Pugnaire, F. and Valladares, F. (eds.) 2007. Functional plant ecology. Taylor and Francis, New York.

4

The Architecture of Plant Crowns: From Design Rules to Light Capture and Performance

Fernando Valladares and Ülo Niinemets

CONTENTS

INTRODUCTION

Plants exhibit a striking diversity of forms and structures, which are difficult to interpret. The functional approach to the study of plant form emerged as a separate discipline at the beginning of the twentieth century with the first classifications of growth forms in relation to climate and with tentative ecophysiological studies of plant responses to the environment (Waller 1986). Physiological ecology now makes detailed predictions on how physical and physiological characteristics affect plant photosynthesis, whereas plant population ecology translates patterns of growth into fitness of individuals and populations. And plant structure remains an essential tool for all these exercises of interpreting plant performance in natural habitats and for scaling from cellular and leaf-level to ecosystem processes (Ehleringer and FIeld 1993). Plant performance can be understood as the crucial link between its phenotype and its ecological success and the form becomes ecologically and evolutionary relevant when it affects performance (Koehl 1996). It is important to consider that misconceptions can arise from studies in which selective advantages of particular structures are not made with a mechanistic understanding of how the structural traits affect performance. Koehl (1996) showed that the relationship between morphology and performance can be nonlinear, context-dependent, and sometimes surprising. Remarkably, new functions and novel ecological consequences of morphological changes can arise simply as the result of changes in size or habitat.

While all would agree that structure is intrinsically coupled with function, the impetus is often stronger to investigate physiological mechanisms rather than the functional implications of plant form. This is not to say that functional plant architecture has been ignored. For instance, the role of canopy architecture in competition for light has been addressed in several works after the keystone study by Horn (1971). However, the architectural constraints of plant success, which is of plant persistence or expansion in the community, have not been explored extensively. Plant architecture involves the manner in which the foliage is positioned in different microenvironments and determines the flexibility of a shoot system to take advantage of unfilled gaps in the canopy, to allocate and utilize assimilates, and to recover from herbivory or mechanical damage (Caldwell et al. 1981, 1983, Küppers 1989). Except in particular or very extreme environments, plant physiology alone does not explain ecological success, since growth and competition have been clearly related to structural features (Küppers 1994). In agreement with Tomlinson (1987), the study of plant morphology is an integrative discipline rather than a subject restricted to the comparison of anatomical details of plant life cycles. We attempt to demonstrate that plant morphology in general and plant architecture in particular belongs more rightly within the fields of plant ecophysiology and plant population biology.

We analyze here plant shape from a functional point of view. The basic plant design and the many interpretations and implications of its modular nature are presented here as an indispensable starting point to enter into discussions on function and adaptive value of crown structural features. We further discuss the relationships between plant shape and light capture. Plants depend on the light energy that they capture by photosynthesis, and solar radiation is the major driving force affecting not only photosynthetic activity, but also leaf temperature, leaf water status, and many other physiological processes of the plant. Crown architecture is crucial for light capture and for the distribution of light to each particular photosynthetic unit of the crown, but must also serve several other functions. The architectural design of a given plant must provide safety margins to cope with gravity and wind; therefore, biomechanical constraints must be taken into account when assessing the influence of morphology and architecture on plant performance. The structural basis of light capture by plant crowns is explored here from the leaf level to the community level with special attention to leaf angle, phyllotaxis, branching patterns, and crown shape. Examples of plant architecture in extreme light environments are included, where the functional implications for light capture of a range of structural features can be better seen. In the analysis of plant shape at the community level, two main functional concepts involving plant interactions are discussed: the occupation of the space and the shading of neighbors. As there are important world-scale modifications in overall light availability and in the various components of solar radiation, in particular in the ratio of direct to diffuse irradiance (Roderick et al. 2001, Gu et al. 2002, Farquhar and Roderick 2003), understanding the fundamental relationships between plant architecture and efficiency of harvesting light is the precondition in grasping the global change effects on vegetation productivity.

PLANT DESIGN

The shape of a given plant is determined by the shape of the space that it fills, but most plants attain a characteristic shape when grown alone in the open due to an inherited developmental program (Horn 1971). This developmental program usually implies the reiterative addition of a series of structurally equivalent subunits (branches, axes, shoots, leaves), which confers plants a modular nature. This developmental program is the result of plant evolution under some general biomechanical constraints. For instance, the shape of the crown of a tree is constrained by the fact that the cost of horizontal branches is greater than that of vertical branches (Mattheck 1991). This section explores the functional implications of these two general aspects, the modular nature of plants and the biomechanical constraints of shape, which in addition to the environment where the plant grows determine plant architecture.

BASIC ARCHITECTURE OF TERRESTRIAL PLANTS

Terrestrial vascular plants must combine the structural requirements of water-conduction and gas-exchange systems with the problems of mechanical support of aerial structures and light capture by the photosynthetic surfaces. Many different solutions to these frequently opposing problems have been found during plant evolution (Niklas and Kerchner 1984, Speck and Vogellehner 1988, Niklas 1990, 1997). The diversification into trees, shrubs, and herbs occurred relatively rapidly (Raven 1986), and by the end of the Devonian, many alternative plant designs were successfully tested in most terrestrial systems. From primitive cylindrical or flat, two-dimensional photosynthetic surfaces restricted to liquid environments, terrestrial plants evolved complex three-dimensional arrangements of the photosynthetic units, which required stomata for control over water loss preventing embolism (Woodward 1998), lignified fibers for support, and a specialized root system for efficient competition for belowground resources (Jackson et al. 1999). However, because no one design dominates in all environments, specialization for efficiency in any given environment involved structural trade-offs that made the same plant less competitive in other environments (Waller 1986). Most of what follows in this chapter aims to explore the ecological implications and the trade-offs involved in the various and varying architectural designs of extant plants.

MODULAR NATURE OF PLANTS

In the crown of most vascular plants, it is easy to recognize a hierarchical series of subunits. The largest subunit is the branch, which is made up of modules (Porter 1983). *Module* is a general term that refers to a shoot with its leaves and buds, and the term can be applied to either determinate (structures whose apical meristem dies or produces a terminal inflorescence) or indeterminate shoot axes (Waller 1986). Modules are, in turn, made up of smaller subunits consisting of a leaf, its axillary buds, and the associated internode. These small subunits have been called metamers (White 1984). Since plants have many redundant modules or organs that have similar or identical functions (e.g., leaves or shoots transforming absorbed light into biomass), plants have been seen as metapopulations (White 1979). Such redundant modules are not fully dependent on one another, and, in fact, individual modules continue to function when neighbor organs are removed (Novoplansky et al. 1989). The existence of hundreds of redundant subunits within a single plant raises the question: To what degree do these structural subunits (e.g., shoots) respond independently to the environment?

Scaling Up and Down

The study of functional modularity of plants can be tackled at different scales. The smallest end is the so-called nutritional or physiological unit, comprising a unit of foliage, the axillary bud, and the corresponding portion of stem (Watson 1986). As pointed out by Sprugel et al. (1991), the opposite end of the spectrum would be the clonal herbs, in which each module (ramet) contains all of the structural parts necessary for independent existence. The branch is an intermediately scaled unit, which is very convenient because it is large enough to integrate most relevant physiological processed, but small enough to be used in ecophysiological experiments. For this reason, branches have been used extensively by ecologists and ecophysiologists to scale from leaf-level measurements to the whole plant or to the plant community (Gartner 1995).

All branches within a plant are structurally and physiologically connected to one another, but the mutual interactions are not always easy to elucidate. To make reliable scaling and generalization exercises, branch autonomy must be investigated thoroughly. Branch autonomy depends on the resource—carbon, water, or nutrients. The most clear aspect of branch autonomy is that related with carbon budget, since most branches fix all the carbon they need, and usually fix more, becoming exporters or sources of carbon in contrast with roots or reproductive structures, which are important carbon sinks (Geiger 1986). Although branches cannot be completely autonomous with respect to water and nutrients, which come from the roots via the stem, they exhibit different levels of uncoupling with the rest of the branches of the crown, that is, different levels of relative autonomy (Tyree 1999). In most species, branches are somewhat hydraulically isolated from the rest of the plant; thus, in words of Tyree (1988), branches can be treated as small, independent seedlings rooted in the main bole. Nevertheless, branches are imperfect substitutes for studies on whole plants, especially when exceptions to the general branch autonomy can be expected (Sprugel et al. 1991).

Ecology of Branch Autonomy

Branch autonomy has two major ecological advantages: (1) control of stress and damage, and (2) a more efficient exploitation of heterogeneous environments (Hardwick 1986). A compartmentalized plant may be less vulnerable to pathogens or herbivores than an integrated plant. It is well known that trees are capable of walling off injured or too-old branches, which provides an efficient protection against spreading of infections and against a net energy drain on the organism, respectively (Sprugel et al. 1991). A similar argument on the advantages of branch autonomy can be built for the prevention of runaway cavitation, for example, the formation of gas bubbles when transpiration rate exceeds water transport that block xylem vessels or tracheids (Tyree 1999, Zimmermann et al. 2000).

Because the different aerial parts of a plant (e.g., branches and leaves) are generally in different light environments, plants frequently face the problem of distributing limited resources in a way that would optimize the performance of units exposed to heterogeneous light conditions. Although plants do not forage in the classical sense of moving around to different prey locations, they do exhibit a foraging behavior (Hutchins and de Kroon 1994). Plants forage because they must spend energy producing the leaves and the associated supporting structures necessary to harvest light, and their fitness is increased if this energy is spent efficiently, that is, if leaves are arranged appropriately to maximize light capture. A plant that has new leaves in high-light areas of the crown has an advantage over one that remains symmetric and sets out leaves equally in all possible locations. Branch autonomy with respect to carbon budget enhances the efficiency of light foraging because branches exposed to high-light grows bigger, shaded branches stops growing, and no energy is wasted in producing leaves in shaded areas (Sprugel et al. 1991). However, this is the case only for woody plants with indeterminate or multiple flushing growth patterns, where photosynthate for new leaves at the top of a shoot has been shown to come primarily from the older leaves of the same shoot (Fujimori and Whitehead 1986). In woody plants with determinate, single-flush growth patterns, efficient light foraging is not achieved via branch autonomy but rather via increased bud production in high-light areas; the buds draws on reserves throughout the tree in the next growing season (Sprugel et al. 1991). Several evidences indicate that branches are interdependent so that a positive carbon budget by itself does not ensure branch survival, and a stressed branch on a tree where all other branches are also stressed does better than a similarly stressed branch on a tree where some branches are relatively unstressed. As stated by Sprugel (2002) although branch autonomy is an important and useful principle, it is not an absolute rule governing branch growth.

Modularity versus Integrity

Despite the ecological relevance and the functional evidence of a certain autonomy of the different modules of a given plant, many different studies suggest that a plant is more than just a population of redundant organs because it responds to the environment as an integrated individual and not as a simple colony with limited mutual aid (Sprugel et al. 1991, Sachs et al. 1993). The simplistic, albeit tempting, concept that a single plant is not a unit but a collection of independent subunitary parts became widespread during the nineteenth century and persisted until modern times (White 1979). It is reminiscent of the assumption that organismal structure and function can be understood by studying the cells, since cells have been considered the building blocks or organism form since the publication of the cell theory in 1938 (Kaplan and Hagemann 1991). In the advocacy of plant integrity, plants have been considered ‘‘metapopulations’’ (White 1979) in the context of the classical etymology of *meta*- as sharing. Therefore, plants are referred to as metapopulations when the shares elements that make up the morphological structure of an individual are emphasized. Under controlled conditions, plants have been shown to do more than respond locally to the degree to which they are damaged: interactions and mutual support between branches allowed treated plants for the comparison of available branches, and for the diversion of resources so as to increase the chances of greatest overall success (Sachs and Hassidim 1996, Sprugel 2002).

Nevertheless, two interesting lines of evidence support the notion that the modules of a plant are functionally independent of one another, at least to some extent: (1) independent patterns of phenology between branches, and (2) competitive interactions between modules for limited resources as a consequence of a eustelic arrangement. Each module undergoes a complete life cycle of birth, growth, maturation, senescence, and death; therefore, a plant can be studied as a dynamic population of modules with a distinct age structure following rigorous demographic analyses (Room et al. 1994). Individual leaves and foliage units are manifestly not all the same due to the two simple facts that they are not of the same age and that they are borne in different positions relative to each other (Harper 1989). In this sense, and considering the remarkable genetic variability of the different modules of a plant and the fitness differentials between modules, individual plants can be tackled as colonies of evolutionary individuals (Gill 1991).

PLANT BIOMECHANICS: COPING WITH GRAVITY AND WIND

While plant architecture is an outcome of many selective pressures, the shapes of plant parts, their elasticity, and resistance to strain, are constrained by well-known mechanical principles (McMahon and Kronauer 1976, Niklas 1992). Because aerial plant parts face the obvious forces of gravity and wind, a fraction of the biomass must be devoted to support. As mechanical structures of similar shape become increasingly inefficient with increasing size, the fraction required to support plants increases rapidly with increasing plant size. For instance, the strength of a column (e.g., a branch or a stem) scales with the square of its diameter, whereas its mass increases with diameter squared times length (Gere and Timoshenko 1997). For any given plant, the mechanical costs associated with its crown geometry must be balanced with the photosynthetic benefits associated with its light-capture efficiency.

The height to which a plant should grow depends on the environment and on the height of the neighboring plants, that is, the goal is not to grow tall, but grow taller than the others (Waller 1986, King 1990). The taller a plant becomes in its competition for light, the more light it needs to support its preexisting biomass and to achieve growth. In fact, the maximum height of tree can be determined by the balance between maximal potential carbon gain that occurs in full sunlight and carbon required for construction and maintenance costs of crown and roots (Givnish 1988). Although small-statured plants have smaller growth maintenance requirements per unit of light-absorbing machinery than large plants, growing taller implies greater access to light. In general, the higher the plant, the more light it intercepts during the course of the day (Jahnke and Lawrence 1965, King 1981, 1990). Thus, there is a payback of investing in height that can be especially relevant under situations of strong competition for light. Of course, the reverse is also true: being tall requires on average higher irradiances due to extensive maintenance costs (Givnish 1988).

Mechanical stability imposes the minimum amount of tissue required to support the crown and its units. The most likely mode of stem failure is elastic toppling, rather than failure under the weight of the crown. Accordingly, stem diameter scales with height, with a safety margin that prevents elastic toppling but not compressive failure (McMahon 1973). For most plants, height varies with trunk diameter in such a way that there is a margin of safety against buckling (Niklas 1994). When trees grow in the open with little competition, their size and shape is conservative, being only one-quarter of their theoretical buckling height (McMahon 1975, McMahon and Kronauer 1976). However, when competition in a forest is strong, trees cannot afford large safety margins, especially when they have not reached the canopy. Based on this, Givnish (1995) predicted that shade-intolerant pioneer species should have lower mechanical safety margins than shade-tolerant species of similar stature. High wood density, usually reached in long-lived species with slow tissue turnover, provides resistance against mechanical failure and against attack by fungi and insects (King 1986). However, it adds extra weight for a given height or length of the stem or branch, so the biomechanical advantages of a stronger building material are frequently neutralized by the additional load. Structural costs are minimized by constructing stems of low-density wood, and for this reason softwoods can grow faster than hardwoods (Horn 1971). Hence, pioneer trees are expected to have light, energetically inexpensive wood, whereas late successional trees should have dense, highly lignified wood. Most studies in temperate and tropical forests confirm this trend (Horn 1971, Givnish 1995). The different biomechanics and associated costs of the crowns of hardwoods and softwoods can be crucial depending on the sign and intensity of factors such as frequency of storms, stability of the substrate, competition for light, or availability of water and nutrients.

Another important biomechanical aspect of the crown is the branching pattern. Branching angles should minimize both structural costs and leaf overlap to achieve optimal plant growth. However, these two features are mutually exclusive because branching patterns and leaf arrangements that reduce leaf overlap often require more investment in supporting tissues (Givnish 1995). Plants segregate in the cost and benefit trade-offs that their crown design entails in a given environment. In general, tree mechanisms concentrate on a good mechanical design only if light capture is sufficient (Mattheck 1991, 1995), but the biomechanical theory of crown design is still insufficient for integrated comparisons of the particular advantages of each crown architecture.

Although gravity leads to static loading of a plant based on the weight of individual parts, the dynamic loading caused by wind is often transitory (Grace 1977, King 1986, Speck et al. 1990). However, the wind exerts permanent modifications of the overall shape of plants and affects the anatomy and density of the wood, inducing biomechanical changes at architectural and anatomical levels (Coutts and Grace 1995, Ennos 1997). The greatest effects of strong winds on trees are seen near the tree line, where most species exhibit the so-called *krummholz* form (Ennos 1997). *Krummholz* refers to environmentally dwarfed trees, in which the crown is a prostrate cushion that extends leeward from the short trunk (Arno and Hammerly 1984). Despite the fact that light harvesting can be decreased by the *krummholz* habit, carbon gain is enhanced in comparison with upright trees in equivalent environmental conditions due to the increased photosynthetic rates exhibited by the leaves, which are deep in the boundary layer and warmed more by the sun (James et al. 1994). Another interesting, albeit little explored aspect of plant biomechanics and wind is the dynamic reconfiguration of crown shape while the wind is blowing. Branches and foliage bend away with the wind, which reduces drag. It has been suggested that drag reduction should lead to flexible twigs in windy environments (Vogel 1996), and also to pinnate or lobed leaves due to the great degree of reconfiguration of these leaves in comparison with that of simple leaves (Vogel 1989). Increasing evidence is pointing to the existence of two main strategies regarding the wind as an ecological factor: (1) pioneer trees in windy habitats with flexible branches and pinnate or lobed leaves to reduce aerodynamic drag; and (2) late-successional trees or species from sheltered sites with simple leaves and rigid branches to maintain optimal light interception (Vogel 1989, Ennos 1997). A similar reasoning was given for woody plants that dwell along shores of streams and torrents: flexible twigs and narrow, willow-like leaves should prove adaptive since they reduce pressure drag during flash floods (van Steenis 1981, Vogel 1996).

Unusual growth forms pose specific biomechanical problems, and precise studies are required to interpret certain plant designs. For instance, in most species of *Opuntia* (Cactaceae), shoots are formed as a sequence of short, flattened stem segments called cladodes. Cladodes have an elliptical base that supports the greatly enlarged upper portion and joins over only a small portion of their periphery so that there is considerable flexing at the cladode–cladode junctions (Nobel and Meyer 1991). Despite the fact that the contact between cladodes is only 20% of that occurring in a similar stem of constant width, the resulting shoot structure is rigid and resistant to typical wind and gravity loadings. The remarkable strength of this cladode–cladode junction cannot be fully explained from a biomechanical point of view (Nobel and Meyer 1991). Other interesting study cases are palm trees. Their lack of secondary thickening exposes them to a risk of toppling that increases with crown height. Mechanical safety of certain palm trees seems to be maintained by increasing the tissue density over time, and by proliferation of existing tissues that leads to an increase in actual cross-section of the stem (Rich 1986, 1987).

DEVELOPMENT OF A CROWN SHAPE

Despite the fact that most plants exhibit an indefinite growth, which produces a remarkable variability in their final size, they have a recognizable form. The many meristems of a plant are integrated into a galaxy of possible but not random morphologies. Understanding the mechanisms behind the production, arrangement, and turnover of plant modules led morphologists to group plants in a small number of architectural models.

CROWN ARCHITECTURE AND MODELS OF GROWTH

Plants exhibit an extraordinary variety of branching patterns and foliage arrangements. The luxuriance of structural details of a forest canopy or the diversity of morphologies displayed by the herbs of a subalpine meadow can be overwhelming. For this reason, botanists and plant ecologists have looked at the developmental organization (architecture) of plants with a reductionist approach, slimming the complexity of plant shape to a sequence of simpler processes, but retaining the holistic features that determine plant construction (Tomlinson 1987). The questions of how many possible ways there are to build a plant and how many architectural models are exhibited by real plants have led to several classifications of plant shape. One of the best-known detailed classifications of plant architecture is provided by Hallé et al. (1978). This review further provides an extensive, comparative study of the ontogenetic changes of the shape of tropical trees. In fact, most systematic descriptions and cataloging of architectural patterns have been based on trees. The most interesting features of these classifications are (1) a revival of the notion of modular construction and its importance in the generation of plant shape, and (2) an emphasis on understanding the mechanisms behind the dynamics of the arrangement, production, and turnover of plant modules and subunits (Porter 1989). This sort of information has made possible the realistic reconstruction of virtual plants, which is leading to in-depth understanding of plant growth in response to the environment and to promising orientations for plant breeding and pests and pathogens management, thanks to the potential of virtual experimentation (Room et al. 1996).

Branching: The Framework of a Crown

Branching complexity ranges from plants with a single axis to large trees with many orders of branching in three-dimensional space. However, the overall complex shape of a tree can be determined by surprisingly few parameters since a new branch is geometrically determined by just two parameters: branching angle and branch length (Honda et al. 1997). Repetition of the branching generates the distinctive complexity of plant crowns, and the relative simplicity of the process has resulted in the generation of numerous computer models that simulate branching and growth of plants with remarkable realism (Waller and Steingraeber 1985, Fisher 1992).

Although some trees have a single axis (e.g., most palms) and some have many similar branching axes, most species of trees have two or more types of axes that can be distinguished by their primary orientation, symmetry, or form. In general, leader axes are radially symmetrical, whereas lateral branch axes are dorsiventrally symmetrical (Fisher 1986). Differences in initial vigor of lateral branches results in a well-defined main axis, which is established commonly in a regular, alternating zigzag pattern (Fisher 1986). The branching and consequent growth of trees and shrubs can be characterized by vertical or longitudinal, and horizontal or lateral symmetries. Vertical symmetry is characterized by growth of branches at the top (acrotony) or at the base (basitony), whereas lateral symmetry is characterized by branch growth at the upper or lower side of the lateral branch (epitony and hypotony, respectively). Logically, shrubs exhibit a basitonic branching, whereas trees are characterized by acrotonic branching. Analogously, while typical trees exhibit a hypotonic branching, most shrubs and small trees exhibit epitonic branching. However, there are many exceptions to these rules. For instance, the pyramidal shape of the crown of many conifers is due to the combination of basitonic branching (typically a shrub pattern) with a monopodial growth of the bole. The dominance of branch development when branch originates from buds on the upper side of stems or main branches (epitonic shoots) appears to be important in shrub competition for space, since hypotonic branching confers the capacity of extending laterally but not overtopping an existing canopy (Schulze et al. 1986). More implications of branching patterns in the way shrubs and trees occupy and compete for space are discussed in Section ‘‘Structural Determinants of Light Capture’’.

