

Light Heterogeneity and Plants: from Ecophysiology to Species Coexistence and Biodiversity

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1 Introduction

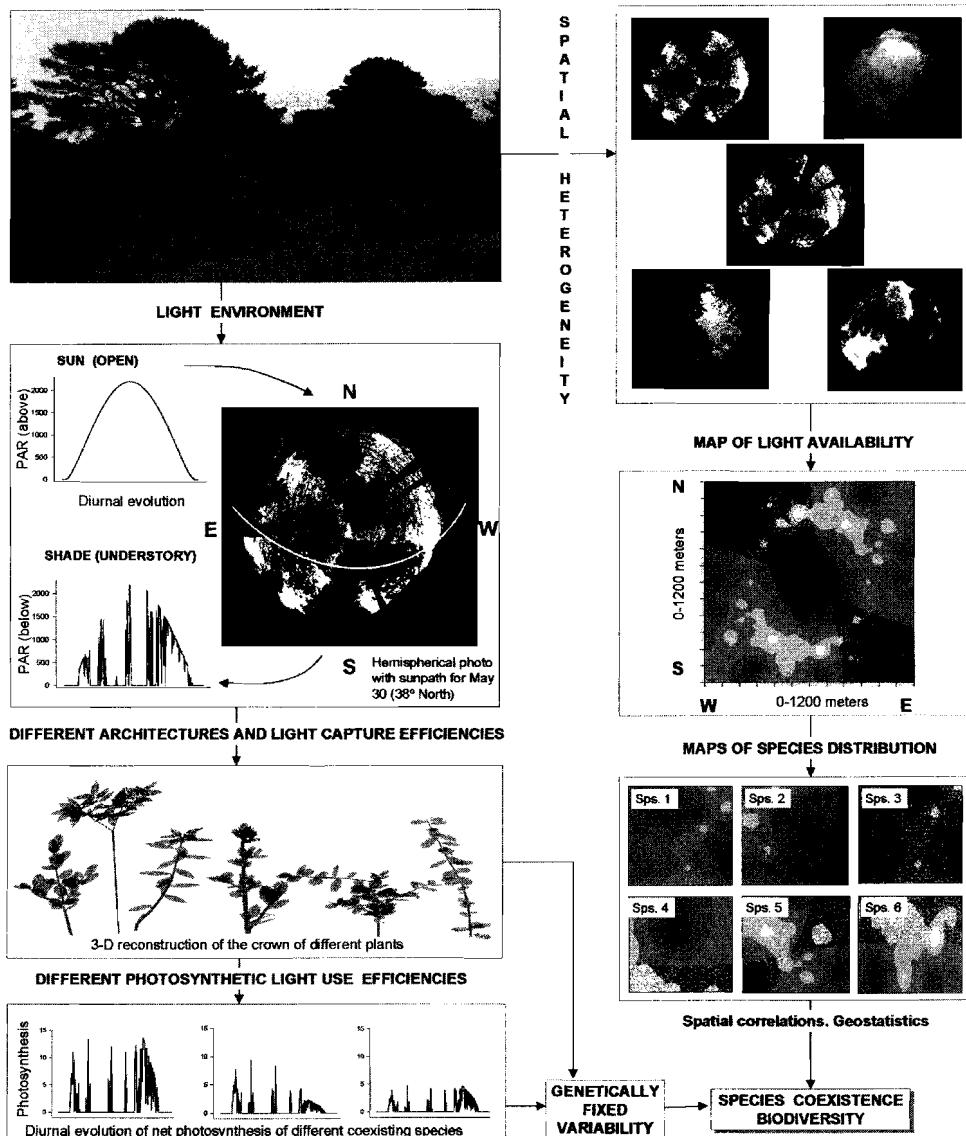
Light is produced by changes in the energy level of electrons (when an electron changes from a high-energy, or excited, state to a low-energy state, its atom will emit a photon), but its dual nature makes it scientifically puzzling: it moves through space as a wave, but when it encounters matter it behaves like a particle, the quantum (Achenbach 2001). In practice "light" is used for the portion of the electromagnetic spectrum in the vicinity of visible light. In plant biology and ecology, photosynthetically active radiation (PAR), which essentially coincides with visible light, is probably the most relevant measure of light. The PAR region is where energy is most abundant (it represents on average 43% of the solar irradiance), and it is strong enough to drive electron transport in photosynthesis, yet weak enough to avoid excessive damage to biological molecules. However, there exists no worldwide network for PAR measurements like the network of actinometric stations, where global, direct, diffuse and reflected solar radiation are measured using unified instruments and methodology and are metrologically based on the world radiometric reference (Ross and Sulev 2000). The dual nature of light, i.e., particle versus wave, affects the way light in general and PAR in particular is measured. One group of sensors measures energy (e.g., W m^{-2}), the other group quanta (e.g., $\mu\text{mol m}^{-2} \text{s}^{-1}$). General conversion factors are 1.814, 1.758, 2.127, and 0.462 $\mu\text{mol PAR W}^{-1}$ for global, direct, diffuse, and reflected radiation, respectively (Ross and Sulev 2000), but these factors should be used with care since they may be different under different environmental conditions.

Light provides the energy used in photosynthesis and the signals used in photoregulation of plant growth and development, and is, among the factors affecting plants, perhaps the most spatially and temporally heterogeneous (Pearcy 1999). PAR in the understory ranges from 50–80% of full sunlight under leafless deciduous trees, to 10–15% in even-aged pine stands, 2.5% in closed spruce canopies, 0.2–0.4% in dense beech forests, and even less than 0.1% in certain tropical rainforests (Barnes et al. 1998). In addition to this quantitative variability, light is also qualita-

tively heterogeneous. A total of five basic light environments can be found in terrestrial ecosystems according to the color of light: (1) forest shade (greenish or yellow-green light due to selective absorption of red and blue by vegetation), (2) woodland shade (bluish or bluish-grey light due to the dominance of the radiation from the sky), (3) small gaps (yellowish-reddish light due to direct sunlight), (4) large gaps, open, or any habitat under cloudy conditions (whitish light due to combination of sun and sky light, or because of the dominance of the white light radiating from clouds), and (5) any habitat early and late in the day, when sun is below 10° from the horizon (purplish light; Endler 1993; Kiltie 1993). Once the vegetation is established, it becomes the main cause of the remarkable spatial heterogeneity of light in most natural habitats (Fig. 1). Forest overstory canopies never close completely and there is a continuous gradient in gap size from those between 1 cm² and 1 m² due to foliage clumping or wind-induced abrasion of adjacent crowns, to those between 50 and 600 m² due to tree falls. Changes in the light environment associated with successional changes are relatively slow and predictable, and allow individual plants to anticipate and respond; the same applies to both seasonal and diurnal variations. Sun flecks, which often contribute a substantial fraction of the total light available in the understory (Pearcy 1983; Chazdon 1988), cause the most rapid

