BIOMECHANICAL PROPERTIES OF TROPICAL TREE SEEDLINGS AS A
FUNCTIONAL CORRELATE OF SHADE TOLERANCE

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2005

To my parents, who let me fly;
and to Abuelita Betty, who gave me the wings.

ACKNOWLEDGMENTS

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Abstract of Thesis Presented to the Graduate School
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May 2005

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Physical disturbances by vertebrates and litterfall are important causes of seedling

mortality in the understory of tropical forests. Thus, the capacity to resist or recover from

mechanical damage should enhance seedling survival in shade. I explored interspecific

variation in seedling biomechanical properties across a shade tolerance gradient, using

eight tropical tree species from Barro Colorado Island (BCI), Panama. The stems and

leaves of shade-tolerant species were constructed of stronger materials than were those of

light-demanding species, as measured by a higher Young's modulus of elasticity, fracture

toughness, and tissue density. These traits were highly correlated with tissue fiber content

(especially % cellulose, but not % lignin) and with seedling survival during the first

6 mo. There were no correlations between seedling survival and structural measurements

that integrated material and morphological traits, such as flexural stiffness, work-to-bend,

and whole stem flexibility. The lack of correlations suggests that investment in strong

material, rather than in large plant size is more beneficial for seedlings at early developmental stages.

Next, I described first-year temporal patterns of seedling mortality, susceptibility to damage agents, and types of damage suffered by seedlings in the forest understory. Seedling mortality was highest during the first 2 mos (due to vertebrate activity) and gradually decreased over the remaining 8 mo. Species differed significantly in their temporal patterns of mortality and in the proportions of seedling surviving at the end of the study. The three main causes of damage were (in order of severity) vertebrate activity, disease, and litterfall. The four main types of mechanical damage (in order of severity) were leaf damage, bent stems, broken stems, and uprooted seedlings. All species suffered similar levels of mechanical damage but shade-tolerant species (which often had stems constructed of strong materials) were less likely to die when damaged than light-demanding species.

My study provides evidence that, in Barro Colorado Island, physical disturbance is a major cause of seedling mortality during the first year, and that shade-tolerant species survive better than light-demanding species after suffering mechanical damage. Higher survival is potentially influenced by higher carbon investment of shade-tolerant tree species into structural support of stems at very early developmental stages. However, greater carbon allocation to structural defense must be accompanied by slower relative growth rates. Thus, functional diversity in biomechanical properties is an important aspect of multiple trait associations that lead to the growth-survival trade-offs observed among coexisting tropical tree species.

CHAPTER 1
BIOMECHANICAL PROPERTIES OF TROPICAL TREE SEEDLINGS AS A
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**Introduction**

Mechanical damage is a major cause of mortality in understory plants, including

tree seedlings (Clark and Clark 1989, Gillman, Wright & Ogden 2002), saplings

(Hartshorn 1972, Aide 1987), and understory herbs (Gartner 1991, Sharpe 1993). Clark

and Clark (1991) found that litterfall caused 11% of the annual mortality of seedlings

$\leq 1$ cm in diameter in a lowland tropical rain forest. In a study in seasonal tropical forest,

Alvarez-Clare (Chapter 2) found that 77% of 755 seedlings, from eight species of tropical

trees transplanted to the forest understory, suffered some type of mechanical damage

after 1 yr. Mechanical damage can be caused by falling debris (Aide 1987, Putz *et al*.

1983), vertebrate activity (Roldan & Simonetti 2001, Gómez, García & Zamora 2004),

water or ice flow (Mou & Warrillow 2000), and herbivory (Coley 1983). In the tropical

rain forest (where there is high frequency of such disturbances) survival of seedlings

depends on their ability to avoid or recuperate from mechanical damage.

An increase in carbon allocation to structural tissues can increase seedling

performance in the forest understory by increasing biomechanical toughness and stiffness

(Sibly & Vincent 1997) and thereby decreasing susceptibility to damage. For example,

Augspurger (1984a) found that from nine species of tree seedlings, species less affected

by pathogen attack were those that became woody more rapidly. Additionally,

mechanical defenses in leaves play a substantial role in deterring loss to herbivores

(Coley 1983, Choong 1996) and are correlated with leaf life span (Wright & Cannon 2001).

Biomechanical strength results from carbon investment in tissues of stems, leaves, and roots, and from the organization and structure of those tissues within the plant. For example, fiber is an important contributor of mechanical strength in leaves. Choong (1996) found that high fracture toughness was correlated with fiber content in leaves of *Castanopsis fissa* (Fagaceae). Resistance to mechanical damage is also influenced by the type and organization of fiber components (e.g., cellulose, hemicellulose, and lignin). Within a tissue, high cellulose content results in increased toughness, while high lignin content increases hardness (Niklas 1992). Additionally, the orientation of the cellulose microfibrils in the S2 layer of the secondary cell wall affects the ability of the material to resist cracking under plastic tension (Lucas *et al*. 2000). In stems of adult trees, high tissue density and cell-wall volume fraction in the xylem increase toughness and stiffness (Barnett & Jeronimidis 2003). Similarly, higher resistance to mechanical stress in root tissues can improve anchoring capacity, and reduce risk of uprooting (Campbell & Hawkins 2004).

Considering the limited carbon budgets of seedlings, increased investments in structural materials must be accompanied by decreases in allocation to growth, to reserves, and/or to chemical defenses, such as tannins and alkaloids (Kitajima 1994, Kobe 1997, Shure & Wilson 1993). Thus, resource limitation leads to trade-offs involving biomechanical attributes, such as light acquisition vs. structural safety, growth vs. tissue density, and photosynthetic capacity vs. leaf toughness (Loehle 1988, Niklas 1992, Givnish 1995, Bazzaz & Grace 1997).

Natural selection should favor stems and leaves with forms, biomechanical properties, and growth dynamics that maximize carbon gain, competitive ability, and safety, but that minimize costs of construction and maintenance (Givnish 1995). Obviously, conflicts among these aspects make it impossible to optimize all factors simultaneously. Thus diverse ecological strategies have evolved, affected by the evolutionary forces dominating particular ecological niches. For example, plants can cope with mechanical damage through investment in resistant structures or by allocating resources to reserves that enable them to replace damaged tissues (Harms & Dalling 1997, Pauw *et al*. 2004). In both cases, a strategy will only be selected for, if it confers a benefit relative to the cost, such as increased survival (Sibly & Vincent 1997). My study focused on the defensive strategy of investing in damage resistance, by exploring the influence of biomechanical traits on seedling survival in shade.

Although biomechanical properties clearly influence plant survival and competitive ability, and potentially influence their ecological distribution (Coley 1983, Niklas 1992, Lucas *et al*. 2000), investigations evaluating plant biomechanical properties in an ecological context are few. Exploring the functional diversity of biomechanical properties in tropical tree seedlings should help in describing multiple trait associations that lead to growth-survival trade-offs observed among coexisting tropical tree species.

My study explored interspecific variation in seedling biomechanical properties across a shade-tolerant gradient, among eight tropical tree species from Barro Colorado Island (BCI), Panama. Because my goal was to understand the ecological role of biomechanical traits in tropical tree seedlings, I evaluated a variety of biomechanical attributes at the material and structural level. Plant stem and leaf material traits consist of

the composite, anisotropic material of which they are composed. At this level,

mechanical (toughness, stiffness, and density) and chemical (fiber fraction) traits were

measured, without considering size or anatomical organization. At the structural level,

material properties combined with morphological traits (e.g., size and shape) were

measured for individual plant organs (stems or leaves). Measurements at the structural

level for stems included flexural stiffness, percent critical height, work-to-bend, and

whole stem flexibility. To describe the structure of leaves, I measured specific leaf area

and force of fracture. Specifically, I addressed the following three questions:

- **Do material properties of stems and leaves of tropical tree seedlings differ among species in relation to their shade tolerance?** Because strong material confers an advantage against mechanical damage and presumably increases survival probabilities, I predicted that shade-tolerant species, which survive better in shade (Wright *et al.* 2003, Chapter 2), should have stronger stem and leaf materials than light-demanding species. More specifically, stems of shade-tolerant species should have higher Young's modulus of elasticity, fracture toughness, and density. In addition, shade-tolerant species should have higher fiber content, which reflects the chemical composition of the material. Likewise, leaves of shade-tolerant species should have higher lamina and midvein fracture toughness, density, and fiber content.

- **What is the relationship between material and structural biomechanical properties, and between material properties of stems and leaves?** Carbon allocation to stronger tissues should also contribute to overall structural strength. Therefore, unless there are important morphological differences between species, material traits should be reflected at the structural level. Stems of shade-tolerant species should have lower percent critical height, higher flexural stiffness, and higher resistance to bending in the field. Leaves of shade-tolerant species should have a lower specific leaf area (SLA) and a higher overall resistance to fracture (force of fracture) than leaves of shade intolerant species. I also expected a concordance of biomechanical attributes between structures. Thus, biomechanical properties of stems and leaves should be correlated. Because it was my ultimate objective to evaluate the implications of biomechanics for seedling performance in the forest, it was key to examine biomechanical traits at the material level but also at the structural level, integrating morphological attributes that can influence overall plant response to mechanical stress.

- **How do biomechanical properties of seedling stems and leaves change over the first 6 mos after initial development?** It has been shown that free-standing plants, as opposed to lianas, increase their stem resistance to bending and breaking during

growth and maturity (Rowe & Speck 1996). Similarly, leaves become tougher with aging (Wright & Cannon 2001). Therefore, I predicted an increase in mechanical strength of stems and leaves, both at the tissue and at the structural level.

## Materials and Methods

The study was conducted in Barro Colorado Natural Monument (BCNM), Panama (9º 10' N, 79º 51' W). Data were collected during the rainy season (May-December), when 78% of the average annual precipitation of 2600 mm falls. Climate, flora, and ecological characteristics of the seasonally moist tropical forest in BCNM are well described by Croat (1978) and by Leigh, Windsor & Rand (1982).

