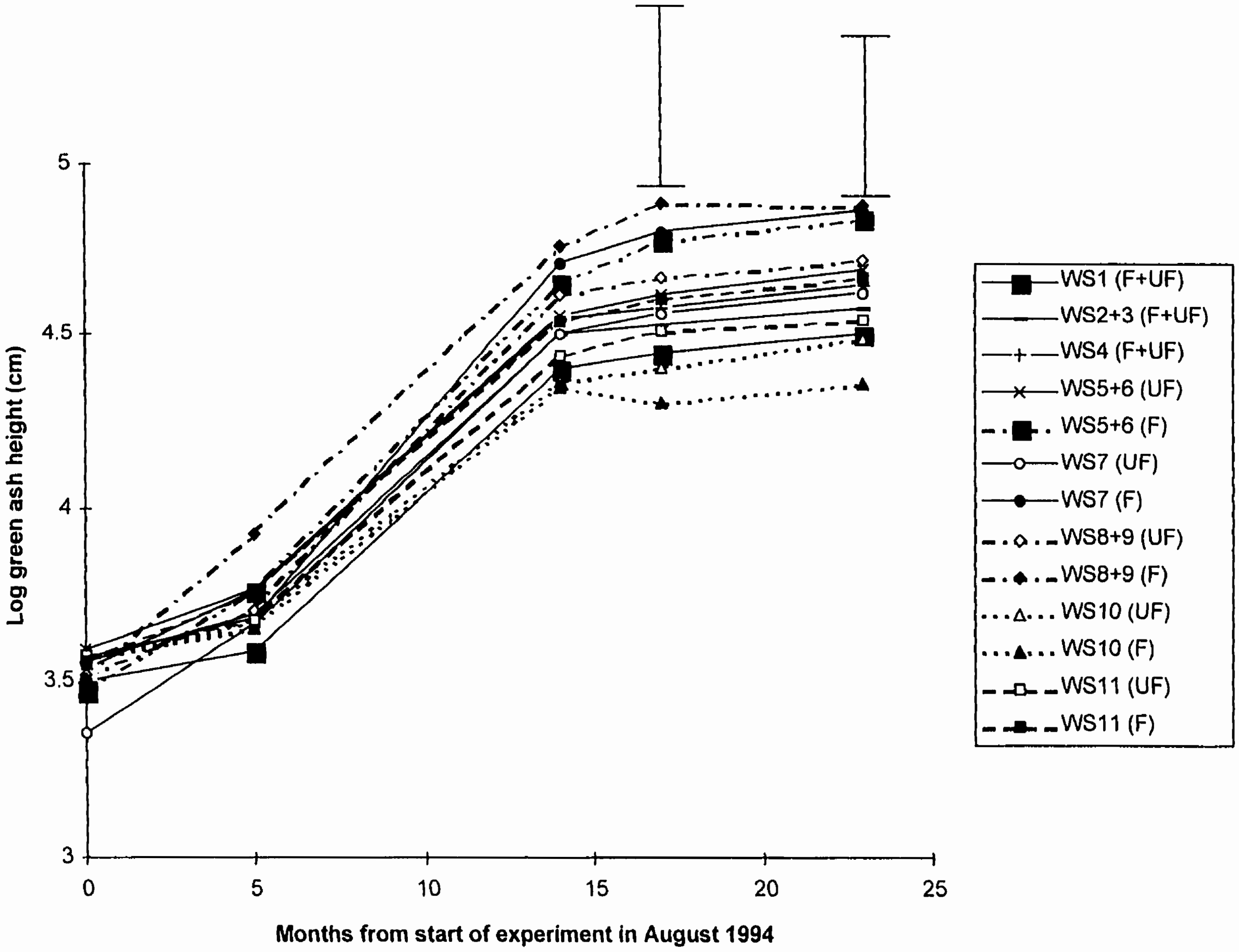
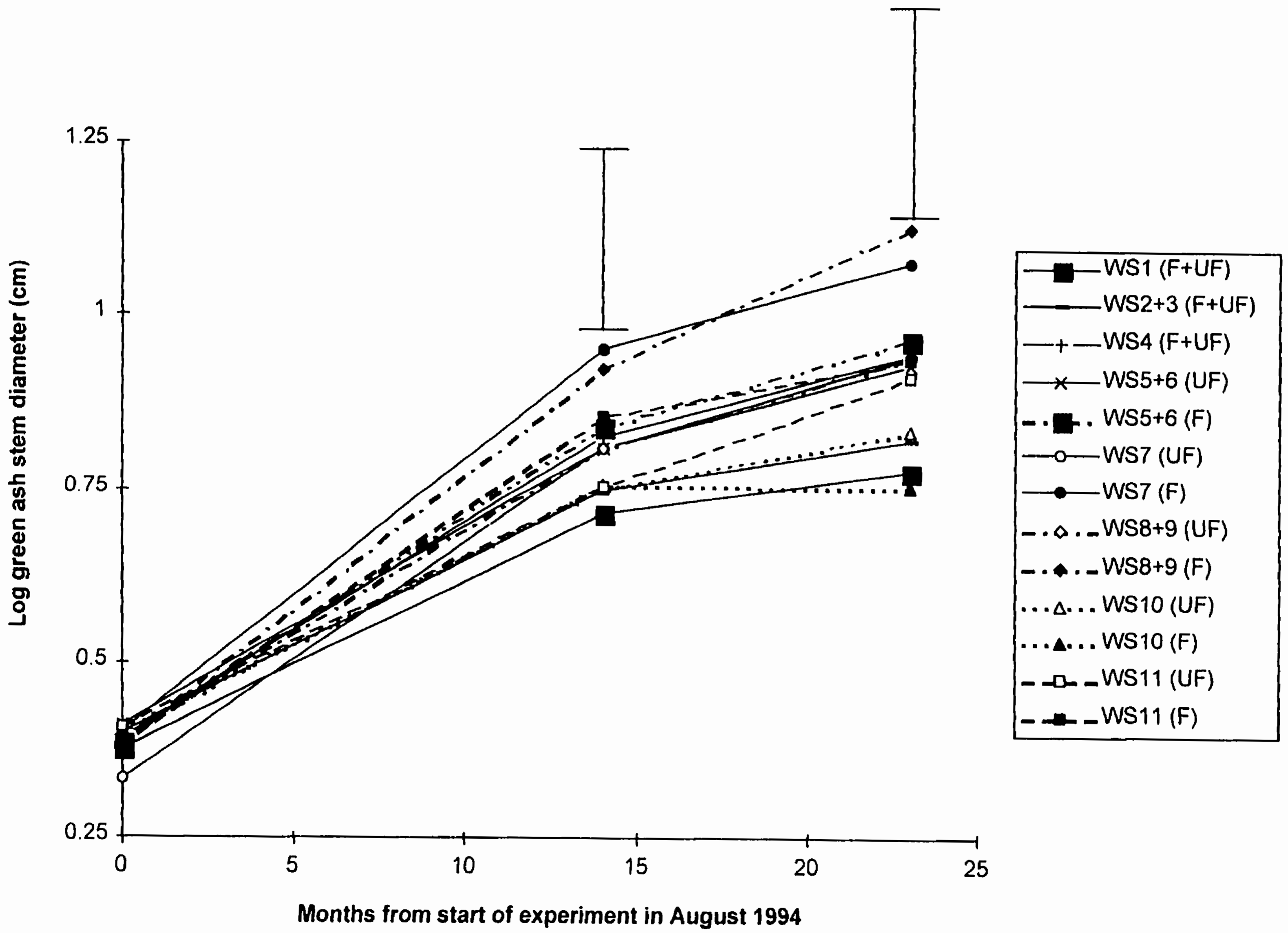

Log green ash height (cm)
5
4.5
4
3.5
3
0
5
10
15
20
25
Months from start of experiment in August 1994
WS1 (F+UF)
WS2+3 (F+UF)
WS4 (F+UF)
WS5+6 (UF)
WS5+6 (F)
WS7 (UF)
WS7 (F)
WS8+9 (UF)
WS8+9 (F)
WS10 (UF)
WS10 (F)
WS11 (UF)
WS11 (F)

Figure 7.4. The effect of fertiliser and weed-shade treatments on green ash diameter from 1994 to 1996. Bars indicate the least significant difference ($p<0.05$) between treatments on each sample date. Twenty-two weed shade treatments were combined into 13 categories to allow for more effective rendering in figures. F: Fertilised. UF: unfertilised.



Log green ash stem diameter (cm)
1.25
1
0.75
0.5
0.25
0
5
10
15
20
25
Months from start of experiment in August 1994
WS1 (F+UF)
WS2+3 (F+UF)
WS4 (F+UF)
WS5+6 (UF)
WS5+6 (F)
WS7 (UF)
WS7 (F)
WS8+9 (UF)
WS8+9 (F)
WS10 (UF)
WS10 (F)
WS11 (UF)
WS11 (F)

Bur oak

Oak trees had relatively poor growth compared with maple and ash. The final tree diameters and heights were less than 50% of those for maple (Table 7.6). Oaks grown in clover had significantly lower heights (Table 7.10) and diameters (Table 7.11) than those in mown-weed (contrast 3), inter-weed (contrast 8), and no-weed (contrast 9) treatments (Figures 7.5 and 7.6). There were no differences in height between mown-weed and either inter-weed (contrast 6) or no-weed (contrast 5) treatments. Neither were there any differences between inter-weed and full-weed (contrast 10) treatments. Oak diameter was more responsive to different weed-control treatments than was height. While there were no differences between trees in mown-weed and no-weed treatments (contrast 5), oaks grown in mown-weed treatments had greater diameters than those in full-weed treatments (contrast 4) and lower diameters than those in inter-weed treatments (contrast 6) (Table 7.6).

There were significant interactions between fertiliser and weed control treatments (Tables 7.10 and 7.11). When fertilised, both oak height and diameter increased in mown-weed treatments, but decreased in clover (contrast 14) and full-weed, no-corn (contrast 17) treatments. Similarly, when fertilised, tree heights and diameters increased in no-corn, inter-weed (contrast 19) and no-corn, no-weed (contrast 18) treatments but decreased in clover treatments (Table 7.6).

The corn shelter crop significantly affected oak growth which, in contrast to maple and ash, was adversely by presence of corn (Tables 7.10 and 7.11). Tree diameter decreased under corn but only for inter-weed treatments (contrast 2) and only in fertilised

Table 7.10. ANOVA for effect of fertiliser and weed-shade treatments on height of bur oak.[1]

Factor	DF	SS	Mean Square	F value	Pr > F
Model	25	380881.35	15235.25	10.04	**0.0001**
Block	3	63661.21	21220.40	13.98	**0.0001**
Fert[2]	1	1430.24	1430.24	0.71	0.5538
Error a	1	2009.28	2009.28		
Wslevel	10	96909.12	9690.91	6.39	**0.0001**
Fert*wslevel	10	85531.74	8553.17	5.64	**0.0001**
Error b	1159	1758634.91	1517.37		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)cn vs nocn (noweed)	1	5835.06	5835.06	3.85	0.0501
2)cn vs nocn (inter)	1	576.08	576.08	0.38	0.5379
3)mow vs clov	1	19370.36	19370.36	12.77	**0.0004**
4)mow vs fullweed, (nocn)	1	2628.37	2628.37	1.73	0.1884
5)mow vs noweed, (nocn)	1	985.28	985.28	0.65	0.4205
6)mow vs inter, (nocn)	1	2484.25	2484.25	1.64	0.2010
7)clov vs fullweed, (nocn)	1	1779.38	1779.38	1.17	0.2791
8)clov vs inter, (nocn)	1	29619.50	29619.50	19.52	**0.0001**
9)clov vs noweed, (nocn)	1	30608.80	30608.80	20.17	**0.0001**
10)full vs inter, (nocn)	1	7310.20	7310.20	4.82	0.0284
11)Fert*(cn1 vs cn2),(noweed, inter)	1	973.30	973.30	0.64	0.4234
12)Fert*(cn vs nocn), (noweed)	1	14537.67	14537.67	9.58	**0.0020**
13)Fert*(cn vs nocn), (inter)	1	675.19	675.19	0.44	0.5049
14)Fert*(mow vs. clov)	1	30483.95	30483.95	20.09	**0.0001**
15)Fert*(mow vs noweed), (nocn)	1	918.55	918.55	0.61	0.4367
16)Fert*(mow vs inter), (nocn)	1	231.30	231.30	0.15	0.6963
17)Fert*(mow vs fullweed), (nocn)	1	14387.03	14387.03	9.48	**0.0021**
18)Fert*(clov vs noweed), (nocn)	1	20438.51	20438.51	13.47	**0.0003**
19)Fert*(clov vs inter), (nocn)	1	17755.78	17755.78	11.70	**0.0006**
20)Fert*(clov vs fullweed), (nocn)	1	28.48	28.48	0.02	0.8911

[1] log-transformed

[2] Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn); low corn density (cn1); high corn density (cn2). Weed contrast: no-weed (noweed); inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

Table 7.11. ANOVA for effect of fertiliser and weed-shade treatments on diameter of bur oak.[1]

