

The Ecophysiology of Leaf Lifespan in Tropical Forests: Adaptive and Plastic Responses to Environmental Heterogeneity

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Abstract Leaf lifespan, the time from leaf expansion to shedding, exhibits wide variation and is a key integrator of relationships with photosynthetic rate, leaf mass per area (LMA), and leaf nitrogen among coexisting tropical tree species. We present a hierarchical view of sources of variation in leaf lifespan in tropical forests, emphasizing the importance of substantial within-species variation, which has rarely been addressed. Interspecific variation in leaf lifespan is positively correlated with LMA, varying from short-lived, low-LMA leaves to long-lived, high-LMA leaves of species associated with resource-rich versus resource-depleted habitats, respectively. Phenotypic responses of leaf lifespan and LMA to light show counter-gradient variation: with acclimation to shade, leaf lifespan increases, and LMA decreases, but both increase with adaptation to shade. In contrast, phenotypic responses to soil fertility are predicted to show co-gradient variation: both leaf lifespan and LMA increase with declining fertility both inter- and intraspecifically. We present new data analyses supporting these predictions, but the interactive effects of light and soil resources can produce complex phenotypic responses. Future studies of leaf lifespan should devote more attention to within-species variation to better quantify and explain how leaf lifespan is central to trade-offs generating the contrasting ecological strategies of tropical tree species.

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Introduction

Leaf lifespan, the duration of time between when a leaf is first expanded and when it is senesced from the plant, differs greatly among species, among individual plants, and also among leaves on a plant (Chabot and Hicks 1982). Since the leaf is the principal photosynthetic organ of higher plants, its lifespan determines how long it will return photosynthetically fixed carbon to the plant (Kikuzawa and Lechowicz 2011). Plant growth and survival are critically dependent upon cumulative net photosynthetic carbon gain, which in turn depends strongly not only on insolation, but also on the availability of nutrients, especially nitrogen, and water in soil (Field 1983). Thus, leaf lifespan and nutrient allocation patterns are functionally linked (Ackerly and Bazzaz 1995; Hikosaka 2005), making leaf lifespan a critically important trait mediating the carbon and nutrient economies of plants that ultimately translate into fitness variation in relation to environmental heterogeneity.

Leaf lifespan is one axis of variation in the worldwide leaf economic spectrum (WLES), which describes a spectrum of coordinated leaf functional trait variation ranging from fast-growing species that produce short-lived, structurally inexpensive leaves with high nutrient concentrations and high photosynthetic productivity to slow-growing species that produce longer-lived, structurally expensive leaves that have lower nutrient concentrations and photosynthetic rates (Reich et al. 1991, 1992, 1997; Wright et al. 2004). Recent analyses of leaf lifespan using increasingly larger databases tend to focus on site and species-level means, neglecting large within-species variation, even though it can be substantial (Westoby et al. 2002). As a result, our knowledge of within-species variation in leaf lifespan in relation to differences in resource availability and other plant functional traits, at both the individual and leaf-levels, is comparatively rudimentary. The ability of a plant to respond to environmental shifts through acclimation will in part dictate responses to climate change, as well as determine patterns of species distribution along environmental gradients (e.g., Vanderwel et al. 2015). Furthermore, an integrated understanding of how multiple sources of natural selection operate on leaf lifespan in relation to the evolution of diverse plant ecological strategies (Donovan et al. 2011) requires quantitative estimates of how leaf lifespans change with environmental variation.

In this review, we seek to call attention to within-species variation in leaf lifespan, some of which can be understood as optimal plastic responses. We focus on tropical forests, where tree species display a wide range of leaf lifespans, including very long-lived leaves. First, we present a hierarchical view of the sources of variation in leaf lifespan and the dynamic underlying physiological mechanisms that influence how lifespan affects a plant's carbon and nutrient economies. Then, we discuss within-versus among-species variation in leaf lifespan and leaf mass per area (LMA) that can be related to variation in light availability and soil fertility from the perspective of theories on optimal leaf lifespan. We show that the direction and strength of the relationship of leaf lifespan with LMA differ among versus within-species, depending on the type of environmental factors considered. In the last section, we discuss knowledge gaps and research questions that are worth

pursuing toward a more mechanistic understanding of leaf lifespan in the carbon and nutrient economies of the whole-tree.

Theories of Optimal Leaf Lifespan

Cost-benefit theories of leaf lifespan have a long history (e.g., Chabot and Hicks 1982). Here, we limit our review to the essential ideas needed for understanding the key elements of optimization of leaf function that have resulted in the global diversity and distribution of leaf lifespans and leaf habits. The fundamental question addressed by optimal leaf lifespan models is, for how long should a tree retain its leaves in a given environment? The optimal answer depends on the costs of leaf construction and maintenance, as well as costs associated with leaf turnover, versus the benefits that the leaf provides, namely photosynthetically fixed carbon and nutrient storage. Table 1 summarizes potential key costs and benefits, which will be described throughout this chapter. The cost of leaf construction is the total cost of acquiring all energy and materials required to build a leaf and its supporting organs (e.g., stem), as well as the cost of the maintaining molecules that make up the leaf (e.g., respiration). However, given the difficulty of assessing some of these costs, what is generally quantified is a minimum leaf construction cost, estimated as the total chemical bonding energy in organic molecules multiplied with a factor for biosynthetic pathway costs (Williams et al. 1987; Poorter et al. 2006). Per unit dry mass, this minimum biosynthetic cost of leaf construction may not differ much among species (Griffin 1994). Hence, leaf construction cost per unit area is approximated by LMA, and leaves with higher LMA require either fast photosynthetic rates or long lifespan to pay back construction costs and generate a net carbon gain.

Since the target of natural selection is individuals, optimization of carbon gain relative to carbon and nutrient costs must be considered at the whole-plant level, even though ecophysiological analyses, including many that we review here, often treat leaves as the unit of study. Leaves are expensive to manufacture: large amounts of limited resources such as nitrogen and phosphorus, as well as carbon to construct systems for structural support, vascular transport, and belowground resource uptake, must be allocated for their construction (Givnish 1988; Williams et al. 1989; Kikuzawa and Ackerly 1999; Reich et al. 2009). Thus, how many leaves a plant should maintain at a given time reflects a dynamic optimization of maximizing benefit, i.e., photosynthetic income, relative to costs of carbon and nutrient allocation for construction and maintenance. It is dynamic, because as a plant produces new leaves or is overtopped by neighbors, old leaves become shaded and less productive (e.g., Mooney et al. 1981). Moreover, aging results in the decrease of net photosynthesis per unit area and photosynthetic nitrogen use efficiency (PNUE) (Field and Mooney 1983; Sobrado 1994; Kitajima et al. 1997b, 2002). In addition, the cost of making and keeping a leaf is not fixed, as it is influenced by variation in structural and chemical defense (McKey 1974;

Table 1 Potential trade-offs that are relevant for cost-benefit models of leaf lifespan