I collected seeds from eight common species in BCNM that differ in ecological characteristics such as dispersal mode, cotyledon type, and seedling establishment probability (Table 1-1). A seedling-recruitment index was calculated as # seeds falling $m^2year^{-1}$ / # seedlings established $m^{-2}year^{-1}$ obtained from a long-term experiment on Barro Colorado Island (BCI). Seed rain density (# seeds $m^{-2}year^{-1}$) was measured in weekly censuses from 1995-1999 in two hundred 1 $m^2$ seed traps. Recruitment of new seedlings (# seedlings $m^{-2}year^{-1}$) was measured once a year from 1995-1998 during the dry season in six hundred, $1m^2$ recruitment plots,[2] each located 2 m from three sides of the seed traps (Wright *et al.* 2003).

Seedling shade tolerance was ranked according to measurements of seedling survival in the shaded understory from four independent studies conducted in BCNM (Table 1-2). Alvarez-Clare (Chapter 2) determined first-year survival of seedlings transplanted to the forest understory at first leaf expansion, and censused weekly for the first 3 mos, then biweekly for the rest of the year. Kitajima (unpublished data) and Myers (2005), both quantified first year survival of seedlings transplanted to fenced enclosures from which vertebrate predators were excluded. Wright *et al.* (2003) estimated survival

probability after 1 yr, using naturally recruited seedlings in the forest understory. Only studies by Alvarez-Clare and by Kitajima included all the species assessed here, and therefore survival per species from these two sources was averaged to determine mean % survival (Table 1-2). Mean % survival was obtained from 2-6 mo survival from Alvarez-Clare, which excludes initial transplant shock and most vertebrate predation (Chapter 2), and survival from 0-4 mo from Kitajima, which was the interval before most plants were harvested. Mean percent survival was correlated with biomechanical traits at 1 and 6 after mos the expansion of the first leaf.

Seeds were germinated in trays in a shaded house where daily total photosynthetic photon flux density was adjusted with shade cloth to approximately 2% of full sun. I transplanted 45 seedlings of each species to each of three 6 x 6 m common gardens located on 70-year-old secondary forest on Buena Vista Peninsula. To standardize by ontogenetic stage based on development of photosynthetic organs, I transplanted seedlings at expansion of the first leaf for all species with reserve cotyledons and at expansion of cotyledons for *Tabebuia rosea*, a species with photosynthetic cotyledons. Time from germination until leaf expansion varied across species from one week for *Anacardium excelsum,* to four weeks for *Eugenia nesiotica* and *Tetragastris panamensis.* Each garden was situated under closed canopy and surrounded by a 1 m tall wire mesh fence to exclude large, ground-dwelling herbivores.

In each garden, seedlings were transplanted 50 cm with each species randomly located within planting positions in each plot. I replaced those that died within the first week after transplanting. Half of the seedlings from each species were harvested after 1 mo (T1), and the remaining plants were harvested approximately 6 mo later (T2).

Forty-five plants (15 per garden) of each species were randomly chosen at T1 and used to perform biomechanical tests *in situ* before being harvested, and then used in the laboratory to test biomechanical properties in different organs (e.g., if stem flexibility was measured in the field, leaves were measured in the laboratory). Because of mortality, at T2 only 30 seedlings per species were measured. After being harvested, all plants were refrigerated for less than 12 h until laboratory biomechanical tests were performed. After testing, plants were separated into stems, roots, and leaves, weighed and then dried at 100 ºC for 1 h and then at 60 ºC for 48 h to determine dry weight. Samples were saved for fiber analysis.

**Biomechanical Measurements**

**Young's modulus of elasticity**

Young's modulus of elasticity ($E$) of stems was measured in a three point bending test with a Portable Universal Tester (Darvell *et al.*1996), as described in Lucas *et al.* (2001). More specifically, Young's modulus was calculated from the slope of the linear regression of the applied bending force vs. deflection. Span distance varied with stem size and bending resistance. Span ratios of >10 were always used, as suggested by Niklas (1992). Young's modulus of elasticity is defined as the ratio between forces of stress and strain, measured within the plastic range of a homogeneous material (i.e., stiffness) In the case of stems, because they are constructed of heterogeneous and composite materials, I measured an apparent Young's modulus, which describes the overall bending properties of a stem independent of size and shape (Niklas 1992).

**Fracture toughness**

I measured fracture toughness for stems and leaves by performing cutting tests with a sharp pair of scissors mounted on a Portable Universal Tester as described by Lucas &

Pereira (1990). Toughness obtained through cutting tests is the work required to propagate a crack over a unit area (Lucas *et al.* 2000) and has been used in leaves as an indicator of resistance to herbivory, pathogens, and other physical damage (Lucas & Pereira 1990, Choong 1996). For leaves, toughness was measured for lamina and midrib separately. When measuring stems, I cut the stem at half of the total length, or just above the cotyledons in *A. excelsum* and *T. panamensiss*, which have epigeal cotyledons.

**Density**

Tissue density was calculated for leaves and stems as the ratio of dry mass to volume. For leaves, volume was calculated as total leaf area (measured in the leaf area meter) multiplied by the lamina thickness, and dry mass was obtained for the total leaf including midrib and veins. For stems, volume was obtained from the formula:

$$V = (\pi r^2)h \qquad\qquad (1\text{-}1)$$

where $r$ is the radius measured at the middle of the stem and $h$ is stem length, both measured in mm. For measuring density and the other biomechanical properties, stems were considered perfect cylinders, ignoring taper.

**Chemical analysis**

To evaluate fiber content and relate it with biomechanical measures, fiber fractions were determined for stem and leaf tissues separately, using a series of increasingly aggressive extractants (Ryan, Melillo & Ricca 1989) with a fiber analyzer system (ANKOM Technology, NY, USA). Dried plants of each species from the same common garden and same harvest were combined and ground as one sample to have a minimal of 0.5 g required for analysis. Because of the small size of *T. rosea*, all harvested plants were combined and ground as one sample. In the first step, each ground sample was weighted and sealed in a chemical resistant filter bag. The bagged samples were

submerged, heated, and agitated in neutral detergent fiber solution removing soluble cell

contents and leaving non-detergent fiber (% NDF). In the second step, the bagged

samples were treated with acid-detergent solution, which removed hemicellulose and left

acid-detergent fiber (% ADF) consisting of cellulose, lignin, cutin and insoluble ash. In

the third step, samples were treated with 70% sulfuric acid, which removed cellulose and

left lignin, cutin and insoluble ash inside the bags. Between steps, sample bags were dried

at 100°C overnight to determine the dry mass, and each fiber fraction was calculated by

subtraction. Afterwards, the remaining sample was combusted at 500ºC to determine

percent insoluble ash. Mass of labile cell contents + hemicellulose + cellulose + lignin +

insoluble ash add up to 100% of the original dry mass.

**Percent critical height**

Percent critical height (% $H_{cr}$) measures the relationship between stem height and

how tall it could be before it buckles under its own weight (Holbrook & Putz 1989).

Percent critical height was calculated for each seedling stem according to the formula

given by Greenhill (1881):

$$H_{cr} = 1.26(E/w)^{1/3} (d_b)^{2/3} \qquad\qquad (1\text{-}2)$$

where $E$ = Young's modulus of elasticity (Pa), $w$ = fresh weight/unit volume ($Nm^{-3}$), and

$d_b$ = diameter at base (m). The ratio of $H_{cr}$ to the actual stem height multiplied by 100 is

% $H_{cr}$, which is an indication of mechanical risk-taking. In other words, the higher the

% $H_{cr}$ the lower the margin of safety for the stem to remain free-standing.

**Flexural stiffness**

Flexural Stiffness (*EI*) describes the ability of a structure to withstand mechanical

loads, taking into account the size and shape of the structure as well as the material

properties of its tissues (Gartner 1991). It is the product of *E*, which describes the

flexibility of the material, and the second moment of area ($I$), which reflects size and the

geometry of the structure to which a force is being applied. I estimated flexural stiffness

($EI$) for cylindrical stems using the formula:

$$I = 0.25\pi r^4 \tag{1-3}$$

where $r$ (mm) is the radius measured in the middle of the stem and the Young's modulus

of elasticity ($E$) obtained with three point bending tests, as described above (Niklas

1992).

**Work-to-bend**

Resistance of stems to bending, here referred to as "work-to-bend", was obtained

empirically in the field by applying a force vertically from above a seedling until the stem

was deflected to 70-60% of its original height. To estimate work-to-bend a 2 L plastic

container was mounted on a 30 cm$^2$ Styrofoam platform and hung from a tripod with a

spring balance just above the seedling. The Styrofoam platform was in contact with the

uppermost part of the seedling, without bending it. Then, water was poured slowly into

the container, until the weighted platform bent the stem to the specified extent. Assuming

that acceleration was nil, water weight (force) times vertical displacement, was calculated

as work to bend the seedling.

**Whole stem flexibility**

To further describe the behavior of intact seedlings rooted in the ground in response

to mechanical stress, I measured whole stem flexibility (Holbrook & Putz 1989) in the

field. A stem was pulled horizontally in four directions with spring balances until bent

20º from vertical. This procedure was repeated in the four canonical directions and the

forces averaged. Whole stem flexibility (WSF) was expressed as angular deflection

divided by applied force (radians/N). In the case of *E. nesiotica*, I bent the stem 40º,

because the force required to bend the stem 20º was too small to be detected in its small seedlings. Whole stem flexibility is a measure of elasticity whereas flexural stiffness is a measure of rigidity; therefore I expected them to be inversely correlated. Because WSF applies a lateral tensile force (the stem is pulled laterally), and work-to-bend applies a vertical compressive force (the plant is pushed down), slightly different stem properties are being measured, and thus I performed both tests.

