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Why are evergreen leaves so contrary about shade?

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Leaf mass per area (LMA) is one of the most widely measured of all plant functional traits. In deciduous forests, there is similarity between plastic and evolutionary responses of LMA to light gradients. In evergreens, however, LMA is lower in shaded than sunlit individuals of the same species, whereas shade-tolerant evergreens have higher LMA than light-demanders grown under the same conditions. We suggest that this pattern of 'counter-gradient variation' results from some combination of (i) close evolutionary coordination of LMA with leaf lifespan, (ii) selection for different leaf constitutions (relative investment in cell walls versus cell contents) in sun and shade environments and/or (iii) constraints on plasticity as a result of genetic correlations between phenotypes expressed in sun and shade.

Co-gradient variation

The traits of organisms respond to environmental variation on various timescales [1]. Phenotypic plasticity (see Glossary) enables a given genotype to produce a range of trait values across environmental gradients and within the lifetime of an individual organism. By contrast, variation in selection pressures along environmental gradients gives rise to heritable differences between populations or species, through the intergenerational process of evolution. There is often strong similarity between the plastic and evolutionary responses of quantitative traits to environmental gradients. For example, within animal lineages, high-latitude species tend to have larger bodies than relatives native to lower latitudes [2], and this is paralleled by evidence that animals reared at low temperatures grow to a larger size than conspecifics reared in warmer environments [3]. This type of parallel has been referred to as 'co-gradient variation' [4] (Figure 1a) and seems consistent with the view that evolutionary divergences in quantitative traits result from selection on the different phenotypes expressed on different parts of a gradient [5,6].

Co-gradient variation is observed in many functional traits of leaves (Table 1). Most leaf trait variation across species and ecosystems can be arrayed along a single axis running from slow to fast metabolism [7,8]. Leaf traits associated with the slow end of this leaf economics spectrum (low photosynthetic capacity and respiration rates, low nitrogen concentrations and long leaf lifespan) are not only found in inherently slow-growing species (e.g. many evergreen conifers such as *Podocarpus* and *Picea*) [7,9,10] but are often also expressed within species when grown in environments unfavorable for rapid growth [10,11]. For example, leaf lifespan is often longer in shaded individuals than in those grown in brighter light [12,13], just as it tends to be longer in shade-tolerant species adapted to late-successional habitats than in light-demanding species, which normally establish under open conditions [11,14,15]. Similarly, photosynthetic capacity and respiration rates are usually lower in shade-grown plants than in conspecifics grown in higher light, paralleling the inherently low gas-exchange rates of shade-tolerant species [11,16]. This is consistent with the idea that a large photosynthetic capacity confers little advantage in

Glossary

Co-gradient variation: similarity of plastic and evolutionary responses to an environmental gradient, such that environmental effects on phenotypic expression reinforce genetically determined differences between populations or species.
Counter-gradient variation: opposition of plastic and evolutionary responses to an environmental gradient, such that environmental effects on phenotypic expression mask genetically determined differences between populations or species.
Environmental gradient: continuous and gradual variation (spatial or temporal) in the level of critical resources (e.g. light) or conditions (e.g. temperature). Environmental gradients can occur as more-or-less stable features of landscapes, such as those associated with variation in latitude or elevation. Pronounced environmental gradients are also associated with the temporal increase in vegetation density during succession.
Functional trait: a trait that is strongly correlated with the growth and/or survival of organisms.
Genetic correlation: correlation between any two phenotypic traits, such as character states expressed in different environments, that leads to linked response of the two traits to a selective pressure. A high genetic correlation across environments implies that the same genes influence the trait or that different genes affect the traits but they are physically close together on the chromosome and thus separate together during recombination.
Leaf economics spectrum: well-documented covariation of a number of physiological, phenological, morphological and chemical traits of leaves. This pattern is believed to represent a universal tradeoff between maximization of the rate of return on biomass investment (fast economics) and prolongation of the duration of the revenue stream obtained from investments (slow economics).
Phenotypic plasticity: the ability of an organism with a given genotype to change its phenotype in response to changes in the environment.
Reaction norm: the pattern of phenotypic expression of a single genotype across a range of environments.
Symplast: the contents of plant cells, inside the plasma membrane.