Relative number of branches has been examined in trees using the Strahler ordering technique, which begins at the edge of the canopy (first-order branches) and works its way toward the trunk, incrementing the order of a branch each time it intersects the junction of two similarly ordered branches (Waller 1986). The bifurcation ratio, an index of the degree of branching from one order to the next, was initially related to the successional status of the tree (Whitney 1976). However, later studies have shown that it varies within a given species (Steingraeber 1982) and even within a given crown (Kellomäki and Väisänen 1995, Kull et al. 1999, Niinemets and Lukjanova 2003). The ratio between terminal and subterminal branches can be of ecological interest, but higher-order bifurcation ratios are difficult to interpret (Steingraeber 1982).

Plant form can be very complex due to the combination of regular and irregular pattern formation processes. While Euclidean geometry is very useful for studying linear, continuous, or regular structural properties of the objects, fractal geometry is a powerful tool to analyze nonlinear, discontinuous, or irregular structural properties, which are characteristic of plants (Hasting and Sugihara 1993). One of the properties of fractal objects is self-similarity, that is, the shape or geometry of the object does not change with the magnification or scale. The reiteration of a branching pattern in trees is a good example of this property, which was qualitatively described and used in the classification of architectural models of trees before fractals became popular (Hallé et al. 1978). Plant architecture has many fractal properties (see e.g., Prusinkiewicz and Lindenmayer 1990). A tree can be modeled as a fractal, and many functional aspects, such as efficiency of occupation of space by the leaves, total wood volume, stem surface area, and number of branch tips, can be calculated with more accuracy by using fractals rather than Euclidean geometry. However, forests, tree branches, plant crowns, or compound leaves, are most likely *multifractals*, because they are not strictly self-similar at every scale, that is, not exactly the same at all magnifications (Stewart 1988). This concept is clearly homologous to the *partial reiteration* concept that Hallé et al. (1978) and Hallé (1995) used in their classification of the architecture of trees.

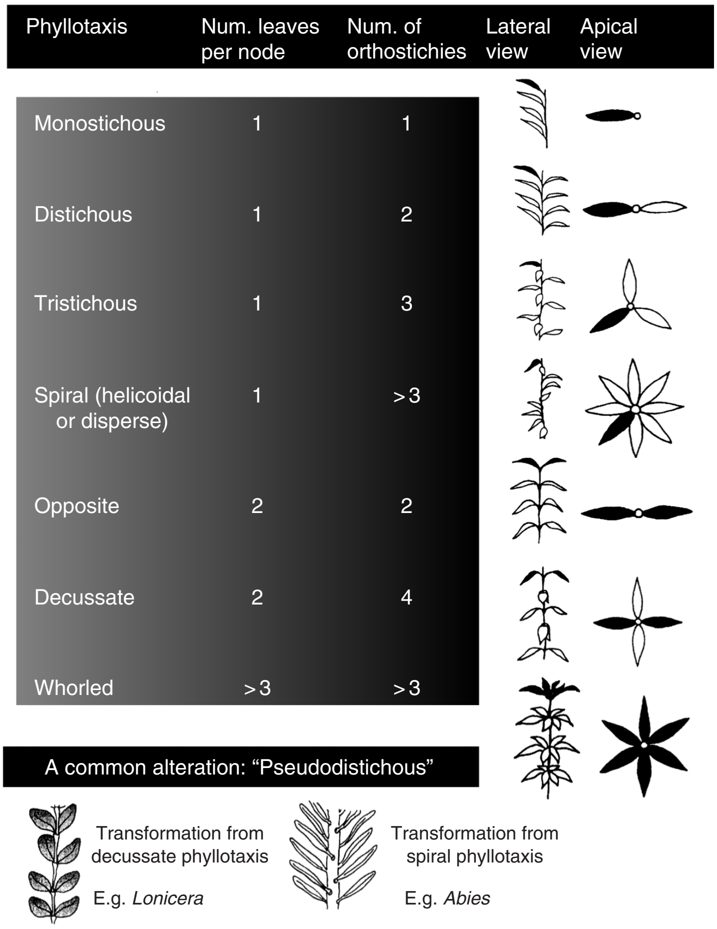
Because symmetries and elegant geometric features of plants have always attracted mathematicians, models of plant shape and growth have received considerable attention. Models can be classified into two main groups: morphological and process-based models (Perttunen et al. 1996). However, the ideal model is a morphological model that deals with physiological processes or a process-based model that incorporates morphological information (Kurth 1994). Models vary greatly in scope and resolution, but very simple models can mimic response of real plants because the complex integrated growth patterns seem to be emergent properties of a simple system (Cheeseman 1993). Metamer dynamics have been simulated using the tools of population dynamics, which have rather simple mathematical formulation; however, this approach ignores structure and allows little scope for geometric analyses (Room et al. 1994). In geometric models, the spatial position and orientation of each structural component is considered, which allows the accurate simulation of interception of light by leaves (Pearcy and Yang 1996), of bending of branches due to gravity, and of collision between branches (Room et al. 1994). Geometric models also provide the information necessary to produce realistic images of plants (see Figure 4.10 and Figure 4.11), which has additional applications in education, entertainment, and art (Prusinkiewicz and Lindenmayer 1990, Prusinkiewicz 1998). For more examples of models and their applications, see reports by Kellomäki and Strandman (1995), Perttunen et al. (1996), and Küppers and List (1997).

From the many models available to simulate plant growth there are two systems that have the widest potential application for plant ecologists and physiologists: L-systems (initiated by Lindenmayer and further developed by Prusienkiewcz) and AMAP (Atelier pour la Modélisation de'Architecture des Plants) originated by de Reffye. AMAP uses stochastic mechanisms, and L-systems, although initially deterministic, can incorporate stochastic mechanisms as well. Despite the fact the AMAP has remarkable utility in agronomy by giving a central role to the structure of plants (Godin 2000), L-systems are inherently more versatile and hold greater promise (Room et al. 1994). Although an ideal growth model takes both internal and external factors into account, models to date focus on either one or the other. Room et al. (1994) revised all the internal and external parameters affecting metamer dynamics that should be considered in modeling plant growth. The advance of plant growth modeling is challenged by the difficulties of making virtual plants responsive to the environment and to neighboring plants in real time, and devising efficient methods of measuring plant structure, which is crucial information for the models that is usually hard to obtain.

Arrangement of Leaves

Fisher (1986) distinguished five different factors that determine the position of leaves. Among them, only two (phyllotaxis, which is addressed in this section, and secondary leaf reorientation by internode twisting, petiole bending, or pulvinus movement, which is addressed in the Section "Structural Determinants of Light Capture") apply to the leaves themselves. The other three concern the branching pattern and the position of the leaf-bearing branches. For instance, internode length affects the longitudinal distribution of leaves along the axis, or the existence of short and long shoots determines whether leaves would be produced every year or not, since, in general, only short shoots continue to produce leaves after one growing season. *Phyllotaxis*, as the sequence of origin of leaves on a stem (Figure 4.1), has a great impact not only on the shape of a crown (it affects the position of axillary buds or apical meristems and thus determines branching patterns), but also in many functional aspects of the crown since it affects the interception of light and the patterns of assimilate movement (Watson 1986). Phyllotaxis is responsible for the morphological contrast between plants with leaves along the sides of horizontal twigs, forming horizontal sprays of foliage, and those with leaves spiraling around erect twigs. With regard to leaves, there can be one per node (as in all monocotyledons and in some dicotyledons) or more than one per node (as in many dicotyledons). Leaves that lie directly above one another at different nodes form vertical ranks called orthostichies. When there is only one leaf per node, the phyllotaxis can be monostichous, distichous, tristichous, or spiral if the stem has one, two, three, or more than three orthostichies, respectively (Figure 4.1). Monostichous is a very rare phyllotaxis and is usually accompanied by a slight twist of the stem that arranges the leaves in a shallow helix; the corresponding phyllotaxis is called spiromonostichous (Bell 1993) (Figure 4.1 and also see Figure 4.10). In a distichous foliage, the two rows of leaves are 18° from each other, whereas in a tristichous foliage, leaves are in three rows with 120° between rows.

Spiral phyllotaxy results when each leaf is at a fixed angle from its predecessor in such a way that a line drawn through successive leaf bases forms a spiral (the genetic spiral) around the stem. This widespread phyllotaxis, also called disperse due to the apparent lack of geometrical pattern, can be mathematically described as a fraction in which the denominator is the number of leaves that develop before a direct vertical overlap between two leaves occurs, and the numerator is the number of turns around the stem before this happens (see Valladares 1999). This fraction times 360 is a measure of the angle around the stem between insertion of any two successive leaves (e.g., for a tristichous phyllotaxis, the fraction is 1/3, meaning that three leaves are developed before vertical overlap between two leaves, and this overlap happens in one turn around the stem, and the 120° between the orthostichies or between two successive leaves results from 1/3 times 360°). When the phyllotactic fraction of plants with spiral phyllotaxis was calculated and ordered, the following series was obtained: 1/2, 1/3, 2/5, 3/8, 5/13, 8/21, and so on. Interestingly, in this series both numerators and denominators form Fibonacci series since each number is the sum of the preceding two numbers. When multiplied by 360°, this series converges toward 137.5° (Fibonacci angle), which is the divergence angle between two successive leaves in most plants with spirally arranged leaves (Leigh 1972, Bell 1993). Other phyllotaxes can be observed when more than one leaf is present on each node. The simplest case is the opposite foliage, with two



Phyllotaxis	Num. leaves per node	Num. of orthostichies	Lateral view	Apical view
Monostichous	1	1		
Distichous	1	2		
Tristichous	1	3		
Spiral (helicoidal or disperse)	1	>3		
Opposite	2	2		
Decussate	2	4		
Whorled	>3	>3		

FIGURE 4.1 Main patterns of leaf arrangement (phyllotaxis) in plants. In the sketches, the black leaf (or leaves) represents the uppermost one in the shoot. A common alteration that results in a phyllotaxis that looks distichous (pseudodistichous), which has been generally interpreted as an adaptation to avoid self-shading, is shown in the lower part of the figure.

leaves 180° apart at each node, forming two orthostichies. A common variation is the decussate phyllotaxis, which has four orthostichies due to the fact that successive pairs of leaves are orientated 90° to each other (Figure 4.1). A more complex variation is the bijugate or spiral decussate phyllotaxis, where successive leaf pairs are less than 90° apart, leading to a double spiral (Bell 1993).

The ease with which the phyllotactic fraction is measured in a given plant is frequently confounded by internode twisting or leaf primordium displacement. It is relatively frequent that several phyllotaxes converge in an apparent distichous foliage. For example, the needles of some *Abies* are in two rows and look distichous, but their real phyllotaxis is spiral, as indicated by the petiole insertion (Figure 4.1). A similar case was found in the shade shoots of the chaparral shrub *Heteromeles arbutifolia*, which exhibited a pseudodistichous phyllotaxis instead of the characteristic spiral phyllotaxis of the species (Valladares and Pearcy 1998). Decussate phyllotaxis might also look distichous, as observed in horizontal shoots of *Lonicera* (Figure 4.1). Spiral and distichous leaf arrangements are also sometimes found in the same plant species. For instance, certain plants may first, as seedlings, set leaves spirally around an erect stem, and then, as mature individuals, develop a distichous foliage on the horizontal branches produced in the axes of the initial leaves. This seems to be the case for the tropical forest understory herb *Dichorisandra hexandra* (see Section "Structural Determinants of Light Capture" and Figure 4.10). Phyllotaxis is a clear case of phylogenetic constraint (Niklas 1988), but plants have solutions to compensate for the functional drawbacks of a given phyllotaxis. Spiral phyllotaxis can render contrasting shoot patterns with a simple change of 2° in the leaf divergence angle (Figure 4.2). However, despite the remarkable change in leaf overlap as seen from the top of the shoot, light capture is little affected by such a phyllotactic change (Valladares and Brites 2004). This negligible influence of the divergence angle on the light capture by spirally arranged shoots is in contrast with theoretical expectations: the intriguing trend of spiral phyllotaxis to converge in the golden angle, which allows for an infinite number of leaves to be arranged along a shoot without anyone fully blocking any other one, has been interpreted as a trend to maximize light capture efficiency (see Figure 4.2 and Valladares and Brites 2004). Significant differences in light capture efficiency are found, however, in comparisons of spiral versus opposite phyllotaxis, with a lower efficiency in the later (Figure 4.2). Nevertheless, the differences in light capture due to a given phyllotaxis can be easily compensated by an increased in either internode or petiole length (Pearcy and Yang 1998, Brites and Valladares 2005).

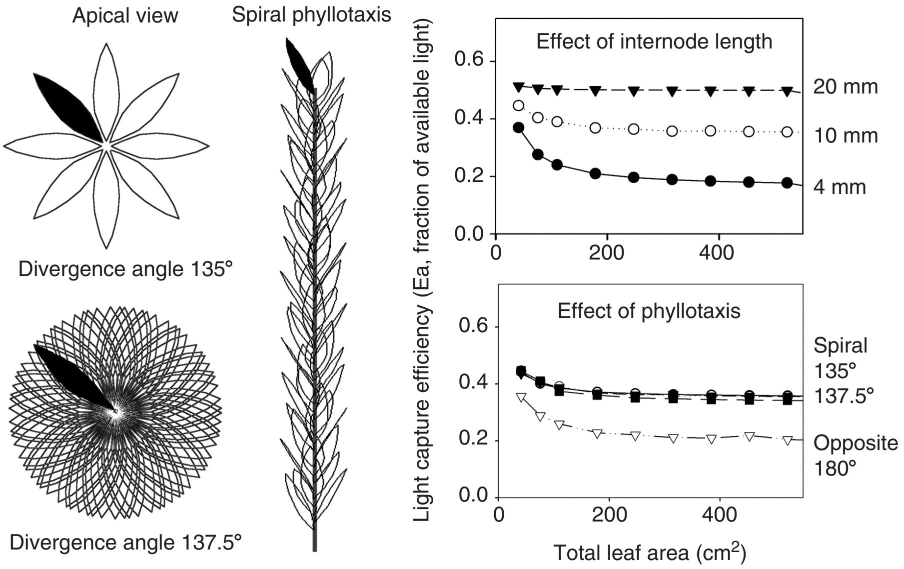


FIGURE 4.2 A vertical shoot such as that of *Heteromeles arbutifolia* (central drawing) generates contrasting views when seen from above (*left* images; the uppermost leaf is shown in black in the three figures). In a shoot with spirally arranged leaves such as the one of the figure, a mere 2.5° change in the divergence angle can dramatically change the number of leaves seen from above from only eight to all in the shoot (a golden angle of 137.5° generates an infinite number of ortostichies—see Figure 4.1). However, this contrasting arrangement had almost no effect in light capture efficiency (*right* graphs, note that values for 135° and 137.5° overlap), particularly when compared with simulations of the same shoot but with opposite phyllotaxis. By contrast, internode length (*upper right* graphs) had a very significant effect in light capture, so by modifying their internode plants can compensate phylogenetic constraints on light capture efficiency such as those imposed by an opposite phyllotaxis. Graphs on the right represent light capture efficiency versus total leaf area of the shoot. (Adapted from Valladares, F. and Brites, D., *Plant Ecol.*, 174, 11, 2004; Brites, D. and Valladares, F., *Trees: Struct. Funct.*, 19, 671, 2005.)

Classifying Crown Architectures

The first, and possibly the best known, classification of tree architecture was reported by Hallé et al. (1978). Basic features of this classification were dichotomic characteristics of the tree crown, such as monopodial or sympodial branching, basitonic or acrotonic branching, orthotropic or plagiotropic shoots, etc. (see Valladares 1999, for terms and for a key to these classic architectural models). From the practical point of view, this classification can be very difficult to use with certain species because the researcher must know the way by which the shape of the crown is achieved during the ontogeny of the tree from the seedling to sexual maturity, something that exceeds the time frame of most field studies dealing with long-lived plants. In addition, certain species exhibit architectural ambiguities, shifting from one model to another during their ontogeny or under different environmental conditions. Leigh (1990, 1998 #43993) modified Hallé et al. classification, simplifying it by merging some models that cannot be easily distinguished.

Architectural models are a convenient starting point for interpreting plant form, but there is a series of variations and exceptions to each program of development that complicates classification and suggests the search of additional descriptions of crown shapes. For instance, *Arbutus* sp. exhibit two different architectural patterns depending on the light environment, and *Acer pseudoplatanus*, as with many other woody plants, undergo significant changes of branching patterns during the ontogeny, switching from one model to another (Bell 1993). There are also many examples of metamorphosis (abrupt change from plagiotropic to orthotropic disposition of a branch) and intercalation of shoots infringing the rules of each model (Bell 1993). Nevertheless, architectural models are useful to predict the form that a plant assumes in the absence of unusual external forces or when affected by the common circumstance of losing a structural subunit (e.g., a branch) through injury. The modules that regrow when a tree loses a subunit usually mirror the architecture of the whole crown of the tree in a process called reiteration (Hallé et al. 1978, Hallé 1995). As the tree grows, the number of reiterated units tends to increase, but their size tends to diminish, and ultimately only parts of the architectural unit are reiterated in a so-called ‘‘partial reiteration’’ (Hallé 1995). This reiteration process that occurs during the growth of a large tree reinforces the idea that most trees are colonies, the elementary individual being not the bud, but the architectural unit. This idea of a plant as a colony (discussed in Section ‘‘Plant Design’’) dates back to eighteenth century: botanists such as de la Hire, Bradley and von Goethe (see references in White 1979), and Charles Darwin and his grandfather Erasmus Darwin thought that coloniality existed in trees. Although reiterated units have largely been considered as leafy branch systems, Hallé (1995) went one step beyond, posing the hypothesis that these units comprise their own root system, and thus the bole is made up of the aggregated root systems of all the reiterated units forming the tree crown. Needless to say, this hypothesis is controversial and may be somewhat heretical to certain readers, as acknowledged by Hallé himself (Hallé 1995 p. 41).

FUNCTIONAL INSIGHTS INTO ARCHITECTURAL CLASSIFICATIONS

Since the shape of the crown influences important aspects of growth and survival of plants, such as light interception and competition for space, the adaptive significance of the architectural models of Hallé et al. (1978) has interested many ecologists dealing with plant form. While all investigators agree that crown shape is generally adaptive, there is no consensus regarding the ecological and evolutionary implications of these architectural models (Porter 1989). On the one hand, as observed by Porter (1989), fossil plants exhibit only three of 23 possible architectural models described by Hallé et al. (1978), mostly due to the remarkable lack of fossil examples of sympodial branching. This clumping of fossil trees among Hallé et al. models suggests that some plant forms may have paid an evolutionary penalty for their mode of whole plant development, that is, the limited number of ancestral architectures may have limited the number of architectural models that have survived. On the other hand, Ashton (1978) pointed out that in West Malaysia, certain models were very rare in shady habitats, whereas a very plastic type of organization (Troll's model) was very widespread. The relatively small number of models found in temperate deciduous forests (the conifer forests of the boreal regions have even fewer models) suggests that some models are selected against in some regions (Ingrouille 1995).

Three arguments have been given to support the notion that these architectural models are not adaptive: (1) all models only coexist in lowland tropical rainforests, so a single ecological region has not favored some models at the expense of others; (2) the same model exists at different levels in the forest canopy, despite the remarkable vertical gradients of light, predation, and nutrients; and (3) the same model exists in different growth forms from very tall trees to small herbs, which clearly do not share the same ecology (Fournier 1979). Actually, developmentally different models can produce functionally similar crown shapes (ecological convergence). And a single model shared by different plant species can produce functionally divergent crowns due to differences in factors such as the relative elongation of axes and the exact arrangements of leaves (Fisher and Hibbs 1982). Additionally, efficiency of leaf display, which is crucial in the ecological strategy of most species (see Section "Structural Determinants of Light Capture"), is not included in the parameters used to define the architectural models (Tomlinson 1987).

There is a wide plasticity allowable within one model of Hallé et al., so these models may lead to unequivocal ecological predictions only for the simplest crowns (Waller 1986). Because development plasticity is an intrinsic characteristic of plant form (see Section "Plasticity, Stress and Evolution"), any attempt to classify the architectural patterns of plants should include the structural response of each species to different environments or perturbations. And a response is a quantitative process, which would make the separation of species into discrete models very difficult. In many plants, and especially in long-lived trees, it is a challenge to distinguish the genetically determined structure from environmental damage and phenotypic plasticity (Fisher 1992). Consequently, searching for a single ecological classification of plant architecture seems a vain endeavor. The critical parameters for the classification of plant shape must vary depending on the problem at hand (Sachs and Novoplansky 1995).

The most widespread architectural classifications have been developed for trees, but they could be used with other plants if characteristics such as multiple stems are considered in detail. The multiple-stemmed characteristic results from the growth of buds from the below-ground level that escape apical dominance to form new stems or modules (Wilson 1995). Multiple-stemmed shrubs exhibit not only a different shape than single-stemmed shrubs, but also a different tolerance to perturbations (e.g., fire and pests). Multiple-stemmed shrubs can survive indefinitely as a clone by producing new stems, whereas single-stemmed shrubs die when the stem dies. The maintenance of an apical control; the tendency of the stems to bend toward the horizontal, producing vigorous vertical shoots in a series of arching segments; or the location of the underground buds of multiple-stemmed shrubs (on the basis of the shoot, along rhizomes, layered branches) are also important features to consider in the description of shrub architecture (Wilson 1995).

REAL CROWNS: IMPERFECT ARCHITECTURES OR CONTROLLED VARIABILITY?

