

Leaf life span spectrum of tropical woody seedlings: effects of light and ontogeny and consequences for survival

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- **Background and Aims** Leaf life span is widely recognized as a key life history trait associated with herbivory resistance, but rigorous comparative data are rare for seedlings. The goal of this study was to examine how light environment affects leaf life span, and how ontogenetic development during the first year may influence leaf fracture toughness, lamina density and stem density that are relevant for herbivory resistance, leaf life span and seedling survival.
- **Methods** Data from three experiments encompassing 104 neotropical woody species were combined. Leaf life span, lamina and vein fracture toughness, leaf and stem tissue density and seedling survival were quantified for the first-year seedlings at standardized ontogenetic stages in shade houses and common gardens established in gaps and shaded understorey in a moist tropical forest in Panama. Mortality of naturally recruited seedlings till 1 year later was quantified in 800 1-m² plots from 1994 to 2011.
- **Key Results** Median leaf life span ranged widely among species, always greater in shade (ranging from 151 to >1790 d in the understorey and shade houses) than in gaps (115–867 d), but with strong correlation between gaps and shade. Leaf and stem tissue density increased with seedling age, whereas leaf fracture toughness showed only a weak increase. All these traits were positively correlated with leaf life span. Leaf life span and stem density were negatively correlated with seedling mortality in shade, while gap mortality showed no correlation with these traits.
- **Conclusions** The wide spectrum of leaf life span and associated functional traits reflects variation in shade tolerance of first-year seedlings among coexisting trees, shrubs and lianas in this neotropical forest. High leaf tissue density is important in enhancing leaf toughness, a known physical defence, and leaf life span. Both seedling leaf life span and stem density should be considered as key functional traits that contribute to seedling survival in tropical forest understoreys.

Key words: Fracture toughness, herbivory, leaf life span, leaf density, leaf toughness, light environment, ontogenetic changes, phenotypic plasticity, seedling survival, stem density, tropical lianas, tropical trees.

INTRODUCTION

Damages from herbivory, disease and fallen litter can be fatal to seedlings in the shaded forest understorey where photosynthetic income is too low to facilitate rapid recovery (e.g. Augspurger, 1984; Clark and Clark, 1985, 1991; Molofsky and Fisher, 1993). Hence, long-term maintenance of carbon gain and survival in shade benefits from robust physical construction of dense and tough leaves, stems and roots (Grime, 1965; Coley, 1983; Kitajima, 1994; Alvarez-Clare and Kitajima, 2007) as well as other traits that enhance defence against such hazards (e.g. Eichhorn *et al.*, 2007), and to a lesser extent from carbohydrate storage to recover from damages (Canham *et al.*, 1999; Myers and Kitajima, 2007; Poorter *et al.*, 2010). According to cost–benefit theory, leaves should live longer when low resource availability restricts daily photosynthetic income as is the case in shade, whereas the optimal strategy in resource-rich environments is rapid turnover of short-lived productive leaves (Chabot and Hicks, 1982; Williams *et al.*, 1989; Kikuzawa, 1991; Ackerly and Bazzaz, 1995). Such environment-dependent

optimization of carbon economy cannot be decoupled from ecological requirements of defending long-lived leaves; undefended leaves cannot achieve their optimal leaf life spans, and well-defended leaves may require high initial construction costs which further increase payback time (Coley *et al.*, 1985). Consequently, shade acclimation and shade adaptation are both accompanied by extension of leaf life span (Kikuzawa and Lechowicz, 2011).

Leaf life span data are relatively rare for woody seedlings despite its relevance for seedling regeneration and community assembly. Unlike deciduous species whose leaf life spans are constrained by the growing season length (Seiwa and Kikuzawa, 1991; Mediavilla and Escudero, 2003), evergreen seedlings and saplings may have leaf life spans extending over multiple years (Kursar and Coley, 1993; Iddles *et al.*, 2003; Osada *et al.*, 2003; Coste *et al.*, 2011; Lusk *et al.*, 2011; Kitajima *et al.*, 2012). Quantifying leaf life span for such juveniles is labour and time intensive, and appropriate comparisons among species require standardization of ontogeny and light environment.

Comparative studies of gap-grown juveniles of neotropical trees show that among multiple putative defence traits, leaf toughness, leaf tissue density, and cellulose concentrations are the best correlates of leaf life span and herbivory rates across species (Coley, 1983; Iddles *et al.*, 2003; Kitajima *et al.*, 2012). A classical study of gap-grown saplings of 46 neotropical tree species by Coley (1983) found that the majority of herbivory damage takes places when leaves are still expanding, but herbivory rates (% leaf area loss per day) of young leaves are uncorrelated with putative defence traits and leaf life span across species. In contrast, herbivory rates of mature leaves are slow, but correlated negatively with physical robustness measured as punch strength ($r = -0.67$, $P < 0.001$) and leaf life span ($r = -0.70$, $P < 0.001$, for 41 species excluding species with zero herbivory rates after log transformation of variables).

While the maximum force recorded during punching through a leaf lamina provides an ecologically meaningful index of physical defence as found by Coley (1983), proper normalization of mechanical properties and measurements of lamina thickness and leaf mass per area (LMA) enhance understanding of the material and mechanical basis of leaf toughness (Read and Stokes, 2006). Leaf toughness measured with a cutting test can be normalized as work-to-shear (= work to fracture per unit cut length), fracture toughness (= work-to-shear divided by lamina thickness) or density-corrected toughness (= fracture toughness divided by leaf density) (Onoda *et al.*, 2011). Species differences in density-corrected toughness reflect concentration per unit leaf mass of cellulose but not other cell wall components (Kitajima *et al.*, 2012). A comparative analysis of 197 neotropical tree species found that leaf density and cellulose concentration are two independent evolutionary paths for changing leaf fracture toughness (Westbrook *et al.*, 2011). LMA, interspecific variation of which reflects either leaf density or thickness (Poorter *et al.*, 2009), is a widely recognized functional trait that contributes to the leaf economic spectrum (Wright *et al.*, 2004) and shade tolerance of evergreen species (Lusk and Warton, 2007). But, LMA is a fuzzy measure of physical defence (Wright and Westoby, 2002), and the relative contributions of lamina thickness versus density to LMA's linkage to leaf life span differ among studies. For Australian species from four sites that contrast in rainfall and soil phosphorus availability, lamina thickness (but not density) correlates with leaf life span within each community (Wright and Westoby, 2002). In contrast, in neotropical forests, lamina density (but not thickness) explains species-difference herbivory resistance, leaf life span and growth-survival trade-offs (Kitajima and Poorter, 2010; Westbrook *et al.*, 2011; Kitajima *et al.*, 2012).

For proper interspecific comparisons of these leaf traits, it is important to consider variation due to phenotypic plasticity in relation to ontogeny and environments (Kikuzawa and Lechowicz, 2011). Leaf density and lamina toughness increase from saplings to adults, which could reflect both ontogeny and light environments (Kitajima and Poorter, 2010). First-year seedlings go through rapid developmental changes, from the first-leaf stage (rapid development of soft organs largely fuelled by seed reserves) to autotrophic development dependent on photosynthetic carbon gain by leaves. Few published studies have examined these initial ontogenetic changes

of leaf and stem density in a comparative framework (Alvarez-Clare and Kitajima, 2007). It is widely recognized that light environments affect leaf traits (Markesteijn *et al.*, 2007), and plants growing under higher light availability exhibit shorter leaf life span (Williams *et al.*, 1989; Osada *et al.*, 2003; Coste *et al.*, 2011). Acclimation to high light is typically associated with greater LMA in intraspecific comparisons, even though interspecific comparisons of evergreen species show that adaptation to high light is associated with lower LMA (Kitajima, 1994; Lusk and Warton, 2007; Lusk *et al.*, 2010; Coste *et al.*, 2011). Given such discordant directional response of LMA and lamina density for light acclimation versus light adaptation, it is important that trait measurements control for light availability. Unfortunately, measurements are often made in representative habitats so that gap-dependent species are measured in gaps and shade-tolerant species are measured in shade. Such comparisons cannot determine whether the observed differences among species reflect intraspecific plasticity or evolutionary differences among species (Endara and Coley, 2011). Indeed, patterns of interspecific correlations between leaf traits, herbivory rates, leaf life span and seedling survival may change across environments (Kitajima *et al.*, 2012).