**Force of fracture**

For leaves, force of fracture was calculated as the product of fracture toughness by lamina thickness. This structural measurement indicates total force necessary to propagate a crack considering leaf thickness (Wright & Cannon 2001).

**Specific leaf area**

Specific leaf area (SLA) was calculated as the ratio of leaf area, measured with a leaf area meter (LICOR-3100), and leaf total dry mass. Because species with low SLA are usually thick and/or dense (Wright & Cannon 2001), I expected SLA to be inversely correlated with leaf fracture toughness and force of fracture.

**Statistical Analyses**

Every biomechanical measurement was averaged for each species, and species means were log-transformed to meet normality assumptions for ANOVA tests (Shapiro-Wilk, $\alpha = 0.05$). For each measurement, the effect of species ($N = 8$) and harvest time ($N = 2$) was evaluated using two-way ANOVAs. When the species*time interaction was significant, the data for each harvest were analyzed separately. To test if means differed between T1 and T2 within each species, t-tests with subsequent Bonferroni corrections were applied. For across-species comparisons between two biomechanical measurements or between a biomechanical measurement and survival,

linear regressions on log-log plots were calculated. For multiple across-species

comparisons between non-normal variables, Spearman rank correlations were applied.

Two means per species (one per harvest) were obtained to evaluate the correlation

between biomechanical traits ($N = 16$). Work-to-bend was only measured at T1 ($N = 8$)

for logistic reasons. For Spearman correlations between biomechanical properties and

% survival in shade, species means were evaluated at each harvest separately ($N = 8$). All

analyses were performed using JMP IN 4.0 (SAS Institute Inc., Cary, NC, USA) with a

significance level of $\alpha = 0.05$.

## Results

### Stem Biomechanics

Mean Young's modulus of elasticity ($E$) of the seedling stems varied 20-fold

among species (Figure 1-1A). Most species increased their resistance to bending ($E$)

during the six-month period between T1 and T2 (Table 1-3) resulting in significant time

effect without a species*time interaction. Mean stem fracture toughness also varied

among species and between harvests (Figure 1-1B), but the amount of increase in fracture

toughness varied among species (Table 1-3). While *E. nesiotica* increased its mean

fracture toughness threefold from 1-6 mos after leaf expansion, *A. exelsum* and *T.*

*panamensis* showed no increase (Figure 1-1B). Mean stem tissue density also varied

among species and between harvests, increasing from T1 to T2 for all species except

*A. cruenta*, which decreased its mean stem tissue density over time (Table 1-3, Table A-

1). Total fiber (% NDF) was generally higher for more shade-tolerant species (Table 1-3),

but *A. cruenta*, the species with highest survival in shade, had a mean % NDF similar to

the three least shade-tolerant species (Figure 1-2A). Mean % NDF did not differ

significantly between harvests (Table 1-3 and Table A-3). All individual fiber fractions varied between species, but only % hemicellulose increased between harvests (Table 1 3).

Most material properties of stems were inter-correlated (Figure 1-3 and Table 1-4). Material mechanical traits, such as toughness and modulus of elasticity, were positively correlated (Figure 1-3A). Additionally, material properties describing mechanical strength (e.g., modulus of elasticity and density) were correlated with chemical indicators of tissue strength (e.g., fiber content; Figure 1-3B-D). Among chemical properties, % cellulose was the best predictor of mechanical strength, as measured by modulus of elasticity, fracture toughness, and density (Table 1-4). Percent lignin was not correlated with toughness or density but was a good predictor of modulus of elasticity (i.e., stem stiffness).

Mean percent critical height (% $H_{cr}$) varied among species and significantly decreased in three out of eight species from T1 to T2 (Figure 1-4A and Table 1-3). All species had low % $H_{cr}$ (their actual height was 14-28% of their critical height), indicating that seedlings were overbuilt relative to their potential maximum height before buckling under their own weight. Mean flexural stiffness (*EI*) varied among species and between harvests, with an interaction between factors (Figure 1-4B and Table 1-3). The significant interaction was apparently influenced by *A. exelsum* and *G. superba*, the species with the largest seedlings (i.e., largest *I*), which disproportionately increased *EI* from T1 to T2. Mean work-to-bend (i.e., work necessary to bend a stem to 70% of its original height) varied four-fold among species (Figure 1-4C and Table 1-3). Stem diameter was a good predictor of work-to-bend ($r^2 = 0.53$, F = 73.0, d.f. = 1,66, $P < 0.001$), and consequently there was a positive correlation between *EI* and work-to-bend (Table 1-4). Mean whole

stem flexibility, measured as angular deflection, varied among species decreasing over time as stems became more lignified (Figure 1-4D and Table 1-3). Plants with large stem diameters were less flexible than plants with small stem diameter ($r^2 = 0.64$, F = 289.70, d.f. = 1,160, $P < 0.001$).

Although mechanical and chemical traits of stem tissues were intercorrelated, they were never correlated with structural measurements that integrated material and morphological traits (Table 1-4). The only exception was % $H_{cr}$, which was negatively correlated with modulus of elasticity ($E$), fracture toughness, % NDF, and % cellulose. This observation indicates that species with stronger material had a lower % $H_{cr}$ and hence a greater safety margin.

Second moment of area ($I$), did not correlate with any of the material properties. In contrast, both $I$ and flexural stiffness ($EI$) correlated positively with structural traits, such as work-to-bend and whole stem flexibility measured on intact seedlings in the field (Table 1-4).

**Leaf Biomechanics**

Material biomechanical traits of leaves differed among species and between harvests, although not all species varied consistently between T1 and T2. Lamina fracture toughness differed among species with a significant interaction between species and time (Table 1-5). Two species increased their lamina toughness, two decreased, and four species did not vary between T1 and T2. Fracture toughness of midveins varied between species and between harvests, with a significant interaction between these two factors (Figure 1-5B, Table 1-5). In general, for each species midvein fracture toughness was lower or similar than stem toughness, but much higher (ca. x10) than lamina toughness. Leaf density also varied among species and between harvests (Table 1- 5). A significant

interaction between species and time was probably because leaf density increased from T1 to T2 in *B. pendula* much more than in other species (Table A-2). Percent NDF differed among species but not between harvest times (Figure 1-2B and Table 1-5). All individual fiber fractions varied among species, but only % lignin changed between harvests (Table 1-5).

Structural properties of leaves, integrating material properties and morphology varied among species, but only SLA differed between harvests (Table 1-5). *Tabebuia rosea* had the highest SLA, while *A. cruenta* had the lowest SLA. Force of fracture was different among species, but not between harvest times (Figure 1-5 and Table 1-5).

Biomechanical attributes of midveins highly influenced mechanical traits of the whole leaf. Across species, there was a positive correlation between lamina and midvein toughness (Table 1-6). Total leaf density was best correlated with midvein than with lamina toughness, suggesting that biomechanical attributes of the midvein significantly influence overall leaf density. Percent cellulose was the chemical trait that most correlated with the rest of the material traits. Force of fracture (toughness*thickness) was more correlated with toughness than with thickness, indicating a stronger effect of leaf material properties than of leaf dimensions.

**Relationship between Biomechanical Traits of Stems and Leaves**

Across species, there was a positive correlation between stem toughness and midvein toughness, but not between stem toughness and lamina toughness (Table 1-7). Tissue density and % NDF were also correlated between stems and leaves, but the other fiber fractions were not (data not shown).

**Relationship between Seedling Biomechanics and Survival**

Several stem material biomechanical properties were positively correlated with % mean survival in shade (Table 1-8). Fracture toughness and tissue density measured at T2 showed the highest correlations with survival in both stems and leaves (Figure 1-6, Table 1-8). Furthermore, if *A. cruenta* (the species with high survival but with low $E$ and % fiber content) was removed from the analyses, all correlations between material biomechanical traits and survival increased. Although individual fiber fractions exhibited no significant correlation with survival, % NDF (i.e., total fiber) was positively correlated with survival in both stems and leaves. Stem and leaf structural properties, at 1 and 6 mos after expansion of the first leaf, were not correlated with survival in shade.

## Discussion

**Stem Biomechanics**

Mechanical traits and chemical composition of seedling stems varied widely among eight species of tropical trees but as predicted, stems of shade-tolerant species were generally stiffer, tougher, and denser, and with higher total fiber content (% NDF) than stems of shade intolerant species (Figures 1-1 and 1-2A). Among the biomechanical properties tested there were positive correlations between Young's modulus of elasticity, fracture toughness, and stem density suggesting a greater overall investment in strong material properties in shade-tolerant species. Similar results were obtained by Cooley, Reich & Rundel (2004) for understory herbs. Although in my study there were positive correlations between mechanical and chemical material traits, the fiber components contributing to these correlations differed, with the mechanical property considered. For example, fracture toughness was correlated with % cellulose and % hemicellulose, but not with % lignin (Table 1-4). As a complex, heterogeneous polymer with strong

covalent bonds, lignin acts as an adhesive agent in the cell wall, and therefore is expected

to increase stiffness rather than toughness (Lucas *at al*. 2000). In fact, the only

mechanical property correlated with % lignin was *E*, a measure of stem stiffness.

Modulus of elasticity, however, can also be affected by other tissue properties such as

volume fraction of cell wall materials (Lucas *et al*. 2000, Niklas *et al.* 2000),

hemicellulose and cellulose contents, and microfibril angles in the cell wall of fiber cells

(Hoffman 2003, Savidge 2003).