In contrast to human designs such as buildings, the final shape of the crown of a plant expresses a remarkable variability, which is evident even in comparisons of two halves of the very same individual (Sachs and Novoplansky 1995). However, there is a characteristic design or architectural pattern for each plant species. Therefore, the general shape of a crown is rather constant for a given species under a given environment, whereas many aspects of branch growth and survival do not follow a strict program, exhibiting an apparently stochastic behavior. At least the following three parameters have been shown to introduce variability in the shape of a plant: (1) the location and number of developing apices; (2) the developmental rates of individual apices; and (3) the shedding of branches (Sachs and Novoplansky 1995). Is this variability in the crown shape due to a malfunction of the genetic program that determines the development of the shape of a plant? How could the general form of a tree be more predictable than the individual events (e.g., production and shedding of branches) that lead to it? Variability in the final shape is not characteristic of primitive or maladapted plants, and it is not the result of errors in the developmental program. On the contrary, it has a crucial ecological role in changing and heterogeneous environments (see Section "Plasticity, Stress and Evolution"). On the other hand, predictable mature structures can result from selection of the most appropriate developmental events from an excess of possibilities that are genetically equivalent (epigenetic selection Sachs 1988). In this way, the final shape or pattern is genetically specified, but the development of the crown gravitates toward this final shape without a detailed genetic program. This tendency toward the final shape is accomplished by means of internal systems that control the variability in the aforementioned parameters, but allow for developmental plasticity. These control systems that constrain development variability include internal correlative interactions between branches, responses to local shading, and programed limitations of successful branches (Sachs and Novoplansky 1995). In conclusion, although the architecture of a plant limits its range of possible shapes, a plant's architectural model does not determine its final shape.

STRUCTURAL DETERMINANTS OF LIGHT CAPTURE

Canopy photosynthesis rate depends on the biochemical capacities of the foliage as well as on the distribution of light within the canopy (Wang and Jarvis 1990, Baldocchi and Harley 1995, Sinoquet et al. 2001). A major outcome of variation in crown architecture is modification of the overall light harvesting and the efficiency of light harvesting. The total leaf area supported by given crowns is the most basic structural property that affects the fraction of absorbed radiation. However, the distribution and arrangement of leaves within a crown can strongly modify the light harvesting efficiency of unit foliage area (Ross 1981, Cescatti and Niinemets 2004). As the three-dimensional arrangement of leaves in a crown is difficult to measure, light interception and canopy photosynthesis is often simulated assuming that foliage is randomly dispersed throughout the canopy volume (Beyschlag and Ryel 1999). However, recent development of three-dimensional ray-tracing models (Pearcy and Yang 1996, Sinoquet et al. 1998) as well as application of more advanced radiative transfer models combined with laborious harvesting of plant material (Baldocchi et al. 1984, Baldocchi and Collineau 1994, Niinemets et al. 2004a) has made it possible to resolve the effects of spatial clumping, foliage inclination angle, and foliage area density on distribution of solar energy in plant stands.

In most radiative transfer models, the sun is also considered as a point light source, and generally two classes of foliage—sunlit and shaded—are separated for any given situation (Wang and Leuning 1998). In reality, the radius of solar disk as seen from the earth is about 0.27 degrees. Due to finite size of solar disk, phytoelements can partially shade each other, resulting in intermediate situations between completely sunlit and shaded foliage, that is, in penumbral radiation. Recent advances in ray tracing approaches has made it possible to evaluate the importance of penumbral radiation for overall distribution of light in the canopy and on photosynthesis (Stenberg 1995, Cescatti and Niinemets 2004).

SHAPING THE FOLIAGE: THE SINGLE-CROWN LEVEL

Crown shape and the arrangement of foliage within the crown are the two most basic characteristics affecting the efficiency of light capture. From a photosynthetic perspective, the most efficient canopy is achieved when all of the leaves are evenly illuminated at quantum flux densities that saturate photosynthesis, that is, at intermediate quantum flux densities. Such ideal canopies are found in the nature rarely, if at all. Various crown shapes and different dispositions of leaves within the crown result in complex diurnal and seasonal patterns of light interception at both the single-leaf and the whole-crown levels. Leaves at the uppermost positions of the canopy are frequently exposed to high irradiances that are often in excess for photosynthesis. Lower leaves, in turn are often heavily shaded, and the light available for these depends not only on the amount of neighboring leaves, but is also affected by the general form of the crown and the angle and orientation of the surrounding units of the foliage (Niinemets and Valladares 2004). In addition, the level of incident photon irradiance can be regulated by diurnal movements of foliage units, that is, crowns can have their geometries changing over a short time interval.

Crown Size and Shape

The questions of whether there is a perfect crown shape that maximizes light interception in a given environment, and how far are the actual crown shapes of an optimal has attracted many researches (Jahnke and Lawrence 1965, Horn 1971, Terjung and Louie 1972, Oker-Blom and Kellomäki 1982, Kuuluvainen 1992, Chen et al. 1994). Probably most stimulating insight into the significance of variation in crown shape has been attained by studies investigating the role of different crown shapes in gradients of overall variation of available light during forest succession (Horn 1971), and in studies looking at the variation of solar radiation and average inclination of beam radiation with latitude (Kuuluvainen 1992).

The shape of the crown can be described by the absolute size, the ratio of height to width, and the convexity or shape of its contour. As the solar inclination angle decreases from equator to higher latitudes, crowns with differing height to width ratio have inherently varying efficiencies of light interception. Specifically, in high latitudes, light penetrates from high solar inclination angles, implying that beam path lengths become increasingly longer with increasing crown flatness. The beam path lengths are similar throughout the entire canopy for the narrow, vertically extended crowns that maximize the direct light interception of entire crown in high latitudes (Figure 4.3, Kuuluvainen 1992). In low latitudes, the beam path lengths are shortest for flat, horizontally extended crowns (Figure 4.3, Kuuluvainen 1992). The dominance of tall and thin conifers at high latitudes, and flat-topped Mediterranean conifers (*Pinus pinea* and *Pinus halepensis*) as well as acacia-like trees at low latitudes, partly confirms and supports the adaptive value of these two general crown shapes at different latitudes.

Crown shape	Latitude of maximum efficiency	Season of maximum efficiency	Season of maximum light interception
	Low to medium	Summer	Summer
	Medium to high	Winter	Spring–autumn

FIGURE 4.3 Latitude and season of maximum efficiency of light interception, and season of maximum light interception for two main types of crown shape: flat and broad versus thin and tall.

Contrary to these suggestions, Chen et al. (1994) discussed that the latitudinal variation of potential sunlight interception by different crown shapes does not match very well with the existing latitudinal gradients of crown shape. They suggested that this mismatch arises because (1) light is not the only factor affecting the crown shape variation along the latitudinal gradient, and that (2) in addition to crown shape, the geometry and distribution of the foliage alter crown light interception, partly compensating for differences in crown shape (Chen et al. 1994). As the result, crowns of different shapes can intercept a similar fraction of the available light.

It is further important that the crown shape can vary at any given height to width ratio. For low-solar inclination angles, the beam path length strongly increases with canopy depth for narrow ellipsoidal crowns. However, the beam path length is essentially the same for narrow conical crowns, in which the branches in lower canopy positions reach farther from the stem, implying that such crown can be very efficient at low latitudes. In general, the more extended the cone, the larger is the fraction of irradiance captured (Jahnke and Lawrence 1965). Simulations demonstrate that for a given latitude, either very small or very large values of the height-to-width ratio result in maximum direct light interception (Chen et al. 1994).

The crown height-to-width ratio must reach a balance between growth in height to reach the brighter areas of the canopy, and growth in width to intercept light and occupy enough space (Horn 1971, Givnish 1988, Küppers 1989). In addition, the greater the convexity of a crown, the greater the irradiance intercepted at most latitudes, but also the greater the amount of supporting and conductive tissues. Horn (1971) predicted that the optimal shape of trees varies in dependence of tree successional position and distinguished three different successional strategies: early successionals, late successionals, and early successionals in the mature forest (Figure 4.4). Because early succession is a race to form a canopy, fast-growing softwoods are favored over stronger hardwoods, and growth in height is favored over growth in width (Horn 1971, King 1991, 1994). For rapid height growth, stems of some early-successional species are even hollow (King 1994). Because of weak wood and relatively thin stems, early-successional trees cannot form extensive wide-reaching crowns.

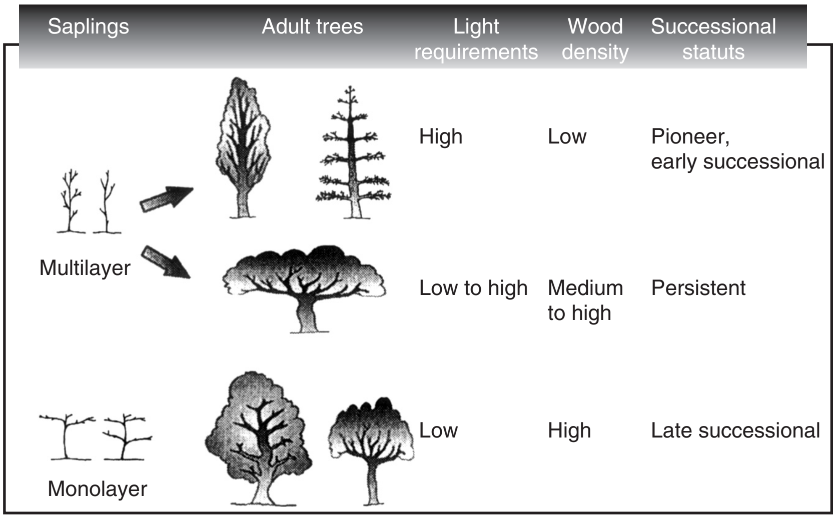


FIGURE 4.4 Crown shape as sapling and adult, light requirements, and wood density predicted for trees of different successional status. (Adapted from Horn, H.S., *The Adaptive Geometry of Trees*, Princeton University Press, Princeton, NJ, 1971.)

Horn (1971) predicted that crown shape of saplings of early-successional, shade-sensitive species is multilayered, consisting of short branches distributed over a long distance from top to bottom of the stem (Figure 4.4). Such a crown allows plants to expose a large leaf area in several independent layers to high irradiance. However, this crown shape is inefficient in low light because it results in extended self-shading within the crown. Late-successional, shade-tolerant species are predicted to be monolayered, distributing total sapling leaf area in a single layer by far-reaching extensive branch framework and thereby capturing more light in low irradiance (Horn 1971). Some multilayered trees persist by invading small openings in the forest and should have a mixed strategy. Because these species must initially race to the canopy, they must be tall, thin, multilayered, and made of softwood. Once they reach the canopy, they should spread out and dominate the forest gap. The height-to-width ratio decreases with age, and their wood should become harder to provide lateral support.

Although the predictions of crown shape variation during succession are based on only a single factor, light, and provide therefore an incomplete theory, as Horn himself acknowledged (Horn 1971 p. 121), these predictions provide an explicit list of testable assumptions. The experimental evidence of the successional sequence of crown shapes and foliage distribution has been scarce, but the available evidence from some temperate and tropical forests supports the gradual change from multilayer to monolayer species during succession (Horn 1971, Niinemets 1998, Sterck et al. 2001, 2003, Pearcy et al. 2005). Many observations reveal that plant species partition canopy light gradients through variation in adult stature and light demand, which has been well characterized in complex tropical forests (Poorter et al. 2005). Adult understory trees are typically shorter than similar-diameter juveniles of high-light species, since wide crowns allow intercepting light over a large area at the expense of a reduced height growth, whereas light-demanding species are characterized by orthotropic stems and branches, and large leaves (Poorter et al. 2005).

Functional analyses of the importance of crown shape often neglect the overall availability of light and the time of the year of maximum irradiance and light interception. Although the maximum efficiency of light interception by narrow-shaped trees is achieved during the winter, they intercept more light in spring and autumn. In broad-shaped trees, both light interception efficiency and the amount of light intercepted reach their maximum values during the summer. In addition, the fraction of diffuse radiation (radiation from all angles) in total irradiance importantly affects the efficiency of a crown light capture. In environments with frequent cloud cover as maritime temperate forests and mountain cloud forests, a large fraction of radiation is received as diffuse radiation, and as a result, the role of the crown shape less strongly affects the overall light interception. Understanding the relations between the latitudinal gradients in crown shape and the latitudinal variation of the light regime, requires both theoretical analyses of crown shape and light interception (like the one by Chen et al. 1994), and further case studies exploring the real light environment experienced by trees of different shapes at different latitudes. These studies should necessarily also investigate the modification of crown shape by other interfering factors and constraints, such as water, snow, gravity, and wind.

Geometry of Foliage Arrangement within the Crown

The amount of foliage supported by a given crown is measured by crown leaf area index, L ($m^2\ m^{-2}$), defined as total leaf area divided by the total ground area where it stands. The distribution, dispersion, and inclination of leaf area in space defines the probability for light beam penetration though a canopy gap to the lower leaves. Crowns with the same values of L can have widely differing efficiencies of light capture (Ross 1981, Baldocchi and Collineau 1994, Cescatti and Niinemets 2004).

Foliage Dispersion

Foliage dispersion is a major factor affecting the light-harvesting efficiency of unit foliage area. Simple light interception algorithms assume that plant canopies consist of randomly dispersed foliage elements. In real canopies, the foliage is often clumped to branches and shoots, resulting in greater fraction of canopy gaps and significantly larger light transmission relative to a clumped canopy (Figure 4.5, Ross 1981, Baldocchi and Collineau 1994, Cescatti and Niinemets 2004, Sinoquet et al. 2005). While clumped canopies intercept light less effectively, clumping allows the plants to expose larger leaf areas. Canopies with random dispersion intercept essentially all light above a L of 5 m^2 m^{-2}, whereas canopies with extensively aggregated foliage, as in some conifers, can support leaf area indices as high as 15 m^2 m^{-2} and more (Figure 4.5, Margolis et al. 1995, Van Pelt and Franklin 2000).

In addition to random and clumped foliage dispersions, which result in a relatively large canopy gap fraction, foliage can be arranged regularly. Arranging leaves side-by-side in a planar layer efficiently fills the gaps in the canopy and thereby results in greater light harvesting at a common L than either random or clumped dispersion (Figure 4.5). As regular dispersion is an extremely efficient strategy for light interception, it is favored in low-light environments and in late-successional mono-layer species (Horn 1971, Cescatti and Niinemets 2004).

It is possible to derive the estimates of whole canopy foliage aggregation structure from light transmission measurements that provide effective leaf area index (L_{eff}) and separately harvesting plants to estimate L (Kucharik et al. 1999 for a review). However, modification of foliage clumping can occur at the level of individual crowns, branching patterns and individual shoots (Oker-Blom 1986, Cescatti 1998). Crown-level clumping arises because crowns

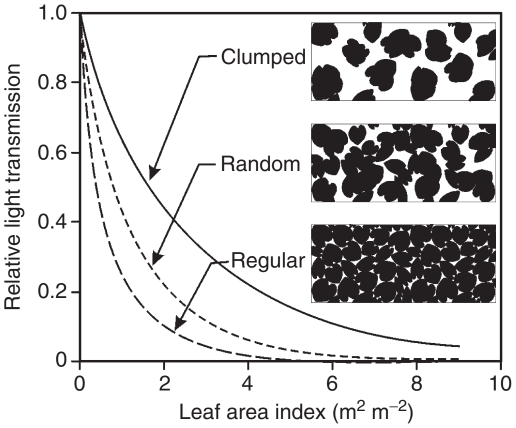


FIGURE 4.5 Light transmission relative to cumulative leaf area index for three hypothetical canopies. Relative to canopies with random foliage dispersion, canopies with clumped foliage intercept less light, and canopies with regular dispersion intercept more light. In these simulations, leaf angular distribution was assumed to be spherical, and light transmission was integrated over the entire sky hemisphere. Light transmission for nonrandom canopies was simulated using the theory of light penetration in nonrandom media (see Nilson 1971, Cescatti and Niinemets 2004 for details of light models). For the clumped canopy, we used a Markov model, using a clumping coefficient, $\lambda_0 = 0.5$, that corresponds to a moderately clumped canopy (λ_0 varies between 1 and 0, 1 corresponding to random dispersion and 0 to completely aggregated canopy) (Nilson 1971, Cescatti and Niinemets 2004). For the regular dispersion, we used a positive binomial model, with the parameter Δ_L (thickness of an independent leaf layer), set at 1.5 ($\Delta_L \rightarrow 0$ for a random dispersion, and the values increasing with the degree of regularity). In the boxes illustrating the concept of foliage dispersion, the number of leaves is equal for all dispersion types.

with different size and shapes result in different fraction of gaps in the canopy (Oker-Blom 1986, Cescatti 1998).

Branching modifies foliage dispersion via the frequency of branching (bifurcation ratio) and the branching angles. Modifying both of these characteristics can result in foliar displays that either minimizes the overlap among the leaf clusters on a horizontally spreading branch and results in regular foliage dispersion or results in strongly clumped foliage (Honda and Fisher 1978, Takenaka 1994b). As described earlier, there is a vast heterogeneity in the branch architectural models, but it is important to understand, that from a functional perspective, the branching architectural models mainly differ in the extent of foliage aggregation. For instance, the Aubréville's architectural model investigated in *Terminalia* results in arrangement of leaves side by side, minimizing the branch gap fraction and resulting in essentially regular leaf display (Honda and Fisher 1978, Fisher and Honda 1979a,b). In general, increases in the bifurcation ratio result in more clumped canopies, whereas lower bifurcation ratios result in random or regular canopies (Whitney 1976, Canham 1988). A branch system with a high bifurcation ratio allows plants to achieve a greater amount of foliar area for a given biomass investment in stem tissue, but such branch with enhanced clumping requires higher irradiance for full activity. Overall, the bifurcation ratio increases with increasing light availability (Kellomäki and Strandman 1995, Niinemets and Lukjanova 2003), demonstrating a general shift from highly divided branches with strong foliage clumping that require high light to less frequently bifurcating branches with more regular foliage display that require less light since they intercept it very efficiently.

At the shoot scale, light interception efficiency varies due to variations in the number of leaves per unit stem length, and differences in petiole length and leaf extension that modify the distance between the bulk of leaf area and shoot axis. Foliage is considered especially clumped in the shoots of conifers (Oker-Blom and Smolander 1988, Niinemets 1997, Stenberg et al. 2001), where the foliage in the shoots harvests light only with 10%–40% efficiency relative to the equivalent foliage area on an horizontal plane (Figure 4.6, Stenberg et al. 2001, Niinemets et al. 2002, Cescatti and Zorer 2003, Niinemets et al. 2006).

Increases in overall leaf extension and length of petioles strongly reduce shoot-level clumping, because these modifications reduce the shading by shoot axis as well as reduce the overlap of neighboring leaves (Figure 4.7, Takenaka 1994a, Figure 4.7, Pearcy and Yang 1998). At a global scale, there is a large variation in petiole length and foliage length. For instance, needle length varies between 2 and 35 cm among *Pinus* species (Figure 4.6). For the six conifer species depicted in Figure 4.6, which had contrasting foliage element length and shoot architecture, there was a uniform negative relationship between the degree of foliage clumping and foliage element length (Niinemets et al. 2006). However, an increase in the foliage element length and reduced clumping brings about lower foliage area density in the shoots with longer foliage elements (Figure 4.6). This implies that the canopies consisting of long-needled shoots do not cast deep shade and are open to invasion by competitors that can create denser foliage. Another disadvantage of increasing the length of foliage elements and petioles is the enhanced cost of support. In 17 clonal poplar stands, the whole canopy aggregation decreased with increased petiole length (Figure 4.7), but this resulted in overall greater fraction of foliage biomass invested in support (Niinemets et al. 2004a), implying a fundamental trade-off between efficiency of light harvesting and biomass investment in support.

In addition to the foliage and petiole lengths, shoot-level clumping can strongly vary with the distance between neighboring leaves on the shoot axis. Shorter distance between the leaves on shoot axis implies greater self-shading and aggregation within the shoot. Often, leaf number per unit shoot axis length increases in stressful environments due to stronger limitations on shoot length growth than on formation of leaves. Greater packing of needles on shoot axis explains greater aggregation and lower light harvesting efficiency of conifers on less

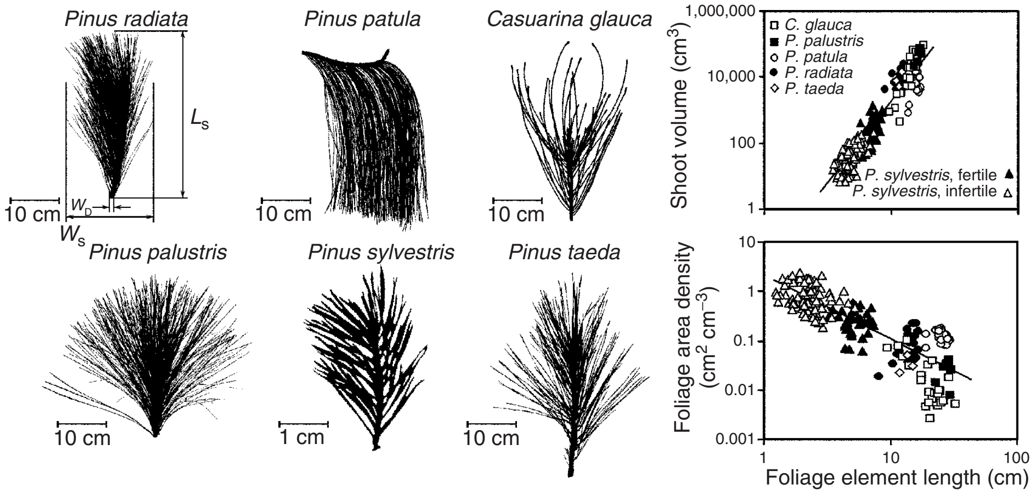


FIGURE 4.6 Illustration of shoot architecture in five *Pinus* species of contrasting needle length and in angiosperm conifer *Casuarina glauca*, and the relationships between shoot volume and foliage area density (ratio of half of the total foliage area to shoot volume) with the length of foliage elements (modified from Niinemets, Ü., Tobias, M., Cescatti, A., and Sparrrow, A.D., *Int. J. Plant Sci.*, 167, 19, 2006). Trees of *Pinus sylvestris* were sampled in two sites of contrasting fertility; needles were significantly shorter and shoots more clumped in the infertile site (Niinemets et al. 2002, 2006). Conifers have extensive clumping of foliage elements in the shoot. Light interception efficiency of unit leaf area, that is, the amount of light harvested by needles in their specific position in the shoot and with their specific cross-sectional geometry relative to the amount of light harvested by an equivalent flat surface, scales with the spherical average shoot silhouette area to total foliage area ratio $\overline{S_S}$ (Niinemets et al. 2002, Cescatti and Zorer 2003). The values of $\overline{S_S}$ (average ± SE for all shoots sampled per given species) were 0.2149 ± 0.0036 for *C. glauca*, 0.141 ± 0.008 for *Pinus palustris*, 0.1066 ± 0.0046 for *Pinus patula*, 0.0901 ± 0.0047 for *Pinus radiata*, 0.1562 ± 0.0047 for *P. sylvestris*, fertile site, 0.1147 ± 0.0019 for *P. sylvestris*, infertile site, and 0.147 ± 0.018 for *Pinus taeda*, demonstrating extreme inefficiency of light harvesting in these conifers. (Averages calculated from Niinemets, Ü., Tobias, M., Cescatti, A., and Sparrrow, A.D., *Int. J. Plant Sci.*, 167, 19, 2006.)

fertile sites (Niinemets et al. 2002, Palmroth et al. 2002). Analogously, greater clumping, and lower efficiency of shoot light harvesting in mature conifer trees relative to young trees is mainly associated with shorter and more densely leafed shoots in mature trees (Figure 4.8, Niinemets and Kull 1995, Niinemets et al. 2005). Several hypotheses have been advanced to explain the tree productivity decreases with tree age, mainly focusing on foliage physiological characteristics (Ryan et al. 1997), but there are important data demonstrating that the foliage clumping does increase in older stands (Brown and Parker 1994). Shoot-level observations suggest that enhanced foliage clumping due to arrested shoot growth may partly explain the curbed productivity in older trees.