Growth form difference may also influence herbivory resistance and leaf life span in woody seedling communities. Lianas (woody vines) as a group may include more light-demanding species than trees (Schnitzer and Bongers, 2002), and their climbing habits may influence leaf life span and functional traits of seedling leaves and stems. Given their climbing habit and greater phenotypic plasticity, adult lianas differ from trees in tissue density and biomechanical properties (Gartner, 1991) and canopy leaves of lianas and trees differ in LMA and chemical compositions (Asner and Martin, 2012). Lianas, however, may grow as free-standing woody seedlings for a prolonged time (Caballe, 1998), and thus trees and lianas may exhibit similar relationships of demographic and functional traits. But, this possibility remains unexplored despite potential importance of seedling regeneration ecology of lianas and trees for forest community dynamics (Schnitzer and Bongers, 2002).

Defending leaves alone would not be sufficient for small seedlings; biomechanical strength of stems may be more important than leaf toughness in enhancing seedling survival because their stems can be easily chewed off by herbivores and crushed by trampling and litter falls (Alvarez-Clare and Kitajima, 2009). Adult wood density is widely recognized as a positive correlate of survival of first-year seedlings survival (Augsburger, 1984) and older juveniles (Muller-Landau, 2004; Poorter *et al.*, 2008; Chave *et al.*, 2009; Kraft *et al.*, 2010; Wright *et al.*, 2010). However, studies that examine relationships between survival and stem tissue density with both measured for earlier ontogenetic stages remain rare. Soft stems – hypocotyls in particular – of young seedlings make them vulnerable to attack by herbivores, including invertebrate grazers (Hulme, 1994; Hanley *et al.*, 2003; Green *et al.*, 2004) and vertebrate browsers (Sork, 1987; Kitajima and Augsburger, 1989; Molofsky and Fisher, 1993). In a study of eight neotropical species, high stem density is associated with greater stem toughness and modulus of elasticity, which in turn reduce mortality subsequent to being damaged by

litter fall and herbivory (Alvarez-Clare and Kitajima, 2009). Furthermore, interspecific variations in stem tissue density and biomechanical strength are likely to be concordant between leaves and stems (Alvarez-Clare and Kitajima, 2007). Yet, no published work has simultaneously examined the relevance of leaf toughness, stem density and related traits for seedling leaf life span and survival, all measured at the same ontogenetic stage.

In this paper, we focus on relationships between leaf toughness, leaf density and stem density versus leaf life span and seedling survival across common woody species in a tropical moist forest. To do so, we have combined data from a long-term monitoring study and experiments conducted in shade houses and field common gardens. We evaluated the following predictions: (a) leaf life span exhibits phenotypic plasticity to gap versus shade environments, with shorter leaf life span in gaps than in shade; (b) fracture toughness of leaf lamina and vein determined in the shade houses correlates positively with leaf life span in both gaps and shade; (c) tissue densities of leaves and stems increase with seedling ontogeny, from rapidly developing young seedlings to older seedlings; (d) leaf density and stem density are correlated with each other and with leaf life span and seedling survival in shade, but not with survival in gaps.

Our leaf demography data were summarized from approx. 39 000 individually marked leaves on seedlings of 70 and 84 woody species in 5-year common-garden experiments in gaps and shade, respectively. Whole seedling survival was evaluated in the gap and shade common gardens, as well as for 39 500 naturally recruited seedlings over 17 years in 800 1-m² forest census plots. Leaf lamina and vein fracture toughness, leaf density and stem density were quantified for 70–89 species with growth experiments that carefully standardized shade environments and ontogenetic developmental stages. A given pair-wise correlation analysis involved 38–89 species. As to species difference in susceptibility to herbivory in the field, we quantified herbivory frequency (proportion of marked leaves that exhibited conspicuous herbivory) but not herbivory rates (% leaf area lost per day). Thus, we examined pair-wise trait correlations with herbivory rates of mature leaves quantified in gaps in the same forest by Coley (1983) for 14–20 species that overlap between the two datasets.

MATERIALS AND METHODS

Site and species

We combine results from three studies conducted in the Barro Colorado Nature Monument (BCNM, 9°98' N, 79°51') in Panama. The three studies include (a) a long-term observation of seedling recruitment, growth and survival on Barro Colorado Island (BCI) from 1994 to 2012 (Wright *et al.*, 2005; Gilbert *et al.*, 2006), (b) a growth experiment with potted seedlings in shade houses established in a clearing on BCI (2001–2006), and (c) a field experiment with transplanted seedlings in gap and shade common gardens on the nearby Buena Vista Peninsula in the BCNM (2002–2006) (Kitajima *et al.*, 2012). Leigh *et al.*, (1982) describe the climate, flora and ecology of the seasonal moist tropical forests of the BCNM. Annual rainfall averages 2600 mm, 90 % of which

falls between May and December. The 104 woody species included in our analyses (Table 1) are common trees, shrubs and lianas for which at least two of the functional traits were quantified, along with leaf and plant demographic traits. Because seed availability, germination success and transplant success limited species number in the shade-house and common-garden experiments, a given pair-wise correlation analysis included 38–89 species, with 90 % of the pairwise correlations including 45–70 species (Table 2).

Mortality rates of naturally recruited seedlings

Wright *et al.* (2005) describe the details of the design of this on-going experiment of naturally recruited seedlings. For our purposes, each year during the dry season between January and April, all new woody seedlings are marked and identified to species in 800 1-m² plots, and their survival is recorded in the next census 1 year later. All 800 seedling-census plots are within a 50-ha forest dynamics plot from which annual mortality rates of saplings (10–100 mm diameter at breast height) have been published (Condit *et al.*, 2006). We pooled all newly recruited seedlings of each species recorded in 1995 through 2011 (17 years), and calculated the mortality rate (% d⁻¹) as $100 \times [\ln(\text{total number of new recruits}) - \ln(\text{total number of 1-year-old seedlings})]/365$. We included 72 species with a minimum of 20 new recruits for which at least one additional trait was also quantified. Supplementary Data Table S1 reports the sample size and mortality rates for each species included in the analysis. On BCI, seeds of most species germinate during the early to mid-rainy season (mid-May through to September) (Garwood, 1983) and, thus, the seedlings were typically 4–10 months old when they were first enumerated as new recruits. The mortality rates of younger seedlings were quantified experimentally in the common-garden experiments described below.

Field common gardens in gaps and shaded understorey

In a 20-m tall secondary forest on the Buena Vista Peninsula, we established six common gardens (7–8 m × 8–10 m each) enclosed by fences (hardware cloth with 2-cm mesh) to exclude ground-dwelling vertebrates. Three common gardens were located in the shaded understorey and received 0.5–0.8 % of above-canopy photosynthetically active radiation (PAR), and three common gardens were established in natural treefall gaps whose centres received 23.4, 37.7 and 50.7 % of above-canopy PAR. Between April 2002 and May 2004, seeds were collected from forests within the BCNM, and germinated under 30 % or 1 % light availability in plastic trays filled with washed sand and forest soil from the top 30 cm of the soil profile. After radicle emergence and before full expansion of the first leaf, 6–12 seedlings of each species were transplanted to two randomly chosen sections of each common garden (i.e. 18–36 seedlings per environment, transplanting seeds germinated under high and low light conditions to gap and shade gardens, respectively). Seedling survival was recorded weekly. Mortality rates were calculated for 3 months after first leaf full expansion and before destructive harvests reduced sample size. The analysis excluded a small number of seedlings that died within 1

TABLE 1. The 104 tropical woody species included in the study, along with their family, growth form (T, trees; M, mid-story trees; U, understory trees; S, shrubs; L, lianas), median leaf life span (d) determined in the shade houses and in common gardens (CGs) in gaps and the shaded understory, and mean lamina fracture toughness determined in the shade houses