Property	Benefit	Cost
Slower leaf turnover	<ul style="list-style-type: none"> • Leaf construction costs are infrequently incurred • Nutrient resorption and translocation costs are infrequently incurred • Nutrient and carbon losses are minimized, and leaves may store nutrients and carbohydrates, contributing to better nutrient retention and nutrient use efficiency • Cost of allocation to roots for uptake of belowground resources is reduced • Slower development of self-shading enables leaf to remain near its maximal productivity for longer time period 	<ul style="list-style-type: none"> • Leaf area of tree does not always maximize light interception • Slower height and crown growth rate limit competitive ability • Slower leaf turnover delays the response to spatio-temporal fluctuations of light • Lost opportunity cost due to less optimal allocation to maximize the compounding interest of photosynthetic production
Slower A_{\max}	<ul style="list-style-type: none"> • Lower nutrient demands alleviate need for extensive belowground investment • Slower transpiration rates reduce need for extensive water uptake • Photosynthetic machinery requires less maintenance respiration 	<ul style="list-style-type: none"> • Slower rate of return of photosynthetic carbon requires longer lifespan to repay initial carbon construction cost • Plants fail to benefit from compounded interest associated with high A_{\max}
Greater investment in defense	<ul style="list-style-type: none"> • Durability is enhanced through greater resistance to damage agents, such as physical forces and natural enemies • Functional deterioration with leaf age may be slower <i>via</i> slower accumulation of damage to the leaf 	<ul style="list-style-type: none"> • Larger construction cost per unit leaf area means longer payback time

The benefits and costs at the plant level of three key properties associated with extending leaf lifespan for evergreen tropical species are summarized. Abbreviations: A_{\max} , maximum rate of photosynthesis at the leaf level

Coley 1983), lost-opportunity costs of not allocating nutrients to newer leaves or non-leaf tissues (Harper 1989; Westoby et al. 2000), and costs of stem and root tissues to support leaves (Kikuzawa and Ackerly 1999; Givnish 2002). Thus, dynamic optimization of leaf lifespan involves processes operating at both the leaf and whole-plant levels, and it is adaptive for plants to adjust leaf phenotype and lifespan to acclimate to spatio-temporal variation in the environment and resource availability (Ackerly and Bazzaz 1995).

Sources of Variation in Leaf Lifespan

Here, we present a hierarchical view of the total phenotypic variation in leaf lifespan across all individuals, which can be partitioned into mechanisms operating at different levels of organization (Fig. 1).

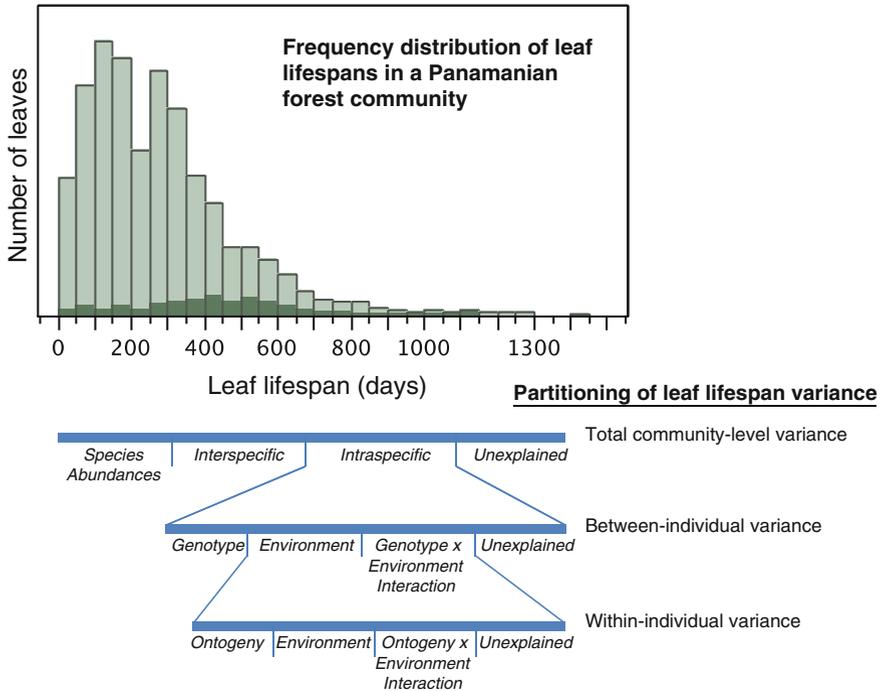


Fig. 1 Conceptual diagram of how the total variation in leaf lifespan within a forest community is hierarchically partitioned among different sources of variation at different levels of biological organization (*lower portion*), along with an example of leaf-level variation in estimates of leaf lifespan of seedlings across 58 species in a Panamanian forest community (*upper portion*). The part of the histogram in *darker green* indicates data for one species, *Virola surinamensis* (Myristicaceae), demonstrating substantial within-species variation in leaf lifespan, some of which reflects plasticity in response to light. Different species in a community contribute disparate amounts to the total variance of the community, depending on their intraspecific variation

Interspecific Variation

The covariation of leaf lifespan with other leaf functional traits defines key axes in the WLES describing interspecific variation in species ecological strategies (Reich et al. 1991, 1992, 1997; Wright et al. 2004). Tropical tree species vary enormously in their leaf lifespans, from pioneer species that exchange leaves within several weeks (e.g., *Heliocarpus appendiculatus*, Ackerly and Bazzaz 1995) to shade tolerant species that retain leaves over multiple years (e.g., 25 years reported for *Araucaria* by Molisch (1928), cited by Chabot and Hicks (1982); 12 years reported for a dicot tree sapling in Panama, pers. comm., P.D. Coley). Although phylogenetic history can constrain evolutionary changes, it is widely accepted that

interspecific variation in leaf lifespan, and the shape of the WLES axes, arise through natural selection (Donovan et al. 2011), which has produced a diversity of convergent solutions, even within a given tropical forest community (e.g., Reich et al. 1991). Overall, we can interpret the trait syndromes associated with leaf lifespan as being evolutionary answers to optimization problems posed by complex, interacting trade-offs related to the carbon and nutrient economies of plants and their consequences for fitness in heterogeneous environments.

One of the widely-reported patterns from tropical forest tree communities is that species with shorter leaf lifespans tend to have faster maximum rates of photosynthesis and higher leaf nitrogen concentrations per unit leaf mass (Williams et al. 1989; Reich et al. 1991, 1992, 1997; Wright et al. 2004). They also generally occupy more productive habitats that can support the faster growth rates that make such a strategy advantageous, such as moist soils with high nutrient availability and irradiance. Since rapid shoot growth also causes self-shading, decreasing the insolation and productivity of older leaves (Hikosaka 1996; Ackerly 1999; Yamada et al. 2000), the rate of decline in photosynthetic rate with leaf age tends to be faster for species with shorter-lived leaves (Kitajima et al. 1997a, b, 2002). In such productive environments, greater whole-plant photosynthetic income may be gained by reallocating nutrients in aging leaves to support production of new leaves and rapid height growth (Field 1983; deJong 1995; Hikosaka 2005; Marty et al. 2010), and there would be little to gain by investing in structural durability beyond the minimal need to achieve the short optimal leaf lifespan.

Conversely, long-lived leaves with high LMA are generally found on slower-growing tree species that persist in less productive habitats, such as nutrient-depleted, well-drained soils or the shaded understory, where diurnal photosynthetic carbon gain is constrained by light, nutrient, or water availability. Longer leaf lifespan is advantageous because it prolongs the time over which such high carbon construction costs can be recouped (Chabot and Hicks 1982; Poorter et al. 2006). Moreover, in these habitats, allocation of limited resources to roots may constrain allocation to leaf construction (Bryant et al. 1983; Poorter et al. 2012), and leaves may have lower nutrient concentrations per unit mass (Reich et al. 1991, 1992, 1997; Wright et al. 2004). Longer lifespans are also selected because they reduce the nutrient loss associated with leaf turnover, and thus increase the whole-plant retention time of expensive-to-acquire nutrients (Monk 1966; Small 1972; Chapin 1980; Aerts and de Caluwe 1994). Likewise, defense (often carbon-based structural and chemical defenses, rather than nitrogen-based chemical defense, on infertile soils; Bryant et al. 1983) to avoid damage and premature leaf loss from herbivory or other hazards should also be favored (Janzen 1974; McKey 1979; Coley and Barone 1996).