Factor	DF	SS	Mean Square	F value	Pr > F
Model	25	69.23	2.77	16.41	**0.0000**
Block	3	11.66	3.89	23.02	**0.0001**
Fert[2]	1	1.03	1.03	0.50	0.6080
Error a	1	2.06	2.06		
Wslevel	10	31.48	3.15	18.65	**0.0001**
Fert*wslevel	10	8.40	0.84	4.98	**0.0001**
Error b	1159	195.58	0.17		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)cn vs nocn (noweed)	1	0.04	0.04	0.22	0.6380
2)cn vs nocn (inter)	1	2.81	2.81	16.64	**0.0001**
3)mow vs clov	1	7.41	7.41	43.93	**0.0001**
4)mow vs fullweed, (nocn)	1	2.64	2.64	15.66	**0.0001**
5)mow vs noweed, (nocn)	1	0.79	0.79	4.70	0.0303
6)mow vs inter, (nocn)	1	2.18	2.18	12.94	**0.0003**
7)clov vs fullweed, (nocn)	1	0.03	0.03	0.18	0.6734
8)clov vs inter, (nocn)	1	15.22	15.22	90.20	**0.0001**
9)clov vs noweed, (nocn)	1	13.89	13.89	82.29	**0.0001**
10)full vs inter, (nocn)	1	6.93	6.93	41.09	**0.0001**
11)Fert*(cn1 vs cn2),(noweed, inter)	1	0.00	0.00	0.00	0.9545
12)Fert*(cn vs nocn), (noweed)	1	1.29	1.29	7.63	0.0058
13)Fert*(cn vs nocn), (inter)	1	1.81	1.81	10.70	**0.0011**
14)Fert*(mow vs. clov)	1	1.78	1.78	10.57	**0.0012**
15)Fert*(mow vs noweed), (nocn)	1	0.00	0.00	0.00	0.9648
16)Fert*(mow vs inter), (nocn)	1	0.04	0.04	0.22	0.6421
17)Fert*(mow vs fullweed), (nocn)	1	1.52	1.52	9.02	**0.0027**
18)Fert*(clov vs noweed), (nocn)	1	1.87	1.87	11.09	**0.0009**
19)Fert*(clov vs inter), (nocn)	1	1.81	1.81	10.74	**0.0011**
20)Fert*(clov vs fullweed), (nocn)	1	0.14	0.14	0.82	0.3657

[1] log-transformed

[2] Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn); low corn density (cn1); high corn density (cn2). Weed contrast: no-weed (noweed); inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

Figure 7.5. The effect of fertiliser and weed-shade treatments on bur oak height from 1994 to 1996. Bars indicate the least significant difference ($p<0.05$) between treatments on each sample date. Twenty-two weed shade treatments were combined into 13 categories to allow for more effective rendering in figures. F: Fertilised. UF: unfertilised.

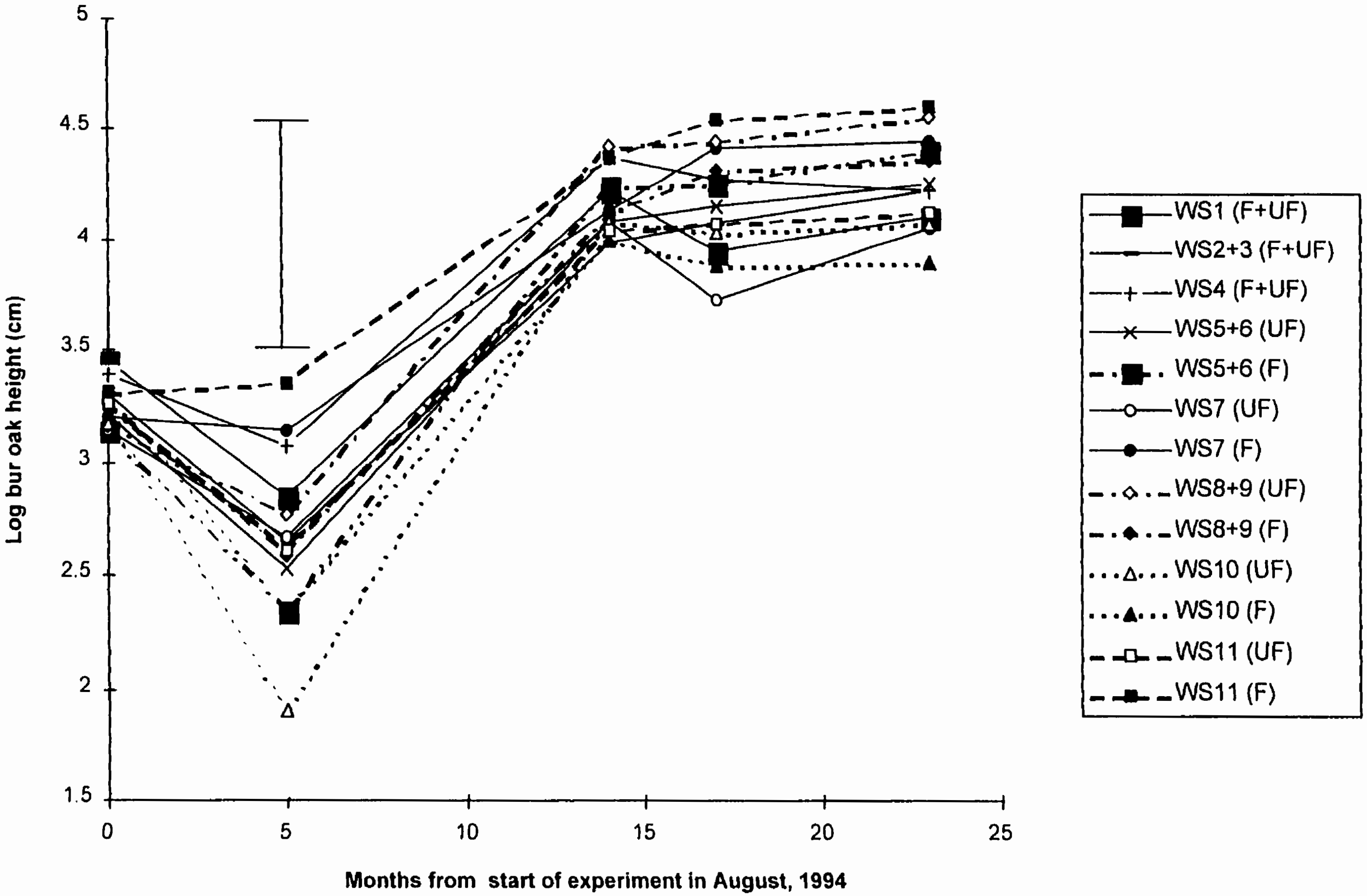
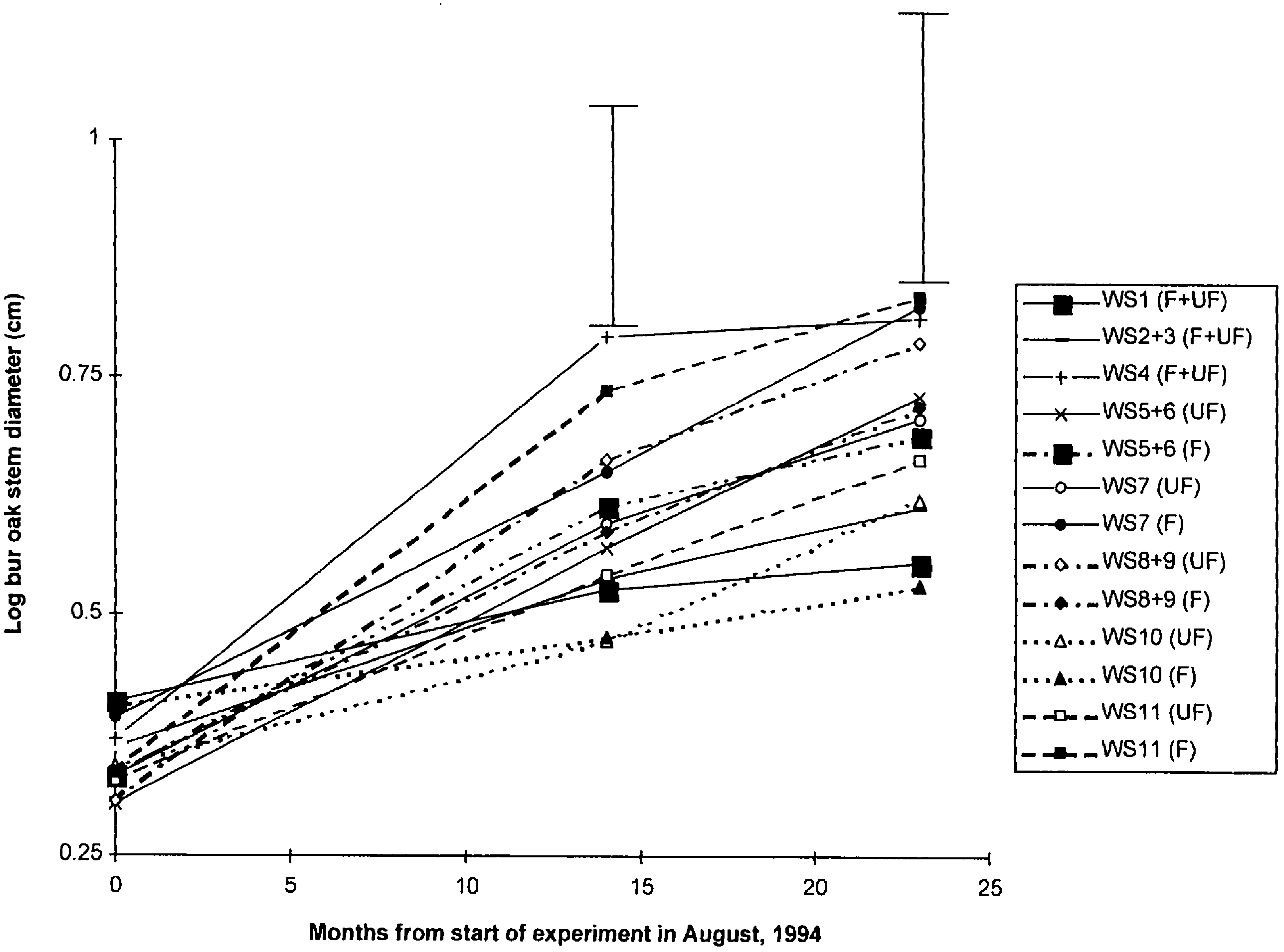

Log bur oak height (cm)
5
4.5
4
3.5
3
2.5
2
1.5
0
5
10
15
20
25
Months from start of experiment in August, 1994
WS1 (F+UF)
WS2+3 (F+UF)
WS4 (F+UF)
WS5+6 (UF)
WS5+6 (F)
WS7 (UF)
WS7 (F)
WS8+9 (UF)
WS8+9 (F)
WS10 (UF)
WS10 (F)
WS11 (UF)
WS11 (F)

Figure 7.6. The effect of fertiliser and weed-shade treatments on bur oak diameter from 1994 to 1996. Bars indicate the least significant difference ($p<0.05$) between treatments on each sample date. Twenty-two weed shade treatments were combined into 13 categories to allow for more effective rendering in figures. F: Fertilised. UF: unfertilised.


Log bur oak stem diameter (cm)
1
0.75
0.5
0.25
0
5
10
15
20
25
Months from start of experiment in August, 1994
WS1 (F+UF)
WS2+3 (F+UF)
WS4 (F+UF)
WS5+6 (UF)
WS5+6 (F)
WS7 (UF)
WS7 (F)
WS8+9 (UF)
WS8+9 (F)
WS10 (UF)
WS10 (F)
WS11 (UF)
WS11 (F)

plots (contrast 13). Similarly, tree heights decreased and diameters tended to decrease in weed-free treatments under the corn, when fertilised (contrast 12). There were no significant interactions between corn density and fertiliser for either oak height or diameter (contrast 11) (Tables 7.10 and 7.11).

Tree mortality

Mortality varied from 5-18% for the three tree species and that of the oak was highest ($G=51.52$, $p<0.001$) (Table 7.12). This relatively high mortality was likely associated with selective deer grazing as significantly more oak were grazed by deer than ash or maple ($G=149.76$, $p<0.001$) (Table 7.12). Furthermore, mortality was unaffected by fertilisation or WS for maple ($F_{57,30}=1.31$, $p=0.2160$), ash ($F_{57,30}=1.05$, $p=0.4515$), or oak ($F_{57,30}=1.66$, $p=0.0660$). Hickory mortality was much higher than the other tree species and had reached 82% by August 1994 and 99% by May 1996. The high mortality was likely due to shallow planting of the trees.

Weed biomass

Weed biomass (g/m^2) was affected by WS treatments (Tables 7.13 and 7.14). In particular, in inter-weed treatments, total weed biomass was significantly lower in corn plots than in no-corn plots (contrast 5). Similarly, in corn plots, total weed biomass was lower in inter-weed than in full-weed treatments (contrast 8). Total percentage cover was similarly affected by WS treatments (Tables 7.14 and 7.15). However, percentage cover was also lower in corn plots than in no-corn plots for full-weed treatments (contrast 4).