Fig. 1. Influence of light heterogeneity on the structure and dynamics of plant populations and communities can be explored via mechanistic approaches (*left panels*) or correlation studies (*right panels*). In the understory the low, diffuse, background light is punctuated by sun flecks of various durations and intensities, which can be seen in diurnal cycles estimated from hemispherical photographs of the canopy (*central photo in left panels*). This temporally heterogeneous light can be exploited by plant species of different crown architectures, i.e., with different light capture efficiencies and allocation patterns. Light capture efficiency by the whole crown can be simulated by realistic 3-D reconstructions using computer models (plant images in *left panels* were obtained with Y-plant; Pearcy and Yang 1996). Plant species also differ in their photosynthetic capacity to use this variable and dynamic light (Valladares et al. 1997). Frequently, many of these differences are genetically fixed (Arntz and Delph 2001). These different plants coexist in the understory either by being functionally equivalent (e.g., two contrasting architectures might have the same light capture efficiency, two different photosynthetic physiologies might lead to the same daily total carbon gain), by converging by phenotypic plasticity, or by the fact that other traits (tolerance to herbivory or water stress, efficient reproduction, dispersal or recruitment) counteract suboptimal morphologies and physiologies. Functional convergence in response to shade could explain the relatively high levels of biodiversity in tropical understories where light is the limiting factor (see, e.g., Valladares et al. 2002b). However, light in most natural ecosystems is heterogeneous not only in time but also in space and many forest ecosystems exhibit a complex spatial distribution of mean daily photosynthetically active radiation (PAR). Correlation studies considering spatial patterns explicitly (e.g., by means of geostatistics) are enhancing our understanding on where, when and to which extent light heterogeneity contributes to species coexistence and promotes biodiversity (see, e.g., Nicotra et al. 1999; Bascompte and Rodriguez 2001)

scale of temporal heterogeneity: from seconds to minutes. The spatial scale of sun flecks typically vary from 0.1 to 1 m, so that often only part of the crown of an understory plant will be influenced by a given sun flea (Baldocchi and Collineau 1994). Spatial autocorrelation explored with arrays of photosensors revealed very fine grain heterogeneity (auto-correlation of 0.4 within 0.2 m and almost none for 0.5 m) due to the interplay of the overstory canopy and the self-shading within the crown of the understory plant (Chazdon et al. 1988). The spatial heterogeneity



observed for a day is noticeably decreased when monthly or annual means are considered due to seasonal changes in the solar elevation angle. For this reason, spatial analysis carried out with hemispherical photographs (Fig. 1) generally reveals heterogeneity of coarser grain: autocorrelation was still significant at 2.5 m in a tropical forest (Becker and Smith 1990). Autocorrelation was significant at even longer distances (>10 m) when only the spatial heterogeneity of diffuse light was considered in a study of different tropical forests (Nicotra et al. 1997). The distinction between spatial and temporal heterogeneity of light is convenient but also rather artificial (Pearcy 1999). The spatial and temporal scales are highly correlated and, in terms of analysis, they are frequently interchangeable (Baldocchi and Collineau 1994).

Light quantity and quality affect ecosystem properties in general and plant performance in particular, but the effects are in many cases difficult to unveil due to correlations (e.g., high light–high temperature–high water stress) and complex interactions with other environmental factors (e.g., water stress reduces the photosynthetic capacity to use light, ultraviolet light affects plants directly but it also alters herbivore and microbial activity which in turn affects plants both directly and indirectly via changes in nutrient cycling). The purpose of this chapter is to review a selection of the abundant literature on this rapidly developing field to illuminate some of the most promising areas for future research. The task of integrating the information has been challenging due not only to the large number of publications, but also to the variety of interrelated topics, techniques and approaches that have appeared since the earlier and now classical attempts of exploring light as an ecological factor (e.g., Shirley 1929; Bainbridge et al. 1966; Horn 1971).

2 Light Capture and Photosynthesis: Scaling Up to the Plant

a) Crown Architecture, a Compromise of Multiple Functions

Leaves are the ultimate sink for light and their optical properties can significantly affect light capture by the whole plant, while their photosynthetic characteristics dramatically influence whole plant photosynthetic performance. Leaf morphological and physiological adaptations to high and low irradiances received intense attention during the 1970s and 1980s, which led to a thorough description of the so-called sun and shade types of leaf (Björkman 1981; Evans et al. 1988; Larcher 1995). The last decades of the twentieth century have witnessed a change in the research priorities of most plant ecologists, with the whole plant and not the leaf as the main target. This in turn has led to a renovated, more functional interest in plant architecture (Valladares 1999; Valladares and Pearcy 2000).

A striking feature of understory vegetation in neotropical rainforests is the large variation in plant appearance and leaf morphology (Bongers and Popma 1990; Leigh 1998; Turner et al. 2000). Are these contrasting habits and morphologies rendering a functionally equivalent architecture in terms of light capture efficiency? Branching pattern and leaf arrangement in the crown of a plant have a direct impact on the efficiency of leaf display and consequently on light capture and photosynthesis (Valladares 1999). However, crown architecture influences numerous aspects of whole-plant function and not only light capture efficiency (Pearcy and Valladares 1999). Thus, real plants in low-light environments may deviate considerably from the predicted, optimal pattern for light capture as a result of other constraints on crown form (e.g., water transport, mechanical stability). For example, optimal display of foliage for light capture may be prohibited by requirement for high resources for supporting tissues (King 1991; Pearcy and Yang 1998; Poorter and Werger 1999). Or, selection in trees for a fast increase in height to attain a position in the canopy can be at the cost of a narrow crown far from optimal in terms of light capture during the understory phase (King 1990; Clark and Clark 2001). Crown architecture has a static function (i.e., efficient leaf display at the current light environment) and, since light is predictably more available at increasing heights, also a dynamic function (i.e., increasing in height at the lowest construction cost), which translates into a trade-off between height growth and leaf area extension (Kohyama and Hotta 1990). All these constraints and trade-offs could explain why among all the plants in a comparative study of 24 co-occurring understory plants none had a light absorption efficiency greater than 0.75 (Valladares et al. 2002b). When natural selection acts on two or more traits simultaneously, evolutionary responses may be limited by genetic correlations that reflect genetic, physiological and/or developmental constraints (Ackerly 2000). Diversity in architecture may reflect different ways of using light resources and thus may enable species coexistence (Aiba and Kohyama 1997; Fig. 1). As argued by Kohyama (1987), the architectural and allometric diversity found in the forest understory can be related to the alternative of "choosing" any of these combinations of traits.