In summary, variation among species in leaf lifespan should be viewed as an important part of the functional variation underlying the interspecific trade-off between growth and survival rates, which represents plant species' ecological strategies spanning fast growth and low survival to slow growth and high survival

(Kitajima 1994; Kobe 1999; Hubbell 2001; Kitajima and Myers 2008; Russo et al. 2008). Indeed, interspecific variation in leaf lifespan is positively correlated with survival rate in shade for seedlings and saplings in neotropical forests (Poorter and Bongers 2006; Kitajima and Poorter 2010; Kitajima et al. 2013) and saplings in Bornean rain forests (Russo, unpub. data).

Intraspecific Variation

Many studies, including those cited above, focus on interspecific variation, comparing mean or median lifespan of species, ignoring large variation within species (Fig. 1). Tree species with evergreen leaf habits should have evolved the capacity to produce leaves with varying lifespans, given that leaf structural and biochemical traits show such ecological plasticity (Valladares et al. 2007) and that plasticity in leaf lifespan enables trees to respond to environmental changes to maintain positive net carbon gain. The total variance within a population of a phenotypic trait such as leaf lifespan can be partitioned into four sources, plus unexplained variance (Fig. 1): (1) variation attributable to genes, (2) variation attributable to the environment, (3) variation attributable to ontogeny, (4) variation attributable to genotype-by-environment interaction (genetic variation for phenotypic plasticity).

Within-species variation in leaf lifespan may arise because the genotypes in the population differ in their leaf lifespan, and the relative proportion of these genotypes may differ among populations. Environmental heterogeneity can also be a significant source of variation in leaf lifespan both between habitat types and between microenvironments within a habitat due to differences in forest canopy structure, microtopography, or tree-size, which all influence access to above- and belowground resources (Weiner 1990). Even individual leaves and branches on a tree experience contrasting environments. In seasonally dry tropical forests, leaves produced in the early wet season function for a longer time under lower light availability of the cloudy rainy season, whereas those produced prior to the dry season can achieve higher productivity under a brighter sky, but are limited in maximum leaf lifespan due to dry-season deciduousness (Kitajima et al. 1997a). The shapes of leaf survival curves, which show the proportion of leaves remaining versus leaf age, demonstrate that leaf-level variation in lifespan can be substantial, even within a species (Fig. 2). When most leaves have similar lifespans, the survival curve shows low mortality before declining dramatically, which coincides with a short phase of synchronous senescence (Fig. 2a). Alternatively, the survival curve can decline more gradually, indicating steady mortality from early to late leaf ages, which reflects greater variation leaf lifespan among individual leaves (Fig. 2b).

Phenotypic plasticity is the capacity of a genotype to produce different phenotypes in different environments (Sultan 1995). It is considered by some to be a trait under selection that is favored when the environment is highly and unpredictably variable (Via and Lande 1985) or when it enables a plant to take maximal

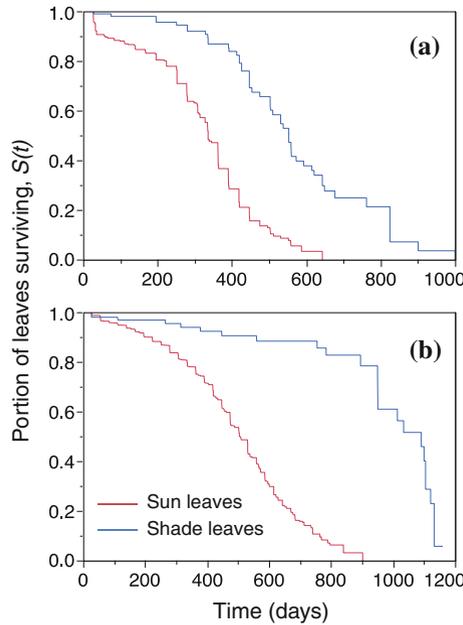


Fig. 2 Examples from two Panamanian tree species to demonstrate how the shapes of leaf survivorship curves differ between environments and species. Panels show Kaplan-Meier estimates of the survival function for sun leaves in the canopy (red) and shade leaves in the understory (blue). In the case of *Bombacopsis sessilis* (Bombacaceae) (a), sun and shade leaves show similar magnitudes of leaf-level variation in leaf lifespan across contrasting light environments, but for *Virola surinamensis* (Myristicaceae) (b), the survival function is steeper for shade than for sun leaves, indicating less variance in observed leaf lifespans among individual leaves in the former

advantage of ephemeral pulses of resources, and so faster-growing species are thought to have greater plasticity (Bazzaz 1979; Lambers and Poorter 1992; Valladares et al. 2000). Quantifying phenotypic plasticity at the individual level is challenging because genetic clones are rarely available for wild tree species, hence, environmentally induced phenotypic variation in leaf lifespan is measured at the population level using maternal siblings grown in contrasting environments. Even so, studies of plasticity in leaf lifespan of tropical species are rare (Ackerly and Bazzaz 1995; Kitajima et al. 2013). However, they still yield insights because even though the variation due to genotype and genetic variance for phenotypic plasticity are unknown, total phenotypic variation can be partitioned into what is explained by the environment versus all other sources (Whitman and Agrawal 2009).

Ontogenetic plasticity, in which the phenotype depends on an individual's developmental stage, also contributes to within-species variation. The tissue density and toughness of the leaf lamina increase from saplings to adults in tropical trees (Kitajima and Poorter 2010), and in a Malaysian forest, Osada et al. (2001) found that more sunlit leaves at taller heights within tree crowns had shorter lifespans relative to more shaded leaves at shorter heights. Because the environment changes

dramatically with tree size in closed canopy tropical forests, the proportion of this variation due to purely environmental versus developmental influences is unknown.

Leaf Structure and Nitrogen: Key Aspects of Leaf Construction Cost and Lifespan

LMA and nitrogen concentrations vary with leaf lifespan among species, as described in the WLES, and also plastically within species (Ackerly and Bazzaz 1995). It is overly simplistic to consider LMA only as a measure of structural defense or to assume that a fixed proportion of nitrogen resides only in the carboxylation enzymes. It is therefore important to consider a leaf as a heterogeneous structure (Terashima et al. 2011). In mesic tropical forests, trees with needle-shaped leaves are rare. A common design that simultaneously allows for efficient harvest of light energy under a shaded canopy while enabling CO₂ uptake is for a plant to have multiple layers of thin and flat leaf blades arranged in its crown (Horn 1971; Halle et al. 1978; Hikosaka 2005). The leaf blade is a complex structure consisting of photosynthetic and vascular cells sandwiched between cuticles that provide protection from desiccation and physical damage. Within the leaf blade, metabolically active molecules reside in cells surrounded by cell walls of different thickness and mechanical properties (Onoda et al. 2015). There are many sources of structural and mechanical variation in the leaf blade that contribute to its toughness and density, two correlates of leaf lifespan (Coley 1983; Kitajima and Poorter 2010; Westbrook et al. 2011; Kitajima et al. 2012).