Table 7.12. Mortality and deer-grazing pressure for each of the three tree species in the study

Species	**Mortality** (% trees dead)	**Deer-grazing** (% trees grazed)
Silver maple	7.1	0.2
Green ash	4.8	0.8
Bur oak	18.0	14.5

Table 7.13. ANOVA for effect of fertilizer and weed-shade treatments on total weed biomass per m^2 in 1995.[1]

Factor	DF	SS	Mean Square	F value	Pr > F
Model	42	66.96	1.59	3.28	**0.0024**
Blk[2]	3	3.65	1.22	2.05	0.0875
Fert	1	1.35	1.35	2.95	0.1843
Error a	3	1.37	0.46	0.94	0.4388
Wslevel	7	46.60	6.66	13.69	**0.0001**
Fert*wslevel	7	3.71	0.53	1.09	0.4052
Blk*fert	21	10.27	0.49	1.02	0.4112
Error b	21	10.21	0.48		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)clov vs fullweed, (nocn)	1	0.46	0.46	0.95	0.3410
2)clov vs mow	1	0.10	0.10	0.21	0.6527
3)fullweed (nocn) vs mow	1	1.00	1.00	2.05	0.1672
4)cn vs nocn, (fullweed)	1	0.13	0.13	0.27	0.6109
5)cn vs nocn, (inter)	1	13.13	13.13	27.00	**0.0001**
6)fullweed vs inter, (nocn)	1	1.61	1.61	3.31	0.0832
7)fullweed vs inter, (cn)	1	33.54	33.54	68.96	**0.0001**

[1] log-transformed

[2] Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn). Weed contrast: inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

Table 7.14. Effect of WS treatment combinations on weed growth in 1995. Weed-shade (WS) treatments were: full-weed, no-corn (WS1); full-weed, low-corn (WS2); full-weed, high density corn (WS3); inter-weed, no-corn (WS4); inter-weed, low density corn (WS5); inter-weed, high density corn (WS6); clover cover crop, no-corn (WS10); mown-weed, no-corn (WS11). All values are calculated on a means per quadrat basis.

WS level	Species number		Percentage cover		Broadleaf biomass (g dwt m^{-2})		Grass biomass (g dwt m^{-2})		Total weed biomass (g dwt m^{-2})	
Treatment no.	**UF**	**FF**	**UF**	**FF**	**UF**	**FF**	**UF**	**FF**	**UF**	**FF**
1	10.3	10.0	135.3	165.1	264.9	348.7	136.0	214.6	400.9	563.3
2	10.2	9.3	87.8	142.3	209.1	703.3	95.3	46.2	304.4	749.5
3	11.1	9.6	92.9	172.9	166.2	335.5	136.0	152.2	302.2	487.7
4	9.9	9.0	135.6	223.2	120.0	130.0	138.4	168.3	258.4	298.3
5	9.4	9.4	59.4	86.5	33.1	97.2	45.3	10.4	78.4	107.5
6	9.5	8.1	58.7	45.6	55.9	25.8	48.3	13.8	104.1	39.6
10	8.4	9.4	148.8	142.8	323.5	462.8	0.3	7.2	323.8	470.0
11	9.4	10.4	89.9	136.5	102.6	348.5	130.6	56.3	233.2	404.8

Table 7.15. ANOVA for effect of fertilizer and weed-shade treatments on weed percentage cover per m^2 in 1995.[1]

Factor	DF	SS	Mean Square	F value	Pr > F
Model	63	52.46	0.83	1.42	**0.0433**
Blk[2]	3	7.61	2.54	4.34	**0.0058**
Fert	1	0.90	0.90	7.06	0.0765
Error a	3	0.38	0.00		
Wslevel	7	23.90	3.41	5.84	**0.0001**
Fert*wslevel	7	3.37	0.48	0.82	0.5689
Blk*wslevel	21	11.55	0.55	0.94	0.5403
Blk*fert*wslevel	21	7.01	0.33	0.57	0.9321
Error b	144	84.21	0.58		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)clov vs fullweed, (nocn)	1	0.09	0.09	0.16	0.6876
2)clov vs mow	1	2.66	2.66	4.55	0.0346
3)fullweed (nocn) vs mow	1	3.76	3.76	6.43	0.0123
4)cn vs nocn, (fullweed)	1	5.07	5.07	8.68	**0.0038**
5)cn vs nocn, (inter)	1	11.38	11.38	19.45	**0.0001**
6)fullweed vs inter, (nocn)	1	0.02	0.02	0.04	0.8513
7)fullweed vs inter, (cn)	1	5.35	5.35	9.16	**0.0029**

[1] log-transformed

[2] Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn). Weed contrast: inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

When weed biomass was divided into forb (including clover) (Tables 7.14 and 7.16) and graminoid classes (Tables 7.14 and 7.17), both forb and graminoid biomass were greater in the no-corn plots than under the corn plots (contrast 5) and, in the corn plots, were greater in the full-weed than in the inter-weed treatments (contrast 8). Graminoid biomass was lower in the clover treatment than in the mown-weed (contrast 2) and the no-corn, full-weed (contrast 1) treatments. There was a significant effect of WS on species richness (Tables 7.14 and 7.18) which was lower in the clover treatment than in the no-corn, full-weed treatment (contrast 1).

Composition of weed communities

The three most common weed species occurring in plots were *Echinochloa crus-galli*, *Xanthium strumarium*, and *Ambrosia artemisiifolia*. When classified as a weed, *Trifolium repens* was also very common. In general, principal components analysis (PCA) indicated the importance of clover, fertilisation, and shelter treatments and whether the sampling areas had been mechanically cultivated (inter) or not (intra). Axis 1 separated unfertilised, clover quadrats associated with *Trifolium repens*, from fertilised quadrats associated with *Echinochloa crus-galli* and *Xanthium strumarium* (Appendix 2: Figure 7.7). Axis 2 separated uncultivated plots associated with *Ambrosia artemisiifolia* and *Polygonum persicaria* from clover plots associated with *Trifolium repens* . Axis 3 (not shown) separated uncultivated, fertilised quadrats in block 3 associated with *Ambrosia artemisiifolia* and *Ambrosia trifida* from those that were inter-cultivated, corn-free and associated with *Xanthium strumarium* and *Abutilon theophrasti*. Finally, axis 4

Table 7.16. ANOVA for effect of fertilizer and weed-shade treatments on forb biomass (including *Trifolium repens*) per m^2 in 1995.[1]

Factor	DF	SS	Mean Square	F value	Pr > F
Model	42	148.54	3.54	2.63	**0.0098**
Blk[2]	3	3.74	1.25	0.93	0.4450
Fert	1	2.09	2.09	0.79	0.4408
Error a	3	7.97	2.66		
Wslevel	7	72.24	10.32	7.68	**0.0001**
Fert*wslevel	7	20.91	2.99	2.22	0.0742
Blk*wslevel	21	41.60	1.98	1.47	0.1909
Error b	21	28.24	1.34		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)clov vs fullweed, (nocn)	1	0.09	0.09	0.07	0.7985
2)clov vs mow	1	2.89	2.89	2.15	0.1572
3)fullweed (nocn) vs mow	1	1.96	1.96	1.46	0.2403
4)cn vs nocn, (fullweed)	1	0.88	0.88	0.66	0.4265
5)cn vs nocn, (inter)	1	13.19	13.19	9.81	**0.0050**
6)fullweed vs inter, (nocn)	1	4.57	4.57	3.40	0.0793
7)fullweed vs inter, (cn)	1	39.96	39.96	29.72	**0.0001**

[1] log-transformed

[2] Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn). Weed contrast: inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

Table 7.17. ANOVA for effect of fertilizer and weed-shade on graminoid biomass per m^2 in 1995.[1]

Factor	DF	SS	Mean Square	F value	Pr > F
Model	42	162.96	3.88	4.39	**0.0003**
Blk[2]	3	22.44	7.48	8.46	**0.0007**
Fert	1	2.86	2.86	3.06	0.1785
Error a	3	2.81	0.94		
Wslevel	7	102.64	14.66	16.58	**0.0001**
Fert*wslevel	7	11.77	1.68	1.90	0.1202
Blk*wslevel	21	20.45	0.97	1.10	0.4136
Error b	21	18.57	0.88		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)clov vs fullweed, (nocn)	1	66.87	66.87	75.63	**0.0001**
2)clov vs mow	1	39.89	39.89	45.12	**0.0001**
3)fullweed (nocn) vs mow	1	3.46	3.46	3.92	0.0610
4)cn vs nocn, (fullweed)	1	2.54	2.54	2.87	0.1050
5)cn vs nocn, (inter)	1	18.11	18.11	20.49	**0.0002**
6)fullweed vs inter, (nocn)	1	0.08	0.08	0.09	0.7676
7)fullweed vs inter, (cn)	1	13.39	13.39	15.14	**0.0008**

[1] log-transformed

[2] Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn). Weed contrast: inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

Table 7.18. ANOVA for effect of fertilizer and weed-shade treatments on species richness per m^2 in 1995.[1]

Factor	DF	SS	Mean Square	F value	Pr > F
Model	63	3.00	0.05	2.10	**0.0001**
Blk[2]	3	0.44	0.15	6.50	**0.0004**
Fert	1	0.05	0.05	0.28	0.6308
Blk*fert	3	0.55	0.18		
Wslevel	7	0.41	0.06	2.60	**0.0149**
Fert*wslevel	7	0.40	0.06	2.54	**0.0171**
Blk*wslevel	21	0.47	0.02	0.99	0.4778
Blk*fert*wslevel	21	0.46	0.02	0.97	0.5098
Error	144	3.27	0.02		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)clov vs fullweed, (nocorn)	1	0.21	0.21	9.07	**0.0031**
2)clov vs mow	1	0.13	0.13	5.71	0.0182
3)fullweed (nocorn) vs mow	1	0.01	0.01	0.39	0.5348
4)cn vs nocn, (fullweed)	1	0.01	0.01	0.30	0.5838
5)cn vs nocn, (inter.)	1	0.01	0.01	0.50	0.4822
6)fullweed vs inter, (nocn)	1	0.05	0.05	2.00	0.1596
7)fullweed vs inter, (corn)	1	0.14	0.14	5.99	0.0156
8)fert*(mow vs clov)	1	0.00	0.00	0.07	0.7890
9)fert*(cn vs nocn), (fullweed)	1	0.03	0.03	1.32	0.2529
10)fert*(cn vs nocn), (inter)	1	0.00	0.00	0.01	0.9073
11)fert*(fullweed vs inter), (nocn)	1	0.00	0.00	0.17	0.6844
12)fert*(fullweed vs inter), (cn)	1	0.01	0.01	0.54	0.4625
13)fert*(fullweed vs clov), (nocn)	1	0.07	0.07	3.11	0.0799
14)fert*(fullweed vs mow), (nocn)	1	0.05	0.05	2.24	0.1369

[1] log-transformed

[2] Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations). Shelter crop contrast: corn (cn); no-corn (nocn). Weed contrast: inter-weed (inter); mown-weed (mow); clover (clov); full-weed (fullweed).

Figure 7.7. Principal components analysis (PCA) diagram for herbaceous percentage cover data at Sturgeon Creek (axes 1 and 2). The quadrat labeling is as follows: combined weed-shade treatment:1-11; fertilisation treatment: fertilized (F), unfertilized (UF); tillage effect: quadrat situated in intra-row (ra), quadrat situated in inter-row (er). Species codes are listed in Appendix 2.


PCA axis 2 (S.D.)
10.0
8.0
6.0
4.0
2.0
0
-2.0
-4.0
-10.0
-5.0
0
5.0
10.0
PCA axis 1 (S.D.)
Ambart
2Fra
Trirep
Echcru
Xanstr
Polper
1UFra
3Fra
Ambtri
1UFra
11Fer
3Fra
3UFra
Taxoff
11Fra
2Fra
Abuthe
1UFra
4Fer
10Fra
11UFer
4Fer
1Fra
4UFer
10Fer
11UFer
10UFer
10Fer
4Fer
3Fra
1Fer
2UFra
10UFra
10UFra
10Fra
10Fer
10UFra
10UFer
10UFer
10UFra
3Fra
10Fra

(not shown) separated no-corn plots associated with *Echinochloa crusgalli*, *Trifolium repens*, and *Polygonum persicaria* from those that were fertilised, corn-shaded and associated with *Cirsium vulgare* and *Aster hirsuta*.(Figure 7.7)

Growth of the corn shelter crop

Corn responded significantly to both fertiliser and weed-control (Table 7.19). Total corn biomass and biomass per plant were significantly affected by fertiliser and WS treatment combinations in both 1994 and 1995 (Tables 20-23). In both years, fertilised corn plants had higher biomass per quadrat (Table 7.20 and 7.21). In 1995, corn biomass per quadrat was higher in no-weed than either inter-weed (contrast 3) or full-weed (contrast 2) (Table 7.21). Biomass per corn plant was lower in full-weed than no-weed in both 1994 and 1995 (contrast 2) and lower in high corn-density treatments in 1994 (contrasts 4 and 5) (Table 7.22 and 7.23). Predictably, corn plant number was greater in high-density treatments for both 1994 (Table 7.24) and 1995 (Table 7.25) (contrasts 4 and 5). Furthermore, in 1995, plant number was lower in full-weed than no-weed treatments (contrast 2) (Table 7.19).

Neither kernel weight per quadrat ($F_{32,15}$= 0.94, p=0.1659) nor kernel weight per cob ($F_{32,15}$=1.14, p=0.4522) had any significant treatment effects in 1995 although kernel weight per quadrat tended to be greater in fertilised plots. There was more herbivory on corn cobs in no-weed than in either inter-weed or full-weed plots (G=9.126, p=0.010) and small mammals tended to prefer to graze on corn in the no-weed treatments (G=5.001, p=0.082) (Table 26).

