

Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences

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Annu. Rev. Ecol. Syst. 2008. 39:237–57

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev.ecolsys.39.110707.173506

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1543-592X/08/1201-0237\$20.00

Key Words

drought, global change, interactive factors, multiple stresses, ontogenetic effects, phenotypic plasticity

Abstract

Light gradients are ubiquitous in nature, so all plants are exposed to some degree of shade during their lifetime. The minimum light required for survival, shade tolerance, is a crucial life-history trait that plays a major role in plant community dynamics. There is consensus on the suites of traits that influence shade tolerance, but debate over the relative importance of traits maximizing photosynthetic carbon gain in low light versus those minimizing losses. Shade tolerance is influenced by plant ontogeny and by numerous biotic and abiotic factors. Although phenotypic plasticity tends to be low in shade-tolerant species (e.g., scant elongation in low light), plasticity for certain traits, particularly for morphological features optimizing light capture, can be high. Understanding differential competitive potentials among co-occurring species mediated by shade tolerance is critical to predict ecosystem responses to global change drivers such as elevated CO₂, climate change and the spread of invasive species.

LIGHT HETEROGENEITY AND SHADE TOLERANCE

High versus Low Light Plants

Light is a highly heterogeneous environmental factor influencing plant growth and survival and competitive interactions in the community (Canham et al. 1990, Valladares 2003). As shading in natural communities primarily results from plant canopies, the composition and dynamics of plant communities are cause and, to a large extent, also consequence of light heterogeneity (Canham et al. 1994, Denslow 1987, Kelly & Canham 1992). Contrasting light gradients occur both within the crowns of individual plants and within plant canopies, so all plants are exposed to at least some degree of shade during their lifetime. Although light is an inevitable resource for photosynthesis, both low and high sunlight can limit plant performance. Shortages of key resources, such as light, compromise survival and growth (Grubb 1998), whereas plants face heat, desiccation, excessive irradiance, and UV radiation stresses in high sunlight, and coping with these stresses requires high protective investments (Demmig-Adams & Adams 2006).

Because morphological and physiological adaptations for coping with the lower end of the light gradient are frequently incompatible with those for coping with the upper end, no plant can perform optimally over the entire light gradient. Consequently, species segregate in their light preference and in their tolerance of the extremes. As light is a key limiting resource in many ecosystems, particularly in productive ecosystems supporting high plant foliage areas, differences in minimum light requirement for survival of co-occurring species are central for ecosystem dynamics and community ecology (Bazzaz 1979, Canham et al. 1994, Kobe et al. 1995, Zavala et al. 2007). In fact, shade tolerance is one of the key attributes required to realistically predict forest dynamics (Bugmann 1996), with understory vegetation being a key ecosystem driver that is frequently neglected or underestimated (Nilsson & Wardle 2005).

Basics of Shade Tolerance

Shade tolerance is an ecological concept that refers to the capacity of a given plant to tolerate low light levels. Nevertheless, the term is used in a wide range of disciplines beyond ecology, spanning plant physiology, forestry, agriculture, and horticulture, as well as landscaping and gardening. Shade tolerance has been extensively studied in forests, because light competition and interspecific differences in shade tolerance are frequently important determinants of forest structure and dynamics (Canham et al. 1994, Gravel et al. 2008). From a physiological point of view, the shade tolerance of a given plant is defined as the minimum light under which a plant can survive. A simple field measure of shade tolerance is, in fact, the whole-plant light compensation point (see Baltzer & Thomas 2007). The “carbon gain hypothesis” defines shade tolerance as the maximization of light capture and use in photosynthesis together with the minimization of respiration costs for maintenance (Givnish 1988). An extension of the carbon gain hypothesis is the growth and survival trade-off hypothesis, which predicts that growth rates in high light and survivorship in low light are inversely correlated across species (Kobe et al. 1995). However, shade tolerance is associated with a wide range of traits (**Table 1**), and though many plants can tolerate low light conditions, only a fraction of them can reproduce under these conditions. Thus, a biological definition of shade tolerance must consider the whole life cycle of the plant from early survival and growth to reproduction. We argue that shade tolerance is not an absolute value of the minimum light availability required by a given species, but a relative concept, the meaning of which depends on the specific ecological context. The duration of the growing season and the co-occurrence of multiple stresses can dramatically alter the capacity of a given species to tolerate low light (**Figure 1**). As

Table 1 Plant features associated with shade tolerance

Feature	Expected value ^a	Challenged ^b	Ontogenetic effects ^c
Leaf physiology and biochemistry			
Light compensation point	Low	No	Yes
Quantum yield	High	Yes	Yes
Dark respiration rate	Low	No	Yes
Net photosynthetic rate	Low	Yes	Yes
Sunfleck utilization efficiency	High	Yes	No
Electron transport rate	Low	No	No
Sensitivity to photoinhibition	High	Yes	Yes
Stomatal conductance	Low	No	No
Carboxylation efficiency	Low	No	No
Rubisco content	Low	No	No
Nitrogen content per area	Low	No	Yes
Nitrogen content per dry mass	High	Yes	Yes
Chlorophyll content per area	High	Yes	No
Chlorophyll content per dry mass	High	Yes	Yes
Chlorophyll a/b ratio	Low	Yes	No
Xanthophyll cycle pigments	Low	Yes	No
Lutein epoxyde cycle	High	No	No
Antitherbivore metabolites	High	Yes	Yes
Leaf anatomy and morphology			
Leaf mass per area (M_A)	Low	Yes	Yes
Lamina thickness	Low	Yes	Yes
Fraction of leaf weight invested in supporting tissues	Low	Yes	Yes
Stomatal density	Low	No	No
Leaf size	Large	Yes	No
Leaf margin toothedness	Low	Yes	No
Crown level			
Leaf clumping	Low	No	Yes
Leaf turnover rate	Low	No	No
Apical dominance	Low	Yes	Yes
Canopy light transmittance	Low	Yes	No
Branching frequency	High	Yes	Yes
Elongation response to shade	Low	No	No
Wood density	High	No	No
Number of foliage layers	Low	Yes	Yes
Leaf inclination angle	Low	No	No
Whole plant			
Root-shoot ratio	Low	Yes	Yes
Relative growth rate (RGR)	High	Yes	Yes
Fractional investment of plant mass in leaves (f_L)	High	Yes	Yes
Leaf area ratio (LAR)	High	Yes	Yes
Carbohydrate storage	High	Yes	Yes
Fecundity	Low	Yes	Yes
Longevity	High	Yes	N.A. ^d

^aExpected value for a typical shade-tolerant plant in low light conditions. Most of these features are affected by biotic and abiotic factors other than light.