When a plant should shed a leaf is a function of nutrient, as well as carbon balance (Field 1983; Aerts and Chapin 2000). Shorter leaf lifespan should be favored when the cost of acquiring nutrients is low, whereas the reverse is true in nutrient-depleted soils, and only by accounting for the cost of nutrient acquisition can models accurately predict an evergreen leaf habit in highly seasonal, nutrient-limited, boreal environments (Givnish 2002). Consistent with these predictions, in an Argentine subtropical forest, leaf lifespans of seedlings of five tree species grown in high-light gaps declined with N and P fertilization, although some only marginally so (Villagra et al. 2013). Similar results were seen by Cordell et al. (2001) for *Metrosideros polymorpha* (Myrtaceae), but only on N-limited substrates. On P-limited substrates, fertilization with N and P had no effect on leaf lifespan. Thus, the effects of nutrient limitation on leaf lifespan are likely to depend upon the nutrient in question.

In some leaf lifespan models that consider costs and benefits only in terms of carbon, the predicted optimal time of leaf shedding is the time at which the leaf can no longer off-set its own carbon costs of maintenance respiration (Monsi and Saeki 2005; translated from Monsi and Saeki 1953). Consideration of optimum nitrogen allocation strategy in the plant canopy, however, is critical (Hirose 2005). For example, Oikawa et al. (2006) showed that this prediction is met for an herb when it was grown under high nitrogen availability, but that under low nitrogen availability,

leaves were shed despite still having positive net carbon gain. When nitrogen availability limits the maximum leaf area within the plant canopy, the effects of leaf area index and self-shading are less pronounced, such that the oldest leaves at lower positions may be receiving sufficient light to allow C-gain to remain positive up until the time of leaf shedding (Ackerly and Bazzaz 1995). To maximize net carbon gain over all leaves in an entire, heterogeneously illuminated plant canopy, nitrogen should be allocated so that the most sun-lit leaves contain the greatest photosynthetic nitrogen concentrations, and such differential nitrogen allocation is expected to be more pronounced in species with a steep self-shading gradient (Hikosaka 2005; Hirose 2005). In a tropical forest canopy, *Cecropia* species with a low leaf area index (<1) had a shallower nitrogen gradient compared to species with greater LAI and self-shading (Kitajima et al. 2002, 2005). Thus, there are complicated interactions between insolation at the top of the crown and soil nutrient availability that influence LAI and the steepness of the self-shading gradient, which together affect differential nitrogen allocation among leaves and leaf lifespan. Moreover, how these processes interact to affect whole-plant C-gain is likely to vary among species with different ecological strategies.

One of the most commonly used, but deceptively simple, ecological measures of leaf structure is LMA (Osnas et al. 2013). However, LMA is a complex trait that can be decomposed into lamina thickness and density, which play different functional roles (Witkowski and Lamont 1991; Poorter et al. 2009). Sun-exposed leaves have multiple layers of elongated palisade mesophyll cells for more thorough absorption of high irradiance, resulting in greater lamina thickness and high LMA (Goldstein et al. this volume; Givnish 1988; Terashima et al. 2011). Greater LMA of sun leaves compared to shade leaves also involves change in the abundance of thick-walled vascular cells to meet high transpirational water demand and consequent increases in tissue density (Poorter et al. 2009). In contrast to these sun-shade acclimation responses, adaptation to high versus low-light habitats exhibit different directional responses: the leaves of light-demanding tree species have lower LMA than those of shade-tolerant tree species (Kitajima 1994; Walters and Reich 1999; Rozendaal et al. 2006; Markesteijn et al. 2007). This interspecific trend in LMA can be understood as adaptation to resource-limited environments, such as the shaded forest understory or infertile soils, in which longer time is required for paying back leaf construction cost (Mooney and Gulmon 1982; Williams et al. 1989).

Selection for Leaf Lifespan—What Is the Role of Defense?

If leaf lifespan is merely a function of how quickly a leaf wears out under the bombardment of attacks from herbivores and physical stresses, it may be reasonable to hypothesize a positive association between defense and leaf lifespan. But, a casual walk in a tropical forest reveals many “holey” leaves that exhibit extensive damage (e.g., 11-year old leaves in a Bornean rain forest Fig. 3). Coley (1983) evaluated saplings of 46 tropical tree species in Panama under a standardized

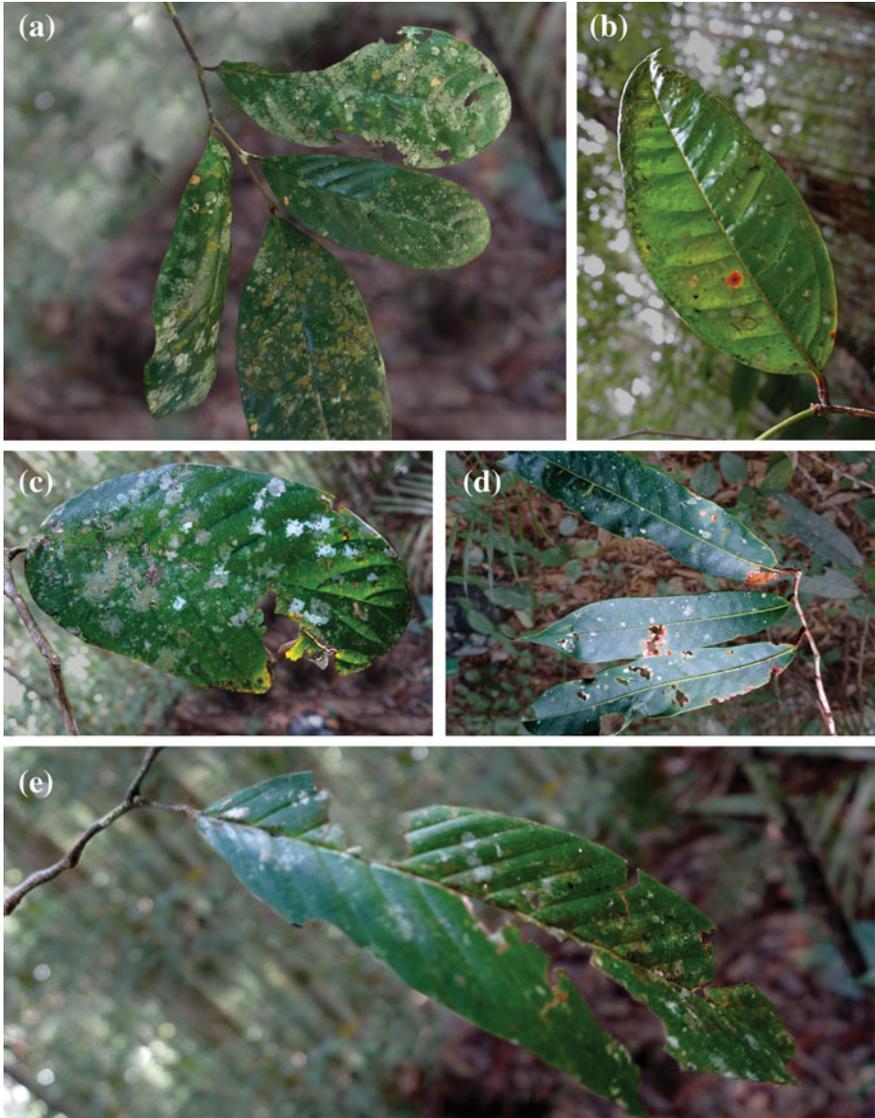


Fig. 3 Portraits of leaves that are greater than 11 years old on saplings of five tree species in the mixed dipterocarp forest of Lambir Hills National Park, Borneo, **a** *Polyalthia sarawakensis* (Annonaceae), **b** *Syzygium cf. grande* (Myrtaceae), **c** *Shorea laxa* (Dipterocarpaceae), **d** *Knema galleata* (Myristicaceae), **e** *Dipterocarpus globosus* (Dipterocarpaceae)

environment of treefall gaps to examine which leaf traits best explain differences in herbivory of young and mature leaves, leaf lifespan, and inherent differences in growth rates. The results show that interspecific variation in herbivory rates of young leaves is not explainable by most putative defense traits except for

toughness. In contrast, differences between species in herbivory rates of mature leaves, although they are overall much lower than in young leaves, can be explained by toughness, cellulose contents, and pubescence, but not by carbon-based chemical defense of tannins and phenols. Similar results are reported for 24 species from the same Panamanian forest in Kitajima et al. (2012), in which leaf toughness is measured as fracture toughness and work-to-shear, along with their material bases.