Species	Family	Growth form	Median leaf life span (d)			Lamina toughness (J m ⁻²)
			Gap CGs	Shade CGs	Shade house	
<i>Allophylus psilospermus</i>	Sapindaceae	M			259	181.7
<i>Alseis blackiana</i> *	Rubiaceae	T	246			
<i>Anacardium excelsum</i>	Anacardiaceae	T	161	167	490	251.6
<i>Annona spraguei</i> *	Annonaceae	M	168			
<i>Apeiba membranacea</i> *	Malvaceae	T				159.4
<i>Aspidosperma spruceanum</i>	Apocynaceae	T	867		> 1792	232.6
<i>Beilschmiedia pendula</i>	Lauraceae	T	420	1119	> 1157	211.0
<i>Brosimum alicastrum</i>	Moraceae	T	614	1028	1047	329.1
<i>Callichlamys latifolia</i>	Bignoniaceae	L	301	699	1139	278.0
<i>Calophyllum longifolium</i>	Clusiaceae	T	701	1253	860	269.6
<i>Casearia guianensis</i> *	Salicaceae	U			307	220.6
<i>Castilla elastica</i>	Moraceae	T	140	224	275	85.8
<i>Ceiba pentandra</i> *	Malvaceae	T	140		249	
<i>Chrysophyllum cainito</i>	Sapotaceae	T	398		1227	177.0
<i>Combretum decandrum</i> *	Combretaceae	L	168			190.8
<i>Connarus turczaninowi</i>	Connaraceae	L			> 909	275.6
<i>Cordia alliodora</i> *	Boraginaceae	T	196		303	114.9
<i>Cordia bicolor</i> *	Boraginaceae	T	261		302	79.7
<i>Coussarea curvigemma</i> *	Rubiaceae	U	447	923		
<i>Cupania seemannii</i>	Sapindaceae	U			> 892	216.1
<i>Davilla nitida</i> *	Dilleniaceae	L	222			
<i>Dendropanax arboreus</i> *	Araliaceae	T			749	195.4
<i>Desmopsis panamensis</i>	Annonaceae	U			> 452	260.0
<i>Dipteryx oleifera</i>	Fabaceae	T	280			196.0
<i>Dolioscarpus major</i> *	Dilleniaceae	L				162.2
<i>Dolioscarpus olivaceus</i> *	Dilleniaceae	L	468			
<i>Eugenia coloradoensis</i>	Myrtaceae	T			1166	282.6
<i>Eugenia nesiotica</i>	Myrtaceae	M	307	636	677	309.6
<i>Eugenia oerstediana</i>	Myrtaceae	M			> 884	316.4
<i>Faramea occidentalis</i>	Rubiaceae	T	418	754	> 965	389.1
<i>Ficus insipida</i> *	Moraceae	T			151	
<i>Garcinia intermedia</i>	Clusiaceae	M			> 1220	275.8
<i>Garcinia madruno</i>	Clusiaceae	M			1714	
<i>Genipa americana</i> *	Rubiaceae	M	197	532	612	236.8
<i>Guapira standleyana</i> *	Nyctaginaceae	T	217			239.7
<i>Guarea Guidonia</i>	Meliaceae	M	405	> 747	503.5	210.3
<i>Gustavia superba</i>	Lecythydaceae	M	643	> 1120	1105	281.8
<i>Heisteria acuminata</i> *	Olacaceae	U				249.0
<i>Heisteria concinna</i> *	Olacaceae	M			> 1750	
<i>Herrania purpurea</i>	Malvaceae	S	141	504	567	181.6
<i>Hippocratea volubilis</i>	Celastraceae	L	223	635	> 678	138.5
<i>Hirtella triandra</i>	Chrysobalanaceae	M				195.2
<i>Hybanthus prunifolius</i> *	Violaceae	S	224	350	393	103.0
<i>Hyeronima alchorneoides</i> *	Euphorbiaceae	T			> 248	
<i>Hylenaea praecelsa</i>	Celastraceae	L			> 369	254.7
<i>Inga marginata</i>	Fabaceae	T				243.0
<i>Inga ruiziana</i>	Fabaceae	T			490	
<i>Jacaranda copaia</i> *	Bignoniaceae	T	224			
<i>Lacistema aggregatum</i> *	Salicaceae	U	391	584	797	146.9
<i>Lacmellea panamensis</i>	Apocynaceae	M			> 425	168.2
<i>Lafoensia punicifolia</i> *	Lythraceae	T	222			
<i>Licania platypus</i>	Chrysobalanaceae	T	469			250.2
<i>Lonchocarpus heptaphyllus</i>	Fabaceae	T	232	> 459	541	201.1
<i>Luehea seemannii</i> *	Malvaceae	T	139			
<i>Macfadyena unguis-cati</i>	Bignoniaceae	L			683	165.9
<i>Machaerium arboreum</i>	Fabaceae	L	329	469	518	211.8
<i>Maquira guianensis</i>	Moraceae	T	475	811	874	140.2
<i>Maripa panamensis</i>	Convolvulaceae	L	401		> 385	325.2
<i>Mouriri myrtilloides</i>	Melastomataceae	T			1080	460.4
<i>Myrcia gatunensis</i> *	Myrtaceae	U			1087	523.8
<i>Odontadenia macrantha</i>	Apocynaceae	L			847	163.0
<i>Oenocarpus mapora</i>	Araliaceae	M	672	> 1250	> 1150	227.9

Continued

TABLE 1. Continued

Species	Family	Growth form	Median leaf life span (d)			Lamina toughness (J m ⁻²)
			Gap CGs	Shade CGs	Shade house	
<i>Ormosia macrocalyx</i>	Fabaceae	T			>1608	418.2
<i>Pachira sessilis</i> *	Malvaceae	T	336	553	>1058	126.4
<i>Pentagonia macrophylla</i> *	Rubiaceae	U	252	483		79.6
<i>Pithecoctenium crucigerum</i>	Bignoniaceae	L	112		276	156.2
<i>Platymiscium pinnatum</i>	Fabaceae	T	330	468	1078	189.4
<i>Platyopodium elegans</i>	Fabaceae	T	154	335	814	283.7
<i>Posoqueria latifolia</i> *	Rubiaceae	S	523	1104	>1320	235.8
<i>Pouteria reticulata</i>	Sapotaceae	T	447		777	176.6
<i>Prionostemma aspera</i>	Celastraceae	L	>690		>1793	175.6
<i>Prioria copaifera</i>	Fabaceae	T			>1403	333.4
<i>Protium panamense</i>	Burseraceae	M			832	214.7
<i>Protium tenuifolium</i> *	Burseraceae	M			643	348.1
<i>Psychotria acuminata</i> *	Rubiaceae	S			>384	182.8
<i>Psychotria deflexa</i> *	Rubiaceae	U			>229	
<i>Psychotria grandis</i> *	Rubiaceae	U			725	298.2
<i>Psychotria hoffmannseggiana</i> *	Rubiaceae	U	300	386		194.3
<i>Psychotria horizontalis</i> *	Rubiaceae	S	301	489	307	166.5
<i>Psychotria marginata</i> *	Rubiaceae	S	364		684	236.8
<i>Psychotria micrantha</i> *	Rubiaceae	S			373	204.7
<i>Quararibea asterolepis</i>	Malvaceae	T			818	174.2
<i>Randia armata</i> *	Rubiaceae	U	531	957	703	223.3
<i>Rinorea sylvatica</i>	Violaceae	S	>386		>422	193.8
<i>Serjania mexicana</i>	Sapindaceae	L	345		370	179.7
<i>Simarouba amara</i>	Simaroubaceae	T	272		637	138.0
<i>Socratea exorrhiza</i>	Araliaceae	T			1106	
<i>Sorocea affinis</i>	Moraceae	S			1177	332.4
<i>Spondias mombin</i>	Anacardiaceae	T	112		213	104.0
<i>Sterculia apetala</i>	Malvaceae	T	251	>371	362	91.2
<i>Swartzia simplex</i> .var.gr	Fabaceae	U	>294	560	1224	291.4
<i>Tabebuia guayacan</i> *	Bignoniaceae	T	196		>336	234.7
<i>Tabebuia rosea</i> *	Bignoniaceae	T	168	319	278	127.2
<i>Tabernaemontana arborea</i> *	Apocynaceae	T	252	441	640	120.9
<i>Tachigali versicolor</i>	Fabaceae	T				215.8
<i>Terminalia amazonia</i> *	Combretaceae	T	205			158.6
<i>Tetragastris panamensis</i>	Burseraceae	T	672	1044	>380	396.1
<i>Thinouia myriantha</i>	Sapindaceae	L	345			222.3
<i>Tocoyena pittieri</i> *	Rubiaceae	M	252	593	639	202.4
<i>Trichilia tuberculata</i>	Meliaceae	T	643	>1260	>1128	192.7
<i>Triplaris cumingiana</i> *	Polygonaceae	M	195		506	207.9
<i>Virola sebifera</i>	Myristicaceae	M			>298	141.9
<i>Virola surinamensis</i>	Myristicaceae	T	504	1091	645	304.8
<i>Vochysia ferruginea</i> *	Vochysiaceae	T	280	728		

See Supplementary Data Tables S1 and S2 for additional species-level data including sample sizes. For species for which median leaf life span exceeded the maximum possible observation time (T_{\max}), median leaf life span is indicated as $>T_{\max}$. T_{\max} varied among species because planting dates varied. Missing cells indicate no data available due to low sample size (total number of marked leaves <20), low seed availability or high mortality.

* Species which have photosynthetic cotyledons.

week of transplanting apparently from transplant shock. The exact number of days since transplanting varied among species, because species varied in developmental rates and time from transplanting to the first leaf full expansion. Mortality rates were calculated as $100 \times [\ln(\text{total number of transplanted seedlings in each environment}) - \ln(\text{total number of survivors at the 3-month harvest})]/(\text{number of days since transplanting})$. Mortality rates were available for 72 species, 60 of which overlap with the 1-year mortality of naturally recruited seedlings (Supplementary Data Fig. S1).