^bAt least one study has challenged the expectations.

^cImportant confounding ontogenetic effects have been observed and may alleviate controversy.

^dN.A., not applicable.

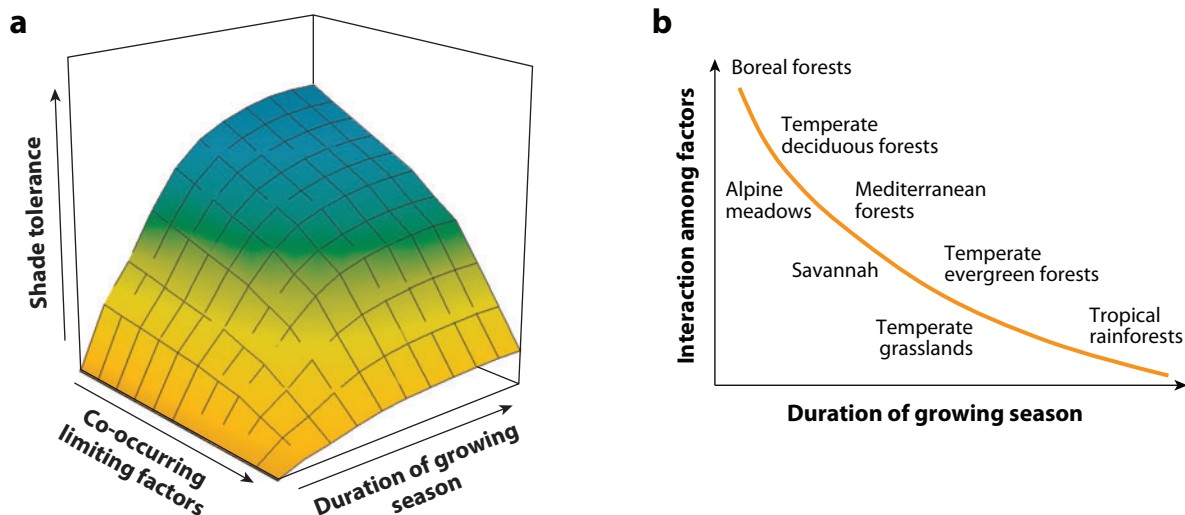


Figure 1

Shade tolerance is inversely associated with tolerance to other limiting factors, for instance, with tolerance to drought and flooding (Niinemets & Valladares 2006). The extent to which a plant can tolerate interacting stresses in low light depends on the length of the growing season. (a) The interaction among co-occurring limiting factors (e.g., low light plus drought stress or low light plus herbivory) and trade-offs between tolerances to different stresses become more intense and relevant for the plant as the growing season becomes shorter. (b) Ecosystems differ in both the duration of the growing season and in the importance of the interactive effects of low light and other limiting factors. For instance, conflicting requirements for shade tolerance (high foliage area) and drought tolerance (high biomass investments in roots, robust leaves with high support biomass fraction) cannot be simultaneously fulfilled in temperate forests where plants have positive carbon balance only during a short period of the year. A significant drought spell during the growing season seriously reduces annual carbon gain and implies that the plant should intercept higher light during the rest of the growing season. Thus, being able to grow in low light and resisting drought are incompatible. In contrast, in wet tropics, the growing season is at least double that in temperate forests. Accordingly, a drought spell with equal length affects the annual carbon balance of tropical plants less. Thus, tolerance of drought and shade simultaneously is not necessarily exclusive in biomes with a longer growing season.

we illustrate in the following, shade tolerance is in fact a complex, multifaceted property of plants that is achieved by different suites of traits in different species (**Table 1**).

Novel Insights and Controversies

Although shade tolerance is a classic topic in plant ecology, recent years have seen an increased interest in research on shade tolerance. Only six articles with the keyword “shade tolerance” are included in the ISI Web of Science (www.thomsonscientific.com) for the period 1980–1985, whereas 100 times more articles can be found for the past five years (2003–2007). The increase is remarkable also in relative terms. Although shade tolerance was included in 7% of the articles with “plant ecology” as a keyword published in 1980–1985, it was included in 15% of the articles with the latter keyword in 2000–2005, further increasing to 17% in the past two years. We argue that this expanding interest in shade tolerance has been triggered by new findings regarding plant features involved in shade tolerance, by controversies about classic ecological and evolutionary hypotheses, and by an emerging understanding of the importance of shade tolerance in global change.

Novel insights into shade tolerance include reappraisals of species rankings according to their low-light tolerance (Humbert et al. 2007, Niinemets & Valladares 2006), recognition of the importance of crown architecture (Valladares & Niinemets 2007), leaf phenology (Kikuzawa 2003), phenotypic plasticity (Portsmouth & Niinemets 2007, Valladares et al. 2007), and plant ontogeny

(Lusk et al. 2008, Niinemets 2006); identification of multiple factors affecting shade tolerance (Moser & Schutz 2006, Niinemets & Valladares 2006, Sánchez-Gómez et al. 2006a), and appreciation that important impacts of global change on plant communities are mediated by the shade tolerance of coexisting plant species (Abrams 2007, Manrique et al. 2007, Reinhart et al. 2006).

Among the main controversial issues, the mechanisms and traits enhancing survival under low light are under vigorous dispute (**Table 1**). Although it has been suggested that shade-tolerant species have higher growth rates in low light than intolerant species (e.g., Givnish 1988), this statement has been challenged by evidence demonstrating lower photosynthetic capacities and inferior whole-plant relative growth rates (RGRs) in both high and low irradiance in seedlings of shade-tolerators (Kitajima 1994, Walters & Reich 1999). The growth-survival trade-off is controversial as well (Gravel et al. 2008). The issue of whether shade tolerance is affected by other environmental factors such as drought is also under debate because experimentally quantified shade and drought tolerances have been shown to vary independently in certain studies (Sack 2004) but not in others (Sánchez-Gómez et al. 2006a).