Interestingly, these putative structural and mechanical defenses explain species differences in leaf lifespan and growth rates better than herbivory rate does. Thus, there is a paradox. Leaf lifespan, rather than herbivory, is associated with leaf functional traits associated with physical defense. But, a cafeteria experiment with a generalist herbivore has shown a clear negative correlation between toughness and herbivory rate ($r = -0.78$), which were as strong as positive correlations of toughness with leaf lifespan ($r = 0.88$) and sapling survival rate ($r = 0.78$) (Kitajima and Poorter 2010). Perhaps, specialist herbivores are responsible for herbivory in the field, but they may be influenced differently by different chemical defenses, such that comparison of a broad range of species does not reveal significant association between herbivory and putative leaf defense traits.

Recent comparative studies also shed light on how LMA is linked to leaf structural properties through evolution and acclimation. In comparative analysis of subcanopy leaves of 197 species, Westbrook et al. (2011) asked, “what makes leaves tough?” from an evolutionary perspective, using structural equation models with phylogenetic independent contrasts. The results showed lamina density and cellulose per unit dry mass as two alternative paths to evolutionarily increase leaf fracture toughness, which was greater for species with high survival in shade. Their results also suggested that lamina thickness evolved independently of density and cellulose per unit mass. Perhaps, fracture toughness and its material bases should be viewed as the physical robustness necessary to set the upper limit for maximum lifespan. For a given leaf, realized leaf lifespan, however, may be shorter than this potential maximum. Even if a leaf is built to last for five years, it is perhaps not adaptive for a sapling to keep it that long. Particularly when a canopy opening forms, it may be more beneficial to senesce old leaves, translocate nitrogen and phosphorus to new leaves at higher and sunnier positions, and thereby extend the main stem.

For a given leaf, LMA is a product of lamina thickness and tissue density (dry mass per volume). Both lamina thickness and density may have plastic responses to light and nutrient availability as described in later sections with respect to LMA. Higher light availability in treefall gaps is associated with thicker, denser, and tougher leaves, but leaf lifespan is shorter, and herbivory is more common in gap seedlings than in understory seedlings (Kitajima et al. 2012). Hence, it is overly simplistic to interpret LMA as a putative structural defense trait. For interspecific variation, the tissue-density aspect of LMA enhances leaf lifespan, but the lamina thickness appears to be of lesser importance. For intraspecific variation associated with sun-shade gradients, leaf lifespan may decrease while LMA increases from shade to sun. Such counter-gradient variation (Lusk et al. 2008) is also found for putative chemical defense as well (Coley 1993); for temperate tree saplings, Shure

and Wilson (1993) found that within species, acclimation to larger gap size (i.e., more light) resulted in higher tannin concentrations, but among species, higher tannin was associated with adaptation to shade.

Empirical Tests of Conceptual Models for Acclimation and Adaptation to Varying Resources

As discussed above, acclimation to variable light availability versus adaptive specialization to contrasting irradiance habitats may exhibit different relationships of leaf lifespan with LMA and other leaf functional traits. The interaction of nitrogen and light availability is also key to understanding the optimization of leaf lifespan. Unfortunately, much less is known about how acclimation and adaptation exhibit co-variation of leaf lifespan and LMA within and among species in relation to soil fertility variation in tropical forests. In this section, we first present conceptual predictions of covariation of leaf lifespan and LMA (Fig. 4). We then test them with empirical data on plasticity of species specialized to habitats with contrasting resource availabilities, using data on leaves from Panama (seedlings grown under contrasting light environments) and Borneo (seedlings grown under contrasting light and soil environments). Our goal is to interpret these patterns in adaptive ecological plasticity with respect to the resource economic strategies of tree species.

Acclimation Versus Adaptation to Light Availability: Counter-Gradient Variation

As discussed in the previous section, the among-species correlation in leaf lifespan and LMA is positive (WLES), whereas plastic covariation within species is negative. Such counter-gradient variation is summarized graphically for light (Fig. 4a): acclimation to shade causes a decrease in LMA (Arrows 1 and 3 in Fig. 4a) and an increase in lifespan (Arrows 2 and 4 in Fig. 4a) within species, whereas between species, longer leaf lifespan is associated with higher LMA (positive slope of across species in the same light environment). This conceptual model is similar to the one by Lusk et al. (2008), but our model is more explicit about variation in the acclimation response of each species, depending on its resource economic strategy. More specifically, we predict that the degree of plasticity in leaf lifespan is greater, but that of LMA is smaller, for species with longer maximum leaf lifespan (shallower slopes for the gray arrows representing plastic covariance toward the right-hand side of Fig. 4a). For species under selection to have rapid leaf turnover in a resource-rich environment, it may be infeasible to reduce leaf lifespan beyond a

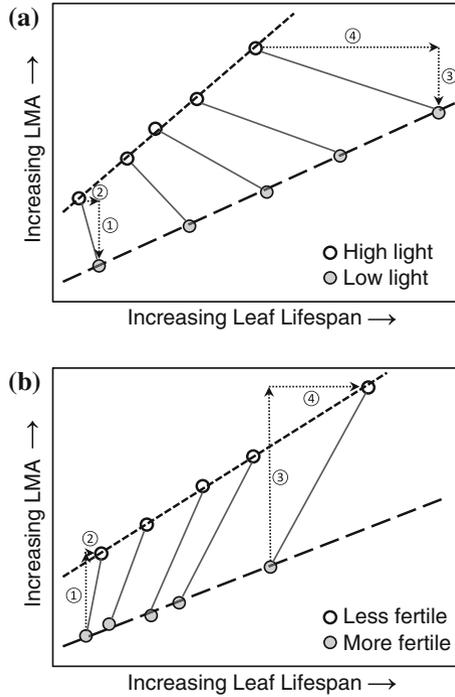


Fig. 4 Conceptual models of how leaf mass per area (LMA) covaries with leaf lifespan across and within species in terms of phenotypic responses to **a** contrasting light regimes (*open symbols* high light, *closed symbols* low light) and **b** contrasting soil types (*open symbols* fertile, *closed symbols* infertile). Each pair of *circles* connected by a *solid gray line* corresponds to an individual species and its phenotypic reaction norm. The interspecific relationship of LMA versus lifespan in a given environment is shown as *dotted* or *broken lines*: in high or low light (*short* and *long-dash*, respectively) and in more or less fertile soil types (*long* and *short-dash*, respectively). *Small circled numbers* indicate directional changes in LMA and lifespan, and the mechanisms involved for each are described in the main text

certain minimum, due to ever-increasing costs associated with leaf-turnover, even though they may exhibit a high degree of plasticity in LMA under higher light availability. At the other end of the LMA-lifespan spectrum, species selected to have structural defense to enable longer leaf lifespans have more latitude for plastic lifespan responses, which may result in greater shifts in response to light environment. There is also likely to be an upper limit on LMA, since light attenuates within thick mesophyll layers, and severely decreased lamina area may reduce photosynthetic surface area. Thus, the degrees of plasticity in LMA and leaf lifespan may differ across species with different ecological strategies, influencing the slope of the interspecific LMA-lifespan relationship (Fig. 4a).