Shade-house experiment

Three shade houses were covered with standard window screening and surrounded by 15- to 30-cm-wide water-filled

moats to exclude insect herbivores. In the first shade house, shade was created with a combination of shade film (Scotch tint Dark Panther; 3M, St Paul, MN, USA) and multiple layers of shade cloth (80% grade; Pak Unlimited, Perkins Ave, Willacoochee, GA, USA) to achieve 0.8% of above-canopy PAR and a red:far-red ratio of 0.5 which simulates the light environment in the forest understory. In the other two shade houses, due to the high cost of shade film, only neutral shade cloth was used to achieve 0.8% PAR. All seeds germinated in the first shade house where seedlings stayed until they were sequentially moved to the second and third shade houses at 3 months and 1 year, respectively, after full expansion of the first leaf or photosynthetic cotyledons depending on the species. Table 1 identifies which species have photosynthetic cotyledons (cf. Garwood, 2009). Seedlings

TABLE 2. Pairwise Pearson correlation coefficients (r) for seedling traits and mortality rates of common woody species on Barro Colorado Island (BCI), Panama, with sample size (n , number of species included in each pair-wise correlation)

	LL-gap*		LL-shade*		Tuf-lamina*		Tuf-vein*		LeafD		StemD*		MRT_3mo_gap*		MRT_3mo_shade*		MRT_1yr*		
	n	r	n	r	n	r	n	r	n	r	n	r	n	r	n	r	n	r	
LL-shade*	45	0.811																	
Tuf-lamina*	54	0.472	57	0.623															
Tuf-vein*	58	0.536	58	0.655	87	0.742													
LeafD	49	0.421	48	0.441	71	0.350	72	0.504											
StemD*	61	0.578	61	0.602	84	0.582	89	0.558	73	0.382									
MRT_3mo_gap*	64	-0.062	52	-0.030	66	-0.069	71	0.106	59	0.120	75	-0.079							
MRT_3mo_shade*	58	-0.533	48	-0.408	62	-0.231	66	-0.154	55	-0.172	70	-0.432	72	0.244					
MRT_1yr*	48	-0.610	44	-0.533	64	-0.387	68	-0.394	54	-0.328	71	-0.594	61	0.235	56	0.462			
MRT_saplings*	42	-0.427	42	-0.434	59	-0.281	60	-0.369	46	-0.185	65	-0.445	51	0.085	47	0.363	54	0.232	

Leaf traits include median leaf life span (LL) in gap and shade common gardens, fracture toughness (Tuf)* of lamina and vein, leaf density (dry mass per volume) of 3-month-old seedlings (LeafD), stem density of first-leaf stage seedlings (StemD), and mortality rates for the first three months following germination (MRT_3mo)* in gap and shade common gardens, and first-year mortality rates (MRT_1yr)* determined from 18 annual censuses of naturally recruited seedlings in 800, 1-m² plots in the mostly shaded forest. MRT_saplings is derived from Condit *et al.* (2006). Bold italic, $P < 0.001$; bold, $0.001 < P < 0.01$; italics, $0.01 < P < 0.05$.

* \log_{10} -transformed to improve normality of the data distribution.

were rotated weekly within each shade house. This scheme simulated understory light quality for initial seedling development, which is particularly sensitive to light quality (Kitajima, 1994; Lee *et al.*, 1996), and standardized environmental conditions experienced at each ontogenetic stage across species.

Seeds were kept moist in plastic trays filled with a 2 : 1 mix of washed sand and vermiculite and checked every 3–7 d for germination. Thirty to fifty seedlings of each species were transplanted individually to plastic pots immediately after emergence of the radicle and the hypocotyl or epicotyl. Seedlings were randomly pre-assigned to four groups. The four groups were harvested at full expansion of the first photosynthetic leaf or cotyledon (first-leaf stage), 3 months (3-month stage) and 1 year later (1-year stage) or monitored for leaf demography until the end of the study (up to 4 years). Pot size varied among species. Species with seed length < 3 mm were transplanted to 1-L pots, while those with larger seeds were transplanted to larger pots up to 3 L. Pots were filled with a 1 : 2 mix of washed sand and topsoil collected from the nearby forest edge, and watered twice per week. For every transplanted seedling, one of the first photosynthetic cotyledons or leaves was marked while partially expanded and measured for length weekly. Length was measured from blade base to tip for simple leaves or from the base of the most basal leaflet to the tip of the terminal leaflet for compound leaves. When two sequential measurements differed by < 1 mm, the marked leaf (or cotyledon) was considered to be fully expanded, and, if the plant was pre-assigned to the first-leaf stage harvest, it was harvested within 1–5 d. Thus, we knew the time of first leaf (or cotyledon) full expansion for every seedling. This method standardized the ontogenetic developmental stage despite wide variation in germination and initial developmental rates among individuals and species. Seeds of 130 species were collected and planted in this experiment as they became available between 2001 and 2005. Due to limited seed availability, germination or early survival in 33 species, we were only able to harvest six or more seedlings of 97 species.

Determination of leaf life span and herbivory frequency

Leaf demography was monitored for three or more seedlings in each of the six common gardens and for 10–12 seedlings in the shade house for each species. At each monthly census, we marked newly expanded leaves sequentially with a non-toxic permanent marker, and recorded presence/absence of previously marked leaves. Both censuses continued through July 2006. The age of leaf death was analysed using the Kaplan–Meier method, which accounts for right censored leaves that were removed from the census due to harvest or death of the plant (see Supplementary Data Table S1 for sample sizes and quartile statistics). Median leaf life span could not be determined in some species because it exceeded the duration of the study, or because plant survival was too low to obtain sufficient samples. At the time of weekly censuses of seedling survival, any symptoms of disease or extensive herbivory (approx. > 30 % of leaf area missing) were noted. For each species and light environment, the proportion of all marked leaves that exhibit conspicuous herbivory was calculated as an index of herbivory frequency. When a seedling lost all

leaves and the main stem became necrotic, it was considered to be dead and the date of death was recorded. Leaves that died within 2 months of plant death from disease were considered to be right censored in the statistical analysis.

Median leaf life span did not differ significantly between the shade common gardens and the shade houses with a comparable light availability (0.8 % of total daily PAR) (two-sided $P = 0.07$ with paired t -test for 21 species for which median leaf life span could be determined in both shade environments). Thus, leaf life span data from both shade environments were merged to estimate median leaf life span in shade for each species. We also assessed whether leaf life span differs among leaf cohorts produced during the first and second year for 18 species in the shade-house experiment (for other species, median leaf life span was too long relative to the study duration to do this assessment). There was no consistent ontogenetic change of leaf life span for leaves produced during the first two years; ten species showed no significant difference, six species had longer leaf life span for those born in the first year, while two species had the opposite.

Determination of leaf density, fracture toughness and stem density

Shade-house grown seedlings were harvested at three ontogenetic stages (first-leaf, 3 months and 1 year) and also at 2–4 years if sufficient numbers of seedlings were available without compromising determination of median leaf life span. All remaining seedlings were harvested at the end of the study in September 2006. The whole pot was submerged in a bucket of water to loosen the soil and to collect and rinse all roots carefully. Seedlings were kept individually in plastic bags in a cooler lined with ice until measurements with fresh seedlings were completed within 36 h after harvest (mostly within 6 h).

Fracture toughness of lamina and vein was measured for one or two of the most recent fully expanded leaves with the cutting method developed by Lucas and Pereira (1990), using a pair of scissors mounted on a portable universal tester (Darvell *et al.*, 1996). A small strip approx. 8–10 mm wide and 20 mm long was excised (including the mid-vein along a long edge) and subjected to the cutting test to measure fracture toughness of lamina and vein separately (Lucas *et al.*, 2001). Fracture toughness (J m^{-2}) was calculated as the work per unit cross-sectional area of vein and lamina, which were estimated from vein diameter and length of the cut times lamina thickness, respectively. Lamina thickness was measured with an analogue thickness gauge (Teclock SM112; Nagano, Japan). A minimum of three seedlings per species per ontogenetic stage was measured with the cutting test, but when there was wide variation among the first three measurements, leaves from an additional two to four seedlings were also measured. At the first-leaf stage as defined in this study, some species had only photosynthetic cotyledons but not leaves. Although cotyledon toughness was also measured, the current analysis includes only measurements with true leaves. The excised sections were reunited with the remainder of the leaf and included in subsequent measurements of leaf area and mass.