Relative growth rate (RGR): dry mass increment per unit of dry mass and time

TOWARD A MECHANISTIC UNDERSTANDING OF SHADE TOLERANCE

Species with varying shade tolerances differ in a large number of physiological and structural traits (**Table 1**; see, for example, Abrams & Kubiske 1990, Baltzer & Thomas 2007, Janse-ten Klooster et al. 2007). Two partly opposing hypotheses on the suites of traits responsible for species' shade tolerance have been proposed: maximization of net carbon gain in low light (Givnish 1988 for review) and maximization of the resistance to biotic and abiotic stresses in the understory, i.e., the stress tolerance hypothesis (Kitajima 1994). Although the carbon gain hypothesis has been recently challenged by several contrasting findings on the variation of suites of traits responsible for carbon gain among species groups with different shade tolerance, consideration of species life history and ontogeny can alleviate controversies (**Table 1**). In the following section, we critically review the key points and supporting evidence of both major hypotheses and argue that shade tolerance depends both on the efficiency of carbon gain in low light and on the tolerance of stresses interacting with light availability.

The Carbon Gain Hypothesis: Leaf Chemistry and Physiology

According to the carbon gain hypothesis, any trait that improves the use efficiency of light, and therefore improves carbon gain, increases species shade tolerance (Givnish 1988). Carbon gain can be increased by a number of traits spanning from tissue to whole plant scales. At leaf scale, the carbon gain hypothesis suggests that shade-tolerant species have higher leaf chlorophyll contents and higher photosynthetic capacity in low light than intolerant species (**Table 1**). There is some evidence of greater fractional investment of foliage nitrogen in chlorophyll and associated pigment-binding proteins in shade-tolerant species, implying greater leaf light harvesting efficiency (Niinemets 1997; but see Niinemets et al. 1998), whereas the variations in photosynthetic capacity (light-saturated photosynthetic rate) do not correspond to predictions of carbon balance hypothesis at all. In fact, photosynthetic capacity in seedlings of intolerant species is consistently larger in both high and low light than photosynthetic capacity of tolerant species (Kitajima 1994, Reich et al. 2003, Valladares et al. 2000b, Walters & Reich 1996).

To reconcile the discrepancy with the carbon gain hypothesis, it has been suggested that steady-state photosynthetic rates poorly reflect carbon assimilation in understory environments where light strongly fluctuates; accordingly certain shade-tolerant species were found to be more

M_A : leaf dry mass per unit area (inverse of the also common term specific leaf area, i.e., SLA)

f_L : fractional investment of plant mass in leaves

Leaf area ratio

(LAR): total leaf area per total plant mass ($LAR = f_L/M_A$)

efficient in using sunflecks and could therefore still have higher single leaf-level carbon gain, despite their lower steady-state photosynthetic rates (Küppers et al. 1996, Valladares et al. 1997). However, review of a series of studies indicates no consistent differences in sunfleck-use efficiency among species with different shade tolerances (Naumburg & Ellsworth 2000), so differences in steady-state photosynthesis can be considered to adequately reflect differences in leaf-level gas exchange potentials.

Although the variation in leaf-level photosynthetic potentials does not agree with the carbon gain hypothesis, daily net carbon gain is the difference between photosynthesis and respiration rates. As high photosynthesis and growth rates require a high concentration of photosynthetic enzymes that are bound to have large maintenance costs, advanced performance of shade-tolerant species in low light has been explained by their lower dark respiration rates, which results in a lower light compensation point (Craine & Reich 2005, Walters & Reich 2000). Actually, dark respiration was the strongest determinant of whole-plant light requirements in tropical tree saplings, and it was considered a reliable and simple estimate of shade tolerance (Baltzer & Thomas 2007). According to the revised carbon gain hypothesis, shade-tolerant species achieve superior performance in low light by minimizing CO_2 losses in low light rather than by enhancing maximum potential carbon gain (Craine & Reich 2005, Walters & Reich 2000).

The Carbon Gain Hypothesis: Leaf Area, Seedling Growth, and Seed Size

At the whole-plant level, the carbon gain hypothesis proposes that shade-tolerant plants have higher leaf area than that in intolerant species (**Table 1**). This can be achieved by forming thinner leaves with low dry mass per unit area (M_A) and/or with a greater fraction of plant mass in leaves (f_L), collectively resulting in greater leaf area per total plant mass (leaf area ratio, $LAR = f_L/M_A$). Shade-tolerant temperate gymnosperms do have greater LAR than intolerant gymnosperms (**Figure 2**), but intolerant seedlings of temperate and tropical angiosperms have lower M_A and larger LAR and RGR in both high and low light (Kitajima 1994, Reich et al. 2003, Walters & Reich 1996). Despite having higher RGR in shade and other traits that are predicted to increase shade tolerance, low-light mortality is still consistently higher in these seedlings of shade-intolerant species than in seedlings with lower RGR and LAR (Walters & Reich 1996).

To explain the striking discrepancy among studies evaluating the carbon gain hypothesis in angiosperms, it is important to consider that most of the work on the determinants of shade tolerance has been carried out with seedlings (Niinemets 2006, Walters & Reich 1999). Thus, negative relationships between RGR and seedling mortality can be explained, at least in part, by differences in seed size among tolerant and intolerant species. Shade-tolerant angiosperms generally possess larger seeds than intolerant species, and this difference in seed size is associated with greater seedling size (Osunkoya et al. 1994, Poorter & Rose 2005). Although LAR and RGR are lower in shade-tolerant species, shade tolerators with larger initial sizes have greater total plant leaf area, absolute growth rates, and lower mortality than shade-intolerant species, which leads to larger absolute size even after one or two growing seasons (Niinemets 2006). Clearly, RGR as a relative measure of plant performance does not adequately describe species differences in low light performance. Despite shade-intolerant species having a higher RGR, it takes months to years to catch up with shade-tolerant ones (Niinemets 2006, Poorter & Rose 2005). Although it has been disputed that the relationship between shade tolerance and seed size is not general (at least in the tropics, see Metcalfe et al. 1998), small-seeded plants inevitably have very short windows of opportunity for establishment (Poorter & Rose 2005) and high mortality in understory (Metcalfe et al. 1998).