b) Plant Movements Influenced by Light

Crown architecture is rather dynamic. Changes in its geometry and size can be due to external factors (e.g., mechanical damage) and also to internal responses to environmental clues (Valladares 1999). Leaves can be arranged either to increase or to decrease light capture, and, as in the case of chloroplasts, leaf movements can be triggered by light itself (Koller 1990). Leaves of many terrestrial plants perform "sleep move-

ments", assuming a compactly folded configuration during the night and an unfolded one in daytime, increasing interception of light by the lamina (Koller 2000). Photonastic movements (such as sleep movements) take place in a determined direction but are independent of the direction of the light, while phototropic movements take place according to the direction of light and are more prone to modifications by environmental stresses (Ehleringer and Werk 1986; Koller 2000). Heliotropic movements track the daily solar transit and after sunset they reverse direction; they can be diaheliotropic, when leaves are kept perpendicular to the sunrays, or paraheliotropic when they are kept parallel to the sunrays, which minimizes light and heat loads and can be advantageous under water stress (Ehleringer and Werk 1986). Leaf movements are effective in regulating light capture by the whole crown only when mutual shading by leaves is reduced, i.e., when individuals are widely spaced and leaf area indices are lower than 1.5 (Ehleringer and Forseth 1989). Leaf movements require a high direct-to-diffuse light ratio, so they are restricted to the upper layer of a canopy and are scant in the understory, except certain downwards movements in the presence of high light that can prevent photoinhibition of deep shade plants during sun flecks (Powles and Björkman 1981). Not only leaves, but also apical parts of the shoot may exhibit heliotropic movements, which have been described not only in the domestic sunflower and its wild relatives, but also in *Crozophora tinctoria*, *Xanthium strumarium*, and in a number of Arctic and alpine plants (Kevan 1975; Stanton and Galen 1993; Koller 2000).

c) Morphological and Structural Photoprotection

Certain features of the shape and architecture of the crown, such as self-shading and steep leaf elevation angles, can prevent excessive light from reaching the photosystems together with leaf attributes such as pubescence or thick cuticular or epidermal layers (Valladares 1999; Valladares and Pugnaire 1999). This morphological or structural protection can be efficient not only against excessive PAR, avoiding photoinhibition and overheating, but also against ultraviolet radiation, avoiding DNA mutations and growth alterations (Day 1993; Skaltsa et al. 1994; Kyparissis et al. 1995; Grammatikopoulos et al. 1998). In fact, certain plant life forms have been shown to be more effective than others in screening out UV-B radiation (Day et al. 1992). Structural and physiological protection against excessive light interact and complement each other. Carotenoids, primarily photoprotective (Young 1991), exhibited higher concentrations in leaves than in stems in a comparison of six leguminous, green-stem shrubs (Valladares et al. submitted), which was in agreement with the different exposure to high light and risk of photoinhibition associ-

ated with the different mean elevation angle of leaves and stems (Ehleringer and Cooper 1992; Valladares and Pearcy 1999). This finding agrees with previous studies where the particular orientation and daily light interception of each individual leaf correlated with the concentration of the photoprotective carotenoids of the xanthophyll cycle (Lovelock and Clough 1992).

d) Geometry of the Crown, Curiosity or Function?

In most plants, leaf primordia at the apex appear as far as possible from each other (Hofmeister's rule; Jean 1984), which in plants with helical leaf arrangement commonly leads to a divergence angle between consecutive leaves near the "golden angle" of 137.5° at which there is no complete overlap between any two leaves on a vertical stem (Bell 1993). For plants in shaded habitats, minimum leaf overlap is a predicted characteristic. For that reason, phyllotaxis (the geometry of leaf arrangement on stems) and the mathematically intriguing properties of the Fibonacci series in divergence angles have been historically dealt with in terms of selection pressures favoring light interception (Sekimura 1995; Adler et al. 1997; Jean and Barabé 1998). Unusual patterns such as the monostichous phyllotaxis of *Costus*, with a divergence angle as low as $30\text{--}40^\circ$, has attracted and puzzled many botanists. However, after more than 120 years of study, the mystery of costoid phyllotaxy still remains (see Kirchoff and Rutishauser 1990 and references cited therein). The small divergence angles of *Costus* are correlated in certain species with helical twining of the stem to give the shoot the appearance of a spiral staircase (in this case the phyllotaxis is referred as spironostichous; Bell 1993). Is this staircase-like crown compensating for the small divergence angle between consecutive leaves? The answer after a comparative study of 24 species cooccurring in a tropical understory is yes (Valladares et al. 2002b). Distichy, characteristically orthodistichy, is the typical kind of phyllotaxy among monocotyledons (Wilder 1992 and references cited therein); this implies the existence of two straight rows of leaves and thus, a potentially large mutual shading among leaves in vertical stems. This potentially inefficient leaf display was overridden by either an arced stem, by plagiotropic shoots, or by long petioles in the same comparative study of understory plants (Valladares et al. 2002b). The extent to which phyllotaxis influences light capture of real plants still remains poorly understood, but the fact that a suite of morphological features can compensate for suboptimal phyllotactic arrangements (Niklas 1988; Brites and Valladares, submitted) suggests that phyllotaxis involves more geometric and mathematic curiosity than functional implications. Other geometric characteristics of the foliage, such as the elevation angle of the leaf and the internodal length, have been confirmed as important de-

terminants of light capture in a number of quantitative, functional studies of plant crowns (McMillen and McClendon 1979; Smith and Ullberg 1989; Herbert 1996; Valladares and Pearcy 1998).