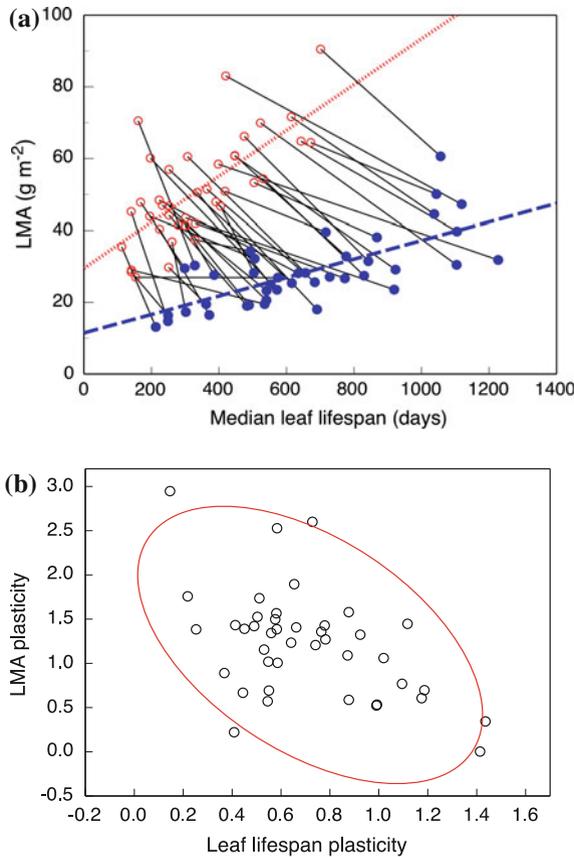


Fig. 5 **a** Interspecific variation and plasticity of leaf lifespan and LMA across seedlings of 41 Panamanian tropical tree species. Seedlings were grown from seeds in common gardens in treefall gaps (*red, open circles*) or understory common gardens or shade house (0.8 % of total daily PPFD in both; *blue, closed circles*). Each *solid line* connecting two data points from a given species shows the direction of phenotypic co-variation in LMA and leaf lifespan. The *dotted* and *broken lines* indicate the interspecific relationship. Species with estimates of median leaf lifespan exceeding 1300 days were not included, nor were species that were raised or could survive only in one of the environments. See Kitajima et al. (2013) for further details. **b** Relationship between plasticity in LMA and leaf lifespan derived from the data shown in (a), with the 95 % confidence ellipse in red. The plasticity index was calculated as the difference in trait values between contrasting light environments divided by the geometric mean of those values

We tested these predictions using data on the LMA and leaf lifespans of seedlings from 41 Panamanian tree species that were experimentally grown in replicated common gardens in gaps and shaded understory. These species represent a range of shade-tolerance strategies, from light-demanding pioneers to shade tolerant late-successional species (Kitajima et al. 2012, 2013). Overall, the results shown in

Fig. 5a support the conceptual model predictions (Fig. 4a). Within-species, acclimation to shade involved an increase of leaf lifespan and decrease of LMA (negative correlation). Among species, longer leaf lifespans were associated with increased LMA under each standardized light environment (positive correlation). Also, light-demanding species with short leaf lifespan exhibited large degrees of plasticity in LMA, but relatively smaller changes in leaf lifespan between the two light environments. Consistent with our conceptual model, plasticity in LMA declined with increasing plasticity in leaf lifespan ($r = -0.491$, $P = 0.001$; Fig. 5b).

Acclimation Versus Adaptation to Soil Resource Availability: Co-gradient Variation

Among and within tropical forests, soil properties vary greatly in terms of availability of mineral nutrients, such as nitrogen and phosphorous, and water, even under the same climate (Ashton 2015). Co-variation of leaf lifespan and LMA in relation to natural soil gradients is widely demonstrated both in temperate and tropical ecosystems (e.g., Cordell et al. 2001; Wright et al. 2002), although in many such studies, variation due to acclimation versus adaptation are confounded. While we recognize that different types of belowground resources may produce varying responses (e.g., low-rainfall vs. low-nutrient sites, Wright et al. 2002; nitrogen vs. phosphorus, Cordell et al. 2001), here we develop a general conceptual model for inter- and intraspecific variation in leaf lifespan and LMA due to soil fertility.

Variation in soil fertility is expected to produce co-gradient variation (Fig. 4b), unlike the case for insolation (Fig. 4a), since lower soil fertility should be associated with increases in both LMA (Arrows 1 and 3 in Fig. 4b) and leaf lifespan (Arrows 2 and 4 in Fig. 4b) both within and between species. Species with contrasting soil associations across fertility gradients experience and are presumably adapted to different soil nutrient and moisture regimes, and so we expect them to differ in LMA and leaf lifespan plasticity, causing the slope of the interspecific LMA-lifespan relationship to vary across soil habitat types, analogous to light-related patterns.

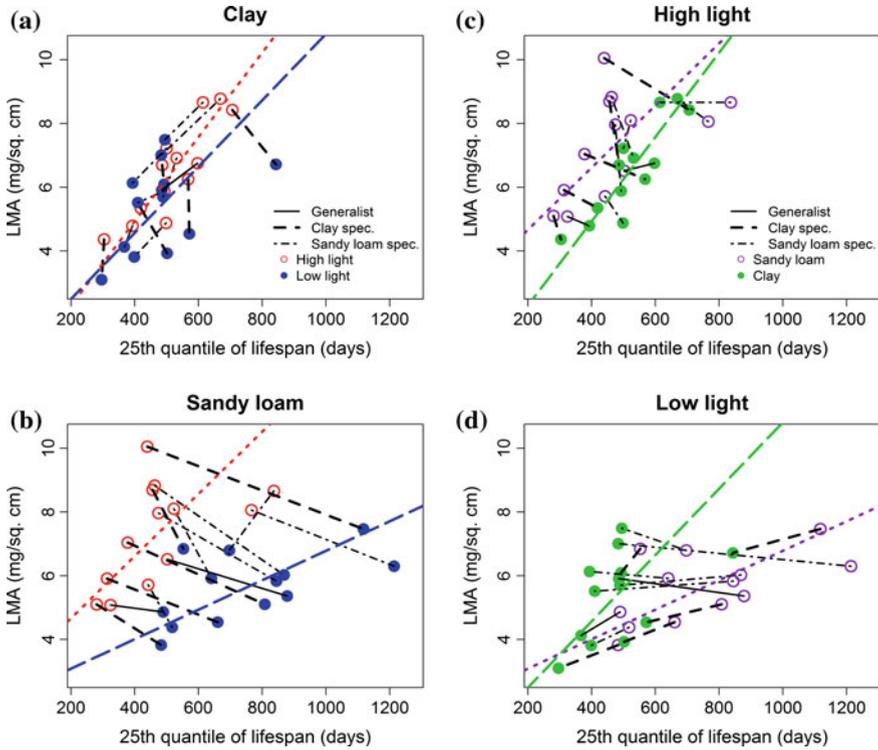
Patterns of within-species variation in leaf lifespan with soil fertility, however, can be quite inconsistent across studies, often with apparently non-adaptive phenotypic responses, such as reduced leaf lifespan in less fertile soils (Aerts and Caluwe 1995; Richardson et al. 2010; Pornon et al. 2011). Pornon et al. (2011) proposed a conceptual model to explain these counter-intuitive soil-related responses, in which they consider that sink activity due to growth accesses endogenous, more than exogenous, nitrogen when soil nitrogen is very low, accelerating leaf senescence (Marty et al. 2009; Pornon et al. 2011). However, this logic only makes sense if a plant species does not sufficiently down-regulate sink activity in resource-depleted environments via regulation of leaf production and growth rates, which would reduce demand for nitrogen in the first place. Although

height competition is less intense in nutrient-depleted soils, down regulation of height growth may not be an evolutionarily stable strategy in some circumstances (Anten 2005). There is ample evidence that growth rates vary depending on resource availability, but there are likely to be limits to the amount by which a species can adjust inherent variation in growth rate (*sensu* Lambers and Poorter 1992).