Foliage Inclination and Orientation

Variation in vertical foliage angle and azimuthal orientation can generate large differences in diurnal patterns of light interception in canopies with similar degree of foliage aggregation. Steep leaves project a small fraction of their area to the sun during the central hours of the day, but the overall effect depends on foliage azimuth. Although steep leaf angle always reduces the light interception at individual leaf level, this reduction can vary from strongly limiting to negligibly affecting photosynthetic carbon fixation (Valladares and Pearcy 1999). Since crowns consist of large number of leaves that interact in determining the whole canopy

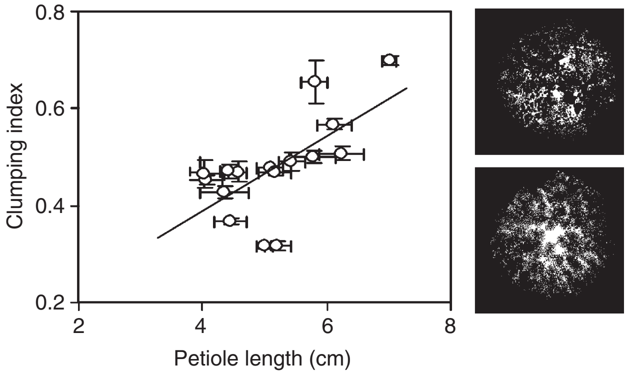


FIGURE 4.7 Relationship between the canopy clumping index (λ_0, Markov model of radiative transfer, Figure 4.5) and average petiole length for 17 different clonal stands of *Populus* (Niinemets et al. 2004a). The clumping index was derived from measurements of leaf area index by hemispherical photography (effective leaf area index L_{eff}) and actual measurements (L) and is given as $\lambda_0 = L_{\mathrm{eff}}/L$. $L_{\mathrm{eff}} = L$ ($\lambda_0 = 1$) for canopies with random dispersion, whereas L_{eff} becomes relatively smaller with increasing foliage aggregation. The hemispherical photographs illustrate two poplar canopies with similar effective leaf area index, but different total leaf area index and λ_0. Upper canopy photograph—*Populus deltoides* × *Populus nigra* 'Gibecq' ($\lambda_0 = 0.67$, $L_{\mathrm{eff}} = 2.33$, $L = 3.74$ m^2 m^{-2}). Lower canopy photograph—*Populus nigra* 'Wolterson' ($\lambda_0 = 0.30$, $L_{\mathrm{eff}} = 2.07$, $L = 6.84$ m^2 m^{-2}). (Modified from Niinemets, Ü., Al Afas, N., Cescatti, A., Pellis, A., and Ceulemans, R., *Tree Physiol.*, 24, 141, 2004a.)

light interception and light distribution, and single crowns can have leaves with differing angles, it is more appropriate to use leaf surface angle distributions to simulate the role of leaf angles in whole canopy light interception (Campbell and Norman 1989). To understand the effect of leaf angular distribution on whole canopy light harvesting, it is further important to integrate the light harvesting of the canopy over the entire day (Figure 4.7). Because solar position changes during the day, leaf angular distribution has generally a minor effect on total light interception and canopy photosynthesis for sparse canopies with a leaf area index (L) less than approximately 3 (Duncan 1971, Gutschick and Wiegel 1988). The effects of leaf angular distribution on canopy photosynthetic production are stronger for canopies with large leaf area (Duncan 1971, Gutschick and Wiegel 1988).

Horizontal leaves at the top of the crown exhibit their maximum light interception efficiency at times of the day and the year (midday and summer, respectively) when irradiance in sunny environments is well above the light saturation point for photosynthesis. Therefore, the superior light capture of horizontal leaves in high light usually translates into a negligible increase of potential carbon gain (Figure 4.9). For these reasons, erectophile crops have a marked yield advantage over those with horizontal leaves, especially at high values of L and at high solar elevations (Isebrands and Michael 1986). However, light interception by steep leaves themselves is poor, and if they represent a large fraction of the foliage or if their angle is too steep and if this is further combined with extensive clumping because the leaf blades are too close to each other (see computer images in Figure 4.9), light interception and potential carbon gain by the whole plant decrease. In a simulation of light interception and potential carbon gain by shoots of *H. arbutifolia* with leaves set at different angles, vertical foliages absorbed 20%–30% less photosynthetic photon flux density (PPFD) and had 30% lower daily carbon gain than normal shoots (average leaf angle = 71°) (Valladares and Pearcy 1998).

Leaf angular distribution is often considered constant in the canopy, but numerous observations demonstrate that leaves are more vertical in the upper canopy and become gradually horizontal in the lower canopy (e.g., Thomas and Winner 2000, Niinemets et al. 2004b, 2005).

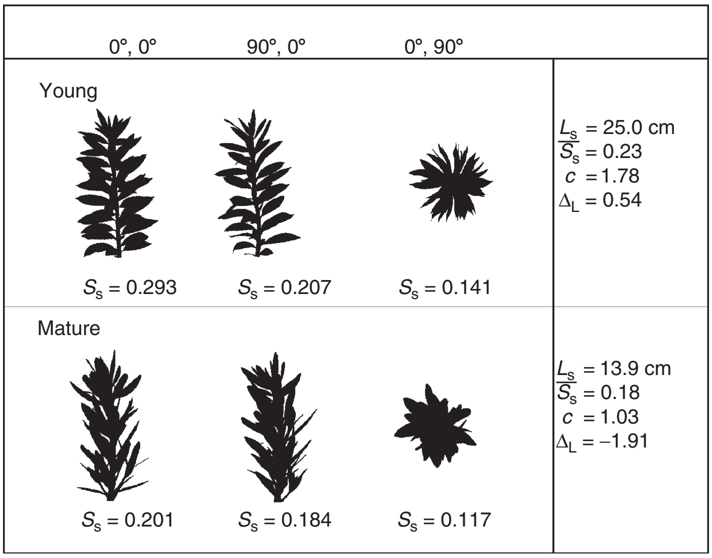


FIGURE 4.8 Representative shoot silhouettes for a young (tree height, $h = 4$ m) and a mature tree ($h = 18$ m) of temperate broadleaved conifer *Agathis australis* (data from Niinemets, Ü., Sparrow, A., and Cescatti, A., *Trees: Struct. Funct.*, 19, 177, 2005). The shoots were taken from similar high-light environments for both young (daily integrated seasonal average quantum flux density, $Q_{\text{int}} = 25.6$ mol m^{-2} day^{-1}) and mature ($Q_{\text{int}} = 26.8$ mol m^{-2} day^{-1}) tree. Shoots were photographed from various view directions. For the projection 0°, 0° (rotation, inclination angle) the upper part of the shoot is facing the view direction, for the 90°, 0° projection, the shoot is rotated 90° around its axis, and the projection 0°, 90° gives the shoot axial view. These and additional shoot projections were employed to derive the parameter of ellipsoidal distribution of leaf surface angles (c) and the degree of leaf clumping (Δ_L, defined in Figure 4.5) as described in detail in Niinemets et al. (2005). Ellipsoidal distribution of leaf angles assumes that the leaves are distributed parallel to an ellipsoid, and the parameter c is the ratio of ellipsoid major and minor semiaxes (Campbell 1986, Norman and Campbell 1989). $c = 1$ for a spherical distribution of leaf surface inclination angles, $c > 1$ for horizontal distributions, and $c < 1$ for vertical distributions. The clumping characteristic, $\Delta_L \rightarrow 0$ for a random dispersion, whereas positive values of Δ_L correspond to regular canopies (positive binomial model) and negative values (negative binomial model) to clumped canopies (Nilson 1971, Baldocchi and Collineau 1994). For every shoot projection, the ratio of silhouette to total surface area (S_S) and for every shoot, the spherical average of S_S ($\overline{S_S}$) and shoot length (L_S) are also provided.

As this pattern results in larger penetration of light to lower canopy layers, it results in a more uniform profile of light with the canopy than a distribution with constant leaf angles and maximizes whole-plant photosynthesis (Herbert 1991, Herbert and Nilson 1991). In a canopy with vertical inclination angles in the upper canopy and more horizontal leaves in the lower canopy, only a few leaves are light-saturated in the upper canopy, and the leaves at the base of the crown receive enough light for photosynthesis. Therefore, canopies with varying inclination angles can sustain greater foliage areas than canopies with constant inclination angles (Russell et al. 1989).

A little-explored aspect of leaf angle is how it interacts with leaf internal anatomical structure in modifying light harvesting and utilization at the chloroplast level. Leaf inclination affects the distribution of light between lower and upper surfaces, and depending on how efficiently foliage photosynthetic characteristics upper and lower surface of leaf acclimate to the long-term irradiance, modification of the fractional distribution of light interception between upper and lower surfaces of leaf can alter whole leaf photosynthesis (Poulson and DeLucia 1993, Valladares and Pearcy 1999). Large differences in mesophyll photosynthetic properties between the two sides of the leaves seem to depend on a complex interaction

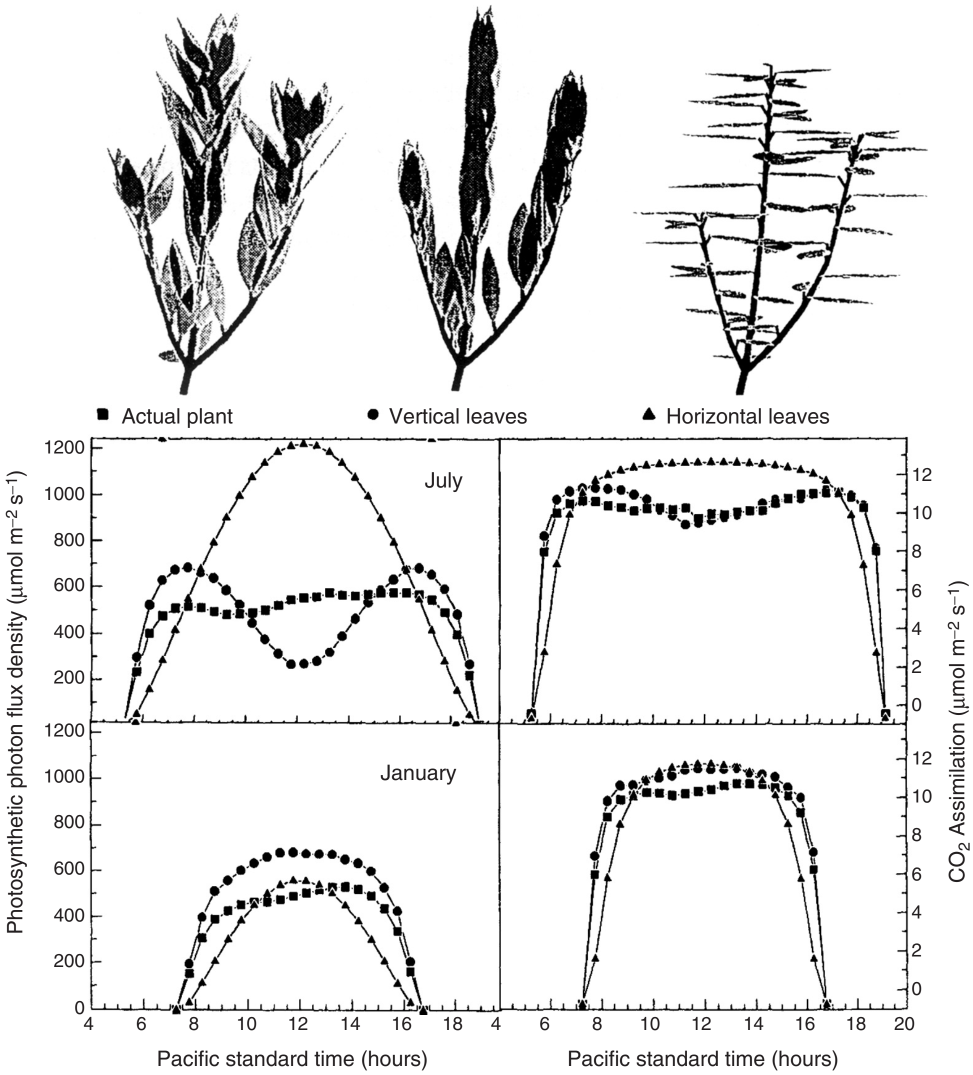


FIGURE 4.9 Diurnal course of interception of photosynthetically active radiation and CO$_2$ assimilation calculated for whole shoots of the chaparral shrub *H. arbutifolia* on a clear day of winter (*lower* graphs) and summer (*upper* graphs). Data were calculated for real shoots and for the same shoots with either vertical or horizontal leaves. Simulations were performed using the three-dimensional YPLANT model (Pearcy and Yang 1996). (Data from Valladares, F. and Pearcy, R.W., *Oecologia*, 121, 171, 1999.)

among light environment, leaf anatomy, and leaf angle (Myers et al. 1997). In addition, mesophyll cells (Smith et al. 1997) and bundle sheath extensions (Nikolopoulos et al. 2002) can function as optical fibres canalizing light into deeper leaf interior. However, to function as an optical fiber the leaf surface must be perpendicular to solar beams, implying that leaf inclination can modify the diurnal distribution of light penetration into the leaf.

Diffuse Light

We have so far considered the importance of leaf angular distribution for direct radiation interception, but diffuse light is an important component of incident radiation (Gutschick and Wiegel 1988, Herbert 1991). While the leaf angular distribution affects diffuse light transfer to a minor degree, foliage dispersion modifies diffuse light interception similarly to direct light interception (Cescatti and Zorer 2003). While the leaf angular distribution affects diffuse light transfer to a minor degree, foliage dispersion modifies diffuse light interception similarly to direct light interception (Cescatti and Zorer 2003). The geometry of the foliage, basically proximity of leaves and distribution of leaf angle throughout the canopy, affect the transport of diffuse light to lower layers. This can be relevant for whole-plant photosynthesis in both low- and high-light environments (Valladares and Pearcy 1998). Studies further demonstrate that the orientation of the crown and its leaves in the vicinities of forest gaps frequently respond to diffuse light rather than direct light (Ackerly and Bazzaz 1995, Clearwater and Gould 1995).

Penumbra

The majority of radiative transfer models assume that the sun is a point light source and separate only between shaded and sunlit foliage. As illustrated in Valladares (1999), this assumption can lead to significant errors in simulation of light interception and photosynthesis. The relevant parameter describing the relevance of considering that the solar disk has a finite size, is the ratio of canopy height to foliage element diameter (Cescatti and Niinemets 2004). The solar disk is completely blocked by a leaf (umbra) at a theoretical distance of 108 times the leaf diameter. An object farther than this distance is lit by at least part of the sun (penumbra). Empirically, this distance is approximately 50–70 times the leaf diameter with the sun at the zenith on a clear day (Horn 1971). Thus, long crowns with small leaves intercept a large fraction of light as penumbral radiation. In fact, in conifers, penumbral radiation can be more than 95% of total, whereas in broad-leaved herbs, penumbral radiation constitutes only a few percent (Cescatti and Niinemets 2004). Given the strong nonlinearity in photosynthetic light response, lack of consideration of penumbral radiation results in major underestimation of canopy productivity (Cescatti and Niinemets 2004). Overall, this discussion suggests that leaf size per se can play a major role in light harvesting by the whole crown and that future advancements of ray-tracing models can facilitate further insights into complex geometrical phenomena such as penumbra.

Changing Geometries: Leaf Movements and Rolling

Leaves from a number of species move during the day, keeping leaf blade either perpendicular (diaheliotropic movements) or parallel (paraheliotropic movements) to the direct rays of the sun. For the leaves tracking the sun, light interception can be enhanced by as much as 35% compared with a fixed leaf with a horizontal position (Ehleringer and Forseth 1980, Ehleringer and Werk 1986). For the leaves remaining parallel to the sunrays, can significantly reduce light interception and heat loads relative to a leaf remaining in a fixed position. Leaf solar tracking occurs in herbaceous species that do not form an extensive canopy and is most common in annuals (Ehleringer and Werk 1986). In drier sites, the frequency of leaf solar-tracking species seems to be inversely related to the length of the growing season, reaching values as high as 75% of the flora in the summer annuals of the Sonoran Desert (Ehleringer and Forseth 1980).

Leaf solar tracking poses a physiological dilemma when photosynthesis is impaired at midday by water or heat stress. Under these far-from-optimum conditions, diaheliotropic leaves can intercept excessive radiation that is potentially damaging to the photosynthetic apparatus. Certain species, such as the desert annual *Lupinus arizonicus*, avoid the dilemma, exhibiting either diaheliotropic or paraheliotropic leaf movements depending on the availability of water (Ehleringer and Werk 1986).

The overall effect of leaf movements on canopy productivity depends on stand leaf area index. When leaf area index is low, solar tracking enhances canopy productivity since leaves absorb photons that would otherwise pass through the sparse canopy. However, when leaf area index is greater than 4, leaf solar tracking reduces canopy productivity because the bulk of the canopy photosynthesis is restricted to the leaves of the upper parts of the crown (Ehleringer and Forseth 1989). In dense or very large crowns, leaf movements are restricted to the external layer of leaves, because the leaf movements require a high ratio of direct to diffuse components of the solar radiation (Ehleringer and Forseth 1989). By the same token, leaf movements are not expected to occur in habitats with a high incidence of overcast days or in understory habitats.

In addition to these short-term leaf movements, many species, in particular grasses, respond to drought by leaf rolling (Corlett et al. 1994, Turgut and Kadioglu 1998, Fernandez and Castrillo 1999). Leaves of these species have specific bulliform cells located near the vascular bundles. During drought, water is absorbed from these cells, resulting in inward rolling of the foliage (Moulia 1994).

CROWN ARCHITECTURE IN EXTREME LIGHT ENVIRONMENTS

Light can be a limiting resource in understories of dense stands or for plants subject to strong neighborhood competition, whereas light can be excessive and even harmful in open environments where plant metabolism is impaired by environmental stresses. Plant shape and size have been shown to change as a function of the light environment, and plants are capable of orienting their light-capturing surfaces in different ways to increase or decrease the leaf surface area projected in the direction of ambient light (Ellison and Niklas 1988, Stenberg et al. 1998, Cescatti and Niinemets 2004).

Plants exhibit a remarkable within-species and within-individual variability in their structural features. For instance, branching pattern of trees is not stationary, and it has been shown that the variation of branching pattern can be the result of developmental–phenotypic interaction (Steingraeber 1982). While in some cases it can be due to a malfunction of the genetic program, in most cases this variability is a plastic response to local conditions, and light is possibly the most spatially and temporally heterogeneous environmental factor affecting plant survival and growth. Structural plasticity of plants enables a fine-tuning with environmental changes so that the efficiency of the limiting processes at each stage is maximized. A common environmental change experienced by plants is the decreasing availability of light with the advance of succession. It has been shown for the succulent halophyte *Salicornia europaea* that morphological changes in the branching patterns during succession maximized light interception (Ellison and Niklas 1988). However, even phylogenetically close species differ in their capacity for a plastic response to the light environment (Valladares et al. 2000). Interestingly, certain species that exhibit an architecture suited to high irradiance conditions do not change significantly when grown in the shade. That was the case for mangroves in Malaysia: architecture and allometry of shaded mangroves were consistently more similar to those of exposed mangroves than to shaded, broad-leaved, evergreen, rainforest trees (Turner et al. 1995).

When Light is Scarce

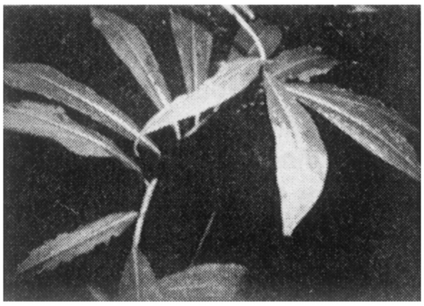
When plants grow in dense stands or in the understory, the resource of radiant energy becomes scarce, unpredictable, and patchy. In these environments, evolution has led to two principal approaches for survival: shade avoidance and shade tolerance. Angiosperms, in particular, have evolved an impressive capacity to avoid shade. The so-called shade-avoidance syndrome involves accelerated extension growth, strengthened apical dominance, and retarded leaf and chloroplast development, among other processes (Smith and Whitelam 1997, see Section ‘‘Plasticity, Stress and Evolution’’). Here the focus is on the functional aspects of the crown of plants that tolerate shade and on the structural features that are relevant for such tolerance.