These data collectively indicate that the apparent contradiction between whole-plant allocation and size in seedlings and the carbon gain hypothesis is mainly driven by inappropriate use of a

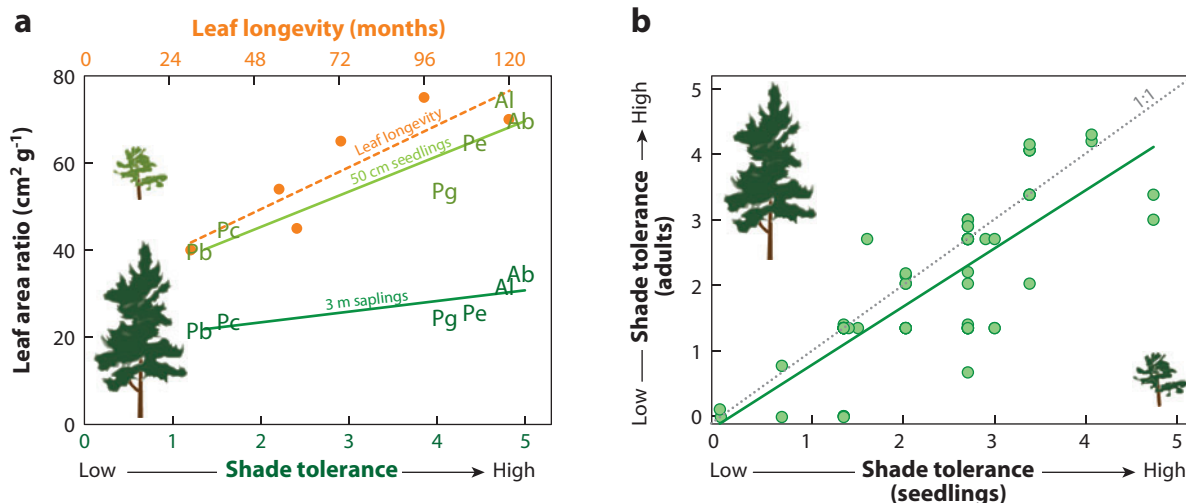


Figure 2

(a) Leaf area ratio (LAR, $\text{cm}^2 \text{g}^{-1}$) versus shade tolerance (lower x-axis) and leaf longevity (upper x-axis) in six sub-boreal, conifer species. The trend of increasing LAR with shade tolerance was significant for small seedlings (50 cm high; upper light green line) but not for 3-m-high saplings (lower dark green line). LAR is larger in seedlings than in saplings and it is significantly correlated with leaf longevity (orange), which is also correlated to shade tolerance. The species are *Pinus banksiana* (Pb), *Pinus contorta* (Pc), *Abies balsamea* (Ab), *Abies lasiocarpa* (Al), *Picea glauca x engelmannii* (Pe) and *Picea glauca* (Pg). Elaborated from the data in Claveau et al. (2005), with leaf longevity data from Reich et al. (1998), Niinemets & Lukjanova (2003), Amponsah et al. (2005) and Wright et al. (2004). The scale of shade tolerance (0 = no tolerance, 5 = tolerance of very deep shade) was obtained after cross-calibrating different scales and databases for 800 woody species of the Northern hemisphere by Niinemets & Valladares (2006). (b) Shade tolerance of adults is correlated with that of juveniles, but there is an important scatter in the relationship, and the slope slightly but significantly departs from the 1:1 relationship (dotted line), with a trend for lower shade tolerance in adults than in juveniles for this particular dataset. Elaborated for 65 tree species of Central Europe from the data in Glenz (2005).

relative growth measure, RGR, to characterize plant growth potential of seedlings vastly differing in size. When the absolute plant growth potential and the total plant leaf area is used, shade-tolerant seedlings of angiosperms do have larger carbon gain in low light, and this corresponds to their greater survivorship. RGR and LAR are appropriate characteristics to compare plant growth potentials of plants of similar size. As noted, LAR and total leaf area increased with increasing shade tolerance in gymnosperms (Figure 2), where seed size was not related to shade tolerance (Hewitt 1998).

In addition to affecting the initial seedling size, large-seededness also results in faster completion of shoot growth (Poorter & Rose 2005, Seiwa 1999). In temperate deciduous forest, faster completion of shoot development allows larger-seeded plants to take advantage of high irradiance under a leafless canopy and, thus, additionally contributes to superior initial absolute growth rates in large-seeded species (Seiwa & Kikuzawa 1991).

The Carbon Gain Hypothesis: Crown Architecture and the Combined Perspective

Whole-plant energy capture in plants critically depends on the integration of foliage into an effective canopy (Givnish 1988). Although crown architectural variation is a classic topic, recent progress in light interception models, in particular enhanced employment of models based on ray-tracing algorithms, has enabled a more quantitative insight into the functional significance of

various architectural attributes (Valladares & Niinemets 2007). At the shoot scale, shoot silhouette to total leaf area ratio, which characterizes the efficiency of light harvesting relative to a flat leaf, is generally larger in more tolerant species, especially in conifers (Leverenz et al. 2000); it must be noted that the information on variation in shoot architecture among broad-leaved species is scarce. At a crown scale, leader extension growth of shade-tolerant species is generally smaller than in intolerant species (Ishida & Peters 1998, Marks 1975), so the crowns are more narrow and vertically extended in shade-intolerant species (Delagrange et al. 2004). This architectural pattern benefits rapid gain in height and whole canopy photosynthesis, but narrow crowns with many leaf layers (multilayers) can grow only in larger gaps, because in dense canopies most light comes from high solar inclination angles such that deeper leaf layers are inevitably shaded (Horn 1971). In contrast, many shade-tolerant species possess, in low light, wide crowns with leaves arranged in a planar layer (monolayers), which maximizes light interception in deeply shaded understories (Horn 1971, Kohyama 1980, Niinemets 1996). Although multilayer versus monolayer differentiation among species of different shade tolerances has been widely accepted, the generality of such differentiation has been questioned (Poorter & Werger 1999). Besides, detailed computer model analyses show that highly contrasting crown architectures can have similar light capture efficiencies (Valladares et al. 2002). In artificial and dense stands, species of contrasting shade tolerance exhibited similar light capture efficiencies at equivalent size and irradiance (Delagrange et al. 2006) so shade tolerance is not directly related to an efficient foliage display.