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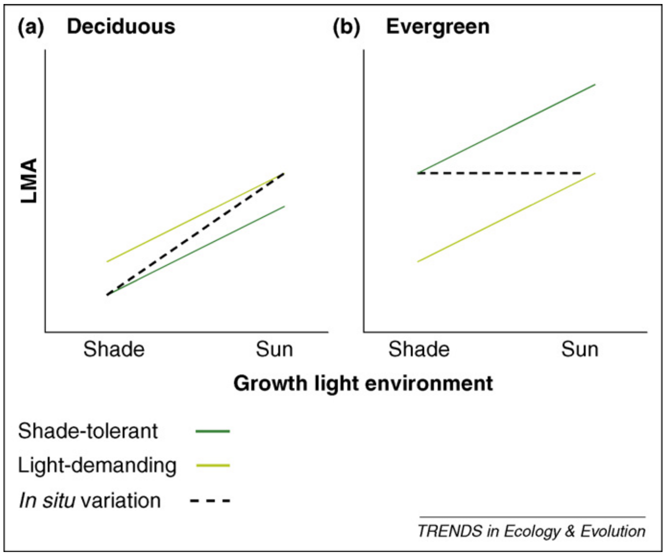

Figure 1. Schematic representation of plastic and evolutionary responses of LMA to light gradients. **(a)** Co-gradient variation in deciduous forests. **(b)** Counter-gradient variation in evergreen forests. Light and dark green lines show the responses of light-demanding and shade-tolerant species to light availability. Our use of parallel lines is arbitrary; there is little agreement on the relative magnitude of plasticity in LMA of light-demanding and shade-tolerant species [11,20,42], and many comparisons of plasticity are confounded with ontogenetic drift [43]. The broken line shows the contrast to be expected if plants are sampled randomly or haphazardly in the field, with shade-tolerant species naturally occurring in deeper shade than light-demanders. Inherent differences in LMA can be either accentuated (deciduous forests) or masked (evergreen forests) by these field comparisons.

Box 1. Leaf mass per area

Leaf mass per area (LMA) is the amount of biomass per unit of leaf area, the product of the average thickness and density of a leaf blade [44]. The inverse of LMA (specific leaf area; SLA) is also commonly used in the literature. LMA is among the easiest of plant functional traits to measure. However, because it appears to index so much information of ecological importance, it has come to hold enormous interest for plant ecologists and ecophysiologists during the past 20 years.

LMA varies over about two orders of magnitude across species, and this variation is seen as representing a key tradeoff between performance and persistence of leaves [7,8]. LMA has therefore come to be regarded as a key dimension of plant ecological strategies [7,27]. Globally, across species it is positively correlated with leaf lifespan and negatively correlated with mass-based nitrogen content, photosynthetic capacity, transpiration rate and respiration rate [7,8]. Inherently large LMA is characteristic of perennials native to a range of chronically unproductive environments such as low-rainfall or infertile sites. Low LMA is typical of herbaceous plants, and of perennials native to environments that offer sustained periods of favorable growth conditions (e.g. early stages of secondary succession, or deciduous forests on fertile soils) [19,27]. Interspecific variation in LMA shows a strong negative correlation with seedling growth rates [9], reflecting its value as an indicator of the cost of constructing leaf area [45]. Interspecific variation in LMA is also negatively correlated with decomposition rates of leaf litter, and so can have ‘posthumous’ influences on nutrient cycling and other ecosystem processes [46].

Intraspecific variation in LMA has also received much attention. Notwithstanding the inherent species differences seen when plants are compared at a common size in a common environment, LMA of a given species increases markedly as seedlings grow bigger [20,47]. It is also subject to strong environmental influences, being affected by availabilities of light, water and other resources [1,48].

low light, but instead brings the associated disadvantage of high respiration rates [17–19]. In summary, co-gradient variation appears to be the rule, rather than the exception, in leaf functional traits.