Table 7.19. Effect of WS treatments combinations on corn growth in a) 1994 and b) 1995. Weed-shade (WS) treatments are: full-weed, low density corn (WS2); full-weed, high density corn (WS3); inter-weed, low density corn (WS5); inter-weed, high density corn (WS6); no-weed, low density corn (WS8); and no-weed, high density corn (WS9). All values are calculated as means per sample area.

a)

	1994					
WSLEVEL	**Total weight (g dwt m^{-1})**		**Plant number (m^{-2})**		**Weight per plant (g dwt $plant^{-1}$)**	
Treatment no.	**UF**	**FF**	**UF**	**FF**	**UF**	**FF**
2	3.6	4.8	9.8	9.3	0.4	0.5
3	4.2	5.6	15.3	14.8	0.3	0.4
5	4.1	5.4	9.8	10.0	0.4	0.6
6	4.2	7.2	14.0	14.0	0.3	0.6
8	4.7	5.5	9.8	8.8	0.6	0.7
9	4.9	7.3	15.5	13.3	0.3	0.5

b)

	1995											
WSLEVEL	***Total weight* (g dwt m^{-1})**		***Plant number* (m^{-2})**		***Weight per plant* (g dwt $plant^{-1}$)**		***Cob number* (m^{-1})**		***Kernel weight* (g dwt $plant^{-1}$)**		***Kernel weight per cob* (g dwt cob^{-1})**	
Treatment no.	**UF**	**FF**	**UF**	**FF**	**UF**	**FF**	**UF**	**FF**	**UF**	**FF**	**UF**	**FF**
2	1.2	2.4	3.8	7.5	0.3	0.3	2.3	2.8	253.2	475.3	36.4	60.0
3	2.2	3.4	10.3	10.0	0.2	0.4	3.0	3.4	321.7	839.7	36.6	73.2
5	1.3	2.7	7.0	8.3	0.2	0.3	2.2	2.8	266.4	679.1	52.6	82.4
6	2.7	4.4	10.3	12.0	0.3	0.4	2.8	3.8	316.9	1080.6	42.6	70.9
8	2.6	5.0	8.0	8.5	0.3	0.6	2.5	3.1	554.1	712.8	70.1	73.5
9	3.3	6.1	12.5	14.0	0.3	0.5	3.5	3.9	564.2	1195.2	45.4	79.7

Table 7.20. ANOVA for effect of fertilizer and weed-shade treatments on corn plant biomass in 1994.

Factor	DF	SS	Mean Square	F value	Pr > F
Model	32	98.21	3.07	2.32	**0.0433**
Blk[1]	3	19.86	6.62	4.99	**0.0134**
Fert	1	34.07	34.07	40.93	**0.0077**
Error a	3	2.50	0.83		
Wslevel	5	19.65	3.93	2.97	**0.0467**
Fert*wslevel	5	6.91	1.38	1.04	0.4289
Blk*wslevel	15	15.23	1.02	0.77	0.6939
Error b	15	19.88	1.33		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)fullweed vs interweed	1	3.73	3.73	2.81	0.1143
2)fullweed vs noweed	1	9.27	9.27	6.99	0.0184
3)inter vs noweed	1	1.24	1.24	0.94	0.3487
4)corn density	1	9.97	9.97	7.53	**0.0151**
5)corn density, (noweed)	1	4.16	4.16	3.14	0.0967

[1] Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations).

Table 7.21. ANOVA for effect of fertilizer and weed-shade treatments on corn biomass in 1995.

Factor	DF	SS	Mean Square	F value	Pr > F
Model	32	126.10	3.94	3.4	**0.0091**
Blk[1]	3	9.70	3.23	2.78	**0.0796**
Fert	1	34.11	34.11	17.99	**0.0240**
Error a	3	5.69	1.90		
Wslevel	5	50.02	10.00	8.62	**0.0007**
Fert*wslevel	5	4.54	0.91	0.78	0.5792
Blk*wslevel	15	17.87	1.19	1.03	0.4830
Error b	14	16.25	1.16		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)fullweed vs interweed	1	1.91	1.91	1.64	0.2209
2)fullweed vs noweed	1	30.77	30.77	26.51	**0.0001**
3)inter vs noweed	1	15.28	15.28	13.16	**0.0027**
4)corn density	1	15.32	15.32	13.20	**0.0027**
5)corn density, (noweed)	1	3.15	3.15	2.71	0.1217

[1] Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations).

Table 7.22. ANOVA for effect of fertilizer and weed-shade treatments on corn biomass per plant in 1994.[1]

Factor	DF	SS	Mean Square	F value	Pr > F
Blk[2]	3	0.06	0.02	3.52	**0.0412**
Fert	1	0.17	0.17	63.22	**0.0041**
Error a	3	0.01	0.00		
Wslevel	5	0.18	0.04	5.91	**0.0033**
Fert*wslevel	5	0.01	0.00	0.31	0.8967
Blk*wslevel	15	0.04	0.00	0.48	0.9165
Error b	15	0.09	0.01		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)fullweed vs interweed	1	0.04	0.04	6.71	**0.0205**
2)fullweed vs noweed	1	0.06	0.06	9.40	**0.0078**
3)inter vs noweed	1	0.00	0.00	0.23	0.6415
4)corn density	1	0.10	0.10	17.06	**0.0009**
5)corn density, (noweed)	1	0.07	0.07	11.35	**0.0042**

[1] log-transformed

[2] Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations).

Table 7.23. ANOVA for effect of fertilizer and weed-shade treatments on corn biomass per plant in 1995.[1]

Factor	DF	SS	Mean Square	F value	Pr > F
Model	32	0.75	0.02	2.17	0.0622
Blk[2]	3	0.02	0.01	0.52	0.6778
Fert	1	0.20	0.20	15.06	**0.0303**
Error a	3	0.04	0.01		
Wslevel	5	0.19	0.04	3.53	**0.0283**
Fert*wslevel	5	0.10	0.02	1.78	0.1811
Blk*wslevel	15	0.20	0.01	1.21	0.3622
Error b	***				

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)fullweed vs interweed	1	0.01	0.01	0.49	0.4965
2)fullweed vs noweed	1	0.11	0.11	10.17	**0.0066**
3)inter vs noweed	1	0.06	0.06	5.49	0.0344
4)corn density	1	0.00	0.00	0.11	0.7404
5)corn density, (noweed)	1	0.04	0.04	3.36	0.0881

[1] log-transformed

[2] Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations).

Table 7.24. ANOVA for effect of fertilizer and weed-shade treatments on corn density in 1994.

Factor	DF	SS	Mean Square	F value	Pr > F
Model	32	402.92	12.59	6.49	**0.0002**
Blk[1]	3	27.33	9.11	4.70	**0.0166**
Fert	1	5.33	5.33	0.77	0.4437
Error a	3	20.67	6.89		
Wslevel	5	295.75	59.15	30.51	**0.0001**
Fert*wslevel	5	7.92	1.58	0.82	0.5563
Blk*wslevel	15	45.92	3.06	1.58	0.1932
Error b	15	29.08	1.94		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)fullweed vs interweed	1	0.78	0.78	0.40	0.5351
2)fullweed vs noweed	1	1.53	1.53	0.79	0.3882
3)inter vs noweed	1	0.13	0.13	0.06	0.8030
4)corn density	1	290.08	290.08	149.61	**0.0001**
5)corn density, (noweed)	1	105.06	105.06	54.19	**0.0001**

[1] Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations).

Table 7.25. ANOVA for effect of fertilizer and weed-shade treatments on corn density in 1995.

Factor	DF	SS	Mean Square	F value	Pr > F
Model	32	615.48	19.23	3.25	**0.0111**
Blk[1]	3	112.11	37.37	6.32	**0.0062**
Fert	1	29.81	29.81	3.77	0.1475
Error a	3	23.73	7.91		
Wslevel	5	276.85	55.37	9.37	**0.0004**
Fert*wslevel	5	21.62	4.32	0.73	0.6114
Blk*wslevel	15	133.02	8.87	1.50	0.2270
Error b	14	82.73	5.91		

Contrast	DF	Contrast SS	Mean Square	F value	Pr > F
1)fullweed vs interweed	1	10.18	10.18	1.72	0.2104
2)fullweed vs noweed	1	66.13	66.13	11.19	**0.0048**
3)inter vs noweed	1	20.81	20.81	3.52	0.0816
4)corn density	1	191.17	191.17	32.35	**0.0001**
5)corn density, (noweed)	1	100.00	100.00	16.92	**0.0011**

[1] *Blk: Block; Fert: fertilizer, wslevel (weed-shade treatment combinations).*

Table 7.26. Amount of corn grazed (%) in different weed treatment plots in 1995.

Weed treatments	Small-mammal %	Bird/Deer %	Combined %
Full-weed (WS 2+3)	15	20	31
Inter-weed (WS5+6)	11	22	33
No-weed (WS8+9)	22	13	46

Discussion

In this study, weed management, the use of a shelter-crop, and fertilisation all significantly increased tree growth in plantations established on post-agricultural land. The results for weed treatments supported the past emphasis on weed control in afforestation activity, which still influences most current efforts (Von Althen,1987, 1991; Ponder, 1991).

Historically, monocultures of high-value trees were managed identically to the agricultural crops they replaced. Weed control was achieved by repeated mechanical cultivation and the broadcasting of herbicides (Ponder, 1991). More recently, however, environmental concerns over nutrient runoff, soil erosion, and herbicide use in agriculture-intensive areas have prompted the development agronomic practices that mitigate this degradation. These practices tend to result in increased vegetation cover and to reduce the need for mechanical cultivation (Swanton and Weise, 1991). Such agricultural innovations have, in turn, prompted equivalent changes in the management of plantations. Alternative forms of weed control in plantations include the use of organic mulches, black plastic, and, especially, legume cover crops which may supplement soil nutrients through nitrogen fixation (Van Sambeek et al., 1986). Their benefits for tree growth have been largely equivocal and species-dependent (Lambert et al., 1991; Siipilehto and Lyly, 1995). The use of *Trifolium repens* as a cover crop between tree rows is currently recommended by local agencies in Essex county (e.g. Ontario Ministry of Natural Resources, Essex Regional Conservation Agency) and combined with the banding of herbicides within the tree row, is aimed at reducing potential competition between trees and cover crop. However, in our study, the growth of all three tree species was poorest for those grown in clover plots.

The poor tree performance in the clover treatments was, in large part, related to the spread of *Trifolium repens* into the tree row (Calkins and Swanson, 1996). This was despite the application of herbicides (simazine, glyphosate) within the tree row and repeated mowing between rows. Clover suppressed the growth of weed forbs and graminoids but when clover was classified as a weed, total weed and forb biomass were not significantly different from the full weed treatment plots. As with the full-weed treatments, tree growth decreased when clover plots were fertilised because faster growing weeds and clover were better able to exploit these nutrients (Remphrey and Davidson, 1996).

The mowing of weeds in the tree inter-row is often suggested to be ineffective and may stimulate the root growth of weeds (von Althen, 1984; Ponder, 1991). However, our study showed that tree growth in mown-weed treatments was greater than in both full weed and clover treatments, although less than in both inter-weed and no-weed treatments. As with no-weed and inter-weed treatments, ash diameter in mown-weed treatments increased when fertilised, suggesting that mowing had reduced weed growth. These results suggest that mowing should be further investigated as a form of weed control. The greatest tree growth occurred in the no-weed and the inter-weed treatments. Although, weed control was achieved within the tree row by repeated hoeing, the banding of effective residual herbicides within the tree row might have generated similar results.

In the early stages of plantation establishment, prior to tree canopy closure, there was no effect of trees on weeds, even though canopy cover approached 60% in weed-free, fertilised treatments (S. McLachlan, pers. comm.). However, weed biomass in the inter-row of fertilised plots was being reduced by corn. Once the tree canopy exceeds 90% cover, shade levels should be high enough that weed control will become unnecessary (Buckley and Knight, 1989). At that time, shade-tolerant understorey and woody species might be introduced.

The use of fertilisers remains controversial in afforestation (Hunter and Smith, 1996). In our study, they provided little benefit to trees and reduced tree growth if adequate weed control was not achieved, as they preferentially benefited faster-growing weedy species (Remphrey and Davidson, 1996). In fact, nutrient exhaustion is frequently recommended for post-agricultural fields either through continuous cropping (Bruns, 1988), or the direct removal of soil (Marrs and Gough, 1989). These results were consistent with the expectation that past intensive agricultural use in our site would have a residual effect on soil nutrient levels. However, a lack of consistent, strong fertiliser effects may also have been due to low degrees of freedom associated with the higher-model error terms (Sokal and Rohlf, 1981).

We investigated the effects of a nurse crop on tree growth because the study site is located adjacent to Lake Erie and is subjected to high, year-round winds which frequently reduce tree growth in exposed sites (Sun and Dickinson, 1995). The minimal snow cover, high ambient temperatures, and lack of rainfall typical of this region were also expected to adversely affect tree growth. Both maple and ash had significantly greater growth under the corn, but only when plots were fertilised and adequate weed control achieved. In contrast, oak growth was adversely affected by the nurse crop. This might be associated with the decreased light levels under the corn canopy. Oak is a savannah species that favours open, dry sites and, thus, might be less shade-tolerant than either maple or ash. We do not know whether critical shelter was provided during the winter or summer. However, William and Gordon (1994) found that trees grow more rapidly when intercropped with corn than either soybean and winterwheat. They attributed this to reduced wind speed in the corn plots and early-season competition between winter wheat and trees

It should be noted that external factors (e.g. deer grazing, tree species, recreation) can have major effects on tree growth in plantations. In our study, the relatively poor growth and high mortality of oak was associated with selective deer grazing. Deer are a problem in many plantations and deer-grazing levels were great enough that, for this species, the use of tree shelters might be necessary in order to achieve adequate growth.