Tropical rainforests exhibit an outstanding diversity of plant species and growth forms (Medina 1999, Wright 1999). Despite the extremely low levels of irradiance experienced in the understory of late-successional rainforests, a relatively large number of shrubs, herbs, and seedlings can be found within a few hectares. These plants suffer shading not only from the forest canopy and neighboring plants, but also from the leaves of their own crowns. The efficiency of light capture of 24 understory species differing in their habit and growth form was compared, and the influence of phyllotaxis and leaf size and shape in the avoidance of self-shading was explored in a field study in a lowland tropical rainforest in Barro Colorado Island (Valladares et al. 2002c). The species studied included understory palms, saplings of canopy trees, shrubs, and a wide variety of monocots of contrasting architectures. Plant size and total leaf surface area also varied significantly among the species considered. Most of the phyllotaxes shown in Figure 4.1 were represented, and leaf size ranged from a few to several hundred square centimeters. Light harvesting efficiency was calculated with the three-dimensional plant architecture model YPLANT (Pearcy and Yang 1996). The most remarkable result of this study was the functional convergence of the different plant species co-occurring in the forest understory: most of the species intercepted between 80% and 90% of the available radiation, and mutual shading of the leaves during the brightest hours of the day was little, approximately 10% of the foliage area in most cases (Figure 4.10). Thus, the rare spiromonostichous phyllotaxis of *Costus pulverulentus* (Figure 4.10), apparently a unique solution to avoid self-shading, was no better for this purpose than the spiral phyllotaxis of the saplings of *Thevetia ahouai* or the pseudodistichous foliage of the shrub *Hybanthus prunifolius*. Nevertheless, significant differences among species were found when the fraction of the plant biomass invested in support was considered in the analysis of the efficiency of the different architectures. Monocots, with a lower investment in dry weight, generally reached a more favorable compromise in this simple cost–benefit analysis of plant architecture under limiting light conditions (Valladares et al. 2002c). The drawbacks of the monocot strategy are a reduced survival to mechanical damage, and in some cases, a shorter plant longevity and a limited capacity to reach the forest canopy.

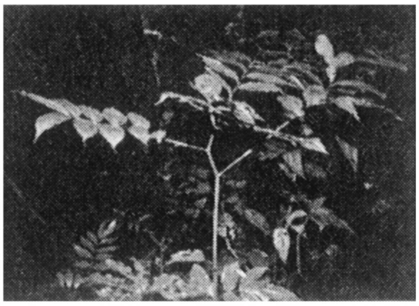
There is evidence that both spiral and distichous phyllotaxis are more frequent in low-light environments, whereas opposite phyllotaxis are more frequent in open, high-light environments (Brites and Valladares 2005). Several plant species first set leaves spirally around an erect stem, and then produce horizontal branches bearing distichous leaves (Leigh 1998). This combination of two phyllotaxes has been interpreted as a way of minimizing leaf overlap. *Dichorisandra hexandra* exhibits this combination of spiral leaves around vertical stems and distichous leaves around horizontal branches (Figure 4.10), but leaf overlap is as reduced as in other understory species with different leaf arrangements. It seems more likely that this combination of two phyllotaxes is an efficient way of filling the space with leaves while growing in height.

Where there are many leaves in one spiral, long petioles in older leaves or narrow leaf bases in certain species can minimize leaf overlap (Leigh 1998). In the redwood forest understory plant *Adenocaulon bicolor*, which exhibits a spiral phyllotaxis with a mean divergence angle of 137° (phyllotactic fraction of 8/21), leaf overlap was reduced by particular combinations of leaf size and petiole length at successive nodes (both increasing initially and then decreasing). The petiole length observed in this plant corresponded to the optimal petiole length obtained in simulations of the dependence of light absorption efficiency on petiole length (Pearcy and Yang 1998).

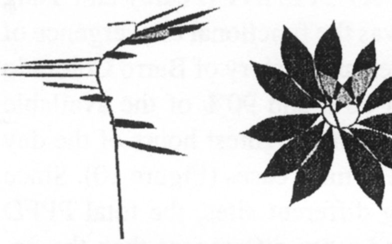
In the search for light, the crown of certain plants becomes thin instead of broad and flat in the shade. Light interception is not favored by such transformation, which usually represent an escape strategy of shade-intolerant species (Peer et al. 1999). In some cases, the whole developmental sequence of the plant is changed in the shade. Shrubs such as *Arbutus* switch from a sympodial growth in the open (Leeuwemberg architectural model) to a monopodial



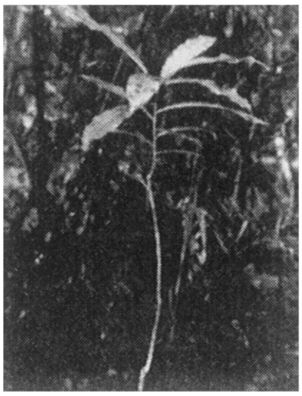
Costus pulverulentus

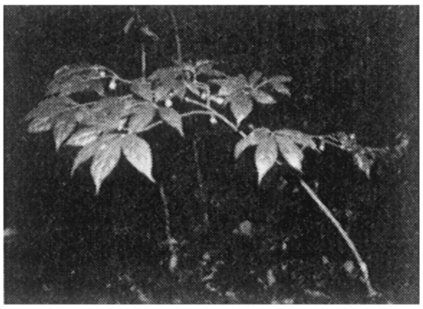


Dichorisandra hexandra



0.07	Fraction of leaf area self-shaded during the central hours	0.06
0.84	Fraction of leaf area displayed during the central hours	0.85
0.49	Intercepted PPFD in a clear day of spring (mol m^{-2} day^{-1})	0.75
0.90	Intercepted PPFD in a clear day of spring (fraction of available)	0.93





Hybanthus prunifolius

Thevetia ahouai

0.12	Fraction of leaf area self-shaded during the central hours	0.07
0.77	Fraction of leaf area displayed during the central hours	0.81
0.30	Intercepted PPFD in a clear day of spring (mol m^{-2} day^{-1})	0.26
0.86	Intercepted PPFD in a clear day of spring (fraction of available)	0.87

trunk (according to the model of Scarrone) in low-light environments (Bell 1993). Many plants accommodate their structure to the light environment, enhancing light interception efficiency under low-light conditions. This is the case of the chaparral shrub *H. arbutifolia*, which changes from orthotropic stems with spirally arranged leaves in the open to plagiotropic stems with pseudodistichous foliage when exposed to the moderate shade of a *Quercus* woodland (Valladares and Pearcy 1998). This structural change, in contrast to the escape strategy of more shade-intolerant species, significantly enhances light interception on a leaf area basis.

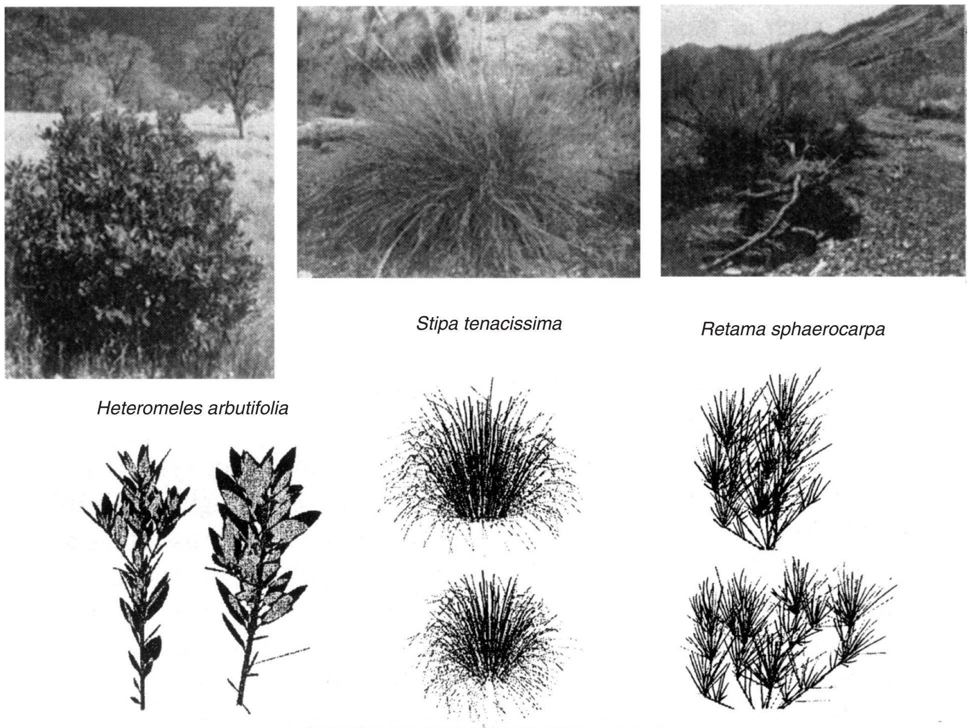
When Light is Excessive

Plants in open environments are exposed to high irradiance, which frequently leads to a decline in the efficiency of photosynthesis (photoinhibition), particularly under adverse conditions (Horton et al. 1996, Osmond et al. 1999). Under these circumstances, plants exhibit remarkable physiological and architectural plasticity. Physiological adjustments result in protection of photosynthetic apparatus against light intensities in excess to those that can be used in photosynthesis (Osmond et al. 1999). Structural adjustments lead to the avoidance of excessive irradiance by structural features, overall reducing the total leaf area or the fraction of leaf area directly exposed to the sun.

Sun shoots of the chaparral shrub *H. arbutifolia* exhibited a remarkable structural photoprotection, and despite having seven times more photosynthetically active radiation available, they intercepted only four times more and had potential daily carbon gains only double of those of shade shoots (Valladares and Pearcy 1998). The resulting fraction of leaf area that was displayed during the central hours of a typical day of spring was only one-third of the total leaf area of the shoot (Figure 4.11). Leaf angle, the most plastic character in the response of *H. arbutifolia* shoot to high light, played a key role in achieving an efficient compromise between maximizing carbon gain while minimizing the time that the leaf surfaces were exposed to irradiance in excess of that required for light saturation of photosynthesis, and therefore potentially photoinhibitory (Figure 4.9). For relatively simple canopies, leaf angle and orientation are the main structural photoprotective features (Werk and Ehleringer 1984, Smith and Ullberg 1989), but mutual shading among leaves can be even more important in complex, multilayered canopies (Roberts and Miller 1977, Caldwell et al. 1986). In *H. arbutifolia*, 27% of the foliage was self-shaded during the central hours of a clear spring day (Figure 4.11), but this percentage was far higher for leaves of certain orientations, such as those facing south. A steeply oriented foliage and moderate self-shading that reduces the photosynthetic surface area displayed during the central hours of the day were also characteristic structural features of the crowns of two other plants from high-light environments: *Stipa tenacissima*, a tussock grass, ad *Retama sphaerocarpa*, a leguminuous, leafless shrub (Valladares and Pugnaire 1999). These two species exhibited similar leaf display and PPFD interception efficiencies to those of *H. arbutifolia* (Figure 4.11). The costs in terms of missed

---

FIGURE 4.10 Four plant species co-occurring in the understory of a tropical rainforest (Barro Colorado Island, Panama). *Costus pulverulentus* and *Dichorisandra hexandra* are monocot herbs, *Hybanthus prunifolius* is an understory shrub, and the individual of *Thevetia ahouai* (a canopy tree) presented is a 2-m-high sapling. Beneath each photograph, to computer images at dawn (*left*) and at noon (*right*) of a representative of each species are provided. A lighter gray in the computer images indicates overlap between two or more leaves as seen from the sunpath. For each species, the fraction of the total leaf area that is either self-shaded or displayed during the central hours of the day, and the PPFD intercepted in a clear day of spring (both as daily total and as a fraction of available) were calculated using the three-dimensional YPLANT model (Pearcy and Yang 1996). (Data from Valladares, F., *Handbook of Functional Plant Ecology*, F.I. Pugnaire and F. Valladares, eds, Marcel Dekker, Inc., New York, 1999.)



	Fraction of leaf area self-shaded during the central hours	
0.27	0.25	0.20
	Fraction of leaf area displayed during the central hours	
0.34	0.16	0.37
	Intercepted PPFD in a clear day spring (mol m^{-2} day^{-1})	
18.1	16.3	30.0
	Intercepted PPFD in a clear day of spring (fraction of available)	
0.33	0.30	0.55

FIGURE 4.11 Three plant species from open, dry environments. *Heteromeles arbutifolia* is an evergreen sclerophyll of the California chaparral, *Stipa tenacissima* is a tussock grass frequent in the driest regions of the Iberian Peninsula, and *Retama sphaerocarpa* is a leguminous, leafless shrub also frequent in dry and warm areas of the Iberian Peninsula. Beneath each photograph, two computer images of a representative of each species are provided. A lighter gray in the computer images indicates overlap between two or more leaves as seen from the sunpath. For each species, the fraction of the total leaf area that is either self-shaded or displayed during the central hours of the day, and the photosynthetic photon flux density (PPFD) intercepted in a clear day of spring (both as daily total and as a fraction of available) were calculated using the three-dimensional YPLANT model (Pearcy and Yang 1996). (Data from Valladares, F. and Pearcy, R.W., *Oecologia*, 114, 1, 1998; Valladares, F. and Pugnaire, F.I., *Ann. Bot.*, 83, 459, 1999.)

opportunity for carbon gain (comparing plant crowns with equivalent horizontal photosynthetic surfaces) for these two species were similar to those imposed by the summer drought (approximately 50% of the potential carbon gain), the main limiting factor for plant survival in semiarid environments. This elevated cost of structural photoprotection emphasizes the ecological relevance of avoidance of high irradiance stress in these species.

Other stress factors occurring in high-light ecosystems, such as heat and water deficits, also favor increased inclination angles of leaves (Shackel and Hall 1979, Ehleringer and Forseth 1980, Comstock and Mahall 1985, Lovelock and Clough 1992) as well as greater degree of leaf rolling and folding (Fleck et al. 2003). Since different stresses co-occur at certain times of the day or during certain seasons (Niinemets and Valladares 2004), a protective strategy that is triggered by one type of stress (heat, water deficit, or excessive light) also increases protection or tolerance to other simultaneously occurring stresses is very adaptive. In addition to a series of structural features that clearly constitute an adaptive strategy helping to cope with multiple stress, a series of physiological responses such as down-regulation of photosynthesis and heat tolerance has been observed in plants from Mediterranean-type climates. As the structural adjustments, these physiological responses were found to be very efficient in protecting the high-light exposed plants to multiple stresses during the summer (Valladares and Pearcy 1997, Valladares et al. 2005).

Leaves of broad-leaved species are also often significantly rolled and curved, especially at high-upper canopy where high irradiances can be combined with water limitations (Farque et al. 2001, Fleck et al. 2003). Leaf rolling results in extreme reduction of leaf area, and therefore, in large decreases in radiation interception and transpiration (Figure 4.12). In fact, the leaves of broad-leaved species are never completely flat (Sinoquet et al. 1998). Leaf rolling in broad-leaved trees strongly reduces radiation interception of these leaves and can be a beneficial attribute in reducing photoinhibitory damage, heat stress, and transpiratory water loss.

It has been shown that structural avoidance of excessive irradiance by any of the means illustrated earlier can be crucial for survival under extreme conditions, even in plants capable of extensive physiological adjustment to stress (Valladares and Pearcy 1997). Stress itself can also direct influence crown architecture as it can modify the allocation patterns and the developmental processes of the plant. High irradiance can lead to high-leaf temperatures, especially in warm regions and when transpirational cooling is reduced due to water deficits, as in arid or Mediterranean-type environments (Figure 4.12 and Figure 4.13). The complex interplay between leaf size and shape, phyllotaxis, branching, and mutual shading among neighboring leaves can lead to contrasting temperatures in different plants and even in different leaves within the same plant as revealed by infrared thermographies (Figure 4.12 and Figure 4.13). Infrared thermography is a powerful tool to study the complex and heterogeneous pattern of leaf temperatures in plant crowns exposed to high light, which is the result of the combined effect of a large number of morphological, physiological, and environmental variables (Jones 2004).

OCCUPYING SPACE AND CASTING SHADE: THE COMMUNITY LEVEL

Many analyses of adaptations in plant form have assumed that natural selection favors traits that tend to maximize the growth rate of a given plant (Givnish 1986). One important objection to this approach is the lack of consideration of the role of competitors. As Givnish (1986) has shown, certain features of plant architecture, such as leaf height, are examples of a trait in which the strategy that maximizes growth in the absence of competitors is the one that does most poorly in their presence. In addition, certain structural features are not very efficient for their primary function, but provide a competitive advantage. For instance, the generous amount of leaves within certain crowns, well above what could be strictly needed, appears to be competitively more effective by intercepting light that competitors might use than in providing photochemical energy (Margalef 1997). Thus, the evolution of plant form must be interpreted considering not only the immediate function of the organs and structures involved (e.g., light interception), but also its effect on the efficiency with which competitors exploit the resources.

Whenever plants are grown in close proximity there is competition for light and space. Branching poses an ecological dilemma to many plants, because a wide and low crown with a

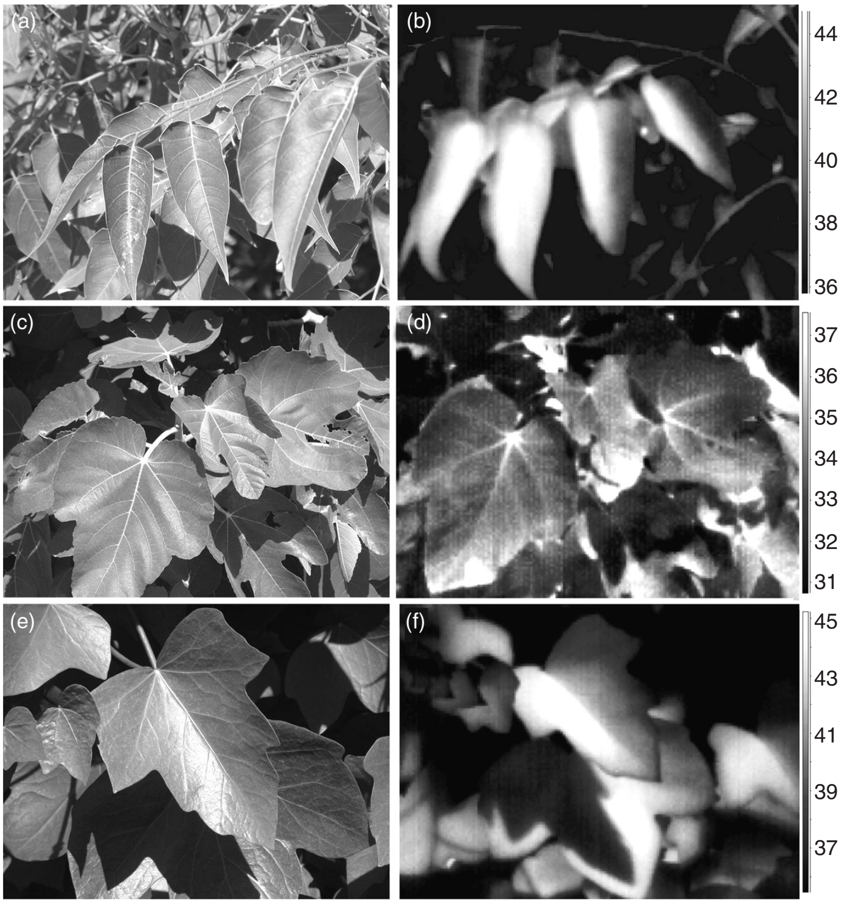


FIGURE 4.12 Leaf size and shape, and their relative position in the shoot determine the exposure of leaf surfaces to sunlight, which in turn translates into different leaf temperatures under the same environmental conditions, particularly under clear skies. Left-hand side images (a, c, and e) are normal, visible photographs, whereas those at their right (b, d, and f) are the corresponding infrared thermal images. The curved leaves of *Ailanthus altissima* (a, b) generated within-leaf shading and this curling protected some leaf zones against overheating. The large leaves of *Ficus carica* (c, d) exhibited large within-leaf thermal ranges which were due to differential transpirational cooling and thermal properties over the leaf surface since leaves were almost flat; note the relatively high temperatures of major leaf veins. The multilayered crown of the climber *Hedera helix* (e, f) rendered contrasting leaf temperatures depending on the relative position of each leaf; note the 8.5°C difference between the exposed leaf and the shaded leaf immediately underneath. The scale at the right is in Celsius degrees. All images were taken with a Flir B50 thermal camera in the afternoon of a clear spring day in Madrid (Spain); air temperature during the measurements was 35°C, air relative humidity was 23%, and wind speed was 0.15 m s^{-1}.

lot of branches is highly efficient in terms of light capture versus construction costs, but is easily overtopped, whereas a tall crown with little branches represents the opposite trade-off. Certain plants have reached an interesting compromise by building compound leaves whose long rachises act as throw-away branches, extending the photosynthetic surface of the crown without investing in permanent and expensive support tissue (Givnish 1978). Probably one of the most extreme examples of this strategy is that of the Devil's walking stick *(Aralia spinosa)*, which avoids branching by producing long, light leaves, allowing for a fast growth of the

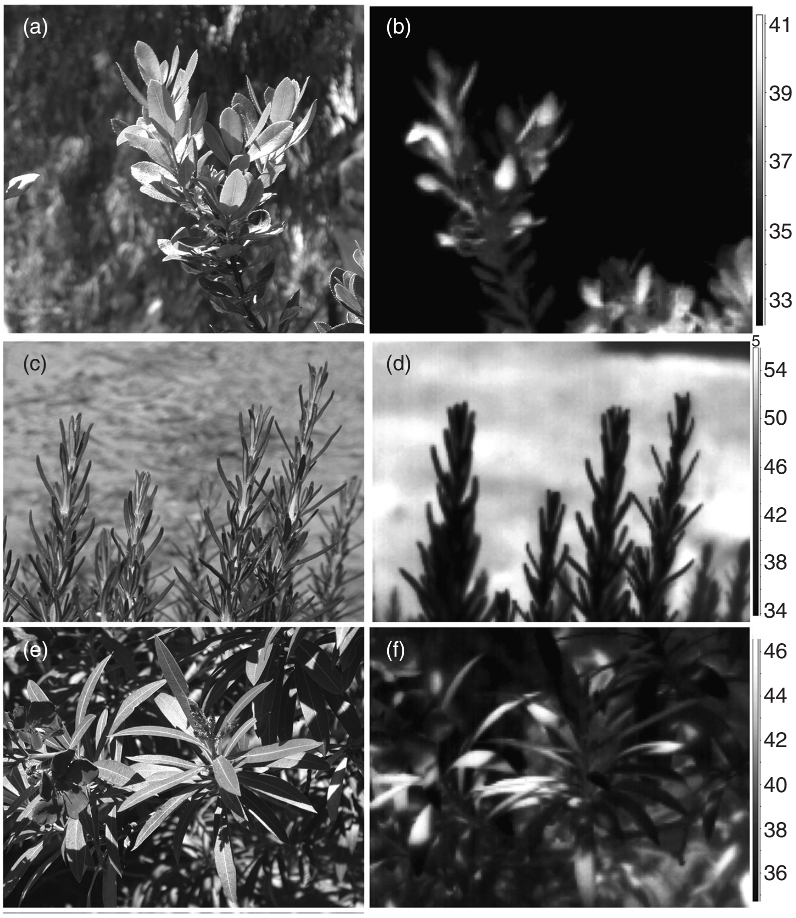


FIGURE 4.13 Phyllotaxis and shoot architecture influence the energy balance of individual leaves and of the whole plant. Steep and aggregated, spiral leaves of *Arbutus unedo* (a, b) reduce the exposure of leaf area leading to an important degree of self-shading; only some leaves with their laminas oriented to the south exhibit temperatures significantly above air temperature (up to 6°C higher). The erectophile foliage of *Rosmarinus oficinalis* (c, d), made up of thin and small leaves very close to each other (short internodes), is entirely at air temperature, in contrast with the surrounding soil, which is 20°C above air temperature. The complex and multi-branched crown of *Nerium oleander* (e, f) generates an intricate pattern of leaf temperatures. Left-hand side images (a, c, and e) are normal, visible photographs, whereas those at their right (b, d, and f) are the corresponding infrared thermal images. The scale at the right is in Celsius degrees. All images were taken as in Figure 4.12.

trunk. To support the same leaf area, a co-occurring tree, the flowering dogwood *(Cornus florida)*, has to invest 7–15 times more in wood (White 1984).