Seedlings were separated to cotyledons (if present), leaves, petioles, stems and roots. On fresh material, we measured

the area and fresh mass of photosynthetic cotyledons and leaves, stem length (from the stem base to the apical meristem), and stem diameter at the midpoint of the stem. We then dried everything at 60 °C in paper envelopes for a minimum of 1 week and determined dry masses. Leaf density (dry mass per unit volume) was estimated from the total leaf mass divided by leaf area and lamina thickness. Because major veins were not separated, our measure of leaf density was higher than the density of lamina *per se*. However, previous studies have confirmed that this measure of bulk leaf density correlates strongly and linearly ($r^2 = 0.99$) with lamina-specific leaf density determined for leaf discs free of major veins (Kitajima and Poorter, 2010; K. Kitajima and S. J. Wright, unpubl. res.). Stem volume was estimated by assuming that the stem was a linear rod (with the midpoint diameter and the measured stem length), ignoring the slight tapering from the base to the tip. Stem density (g cm^{-3}) was estimated as stem dry mass divided by stem volume. Seedling growth was slow in the shade houses, and none of the seedlings branched during the study.

Statistical analyses

We conducted pair-wise correlation analyses and paired t -tests for evaluation of differences in species mean trait values among ontogenetic stages and environments with JMP v. 9.0 (SAS Institute, Cary, NC, USA). For trait–trait relationships, we also evaluated differences in slopes and intercepts for free-standing species versus lianas using standard major-axis regression analysis with the SMATR software (Warton *et al.*, 2006). Fracture toughness was used consistently as the measure of leaf toughness for correlation analysis with demographic traits. The results of analyses with leaf toughness normalized by two other schemes (i.e. work-to-shear, density-corrected toughness) are reported in Supplementary Data Table S3. Previous species-level and phylogenetically independent contrast (PIC) correlations found largely convergent patterns for leaf functional traits (Westbrook *et al.*, 2011; Kitajima *et al.*, 2012). Thus, we examined PIC correlations for only trait pairs of *a priori* interests to confirm that the patterns were robust from an evolutionary perspective (Supplementary Data Table S4). All values were log-transformed to achieve normality prior to analysis, except for comparison of stem and leaf density values among ontogenetic stages.

RESULTS

Leaf life span, herbivory frequency, toughness and density

Median leaf life span of the woody species in the study varied over a 15-fold range from 112 d for *Spondias mombin* in gaps to >1793 d for *Aspidosperma spruceanum* in shade (Table 1). Some species such as *A. spruceanum*, *Heisteria concinna*, *Ormosia macrocalyx* and *Prionostema aspera* exhibited an extremely long leaf life span in the shade houses, with the median exceeding the study duration (>1600 d). Median leaf life span was strongly and linearly correlated between gaps and shade ($r = 0.811$; Table 2 and Fig. 1A), and shade medians were 46 % longer relative to the gap medians on

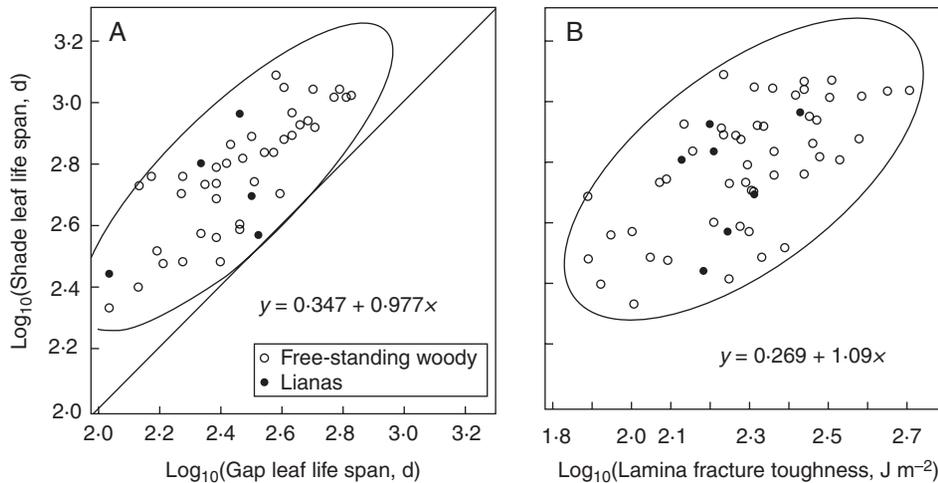


FIG. 1. Scatter plots for (A) \log_{10} (median leaf life span in days) in gaps and shade, and (B) \log_{10} (median leaf life span in shade) and \log_{10} (lamina fracture toughness, J m^{-2}). Points represent species means. The ovals represent 95% confidence ellipses. In (A) points above the diagonal indicate a greater leaf life span in shade than in gaps (paired t -test, $P < 0.001$). Free-standing woody species and lianas are as indicated in the key. Standard major axis regressions indicate that the slope was not significantly different from 1.0. See Table 2 for sample size and correlation coefficients.

average across 45 species. Leaf life span, leaf life span–trait relationships, and trait–trait relationships never differed significantly between lianas and free-standing species in standard major axis regression analyses ($P > 0.05$). Lianas and free-standing species were therefore pooled for subsequent analyses.

Median leaf life span of gap-grown seedlings was positively correlated with leaf life span of gap-grown saplings determined by Coley (1983) for 14 species that overlap between the two studies ($r = 0.92$, $P < 0.001$). The proportion of marked leaves of each species that exhibited conspicuous herbivory (= herbivory frequency; Supplementary Data Table S1) was higher in gaps than in shade common gardens (paired t -test, $n = 69$ species, $P < 0.001$), with positive correlation between the two environments ($n = 69$ species, $r = 0.33$, $P = 0.006$). But neither was correlated with median leaf life span ($r < 0.19$, $P > 0.1$) or herbivory rates (% leaf area lost per day) of young or mature leaves determined by Coley (1983) ($n = 20$ species, $P > 0.2$).

Mean fracture toughness was correlated across ontogenetic stages for lamina (Supplementary Data Fig. S2) and vein (data not shown), with marginal increases from early to later ontogenetic stages (paired t -tests for lamina fracture toughness, $P > 0.05$ for change between two sequential stages, $P = 0.02$ for first-leaf stage to 1 year later). Therefore, fracture toughness was averaged across ontogenetic stages for further analysis. Mean lamina fracture toughness of shade-house-grown plants differed among species from 79.7 to 523.8 J m^{-2} (Table 1; the mean for 87 species = 221.2 J m^{-2}), and vein fracture toughness was much higher in all species (ranging from 318 to 6410 J m^{-2} ; the mean for 92 species = 1759 J m^{-2} ; Table S1).

Leaf density and stem density were significantly correlated across ontogenetic stages (Fig. 2, Table 2 and Supplementary Data Fig. S3). However, both leaf and stem density values exhibited significant increases with ontogeny (paired t -test, $P < 0.001$; model II regression slope > 1 or intercept > 0 , $P < 0.05$; Supplementary Data Table S2 lists species means at

all ontogenetic stages). The only exception was that stem density did not change significantly from first-leaf stage to 3 months later. Given these ontogenetic patterns, we used leaf density determined at the 3-month stage and stem density determined at the first-leaf stage for subsequent analyses to maximize the number of species included in the analysis.

Functional trait correlations with leaf life span and seedling survival

Lamina fracture toughness and vein fracture toughness were correlated with each other, and both were correlated with median leaf life span determined in gaps and shade (Fig. 1B and Table 2; $P < 0.001$). The log–log relationship between leaf life span and lamina toughness exhibits a model II regression slope of 1.09 (95% CI = 0.89–1.35). Median leaf life span in gaps and shade was also positively correlated with lamina density and stem density (Table 2). Due to these correlations and a weak positive correlation between lamina thickness and leaf life span ($r = 0.35$, $P = 0.014$), LMA (= lamina density \times lamina thickness) and work-to-shear (= fracture toughness \times lamina thickness) were also positively correlated with median leaf life span (Supplementary Data Table S3). The PIC correlations for these trait relationships were significant with correlation coefficients similar to the non-phylogenetic, species-level correlations (Supplementary Data Table S4).