Management implications

Forest plantations can play an important conservation role by functioning as primary natural habitat, by increasing the protection of existing habitat (Hobbs, 1993), and by increasing landscape connectivity (Llewellyn et al., 1996). This is especially true for regions with little natural forest cover such as Essex County (Frielinghaus, 1996). In Essex, the costs of trees, their planting and subsequent maintenance have been largely subsidised and, as a result, millions of trees have been planted (ERCA, 1995). Many of the plantations use fast-growing, locally grown deciduous native trees of low economic worth and are of multiple species (NHRP, 1994). Consequently, intensive weed control and fertilisation, which may be justified in monocultures of high-value trees, are likely to be impractical in these systems. However, the benefits of multi-species planting and intercropping with shelter crops are beginning to become apparent. For example, the interplanting of high value trees with leguminous trees increased tree growth (Clark and Williams, 1979). Buffer systems that incorporate both shrubs and trees have been shown to reduce nutrient runoff (Lowrance, 1992; Schultz et al., 1993, 1995) while plantations including understorey shrubs are used more frequently by wildlife (Zebehazy and Rossell, 1996). However, one draw back is that, when shrubs are planted, subsequent successional change and tree growth may be slowed and they may be difficult to control or remove (Niehring, 1987). Furthermore, although shrubs tend to grow more rapidly than trees, it often is not rapid enough to provide shelter during plantation establishment when weed control is crucial. For example, *Cornus florida* planted as an edge wind break in our study site grew more slowly than either maple or ash. In contrast, a rapidly growing annual such as corn, which is tall enough to provide shelter, may be more effective as a shelter crop.

Agroforestry, or the inter-planting of crops and trees in designed management systems, is extensively used in the tropics (Schultz et al., 1995; It is relatively rare in temperate regions (Von Maydell, 1995), but is increasing in popularity, especially in high-value tree plantations. The inter-planting of crops with trees can increase vertical complexity compared to the relative simple stand structure of even-aged, single-species plantations. The resultant increases in habitat heterogeneity can facilitate wildlife use especially if crops can be used as food source and shelter, as was the case in our study (Gallina et al., 1996). Furthermore, the interplanting of trees and row crops may facilitate the movement by small mammals, which tends to deterred by dense vegetation at one extreme and by predation in open habitats at the other extreme (Merriam and Lanoue. 1990). The inter-weed treatment used in this study may act together with corn to increase habitat heterogeneity and movement without compromising tree and crop growth. In contrast, the clover cover crop reduced species richness, vertical complexity, and habitat heterogeneity, and likely impeded small animal movement.

Agroforestry holds much promise for intensely farmed regions such as Essex county, where compromises between conservation and production are needed. Low-growing vegetables such as tomatoes and peppers are grown extensively in this region and might be planted successfully with trees. Although they would provide little shelter, they are frequently hand harvested and would generate greater short-term income. Additionally, instead of trees, other woody species such as grape might be planted.

Essex County is one of the most rapidly developing wine-growing regions in Canada. This growth is great enough that local grape production is continually in short-supply. Although grape-concentrate is imported, only wine made entirely of domestically-grown grapes can be given the highest Vintner's Quality Association (VQA) certification. It takes 5-10 years for a vineyard to become fully productive which deters land-use conversions, especially if the land is currently under production. The use of a vine/vegetable intercrop system would provide short-term income until vineyards were fully operational. Hypothetically, these intercropping systems could be maintained even when the vineyards were mature.

The use of crops in afforestation also allows a dramatic change in stand structure from that of the densely planted plantations. Conventionally spaced plantations are unnatural looking, of low stand complexity and tend to impede wildlife and recreational use (Williams and Gordon, 1994). The use of crops would allow areas that managers desire to keep tree-free in the future, from undergoing succession. Open areas could eventually be planted with shrubs or restored as early successional natural habitats including tall grass prairies and savannahs. Despite being relatively fast-growing, light tolerant tree species that are commonly planted in parks and urban spaces, both maple and ash responded favourably to the shelter system. This system would likely be of even greater use when planting slower growing, shade-tolerant species. The use of fast growing exotics as nurse-crops has been recommended for when creating late-successional tropical forests (Brown and Lugo, 1994; Otsamo et al., 1996), but has yet to be fully explored in temperate regions.

Overall, the inter-weed treatment seemed to represent a good compromise when tradeoffs between tree/crop productivity and wildlife benefits are desired. This corn shelter system should provide additional benefits for trees that were not as light-tolerant as these species, that have higher growth rates in partial shade, and that are consequently excluded from most afforestation efforts. In contrast our results do not support the use of the agency-recommended cover crop.

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CHAPTER 8

MANAGEMENT IMPLICATIONS OF RESEARCH FINDINGS

Most ecological research is not "management-friendly" either in content or form (W. Stephenson, pers. comm.). As management concerns played a fundamental role in defining the scope of this research, I decided to make this connection between theoretical and management interests explicit. Included below are the management implications of this study's research findings grouped according to the thesis chapters

GIS AND RESTORATION (CHAPTER 2)

Observation	***Management response***
- landscape highly fragmented (<10% forest cover) -area immediately surrounding PPNP less than 3% cover - inter-patch distances greatest around PPNP - other main areas (Cedar Creek and Pelée Island) show much higher forest cover and lower inter-patch distances	- in area surrounding PPNP: focus on conservation (further protecting what little remains) through purchases and land-trusts - restoration not recommend in this area (no functional value) as fragmentation so great - in Cedar Creek and Pelee Island: focus on restoration (to increase connectivity)
- satellite imagery classified forest with high confidence (in Pelee Island and Cedar Creek) -less successful in area surrounding PPNP (due to low forest cover)	- use satellite imagery to identify "clusters" of forest patches in area around PPNP that show additional conservation value - identify clusters in Cedar Creek and Pelee Island where connectivity can be increased through restoration
- WIAs (representing greatest restoration efforts in region) located in Cedar Creek and around PPNP but Pelee Island underrepresented -few located near existing forest, - spread throughout main areas	-should subsidize or encourage restoration in Cedar Creek and Pelee Island - emphasize clustered rather than dilute planting - as density/unit area increases so does connectivity
-impact of differences in forest fragmentation on use of one of three main areas as core habitat in "bioreserve" management -absence of "buffer zone" around PPNP (only 'zone of interference")	-question whether PPNP should be used as core area, although largest and best - high visibility area but: - highly and widely disturbed - very isolated (surrounded on three sides by water) - single owner (Parks Canada) - little marginal land; land prices very high *versus* - Cedar Creek (or Pelee Island): much less disturbed - multiple partner, - functional basis to management unit (watershed), - much higher forest cover and connectivity between patches; - more marginal land; land prices much lower
- LANDSAT TM data not identify disturbed forest accurately but can supplement satellite imagery with information from recent (1989) aerial photos taken by Essex Regional Conservation Authority and recent NTS (1:50,000) maps (updated in 1990)	- create data base identifying disturbed forest that benefits from restoration - co-ordinate restoration of disturbed forest at landscape level

IN-PARK RESTORATION OF FORMER COTTAGE AND ROAD SITES (CHAPTER 3)

Observation	**Management response**
- use of similarity between restored sites and references sites as primary indicator of recovery - similarity greatest for 30+ year-old sites - *similarity increases over time*	- passive restoration (removal of roads and cottages) largely successful - proximity to seed source affect recovery patterns - facilitate by attracting seed dispersers and planting "seeding nuclei" (e.g. shrubs, perches) - application of top soil from other areas (especially if under development)
- seedbanks of newly restored sites have few native species	- dependent upon external seed source for recovery
- distance to continuous forest, and shape index affect recovery - roads faster recovery than cottages (greater proximity to seed source, - relative absence of inhibiting former lawn species (*Poa* spp.)	- remove exotic grasses if present - if disturb sites (for park infrastructure): avoid planting *Poa* spp. in lawn : avoid circular shaped disturbance
- actively restored sites (planting of trees, removal of non-native vegetation, return of topography) still dominated by exotic ruderals after 5 years - show reduced cover of Eurasian grasses (*Poa* spp. *Bromus* spp.)	- monitor to see if extra expense is justified

VULNERABLITY OF NATIVE UNDERTOREY (CHAPTER 4)

Observation	**Management response**
- no difference in native diversity between reference and restored sites but differences in native species composition	- caution about using diversity measures as indicator of recovery - (or more generally, for any kind of vegetation management)
- use of guilds (groups of species with similar "functional" traits suggest that vulnerable species are: 1) spring ephemerals 2) restricted seed dispersers -if traits combined, especially vulnerable	- use of phenology and dispersal-based characteristics to predict response to long-term disturbance and subsequent speed of recovery - unlike species-level responses, these guilds allow prediction of response of species or sites that have not been studied
- species of intermediate vulnerability (VR3) show recovery over time	- use these as indicators of recovery (not necessary to monitor entire community)
- species of high vulnerability (VR1, VR2) show no recovery	- candidates for reintroduction (combine with habitat-restoration as ephemerals (like weeds) need high-light environments to grow - use as indicators of disturbance
- wet/mesic sites have more rapid recovery than dry sites	- avoid disturbing dry sites in future development
- some mesic sites show "complete recovery" after 35 years	- likely that most sites will recover without active management but will take many decades (if not centuries) to recover

SUCCESSION-BASED MANAGEMENT OF NON-NATIVES (CHAPTER 5)

Observation	**Management response**
- non-natives decline as regeneration proceeds	- accelerate regeneration - increase canopy cover - facilitate seed dispersal (increase vertical structure, plant fruit-bearing shrubs and trees
-decline in early successional "savannah" species	-remove dominant "Eurasian" grasses (e.g. *Bromus* spp., *Poa* spp.) - repeated cutting, sod removal, herbicides, prescribed burns, cultivation,
-absence of "savannah" species in seedbank	- seed collection programs, - reintroduction (seeds and seedlings)
- not all classes of exotics respond similarly to regeneration -class 1 (hybridizing: white mulberry) no change -class 2 (competitors: garden escapes) prefer disturbed habitat -class 3 (impact unknown, ruderals) sharpest decline -class 4 (inhibitors: Eurasian grasses, lawn species): eventual decline - increased *Bromus inermis* cover- natives decline	- class 1: removal (but combined with planting of native cover species (e.g. sweet cicely, appendaged waterleaf, shorts aster) or facilitate other invasion - class 2: recover over time, as largely localized could remove successfully - but recommend occasional monitoring only - exception: garlic mustard which pervasive through park (no control program in place). See (Chapter 6) - class 3: no control necessary - class 4: accelerate eventual decline by removal (Chapter 3)
- slower decline over time in dry habitat	- accelerate successional change by planting if forest desired, disturb if savannah desired - avoid disturbing dry habitat
- removal of exotics disturbs native cover, encourage further invasion	- ecosystem management: combined methods (reintroduction + removal + canopy)

EFFECT OF GARLIC MUSTARD ON NATIVE UNDERSTOREY (CHAPTER 6)

Observation	**Management response**
- decline in native diversity as cover of garlic mustard (GM) increase - only as 100% cover approached	- abandon idea of eliminating GM, if active management desired, - lower GM cover (to 60%) by least intrusive methods (herbicides, mulches) - minimize disturbance
- effect of competition between rosette and adult lifestage of GM greater than effect on native diversity: at high densities life stages cannot coexist - wave effect between years at high densities - long-term "bust and boom" cycle - species respond differently to each lifestage	- GM will not likely eliminate native species - incorporate biennial lifehistory and transient seedbank into control measures (e.g. short-term use of black-plastic mulches, use of life-stage-specific herbicides e.g. sulfonyl ureas)
-GM a biennial. - majority of native understorey perennial seeds only viable for 2-3 years	- periodic intervention will likely keep GM in check until native understorey recovers
- long-term invaded sites seem to show native understorey similar to newly invaded sites -no long-term effects of GM invasion in these sites	- likely that native understorey will stabilize and GM naturalized; - ultimately no active management necessary
-our study is a chronosequence	-need long term studies with permanent plots

MULTIPLE-USE AFFORESTATION (CHAPTER 7)

Observation	**Management response**
- fertilization no overall effect - increase tree growth if weeds adequately controlled - decrease tree growth if weeds not adequately controlled	-not fertilize except: - if using shelter crop - if weeds are adequately controlled
- shelter crop (corn) increased growth of silver maple and green ash but only if fertilized	- require fertilization if use shelter crops - further study of use of shelter crops especially for slow-growing, shade-tolerant tree species - explore use of agroforestry in other systems (e.g. vineyards)
- clover decreased tree growth (weeds in intra-row not adequately controlled - trees show less growth than full-weed treatment	-reconsider use of highly-aggressive clover species as cover crop -replace with less aggressive species (e.g. vetch), or those with commercial value (e.g. winter wheat)
- inter-weed (weed control only in the tree row) show tree growth second only to weed-free treatment	-if can achieve weed control within tree-row, no further control necessary
- mown-weed treatment better tree growth than either full-weed or clover	- reinvestigate mowing as weed management tool (especially if can achieve further control within tree row)
- silver maple and green ash respond similarly to treatments, bur oak showed much less growth (associated with species-specific grazing by white-tailed deer in winter)	-use of tree shelters on grazing-prone tree species (e.g. bur oak) only