Canopy trees of shade-tolerant species generally accumulate more leaf area and form denser crowns with lower light transmittance than the canopy trees of intolerant species (Figure 3a; Canham et al. 1994, Reich et al. 2003). Denser crowns reflect a larger branching density (number of twigs per unit leaf area) of shade-tolerant species (White 1983) and possibly also greater foliage

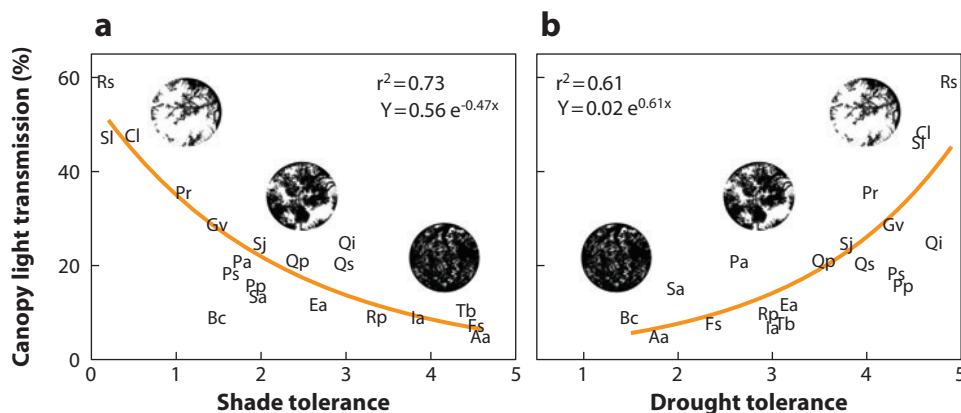


Figure 3

Transmission of light through the canopy of twenty contrasting woody species from the Iberian Peninsula versus their shade (a) and drought tolerances (b). Although light transmission significantly decreases with increasing shade tolerance as observed in other ecosystems, it increases with drought tolerance, revealing interactive effects of the tolerance to these two factors on the optical properties of the crown of a given plant. Light transmission was calculated by hemispherical photography analysis, and representative hemispherical photographs are also shown as examples. The species are *Abies alba* (Aa), *Betula celtiberica* (Bc), *Cistus ladanifer* (Cl), *Erica australis* (Ea), *Fagus sylvatica* (Fa), *Genista versicolor* (Gv), *Ilex aquifolium* (Ia), *Pinus pinea* (Pp), *Pinus sylvestris* (Ps), *Populus alba* (Pa), *Prunus ramburii* (Pr), *Quercus ilex* (Qi), *Quercus pyrenaica* (Qp), *Quercus suber* (Qs), *Retama sphaerocarpa* (Rs), *Rhododendron ponticum* (Rd), *Salix alba* (Sa), *Salvia lavandulifolia* (Sl), *Spartium junceum* (Sj), and *Taxus baccata* (Tb). Elaborated from unpublished data (F. Valladares); shade and drought tolerances cross-validated with those in Niinemets & Valladares (2006).

shade tolerance (lower photosynthetic light compensation point) in shade-tolerant species (Craine & Reich 2005). Apart from the overall differences in crown leaf area density, there is also evidence of a more complex outline of crown surface with a larger degree of penetrating cavities (larger canopy fractal dimension) in shade-tolerant species, allowing the plants to sustain more foliage in the interior of the canopy (Körner 2005, Osawa 1995).

Although there is a long-standing consensus that crowns are more efficiently organized for light capture in shade-tolerant species (Horn 1971, Valladares & Niinemets 2007), the recent evidence summarized here demonstrates that a hierarchy of traits from leaf physiology to whole-plant architecture is involved in determining the species capacity for effective carbon gain in low light (**Table 1**). The effect of seed size on plant absolute growth is necessarily short-lived, influencing plant characteristics after seed germination for four years at most (Poorter & Rose 2005). However, suppressed saplings of shade-tolerant trees can survive in deeply shaded forest understories for 10–30 years before a gap is created, exhibiting higher absolute growth rates in these conditions than do shade-intolerant species (Lin et al. 2002). This suggests that superior light use efficiency does play an important role in shade tolerance after the seed effect is abolished.

The Stress Tolerance Hypothesis

Based on the finding that LAR and RGR were higher and M_A lower in young seedlings of shade-intolerant species in both high and low light, Kitajima (1994) proposed that the carbon gain hypothesis should be abandoned and that survival in shade is more strongly related to plant resistance to biotic and abiotic stresses (stress tolerance hypothesis). Although this suggestion partly relies on uncritical use of RGR in evaluating carbon gain in young plants differing in size (see also Sack & Grubb 2001, Kitajima & Bolker 2003), and shade-tolerant plants likely have higher carbon gain in low light as discussed above, shade tolerance does correlate positively with wood density and with resistance to pathogens and diseases in the shade (Augspurger 1984). Two corollaries of this survival hypothesis of shade tolerance, i.e., that growth rate crossovers do not occur across the light gradient and that more shade-tolerant species require higher light environments for growth than for survival, were not supported by a comparative study of saplings of tropical trees that, on the contrary, did support the carbon gain hypothesis (Baltzer & Thomas 2007).

Larger M_A of shade-tolerant species, compatible with greater robustness of leaves, has been suggested to support the stress tolerance hypothesis (Walters & Reich 1996). However, in temperate deciduous species, high M_A in shade tolerators likely reflects initial differences in size and a crossover occurs during plant ontogeny (see ontogeny effects, below). In evergreens, larger M_A is associated with higher leaf longevity (Wright et al. 2004), which allows the plants to accumulate more leaf area (higher LAR), a key mechanism enhancing low-light carbon gain in these species (Lusk 2004, **Figure 2**). In addition, evergreenness allows the plants to take advantage of phenological changes in overstory. For instance, in warm temperate deciduous forests, evergreen shade-tolerant species can obtain more than 50% of annual carbon gain during the autumn to spring months when overstory is leafless (Miyazawa & Kikuzawa 2005). Under this perspective, the larger M_A in evergreen shade-tolerant species is in agreement with the carbon gain hypothesis and does not necessarily support the stress tolerance hypothesis.

The storage hypothesis of shade tolerance (e.g., Canham et al. 1999, Kobe 1997) is akin to the stress hypothesis. According to this hypothesis, shade-tolerant species do not maximize growth in low light, but invest a larger fraction of production in storage, permitting the plants to tolerate periods of low light close to or below the whole-plant light compensation point. Some empirical studies have revealed higher storage capacity of shade-tolerant plants, supporting the hypothesis (e.g.,

Gaucher et al. 2004). Empirical data also show a positive correlation between the size of the storage and survival in low light (Canham et al. 1999, Kobe 1997), and survival of completely defoliated plants was weakly related to shade tolerance, suggesting that the capacity for canopy reconstruction needed to refill the storage may differ among species differing in shade tolerance. In fact, there is evidence that shade-tolerant species have a determinate growth pattern and stop growth earlier than intolerant species, which often have an indeterminate growth pattern and a much longer growth period (Marks 1975, Kikuzawa 2003). This difference implies that shade-tolerant species have a more conservative growth strategy with significantly longer time available to fill the storage.