Interactions of Light and Soil Resource Availability on Leaf Lifespan Variation

Both light and soil resources vary in time and space, and in the forest understory, they are often interdependent (Coomes and Grubb 2000; Russo et al. 2012), and so it makes sense to examine their interactive effects on acclimation of LMA and leaf lifespan. We examined these patterns using data from seedlings of 13 Bornean tree species that were reciprocally transplanted into contrasting light and soil environments in forest experimental plots. Leaf lifespan was estimated on seedlings of each species sown on clay and sandy loam soils in gaps and understory. All study species are shade tolerant, but differ in soil specialization, ranging from species associated with nutrient-depleted, well-drained sandy loam soil, to clay soil with greater nutrient concentrations and water-holding capacity, and generalist species associated with both soil types (Davies et al. 2005). Moreover, the sandy loam specialists have slower diameter growth and higher survival rates compared to clay specialists (Russo et al. 2005).

The patterns among the Bornean species across light and soil treatments (Fig. 6) were considerably more complex than the pattern due to insolation alone (Fig. 5). As predicted by our conceptual models (Fig. 4), the results show counter-gradient variation for acclimation versus adaptation of LMA and leaf lifespan with light environment, and co-gradient variation with contrasting soil environments. However, the direction and magnitude of plasticity of both traits depended on the soil and light environment, as well as the species' soil specialization. Among species, increases in leaf lifespan were associated with increases in LMA, and, consistent with our conceptual model, the slopes of these relationships depended upon the environment. Within-species, acclimation to shade produced an increase in leaf lifespan and a decrease in LMA (negative slopes of the black lines in Fig. 6a, b). These relationships were most consistently seen on sandy loam (Fig. 6b), which exhibited counter-gradient selection and resembled patterns for the Panamanian species (Fig. 5a). On the more fertile clay (Fig. 6a), LMA decreased for all species with acclimation to shade, as expected. However, leaf lifespan on clay showed variable patterns with acclimation to shade, increasing or showing little change, as expected for clay specialists, but counterintuitively decreasing for sandy loam



specialists and generalists. One explanation is that the sandy loam specialist seedlings may have accelerated leaf senescence in order to reduce carbohydrate consumption (Sevanto et al. 2014), since the understory on clay is shadier than the understory on their home sandy loam soil to which they are presumably adapted (Russo et al. 2012).

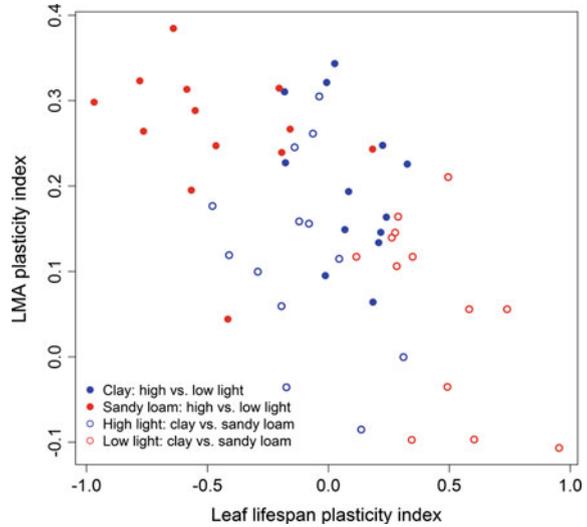
Within-species, acclimation from sandy loam to clay produced a decrease in leaf lifespan and either little change or a decrease in LMA (Fig. 6c, d), co-gradient variation that is most consistently seen in the low light understory (Fig. 6d). In gaps, however, patterns were complex, with some species exhibiting counter-gradient selection or little change in leaf lifespan across contrasting soils (Fig. 6c). These disparate responses could be related to whether species are N or P-limited. On a P-limited substrate, Cordell et al. (2001) found no change in the leaf lifespan of *M. polymorpha* in response to fertilization with N, P, or their combination, in contrast to an N-limited substrate, on which leaf lifespan declined with fertilization. Although responses of individual species varied, at a given LMA, leaf lifespan was always longer for seedlings in low light especially on sandy loam (Fig. 6a, b). However, at a given LMA, leaf lifespan was on average longer for seedlings on sandy loam than on clay soil only in low light (Fig. 6d); in high light, leaf lifespan

◀ **Fig. 6** Interspecific variation and plasticity of leaf lifespan and LMA of seedlings of 13 tropical, shade-tolerant tree species in the Dipterocarpaceae specializing on sandy loam soil, clay soil, or neither (generalists). Seedlings were grown from newly germinated seeds in a field reciprocal transplant experiment in plots in Bornean forest (Lambir Hills National Park, Malaysia) located on sandy loam (*purple, open circles*) or clay (*green, closed circles*) and in treefall gaps (*red, open circles*) or shaded understory (*blue, closed circles*). Responses in the four environmental regimes are in each panel, comparing plots in high versus low light (**a** and **b**) or sandy loam versus clay (**c** and **d**), holding either soil or light environment constant, respectively. The two data points for each species are connected by a *black line* showing the phenotypic reaction norm, with the *dashing pattern* indicating soil specialization (*solid*, generalist; *long dash*, clay specialist; *dot-dash*, sandy loam specialist). *Colored dotted and broken lines* (colors correspond to the symbol colors for the different environments) indicate the interspecific relationship of LMA with the 25th quantile of leaf lifespan within each soil or light environment. LMA was determined for all true leaves at approximately 1.5 years after seeds were sown. Species' 25th quantile leaf lifespan was determined for marked true leaves for up to 1200 days. The 25th quantile of lifespan was used because the median lifespan could not be estimated for all species based on the study duration (3.25 years) and long leaf lifespans. Study species are shade-tolerant and either canopy or emergent tree species. Congeneric species of contrasting soil associations include the following: sandy loam specialists, *Dryobalanops aromatica*, *Hopea beccariana*, *Dipterocarpus globosus*, *Shorea beccariana*, *Shorea laxa*, *Vatica nitens*; clay specialists, *Dryobalanops lanceolata*, *Hopea dryobalanoides*, *Dipterocarpus palembanicus*, *Shorea macrophylla*, *Shorea xanthophylla*; and generalists, *Anisoptera grossivenia* and *Dipterocarpus acutangulus*. Soil associations are based on Poisson cluster model analyses in Davies et al. (2005; see also Russo et al. 2005), with stems of specialists being significantly aggregated on that soil type and generalists showing no significant aggregation due to soil type

at a given LMA was shorter for seedlings on sandy loam than on clay (Fig. 6c). This unexpected response resembles findings from Reich et al. (1999) and Wright et al. (2002) in relation to water availability: at a given LMA, species associated with lower rainfall sites had shorter leaf lifespan than those at wetter sites. For these Bornean species, the LMA required to achieve a given lifespan is higher on sandy loam, potentially owing to lower soil moisture (Russo et al. 2010). Higher LMA may confer better tolerance to low soil water potentials experienced at low-rainfall sites or well drained soils (Niinemets 2001; Wright et al. 2002). Thus, soil-related plasticity in leaf lifespan when light is not limiting may depend upon the particular belowground resource in question, as well as variation among species in which resource is most limiting to growth.