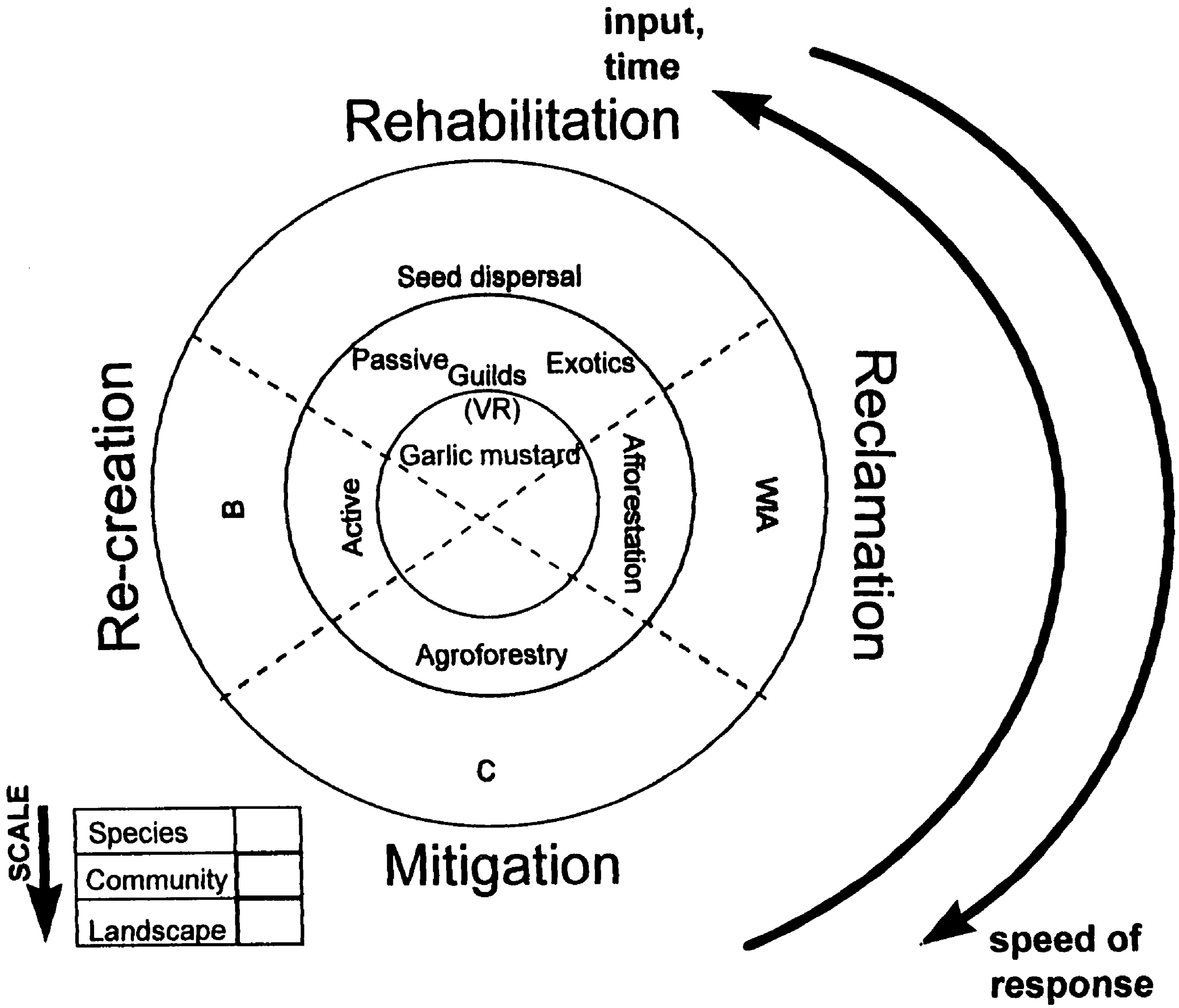
CHAPTER 9

SYNTHESIS

The present study represents a multiple-scale, process-based approach to restoration which incorporates mitigation, reclamation, rehabilitation, and re-creation. Each of these four restoration types, the level of organization it occupies, and the way it interacts with the others, conforms to a larger integrative, multiple-approach strategy to deciduous forest restoration required for settled landscapes (Figure 9.1).

In the past, the management of what remains of the forest in the Carolinian region of Ontario has been mainly limited to protection (i.e. conservation). While this has resulted in a fragile network of protected areas throughout the region (Allen et al., 1990), attempts at habitat protection have been compromised by a number of factors: most of the forest remnants are privately owned (Hilts, 1985), many have been degraded by mismanagement and surrounding landuse (Matlack, 1993b; Robinson et al., 1994), the surrounding matrix is of high agricultural and economic value, and there is a longstanding public preoccupation with nature as "wilderness" and an associated devaluation of natural habitat in settled landscapes (Caldicott, 1991). Restoration, as a new subdiscipline of ecology, seems likely to play an important role in, and in fact draws its existence from, the management of degraded natural habitat (Turner, 1994; Jordan et al., 1994). In the past, this activity has focused on natural habitat at the site or species level of organization (Naveh, 1994) and has effectively ignored the landscape matrix. In settled landscapes such as Essex county, Ontario, however, restoration efforts could be multi-scaled, thereby incorporating species, ecosystem, and landscape levels of organization. Past restoration efforts in this region have tended to be end-point oriented such as the planting of late-

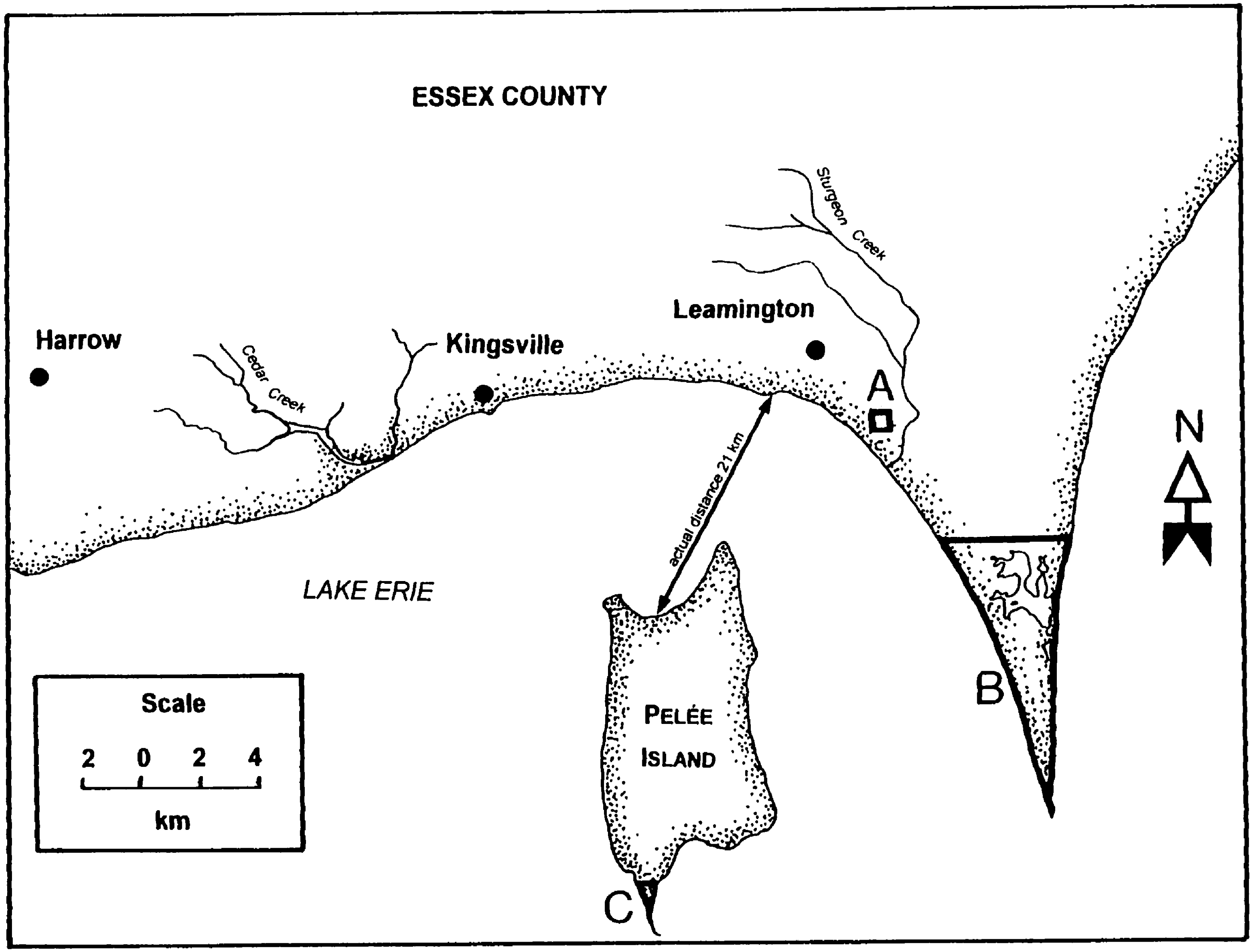
Figure 9.1. Relationship between different components this study, levels of organization (i.e. species, community, landscape), and types of restoration (i.e. mitigation, reclamation, rehabilitation, and restoration). Also indicated are expected input and speed of response.


input,
time
Rehabilitation
Seed dispersal
Passive
Guilds
Exotics
(VR)
Garlic mustard
Re-creation
B
Active
Afforestation
WIA
Reclamation
Agroforestry
C
Mitigation
SCALE
Species
Community
Landscape
speed of
response

successional trees in post-agricultural fields. However, process-oriented studies that focus on the mechanisms that underlie vegetation change may be more cost-effective, and encounter greater success (Lockwood, 1997).

The first step in conducting forest restoration in the Carolinian region was to fully describe the landscape (Figure 9.2). In this case, these data did not exist for Essex county and were generated from satellite imagery and preliminary GIS-derived spatial analyses. These data were used to compare three main areas in the county, each of which had a "high-integrity" natural core area, potentially suitable as a nucleus of a landscape-based "bioreserve" management model (Chapter 2, Figure 9.1) (Stephenson, 1994; Francis, 1994). Preliminary analysis suggested that the natural habitat in Pelée-north (the area immediately north of Point Pelée National Park (PPNP)) is so highly fragmented that conservation of the forest remnants, rather than habitat restoration should be a first priority there. In fact, it was questionable, whether the use of a "buffer zone", in which conservation and production priorities are balanced, would have any ecological meaning in Pelée-north since the forest cover outside PPNP is so low. In contrast, Cedar Creek, and Pelée Island, with their substantially greater surrounding forest cover, shorter inter-patch distances, and the greater availability of marginal land, might function more adequately as core areas since restoration in this buffer may facilitated by the lower land value. Another approach would be to combine all three cores into a larger regional "metacore" management model. However, these analyses were strictly preliminary and need to be taken further. The classified images need to be expanded by further ground truthing and the use of aerial photos and historical records. Furthermore, narrow fence-rows, which likely represent the greatest amount of natural habitat remaining in Pelée-

Figure 9.2. Map of southwestern Ontario showing portion of Essex county, towns, and study areas in Sturgeon Creek (A), Point Pelée National Park (B), and, on Pelée Island, FishPoint Nature Preserve (C).


ESSEX COUNTY
Harrow
Cedar Creek
Kingsville
Leamington
Sturgeon Creek
A
c.
B
N
LAKE ERIE
actual distance 21 km
PELÉE
ISLAND
C
Scale
2 0 2 4
km

north, still need to be identified and classified. Assumptions about fence row-mediated landscape connectivity could then be tested, along with the effects of patch size, shape, and adjacent land use on composition of understorey plant communities, and both inter-patch and intra-matrix movement. Past restoration activities could be located on these images and future restoration and conservation strategies co-ordinated at the landscape level. Finally, in the highly fragmented areas (e.g. Pelée-north) changes in agricultural practices that might increase landscape connectivity (e.g. intercropping, agroforestry, cover cropping) could be further explored and modeled using GIS.

Once potential sites for restoration were identified, different approaches to restoration appropriate for settled landscapes, including mitigation, reclamation, rehabilitation, and re-creation (Hobbs, 1993; Cairns, 1993), could be assessed, and have been used in this multiple-scale, multiple-approach study.

Mitigation suggests that the integrity of the ecosystems under management can be recovered, without any substantial change in land-use (Hobbs and Norton, 1996). In this study, mitigation was characterized by the agroforestry study (Chapter 7) (Figure 9.1). Agroforestry, i.e. the interplanting of crops and trees, is mitigative as it reconciles both production and conservation concerns without requiring a change in land-use. In our study this was achieved by intercropping corn with three deciduous tree species (Chapter 7). Corn growth was dependent upon on fertilization and adequate weed control (i.e. inter-weed and no-weed treatments). Silver maple (*Acer saccharinum*) and green ash (*Fraxinus pennsylvanica*), growing under the corn crop, had the greatest growth if adequate weed control was achieved. To the best of my knowledge, corn shelter crops have never been used to accelerate tree growth in temperate regions. This approach could be further applied to shade-tolerant, late-successional tree species, which have grown poorly in nearby plantations (D. Bazely, pers. comm.). Furthermore, this approach could be used in the highly successful wine-growing regions in the Carolinian by combining grape and vegetable production. Domestically grown grapes required for the highest quality wine (Vinters Quality Association (VQA)) are in short supply, and intercropped vegetable production might help offset the decade-long period required for a vineyard to become established. Furthermore, agroforestry allows a multiple-use approach to agriculture and conservation that may hold greater promise for increasing landscape connectivity in these highly fragmented ecosystems than corridors of natural habitat, which have been criticized extensively in the literature (Simberloff, and Cox 1987: Simberloff et al., 1992). The movement of small mammals, birds, and understorey plants within these "combined-use" areas also requires further study. Once understood on a local scale, the impact of these and other changes in agronomy could be modeled at the landscape level using GIS and Landsat TM data. Furthermore, this approach would allow predictions to be made about the effects of various restoration schemes on, for example, landscape connectivity. Finally, one could compare the effect of dilute, uniform, corridor/wind break planting against that of cluster planting in marginal habitats, on connectivity.