Mortality rates of young seedlings in shade (MRT_3mo_shade) were positively correlated with mortality rates of older first-year seedlings (MRT_1yr) (Table 2 and Fig. 3A; $P < 0.001$), and only weakly so with mortality rates of saplings (MRT_saplings) (Table 2 and Fig. 3B; $P = 0.012$). All three mortality rates were negatively correlated with shade leaf life span (Fig. 4A, C), gap leaf life span (Table 2) and stem density of shade-grown seedlings (Fig. 4B, D). Seedling leaf density and lamina fracture toughness showed the expected negative correlation only with MRT_1yr and not with MRT_3mo_shade (Table 2). In contrast to mortality in shaded understorey, early seedling mortality in gaps

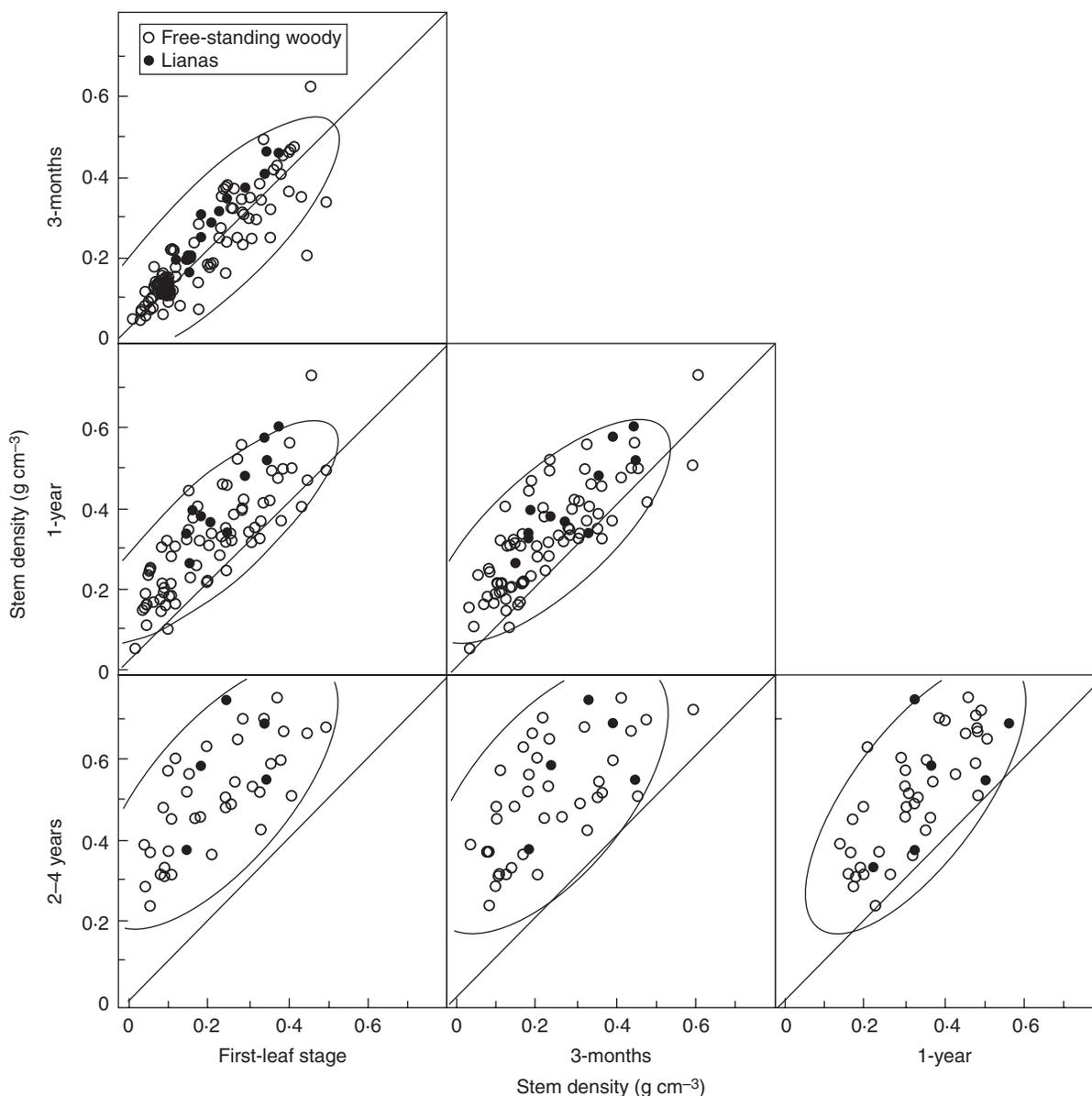


FIG. 2. Scatter plots for stem density (g cm^{-3}) between ontogenetic stages of seedlings (first-leaf stage, 3-months later, 1-year later, and 2- to 3-year-old seedlings). Points represent species means. Free-standing woody species and lianas are as indicated in the key. The ovals represent 95 % confidence ellipses. Points above the diagonal indicate greater stem density at the later ontogenetic stage in each panel (paired t -test, $P < 0.001$ in all pair-wise comparisons). Standard major axis regressions indicate that the slope was not significantly different from 1.0, but the intercept was significantly greater than zero, except for first-leaf versus 3-months and 1-year versus 2–4 years.

(MRT_3mo_gap) was uncorrelated with any traits of shade-grown seedlings examined in the study (Table 2). But, MRT_3mo_gap was negatively correlated with herbivory frequency ($n = 73$ species, $r = -0.30$, $P = 0.01$), indicating that species whose leaves were damaged by herbivores more frequently tended to survive better in gaps.

DISCUSSION

The seminal work of Coley (1983) comparing gap-grown saplings firmly established the relevance of the spectrum of seedling leaf life span for herbivory resistance and shade tolerance of tropical trees, whereas our study was the first to compare

leaf life span for gap-grown and shade-grown seedlings and to shade-leaf traits across similarly large numbers of species. Leaf life span, which varied >15 -fold across species, was correlated positively with leaf and vein fracture toughness, leaf density and stem density, and negatively with seedling mortality (Figs 1 and 4 and Table 2). This key result from comparisons with careful standardization of ontogenetic stages and light environments is largely concordant with the results from other studies that compared traits of naturally recruited saplings (Coley, 1983; Kitajima and Poorter, 2010), as well as older seedlings in the gap common gardens (Kitajima *et al.*, 2012). The current study went beyond these earlier studies by directly assessing relationships between leaf

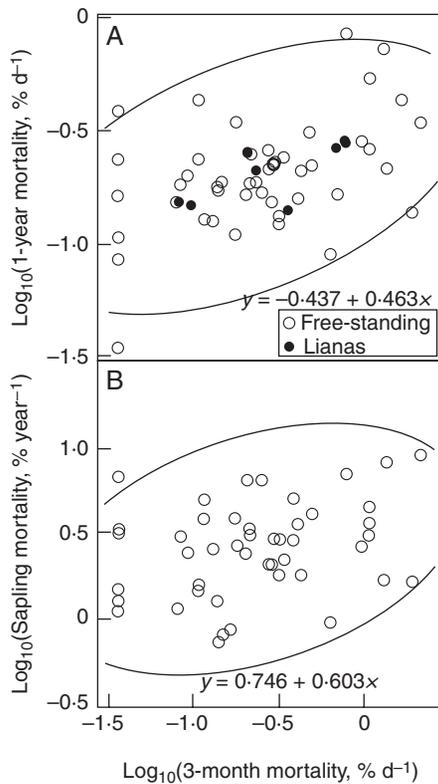


FIG. 3. Relationships of the mortality rate at early seedling stage (0–3 months) in the shade common gardens with (A) mortality rate of new recruits in the field for 1 year ($n = 56$ spp., $r^2 = 0.213$, $P < 0.001$) and with (B) mortality rate of 1- to 10-cm-diameter saplings ($n = 47$ spp., $r^2 = 0.132$, $P = 0.012$). Points represent free-standing species or lianas, as indicated in the key. The ovals represent 95% confidence ellipses. The standard major axis regression slopes were significantly >0.0 and <1.0 , meaning mortality reduction with ontogeny was greater for species with high early mortality.

functional traits of shade-grown seedlings and seedling survival in the shaded forest understorey.

Leaf life spans in gaps, shaded understorey and shade houses

All species exhibited shorter leaf life span in gaps than in shade, as predicted by the optimization theory of leaf carbon economy and earlier reports (Williams *et al.*, 1989; King, 1994). Although there were substantial variations among species, there appears to be a generalizable pattern of leaf life span plasticity (Fig. 1A). Vincent (2006) reports that seedling leaf life span plasticity (% change relative to the mean across the environments) ranged from 29 to 84% among four Brazilian trees grown under 12–100% full sun. In our study, leaf life span plasticity averaged 31% across 45 species (ranging 3.5–58.1%) for seedlings grown under 0.8–51% full sun. Because we could not determine median leaf life span in shade for species with long-lived leaves (e.g. median >1600 d), the actual range of leaf life span plasticity may be even greater.