e) Photosynthetic Stems

It is well known that plant parts other than leaves can be green and photosynthetically active, and, in the case of green stems, they can have remarkable implications for the overall carbon gain of the plant (Pfanz and Aschan 2001). Net photosynthetic capacity of green stems contributes to an average of 50% of whole plant carbon gain in habitats like deserts, tropical dry or thorn woodlands and Mediterranean type ecosystems (Nilsen 1992a,b). Stem photosynthesis has a number of possible benefits: extension of period of carbon gain in environments with periodic droughts (Smith and Osmond 1987; Nilsen 1992a), heat (DePuit and Caldwell 1975; Smith and Osmond 1987) or excessive irradiance (Valladares 1999; Valladares and Pugnaire 1999), and tolerance to herbivory (Bossard and Rejmanek 1992). Even though green stems are photosynthetically not efficient in a number of woody species (Comstock and Ehleringer 1988; Pfanz and Aschan 2001), photosynthetic activity of the cortical tissues of leguminous shrubs like *Retama*, *Spartium* or *Cytisus* is as high and efficient as that reported for leaves (Bossard and Rejmanek 1992; Nilsen 1992b; Haase et al. 1999). Leguminous shrubs with green stems differ in the relative importance of leaves for whole plant carbon gain, from species such as *Retama sphaerocarpa*, practically leafless, to species like *Cytisus scoparius* and *Spartium junceum*, where leaves contribute 50–70% of whole plant carbon gain (Nilsen 1992b; Nilsen et al. 1993). A recent comparative study of six leguminous species has shown that the relative amount of leaves determines the short-term survival in deep shade (Valladares et al., submitted). Thus, species with green stems and a low number of leaves seem to be morphologically restricted to well-lit habitats. In fact, the poor light harvesting efficiency of vertical stems becomes a potential advantage in high-light habitats since it provides protection against excessive radiation, enhancing survival and performance in arid environments (Valladares and Pugnaire 1999).

f) Leaf Phenology and Light Capture

Leaf phenology, or the arrangement of leaves in time, is also an important aspect of the light-harvesting strategy of plants (Kikuzawa 1989, 1991). Interrelationships among the three components of leaf phenology, i.e., leaf longevity, leaf habit (evergreenness or deciduousness) and leaf

emergence pattern (simultaneous or successive), together with shoot architecture and photosynthetic capacity, affect plant productivity (Kikuzawa 1995; Kikuzawa et al. 1996). Kikuzawa (1995) presented a synthesis between resource-based and climate-based models of leaf phenology. In his model, plants with successive leaf emergence and short leaf longevity (he assumes that the first, unshaded leaf is only replaced by a second leaf when its photosynthetic ability declines) have straight, multilayered shoots and attain high production in resource-rich environments (e.g., early successional stages), while plants with a simultaneous leaf emergence increase the longevity of individual leaves and avoid self-shading by inclining their apical shoot (monolayer canopies) to attain high production in resource-poor environments. The connections between light environment, seasonal variability, canopy architecture, photosynthetic capacity and leaf phenology are appealing but the model oversimplifies the reality. Some of the assumptions (e.g., self-shading is not a serious problem for plants with successive leaf emergence, the replacement takes place only when the photosynthetic ability of the leaf declines) are not universally valid (Valladares and Pearcy 1998, 1999), and the selective pressure for maximizing light capture does not hold in many habitats since self-shading in high-light environments where plant growth is limited by water or extreme temperatures might not be a constraint but an advantage (Valladares 1999; Valladares and Pugnaire 1999).

g) Advantages and Limits of Computer Models

Computer models can handle and integrate complex and interrelated variables and thus are powerful tools to simulate the role of light for net carbon assimilation and plant growth. They have been used in a range of applications, from leaf to canopy photosynthesis (Thornley 1998; Beyschlag and Ryel 1999; Farquhar et al. 2001), and from crown architecture (Pearcy and Yang 1996; Fig. 1) to plant growth (Kramer 1994). The fascinating geometric properties of plant architecture in particular have received considerable attention from modellers (Prusinkiewicz and Lindenmayer 1996; Prusinkiewicz 1999). Empirically based models and mechanistic approaches demand detailed knowledge in a frequently too extensive list of parameters, while goal-seeking methods based on optimality arguments are usually simpler. However, when only a single variable is chosen for optimization, not only realism but also accuracy in the predictions is significantly reduced (Wirtz 2000). Despite the realistic appearance of certain computer simulations, they frequently make broad and sometimes too general assumptions on the physiology underlying the models. The lack of congruence between model predictions and experimental data for the number of primary branches in a 3-D model-

ing of photomorphogenesis of *Trifolium repens* in neutral versus green shading and control light environments (Gautier et al. 2000) reveals that there is still a long way to go before we fully understand and can accurately simulate the integrated response of plants to different light signals. Many processes underlying leaf trait dynamics are quantitatively or even structurally unknown, which confines the number of variables used in mechanistic models such that certain traits that are dynamic have to be treated as constant (Wirtz 2000). For more general reviews and references on models of plant growth that incorporate light capture and photosynthesis, see Hari et al. (1991), Norman and Arkebauer (1991), Room et al. (1996), De Reffye and Houllier (1997), Prusinkiewicz (1998), and Valladares (1999).

3 Acclimation to Light, Tolerance of the Extremes and Phenotypic Plasticity

a) Photomorphogenesis and Whole-Plant Response to Light

Terrestrial plants are developmentally versatile since as sedentary photoreceptors they must accommodate diurnal, seasonal, and long-term changes in light environments (Bradshaw 1965; Schlichting 1986; Niklas 1997). Plants have been shown to adjust their morphology and physiology to available light at different hierarchical levels: crown allometry (e.g., height to diameter ratio, supporting to non-supporting tissues weight ratio), crown architecture (branching pattern, foliage arrangement, leaf area ratio), leaf phenology (longevity, habit, and emergence pattern), specific leaf area (area to weight ratio of leaves), leaf optical properties (absorbance, transmittance), and finally leaf gas exchange properties (photosynthesis, respiration). Responses to variations in the light environment are expressed over a variety of time scales, from the rapid movements of antenna proteins and pigments between the two photosystems (considered part of the acclimation response), to the relatively slow changes in plant architecture (considered part of the plastic response).

The spectral change experienced by the light transmitted through a canopy is sensed by the plants as a low-red/far-red ratio via the phytochrome system, and is capable of modulating a suite of architectural responses often described as the shade-avoidance syndrome (Smith 1982; Ballare 1999). The most important feature of the shade-avoidance response is the elongation of vertical stems and petioles, which results in leaf blades located higher in the canopy profile (Aphalo et al. 1999). Shade avoidance seems to represent an alternative to shade tolerance (Henry and Aarssen 1997). In fact, tropical shade-tolerant species have

not been found to respond to changes in light quality (Kwesiga and Grace 1986; Riddoch et al. 1991).