The second restoration type is *reclamation*, in which landuse is changed to a more natural state which has no resemblance to the pre-existing natural habitat (Cairns, 1993). An example of reclamation is the afforestation of an arable field, in which we examined the effects of fertilization and weed control on the growth of three species of native trees (Figure 9.1). Afforestation in this region, normally involves the one-time planting of rows of trees, between which clover is interseeded in order to achieve weed control (Van Sambeek and Rietveld, 1982; Von Althen, 1991). We found that clover decreased tree growth more than the full-weed treatment (no-weed), while the two other weed control treatments (mown-weed and inter-row weeding) resulted in significantly greater tree growth. Fertilizers only increased tree growth if combined with adequate weed control. Further research might focus on the development of alternate weed-control methods as well as monitoring the use of plantations by small mammals and birds. Colonization by native plant species should also be monitored (M. Kellman, pers. comm.). Process-based afforestation should also incorporate the planting of understorey once canopy closure reaches 90% (Buckley, 1989). The combined planting of trees with fruit-bearing shrubs, especially in non-uniform, "cluster spacing" might increase use by wildlife and seed dispersers (Robinson and Handel, 1993) and should be studied further.

Woodland Improvement Act (WIA)-associated tree planting over the last three decades accounted for the majority of the restoration activity in this region. To the best of my knowledge, the plantations in Essex have never been studied either at the site or landscape level of organization. A preliminary examination (Figure 9.1) suggested that few WIAs were situated close to natural forest patches and only one was located at Pelée Island, although restoration in the latter area holds the greatest promise for increasing connectivity. Furthermore, there seem to be no studies which examine the degree to which these "plantation" patches are used by small mammals and birds. Chronosequence-based studies examining the impact of different practices on the structure and growth of deciduous plantations and the degree to which, if any, that natural regeneration occurs, also need to be undertaken.

The third restoration type is *rehabilitation*, in which existing but degraded natural habitat is regenerated (Cairns, 1993). In our study, this was exemplified by "passive restoration" in PPNP (Chapter 3, Figure 9.1) and the garlic mustard (*Alliaria petiolata*) study in PPNP (Chapter 6, Figure 9.1). With respect to "passive restoration", since 1960, cottages and roads at PPNP have been removed and the native plant community allowed to regenerate. Over time, all sites increased in similarity to largely undisturbed, reference sites at both PPNP and the nearby FishPoint Nature Preserve, with the oldest sites having the greatest similarity. Road sites recovered more rapidly than cottage sites, in part due to the greater proximity of seed sources and the lower abundance of lawn species that inhibit succession. Using this research protocol, the success of forest regeneration could be tested in eastern Ontario where large-scale forest recovery has occurred over the last 100 years (Pearce, 1992). Further research directly measuring seed dispersal which underlies differences in regeneration rates is also necessary. Landscape-level characteristics (i.e. distance to continuous forest, proportion of the site adjacent to continuous forest.) (Figure 9.1) also affected rates of regeneration and species composition. We used plant guilds (as an intermediate level between individual species and entire communities) as predictors of recovery (Chapter 4, Figure 9.1). The composition of these guilds was based on flowering phenology and seed dispersal. Spring ephemerals and herbs with restricted seed dispersal (e.g. gravity, ant dispersal) are slowest to re-colonize restored sites. This guild approach could be used to predict recovery patterns of little known species and ecosystems. Similarly, the suggestion that highly vulnerable (VR1) species be actively reintroduced to restored habitats should be examined further. Likewise, the relative success of different types of native transplanting (e.g. seed, seedling, sod, topsoil) should also be examined in restored habitats.

The effect of rehabilitation on the non-native component of forest understorey plant communities was also examined in PPNP (Chapter 5, Figure 9.1). There was an overall decrease in species richness of the non-natives as time-since-restoration (TSR) increased. This decline was more rapid in wet/mesic sites than in dry sites. However, not all non-natives responded equally to succession-based regeneration. Non-native species were classified according to the park-defined threat that they represented. Class 3 species that had unknown effects and which were often ruderals, declined most rapidly as TSR increased. Class 4 species, which were largely lawn species that constrain succession, inhibited overall recovery but eventually declined as TSR increased. Class 2 species, which were perceived to be displacing native species and which were largely garden escapes, did not decline over time but tended to favour disturbed sites. In contrast, Class 1 species, which hybridize with natives failed to decline over time and were not associated with disturbed sites. Chapter 5 is one of the few studies that have attempted to distinguish between classes of exotics and relates them to differences in life history and habitats of origin. Unlike most other restoration research, this study was explicitly linked to succession theory and examined the effectiveness of process-based management. Our recommendation, that exotics, once established, might be more effectively managed at the ecosystem-level rather than that of the individual species should be tested further in deciduous forests as well as other ecosystems (see Hobbs and Humphries, 1995). Furthermore, our suggestion, that non-natives are frequently symptomatic of underlying disturbances rather than a cause of habitat degradation, themselves and thus may be appropriate as indicators of habitat integrity, should be further explored.

The second rehabilitation study was the garlic mustard study that was conducted within PPNP (Chapter 6, Figure 9.1). This invasive plant species is assumed to displace native understorey species in deciduous forests throughout northeastern North America (White et al., 1993), and is currently chemically and mechanically controlled (Nuzzo, 1994; Nuzzo, 1991). My study tested whether these claims were substantiated and found that declines in the diversity of native species occurred only when garlic mustard cover approached 100%. Interestingly, in its adult, flowering stage, this biennial seemed to have the greatest effect on its own rosette lifestage. At high densities, rosettes were entirely displaced by the mature lifestage resulting in a "wave effect" in which mature plants alternate with rosettes from year to year. Understorey species seemed to show differential responses to high densities of either lifestage and thus need to be further explored with controlled experimentation. Sites in which garlic mustard had been present for 20 years had diversity levels comparable to newly invaded sites. In rosette years, garlic mustard might be selectively controlled by herbicide application late in the season when most perennial native species have already senesced. Alternatively, the potential of life-stage specific herbicides should be explored (e.g. sulfonyl ureas are specific to the 3-4 leaf stage of development in forbs). That garlic mustard is an obligate biennial and that its seeds are only viable for two-to-three years, might allow managers to "exhaust" the garlic mustard seedbank by preventing seed production for three year periods. This might be achieved by using "black plastic mulches" and herbicides. Personal observation suggests that areas of PPNP within which exotics are controlled, experience a decline in native species and further susceptibility to invasion. The effect of these, and other, control measures on the understorey community has yet to be studied (Anderson et al., 1996). In general, these results seem to support observations by park managers such as Gary Mouland that garlic mustard displays "boom and bust" population cycles and has not irreversibly displaced native plant species. However, additional long-term studies using permanent plots are needed.

The fourth and final type of restoration is *re-creation*, in which previously existing habitats are reconstructed using historical site descriptions. At PPNP, this restoration approach was incorporated by the study of actively restored sites in which topography and hydrology were altered and shrubs planted Chapter 3, Figure 9.1). After five years, actively restored sites showed no difference in native diversity compared to those of similar age that had been passively restored. However, lawn cover did decline, although it remains to be determined whether these grasses, which dominate the seedbank, will recover and inhibit subsequent site-regeneration.

At both management and theoretical levels, this study on the restoration of deciduous forest in settled landscapes of southwestern Ontario represents a significant step forward in the following ways:

(1) It is explicitly applied and reflects the concerns and, in the garlic mustard chapter, the insights of on-site park managers. As such, it shows how the quantitative and methodological skills of researchers can be combined with management expertise to develop theoretically sound solutions to real-world problems (for example the use of guilds of plant species as indicators

of habitat recovery and to identify vulnerable groups of species that might require reintroduction).

(2) It suggests ways in which restoration can change from being end-oriented to being process-based by using succession theory (e.g. succession-based management of exotics) and landscape ecology (e.g. possible bioreserves in Essex county).

(3) It contributed to the development of a landscape-level database for Essex. In the future, this database will be supplemented using aerial photos and historical records and could be used to help prioritize restoration and conservation efforts.

(4) It tests and questions the efficacy of some of assumptions of field managers such as the effect of exotics on native diversity and the effectiveness of clover as weed control in afforestation.

(5) It identifies ways in which conservation and production concerns can be combined into multiple-use solutions (e.g. interplanting of corn and trees and of vineyards and vegetables).

(6) It embodies the multiple-partner research approach that at once takes advantage of individual research strengths but generates solutions that transcend individual specialties.

(7) It combines different restoration types and integrates across scales and shows how this multiple-scale approach to restoration is necessary when confronting the complex conservation issues that face settled landscapes such as the Carolinian.

Restoration ecology represents an important step in challenging the philosophical and political inertia that permeates conservation ecology. There is no question that regions like southern Ontario have been mismanaged for centuries and the resultant degradation to the environment is well documented. However, studies such as this identify ways that we can protect and even restore the surrounding natural environment, while ensuring we continue to produce ample, inexpensive and high-quality foods. What is still missing, however, is the moral and political will to do so.

CHAPTER 10

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Appendix 1. Latin and common names, multivariate species codes, and origins of all herbaceous species found in studies at Point Pelée National Park and FishPoint Nature Preserve, 1994-1996. Also indicated is code used in multivariate analysis (DCA, CCA).

Latin	Common	Origin[1]	Code
Acalypha rhomboidea	Three-sided mercury	N	Aca rho
Acer negundo	Manitoba maple	N	Ace neg
Acer nigrum	Black maple	N	Ace nig
Acer saccharum	Sugar maple	N	Ace sac
Achillea millefolium	Yarrow	N	Ach mil
Agastache nepetoides	Tall yellow hyssop	N	Aga nep
Agrimonia parviflora	Agrimony	N	Agr par
Allium tricoccum	Leek	N	All tri
Ambrosia artemisiifolia	Common ragweed	N	Amb art
Ambrosia trifida	Giant ragweed	N	Amb tri
Amphicarpa bracteata	Hog-peanut	N	Pte tri
Anemone canadensis	Canada anenome	N	Ane can
Anemone riparia	Tmimbleweed	N	Ane rip
Apios americana	Ground nut	N	Api ame
Aquilegia canadensis	Columbine	N	Aqu can
Arabis hirsuta	Hairy rock cress	N	Ara hir
Arabis laevigata	Smooth cress	N	Ara lae
Aralia nudicaulis	Wild sarsaparilla	N	Ara nud
Arisaema triphyllum	Jack-in-the-pulpit	N	Ari tri
Asclepias incarnata	Swamp milkweed	N	Asc inc
Asclepias syriaca	Common milkweed	N	Asc syr
Aster ericoides	Many flowered aster	N	Ast eri
Aster novae-angliae	New England aster	N	Ast nov
Aster pilosus	Heath aster	N	Ast pil
Aster shortii	Short's aster	N	Ast sho
Aster vimineus	Small white aster	N	Ast vim
Boehmeria cylindrica	False nettle	N	Boe cyl
Campanula americana	Tall bell flower	N	Cam ame
Campsis radicans	Trumpet creeper	N	Cam rad
Cardamine bulbosa	Spring cress	N	Car bul
Cardamine douglassii	Purple cress	N	Car dou
Carex crawei	Sedge (crawei)	N	Car cra
Carex oligocarpa	Sedge (oligigocarpa)	N	Car oli
Carya ovata	Shagbark hickory	N	Car ova
Celtis occidentalis	Hackberry	N	Cel occ
Cerastium arvense	Field chickweed	N	Cer arv
Chenopodium foggii	Goosefoot	N	Che fog
Circaea quadrisulcata	Enchanter's nightshade	N	Cir qua
Cornus drummondii	Rough dogwood	N	Cor dru
Cornus obliqua	Silky dogwood	N	Cor obl
Cornus rugosa	Round dogwood	N	Cor rug
Corydalis flavula	Yellow cordalis	N	Cor fla
Cyperus esculentes	Yellow nutsedge	N	Cyp esc