Differences in material properties at the time of first leaf expansion (T1) suggest

that shade-tolerant species invested earlier in stem mechanical construction than shade

intolerant species. Thus, shade-tolerant species potentially had a more developed vascular

cambium and greater secondary cell wall deposits than shade intolerant species. Mean

moduli of elasticity (*E*) for shade intolerant species at T1 were similar to those reported

for stems of understory herbs (Cooley, Reich & Rundel 2004, Niklas 1995). This

suggests that 1 mo after leaf expansion, vascular cambium development (and thus

secondary growth) was still limited, and seedlings were relying on primary tissues for

mechanical support (Niklas 1992, Isnard, Speck & Rowe 2003). In contrast, shade-

tolerant species (e.g., *T. panamensis* and *E. nesiotica*) had moduli of elasticity at T1 of

the same order of magnitude as wood from 15 of 33 adult temperate trees evaluated by

Niklas (1992). Species with stronger material properties had higher fiber contents as well.

Specifically, they had higher % lignin and  % cellulose fractions, which are correlated

with vascular cambium maturation, high cell wall volume fraction, and secondary cell

wall development (Niklas *et al.* 2000, Lucas *et al.* 2000). Because shade-tolerant species

are usually slow growers (Kitajima 1994), it is not likely that further stem maturity at the

time of first leaf expansion in shade-tolerant species was a product of accelerated stem development. On the contrary it reveals an ecological strategy, characterized by substantial investment in material starting very early in ontogeny.

Variation in stem development at T1 could be influenced by leaf emergence times. Kitajima (2002) demonstrated that *T. rosea*, a light-demanding species with photosynthetic cotyledons, became dependent on photosynthetic carbon gain earlier in development than shade-tolerant species with storage cotyledons. Rapid photosynthetic cotyledon expansion after radicle emergence ($22.5 \pm 1.9$ d), allows little time for stem structural development and toughening. In contrast, *T. panamensis* a shade-tolerant species with reserve cotyledons, expands its first leaves relatively quickly ($23.6 \pm 2.4$ d), but has a high modulus of stem elasticity. Although age (time after radicle emergence) may potentially affect stem stiffness and toughness, this is evidently not the sole cause of variation. Among species variation in biomechanical properties of stems at first leaf expansion is a function of differences in material composition and structural arrangement, which suggest the existence of different ecological strategies among species of tropical tree seedlings.

I predicted that material traits of seedling stems would be reflected at the structural level. Thus, I expected stems with stronger material properties per unit area (or mass) to be more resistant to bending and breaking. Results confirmed this prediction, but only when stems of similar size were compared. When different sized seedlings were compared, species with larger seedlings (at comparable developmental stages) were more resistant to bending, both for tests performed in the laboratory and on intact seedlings in the field. A plant can obtain a high flexural stiffness by increasing $E$ (material stiffness),

or by increasing $I$, a measure of size and shape (Niklas 1992). Given that seedlings of all eight species included in my study had circular stems, the observed differences in $I$ reflect differences in size only. Likewise, differences in flexural stiffness among species were mostly influenced by size of the stem ($I$), as opposed to flexibility of the material ($E$). Similar results have been reported for neotropical understory herbs (Cooley, Reich & Rundel 2004), vines (Rowe & Speck 1996), shrubs (Gartner 1991), and trees (Holbrook and Putz 1989). In contrast, other studies have found an influence of both $E$ and $I$ when comparing flexural stiffness of stems growing in environments differing in wind intensity and shade conditions (Cordero 1999, Henry and Thomas 2002), and when comparing stems from congeneric species differing in growth form (Isnard, Speck & Rowe 2003,).

When intact, live stems were tested in the field, work-to-bend and whole stem flexibility correlated with other structural traits, but not with material properties (Table 1-4). The results of these field tests correlated well with flexural stiffness, which was measured using harvested stems in the laboratory. Whole stem flexibility and work-to-bend proved good field indicators of stem rigidity for tropical tree seedlings, and should be taken into account in future research regarding seedling biomechanics.

The structural property that best correlated with material properties was % critical height. Seedlings from shade-tolerant species had higher safety factors (i.e., lower % $H_{cr}$), than seedlings from shade intolerant species. As suggested by Givnish (1995), my results indicate that there is a trade-off between light acquisition and mechanical safety. While some trees maximize their height to reach light and overtop competitors, this increases vulnerability to toppling (Holbrook & Putz 1989, Brüchert, Becker & Speck 2000). Although all species in my study were overbuilt (Figure 1-2A), light-demanding species

had higher % $H_{cr}$ and weaker material traits than shade-tolerant species, suggesting that they were maximizing height growth at the expense of safety and structure.

As predicted, all species increased their mean $E$ between 1 and 6 mos after leaf expansion, although not always significantly (Figure 1-1). In contrast, there was no pattern to the proportional increase in fracture toughness between T1 and T2 among species, revealing that species do not necessarily increase toughness and stiffness proportionally during ontogeny. Thus, for seven out of eight species in which stem fiber content did not increase from T1 to T2, increases in stiffness and toughness over time must have been caused by changes in stem anatomy, such as fiber distribution and packaging, as opposed to increased fiber content (Hoffman *et al*. 2003), but further anatomical and histological analyses are necessary.

**Leaf Biomechanics**

Mean lamina and midvein toughness varied 30-fold among species, with values from 71 to 395 J m$^{-2}$ for laminas and 984 to 3475 J m$^{-2}$ for midveins. In a study performed on BCI with leaves from adult trees and understory saplings, Dominy, Lucas & Wright (2003) reported considerably higher values for lamina and midvein toughness than reported here. Nevertheless, for the three species used in both studies (*A. excelsum, C. elastica,* and *A. cruenta*), the same ranking prevails: *A. excelsum* had the lowest lamina and midvein toughness while *A. cruenta* had the highest. Although the relationship was weaker than in stems, leaves of shade-tolerant species had higher mechanical strength than leaves of shade intolerant species. Potentially, evolutionary forces favoring selection of other leaf traits, such as photosynthetic capacity, vein distribution, presence of secondary compounds, and water-use efficiency also influence differences in leaf toughness among species (Choong *et al*. 1992, Wright *et al*. 2004).

Fiber content is an indicator of biomechanical strength in leaves (Choong 1996). In the present study, mean % cellulose was the fiber fraction that best correlated with leaf fracture toughness, suggesting that cell wall material was the predominant cellular component influencing fracture toughness (Esau 1977), but it is not clear which tissues make a leaf tough. Both the cuticles (Taylor 1971) and the epidermis (Grubb 1986) have been proposed as toughening tissues. Additionally, Wright & Illius (1995) reported that the proportion of sclerenchyma in leaves was correlated with fracture toughness of grasses, and Choong (1996) found that the non-venous lamina contributed little to overall leaf toughness. In the present study, the positive correlation between midvein and lamina toughness suggests that vascular bundles (and probably fibers associated) were the major determinants of fracture toughness in leaves.

Structural measurements integrating leaf dimensions and size were correlated with material traits but not with morphological traits (Table 1-6). For example, force of fracture, calculated as the product of lamina toughness and leaf thickness, was better correlated with lamina toughness than with leaf thickness. Thus, unlike stems, overall leaf biomechanical properties were influenced more by material traits than by leaf dimensions. Similar results were reported by Wright & Cannon (2001) in a study with 17 sclerophyllous species from low-nutrient woodland in eastern Australia.

I expected that biomechanical strength of leaves would increase over time; however, most species did not change, and some even decreased in their mechanical strength between T1 and T2. In fact, for *G. superva* and *T. panamensis* mean lamina fracture toughness decreased significantly after 6 mos. Although there is no evident explanation for this observation, Lucas & Pereira (1990) found the same trend (where

leaves decreased their fracture toughness over time). They suggested that an increase in parenchymatous tissue and air species in older leaves could result in low fracture toughness per unit volume.

**Relationship between Biomechanical Traits of Stems and Leaves**

Measurements of the material traits of stems and leaves were positively correlated for the eight species combined. Species with tough, dense stems also had tough, dense leaves. An exception was *A. cruenta*, which had tough, thick leaves, but stems constructed of weak and flexible material. *Aspidosperma cruenta* also stores substantial amounts of nonstructural carbohydrates in its stems, which may augment its ability to recuperate from damage, rather than avoid it (Myers 2005). Across species, the correlation between stem and midvein toughness was stronger than the correlation between stem and lamina toughness. The strong relationship between stems and midveins could be driving the relationship between stem and leaf density or fiber content, suggesting consistent investments in vascular structure throughout the plant. Collectively, these results suggest that there is a whole-plant pattern of carbon investment in mechanical defenses, as opposed to a trade-off between investment in stem and leaves. Further investigations might evaluate whether this pattern remains consistent in roots.

**Relationship between Seedling Biomechanics and Survival**

Material properties of stems correlated with 0-6 mo survival in shade (Table 1-8, Figure 1-6). Species stems constructed of tougher, stiffer, denser, and more fibrous material showed higher percent survival than species composed of weaker material. This is direct evidence that biomechanical strength of stem tissues increases seedling performance in the tropical forest understory. As suggested in previous studies, strong material is likely to confer an advantage against mechanical damage caused by litterfall,

vertebrate trampling, and herbivory (Augspurger 1984a, Clark & Clark 1991, Moles & Westoby 2004a). The only species that deviated from the trend was *Aspidosperma cruenta*. Seedlings from this species had the highest survival in shade, but its stems were constructed of weak material. Most likely, high survival in *A. cruenta* was due to the presence of chemical defenses and large reserve pools of carbohydrates in stems and roots. *Aspidosperma cruenta* is well known for its poisonous alkaloids (e.g., obscurinervine and obscurinervidine, Harper *et al*. 1993), and well-developed chemical defense that may compensate for its low structural defense, revealing a unique ecological strategy among the eight species tested. It should be noted that chemical defenses confer herbivore resistance (Coley 1983), but do not protect seedlings from mechanical damage due to litterfall or vertebrate trampling. The high survival of *A. cruenta* on BCI, albeit its lack of mechanical defenses, suggests that for this species defense against herbivory and pathogens (through secondary compounds) was more important as a selective factor, than defense against mechanical damage, at least during the first 6 mos.