b) Phenotypic Plasticity

Plants exhibit a remarkable phenotypic plasticity, and a large effort has gone into the investigation of their plastic response to light (Hirose 1987; Strauss-Debenedetti and Bazzaz 1991; Chazdon 1992; Sultan and Bazzaz 1993; Agyeman et al. 1999; Valladares 2000; Valladares et al. 2000b). Phenotypic plasticity is the expression of environmentally induced variability among individuals of identical genotype (Bradshaw 1965; Pigliucci 2001). Since identical genotypes are often difficult to identify and compare, phenotypic plasticity is frequently taken as the variability among individuals of similar genotype (same species and population) that can be unambiguously attributed to environmental variability (Valladares et al. 2000a,b). Even though the degree of expression of plasticity is under genetic control (Hoffmann and Parsons 1991), plasticity is not necessarily adaptive (Pigliucci 2001). Phenotypic plasticity acts as a buffer against spatial or temporal variability in habitat conditions, and serves three main functions: maintenance of homeostasis, foraging for resources, and defense (Grime et al. 1986). Despite the recurring idea that plasticity and developmental instability might be correlated (Tarashev 1995), there is little evidence for this correlation, and, on biological grounds, the relationship is not to be expected if the misconception that plasticity is a disturbance of the developmental trajectory is discarded (Pigliucci 2001). With the exception of sun- and shade-obligate species, phenotypic plasticity can extend the ranges of most plant species along light gradients, since patterns of individual response to environment are a major element in the realized ecological breadth of species (Sultan et al. 1998 and references therein). Consequently, species with a high degree of phenotypic plasticity should express less clinal and/or ecotypic differentiation (Saxe et al. 2001). Plasticity has been traditionally viewed as an alternative to specialization (Sultan 1992), but new approaches and studies have revealed that plasticity itself can be the result of specialization: plasticity of specialized genotypes is enhanced when specialization is associated with favorable ends of an environmental gradient (Lortie and Aarssen 1996; Valladares et al. 2000b; Balaguer et al. 2001). In comparisons of invasive and native species of Hawaii, it was found that the invaders were more plastic in their photosynthetic and dark respiration responses to light than the native species (Pattison et al. 1998; Baruch et al. 2000; Durand and Goldstein 2001). However, even though plasticity is expected to enhance growth under varying environmental conditions, and thus might be an adaptive fea-

ture of invasive species, plasticity does not necessarily lead to increased growth rates (Walters and Reich 1999).

In the case of green-stem species, a plastic response to light can be mediated by responses of either leaves, green stems, or both (Pfanz and Aschan 2001). An inverse relationship between the plasticity of the stems and that of the leaves was found in a comparison of six leguminous shrubs differing in their relative amount of leaves: while mean plasticity of the stem increased with the relative amount of leaves, the mean plasticity of leaves decreased (Valladares et al., submitted). The relative amount of leaves was also a plastic feature, and the plasticity for this trait exhibited significant differences among the species. While morphological adaptations and responses to light tend to enhance shade survival (e.g., enhancing light capture efficiency, as discussed in Valladares et al. 2002b), physiological plasticity seems to enhance high light tolerance (Valladares et al. 2002a). The relationship between plasticities of a series of traits and reproductive fitness is very complex due to phenotypic and plasticity integration (Schlichting 1989). It was found that adaptive constancy of phenotypic traits central to fitness (phenotypic stability) is achieved by plasticity in developmentally related traits (Sultan 1995).

c) Evolution of Phenotypic Plasticity

Phenotypic plasticity can evolve by natural selection as a trait in its own right, but determining how plasticity evolves is not easy (Scheiner and Callahan 1999; Pigliucci 2001). Adaptive phenotypic plasticity can evolve as a strategy to cope with environmental heterogeneity, but it might not be the only possible outcome. Important empirical information can be obtained in comparisons of the plasticity of closely related species, but comparative studies of plasticity are not common, and very few include an explicitly phylogenetic-comparative method approach (Pollard et al. 2001). Examples of interspecific comparisons of plastic responses show that plasticity can evolve rapidly, since it can be very different in closely related species (Valladares et al. 2000b; Pigliucci 2001). Despite the still numerous uncertainties, there is increasing support to the notion that phenotypic plasticity is central to evolution and is not a minor phenomenon secondary to genetic adaptation (Sultan 1987, 1992; West-Eberhard 1989; Scheiner 1993; Soares et al. 1999). Plasticity can play a role in macroevolutionary phenomena by allowing persistence of populations under stressful or novel environments or by generating phenotypic novelties, and the complete spectrum of these evolutionary mechanisms must be incorporated into our interpretation of phenotypic evolution (Pigliucci 2001).

d) To Respond or Not to Respond? Costs of Plasticity

Resources are heterogeneous and plasticity enhances their harvesting; however, there is no plant species perfectly able to adapt by plasticity to any and all environmental conditions. Thus, the evolution of phenotypic plasticity must have some limits. In fact, a conservative resource use strategy involving a low responsiveness seems to be adaptive under stressful or generally adverse conditions (Valladares et al. 2000a,b; Balaguer et al. 2001). In temporally varying environments, the production of a highly differentiated phenotype under favorable conditions might compromise survival when conditions return to normal levels (Waller 1991). Combining the revisions of De Witt et al. (1998) and Pigliucci (2001), the limits and costs of plasticity can be distinguished and summarized as follows:

Limits of plasticity:

1. Information reliability of environmental cues.
2. Deficient sensory capabilities to perceive environmental change.
3. Time lag between the environmental change and the response.
4. Developmental range of possible phenotypes.
5. Functional integration resulting in trade-offs between traits and their plasticities.
6. Lack of genetic variation for plasticity, which can be due to reduced heritability or to strong correlation between plasticity and other traits.

Costs of plasticity:

1. Maintenance of sensory and regulatory mechanisms.
2. Production costs of producing structures plastically versus through fixed genetic responses.
3. Energy expenditures for information acquisition.
4. Developmental instability associated with reduced canalization and developmental "imprecision".
5. Genetic costs due to deleterious effects of plasticity genes through linkage, pleiotropy, or epistasis with other genes.

Once we have a detailed description of costs and limits, how do we actually measure them? As acknowledged by De Witt et al. (1998), it may be very difficult to experimentally disentangle these categories. The most immediate exploration of the costs of plastic responses is by regressions of plasticity and the trait mean within one environment against a measure of fitness (van Tienderen 1991); however, the approach is noisy and frequently fails to reveal costs unless a very large number of genotypes are used (van Klausen et al. 2000). Other approaches involve the experimental usage of hormones to induce different phenotypes and the quantification of the fitness of these phenotypes under different envi-

ronmental conditions. This approach was used in the exploration of costs on stem elongation in the shade-avoidance response of the common bean (Cipollini and Schultz 1999). However, costs of plasticity must not be confused with the fitness decrement associated with the expression of a wrong phenotype in a given environment.