Height growth is extended in the forest understory because light increases exponentially toward the canopy surface, whereas the costs of structural tissues escalate less rapidly with plant height (Givnish 1982 see Section ‘‘Plant Design’’ for further analyses of the economics of plant height). Competition between trees in its most general sense is competition to fill space, quickly in early succession, where r-selection seems to be dominant, but completely in late succession, where K-selection seems to dominate (Horn 1971). The dynamic nature of a forest canopy, with numerous gaps and clearings caused by treefalls, contributes to the coexistence of many more species of trees than could be expected in a theoretical analysis of crown architecture and monopolization of light; therefore, species of different successional status and crown shapes can coexist (Figure 4.4).

Forests are vertically stratified, from the towering emergent trees to the herbs on the forest floor, each strata comprising a distinct suite of plant species adapted for the conditions at each particular level, mainly light conditions. In the initial description of this idea of vertical strata in forests, an explicit mechanism that would account for stratification was not provided (see discussion in Terborgh 1992). One of the questions that remained unanswered in that description was why certain tree species cease their upward growth when they attain a given height, unlike canopy species that pursue an upward trajectory until they reach the open sky or die. Is there an optimum height for a midstory tree? Terborgh (1992) suggested an explanation, considering how direct sunlight passes through the holes of the forest canopy to the lower layers and eventually to the forest floor. As the sun progresses across the sky, sunlight penetrates into the forest over a wide range of angles. In a simplified and regular canopy, the sunlight passing into the forest interior through a single gap forms a triangular area on the way to the ground (Figure 4.14). At the upper parts of the triangle, the number of hours of sunlight is larger than at the lower parts. These triangular areas of direct sunlight

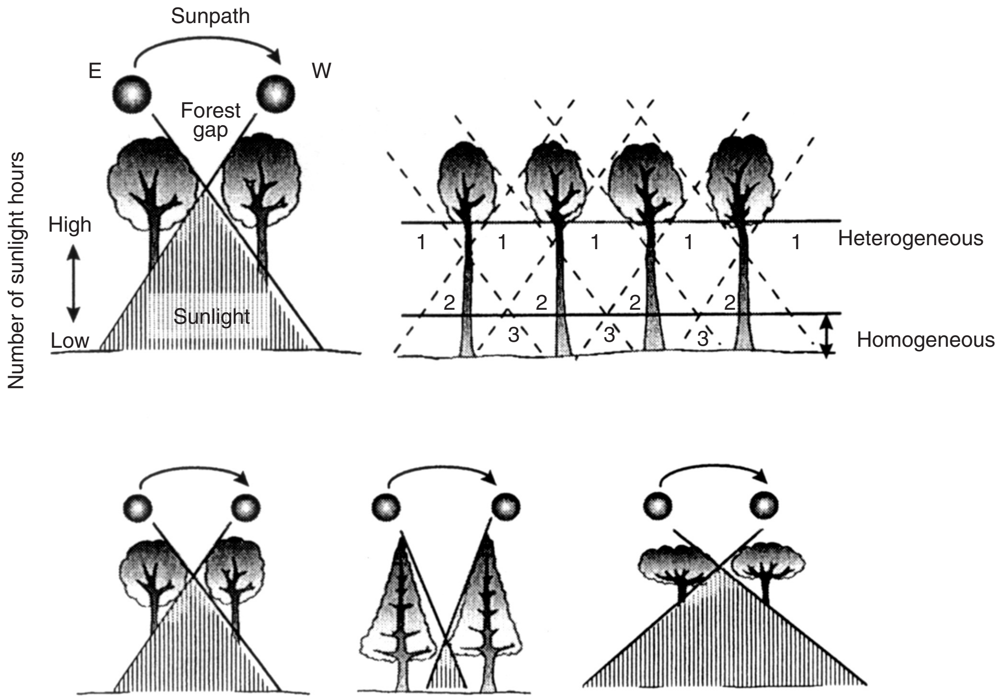


FIGURE 4.14 A gap in the forest canopy allows direct sunlight to reach the understory (*upper left*). The number of sunlight hours increases from the ground to the canopy. When the sunlight passing through more than one gap is considered, a more complex pattern is found (*upper right*), with understory areas affected by one, two, three, or more neighbor gaps (indicated by numbers). Where the cones of several gaps intersect, a spatially uniform light field is produced. Both the distance between the trees forming the limits of the gap, and the shape of the crown of these trees determine the duration of direct sunlight in the understory (lower graphs). Pyramidal crowns allow little sunlight to reach the understory, whereas the reverse is true for flat and broad crowns. (Adapted from Terborgh, J., *Diversity and the Tropical Forest*, Scientific American Library, New York, 1992.)

spread out below the canopy so that areas from adjacent gaps overlap. Some points receive direct sunlight twice a day (intersection of two areas), whereas others lower down in the forest receive sunlight from an increasing number of gaps, although for increasingly briefer periods of time (briefer ‘‘sunflecks’’ see Pearcy 1999). This generates a spatially uniform light field near the ground (Figure 4.14), and it was predicted that a midstory tree must grow as high as the higher limit of this field because above this point, at least part of the tree crown might not receive enough light to pay its costs, and the whole construction and maintenance costs of the tree would be increased at the expenses of other functions such as reproduction (Terborgh 1992). This prediction was found to be true (midstory trees were of the expected height) in a mature temperate forest in North America, but not in the more complex and irregular forests of the tropics. In addition to the fact that the canopy of tropical forests is uneven and complex, Terborgh (1992) pointed to the shape of the crown of the canopy trees as another factor to explain the lack of a predictable, uniform light field. The shape of their crown determines the size of the triangular area of sunlight beneath a gap (Figure 4.14). Crown shape tends to vary with latitude, with mushroom-like trees in the tropics and conical crowns in boreal regions (Figure 4.4), which allows for either generous shafts of direct sunlight or very little sunlight reaching the floor, respectively (Figure 4.14). Thus although the forest has plenty of understory plants in the tropics, it is nearly devoid of them in the boreal regions; temperate forests represent an intermediate situation, with their rather simple canopy structure being very suitable for Terborgh’s theoretical description of vertical light gradients and for the corresponding predictions of optimal height of understory trees. Another prediction regarding crown architecture resulting from the thesis that forests are vertically stratified is that crown shape varies systematically with vertical position. This was found to be true in tropical forests with more than two plant strata, whereas emergent trees possessed crowns that were more broad than deep, those of trees immediately below were more deep than broad (for the rationale, see Terborgh 1992).

In their search for light, understory plants are not only exposed to the vertical gradient of light, but to other physical factors that interact and influence their architecture. If height growth in a low-light environment has the risk of too-expensive construction and maintenance costs, the situation becomes riskier or at least more complicated when the ground is not even, as is the case with hillsides. Since the lines of equal light intensity from the canopy to the ground run parallel to the ground (Horn 1971), the most efficient height growth occurs at right angles to the ground (Figure 4.15). However, to do this on a slope, trees should lean outward (Alexander 1997). Trunk inclination on slopes has been shown to be adaptive (Ishii and Higashi 1997), but the greater the angle of lean, the stronger the trunk of the tree needs to be for biomechanical reasons (Mattheck 1991, 1995), which entails additional costs. Under low-light conditions, leaning trees cannot grow a trunk as tall as it could if it were vertical, so their optimal angle on a slope is neither vertical nor perpendicular to the forest floor (Alexander 1997). Ishii and Higashi (1997) constructed a model to explore tree coexistence on a slope and to predict how tree survival is affected by trunk inclination. The predictions were that survival rate increases with slope angle more sharply under poorer light conditions. These predictions were supported by the understory tree *Rhododendron tashiroi*, which exhibited sharper trunk inclination and coexisted more successfully on steeper slopes with the dominant canopy trees (Ishii and Higashi 1997). Trunk inclination also seems to be affected by the shade tolerance of the species, with the relationship between slope and trunk inclination being more marked in shade-sensitive trees (Figure 4.15). This model provides an explanation based on optimizing processes of evolution by natural selection for the common observation that the trunks of trees on a slope often incline downward. This explanation is more complete and convincing than previous ones alluding to landslides or wind (King 1981, Del Tredici 1991, Mattheck 1991). Another way to enhance light capture on

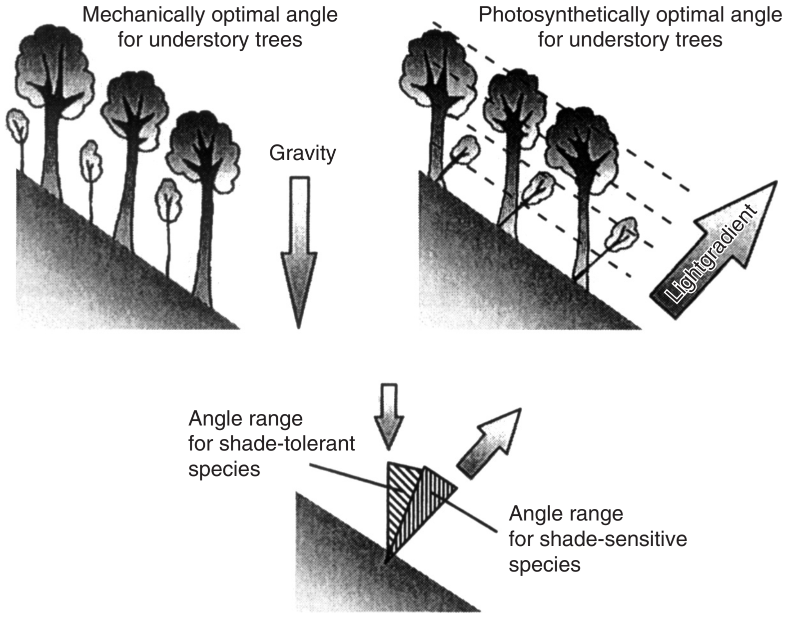


FIGURE 4.15 Understory trees that grow on slope are exposed to the dilemma of growing vertically, which is mechanically optimal, or with their trunks inclined downward, that is, parallel to the light gradient occurring from the ground to the upper canopy, which shortens the distance of their foliage from the canopy surface. Depending on their light requirement or shade tolerance, species are expected to exhibit two ranges of trunk angle, as shown in the lower figure. (Adapted from Alexander, R.M., *Nature*, 386, 327, 1997; Ishii, R. and Higashi, M., *Proc. R. Soc. Lond. Ser. B., Biol.*, 264, 133, 1997.)

slopes is with an asymmetrical crown, with more branches on the downhill side (Hallé et al. 1978, Alexander 1997). Although this architectural solution does not require trunk inclination, it must imply additional construction costs if the trees are not to snap or fall over.

Another interesting study regarding understory plants and slopes is that of leaning herbs that arrange their leaves in a distichous array along an arching stem (e.g., *Disporum, Polygonatum, Smilacina, Streptopus, Uvularia* in the Liliaceae, and *Renealmia* in the Zingiberaceae). Such crown architecture is mechanically less efficient than an umbrella-like arrangement that supports leaves at the same height on a vertical stem. Their competitive advantage derives from their tendency to orient strongly downslope (Givnish 1982, 1986). Above a critical slope inclination, leaning shoots become mechanically more efficient than other herb architectures and tend to supplant them. The correspondence between their observed and predicted distribution relative to slope inclination provides support for their competitive ability on slopes (Givnish 1986).

Hedgerows, linear arrangements of woody species that follow property boundaries between fields, are an interesting case of plant communities with strong competition for light and space. The interactions between carbon relationships, growth, and plant architecture have been thoroughly studied in these systems (Küppers 1994). An important conclusion from these studies was that plant architecture in combination with carbon input can lead to a better understanding of plant success since net primary production by itself is not sufficient to explain competitive relationships between woody species (Schulze et al. 1986). Branching and leaf exposure were principal. Mechanisms in competition: short internodes and thorns were important in early-successional species, whereas shading of neighbors with a minimum of self-shading (capacity for occupying new, higher aerial space coupled with maintenance of a closed leaf cover above the occupied space) provided a competitive advantage to late-successional species (Schulze et al. 1986). Particular branching patterns and lower costs of space occupation permitted late-successional species to grow a crown quickly and then outcompete shade-intolerant pioneers (Küppers 1989, 1994).

Using a stochastic model of plant growth, Ford (1987) reached some interesting conclusions on the implications of crown architecture for plant competition and spatial interference. Growth rates depended on branch probability and also on angle of branching in sympodial plants but not in monopodial plants. In sympodial plants, an optimal branching angle of approximately 30° was found when the ratio of the interference distance to the internode distance was 1.5:5. Sympodial plants with a branching angle of 30° outcompeted monopodial plants (Ford 1987). The light environment of a plant can vary due to the activity of nearby vegetation. Sensing their neighbors, perceiving the light opportunities, and responding in a timely fashion is crucial for plant survival at the community level (Ballaré 1994). An adaptive way of coping with competition is by a plastic response to the environmental changes caused by neighboring plants, an issue briefly addressed in the next section.

In plant communities, however, not everything is competition. In fact, facilitation is becoming better recognized and there is ample evidence pointing to facilitation as an important driver of community dynamics (Callaway and Walker 1997). In arid environments, plants can benefit from an attenuation of the stressful irradiance by being in the shade of others, which can act as nurse plants and improve early establishment and survival of seedlings (Gómez-Aparicio et al. 2004). However, to which extent this effect prevails over competition for water is uncertain, since there is conflicting evidence (Maestre et al. 2005). More studies on the net balance of plant–plant interactions in natural conditions are needed to solve this controversy, particularly in arid conditions where the increase of facilitation with drought stress is not always found (Lortie and Callaway 2006, Maestre et al. 2006).

PLASTICITY, STRESS, AND EVOLUTION

The shape of the crown is an adaptive compromise of conflicting strategies. Multiple functions of an architectural design and functional convergence of alternative architectural features make assessment of optimal design difficult. For instance, phyllotaxis is not strictly a developmental constraint because different phyllotaxes can be functionally equivalent (e.g., in terms of light interception efficiency (Niklas 1988)). The same argument can be built for branching patterns or for the general shape of the crown (Figure 4.3 and Figure 4.4), and these structural features may provide a paradigm for other features in plant evolution. This is the most likely reason why it has proved impossible to describe the many tree architectural models as adaptations. However, there are particular cases in which the several functions of a given structure do not appear to be a constraint in interpreting its functional optimization, such as the analysis of petiole length versus light capture in the understory herb *Adenocaulon bicolor* (Pearcy and Yang 1998). Certain genetic or developmental constraints can be overcome from a functional point of view by changes in other, more plastic structural features, such as petiole and leaf shape, size, and orientation. Consequently, evolution of architectural features cannot be interpreted without a minimum knowledge of the plastic response to the environment of the involved traits.

Shade avoidance, a feature that angiosperms have developed to a remarkable extent, is based on signals that anticipate that shade is going to change (via changes in the red-far red ratio). The so-called shade avoidance syndrome involves a highly plastic response in the shade with strong elongation of internodes and petioles, the production of less dry matter, larger and thinner leaves, a higher shoot–root ratio, and a series of remarkable physiological changes mediated by multiple phytochromes (Smith and Whitelam 1997). The variety of morphogenic programs triggered to move the photosynthetic area toward better-lit canopy regions, and all of the morphological and physiological adjustments to the light environment, correspond to the concept of foraging for light (Ballaré 1994, Ballaré et al. 1997).

Phenotypic plasticity in plants has three main functional roles: maintenance of homeostasis, foraging for resources, and defense. Although plant plasticity has been a commonplace observation, its ecological and evolutionary consequences are only beginning to be thoroughly explored. This is due to the fact that most ecological and ecophysiological studies of plant form to date have focused on adaptive, habitat-based specialization, and plasticity has been interpreted as a feature of generalists. The supposed superiority of specialized ecotypes or taxa over generalists has led biologists to focus on evolutionary specialization and neglect the ecological and evolutionary implications of plastic responses of the phenotype to the environment (Sultan 2004, 2005). Although the adaptive implications of plasticity for relative allocation of biomass or other fitness-related parameters have been widely recognized, plasticity has been traditionally viewed as an alternative to specialization. The evidence that plastic, and thus generalist, species are less able to compete with specialized species is weak at best (Niklas 1997). A different approach to this question has postulated that plasticity in some plant traits may, in fact, represent a product of specialization (Lortie and Aarssen 1996). The predictions for plasticity of specialized genotypes were proposed to depend on whether specialization is associated with the more or the less favorable end of an environmental gradient (Lortie and Aarssen 1996). Specialization to the more favorable end was proposed to increase plasticity, whereas specialization to the less favorable end was proposed to decrease plasticity. In a study of 16 species of the genus *Psychotria* occurring on Barro Colorado Island, Panama, we found that the mean phenotypic plasticity was significantly higher for the high-light species than for the low-light species (Valladares et al. 2000). Selection for greater plasticity may be stronger in the high-light species because forest gaps (high-light environments) exhibit a relatively predictable decrease in PPFD for which this plasticity could be adaptive. In contrast, the low-light species experience relatively unpredictable changes in light caused by infrequent gap formation. Under these conditions, phenotypic stability may have higher adaptive value. The results are consistent with the view that plasticity, rather than being an alternative to specialization, is indeed a specialization to the high-light end of the light gradient in tropical forests. Other studies have found greater photosynthetic plasticity in gap-dependent compared with shade-tolerant species (Bazzaz 1996). On the other hand, the relative stability exhibited by the low-light species is consistent with a stress-tolerant syndrome, with its low potential maximum growth rates, low maximum photosynthetic rates, and low leaf turnover (Valladares et al. 2000). We also found that plasticity was generally greater for the physiological than for the structural characteristics (Valladares et al. 2000). However, the different plasticity in morphological and physiological traits seems to be species-specific, with high-light species showing greater physiological plasticity and low-light species higher morphological plasticity (Valladares et al. 2002b, Niinemets and Valladares 2004).

In the analysis of plant plasticity, choice of which submits to count is essential, since within a plant there is clearly a hierarchy of plasticities, and not all structures exhibit the same degree of plastic response (White 1979). For instance, the range of variation of a phenotype (the norm of reaction) for vegetative structures tends to be broader than that for reproductive traits (Niklas 1997). The adaptive significance of the plasticity of a character becomes clear only when it is scaled up to the performance of the whole plant. Usually, if a plastic response in a feature improves performance, the result at the next level is an enhanced homeostasis (Pearcy 1999).

Since phenotypic plasticity is advantageous for sessile organisms due to the heterogeneous nature of most environments, the question of why all plants are not equally (and maximally) plastic is a very pertinent one. It is rare to find scenarios in which a plastic response to the environment could be maladaptive. Some examples have been pointed out for plants growing under extreme physiological conditions and usually in the absence of strong competition (Chapin 1991, Chapin et al. 1993). Such plants tend to show a conservative pattern involving slow, steady growth, even when conditions are temporarily favorable (Waller 1986). Under ideal growing conditions, these plants are more likely to store nutrients than to accelerate their growth (Chapin et al. 1986, Chapin et al. 1993) to avoid the production of a plant that is too large or structures that are too expensive to be sustained once conditions deteriorate. Specialization to a low-resource environment seems to start with a modification in a key growth-related character, which results in a cascade of effects that triggers the entire stress resistance syndrome (low rates of growth, photosynthesis, and nutrient absorption, high root: shoot ratios, low rates of tissue turnover, and high concentrations of secondary metabolites, Chapin et al. 1993). Low plasticity associated with stressful conditions has been found in several studies of Mediterranean woody plants (Valladares et al. 2002a, 2005).

Examples of proven adaptive plasticity in plants are scarce and most plastic responses actually may be ‘‘passive’’ rather than adaptive, suggesting that the evolution of adaptive plasticity is impeded by constraints (Weinig 2000, van Kleunen and Fischer 2005). And one ubiquitous constrain is stress. Stress dissipates energy that is otherwise available for homeostatic processes such as those controlling development and pattern formation (Parsons 1993). It has been shown that growth pattern and shape-related features are more sensitive to this energy dissipation caused by stress than just size (Alados et al. 1994, 1999). Stress introduces variation in structure, which is not adaptive, in contrast to plastic phenotypic responses to environmental changes. This kind of increased variability is known as developmental instability and the study of the so-called fluctuating asymmetry has been used to detect disruption of homeostasis (Alados et al. 1994, 1999). Stress also causes deviations in radial symmetry and in symmetry of scale, that is, in self-similarity at different spatial scales (Alados et al. 1994). Since both the distance between two successive leaves (internode length) and the internode diameter scale with node order, dispersion about the regression line between length or diameter and node order becomes a measure of the departure from perfect translational symmetry, which is another form of developmental instability (Escós et al. 1997). These are just some examples to illustrate the notions that there are many forms of asymmetry that can be associated with stress and that only a fraction of the phenotypic response to environment is adaptive.