Surprisingly, structural traits that integrate material properties with seedling size and shape were not correlated with six-month survival in shade. Larger seedlings had higher overall resistance to bending (Figure 1-4), but with no apparent consequence for seedling survival. Although previous studies have emphasized the advantages of large size for seedlings (reviewed in Moles and Westoby 2004a), my results suggest that evolutionary pressures selecting for large seedlings are probably related to stress-tolerance (Green & Juniper 2004) and light acquisition (Turner 1990), not to biomechanical strength.

For leaves, there was a positive correlation between some of the biomechanical traits and survival in shade but the trends were not as strong as for stems. Most likely, leaf biomechanical traits are directly correlated with leaf performance (e.g., leaf lifespan or risk of herbivory), but not with whole plant performance (e.g., survival). For example, Wright and Cannon (2001) found that mean leaf toughness, force of fracture, leaf thickness, and leaf area explained between 30 and 40% of variation in leaf life span of 17 species of sclerophyllous plants. In a study with 2,548 species, Wright *et al.* (2004) found that leaf mass per area (LMA), explained 42% of the variation in leaf life span, indicating that thicker, denser leaves, usually live longer. Additionally, the weaker correlations I observed between survival and mechanical traits of leaves suggest that invertebrate herbivores that cause leaf damage are not crucial determinants of whole-plant survival during the first 6 mo, for the eight species considered in my study (Chapter 2).

**Conclusions**

Interspecific variation in material flexibility and fracture toughness of seedling stems as early as one month after leaf expansion, revealed different ecological strategies to cope with mechanical damage in the forest understory. Shade-tolerant species had stems constructed of strong materials, which may promote their survival in shade. However, stronger material properties of stems did not always reflect strength at the structural or whole-plant level. Size and several morphological traits contributed to overall resistance to bending and breaking stress, but they apparently were not crucial for seedling survival from 0-6 mo. As opposed to stems, leaf biomechanical properties were influenced more by material traits than by leaf dimensions, and biomechanical attributes of leaves were not always correlated with whole-plant survival. In tropical tree seedlings,

differential survival in shade is the product of a suit of traits of which biomechanics is an important component.

Table 1-1. Ecological characteristics of eight tropical tree species used in my study, listed by increasing shade tolerance.

| Sp. code | Species | Family | Cot. type | Dispersal | %Rec. index | Seed mass (g) |
|---|---|---|---|---|---|---|
| TABR | *Tabebuia rosea* | Bignoniaceae | PEF | Wind | 0.6 | $0.035 \pm 0.007$ (12) |
| ANAE | *Anacardium excelsum* | Anacardiaceae | PER | Animal | 0.1* | $1.811 \pm 0.316$ (9) |
| CASE | *Castilla elastica* | Moraceae | CHR | Animal | — | $0.315 \pm 0.005$ (8) |
| BEIP | *Beilschmiedia pendula* | Lauraceae | CHR | Animal | 13.7 | $2.360 \pm 0.090$ (10) |
| GUSS | *Gustavia superba* | Lecythidaceae | CHR | Animal | 3.7* | $5.566 \pm 1.746$ (7) |
| TETP | *Tetragastris panamensis* | Burseraceae | PER | Animal | 3.5 | $0.179 \pm 0.026$ (10) |
| EUGN | *Eugenia nesiotica* | Myrtaceae | CHR | Animal | 27.8* | $0.474 \pm 0.067$ (10) |
| ASPC | *Aspidosperma cruenta* | Apocynaceae | PHR[†] | Wind | 2.9* | $0.492 \pm 0.002$ (6) |

Cotyledon types are according to Garwood (1996): PEF = phanerocotylar epigeal foliaceous, PER = phanerocotylar epigeal reserve, CHR = cryptocotylar hypogeal reserve, and PHR = phanerocotylar hypogeal reserve. Percent recruitment (% Rec. Index) refers to percent recruits per seeds per area (Wright *et al.* 2003). Mean $\pm$ 1 SD (*N*) seed mass without seed coat. * Data obtained with between 5 and 10 recruits.† Cotyledons are partially cryptocotylar.

Table 1-2. Percent seedling survival for the eight study species over specified periods from four independent studies in BCNM.

| Sp. code | Mean % survival | Alvarez-Clare [a] | | | Kitajima [b] | | Myers [b] | | Wright [c] |
|---|---|---|---|---|---|---|---|---|---|
| | | 0-2 mo | 2-6 mo | 6-12 mo | 0-4 mo | 4-12 mo | 0-6 mo | 6-12 mo | 0-12 mo |
| TABR | 45.5 | 33 (55) | **44** (18) | 29 (7) | **47** (48) | 30 (23) | 33 (71) | 46(14) | 31 (58) |
| ANAE | 53.0 | 20 (100) | **40** (20) | 11 (9) | **66** (51) | 26 (34) | — | — | — |
| CASE | 65.0 | 40 (100) | **73** (40) | 72 (25) | **57** (28) | 67 (18) | 65 (101) | 86(44) | — |
| BEIP | 82.5 | 8 (100) | **88** (8) | 60 (5) | **77** (61) | 19 (47) | — | — | 52 (826) |
| GUSS | 76.0 | 54 (99) | **83** (54) | 79 (43) | **69** (42) | 86 (32) | — | — | 57 (213) |
| TETP | 82.0 | 62 (100) | **79** (62) | 82 (71) | **85** (20) | 90 (10) | — | — | 64 (361) |
| EUGN | 87.5 | 43 (100) | **100** (42) | 75 (32) | **75** (63) | 96 (47) | — | — | 81 (22) |
| ASPC | 87.0 | 78 (100) | **93** (78) | 82 (71) | **81** (27) | 99 (21) | 98 (111) | 97(104) | — |

Numbers in parentheses indicate sample size, (*i.e.,* the total number of individuals at the beginning of the measurement period). Values shown in bold were averaged for each species and used to calculate mean % survival. Refer to Table 1-1 for species codes. [a]This study. Seedlings transplanted to the forest and monitored for 1 yr (Chapter 2). Time is divided into different stages because initial mortality during 0-2 mo was due mainly to vertebrate activity, and thus is not a good indicator of shade tolerance. [b]Seedlings transplanted at the time of germination (K. Kitajima, unpublished data) or at time of first leaf full expansion (Myers 2005) to exclosures in the forest understory and monitored weekly for 1 yr. These seedlings were protected from vertebrate herbivores. [c]Percent of seedlings that survived at least 1 yr after germinating naturally in the forest understory(Wright *et al*. 2003).

Table 1-3. Effect of species and harvest time on material and structural properties of seedling stems. Shown are F values from two way ANOVAs performed on log-transformed values; d.f. = 7,1; ** $P < 0.001$

| Biomechanical measurement | Effect | | |
| --- | --- | --- | --- |
| | Species | Time | Species*Time |
| Modulus of elasticity (MN m$^{-2}$) | 151.5** | 90.0** | 1.5 |
| Fracture toughness (J m$^{-2}$) | 70.5** | 114.4** | 9.7** |
| Stem tissue density (g cm$^{-3}$) | 219.8** | 85.6** | 19.6** |
| % NDF | 57.7** | 0.8 | 1.9 |
| % Hemicellulose | 25.3** | 17.8** | 4.0** |
| % Cellulose | 30.7** | 0.1 | 1.3 |
| % Lignin | 38.4** | 2.0 | 1.4 |
| % Critical height | 60.8** | 133.8** | 4.8** |
| Flexural stiffness (N cm$^{2}$) | 111.3** | 163.9** | 4.7** |
| Work-to-bend (J) | 18.0** | — | — |
| Whole stem flexibility (radians/ N) | 100.9** | 102.8** | 5.81** |

Table 1-4. Relationships among stem biomechanical traits for seedlings of eight tree species.

| | $E$ (MN m$^2$) | Tough (J m$^{-2}$) | Density (g cm$^{-3}$) | % NDF | %Hemicell | %Cellulose | % Lignin |
|---|---|---|---|---|---|---|---|
| Toughness | **0.80** **(< 0.001)** | | | | | | |
| Density | **0.77** **(<0.001)** | **0.73** **(0.002)** | | | | | |
| % NDF | **0.90** **(<0.001)** | **0.75** **(<0.001)** | **0.83** **(<0.001)** | | | | |
| % Hemicell | **0.51** **(0.041)** | **0.58** **(0.024)** | 0.46 (0.070) | 0.40 (0.128) | | | |
| % Cellulose | **0.77** **(<0.001)** | **0.70** **(0.004)** | **0.60** **(0.014)** | **0.86** **(<0.001)** | -0.11 (0.704) | | |
| % Lignin | **0.63** **(0.009)** | 0.36 (0.191) | 0.33 (0.213) | **0.76** **(<0.001)** | 0.03 (0.905) | **0.62** **(0.011)** | |
| $I$ | 0.27 (0.316) | - 0.19 (0.491) | - 0.45 (0.083) | -0.36 (0.165) | -0.08 (0.837) | -0.29 (0.284) | -0.28 (0.300) |
| % H$_{cr}$ | **-0.68** **(0.004)** | **- 0.71** **(0.003)** | - 0.40 (0.122) | **-0.59** **(0.014)** | -0.44 (0.085) | **-0.67** **(0.005)** | 0.43 (0.094) |
| $EI$ | 0.14 (0.612) | 0.18 (0.526) | -0.17 (0.519) | -0.05 (0.841) | 0.14 (0.593) | -0.01 (0.97) | -0.01 (0.970) |
| Work-to-bend | -0.29 (0.535) | 0.14 (0.760) | -0.57 (0.180) | -0.39 (0.383) | -0.25 (0.589) | -0.25 (0.589) | 0.00 (1.000) |
| WSF | 0.14 (0.612) | 0.06 (0.829) | 0.40 (0.140) | -0.34 (0.221) | -0.11 (0.704) | 0.11 (0.819) | 0.00 (1.00) |
| Seed mass (g) | 0.21 (0.610) | 0.33 (0.420) | 0.24 (0.570) | 0.14 (0.736) | 0.29 (0.493) | 0.21 (0.610) | 0.10 (0.823) |