Desmodium spp.	Tick trefoil	N	Des spp
Dicentra cucullaria	Dutchman's britches	N	Dic cuc
Echinosystis lobata	Wild cucumber	N	Ech lob
Elymus canadensis	Canada wild rye	N	Ely can
Elymus hystrix	Bottle-brush grass	N	Ely hys
Elymus villosus	Wild rye	N	Ely vil
Elymus virginicus	Virginia wild rye	N	Ely vir
Epilobium grandulosum	Northern willow herb	N	Epi gla
Equisetum arvense	Common horsetail	N	Equ arv
Equisetum hyemale	Scouring rush	N	Equ hye
Erigeron annuus	Daisy fleabane	N	Eri ann
Erigeron canadensis	Horseweed	N	Eri can
Erigeron philadelphicus	Common fleabane	N	Eri phi
Erigeron pulchellus	Robin's plantain	N	Eri pul
Eupatorium album	White boneset	N	Eup alb
Euphorbia maculata	Eyebane	N	Eup mac
Festuca obtusa	Sheep's fescue	N	Fes obt
Fragaria virginiana	Strawberry	N	Fra vir
Fraxinus americana	White ash	N	Fra pen
Fraxinus pensylvanica	Red ash	N	Fra ame
Galium aparine	Cleavers	N	Gal tri
Galium trifidum	Fragrant bedstraw	N	Gal apa
Geranium maculatum	Wild geranium	N	Ger mac
Geranium robertianum	Herb Robert	N	Ger rob
Geum canadense	White aster	N	Geu lac
Geum laciniatum	Rough avens	N	Geu can
Glyceria striata	Fowl meadow grass	N	Gly str
Helianthus divaricatus	Woodland sunflower	N	Hel div
Hepatica acutiloba	Sharp-lobed hepatica	N	Hep acu
Heracleum lanatum	Cow parsnip	N	Her lan
Hydrophyllum appendiculatum	Appendaged waterleaf	N	Hyd app
Hydrophyllum virginianum	Virginia waterleaf	N	Hyd vir
Impatiens capensis	Jewelweed	N	Imp cap
Juglans nigra	Black walnut	N	Jug nig
Juncus tenuis	Path rush	N	Jun ten
Juniperus virginiana	Juniper	N	Jun vir
Lactuca biennis	Tall blue lettuce	N	Lac bie
Laportea canadensis	Wood nettle	N	Lap can
Leersia virginica	Leersia virginica	N	Lee vir
Lindera benzoin	Spicebush	N	Lin ben
Lycopus americanus	Water-horehound	N	Lyc uni
Lycopus uniflorus	Bugle weed	N	Lyc uni
Lysimachia ciliata	Fringed loosestrife	N	Lys cil
Maianthemum canadense	Maianthemum	N	Mai can
Menispermum canadense	Moonseed	N	Men can
Mentha arvensis	Wild mint	N	Men arv
Monarda fistulosa	Wild bergamot	N	Mon fis
Muhlenbergia frondosa	Satin grass	N	Muh fro
Muhlenbergia mexicana	Rough grass	N	Muh mex

Muhlenbergia schreberi	Satin grass	N	Muh sch
Oenothera biennis	Evening primrose	N	Oen bie
Onoclea sensibilis	Sensitive fern	N	Ono sen
Onoclea spp.	Bracken fern	N	Ono brk
Osmorhiza claytonii	Wooly sweet cicely	N	Osm cla
Osmorhiza longistylis	Smooth sweet cicely	N	Osm lon
Ostrya virginiana	Hornbeam	N	Ost vir
Oxalis stricta	Wood sorrel	N	Oxa str
Panicum capillare	Panicum capilaire	N	Pan cap
Panicum oligosanthes	Panicum oligosanthes	N	Pan oli
Panicum virgatum	Panicum virginicum	N	Pan vir
Parthenocissus quinquefolia	Virginia Creeper	N	Par qui
Phalaris arundinacea	Phalaris arundinacea	N	Pha aru
Phlox divaricata	Blue phlox	N	Phl div
Phragmites australis	Canary grass	N	Phr aus
Phryma leptostachya	Lopseed	N	Phr lep
Physalis heterophylla	Clammy ground cherry	N	Phy het
Pilea pumila	Clearweed	N	Pil pum
Pinus strobus	White pine	N	Pin str
Podophyllum peltatum	May Apple	N	Pod pel
Polygonatum biflorum	Solomon's-seal	N	Pol bif
Polygonatum canaliculatum	Great Solomon's seal	N	Pol can
Polygonum scandens	False buckwheat	N	Pol sca
Potentilla norvegica	Rough cinquefoil	N	Pot nor
Prenanthes alba	White lettuce	N	Pre alb
Prunus serotina	Black cherry	N	Pru ser
Prunus virginiana	Choke cherry	N	Pru vir
Ptelea trifoliata	Hoptree	N	Amp bra
Quercus muhlenbergia	Chinquipin oak	N	Que muh
Quercus rubra	Red oak	N	Que rub
Quercus velutina	Black oak	N	Que vel
Ranunculus abortivus	Kidney leaved buttercup	N	Ran abo
Rhus aromatica	Fragrant sumac	N	Rhu aro
Rhus radicans	Poison Ivy	N	Rhu rad
Rhus typhina	Staghorn sumac	N	Rhu typ
Ribes americanum	Black current	N	Rib ame
Ribes cynosbati	Prickly gooseberry	N	Rib cyn
Rosa blanda	Smooth rose	N	Ros bla
Rubus occidentalis	Raspberry	N	Rub occ
Rudbeckia trilobia	Cone flower	N	Rud tri
Salix discolor	Pussy willow	N	Sal dis
Salix spp.	Willow	N	Sal spp
Sambucus canadensis	Elderberry	N	Sam can
Sanicula marilandica	Black snakeroot	N	Sanmar
Scrophularia marilandica	Figwort	N	Scr mar
Smilacina racemosa	False solomon's-seal	N	Smi rac
Smilacina stellaria	Starry solomon's-seal	N	Smi ste
Smilax herbacea	Carrion Flower	N	Smi her
Smilax tamnoides	Green briar	N	Smi tam

Solidago altissima	Tall goldenrod	N	Sol alt
Solidago caesia	Blue-stemmed goldenrod	N	Sol cae
Solidago canadensis	Canada goldenrod	N	Sol can
Strophostyles helvola	Wild bean	N	Str hel
Tilia americana	American basswood	N	Til ame
Tovara virginiana	Jumpseed	N	Tov vir
Trillium grandiflorum	Trillium	N	Tri gra
Typha latifolia	Common cattail	N	Typ lat
Ulmus rubra	Slippery elm	N	Ulm rub
Urtica dioica	Stinging nettle	N	Urt dio
Urtica gracilis	Slender nettle	N	Urt gra
Urtica procera	Tall nettle	N	Urt pro
Verbena urticifolia	White vervain	N	Ver urt
Veronica peregrina	Purslane speedwell	N	Ver per
Viola affinis	leConte's violet	N	Vio aff
Viola papilionacea	Common violet	N	Vio pap
Viola pensylvanica	Smooth yellow violet	N	Vio pen
Viola pubescens	Downy yellow violet	N	Vio pub
Viola sororia	Wooly violet	N	Vio sor
Vitis riparia	River Grape	N	Vit rip
Abutilon theophrasti	Velvetleaf	E	Abu the
Agropyron repens	Quack grass	E	Agr rep
Alliaria petiolata	Garlic Mustard	E	All pet
Allium vineale	Onion	E	All vin
Arenaria serpyllifolia	Thyme-leaved Sandwort	E	Are ser
Barbarea vulgaris	Yellow Rocket	E	Bar vul
Berteroa incana	Hoary Alyssum	E	Ber inc
Brassica kaber	Charlock	E	Bra kab
Brassica rapa	Field Mustard	E	Bra rap
Bromus erectus	Upright Brome	E	Bro ere
Bromus inermis	Smooth Brome	E	Bro ine
Bromus tectorum	Chessy Brome	E	Bro tec
Capsella bursa-pastoralis	Sheperd's Purse	E	Cap bur
Centaurea maculosa	Knapweed	E	Cen mac
Chenopodium album	Lambsquarters	E	Che alb
Cirsium arvensis	Canada Thistle	E	Cir arv
Commelina communis	Asiatic Dayflower	E	Com com
Convallaria majalis	Lily-of-the-valley	E	Con arv
Convolvulus arvensis	Field Bindweed	E	Con maj
Dactylis glomerata	Orchard grass	E	Dac glo
Datura stramonium	Jimsonweed	E	Dat str
Daucus carota	Wild Carrot	E	Dau car
Digitaria sanguinalis	Smooth Crab-grass	E	Dig saa
Digitaria sanguinalis	Hairy Crab-grass	E	Dig sab
Eragrostis cilianensis	Stink Grass	E	Era cil
Festuca rubra	Red Fescue	E	Fes rub
Galeopsis tetrahit	Hemp Nettle	E	Gal tet
Glechoma hederacea	Gill-on-the-hill	E	Gle hed
Hedera helix	English Ivy	E	Hed hel

Hemerocallis fulva	Orange Day-lily	E	Hem ful
Hesperis matronalis	Dame's Rocket	E	Hes mat
Lamium amplexicaule	Henbit	E	Lam amp
Lamium purpureum	Purple Dead Nettle	E	Lam pur
Lathyrus latifolius	Everlasting Pea	E	Lat lat
Leonurus cardiaca	Motherwort	E	Leo car
Lepidium campestre	Peppergrass	E	Lep cam
Lonicera japonica.	Japanese Honeysuckle	E	Lon jap
Lychnis alba	White campion	E	Lyc alb
Medicago lupilina	Black Medic	E	Med lup
Melilotus alba	White Sweet Clover	E	Mel alb
Melilotus officinalis	Yellow Sweet Clover	E	Mel off
Morus alba	White Mulberry	E	Mor alb
Narcissus pseudo-narcissus	Daffodil	E	Nar pse
Nepeta cataria	Catnip	E	Nep cat
Ornithogalum umbellatum	Star of Bethlehem	E	Orn umb
Panicum dichotimiflorum	Spreading Witch-grass	E	Pan dic
Phleum pratense	Timothy	E	Phl pan
Phlox paniculata	Garden Phlox	E	Phl pra
Plantago lanceolata	Narrow-leaved Plantain	E	Pla lan
Plantago major	Common Plantain	E	Pla maj
Poa compressa	Canada Bluegrass	E	Poa com
Poa pratensis	Kentucky Bluegrass	E	Poa pra
Poa trivialis	Poa trivialis	E	Poa tri
Polygonum cuspidatum	Japanese knotweed	E	Pol cus
Portulaca oleracea	Milk Purslane	E	Por ole
Potentilla recta	Rough-fruited Cinquefoil	E	Pot rec
Rumex crispus	Curled Dock	E	Rum cri
Saponaria officinalis	Bouncing bet	E	Sap off
Scilla spp.	Scilla spp.	E	Sci spp
Sedum acre	Stonecrop	E	Sed acr
Setaria glauca	Yellow Foxtail	E	Set gla
Setaria magna	Giant Foxtail	E	Set mag
Setaria viridis	Green Foxtail	E	Set vir
Silene cucubalus	Bladder Campion	E	Sil cuc
Silene noctiflora	Night Flowering Catchfly	E	Sil noc
Sisymbrium altissimum	Tumble Mustard	E	Sis alt
Solanum nigrum	Black Nightshade	E	Sol nig
Stellaria media	Common Chickweed	E	Ste med
Stellaria vulgatum	Mouse-eared Chickweed	E	Ste vul
Syringa vulgaris	Lilac	E	Syr vul
Taraxacum erythrospermum	Red-seeded Dandelion	E	Tar ery
Taraxacum officinale	Dandelion	E	Tar off
Thlaspi arvense	Pennycress	E	Thl arv
Trifolium dubium	Least Hop Clover	E	Tri dub
Trifolium repens	White Clover	E	Tri rep
Verbascum thapsus	Mullein	E	Ver off
Veronica arvensis	Corn Speedwell	E	Ver ser
Veronica serpyllifolia	Thyme Speedwell	E	Ver spp

Veronica spp.	Speedwell spp.	E	Ver tha
Vinca minor	Periwinkle	E	Vin min

[1] N: native, E: exotic

Appendix 2. Species and common names of all weed species occurring in Sturgeon Creek study. Each species ranked in importance with respect to total percentage cover (% cov (rank)) and frequency (freq (rank)). Also indicated is code used in Principal Components Analysis (PCA).

Species	PCA code	Common name	%cov (rank)	freq (rank)
Echinochloa crus-galli	Echcru	barnyard grass	1	-
Xanthium strumarium	Xanstr	cocklebur	2	2
Trifolium repens	Trirep	white clover	3	-
Ambrosia artemisiifolia	Ambart	common ragweed	4	4
Ambrosia trifida	Ambtri	giant ragweed	5	6
Chenopodium album	Chealb	common lambsquarters	6	1
Abutilon theophrasti	Abuthe	velvetleaf	7	5
Polygonum persicaria	Polper	smartweed	8	8
Aster hirsuta	Asthir	hairy aster	9	11
Sonchus arvensis	Sonarv	field sowthistle	10	10
Solidagi canadensis	Solcan	Canada goldenrod	11	3
Taraxacum officinale	Taxoff	common dandelion	12	9
Daucus carota	Daucar	wild carrot	13	7
Agropyron repens	Agrpyr	quackgrass	14	-
Cirsium vulgare	Cirvul	bull thistle	15	12
Cirsium arvensis	Cirarv	Canada thistle	16	15
Setaria magna	Setmag	giant foxtail	17	-
Aster vimineus	Astvim	small white aster	18	13
Erigeron philadelphicus	Eriphi	Canada fleabane	19	14
Setaria glauca	Setgla	yellow foxtail	20	-
Erigeron canadensis	Erican	horseweed	21	19
Zea mays	Zeamay	corn	22	18
Euphorbia maculata	Eupmac	eyebane	23	16
Lepidium campestre	Lepcam	peppergrass	24	17
Erigeron pulchellus	Eripul	robin's plantain	25	20
Morus alba	Moralb	white mulberry	26	21