Counter-gradient variation

A more complex pattern is seen in the responses to light gradients of leaf mass per area (LMA; Box 1), one of the most widely measured of all plant functional traits. LMA is the amount of biomass (dry weight) per unit of leaf area. In deciduous forests, there is similarity between plastic and evolutionary responses of LMA to light gradients, when plants are compared at a common size [20,21] (Table 1). By contrast, there is marked divergence between plastic and evolutionary responses of LMA to shade in evergreens [11,22,23]. Within species, individuals grown in shaded habitats invariably have lower LMA than those grown in higher-light habitats (Table 1). By contrast, when evergreens are compared in a common light environment, shade-tolerant taxa tend to have higher LMA than light-demanding taxa (Table 1). This pattern is consistently seen in broad-leaved evergreens [11,20], although there are insufficient data to assess this for evergreen conifers. We note that in addition to the marked divergence of plastic and evolutionary responses of evergreens, there is also a more modest divergence in age-specific comparisons of deciduous seedlings [11,20] reflecting initial size differences between shade-tolerant and light-demanding taxa [20]. However, here we focus on patterns evident in size-specific comparisons.

Divergences between plastic and evolutionary responses to environmental gradients have been termed ‘counter-gradient variation’ [4,24]. This term was originally coined in studies of plastic versus heritable trait variation in animal populations [4], but has also been applied to flowering phenology in plants [25]. The term originally referred to comparisons across and within populations of a single species. However, the paradoxical divergence between plastic and evolutionary responses of LMA to shade in evergreen forests could also be regarded as an

Table 1. Evolutionary and plastic responses of leaf functional traits to shade

Leaf trait	Response to shade				Refs
	Deciduous		Evergreen		
	Evolutionary response	Plastic response	Evolutionary response	Plastic response	
Photosynthetic capacity per unit area	–	–	–	–	[11,31]
Photosynthetic capacity per unit mass	–	–	–	–	[11,31]
Dark respiration per unit area	–	–	–	–	[11,31,41]
Leaf lifespan	+	+	+	+	[11,13,31,36]
Leaf nitrogen (%)	–	Ø	–	Ø	[31,41]
LMA	–	–	+	–	[11,20,22]

Plus and minus signs indicate direction of responses to decreased light availability; Ø indicates the lack of a clear trend in either direction.

example of counter-gradient variation (Figure 1b), contrasting with the co-gradient variation in LMA seen in deciduous forests (Figure 1a).

Why do plastic and evolutionary responses of LMA to shade seem to go in opposite directions in evergreen forests? This issue impinges on questions about the dynamics of natural selection in strongly heterogeneous environments [26]. Our inquiry builds on recent progress in understanding plant ecological strategies [8,19,27,28] and aims to combine this with theory of the evolution of phenotypic plasticity [26]. We argue that this paradoxical divergence in evergreens results from some combination of (i) close evolutionary coordination of LMA with leaf lifespan, (ii) selection for different leaf constitutions (relative investment in symplast versus structure) in sun and shade and/or (iii) constraints on plasticity because of genetic correlations between phenotypes expressed in sun and shade.

Leaf economics and trait interrelationships

The short-term carbon balance advantages associated with expression of low LMA in shade seem clear. Reduction of LMA in the shade (Figure 1) brings potential short-term advantages of lower leaf construction costs per area [29], and lower maintenance costs (i.e. respiration rates per area) [11,17], which are associated with lower rates of photosynthetic carbon gain in low light.

Notwithstanding selection for cost reduction in the shade [17], we would also expect selection for long leaf lifespan, as in other unproductive habitats [19,27]. In environments that limit the possibilities for rapid carbon gain, retention of hard-won resources is at a premium [27,30], and accumulation of overlapping leaf cohorts is the most feasible way of developing an extensive leaf area [15]. Empirical data confirm that shade-tolerant evergreens invariably have longer-lived leaves than their light-demanding associates [11,14,31]. Achievement of long leaf lifespans requires that leaves be resistant to physical stresses and herbivores, properties that have been linked to LMA and other aspects of leaf structure [32]. Global data sets show that in both broad-leaved and needle-leaved species, long leaf lifespan is consistently associated with large LMA [7,8]; selection for long leaf lifespan in the shade should therefore favor relatively high LMA (Figure 2), the opposite of the phenotypic response characteristic of sun–shade plasticity. The empirical pattern of relatively high LMA in shade-tolerant evergreens (Table 1) suggests that the consequences of selection for long lifespan in the shade outweigh those of selection for cost reduction.