Table 1-4. Continued

| | $I$ (mm$^4$) | % H$_{cr}$ | $EI$ (N m$^2$) | Work-to-bend (J)* | WSF (radians/N) |
|---|---|---|---|---|---|
| Toughness | | | | | |
| Density | | | | | |
| % Total fiber | | | | | |
| % Hemicell | | | | | |
| % Cellulose | | | | | |
| % Lignin | | | | | |
| $I$ | | | | | |
| % H$_{cr}$ | 0.17 (0.528) | | | | |
| $EI$ | **0.87 (<0.001)** | -0.12 (0.667) | | | |
| Work-to-bend | **0.86 (0.014)** | 0.00 (1.000) | **0.99 (<0.001)** | | |
| WSF | **-0.81 (<0.001)** | 0.08 (0.790) | **- 0.87 (<0.001)** | **-0.857 (0.014)** | |
| Seed mass (g) | **0.74 (0.037)** | 0.10 (0.823) | **0.79 (0.021)** | 0.64 (0.119) | **-0.82 (0.023)** |

Shown are Spearman correlation coefficients for tests performed on species means obtained at each harvest ($N = 16$) with $P$ values in parentheses and significant correlations in bold. For correlations with work-to-bend and seed mass, only values of T1 were used ($N = 8$). Material properties included modulus of elasticity ($E$), fracture toughness (tough), density, % NDF (non-detergent fiber), % cellulose, % hemicellulose, and % lignin. Structural measurements integrating material traits and morphology included % critical height (% H$_{cr}$), flexural stiffness ($EI$), work-to-bend, and whole stem flexibility (WSF). Second moment of area ($I$) considered only size and shape.

Table 1-5. Effect of species and harvest time on material and structural traits of leaves. Shown are F values from two way ANOVAs performed on log-transformed values; d.f. = 7,1; * $0.001 < P < 0.05$, ** $P < 0.001$.

| Biomechanical measurement | Effect | | |
|---|---|---|---|
| | Species | Time | Species*Time |
| Lamina fracture toughness (J m$^{-2}$) | 32.9** | 1.5 | 10.9** |
| Midvein fracture toughness (J m$^{-2}$) | 47.7** | 49.9** | 6.4** |
| Leaf density (g cm$^{-3}$) | 44.0** | 113.6** | 15.1** |
| % NDF | 5.5** | 1.7 | 1.9 |
| % Hemicellulose | 36.2** | 0.1 | 0.6 |
| % Cellulose | 6.9** | 0.1 | 1.6 |
| % Lignin | 24.4** | 10.4* | 2.2 |
| Specific leaf area (cm$^2$g$^{-1}$) | 119.3** | 46.6** | 2.0 |
| Force of fracture (N) | 46.7** | 2.4 | 5.0** |

Table 1-6. Relationships among leaf biomechanical traits for seedlings of eight tree species.

| | Lamina toughness (J m$^{-2}$) | Midvein toughness (J m$^{-2}$) | Leaf density (g cm$^{-3}$) | % NDF | % Hemicell | % Cellulose | % Lignin | Leaf thickness (mm) | SLA (cm$^2$g$^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|
| Midvein toughness | **0.68** **(0.004)** | | | | | | | | |
| Leaf density | **0.52** **(0.039)** | **0.67** **(0.005)** | | | | | | | |
| % NDF | 0.21 (0.438) | 0.04 (0.897) | 0.31 (0.249) | | | | | | |
| % Hemicell | -0.17 (0.520) | -0.11 (0.664) | 0.15 (0.579) | 0.30 (0.264) | | | | | |
| % Cellulose | **0.74** **(< 0.001)** | **0.67** **(0.005)** | 0.33 (0.213) | 0.29 (0.279) | -0.07 (0.787) | | | | |
| % Lignin | 0.03 (0.914) | -0.33 (0.217) | -0.05 (0.846) | **0.59** **(0.017)** | -0.25 (0.350) | -0.12 (0.664) | | | |
| Leaf thickness | 0.15 (0.580) | -0.03 (0.910) | -0.44 (0.087) | 0.04 (0.871) | (-0.39) (0.131) | 0.29 (0.274) | 0.17 (0.535) | | |
| SLA | **-0.58** **(0.019)** | **-0.67** **(0.005)** | **-0.56** **(0.020)** | -0.33 (0.209) | 0.24 (0.380) | **-0.61** **(0.012)** | -0.01 (0.983) | -0.34 (0.200) | |
| Force (N) | **0.84** **(< 0.001)** | **0.51** **(0.043)** | 0.18 (0.513) | 0.24 (0.374) | -0.41 (0.119) | **0.79** **(< 0.001)** | 0.17 (0.535) | **0.61** **(0.012)** | **-0.65** **(0.006)** |

Shown are Spearman correlation coefficients for tests performed on species means obtained at each harvest ($N$= 16) with $P$ values in parentheses, and significant correlations in bold. Material properties included lamina toughness, midvein toughness, % NDF (nondetergent fiber), % hemicellulose, % cellulose, % lignin, and whole-leaf tissue density. Structural variables integrating material traits and morphology were specific leaf area (SLA) and force of fracture (Force), which was the product of leaf toughness and thickness.

Table 1-7. Relationships among biomechanical traits of stems and leaves for seedlings of eight tree species.

| Biomechanical trait | $r_s$ | $P$ |
|---|---|---|
| Toughness (J m$^{-2}$) | | |
| Lamina | 0.45 | 0.092 |
| Midvein | 0.58 | 0.002 |
| Density (g cm$^{-3}$) | 0.80 | < 0.001 |
| % NDF | 0.58 | 0.019 |

Shown are Spearman correlation coefficients ($r_s$) for tests performed on species means obtained at each harvest ($N = 16$) and corresponding $P$ values.

Table 1-8. Relationships among % survival in shade and various seedling biomechanical traits of stems and leaves for seedlings of eight tree species.

| | T1 | | T2 | |
|---|---|---|---|---|
| | $r_s$ | $P$ | $r_s$ | $P$ |
| STEM | | | | |
| Material properties | | | | |
| $E$ | **0.79** | **0.021** | 0.69 | 0.058 |
| Toughness | 0.60 | 0.120 | **0.89** | **0.007** |
| Density | **0.93** | **<0.001** | **0.90** | **0.002** |
| % NDF | **0.74** | **0.037** | **0.71** | **0.047** |
| % Hemicellulose | 0.50 | 0.120 | 0.52 | 0.183 |
| % Cellulose | 0.48 | 0.233 | 0.45 | 0.260 |
| % Lignin | 0.38 | 0.352 | 0.60 | 0.120 |
| Structural properties | | | | |
| % $H_{cr}$ | -0.17 | 0.693 | -0.38 | 0.352 |
| $EI$ | -0.17 | 0.693 | -0.12 | 0.779 |
| Work-to-bend | -0.68 | 0.094 | - | - |
| WSF | 0.54 | 0.215 | 0.19 | 0.651 |
| LEAF | | | | |
| Material properties | | | | |
| Lamina toughness | 0.33 | 0.420 | **0.76** | **0.028** |
| Midvein toughness | 0.21 | 0.610 | 0.31 | 0.456 |
| Density | 0.64 | 0.086 | **0.93** | **<0.001** |
| % NDF | **0.81** | **0.015** | 0.45 | 0.260 |
| % Hemicellulose | 0.33 | 0.420 | 0.14 | 0.736 |
| % Cellulose | 0.36 | 0.385 | -0.05 | 0.912 |
| % Lignin | 0.43 | 0.289 | 0.24 | 0.570 |
| Structural properties | | | | |
| SLA | -0.52 | 0.183 | -0.60 | 0.120 |
| Force of fracture | 0.29 | 0.493 | 0.048 | 0.911 |