In low light environments, plants tend to converge to a narrow range of light absorption efficiencies (Valladares et al. 2002), though they differ widely in their investments in defense and in their allocation and resource-use strategies (Kitajima 1994, Wright et al. 2003). However, the carbon gain and the stress tolerance hypotheses are not mutually exclusive. This is revealed by studies of shade tolerance of co-occurring species that partially support both hypotheses, which has been interpreted as evidence of adaptation to multiple selective forces (Sánchez-Gómez et al. 2006a,c).

Acclimation and Plasticity in Response to Light

Plants, as sessile organisms in changing light environments, exhibit a remarkable capacity to adjust their morphology and physiology to a particular set of light conditions by acclimation or, more broadly, phenotypic plasticity (Delagrangé et al. 2004, Sultan 2000). Many studies have documented remarkable light-driven structural and functional modifications, with responses spanning from chloroplast to whole plant (Givnish 1988, Niinemets & Valladares 2004, Sultan & Bazzaz 1993). These plastic phenotypic responses enhance light capture and photosynthetic utilization, increasing plant performance in the shade (Valladares & Pearcy 1998). However, compared across species of differing shade tolerance, phenotypic plasticity to light can be inversely related to survival in low light as shown in a study of woody Mediterranean seedlings (Sánchez-Gómez et al. 2006c). Being highly plastic may be associated with costs and risks that compromise long-term survival and may thus preclude such species that respond to changes in light availability from understory environments.

There is conclusive evidence that early- and late-successional species differ in the mode and degree of leaf-level physiological plasticity (e.g., Strauss-Debenedetti & Bazzaz 1991). Low plasticity has been associated with a conservative resource use strategy in Mediterranean oaks and also argued to be part of a shade tolerance syndrome in tropical shrubs (Valladares et al. 2000a,b), which agrees with the low-flexibility strategy as defined by Grubb (1998). A field study of an evergreen Mediterranean oak revealed that growth irradiance affected photosynthesis, but it had little effect on the short-term temperature dependence of leaf respiration; although basal rates of leaf respiration were higher in sun-exposed than shade-exposed leaves, growth irradiance had little impact on the degree of acclimation to seasonal changes in temperature and/or moisture (Zaragoza-Castells et al. 2008). Many studies further show that shade-tolerant species are less plastic (Ellsworth & Reich 1996, Paquette et al. 2007, Portsmouth & Niinemets 2007, Valladares et al. 2000b), concurring with the idea that reduced plasticity to light is part of a general suite of traits linked to a conservative use of resources and a high tolerance of low-light stress (Grime & Mackey 2002, Grubb 1998, Lei & Lechowicz 1998). However, full expression of plasticity in shade-tolerant species strongly depends on the availability of other resources, such as nutrients (Portsmouth & Niinemets 2007) or water (Sánchez-Gómez et al. 2006a).

It must be noted that conclusions on the role of phenotypic plasticity in shade tolerance crucially depend on the suite of traits considered. Although overall plasticity may be low in shade-tolerant

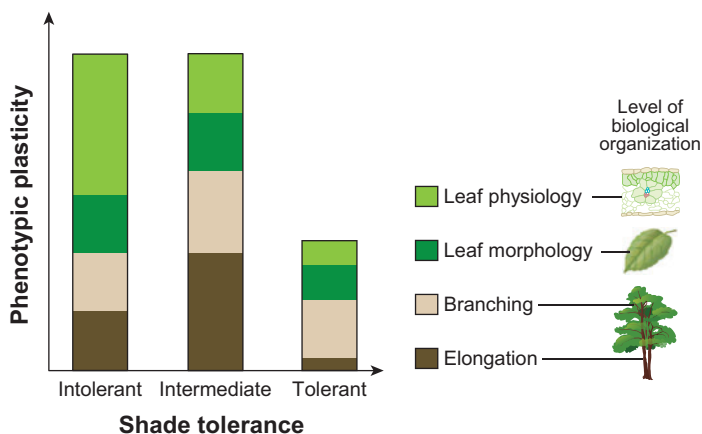


Figure 4

Phenotypic plasticity of shade-tolerant plants is generally lower than that of shade-intolerant species, but differences do not hold constant at each level of biological organization (leaf to whole plant). Although plasticity in leaf morphology tends to be similar among species differing in shade tolerance, high-light plants are more plastic in leaf physiological traits, whereas those adapted to intermediate and highly dynamic light environments are very plastic in traits related to the shade avoidance syndrome such as internode length (stem elongation). Although species do differ in their light-driven plasticity in crown features, such as branching and leaf clumping, the differences are not clearly linked to a distinctively high or low shade tolerance. Plastic responses at one level of organization influence plastic responses at lower levels. For instance, a given elongation or branching pattern determines the heterogeneity of light experienced by the individual leaves of the crown and, thus, the potential extent of the plastic responses of leaf morphology and physiology.

species, certain morphological traits can adjust to light stronger than those in shade-intolerant species (Valladares et al. 2002). Species of varying shade tolerance segregate in their overall plasticity, but also in their plasticity for different traits along the hierarchy from leaf to whole plant (Figure 4; Niinemets & Valladares 2004).

THE INFLUENCE OF ONTOGENY

Ontogenetic Changes in Allometry, Growth, and Shade Tolerance

Ontogeny alters a plethora of plant physiological and structural traits involved in coping with limiting light (Table 1). Foliage photosynthetic capacities invariably decrease, and values of M_A increase with increasing plant size and age (see Bond 2000 for a review). Due to higher M_A , LAR decreases with size and age even if f_L remains constant ($LAR = f_L/M_A$). However, the fractional investment of annual plant production in leaves is not constant; it generally declines with increasing plant size, reflecting the disproportionately scaling requirement for mechanical stability (Sterck & Bongers 1998). As a result, the ratio of assimilative to respiring biomass and the leaf surface to branch and twig surface area decrease with increasing plant size (Delagrange et al. 2004, Gerrish 1990). Lower photosynthetic capacities combined with greater respiratory to photosynthetic biomass ratio and larger self-shading are expected to increase the minimum light requirement for survival (whole plant light compensation point) as trees become larger (Farnsworth & Ellison 1996, Givnish 1988, Kubota et al. 1994). This reasoning is consistent with demographic data from dense forest understories indicating that the probability of mortality of suppressed plants progressively increases in larger size classes (Kneeshaw et al. 2006, Lang & Knight 1983).