4 Population Plasticity by the Coexistence of Genotypes

Environmental variation is important for the maintenance of genetic variation in phenotypic plasticity (De Jong and Gavrilets 2000). Genetic variation in any trait, including phenotypic plasticity, allows for a plastic response to environmental heterogeneity at the population level, which, added to the phenotypic plasticity of the individuals, enhances the chances of species survival in changing or highly heterogeneous environments. In a comparison of three populations of Kermes oak (*Quercus coccifera*), individuals from the most favorable and at the same time most heterogeneous site had both the greatest genetic variability and the highest phenotypic plasticity in response to light (Balaguer et al. 2001), which agrees with the proposal that selection in heterogeneous environments leads to the coexistence of genotypes with greater phenotypic plasticity (Sultan 1987). Environmental heterogeneity of a given habitat interacts with its mean degree of adversity, making generalizations on the effects of heterogeneity on genetic variation and plasticity at the individual and population levels less clear. Favorable environments are frequently more heterogeneous than adverse environments (e.g., tropical forests versus arid shrublands), and they tend to allow for the coexistence of a larger number of genotypes, but whether this is due to heterogeneity, benignity or both is unclear.

The theory of metapopulations has increased our understanding of the consequences of demographic dynamics for patchily distributed plant species (Hanski 1997; Hanski and Gilpin 1997; Porembski and Barthlott 2000). Research on metapopulation dynamics is expected to answer questions about minimum size of populations and the minimum amount of suitable habitat required for long-term metapopulation persistence. Spatially realistic metapopulation models with a limited number of parameters may represent the right compromise between realism and practical prediction capacity (Hanski 1997).

5 Species Replacement Along Light Gradients: the Tropical and Temperate Models

a) Competition and Succession: Negative Correlations Between Adaptations to Sun and Adaptations to Shade

Most of our knowledge on the role of light in vegetation dynamics has been obtained from temperate and tropical forest ecosystems. In fact, light is thought to be an important, and in many cases the most important, determinant of plant establishment, growth and survival in tropical rainforests (Osunkoya et al. 1992; Nicotra et al. 1999). Over time, a typical successional pattern is expressed: plants of greater shade tolerance than that of the overstory species tend to establish and grow-up in the shaded understory (Bazzaz 1996; Barnes et al. 1998). According to this observation, woody species are classified as early or late successional. The common pattern of species replacement in tropical and temperate models of succession is largely a consequence of the negative correlation across species between adaptation to high light, which involves maximization of carbon fixation per unit leaf protein, and adaptation to low light, which involves maximization of light capture (Bazzaz 1979, 1991; Givnish 1988). However, scaling up from species to community responses is complicated by the fact that physiological responses do not remain constant (Bazzaz and Stinson 1999), and important mechanisms enabling coexistence of species differ throughout the developing stages of their life history (Tokeshi 1999; Nakashizuka 2001). Community assembly rules are determined by the response of plant life-history traits to community profiles (horizontal and vertical heterogeneity, disturbances and biotic interactions), but the relative contribution of chance factors is still far from well established. Chance factors seem to be less important in temperate tree communities than in tropical ones (Nakashizuka 2001).

b) Tolerance or Avoidance: Two Alternatives to the Shade?

The sun versus shade adaptation model is too simplistic, since adaptations of plants to cope with shade actually involve two rather opposing strategies: tolerance (the classical view of shade adaptation) and avoidance. However, shade avoidance might not be expressed consistently throughout the life of plants and can be modulated by resource availability (Monaco and Briske 2000), so shade tolerance and shade avoidance may not always be mutually exclusive within one species. In fact, some species display an intermediate combination of both strategies. Henry and Aarssen (1997) presented a model for the trade-off or negative correlation between shade tolerance and shade avoidance, linking

successional stage with shade strategy and phenotypic plasticity. In this model, early successional species have both weak shade tolerance and weak shade avoidance, and shade avoidance should be most common in the early to intermediate stages of succession, where the probability of encountering high irradiance through vertical growth is still high. Plasticity may not only extend the ranges of species along light gradients, but also make the negative correlation between shade avoidance and shade tolerance more difficult to detect.

6 Species Replacement: Particularities and Uncertainties in Dry Environments

a) Competition and Succession in Light Gradients with Water Constraints

Radiation in arid environments is usually excessive due to the photosynthetic limitations imposed by water stress. However, the shade in Mediterranean-type ecosystems is also dry, and plant allocation to the aerial part for enhanced light capture is in conflict with allocation to the underground part for enhanced water uptake, according to the light-moisture trade-off hypothesis (Tilman 1988). While interactions between high light and drought have been the subject of many studies (e.g., Valladares and Pearcy 1997; Faria et al. 1998), interactions between shade and drought have been far less explored (Abrams and Mostoller 1995; Holmgren 2000; Sack et al. 2002; Valladares and Pearcy 2002). Due to these two facts, the interaction of light with drought and the lack of knowledge on plant responses to shade plus drought, succession is less understood in woody Mediterranean-type formations than in temperate and tropical forests, where species can be ranked according to their shade tolerance, which reflects their successional status (Vila and Sardans 1999; Zavala et al. 2000). Plant response to shade is nutrient and moisture dependent and canopy structure is also expected to vary depending on soil moisture and nutrients (Abrams et al. 1992; Abrams and Mostoller 1995; Barnes et al. 1998; Battaglia et al. 1998; Valladares et al. 2000a). Thus, edaphic factors can influence both the light environment experienced by understory plants by affecting the forest canopy, and the ability of understory plants to survive and respond to this light environment. Consequently, in agreement with Henry and Aarssen (1997), both the relationship between sun-shade adaptation and succession, and the relationship between shade tolerance and shade avoidance, must be examined within the context of variable soil moisture and nutrients. This conclusion is especially pertinent in the case of arid environments.

The long-term historical impact of humans on forest composition and dynamics in Mediterranean-type formations superimposed on already

heterogeneous environments has increased biodiversity and complicated the identification of trends in species replacement and coexistence (Zavala et al. 2000). The frequency and importance of disturbances in these formations also introduce complexity in this search for generalizations. Differences in root-to-shoot ratios seem to explain oak species position along soil-moisture gradients (Matsuda et al. 1989), but expectations from the hypothesis of light-moisture allocation trade-off are not found in a number of Mediterranean species. For instance, certain species are relatively drought sensitive despite their large allocation to roots in comparisons of obligate seeders and resprouters (Retana et al. 1999). This is due to the fact that root-to-shoot ratio is only an approximate index of allocation pattern for acquisition of water. Roots serve as storage organs of carbohydrates, nutrients and meristematic tissue in many resprouter species, well adapted to cope with the common disturbances of fire, herbivory, droughts and coppicing (Canadell and Roda 1991).