Mean % survival refers to the first column in Table 1-2. Shown are Spearman correlation coefficients ($r_s$) from tests performed on species means ($N = 8$) and their $P$ values. T1 and T2 = time when biomechanical measurements were taken (1 and 6 mo after leaf expansion, respectively).
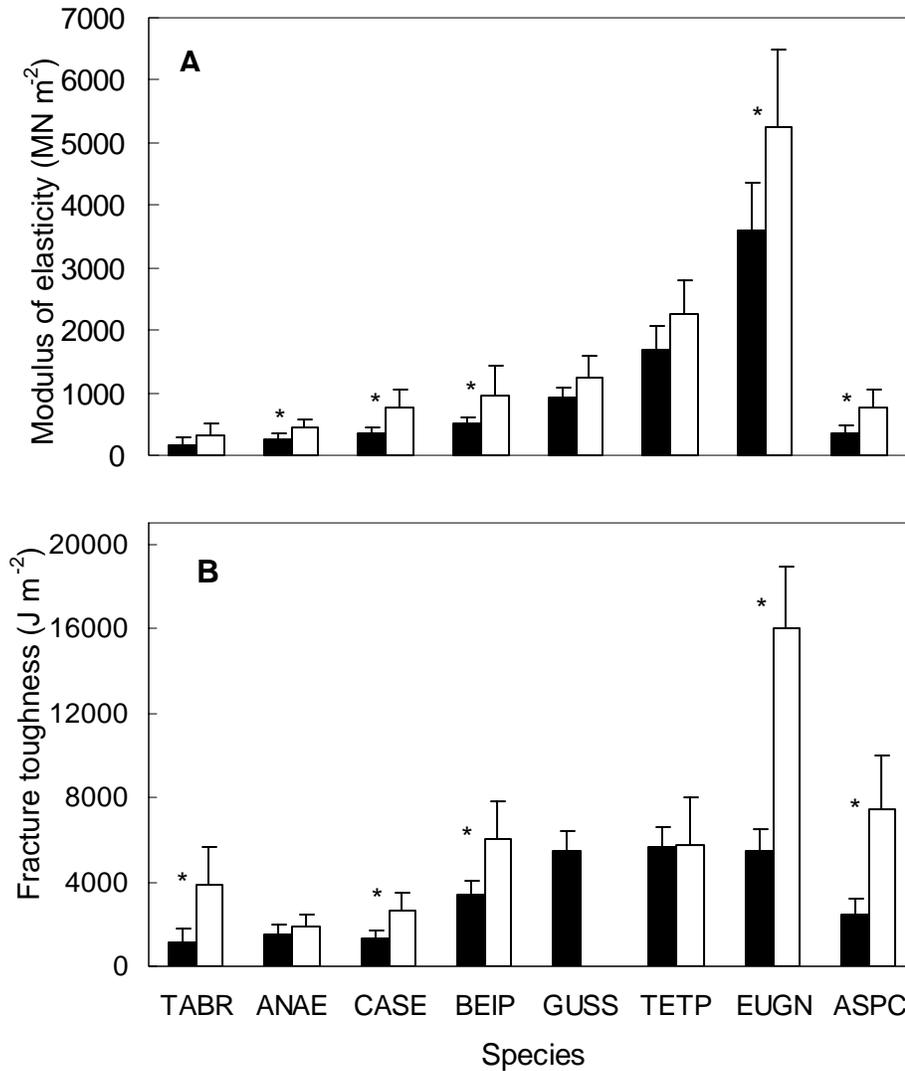
Figure 1-1. Means ($\pm$ 1 SD) material biomechanical traits of stems for seedlings of eight
tree species ordered from left to right by increasing shade tolerance at 1 mo
(T1, filled bars), and 6 mos (T2, open bars) after leaf expansion. A) Young's
modulus of elasticity (*E*). B) Fracture toughness. Asterisks indicate significant
difference between T1 and T2 (*P* value < 0.006 with Bonferroni correction).
Refer to Table 1-1 for species codes. No data available for stem toughness of
GUSS at T2 because the size of the stems exceed size capacity of the tester
(3 mm diameter).
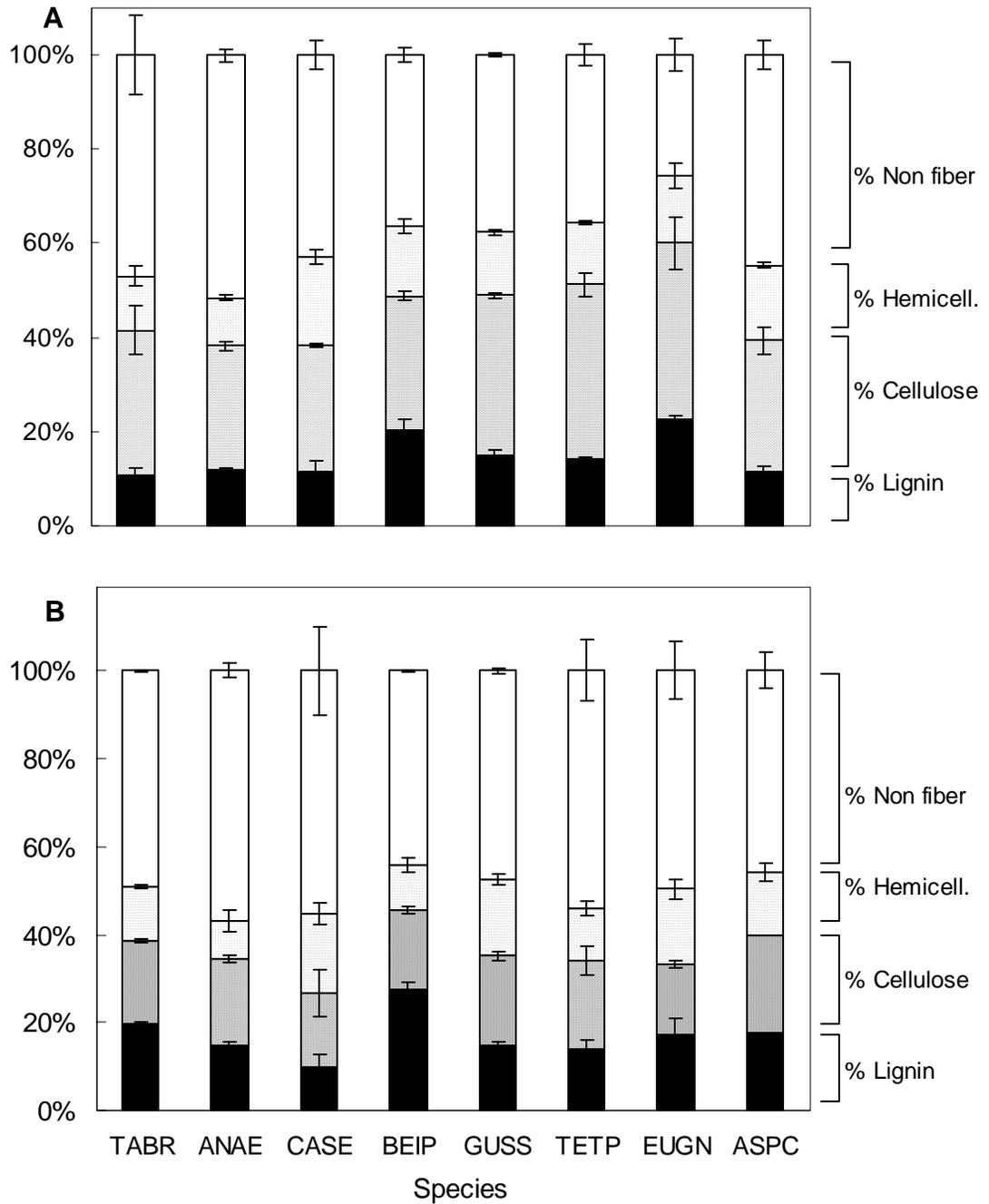
Figure 1-2. Mean ($\pm$ 1 SD) % fiber content (% NDF) for seedlings of eight tree species ordered from left to right by increasing shade tolerance at 6 mos after first leaf expansion (T2). A) Stems. B) Leaves. ANOVA results are shown in Table 1-3 for stems and Table 1-5 for leaves. For species codes refer to Table 1-1.
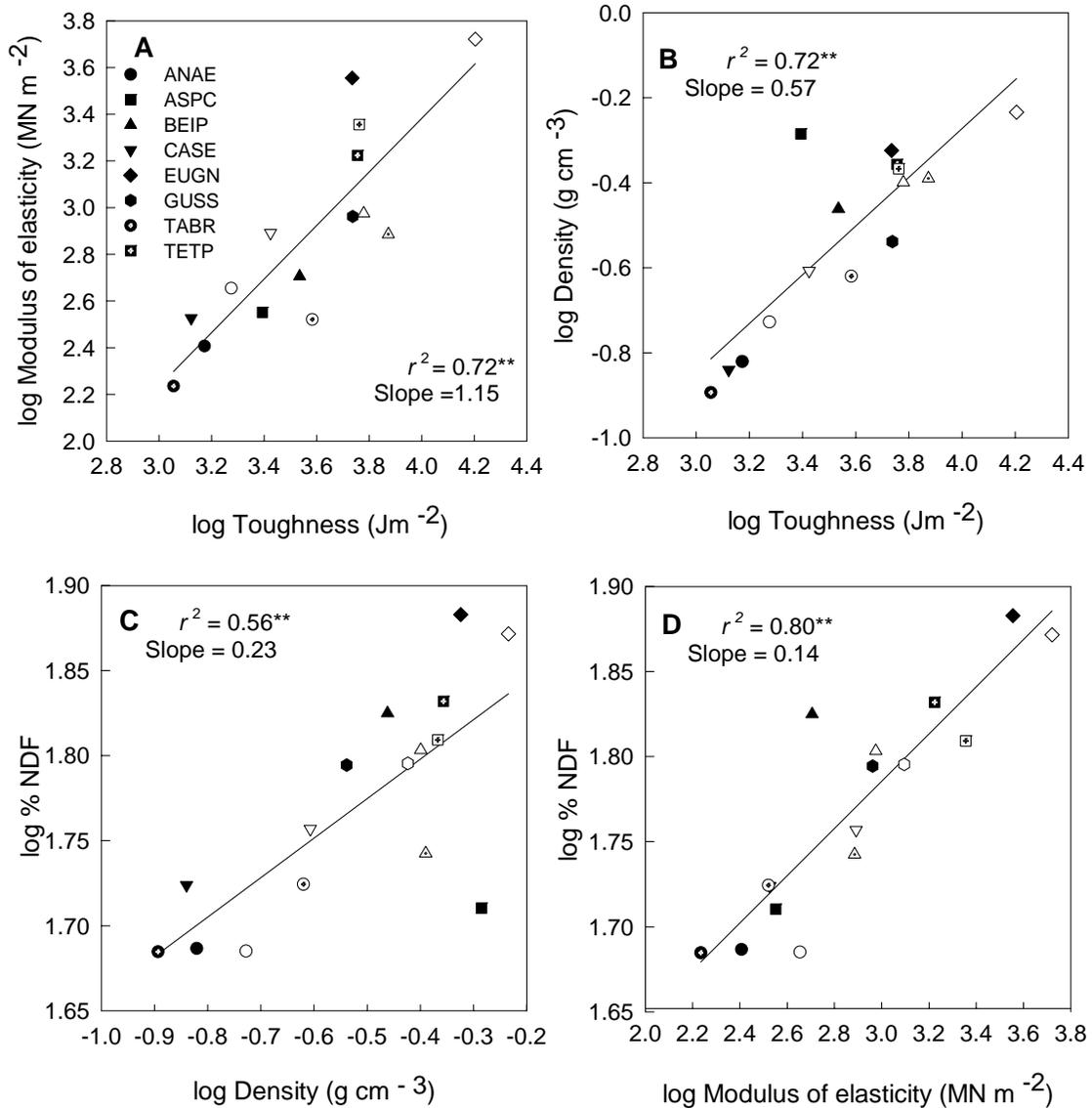
Figure 1-3. Log-log relationships between some material properties of stems for seedlings of eight tree species. Each point is a species mean at 1 mo (T1, filled symbols), and 6 mos (T2, open symbols) after leaf expansion; ** $P < 0.001$. Refer to Table 1-1 for species codes.