ACKNOWLEDGMENTS

Tsvi Sachs has been most generous with his time and expertise in commenting on a first draft of this chapter. This chapter is based on research supported by the Spanish Ministry of Education and Science (grants RASINV, CGL2004-04884-C02-02/BOS, and PLASTOFOR, AGL2004-00536/FOR), by the Estonian Academy of Sciences, Consejo Superior de Investigaciones Científicas (CSIC, Spain) (grant for collaboration between scientific institutions in Estonia and the research institutes of CSIC), the Estonian Science Foundation, and the Estonian Ministry of Education and Science (grant 0182468As03).

REFERENCES

Ackerly, D.D. and F.A. Bazzaz, 1995. Seedling crown orientation and interception of diffuse radiation in tropical forest gaps. Ecology 76: 1134–1146.

Alados, C.L., J.M. Escós, and J.M. Emlen, 1994. Scale asymmetry: A tool to detect developmental instability under the fractal geometry scope. In: M.M. Novak, ed. Fractals in the Natural and Applied Sciences. Elsevier, North-Holland, pp. 25–36.

Alados, C.L., T. Navarro, and B. Cabezudo, 1999. Tolerance assessment of Cistus ladanifer to serpentine soils by developmental stability analysis. Plant Ecology 143: 51–66.

Alexander, R.M., 1997. Leaning trees on a sloping ground. Nature 386: 327–329.

Arno, S.F. and R.P. Hammerly, 1984. Timberline: Mountain and Arctic Forest Frontiers. The Mountaineers, Seattle, WA.

Ashton, P.S., 1978. Crown characteristics of tropical trees. In: P.B. Tomlinson and M.H. Zimmermann, eds. Tropical Trees as Living Systems. The Proceedings of the Fourth Cabot Symposium held at Harvard Forest, Petersham Massachusetts on April 26–30, 1976. Cambridge University Press, Cambridge, New York, Melbourne, pp. 591–615.

Baldocchi, D. and S. Collineau, 1994. The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. In: M.M. Caldwell and R.W. Pearcy, eds. Exploitation of Environmental Heterogeneity by Plants. Ecophysiological Processes Above- and Belowground. Academic Press, San Diego, New York, Boston, London, Sydney, Tokyo, Toronto, pp. 21–71.

Baldocchi, D.D. and P.C. Harley, 1995. Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. II. Model testing and application. Plant, Cell and Environment 18: 1157–1173.

Baldocchi, D.D., D.R. Matt, B.A. Hutchinson, and R.T. McMillen, 1984. Solar radiation within an oak-hickory forest: An evaluation of the extinction coefficients for several radiation components during fully-leafed and leafless periods. Agricultural and Forest Meteorology 32: 307–322.

Ballaré, C.L., 1994. Light gaps: Sensing the light opportunities in highly dynamic canopy environments. In: M.M. Caldwell and R.W. Pearcy, eds. Exploitation of Environmental Heterogeneity by Plants: Ecophysiological Processes Above- and Belowground. Academic Press, San Diego, CA, pp. 73–110.

Ballaré, C.L., A.L. Scopel, and R.A. Sánchez, 1997. Foraging for light: photosensory ecology and agricultural implications. Plant, Cell and Environment 20: 820–825.

Bazzaz, F.A., 1996. Plants in Changing Environments: Linking Physiological, Population, and Community Ecology. Cambridge University Press, Cambridge.

Bell, A.D., 1993. Plant Form. Oxford University Press, New York.

Beyschlag, W. and R.J. Ryel, 1999. Canopy photosynthesis modeling. In: F.I. Pugnaire and F. Valladares, eds. Handbook of Functional Plant Ecology. Marcel Dekker, Inc., New York, pp. 771–804.

Brites, D. and F. Valladares, 2005. Implications of opposite phyllotaxis for light interception efficiency of Mediterranean woody plants. Trees: Structure and Function 19: 671–679.

Brown, M.J. and G.G. Parker, 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. Canadian Journal of Forest Research 24: 1694–1703.

Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Nowak, and R.S. Dzurec, 1981. Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia 50: 14–24.

Caldwell, M.M., T.J. Dean, R.S. Nowak, R.S. Dzurec, and J.H. Richards, 1983. Bunchgrass architecture, light interception, and water-use efficiency: Assessment by fiber optic point quadrats and gas exchange. Oecologia 59: 178–184.

Caldwell, M.M., H.P. Meister, J.D. Tenhunen, and O.L. Lange, 1986. Canopy structure, light microclimate and leaf gas exchange of *Quercus coccifera* L. in a Portugese macchia: Measurements in different canopy layers and simulations with a canopy model. Trees: Structure and Function 1: 25–41.

Callaway, R.M. and L.R. Walker, 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958–1965.

Campbell, G.S., 1986. Extinction coefficients for radiation in plant canopies calculated using an ellipsoidal inclination angle distribution. Agricultural and Forest Meteorology 36: 317–321.

Campbell, G.S. and J.M. Norman, 1989. The description and measurement of plant canopy structure. In: G. Russell, B. Marshall, and P.G. Jarvis, eds. Plant Canopies: Their Growth, Form and Function. Cambridge University Press, Cambridge, New York, New Rochelle, Melbourne, Sydney, pp. 1–19.

Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69: 786–795.

Cescatti, A., 1998. Effects of needle clumping in shoots and crowns on the radiative regime of a Norway spruce canopy. Annales des Sciences Forestieres 55: 89–102.

Cescatti, A. and Ü. Niinemets, 2004. Sunlight capture. Leaf to landscape. In: W.K. Smith, T.C. Vogelmann, and C. Chritchley, eds. Photosynthetic Adaptation. Chloroplast to Landscape. Springer-Verlag, Berlin, pp. 42–85.

Cescatti, A. and R. Zorer, 2003. Structural acclimation and radiation regime of silver fir (*Abies alba Mill.*) shoots along a light gradient. Plant, Cell and Environment 26: 429–442.

Clearwater, M.J. and K.S. Gould, 1995. Leaf orientation and light interception by juvenile *Pseudopanax crassifolius* (Cunn) C. Koch in a partially shaded forest environment. Oecologia 104: 363–371.

Comstock, J.P. and B.E. Mahall, 1985. Drought and changes in leaf orientation for two California chaparral shrubs: *Ceanothus megacarpus* and *Ceanothus crassifolius*. Oecologia 65: 531–535.

Corlett, J.E., H.G. Jones, A. Massacci, and J. Masojidek, 1994. Water deficit, leaf rolling and susceptibility to photoinhibition in field grown sorghum. Physiologia Plantarum 92: 423–430.

Coutts, M.P. and J. Grace, eds. 1995. Wind and Trees. Cambridge University Press, Cambridge.

Chapin, F., 1991. Integrated responses of plants to stress. BioScience 41: 29–36.

Chapin, F.S., III, P.M. Vitousek, and K. Van Cleve, 1986. The nature of nutrient limitation in plant communities. The American Naturalist 127: 48–58.

Chapin, F.S., III, K. Autumn, and F. Pugnaire, 1993. Evolution of suites of traits in response to environmental stress. The American Naturalist 142: S78–S92.

Cheeseman, J.M., 1993. Plant growth modelling without integrating mechanisms. Plant, Cell and Environment 16: 137–147.

Chen, S.G., R. Ceulemans, and I. Impens, 1994. Is there a light regime determined tree ideotype? Journal of Theoretical Biology 169: 153–161.

Del Tredici, P., 1991. Natural regeneration of *Ginkgo biloba* from downward growing cotyledonary buds (Basal Chichi). American Journal of Botany 79: 522–530.

Duncan, W.G., 1971. Leaf angles, leaf area and canopy photosynthesis. Crop Science 11: 482–485.

Ehleringer, J. and I. Forseth, 1980. Solar tracking by plants. Science 210: 1094–1098.

Ehleringer, J.R. and K.S. Werk, 1986. Modifications of solar-radiation absorption patterns and implications for carbon gain at the leaf level. In: T.J. Givnish, ed. On the Economy of Plant Form and Function. Proceedings of the Sixth Maria Moors Cabot Symposium, ‘‘Evolutionary constraints on primary productivity: adaptive patterns of energy capture in plants,’’ Harvard Forest, August 1983. Cambridge University Press, Cambridge, London, New York, New Rochelle, Melbourne, Sydney, pp. 57–82.

Ehleringer, J.R. and I.N. Forseth, 1989. Diurnal leaf movements and productivity in canopies. In: G. Russell, B. Marshall, and P.G. Jarvis, eds. Plant Canopies: Their Growth, Form and Function. Cambridge University Press, Cambridge, New York, New Rochelle, Melbourne, Sydney, pp. 129–142. Ehleringer, J.R. and C.B. FIeld, eds. 1993. Scaling physiological processes. Academic Press, San Diego, CA.

Ellison, A.M. and K.J. Niklas, 1988. Branching patterns on *Salicornia europaea* (Chenopodiaceae) at different successional stages a comparison of theoretical and real plants. American Journal of Botany 75: 501–512.

Ennos, A.R., 1997. Wind as an ecological factor. Trends in Ecology and Evolution 12: 108–111.

Escós, J., C.L. Alados, and J.M. Emlen, 1997. The impact of grazing on plant fractal architecture and fitness of a Mediterranean shrub *Anthyllis cytisoides* L. Functional Ecology 11: 66–78.

Farque, L., H. Sinoquet, and F. Colin, 2001. Canopy structure and light interception in *Quercus petraea* seedlings in relation to light regime and plant density. Tree Physiology 21: 1257–1267.

Farquhar, G.D. and M.L. Roderick, 2003. Pinatubo, diffuse light, and the carbon cycle. Science 299: 1997–1998.

Fernandez, D. and M. Castrillo, 1999. Maize leaf rolling initiation. Photosynthetica 37: 493–497.

Fisher, J.B., 1986. Branching patterns and angles in trees. In: T.J.Givnish, ed. On the Economy of Plant Form and Function. Proceedings of the Sixth Maria Moors Cabot Symposium, ‘‘Evolutionary constraints on primary productivity: adaptive patterns of energy capture in plants,’’ Harvard Forest, August 1983. Cambridge University Press, Cambridge, London, New York, New Rochelle, Melbourne, Sydney, pp. 493–523.

Fisher, J.B., 1992. How predictive are computer simulations of tree architecture? International Journal of Plant Sciences 153: S137–S146.

Fisher, J.B. and D.E. Hibbs, 1982. Plasticity of tree architecture: specific and ecological variations found in Aubrevilles's model. American Journal of Botany 69: 690–702.

Fisher, J.B. and H. Honda, 1979a. Branch geometry and effective leaf area: a study of *Terminalia*-branching pattern. I. Theoretical trees. American Journal of Botany 66: 633–644.

Fisher, J.B. and H. Honda, 1979b. Branch geometry and effective leaf area: a study of *Terminalia*-branching pattern. II. Survey of real trees. American Journal of Botany 66: 645–655.

Fleck, S., Ü. Niinemets, A. Cescatti, and J.D. Tenhunen, 2003. Three-dimensional lamina architecture alters light harvesting efficiency in *Fagus*: A leaf-scale analysis. Tree Physiology 23: 577–589.

Ford, H., 1987. Investigating the ecological and evolutionary significance of plant growth form using stochastic simulation. Annals of Botany 59: 487–494.

Fournier, A., 1979. Is architectural radiation adaptive? Université des Sciences et Techniques du Languedoc, Montpellier, France.

Fujimori, T. and D. Whitehead, 1986. Crown and Canopy Structure in Relation to Productivity. Forestry and Forestal Products Research Institute, Ibaraki, Japan.

Gartner, B.L., 1995. Plant Stems. Physiology and Functional Morphology. Academic Press, San Diego, CA.

Geiger, D.R., 1986. Processes affecting carbon allocation and partitioning among sinks. In: J. Cronshaw, W.J. Lucas, and R.T. Giaquinta, eds. Phloem Transport. Alan R. Liss, New York, pp. 375–388.

Gere, J.M. and S.P. Timoshenko, 1997. Mechanics of Materials, 4th edn. PWS Publishing Company, Boston, MA.

Gill, D.E., 1991. Individual plants as genetic mosaics: ecological organisms versus evolutionary individuals. In: M.J. Crawley, ed. Plant Ecology. Blackwell Scientific Publications, Wiltshire, pp. 321–344.

Givnish, T.J., 1978. On the adaptive significance of compound leaves, with special reference to tropical trees. In: P.B. Tomlinson and M.H. Zimmermann, eds. Tropical Trees as Living Systems. The Proceedings of the Fourth Cabot Symposium held at Harvard Forest, Petersham, Massachusetts on April 26–30, 1976. Cambridge University Press, Cambridge, New York, Melbourne, pp. 351–380.

Givnish, T.J., 1982. On the adaptive significance of leaf height in forest herbs. The American Naturalist 120: 353–381.

Givnish, T.J., 1986. Biomechanical constraints on self-thinning in plant populations. Journal of Theoretical Biology 119: 139–146.

Givnish, T.J., 1988. Adaptation to sun and shade: A whole-plant perspective. Australian Journal of Plant Physiology 15: 63–92.

Givnish, T.J., 1995. Plant stems: Biomechanical adaptation for energy capture and influence on species distributions. In: B.L. Gartner, ed. Plant Stems: Physiology and Functional Morphology. Academic Press, Inc, San Diego, CA, pp. 3–49.

Godin, C., 2000. Representing and encoding plant architecture: A review. Annals of Forest Science 57: 413–438.

Gómez-Aparicio, L., R. Zamora, J.M. Gómez, J.A. Hódar, J. Castro, and E. Baraza, 2004. Applying plant facilitation to reforestation: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14: 1128–1138.

Grace, J., 1977. Plant Response to Wind. Academic Press, New York.

Gu, L., D. Baldocchi, S.B. Verma, T.A. Black, T. Vesala, E.M. Falge, and P.R. Dowty, 2002. Advantages of diffuse radiation for terrestrial ecosystem productivity. Journal of Geophysical Research 107: doi:10.1029/2001JD001242.

Gutschick, V.P. and F.W. Wiegel, 1988. Optimizing the canopy photosynthetic rate by patterns of investment in specific leaf mass. The American Naturalist 132: 67–86.

Hallé, F., 1995. Canopy architecture in tropical trees: a pictorial approach. In: M.D. Lowman and N.M. Nadkarni, eds. Forest Canopies. Academic Press, London, pp. 27–44.

Hallé, F., R.A.A. Oldeman, and P.B. Tomlinson, 1978. Tropical Trees and Forests: An Architectural Analysis. Springer-Verlag, Berlin, Heidelberg, New York.

Hardwick, R.C., 1986. Physiological consequences of modular growth in plants. Philosophical Transactions of the Royal Society of London, Biology 313: 161–173.

Harper, J.L., 1989. The value of a leaf. Oecologia 80: 53–58.

Hasting, H.M. and G. Sugihara, 1993. Fractals: A User's Guide for the Natural Sciences. Oxford University Press, Oxford.

Herbert, T.J., 1991. Variation in interception of the direct solar beam by top canopy layers. Ecology 72: 17–22.

Herbert, T.J. and T. Nilson, 1991. A model of variance of photosynthesis between leaves and maximization of whole plant photosynthesis. Photosynthetica 25: 597–606.

Honda, H. and J.B. Fisher, 1978. Tree branch angle: maximizing effective leaf area. Science 199: 888–890.

Honda, H., H. Hatta, and J.B. Fisher, 1997. Branch geometry in *Cornus kousa* (*Cornaceae*): computer simulations. American Journal of Botany 84: 745–755.

Horn, H.S., 1971. The Adaptive Geometry of Trees. Princeton University Press, Princeton, NJ.

Horton, P., A.V. Ruban, and R.G. Walters, 1996. Regulation of light harvesting in green plants. Annual Review of Plant Physiology and Plant Molecular Biology 47: 655–684.

Hutchins, M.J. and H. de Kroon, 1994. Foraging in plants: The role of morphological plasticity in resource acquisition. In: M. Begon and A.H. Fitter, eds. Advances in Ecological Research. Academic Press Ltd., London, pp. 159–238.

Ingrouille, M., 1995. Diversity and Evolution of Land Plants. Chapman & Hall, London.

Isebrands, J.G. and D.A. Michael, 1986. Effects of leaf morphology and orientation on solar radiation interception and photosynthesis in *Populus*. In: T. Fujimori and D. Whitehead, eds. Crown and Canopy Structure in Relation to Productivity. Forestry and Forest Products Research Institute, Ibaraki, pp. 359–381.

Ishii, R. and M. Higashi, 1997. Tree coexistence on a slope: an adaptive significance of trunk inclination. Proceedings of the Royal Society of London Series B, Biology 264: 133–140.

Jackson, R.B., W.T. Pockman, and W.A. Hoffman, 1999. The structure and function of root systems. In: F.I. Pugnaire and F. Valladares, eds. Handbook of Functional Plant Ecology. Marcel Dekker, Inc., New York, pp. 195–220.

Jahnke, L.S. and D.B. Lawrence, 1965. Influence of photosynthetic crown structure on potential productivity of vegetation, based primarily on mathematical models. Ecology 46: 319–326.

James, J.C., J. Grace, and S.P. Hoad, 1994. Growth and photosynthesis of *Pinus sylvestris* at its altitudinal limit in Scotland. Journal of Ecology 82: 297–306.

Jones, H.G., 2004. Application of thermal imaging and infrared sensing in plant physiology and ecophysiology. Advances in Botanical Research 41: 107–163.

Kellomäki, S. and H. Strandman, 1995. A model for the structural growth of young Scots pine crowns based on light interception by shoots. Ecological Modelling 80: 237–250.

Kellomäki, S. and H. Väisänen, 1995. Model computations on the impact of changing climate on natural regeneration of Scots pine in Finland. Canadian Journal of Forest Research 25: 929–942.

King, D.A., 1981. Tree dimensions: maximizing the rate of height growth in dense stands. Oecologia 51: 351–356.

King, D.A., 1986. Tree form, height growth, and susceptibility to wind damage in *Acer saccharum*. Ecology 67: 980–990.

King, D.A., 1990. The adaptive significance of tree height. The American Naturalist 135: 809–829.

King, D.A., 1991. Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. Functional Ecology 5: 485–492.

King, D.A., 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. American Journal of Botany 81: 948–957.

Koehl, M.A.R., 1996. When does morphology matter? Annual Review of Ecology and Systematics 27: 501–542.

Kucharik, C.J., J.M. Norman, and S.T. Gower, 1999. Characterization of radiation regimes in nonrandom forest canopies: Theory, measurements, and a simplified modeling approach. Tree Physiology 19: 695–706.

Kull, O., M. Broadmeadow, B. Kruijt, and P. Meir, 1999. Light distribution and foliage structure in an oak canopy. Trees: Structure and Function 14: 55–64.

Küppers, M., 1989. Ecological significance of aboveground architectural patterns in woody plants: A question of cost-benefit relationships. Trends in Ecology and Evolution 4: 375–379.

Küppers, M., 1994. Canopy gaps: competitive light interception and economic space filling—a matter of whole-plant allocation. In: M.M. Caldwell and R.W. Pearcy, eds. Exploitation of Environmental Heterogeneity by Plants. Ecophysiological Processes Above- and Belowground. Academic Press, San Diego, New York, Boston, London, Sydney, Tokyo, Toronto, pp. 111–144.

Küppers, M. and R. List, 1997. MADEIRA—a simulation of carbon gain, allocation, canopy architecture in competing woody plants. In: G. Jeremonidis and J.F.V. Vincent, eds. Plant Biomechanics: Conference Proceedings. Centre for Biomimetics, The University of Reading, Reading, pp. 321–329.

Kurth, W., 1994. Morphological models of plant growth: possibilities and ecological relevance. Ecological Modelling 75/76: 299–308.

Kuuluvainen, T., 1992. Tree architectures adapted to efficient light utilization—is there a basis for latitudinal gradients? Oikos 65: 275–284.

Leigh, E.G., 1972. The golden section and spiral leaf-arrangement. In: E.S. Deevey, ed. Growth by Intussusception. Archon Books, Hamden, CT, pp. 163–176.

Leigh, E.G., 1990. Tree shape and leaf arrangement: a quantitative comparison of montane forests, with emphasis on Malaysia and South India. In: J.C. Daniel and J.S. Serrao, eds. Conservation in Developing Countries: Problems and Prospects. Oxford University Press, Bombay, India, pp. 119–174.

Leigh, E.G., 1998. Tropical Forest Ecology. A View from Barro Colorado Island. Oxford University Press, Oxford.

Lortie, C.J. and L.W. Aarssen, 1996. The specialization hypothesis for phenotypic plasticity in plants. International Journal of Plant Sciences 157: 484–487.

Lortie, C.J. and R.M. Callaway, 2006. Re-analysis of meta-analysis: Support for the stress-gradient hypothesis. Journal of Ecology 94: 7–16.

Lovelock, C.E. and B.F. Clough, 1992. Influence of solar radiation and leaf angle on leaf xanthophyll concentrations in mangroves. Oecologia 91: 518–525.

Maestre, F.T., F. Valladares, and J.F. Reynolds, 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. Journal of Ecology 93: 748–757.

Maestre, F.T., F. Valladares, and J.F. Reynolds, 2006. The stress-gradient hypothesis does not fit all relationships between plant–plant interactions and abiotic stress: further insights from arid environments. Journal of Ecology 94: 17–22.

Margalef, R., 1997. Our biosphere. Excellence in ecology 10. Ecology Institute of Germany, Wurzburg.

Margolis, H., R. Oren, D. Whitehead, and M.R. Kaufmann, 1995. Leaf area dynamics of conifer forests. In: W.K. Smith and T.M. Hinckley, eds. Ecophysiology of Coniferous Forests. Academic Press, San Diego, New York, Boston, London, Sydney, Tokyo, Toronto, pp. 181–223.

Mattheck, C., 1991. Trees: The Mechanical Design. Springer-Verlag, Berlin.