Under conditions of high light, ultraviolet light can play an important role at both the individual and the community level especially in high latitudes or elevations. Recent studies in Tierra del Fuego suggest that the increase in UV-B radiation associated with the erosion of the ozone layer might be affecting the functioning of this ecosystem by differentially inhibiting the growth of some plant species and by altering plant-insect interactions (Rousseaux et al. 2001).

b) Facilitation and Positive Plant Interactions

While many ecological studies focus on competition and its implications for species replacement and community organization, less attention has been paid to the roles of cooperative relationships among organisms in promoting species coexistence and biodiversity, but such a view needs to be substantially changed due to ubiquity and importance of cooperation in nature (Wilson and Agnew 1992; Callaway and Pugnaire 1999; Tokeishi 1999). The strong irradiance of most arid environments is likely to cause photoinhibition and overheating of the photosynthetic surfaces, compromising plant survival. For this reason, shrubs, trees or any objects that cast shade can facilitate the establishment of plants in these harsh environments (Pugnaire et al. 1996). It has been argued that competition in these shaded, more favorable microhabitats can be larger than in the open, but it does not seem to be the case in desert or very arid sites (Tielborger and Kadmon 2000a). The balance between competition or interference and facilitation in arid sites is affected by environmental gradients (Tielborger and Kadmon 2000b; Pugnaire and Llueque 2001). A recent comparison of the effect of shrubs on their under-story plant communities in a Spanish semi-arid location has pointed out that not all the different shades created by different shrub species are

equally good shelters due to interactions with the soil properties affected by each shrub species (Pugnaire et al., submitted). The effect of the shrub on the soil properties can vary from enhanced moisture and nutrient content, to enhanced accumulation of inhibitory compounds, which exerts from positive to negative effects on the productivity of the understory plant communities.

7 Species Coexistence and Biodiversity

a) Unveiling Patterns and Integrating Processes

Many attempts have been made to link plant biodiversity and patterns in species richness with abiotic parameters (Tokeshi 1999; Porembski and Barthlott 2000). For instance, O'Brien et al (1998) reported that most of the variation in richness of woody plants in southern Africa was accounted for by climate, with richness being a linear function of liquid water and a parabolic function of energy. However, the fact that similar environments in different geographic regions deviate largely in species richness challenges the view that abiotic patterns are the main determinants of diversity patterns (Latham and Ricklefs 1993), and emphasizes the importance of evolutionary and historical aspects (Herrera 1992; Porembski and Barthlott 2000). Coexistence of species violates the competitive exclusion principle and more than 100 mechanisms have been proposed that delay or prevent competitive exclusion (Tokeshi 1999; Wright 2002). One of the conditions required to realize competitive exclusion is that the environment is temporally constant and has no spatial variation, which is not the case in many natural environments, as shown earlier for the case of light. It is increasingly evident that local levels of habitat diversity significantly promote biodiversity. Pieces of evidence have been provided by studies where habitat diversity was enhanced by either large island size (Kohn and Walsh 1994), small-scale disturbances (Phillips et al. 1994), or fire (Braithwaite 1996). Biologically generated spatial patterns, such as the spatial heterogeneity of light (Fig. 1), have also been shown to allow for the coexistence of competing species (Levin and Pacala 1997; Pacala and Levin 1997; Bascompte and Rodriguez 2001), but spatial variation alone (e.g., without temporal variation) is unlikely to explain high levels of plant biodiversity such as those observed in tropical forests (Wright 2002). The trade-off between survivorship in the shade and growth rate (Welden et al. 1991) must be coupled with spatiotemporal resource variation to lead to species coexistence, as shown in models of temperate forest dynamics (Pacala et al. 1996). Nakashizuka (2001) has recently reviewed the mechanisms enabling coexistence in temperate forests.

Another condition required by the competitive exclusion principle is that species have the opportunity to compete. As discussed by Wright (2002), this condition is violated in the forest shade, where suppressed understory plants rarely come into competition with one another. Thus, every species able to tolerate the understory could potentially coexist. The implications of this possible lack of competition are profound, especially in habitats where shade and understory conditions are temporally and spatially important, as in the tropical rainforests (Wright 2002). Kohyama (1994) has suggested another theoretical framework for how trees in different forest strata can coexist without horizontal spatial heterogeneity, by which large, maximum-size trees with low per capita recruitment affect small, maximum-size trees with high recruitment rates. Larger trees suppress growth and recruitment of smaller trees, but the latter do not affect the former (one-sided competition; Kohyama 1994; Nakashizuka 2001). Survival and coexistence in the understory can be mediated by functional convergence of taxonomically distant and morphologically contrasting species. The efficiency of foliage display and light capture was very similar among 24 contrasting species coexisting in the dark understory of a tropical rainforest (Valladares et al. 2002b). This kind of convergence was found in other cases where differences in crown architecture between plants growing in different environments (sun-shade) were more significant than those between species within the same light environment (Poorter and Werger 1999). Therefore, light environment can play two roles in the maintenance of species diversity by violating two conditions of the competitive exclusion principle: (1) environment is not constant in time and space, which allows coexistence due to tradeoffs in sun-shade adaptations, and (2) persistent, extensive low light conditions in the understory allow coexistence due to either lack of competition or one-sided competition associated with a trade-off between maximum size and per capita recruitment. The relative importance of each role seems to be very habitat specific, since factors like water and nutrient availability or intensity of the suppression by herbivores and canopy plants can profoundly modify the importance of competition. As argued in the case of the coexistence of genotypes within plant populations, habitat heterogeneity and mean degree of adversity interact so trends observed in the field must be combined with manipulative experiments and studies under controlled conditions to disentangle the differential effects of environmental variation versus mean environmental benignity. Both empirical and theoretical approaches are still required to achieve significant advances in this field.

The spatial heterogeneity of light in a forest can have implications on plant populations and communities via its effect on pollinators. The general view is that the mobility of pollinators (and also seed dispersal agents) precludes spatial heterogeneity at scales relevant to alpha diversity. However, an irradiance mosaic in a Mediterranean forest al-

lowed for a wide range of diurnal temperatures in the flowers, and since different insect pollinators differ in their thermal requirements, this heterogeneity generated within- and between-habitat variation in the composition and size structure of pollinator assemblages, with clear implications for plant reproduction (Herrera 1997).