Leaf constitution

If we consider the different components of leaves that contribute to LMA, we can see that the two selection pressures outlined above (cost reduction versus prolongation of leaf lifespan) are not as strongly opposed as we might imagine. We can think of a leaf as composed of structural components (cell walls) and symplastic components (cell contents, including proteins, electrolytes and nonstructural carbohydrates) [28,33]. The structural components provide physical support [34], as well as protection from damage by herbivores and physical stresses [23,32]. Species differ appreciably in the proportions of structural and symplastic components in their leaves: this reflects variation in cell-wall thickness and in the relative abundances of different cell types in the leaf [28,33]. For example, a deep mesophyll will mean a relatively large symplastic component, because mesophyll parenchyma cells have thin walls relative to their volume. Conversely, an abundance of fibers will raise the structural fraction of a leaf, as these cells are usually dead and have thick walls.

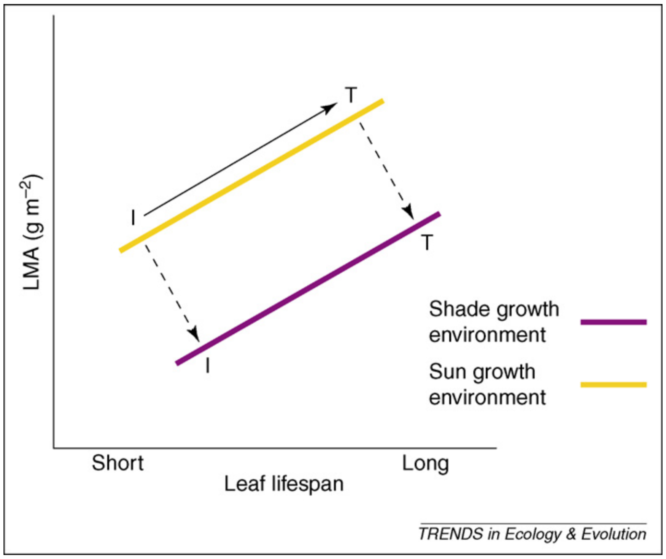

Figure 2. Schematic representation of the influence of selection for long leaf lifespan in shade-tolerant species on the divergence between plastic and evolutionary responses of leaf mass per area (LMA) to shade in evergreen forests. I = shade-intolerant species; T = shade-tolerant species. The dashed lines show plastic responses within all species, expressing lower LMA in the shade. Because of evolutionary coordination of leaf lifespan with LMA, selection for long leaf lifespan in shade-tolerant species also leads to their having a larger LMA than light-demanders grown under the same conditions. The gold and purple lines show the positive interspecific (i.e. evolutionary) relationship between LMA and leaf lifespan in sun and shade environments, respectively. Evolutionary coordination of LMA with leaf lifespan thus leads to the divergence between short-term plastic and long-term evolutionary responses of LMA to shade, in evergreens.

Sun and shade environments likely select for different leaf constitutions, that is, differing investment in structural and symplastic components [20]. Production of leaves with a small symplastic component should be advantageous in the shade, by reducing both construction and maintenance costs [17]. By contrast, a relatively large structural investment (which likely has minimal maintenance costs) is probably selected for in low light. It is this component of LMA that will protect against herbivores and physical stresses, and hence enable prolongation of leaf lifespan. The observed LMA differences between shade-tolerant and light-demanding species in low light (Figure 1b) are therefore likely a result of differences in structural investment.

We are aware of few published data suitable for directly comparing leaf constitutions of shade-tolerant and light-demanding evergreens. A recent study of eight neotropical evergreens [35] did not find a significant correlation between species shade tolerance and cell-wall fraction (i.e. constitution) of leaf tissues. However, data on related traits such as leaf toughness [32,35] are consistent with the proposal [32,35]. There is also support from a recent analysis of a global data set suggesting that short- and long-lived leaves in general differ in tissue composition [28]. The idea of selection for different leaf constitutions in sun and shade therefore seems promising, but in need of further research.