Due to greater exposure of seedlings to biotic and abiotic stress factors in the field, we expected that leaf life span might be shorter in the shade common gardens than in the shade houses. But, the difference was marginal ($P < 0.05$

only with one-sided t -test). In the deep shade employed in the current study (0.8% PAR), leaf turnover was extremely slow, and median leaf life spans of some species exceeded the maximum duration of the experiments (>4.9 years; Table 1). Longer-term monitoring and larger sample size would be necessary for more rigorous quantification of leaf life span for shade-tolerant seedlings of many species. Kursar and Coley (1993) report leaf life span of shade-tolerant saplings to vary from 1 to 5 years among eight species on BCI, and a particular marked leaf on a shaded sapling of *A. spruceanum* survived for 12 years (P. D. Coley, University of Utah, pers. comm.). From leaf production rates, leaf loss rates, and an assumption of steady state-leaf turn-over, King (1994) estimates that leaf life spans of shaded saplings vary from 11 to 45 months for ten species on BCI, whereas Lusk *et al.* (2008a) estimate that sapling leaf life spans vary from 0.8 to 5.3 years for 13 species of Chilean rainforest trees. The steady-state assumption, however, is not valid for smaller shade-tolerant seedlings that accumulate leaves over the first several years of life (Lusk *et al.*, 2011; K. Kitajima, unpubl. res.), and it is necessary to monitor marked leaves over a sufficiently long time.

Leaf traits and herbivory levels in gaps versus shade

In this study, lamina density and fracture toughness are determined for leaves grown in deep shade, whereas in an earlier study, these traits were examined for 3- to 4-year-old seedlings grown in gap common gardens (Kitajima *et al.*, 2012). Because there were no effects of leaf age on these traits, we can use these two studies to compare these traits for gap and shade leaves. Some, but not all measured leaf traits exhibit plastic response to gap versus shade. The results show that leaves of gap-grown plants are denser ($P < 0.001$) and slightly tougher ($P = 0.01$) than shade leaves of the same species (two-sided paired t -test for 21 species). Leaves of gap-grown plants also have greater cellulose and lignin concentration than those of shade-grown plants and, thus, gap leaves are physically more robust than shade leaves, yet herbivory frequency was significantly higher in gaps, most likely because there is greater herbivore abundance in gaps than in shade (Aide and Zimmerman, 1990; Chacon and Armesto, 2006; Richards and Windsor, 2007; Salgado-Luarte and Gianoli, 2010). However, the greater herbivore pressure was unlikely a proximate reason for the shorter leaf life span in gaps. We did not observe any significant difference in leaf life span for leaves with and without conspicuous herbivory (K. Kitajima, unpubl. res.). It was more likely that high production rates of new leaves caused more rapid replacement of self-shading and greater demand for nitrogen retranslocation from older leaves to younger leaves in gaps than in shade (Hikosaka *et al.*, 1994; Ackerly and Bazzaz, 1995).

For 14–20 species, we can also compare our data with those of Coley (1983), who quantified herbivory rates (% leaf area loss per day), leaf life span, and putative defence traits for saplings of 46 species growing in gaps on BCI. The results of this cross-study comparison show that lamina fracture toughness of shade-house-grown seedlings are correlated positively with punch strength ($n = 20$ species, $r = 0.56$, $P = 0.01$) and

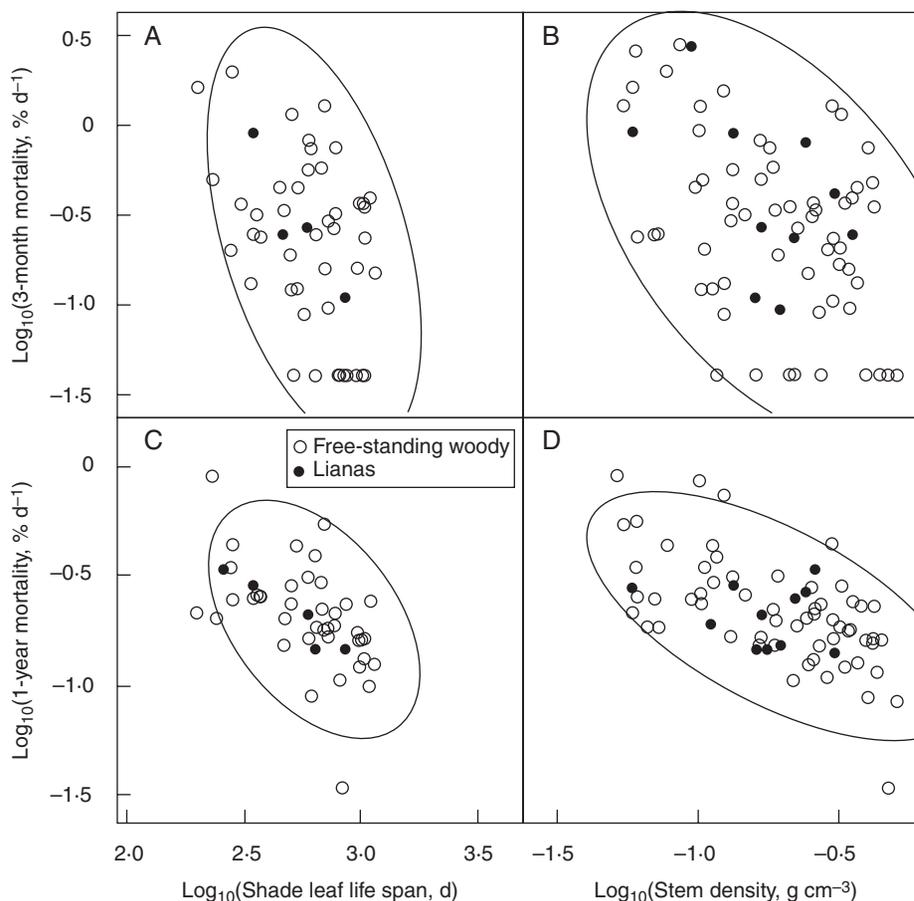


FIG. 4. Scatter plots of seedling mortality rates, (A, B) 0–3 months mortality % per day in shade common gardens and (C, D) mortality % per day of naturally recruited species in 800 1-m² plots till 1 year later, each plotted against (A, C) \log_{10} (median leaf life span of shade-grown plants) and (B, D) \log_{10} (stem density, g cm^{-3}) at the first-leaf stage. Points represent free-standing species or lianas, as indicated in the key, and ovals represent 95 % confidence ellipses. See Table 2 for correlation statistics and Supplementary Data Table S4 for PIC correlations.

negatively with herbivory rates of mature leaves ($n = 20$ species, $r = -0.48$, $P = 0.03$). The same conclusion was reached by Dominy *et al.* (2008) who also compared fracture toughness measured with a cutting test with Coley's data for a different subset consisting of 19 species.

It should be noted that herbivory frequency (proportion of leaves with conspicuous herbivory) was unrelated to herbivory rates (% area loss per day), perhaps because herbivory frequency reflects cumulative herbivory of young leaves during leaf expansion and mature leaves over time. Because species difference in herbivory on soft and expanding leaves is not correlated with many putative defence traits of either young or mature leaves (Coley, 1983), it may not be surprising that herbivory frequency observed in our study showed no correlation with leaf toughness, density and life span of mature leaves. Interestingly, herbivory frequency was lower for species that showed higher 3-month mortality in gaps across 72 species in the current study ($P = 0.01$), but the opposite was the case in a more careful assessment of 24 species (Kitajima *et al.*, 2012). Thus, linkage between leaf herbivory frequency and seedling survival in gaps is ambiguous, perhaps because tolerance strategy with rapid growth rates is a viable alternative to resistance strategy for survival in gaps (Strauss and

Agrawal, 1999; Norghauer *et al.*, 2008). In terms of linkage between herbivory and shade survival, Coley's data of herbivory rates of mature (but not young) leaves were positively correlated with 3-month mortality ($n = 19$ species, $r = 0.50$, $P = 0.03$) and 1-year mortality rate of naturally recruited seedlings ($n = 24$ species, $r = 0.51$, $P = 0.01$). This result is in line with the perspective that lack of herbivory resistance (of mature leaves) constrains light-demanding species from establishing and growing in shade (e.g. Coley, 1983; Salgado-Luarte and Gianoli, 2010), and thus traits conferring herbivory resistance and long leaf life span are central to the functional trait syndrome associated with shade tolerance.

Leaf fracture toughness, density and leaf life span

Fracture toughness values of leaf laminas and veins were positively correlated with leaf life span of shade-grown seedlings and gap-grown seedlings (Table 2), similarly to the pattern reported for 24 species in gap common gardens (Kitajima *et al.*, 2012). Interspecific variation in leaf density reflects variation in the cell wall volume fraction and relative abundance of veins, because veins consist of tissues with thick secondary cell walls and high density (Poorter *et al.*,

2009). In general, vein fracture toughness is much higher than lamina fracture toughness, although the two are highly correlated because fine veins are embedded in lamina (Choong, 1996; Dominy *et al.*, 2003; Westbrook *et al.*, 2011). Perhaps, because abundance and toughness of vascular tissues and bundle sheath extension are the major determinant of leaf toughness (Choong *et al.*, 1992), leaf toughness and life span were more strongly correlated with density of stems (which are rich in vascular tissues) than leaves (Table 2). In other words, density of strong materials (e.g. cellulose abundant in vascular tissues) rather than weak materials (e.g. proteins and carbohydrates) enhances the overall mechanical properties of the leaf as a composite structure (Kitajima *et al.*, 2012).