In interpreting the ontogenetic variation in shade tolerance, it is essential to consider that the rate of change in light requirement with plant age can vary among species with different shade tolerance. Due to smaller seed size, the initial size of shade-intolerant species is smaller (Poorter & Rose 2005). This smaller size is associated with lower M_A , higher leaf photosynthetic capacities and larger LAR and RGR in intolerant species in both low and high light as argued above. M_A increases and LAR decreases rapidly in juveniles of intolerant species; however, the changes are slower in tolerant species (Niinemets 2006). Thus, a crossover in RGR in low light is expected at certain plant size (Lusk 2004, Sack & Grubb 2001, but also see Kitajima & Bolker 2003). This crossover is associated with lower LAR in intolerant species that results from lower f_L in evergreen intolerant species (Lusk 2004) and lower M_A and f_L in deciduous temperate species (King 2003, Niinemets 2006), though the trends are not always clear-cut (Delagrange et al. 2004). A global meta-analysis revealed opposing trends in the relationship of M_A with shade tolerance between deciduous and evergreen taxa, with ontogeny strongly influencing the relationship in deciduous but not in evergreen species (Lusk & Warton 2007). Allometric data further indicate that established saplings of shade-tolerant species can increase the investment in foliage with increasing plant size at the expense of roots, whereas intolerant species cannot (Lusk 2004, Naumburg et al. 2001).

Ontogenetic Changes in Crown Architecture and Phenology

Age-dependent architectural modifications alter self-shading within the canopy and thereby the minimum whole-plant light requirement. Self-shading can increase with increasing plant age and size as foliage accumulates and not enough branches can be constructed because the biomass cost of lateral branches becomes increasingly expensive with adding weight (Gerrish 1990). Although broad canopies provide a very effective architectural structure for light interception in low light, such a structure requires increasingly more biomass for support to avoid toppling and elastic buckling as most of the mass is located farthest from the axis of bending at plant top. Thus, canopies often become relatively longer with increasing tree size (Delagrange et al. 2004, Niinemets 1996). However, as discussed above, more vertically extended canopies require greater light, and again, the speed of such size-driven modifications can vary among shade-tolerant and -intolerant species.

Minimum whole-plant light requirement also critically depends upon the duration of the effective growing season (**Figure 1**). In deciduous temperate forests, there is evidence of earlier bud burst in younger plants relative to adult canopy dominants, on average 8–10 days earlier across different species (Augspurger & Bartlett 2003, Seiwa 1999). Earlier bud-burst allows young plants to intercept high quantum flux densities, 30–60% of full light during a significant part of their growth period, in total contributing between 36–98% of total light intercepted during the growing season (Augspurger et al. 2005). Thus, such phenological differences enhance plant annual carbon gain and improve plant survival during the rest of the growing season under deeply shaded understories with only 1–3% light throughout the bulk of the growing season. This evidence also suggests that progressive delay of bud-opening with increasing plant age is expected to increase the amount of light the plant requires for survival during the full canopy leaf expansion.

The physiological and structural differences between tolerant and intolerant species may decrease over ontogeny (e.g., in boreal forests; Claveau et al. 2005, Delagrange et al. 2004), but they can also increase (e.g., in temperate evergreen forests; Lusk et al. 2008). Long-term successional studies demonstrate that the advantage of shade-tolerant species under suppression is maintained even at adult tree stage (Ward & Stephens 1993) so the canopies of shade-tolerant species do cast deeper shade (**Figure 3**; Canham et al. 1994).

In general, observational estimates of shade tolerance of seedlings, saplings, and canopy trees of a given species are well correlated (**Figure 2**), suggesting that extensive changes in species shade

tolerance ranks during ontogeny are rare. However, the evidence summarized here demonstrates that the value of different traits in characterizing species shade tolerance changes during ontogeny. These changes are reflected in the scattered correlation between adult and seedling shade tolerance that can be observed in European tree species (**Figure 2**).

MULTIPLE FACTOR SCENARIOS

Knowledge of the tolerance to primary abiotic stresses is still scant for many important wild plants and tolerance to simultaneous stresses is poorly understood, despite the ubiquitous coexistence of multiple stresses in nature (Niinemets & Valladares 2006). Tolerance to any given stress depends on specific structural and physiological traits, but it is also strongly affected by the status of other environmental factors. The tolerance to one stress is typically reduced by other co-occurring stresses or by biotic factors such as herbivores, pests, and competition from neighbor plants. For example, shade tolerance is reduced by mildew in temperate forest species like oaks (Birks 2005) and by drought in woody Mediterranean plants (Sánchez-Gómez et al. 2006a,b). Plant species sort out along light gradients in temperate and moist tropical forests, but light alone cannot explain coexistence in sub-Mediterranean forests (Kunstler et al. 2005), and species sort out along drought and fire gradients in dry deciduous forests where light limits plant performance less (Poorter & Kitajima 2007).

Frequent occurrence of inverse gradients of water and light availabilities has led to suggestions that species shade and drought tolerances are negatively associated (Abrams & Mostoller 1995, Niinemets & Valladares 2006, Smith & Huston 1989). Existence of inverse correlations between species ecological requirements involves the ad hoc hypothesis that being tolerant to a certain environmental factor involves a cost such that the plant cannot adjust simultaneously to multiple environmental stresses. In fact, shade and drought tolerance involve conflicting requirements for biomass investment in foliage and branches for efficient light capture versus biomass investment in roots for efficient water uptake coupled with reductions in total foliage area and enhanced leaf clumping to reduce evaporation. In support of this, species drought tolerance is positively, though shade tolerance is negatively, correlated with light transmission through the canopy (**Figure 3**). Conflicting requirements for shade and drought tolerances have been supported by several experimental studies (Kubiske et al. 1996; Sánchez-Gómez et al. 2006a,b). However, this pattern is apparently not general, especially if species of widely varying adult stature are examined simultaneously (Coomes & Grubb 2000, Sack 2004). Tolerance to shade can further compromise tolerance to other environmental limitations: A flooding tolerance/shade tolerance trade-off have been identified in southeastern U.S. floodplains (Battaglia & Shari 2006) and in the main woody flora of the temperate northern hemisphere (Niinemets & Valladares 2006).