As with the results from Panama, plasticity in LMA and leaf lifespan were negatively correlated ($r = -0.56$, $p < 0.001$; Fig. 7). However, on the resource-depleted habitats, the mean plasticity index for leaf lifespan (sandy loam: 0.50 and low light 0.45) was on average two to four-fold higher than that for LMA (sandy loam: 0.26 and low light 0.11), whereas in the more productive environments, the mean plasticity indices for leaf lifespan and LMA were more comparable (lifespan, 0.15 and 0.20, and LMA, 0.19 and 0.14, for clay and high light, respectively), suggesting that in resource-depleted habitats leaf lifespan may be extended by means other than increasing LMA.

Fig. 7 Relationship between plasticity in leaf mass per area (LMA) and leaf lifespan for the data shown in Fig. 6. The plasticity index was calculated as the difference in trait values between contrasting soil or light environments (with the other factor held constant) divided by the geometric mean of those values



Towards a More Mechanistic Understanding of Leaf Lifespan—What Remains Unknown?

Leaf lifespan is central to the carbon and nutrient economies of trees, with direct and indirect links to individual growth and survival. Yet, even very basic information about leaf lifespan in tropical trees is still lacking. Here, we highlight some important knowledge gaps impeding a more mechanistic understanding of the role of leaf lifespan in whole-tree carbon and nutrient dynamics of tropical species.

How Long Is the Longest Leaf Lifespan among Tropical Broad-leaved Species?

Although there are several methods for estimating leaf lifespan (see Kikuzawa and Lechowicz 2011, Chap. 1 for a review) accurate estimates of the distribution of leaf lifespans for evergreen tropical tree species are difficult to obtain. Estimates of leaf lifespan are improved when the data are not censored, i.e., when lifespan of all leaves are followed from their birth to death (Dungan et al. 2003). But data collection campaigns over long time periods for a sufficient number of leaves are logistically challenging, especially for slow-growing species in aseasonal or resource-poor tropical environments. Leaf lifespans of shade-tolerant juveniles in tropical moist forests can be typically five or more years (e.g., Kursar and Coley 1993; King 1994). In saplings of shade-tolerant tree species in an ever-wet Bornean rain forest growing on nutrient-depleted soils, for 14 out of 31 species, even the

25th percentile of the leaf lifespan distribution was not well estimated after 6.5 years of censuses, suggesting that leaf lifespans of these species may routinely exceed 10 years (Russo, unpub. data; Fig. 3). Thus, many published leaf lifespans for evergreen tropical species may not only fail to encompass the full range of within- and between-tree variation, but they may also be underestimates.

Why Are Seemingly Unproductive Leaves Retained?

Juvenile trees of shade tolerant species in closed-canopy tropical forest often survive for long periods of time under deep shade. Given the aged appearance of their often self-shaded leaves, which themselves are frequently covered with lichens and epiphylls (Fig. 3), it is hard to imagine that such leaves are contributing significantly to the tree's carbon economy. So, why are they retained? These leaves may have such low respiratory maintenance costs that they can still achieve positive net carbon balance, in which case, there may be little advantage to senescing the leaf, particularly if the new leaf would not intercept appreciably more insolation as is the case for shaded juveniles. New and young leaves are more likely to be attacked by herbivores (Coley 1983; Coley et al. 2005), and thus replacing old leaves could present a significant risk of resource drain. It is also possible that these leaves are retained because they function to store nutrients, for example, nitrogen in disused proteins, that will be used to produce a flush of new leaves when the growing environment improves. Carbon and nitrogen isotope labelling studies (e.g., Pornon and Lamaze 2007) hold promise for identifying the sources of nitrogen used to form new leaves and the leaf-level photosynthesis-respiration balance of older leaves.

Are Leaves Senesced When Leaf Photosynthetic Function Declines to Zero?

How rapidly photosynthetic rates and PNUE decline with leaf age is a key parameter in theoretical models of optimal leaf lifespan because it strongly influences photosynthetic productivity through the lifetime of the leaf (Kikuzawa 1991, 1995; Ackerly 1999; Escudero and Mediavilla 2003). At least three classes of mechanism likely cause the decline in function with leaf age: self-shading, age-related deterioration per se, and withdrawal of nitrogen from the lamina. With the exception of a few studies (Kitajima et al. 1997b, 2002), how much variation in the age-related decline in leaf function exists among and within tropical tree species, and the environmental controls over this process, remain largely unmeasured.

Estimation of decline-rate functions can be accomplished with either a chronosequence approach, in which leaf position substitutes for exact leaf age, or with a repeated-measurements approach, in which photosynthetic parameters are

repeatedly estimated on the same leaf over its lifetime (Kitajima et al. 2002; Osada et al. 2015). The chronosequence approach is less labor intensive, but it ignores within-plant and within-species variation in leaf lifespan or decline-rate function, which can be substantial, as discussed earlier. This results in substantial bias in estimating functional decline rate with leaf age, and mismatch of empirical data to theoretical predictions of leaf lifespan as to whether leaves are senesced when photosynthetic function declines to zero (Osada et al. 2015). Importantly, the bias worsens as the leaf-level variance in lifespan increases. Given the substantial variation in survival time among individual leaves within-species and even within plants (Figs. 1 and 2), we call attention to the importance of considering variance in age-related changes in leaf function and demography in future tests of optimal leaf lifespan models with empirical data.

Models of Leaf Lifespan—What Are the Key Trade-Offs?

The internal dynamics of carbon and nutrients in trees are complex, are determined by multiple functional traits, and often involve latent physiological and biochemical processes. As a result, the mechanisms by which leaf lifespan affects these dynamics are difficult to quantify with empirical studies. Models of leaf-lifespan that only consider leaf-level processes cannot account for key processes affecting leaf lifespan that are operating at the whole-tree level. Many optimal leaf lifespan models differ in fundamental ways in terms of which mechanisms and physiological processes they incorporate. As a result, each is more appropriate in some ecological contexts than in others. For example, the whole-tree model of Givnish (2002) includes a parameter controlling the fractional carbon allocation to leaves versus roots, and not accounting for this yields predictions of the distribution of deciduous versus evergreen leaf habits in seasonal environments that do not match those found in nature. Somewhat paradoxically, simpler models that do not explicitly consider whole-plant nutrient allocation strategies, in contrast, can also give rough approximation of the prevalence of deciduous versus evergreen habits (Kikuzawa et al. 2013). Although there is no complete consensus as to what are the critical parameters that explain leaf lifespan variation from an ecophysiological perspective, there is a general recognition that trade-offs in resource allocation strategies are key to mechanistic understanding. In Table 1, we summarize some of the critical leaf-level and whole-tree trade-offs in function that mechanistic models of leaf lifespan should capture. Whether we want to explain global variation in leaf habit or the biological mechanisms governing leaf lifespan variation in a forest community in relation to resource availability, dynamic resource allocation models that incorporate these major physiological processes and that accurately capture these critical trade-offs are needed. Development of such models is particularly exciting in species-rich and functionally diverse tropical tree communities.

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