To approximate fracture resistance per unit gram dry mass, ‘density-corrected toughness’ can be calculated by dividing lamina fracture toughness by lamina density (Lusk *et al.*, 2010; Onoda *et al.*, 2011; Kitajima *et al.*, 2012). Because leaf fracture toughness changes little while leaf density decreases significantly from sun to shade, density-corrected toughness increases from sun to shade. This observation has led to the idea that increased density-corrected toughness in shade is adaptive (‘shade leaf punch above their weight’, Lusk *et al.*, 2010). However, adaptive significance of this trait is ambiguous; interspecific variation in density-corrected toughness was not correlated with leaf life span and seedling mortality in shade (Supplementary Data Table S3).

Unlike traits associated with fracture toughness, concentrations of other putative carbon-based defences (lignin, phenolics and tannins per unit mass) may not exhibit significant correlations with herbivory, leaf life span or seedling survival across a broad range of tropical tree species (Coley, 1983; Kitajima *et al.*, 2012). On the other hand, herbivory rates and toughness are not always correlated in other studies that compared seedling herbivory of two to five species (e.g. Blundell and Peart, 1998; Eichhorn *et al.*, 2007), perhaps because toughness sets an upper limit of herbivory, while chemical and other defence traits may constrain herbivory rates of soft leaves (Grubb *et al.*, 2008). We found positive effects of lamina thickness on leaf life span and seedling survival, but they were much weaker than the effects of leaf density and fracture toughness (Table S3), and earlier studies of neotropical tree species report that lamina thickness varies independently of leaf life span and juvenile survival (Alvarez-Clare and Kitajima, 2007; Kitajima and Poorter, 2010; Westbrook *et al.*, 2011).

Ontogeny of leaf and stem density in seedlings

As expected, leaf and stem density increased with seedling ontogeny, from rapidly developing young seedlings to older seedlings (Figs 2 and Supplementary Data Fig. S3). But, lamina and vein fracture toughness showed much weaker changes with ontogeny (Supplementary Data Fig. S2). Lamina fracture toughness also showed only slight changes with light environments despite large decreases of lamina density from sun to shade. This suggests that trait consistency, i.e. maintenance of species-specific leaf toughness despite changes in leaf density (Supplementary Data Fig. S3), may be ecologically and evolutionarily important for a cohesive life-history strategy.

The increase of stem density was surprisingly small during the early interval from the first-leaf stage to the 3-month stage, during which we expected rapid stiffening of stems. In contrast, changes from the 3-month stage to the 1-year stage, and subsequent changes were much more conspicuous (Fig. 2). Alvarez-Clare and Kitajima (2009) reports that risks of seedling damage by vertebrate herbivores decrease dramatically between 0–2 months and 2–12 months for eight tree species on BCI. Perhaps, xylem development and lignification of stems are slow and continuous over multiple years of growth and development of shade-tolerant woody seedlings. How do seedling stem density values compare with adult wood density of the same species on BCI (Wright *et al.*, 2010)? Using the density values derived from wood cores and seedling stems dried at 60 °C, we find that adult wood density is higher than seedling stem density across all four stages, while it exhibits significant correlation with seedling stem density (adult vs. first-leaf stage: $n = 101$ spp., $r = 0.44$, $P < 0.001$; adults vs. 3-month stage: $n = 95$ spp., $r = 0.35$, $P = 0.004$; adult vs. 1-year stage: $n = 80$ spp., $r = 0.33$, $P = 0.003$; adult vs. 2–4 year old seedlings: $n = 45$ spp., $r = 0.49$, $P = 0.006$). Not surprisingly, seedling survival correlates better with seedling stem density than with adult wood density. The 1-year mortality rates of natural recruits were more strongly correlated with seedling stem density ($r = -0.60$ for 71 species) than with adult wood density ($r = -0.36$ for 68 species). Thus, the positive correlations of adult wood density with juvenile survival reported widely in the literature (e.g. Augspurger, 1984; Muller-Landau *et al.*, 2004; Chave *et al.*, 2009; Wright *et al.*, 2010) reflect a trait concordance between adult wood density and seedling stem density. In contrast, correlation of adult wood density is weak with adult mortality ($r = -0.081$) (Wright *et al.*, 2010), possibly because factors other than wood density (e.g. diameter, allometry) also matter for mechanical stability (Larjavaara and Muller-Landau, 2010), or because variation in adult wood density might reflect regeneration niches of juveniles and overall life history of the species (Poorter, 2007).

We also examined whether seedlings of lianas might differ from seedlings of free-standing woody species in traits and trait correlations. Climbing stems have different anatomical and mechanical characteristics from self-supporting stems (e.g. low rigidity, wide vessels) (Gartner, 1991; Putz and Holbrook, 1991). But we did not find any difference between seedlings of lianas and free-standing species for leaf life span, toughness, leaf density, stem density or bivariate correlation between them. Perhaps, this is not surprising because juvenile lianas in shade may develop as free-standing plants for a prolonged time (Caballe, 1998), and during this juvenile phase, their stems exhibit little difference from free-standing woody plants (Rowe and Speck, 2005). Indeed, no shaded liana seedlings exhibited a sign of assuming the climbing habit over the duration of our study. Thus, the leaf life span spectrum and associated traits were similar for shaded seedlings of free-standing and climbing woody species and they do not differ in their growth–survival trade-off relationships (Gilbert *et al.*, 2006), even though significant leaf trait differences must eventually emerge by the time they reach the canopy (Asner and Martin, 2012).

Implications of leaf life span for seedling regeneration in gaps versus shade

We expected that mortality in gaps is independent of leaf life span, because long-lived leaves with low photosynthetic capacity do not provide an advantage to carbon economy in gaps, and might even interfere with adaptive plasticity. This prediction is supported by the lack of correlation between early seedling survival in gaps versus gap leaf life span of 24 species in our earlier study (Kitajima *et al.*, 2012), and in the current study by the lack of correlation of early seedling survival in gaps with gap and shade leaf life spans of a greater number of species (Table 2). Our results are in line with the view that shade tolerance hinges more upon avoidance of herbivory and hazards in combination with long leaf life span (Coley, 1983), because this strategy allows long-term maintenance of positive net carbon balance even though it slows down carbon gain and growth rates over the short term (Kitajima, 1994; Lusk *et al.*, 2008a). In addition, Lusk *et al.* (2011) found that light-use efficiency is lower in more shade-tolerant species with longer-lived leaves, as multiple-layers of leaves result in greater self-shading. The results of Lusk *et al.* (2011) and the current study are also significant in demonstrating that leaf life span is relevant not only in terms of contrast between light-demanding versus shade-tolerant species (as argued by Dominy *et al.*, 2008), but also in terms of variation within the shade-tolerant guild of evergreen species whose seedling life span may span multiple years. In contrast, deciduous tree seedlings, whose maximum leaf life span is truncated by short growing seasons, may employ somewhat different shade survival strategies from evergreen species (Seiwa and Kikuzawa, 1991; Walters and Reich, 1999; Lusk *et al.*, 2008b). Finally, interspecific variations in traits of woody seedling stems, which are long-lasting in both evergreen and deciduous species, deserve more research attention within and across communities in the context of seedling regeneration ecology.

SUPPLEMENTARY DATA

Supplementary data are available online at ww.aob.oxfordjournals.org and consist of the following. Figure S1: histogram of seedling mortality rates (% per day) in shaded forest understoreys. Figure S2: scatter plots of leaf lamina fracture toughness ($J\ m^{-2}$) for three ontogenetic stages of seedlings. Figure S3: scatter plots of leaf density ($g\ cm^{-3}$) for three ontogenetic stages. Table S1: descriptive statistical summary of plant and leaf demography of 104 tropical woody plant species included in the study. Table S2: the species mean values for leaf vein fracture toughness, averaged across three ontogenetic stages. Table S3: correlations of leaf traits that contribute to leaf toughness of seedlings 3 months after the first-leaf full expansion with leaf and seedling demographic traits. Table S4: comparison of correlation coefficients for species correlations (r) and phylogenetically independent contrasts ($rPIC$) for relationships of *a priori* interests, including those that are plotted in the main figures.

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