GLOBAL CHANGE

Global change involves the simultaneous alteration of many factors that, through their effects on plant growth and leaf area production, alter the availability of light in the communities. In particular, elevated CO₂ concentration is expected to reduce the light compensation point of photosynthesis and increase the photosynthetic nitrogen use efficiency (Hättenschwiler 2001), thereby allowing the plants to support a larger leaf area in any given community. Some studies have provided further evidence of greater enhancement of growth and photosynthesis by elevated CO₂ in shade-tolerant species (Naumburg & Ellsworth 2000), but other studies have found no differences in the responsiveness to CO₂ among species varying in shade tolerance (DeLucia & Thomas 2000). In the tropics, enhanced vigor of climbing plants under elevated CO₂ may

accelerate tropical forest dynamics and lead to greater abundance of early-successional tree species (Granados & Körner 2002). Although the relationship between CO₂ responsiveness and shade tolerance is ambiguous, denser canopies alone suggest that species shade tolerance can play a central role in the functioning of future forests (Hättenschwiler 2001). Interspecific differences in the responses to elevated CO₂ may also change species' shade tolerance, further amplifying the changes in the composition of future forests.

Because of inherent trade-offs between shade tolerance and tolerance to other environmental factors, shade tolerance influences the response of plants to many drivers of global change such as elevated temperatures and altered water availabilities (Abrams & Mostoller 1995, Prider & Facelli 2004). These influences, together with the interplay of shade with the other drivers of global change such as habitat fragmentation and enhanced spread of invasive species, point to important global change effects on species relative abundances mediated by species-specific differences in their tolerance to shade (Kursar 1998).

Many examples illustrate how shade tolerance can be involved in altering species performance and distribution under globally changed conditions. Subordinate trees like blackgum (*Nyssa sylvatica*) will have poor chances to successfully cope with rapid climate warming, because they are being outcompeted by fast-growing, high light species (Abrams 2007). The opposite applies to red maple (*Acer rubrum*), a "supergeneralist" that has expanded rapidly after European settlement in North America, outcompeting pines and oaks (Abrams 1998). Invasive plant species are not frequent in dark forest understories because they are, in general, shade intolerant, performing well in high-light and highly disturbed environments (Knapp & Canham 2000, Pattison et al. 1998). However, the high phenotypic plasticity of certain invasive species could facilitate their spread in the understory (Niinemets et al. 2003), which can be further facilitated by elevated CO₂ (Hättenschwiler & Körner 2003). Finally, climate change and land use changes are leading to arrested succession in Mediterranean-type ecosystems, where regeneration of key oak species in the shade is inhibited by multiple mechanisms (Acacio et al. 2007, Valladares et al. 2008). Overall, these pieces of evidence suggest that shade tolerance is a key variable for realistic estimation of the impact of global change on ecosystem structure and function, as revealed by modeling studies of temperate forests (Bugmann 1996).

SUMMARY POINTS

1. The extensive work on shade tolerance carried out over the twentieth century has rendered encyclopedic information still pending to be fully harmonized and condensed in a unified theory.
2. As revealed by similar tolerance of species with contrasting structural and physiological features, shade tolerance can be achieved by alternative combinations of traits.
3. Plant light requirement is affected by other co-occurring stress factors like drought, flooding, nutrient availability, or herbivory, so minimum light availability tolerated by any given species can vary in different ecosystems or under different experimental conditions. In contrast, species relative shade tolerance rankings are remarkably conservative.
4. Although phenotypic plasticity tends to be low in shade-tolerant species (e.g., scant elongation in low light), plasticity for certain traits, particularly morphological features optimizing light capture, can be high in these plants.

5. There are strong ontogenetic modifications in plant light requirement, reflecting enhanced support to photosynthetic biomass ratio in older plants. Light requirements tend to increase faster with increasing plant age and size in less tolerant species.
6. Shade tolerance can importantly affect plant response to global change. Elevated CO₂ may facilitate the spread of tolerant species, whereas warming and ecosystem fragmentation and degradation negatively affect shade-tolerant species.

FUTURE ISSUES

1. Major controversies over traits conferring shade tolerance require novel experiments that (*a*) explicitly quantify irradiance (not expressing it merely as a fraction of sunlight) and light quality (red-far red ratio, fraction of diffuse light, lateral versus vertical light) affecting individual plants; and that (*b*) control for ontogenetic effects, effects of seed size, limited rooting space (e.g., pot effects), and interacting environmental drivers.
2. Further experiments are needed to provide a mechanistic basis for quantitative prediction of species rank changes by addressing the influences of ontogeny and interacting biotic and abiotic factors on shade tolerance. These studies should focus on comparisons of suites of structural and physiological traits rather than on single traits.
3. The research also needs to be concentrated on modifications of shade tolerance by and the role of shade tolerance in mediating community and ecosystem responses to global change drivers. Global change generates novel combinations of factors that can crucially alter shade tolerance and affect both the role of species early life-history traits and the resilience of established individuals.
4. More experimental work is needed in ecosystems of the Southern Hemisphere as well as in tropical and subtropical ecosystems of the Northern Hemisphere to test the generality of features conferring shade tolerance and to better delineate the role of shade tolerance in vegetation dynamics. Anecdotal or incomplete studies from major Earth biomes generate paradoxical pieces of evidence and seriously hamper inclusion of species life-history information in large-scale vegetation models.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Our thanks to Niels P. R. Anten, Frank J. Sterck, Christian Messier, Rebecca Montgomery, Kaoru Kitajima, Robert W. Pearcy, and the members of the Spanish thematic network GLOBIMED (www.globimed.net) for providing germane information and suggestions during preparation of the manuscript. Financial support was provided by the Spanish Scientific Council (CSIC) and the Estonian Academy of Sciences (collaborative project between research institutions of CSIC and research institutions in Estonia), the Spanish Ministry of Education and Science (ECOCLIM,

CGL2007-66066-C04-02/BOS) to E.V., and the Estonian Ministry of Education and Science (grant SF1090065s07) to Ü.N.

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