b) Management of Forests for the Conservation of Biodiversity

Forest management alters forest structure and influences a number of processes, some purposely, as with productivity, some inadvertently, as with environmental heterogeneity, population dynamics and biodiversity. Intensive forestry according to traditional methods has little ecological similarity to natural disturbances, which generate a more variable patch mosaic than does intensive forestry (Sharitz et al. 1992). The most vulnerable habitats in an intensive forestry regime are associated with forests older than harvest age, which are unique and biologically rich (Perry 1998). The standard approach to conserving forest biodiversity has been to establish reserves, but in most cases they do not adequately protect regional diversity (Perry 1998). The new forestry is aimed at mimicking nature, acknowledging that biodiversity is a complex concept that includes many different aspects of ecosystems. For instance, one of the three main objectives of leaving a certain number of large, green trees at harvest is to enhance the vertical and horizontal heterogeneity (Kohm and Franklin 1997). Mediterranean-type ecosystems are an example of how evolution can accommodate biodiversity under different human activities, and human intervention in this case is not only compatible with biodiversity, but also a source of habitat heterogeneity (Zavala and Oria 1995). The true role of light spatial and temporal heterogeneity for species coexistence is not fully understood yet, and it is clear that it varies significantly among habitats. Sustainable management of forests requires advances in this knowledge since forest management is to a large extent the management of light. Even though we cannot manage what we do not understand, adaptive management can tell us whether we are doing it right. Research programs driven solely by the immediate needs of management and not focused on a detailed understanding of ecosystem processes risk overlooking new insights (Christensen 1997). Scientists are playing a role of increasing importance in forest management, and the scientific challenges of the new, multiple-use forestry are those confronting ecology: understanding the relationships among structure, function, and spatiotemporal dynamics of complex systems interconnected at many scales (Zavala and Oria 1995; Hanski 1997; Perry 1998).

8 Concluding Remarks: the Challenge of Scaling and Integrating Processes

As presented in this paper, a large research effort has gone into the characterization of plant responses to sun and shade, from molecular and leaf biochemical features to the whole plant, but comprehensive scaling exercises are scant (Table 1). What is the relative contribution to plant performance and success of each scale of the response to light? Responses at each scale are likely to vary in both their global costs and their benefits for the plant, and responses at one scale might be obscured by responses (or the lack of adequate responses) at another scale. For instance, all the very precise structural and physiological responses of leaves to the low but highly dynamic light of the forest understory (efficient chloroplast distribution, enhanced light harvesting by pigments and antenna complexes, enhanced photosynthetic utilization of sunflecks) may have no implications for whole plant light capture and carbon gain if the mutual shading among leaves is not minimized by an efficient crown architecture. Thus, what is the hierarchical order of importance in the series of adaptations and acclimations leading to an efficient light capture and utilization by the plant? It is clear that the hierarchical order of importance differs depending on whether light is limiting or excessive, but is it constant across habitats or under the influence of other factors (drought, heat, low temperatures, wind)? Despite the significant scientific progress in the last decades in different complementary and interrelated areas within plant molecular biology, functional morphology, physiology, ecology and evolution, the specific role of light in plant ecology and evolution and the accurate description of both the heterogeneity of light in many natural environments and the integrated responses of plants to it still deserve more attention (Table 1). The cost-benefit analysis of fascinating aspects of plant response to light, such as those affecting the optical properties of the leaf, light capture by the whole crown and the general stability of the phenotype by phenotypic integration, is far from well explored. More knowledge (technical and scientific) is required for realistic scaling exercises, both in computer modeling of light utilization by crowns and canopies, and in remote sensing of ecosystem processes analyzing the radiation reflected on the vegetation. Research is also needed, and expected to be challenging, on the connection between individual responses to light and the ecological and evolutionary responses to future environmental conditions, where light interacts with many factors and constraints in a global change scenario.

Table 1. Fifteen areas of research where there have been relevant progress or reviews in the last decade, and 15 areas where current knowledge is still insufficient and more research is required. Areas are arranged according to the structure of this paper. Key references are provided as either examples or starting points for further discussion and research

Relevant progress	Insufficient knowledge
1. Techniques for quantitative description of the light environment: hemispherical photography, miniaturized data-loggers and light sensors (Pontailler and Gent 1996; Englund et al. 2000)	Precise descriptions of the light environment (quantity and quality of light available for plants, temporal dynamics, spatial heterogeneity) in natural habitats (Canham et al. 1990)
2. Photosynthetic pigments (Nishio 2000)	Plant photoreceptors: blue-light receptors and interactions among phytochromes and cryptochromes (Lin 2000; Mazzella and Casal 2001)
3. Leaf anatomy and optical properties (Smith et al. 1997)	Plant response and survival in shade combined with drought (Sack et al. 2001; Valladares and Pearcy 2002)
4. Remote analysis of plant biomass and physiological status (Filella and Peñuelas 1998; Gamon and Qiu 1999)	Costs of photoinhibition under natural conditions (Werner et al. 2001)
5. Global trends in leaf form and function (Press 1999)	Relative importance and general trends in structural versus physiological protection against excessive light (Valladares 1999; Werner et al. 1999)
6. Whole plant general responses to shade (Henry and Aarssen 1997)	Precise information on the influence of light on plant morphogenesis for parameterization of realistic 3-D modeling of plant growth (Gautier et al. 2000)
7. Quantum yield and photosynthesis models (Farquhar et al. 2001; Singsaas et al. 2001)	Whole plant photosynthetic photon use efficiency under real conditions (Pearcy and Sims 1994)
8. Models of photoinhibition (Han et al. 2000; Marshall et al. 2000)	Phenotypic correlation and functional integration of traits (Schlichting 1989; Shipley and Lechowicz 2000)
9. Photoprotective pigments (Bungard et al. 1999; Demmig-Adams and Adams 2000)	Costs of phenotypic plasticity (DeWitt et al. 1998; Cipollini and Schultz 1999)

Table 1 (continued)

Relevant progress	Insufficient knowledge
10. Effects of ultraviolet light and plant response to UV-B (Mackerness 2000; Paul 2001; Rousseaux et al. 2001)	Trends among species and habitats in phenotypic plasticity in response to light (Valladares et al. 2000a,b)
11. Photosynthesis under fluctuating light (Pearcy et al. 1995)	Implications of morphology and physiology for fitness and population and community dynamics (Bell 1984; Arntz et al. 2000)
12. Canopy modeling for light capture and carbon gain (Beyschlag and Ryel 1999)	Genetic basis of phenotypic variability in functional traits (Arntz and Delph 2001)
13. Incorporation of the general effects of light in 3-D models of plant growth (Prusinkiewicz 1999)	Links between ecophysiology and evolution (Ackerly et al. 2000)
14. Functional and adaptive meaning of phenotypic plasticity in response to light (Dudley and Schmitt 1996; Sultan 2000)	Precise knowledge on how light, specially its spatial and temporal heterogeneity, influence coexistence and community composition (Nicotra et al. 1999; Schnitzer and Carson 2001)
15. Models for the coexistence of competing species with emphasis on the role of light (Pacala and Rees 1998; Deutschman et al. 1999)	Light and plant communities of arid environments: facilitation, competition or neutral effects? (Zavala et al. 2000; Pugnaire et al., submitted)

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