Mattheck, C., 1995. Biomechanical optimum in woody stems. In: B.L. Gartner, ed. Plant Stems: Physiology and Functional Morphology. Academic Press, San Diego, CA, pp. 3–49.

McMahon, T., 1973. Size and shape in biology. Elastic criteria impose limits on biological proportions, and consequently on metabolic rates. Science 179: 1201–1204.

McMahon, T., 1975. The mechanical design of trees. Scientific American 233: 92–102.

McMahon, T.A. and R.E. Kronauer, 1976. Tree structures: Deducing the principle of mechanical design. Journal of Theoretical Biology 59: 443–466.

Medina, E., 1999. Tropical forests: Diversity and function and dominant life-forms. In: F.I. Pugnaire and F. Valladares, eds. Handbook of Functional Plant Ecology. Marcel Dekker, Inc., New York, pp. 407–448.

Moulia, B., 1994. The biomechanics of leaf rolling. Biomimetics 2: 267–281.

Myers, D.A., D.N. Jordan, and T.C. Vogelmann, 1997. Inclination of sun and shade leaves influences chloroplast light harvesting and utilization. Physiologia Plantarum 99: 395–404.

Niinemets, Ü., 1997. Distribution patterns of foliar carbon and nitrogen as affected by tree dimensions and relative light conditions in the canopy of *Picea abies*. Trees: Structure and Function 11: 144–154.

Niinemets, Ü. 1998. Growth of young trees of *Acer platanoides* and *Quercus robur* along a gap—understory continuum: interrelationships between allometry, biomass partitioning, nitrogen, and shade-tolerance. International Journal of Plant Sciences 159: 318–330.

Niinemets, Ü. and O. Kull, 1995. Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies*: Variation in shoot structure. Tree Physiology 15: 791–798.

Niinemets, Ü. and A. Lukjanova, 2003. Total foliar area and average leaf age may be more strongly associated with branching frequency than with leaf longevity in temperate conifers. The New Phytologist 158: 75–89.

Niinemets, Ü. and F. Valladares, 2004. Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. Plant Biology 6: 254–268.

Niinemets, Ü., A. Cescatti, A. Lukjanova, M. Tobias, and L. Truus, 2002. Modification of light-acclimation of *Pinus sylvestris* shoot architecture by site fertility. Agricultural and Forest Meteorology 111: 121–140.

Niinemets, Ü., N. Al Afas, A. Cescatti, A. Pellis, and R. Ceulemans, 2004a. Determinants of clonal differences in light-interception efficiency in dense poplar plantations: petiole length and biomass allocation. Tree Physiology 24: 141–154.

Niinemets, Ü., A. Cescatti, and R. Christian, 2004b. Constraints on light interception efficiency due to shoot architecture in broad-leaved *Nothofagus* species. Tree Physiology 24: 617–630.

Niinemets, Ü., A. Sparrow, and A. Cescatti, 2005. Light capture efficiency decreases with increasing tree age and size in the southern hemisphere gymnosperm *Agathis australis*. Trees: Structure and Function 19: 177–190.

Niinemets, Ü., M. Tobias, A. Cescatti, and A.D. Sparrrow, 2006. Size-dependent variation in shoot light-harvesting efficiency in shade-intolerant conifers. International Journal of Plant Sciences 167: 19–32.

Niklas, K.J., 1988. The role of phyllotactic pattern as a ‘‘developmental constraint’’ on the interception of light by leaf surfaces. Evolution 42: 1–16.

Niklas, K.J., 1990. Biomechanics of *Psilotum nudum* and some early Paleozoic vascular sporophytes. American Journal of Botany 77: 590–606.

Niklas, K.J., 1992. Plant Biomechanics. An Engineering Approach to Plant Form and Function. The University of Chicago Press, Chicago, London.

Niklas, K.J., 1994. Interspecific allometries of critical buckling height and actual plant height. American Journal of Botany 81: 1275–1279.

Niklas, K.J., 1997. The Evolutionary Biology of Plants. The University of Chicago Press, Chicago, IL.

Niklas, K.J. and V. Kerchner, 1984. Mechanical and photosynthetic constraints on the evolution of plant shape. Paleobiology 10: 79–101.

Nikolopoulos, D., G. Liakopoulos, I. Drossopoulos, and G. Karabourniotis, 2002. The relationship between anatomy and photosynthetic performance of heterobaric leaves. Plant Physiology 129: 235–243.

Nilson, T., 1971. A theoretical analysis of the frequency of gaps in plant stands. Agricultural Meteorology 8: 25–38.

Nobel, P.S. and R.W. Meyer, 1991. Biomechanics of cladodes and cladode–cladode junctions for Opuntia ficus-indica (Cactaceae). American Journal of Botany 78: 1252–1259.

Norman, J.M. and G.S. Campbell, 1989. Canopy structure. In: R.W. Pearcy, J.R. Ehleringer, H.A. Mooney, and P.W. Rundel, eds. Plant Physiological Ecology. Field Methods and Instrumentation. Chapman & Hall, London, New York, pp. 301–325.

Novoplansky, A., D. Cohen, and T. Sachs, 1989. Ecological Implications of Correlative Inhibition Between Plant Shoots. Physiologia Plantarum 77: 136–140.

Oker-Blom, P., 1986. Photosynthetic radiation regime and canopy structure in modeled forest stands. Acta Forestalia Fennica 197: 1–44.

Oker-Blom, P. and S. Kellomäki, 1982. Theoretical computations on the role of crown shape in the absorption of light by forest trees. Mathematical Biosciences 59: 291–311.

Oker-Blom, P. and H. Smolander, 1988. The ratio of shoot silhouette to total needle area in Scots pine. Forest Science 34: 894–906.

Osmond, C.B., J.M. Anderson, M.C. Ball, and J.G. Egerton, 1999. Compromising efficiency: The molecular ecology of light-resource utilization in plants. In: M.C. Press, J.D. Scholes, and M.G. Barker, eds. Physiological Plant Ecology. The 39th Symposium of the British Ecological Society held at the University of York, 7–9 September 1998. Blackwell Science, Oxford, pp. 1–24.

Palmroth, S., P. Stenberg, S. Smolander, P. Voipio, and H. Smolander, 2002. Fertilization has little effect on light-interception efficiency of *Picea abies* shoots. Tree Physiology 22: 1185–1192.

Parsons, P.A., 1993. The importance and consequences of stress in living and fossil populations: From life-history variation to evolutionary change. American Naturalist 142: S5–S20.

Pearcy, R.W., 1999. Responses of plants to heterogeneous light environments. In: F.I. Pugnaire and F. Valladares, eds. Handbook of Functional Plant Ecology. Marcel Dekker, New York, pp. 269–314.

Pearcy, R.W. and W. Yang, 1996. A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. Oecologia 108: 1–12.

Pearcy, R.W. and W. Yang, 1998. The functional morphology of light capture and carbon gain in the redwood forest understorey plant, *Adenocaulon bicolor* Hook. Functional Ecology 12: 543–552.

Pearcy, R.W., H. Muraoka, and F. Valladares, 2005. Crown architecture in sun and shade environments: Assessing function and trade-offs with a three-dimensional simulation model. The New Phytologist 166: 791–800.

Peer, W.A., W.R. Briggs, and J.H. Langenheim, 1999. Shade-avoidance responses in two common coastal redwood forest species, *Sequoia sempervirens* (*Taxodiaceae*) and *Satureja douglasii* (*Lamiaceae*), occurring in various light quality environments. American Journal of Botany 86: 640–645.

Perttunen, J., R. Sievänen, E. Nikinmaa, H. Salminen, H. Saarenmaa, and J.Väkevä. 1996. LIGNUM: a tree model based on simple structural units. Annals of Botany 77: 87–98.

Poorter, L., L. Bongers, and F. Bongers, 2005. Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. Ecology (Tempe) 87: 1289–1301.

Porter, J.R., 1983. A modular approach to analysis of plant growth. I. Theory and principles. New Phytologist 94: 183–190.

Porter, J.R., 1989. Modules, models and meristems in plant architecture. In: G. Russell, B. Marshall, and P.G. Jarvis, eds. Plant Canopies: Their Growth, Form and Function. Cambridge University Press, Cambridge, New York, New Rochelle, Melbourne, Sydney, pp. 143–159.

Poulson, M.E. and E.H. DeLucia, 1993. Photosynthetic and structural acclimation to light direction in vertical leaves of *Silphium terebinthinaceum*. Oecologia 95: 393–400.

Prusinkiewicz, P., 1998. Modeling of spatial structure and development of plants: A review. Scientia Horticulturae 74: 113–149.

Prusinkiewicz, P. and A. Lindenmayer, 1990. The Algorithmic Beauty of Plants. Springer-Verlag, New York.

Rich, P.M., 1986. Mechanical architecture of arborescent rainforest palms. Principles 30: 117–131.

Rich, P.M., 1987. Developmental anatomy of the stem of *Welfia georgii*, *Iriartea gigantea*, and other arborescent palms: Implications for mechanical support. American Journal of Botany 74: 792–802.

Roberts, S.W. and P.C. Miller, 1977. Interception of solar radiation as affected by canopy organization in two Mediterranean shrubs. Acta Oecologica/Oecologia Plantarum 12: 273–290.

Roderick, M.L., G.D. Farquhar, S.L. Berry, and I.R. Noble, 2001. On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. Oecologia 129: 21–30.

Room, P., J. Hanan, and P. Prusinkiewicz, 1996. Virtual plants: new perspectives for ecologists, pathologists and agricultural scientists. Trends in Plant Science 1: 33–38.

Room, P.M., L. Maillette, and J.S. Hanan, 1994. Module and metamer dynamics and virtual plants. Advances in Ecological Research 25: 105–157.

Ross, J. 1981. The Radiation Regime and Architecture of Plant Stands. Dr. W. Junk, The Hague.

Russell, G., P.G. Jarvis, and J.L. Monteith, 1989. Absorption of radiation by canopies and stand growth. In: G. Russell, B. Marshall, and P.G. Jarvis, eds. Plant Canopies: Their Growth, Form and Function. Cambridge University Press, Cambridge, New York, New Rochelle, Melbourne, Sydney, pp. 21–39.

Ryan, M.G., D. Binkley, and J.H. Fownes, 1997. Age-related decline in forest productivity: Pattern and process. Advances in Ecological Research 27: 213–262.

Sachs, T., 1988. Epigenetic selection: an alternative mechanism of pattern formation. Journal of Theoretical Biology 134: 547–559.

Sachs, T. and M. Hassidim, 1996. Mutual support and selection between branches of damaged plants. Vegetatio 127: 25–30.

Sachs, T. and A. Novoplansky, 1995. Tree form: Architectural models do not suffice. Israel Journal of Plant Sciences 43: 203–212.

Sachs, T., A. Novoplansky, and D. Cohen, 1993. Plants as competing populations of redundant organs. Plant, Cell and Environment 16: 765–770.

Schulze, E.D., M. Küppers, and R. Matyssek, 1986. The roles of carbon balance and branching pattern in the growth of woody species. In: T.J. Givnish, ed. On the Economy of Plant Form and Function. Proceedings of the Sixth Maria Moors Cabot Symposium, "Evolutionary constraints on primary productivity: adaptive patterns of energy capture in plants," Harvard Forest, August 1983. Cambridge University Press, Cambridge, London, New York, New Rochelle, Melbourne, Sydney, pp. 585–602.

Shackel, K.A. and A.E. Hall, 1979. Reversible leaflet movements in relation to drought adaptation of cowpeas, *Vigna unguiculata* (L.) Walp. Australian Journal of Plant Physiology 6: 265–276.

Sinoquet, H., S. Thanisawanyangkura, H. Mabrouk, and P. Kasemsap, 1998. Characterization of the light environment in canopies using 3D digitising and image processing. Annals of Botany 82: 203–212.

Sinoquet, H., X. Le Roux, B. Adam, T. Ameglio, and F.A. Daudet, 2001. RATP: A model for simulating the spatial distribution of radiation absorption, transpiration and photosynthesis within canopies: Application to an isolated tree crown. Plant, Cell and Environment 24: 395–406.

Sinoquet, H., G. Sonohat, J. Phattaralerphong, and C. Godin, 2005. Foliage randomness and light interception in 3D digitized trees: An analysis of 3D discretization of the canopy. Plant, Cell and Environment 29: 1158–1170.

Smith, H., and G.C. Whitelam, 1997. The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. Plant, Cell and Environment 20: 840–844.

Smith, M. and D. Ullberg, 1989. Effect of leaf angle and orientation on photosynthesis and water relations in *Silphium terebinthinaceum*. American Journal of Botany 76: 1714–1719.

Smith, W.K., T.C. Vogelmann, E.H. DeLucia, D.T. Bell, and K.A. Shepherd, 1997. Leaf form and photosynthesis. Do leaf structure and orientation interact to regulate internal light and carbon dioxide? BioScience 47: 785–793.

Speck, T. and D. Vogellehner, 1988. Biophysical examinations of the bending stability of various stele types and the upright axes of early "vascular" land plants. Botanica Acta 101: 262–268.

Speck, T., H.C. Spatz, and D. Vogellehner, 1990. Contributes to the biomechanics of plants. I. Stabilities of plant stems with strengthening elements of differing cross-sections against weight and wind forces. Botanica Acta 103: 111–122.

Sprugel, D.G. 2002. When branch autonomy fails: Milton's Law of resource availability and allocation. Tree Physiology 22: 1119–1124.

Sprugel, D.G., T.M. Hinckley, and W. Schaap, 1991. The theory and practice of branch autonomy. Annual Review of Ecology and Systematics 22: 309–334.

Steingraeber, D.A., 1982. Phenotypic plasticity of branching pattern in sugar maple (*Acer saccharum*). American Journal of Botany 69: 638–640.

Stenberg, P., 1995. Penumbra in within-shoot and between-shoot shading in conifers and its significance for photosynthesis. Ecological Modelling 77: 215–231.

Stenberg, P., H. Smolander, D.G. Sprugel, and S. Smolander, 1998. Shoot structure, light interception, and distribution of nitrogen in an *Abies amabilis* canopy. Tree Physiology 18: 759–767.

Stenberg, P., S. Palmroth, B.J. Bond, D.G. Sprugel, and H. Smolander, 2001. Shoot structure and photosynthetic efficiency along the light gradient in a Scots pine canopy. Tree Physiology 21: 805–814.

Sterck, F.J., F. Bongers, and D.M. Newbery, 2001. Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. Plant Ecology 153: 279–292.

Sterck, F., M. Martinez-Ramos, G. Dyer-Leal, J. Rodriguez-Velazquez, and L. Poorters, 2003. The consequences of crown traits for the growth and survival of tree saplings in a Mexican lowland rainforest. Functional Ecology 17: 194–200.

Stewart, I., 1988. A review of the science of fractal images. Nature 336: 289.

Strauss-Debenedetti, S., and F.A. Bazzaz, 1996. Photosynthetic characteristics of tropical trees along successional gradients. In: S.S. Mulkey, R.L. Chazdon, and A.P. Smith, eds. Tropical Forest Plant Ecophysiology. Chapman & Hall, New York, pp. 162–186.

Sultan, S.E., 2004. Promising directions in plant phenotypic plasticity. Perspectives in Plant Ecology Evolution and Systematics 6: 227–233.

Sultan, S.E., 2005. An emerging focus on plant ecological development. New Phytologist 166: 1–5.

Takenaka, A., 1994a. Effects of leaf blade narrowness and petiole length on the light capture efficiency of a shoot. Ecological Research 9: 109–114.

Takenaka, A., 1994b. A simulation model of tree architecture development based on growth response to local light environment. Journal of Plant Research 107: 321–330.

Terborgh, J., 1992. Diversity and the Tropical Forest. Scientific American Library, New York.

Terjung, W.H. and S.S.F. Louie, 1972. Potential solar radiation on plant shapes. International Journal of Biometeorology 16: 25–43.

Thomas, S.C. and W.E. Winner, 2000. A rotated ellipsoidal angle density function improves estimation of foliage inclination distributions in forest canopies. Agricultural and Forest Meteorology 100: 19–24.

Tomlinson, P.B., 1987. Architecture of tropical plants. Annual Review of Ecology and Systematics 18: 1–21.

Turgut, R., and A. Kadioglu, 1998. The effect of drought, temperature and irradiation on leaf rolling in *Ctenanthe setosa*. Biologia Plantarum 41: 629–633.

Turner, I.M., W.K. Gong, J.E. Ong, J.S. Bujang, and T. Kohyama, 1995. The architecture and allometry of mangrove saplings. Functional Ecology 9: 205–212.

Tyree, M.T., 1988. A dynamic model for water flow in a single tree: Evidence that models must account for hydraulic architecture. Tree Physiology 4: 195–217.

Tyree, M.T., 1999. Water relations and hydraulic architecture. In: F.I. Pugnaire and F. Valladares, eds. Handbook of Functional Plant Ecology. Marcel Dekker, New York, pp. 221–268.

Valladares, F., 1999. Architecture, ecology, and evolution of plant crowns. In: F.I. Pugnaire and F. Valladares, eds. Handbook of Functional Plant Ecology. Marcel Dekker, Inc., New York, pp. 121–194.

Valladares, F. and D. Brites, 2004. Leaf phyllotaxis: Does it really affect light capture? Plant Ecology 174: 11–17.

Valladares, F. and R.W. Pearcy, 1997. Interactions between water stress, sun-shade acclimation, heat tolerance and photoinhibition in the sclerophyll *Heteromeles arbutifolia*. Plant, Cell and Environment 20: 25–36.

Valladares, F. and R.W. Pearcy, 1998. The functional ecology of shoot architecture in sun and shade plants of *Heteromeles arbutifolia* M. Roem, a Californian chaparral shrub. Oecologia 114: 1–10.

Valladares, F. and R.W. Pearcy, 1999. The geometry of light interception by shoots of *Heteromeles arbutifolia*: Morphological and physiological consequences for individual leaves. Oecologia 121: 171–182.

Valladares, F. and F.I. Pugnaire, 1999. Tradeoffs between irradiance capture and avoidance in semi-arid environments assessed with a crown architecture model. Annals of Botany 83: 459–469.

Valladares, F., S.J. Wright, E. Lasso, K. Kitajima, and R.W. Pearcy, 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81: 1925–1936.

Valladares, F., L. Balaguer, E. Martínez-Ferri, E. Perez-Corona, and E. Manrique, 2002a. Plasticity, instability and canalization: Is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? The New Phytologist 156: 457–467.

Valladares, F., J.M. Chico, I. Aranda, L. Balaguer, P. Dizengremel, E. Manrique, and E. Dreyer, 2002b. The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. Trees: Structure and Function 16: 395–403.

Valladares, F., J.B. Skillman, and R.W. Pearcy, 2002c. Convergence in light capture efficiencies among tropical forest understory plants with contrasting crown architectures: A case of morphological compensation. American Journal of Botany 89: 1275–1284.

Valladares, F., I. Dobarro, D. Sánchez-Gómez, and R.W. Pearcy, 2005. Photoinhibition and drought in Mediterranean woody saplings: Scaling effects and interactions in sun and shade phenotypes. Journal of Experimental Botany 56: 483–494.

van Kleunen, M. and M. Fischer, 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. New Phytologist 166: 49–60.

Van Pelt, R. and J.F. Franklin, 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. Canadian Journal of Forest Research 30: 1231–1245.

van Steenis, C.G.G.J., 1981. Rheophytes of the world: An account of flood-resistant flowering plants and ferns and the theory of autonomous evolution. Sijthoff and Noordhoof, Alphen aan den Rijn, The Netherlands.

Vogel, S., 1989. Drag and reconfiguration of broad leaves in high winds. Journal of Experimental Botany 40: 941–948.

Vogel, S., 1996. Life in moving fluids: The physical biology of flow. Princeton University Press, Princeton, NJ.

Waller, D.M., 1986. The dynamics of growth and form. In: M.J.Crawley, ed. Plant Ecology. Blackwell Scientific Publications, Oxford, London, Edinburgh, Boston, Palo Alto, Melbourne, pp. 291–320.

Waller, D.M. and D.A. Steingraeber, 1985. Branching and modular growth: Theoretical models and empirical patterns. In: J.B.C. Jackson, L.W. Buss, and R.E. Cook, eds. Population Biology and Evolution of Clonal Organisms. Yale University Press, New Haven, London, pp. 225–257.

Wang, Y.P. and P.G. Jarvis, 1990. Influence of crown structural properties on PAR absorption, photosynthesis, and transpiration in Sitka spruce: Application of a model (MAESTRO). Tree Physiology 7: 297–316.

Wang, Y.P. and R. Leuning, 1998. A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. I. Model description and comparison with a multi-layered model. Agricultural and Forest Meteorology 91: 89–111.

Watson, M.A., 1986. Integrated physiological units in plants. Trends in Ecology and Evolution 1: 119–123.

Weinig, C., 2000. Limits to adaptive plasticity: Temperature and photoperiod influence shade-avoidance responses. American Journal of Botany 87: 1660–1668.

Werk, K.S. and J.Ehleringer, 1984. Non-random leaf orientation in *Lactuca serriola* L. Plant, Cell and Environment 7: 81–87.

White, J., 1979. The plant as metapopulation. Annual Review of Ecology and Systematics 10: 109–145.

White, J., 1984. Plant metamerism. In: R. Dirzo and J. Sarukhán, eds. Perspectives on Plant Population Ecology. Sinauer, Sunderland, MA, pp. 176–185.

Whitney, G.G., 1976. The bifurcation ratio as an indicator of adaptive strategy in woody plant species. Bulletin of the Torrey Botanical Club 103: 67–72.

Wilson, B.F., 1995. Shrub stems: Form and function. In: B. Gartner, ed. Plant Stems. Physiology and Functional Morphology. Academic Press, San Diego, CA, pp. 91–103.

Woodward, F.I., 1998. Do plants really need stomata? Journal of Experimental Botany 49: 471–480.

Wright, S.J., 1999. Plant diversity in tropical forests. In: F.I. Pugnaire and F. Valladares, eds. Handbook of Functional Plant Ecology. Marcel Dekker, Inc., New York, pp. 449–471.

Zimmermann, U., H.-J. Wagner, H. Schneider, M. Rokitta, A. Haase, and F.-W. Bentrup, 2000. Water ascent in plants: The ongoing debate. Trends in Plant Science 5: 145–146.