Constraints on plasticity

Constraints on plasticity of leaf constitution might help explain why shade-tolerant evergreens consistently have higher LMA than light-demanders, in all light environments (Figures 1,2). In theory, the optimal plastic response of a shade-tolerant species to an increase in light availability would involve development of leaves with a larger amount of symplast per area (enabling larger photosynthetic capacity), and a smaller structural fraction. Relatively little structural investment would be required to ensure survival of a sun leaf until the end of its useful life in resource-rich, well-lit environments, where progressive shading resulting from rapid growth often curtails the useful life of a leaf by quickly driving it into an unfavorable carbon balance [12].

Yet sun and shade leaves of a given species seem to differ little in constitution. Data from ten European tree species (three evergreen, seven deciduous) [29] showed that the average cell-wall fraction was almost identical in sun and shade leaves, despite large differences in LMA. The percentage contributed by protein was also very similar in sun and shade leaves. These data suggest that the proportional abundances of different cell types, and the thickness of cell walls, change little between sun and shade leaves of a given species. When, for example, a shade-tolerant species responds to high light by developing sun leaves, the increase in structural investment per area scales roughly proportionally with the (clearly adaptive) increase in symplastic investment. This might reflect genetic correlations between phenotypes expressed in sun and shade, preventing a given species from expressing optimal phenotypes in both environments [26]. Species leaf constitutions, and reaction norms of LMA to light, would thus be shaped foremost by those light environments that contribute most individuals to the mating pool of a given species [26], such as shaded environments in the case of shade-tolerant species. Genetic constraints on flexibility in leaf constitution might thus at least partly explain the consistent differences in LMA between shade-tolerant and light-demanding evergreens across the full range of light environments (Figure 1b).

Why the co-gradient pattern in deciduous species?

Selection for low construction and maintenance costs probably explains the approximate congruence between plastic and evolutionary responses of LMA to shade in deciduous forests [21] (Figure 1a). Because of seasonal constraints on leaf lifespans in deciduous forests, we would expect much less interspecific variation in structural investment than in evergreen forests. Leaves of shade-tolerant deciduous trees do tend to live somewhat longer than those of light-demanding associates [11,36], suggesting that the former might have slightly greater investment in cell walls. However, the rather weak negative correlation of LMA with shade tolerance of deciduous species [20] suggests that any differences in structural reinforcement are outweighed by the countervailing effects of thicker palisade mesophyll (larger symplastic investment) in the light-demanding taxa [36].

Priorities for future research

We think the perspectives offered here go some way toward explaining why evolutionary and plastic responses of LMA to shade are congruent in deciduous forests but divergent in evergreens. Although there is abundant empirical evidence for one of our hypothesized drivers of this evergreen contrariness, the evolutionary coordination of LMA with leaf lifespan [7,8], we are not aware of published data suitable for directly testing our complementary hypothesis that sun and shade select for differences in leaf constitution. Nevertheless, this hypothesis seems a reasonable deduction from recent modeling work suggesting that short- and long-lived leaves in general differ in relative investment in structure versus symplast [28]. Data on related parameters such as leaf toughness are also consistent with the hypothesis [32,35]. Comparative data on interspecific variation in the contributions of cell walls versus cell contents to LMA [29] in shade-tolerant and light-demanding species would help evaluate this hypothesis, but studies of phenotypic selection [37,38] in sun and shade environments would provide the most direct test. Our hypothesis about constraints on plasticity rests on a very limited empirical foundation [29], and on theory of the genetic control of phenotypic plasticity [26]. A useful step in evaluating this proposal would be to expand the empirical evidence on intraspecific variation of leaf constitution across light gradients. Further progress on the genetic basis of plasticity [39,40] would also help us understand the nature of constraints on the ability of species to adapt to environmental heterogeneity. Together, these steps would give us a clearer picture of how plant traits evolve under the complex selection pressures associated with the dynamic light environments of forests.

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