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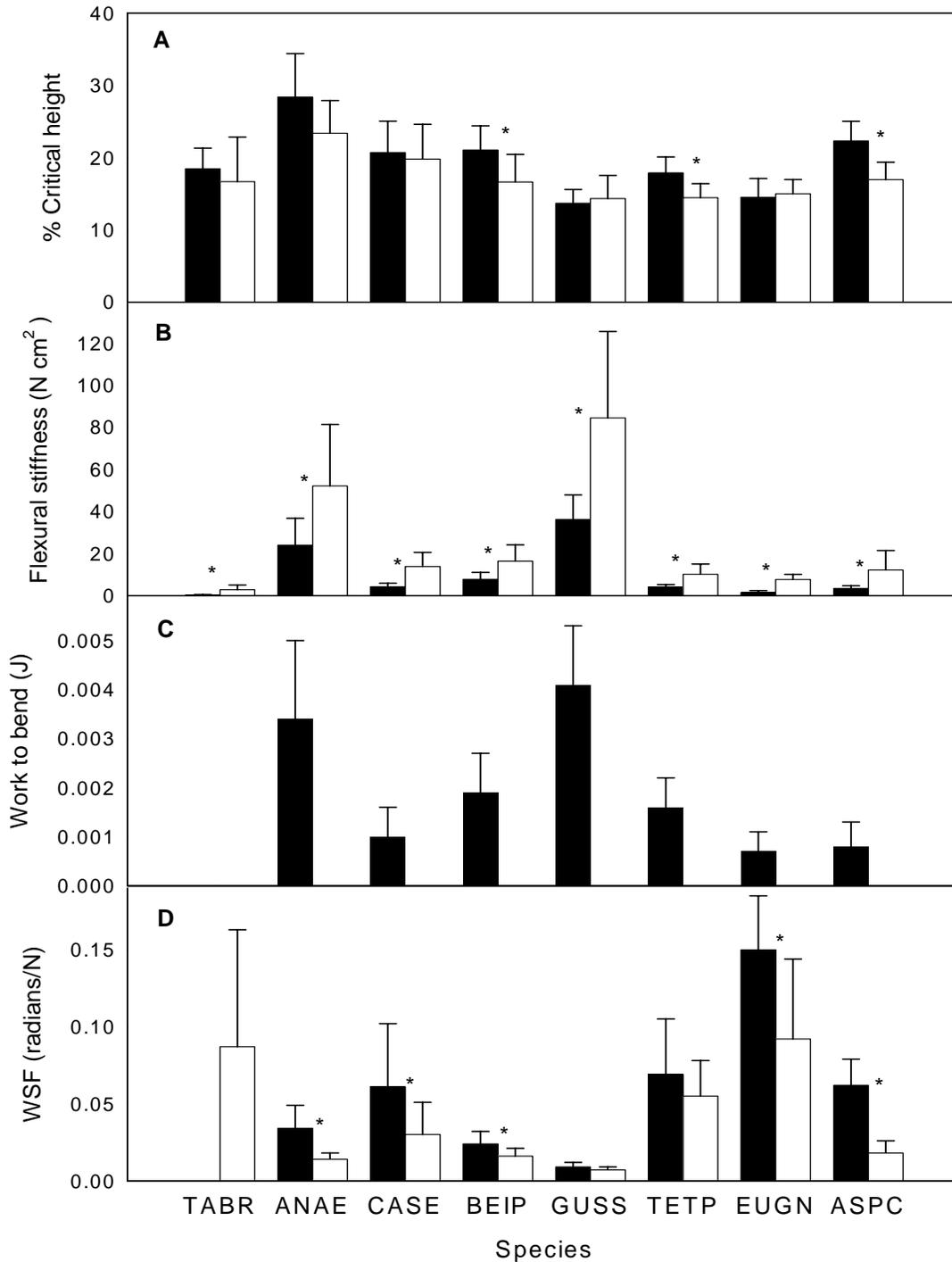


Figure 1-4. Means ($\pm$ 1 SD) structural biomechanical traits of stems for seedlings of eight tree species ordered from left to right by increasing shade tolerance at 1 mo (T1, filled bars), and 6 mos (T2, open bars) after leaf expansion. A) Percent critical height. B) Flexural stiffness. C) Work-to-bend. D) Whole stem flexibility (WSF). Asterisks indicate significant difference between T1 and T2 (*P* value < 0.006 with Bonferroni correction). Refer to Table 1-1 for species codes. Work-to-bend was only measured at T1. Work-to-bend and WSF could not be measured for TABR at T1 because of small size of seedlings.
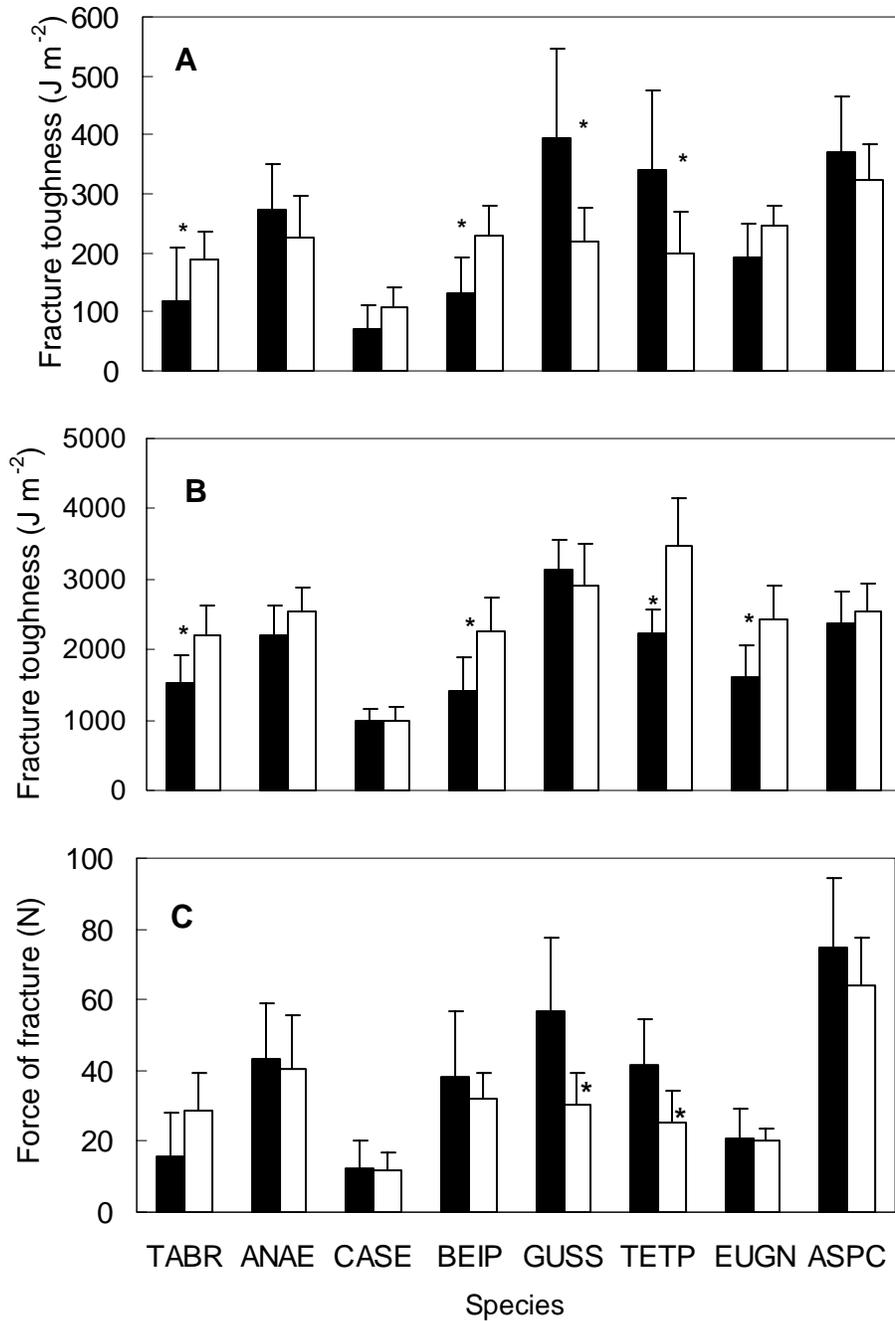
Figure 1-5. Means (± 1 SD) biomechanical traits of leaves for seedlings of eight tree
species ordered from left to right by increasing shade tolerance at 1 mo (T1,
filled bars), and 6 mos (T2, open bars) after leaf expansion. A) Lamina
fracture toughness. B) Midvein fracture toughness. C) Leaf force of fracture.
Asterisks indicate significant difference between T1 and T2 (*P* value <0.006
with Bonferroni correction). Notice the different scales between A and B.
Refer to Table 1-1 for species codes.
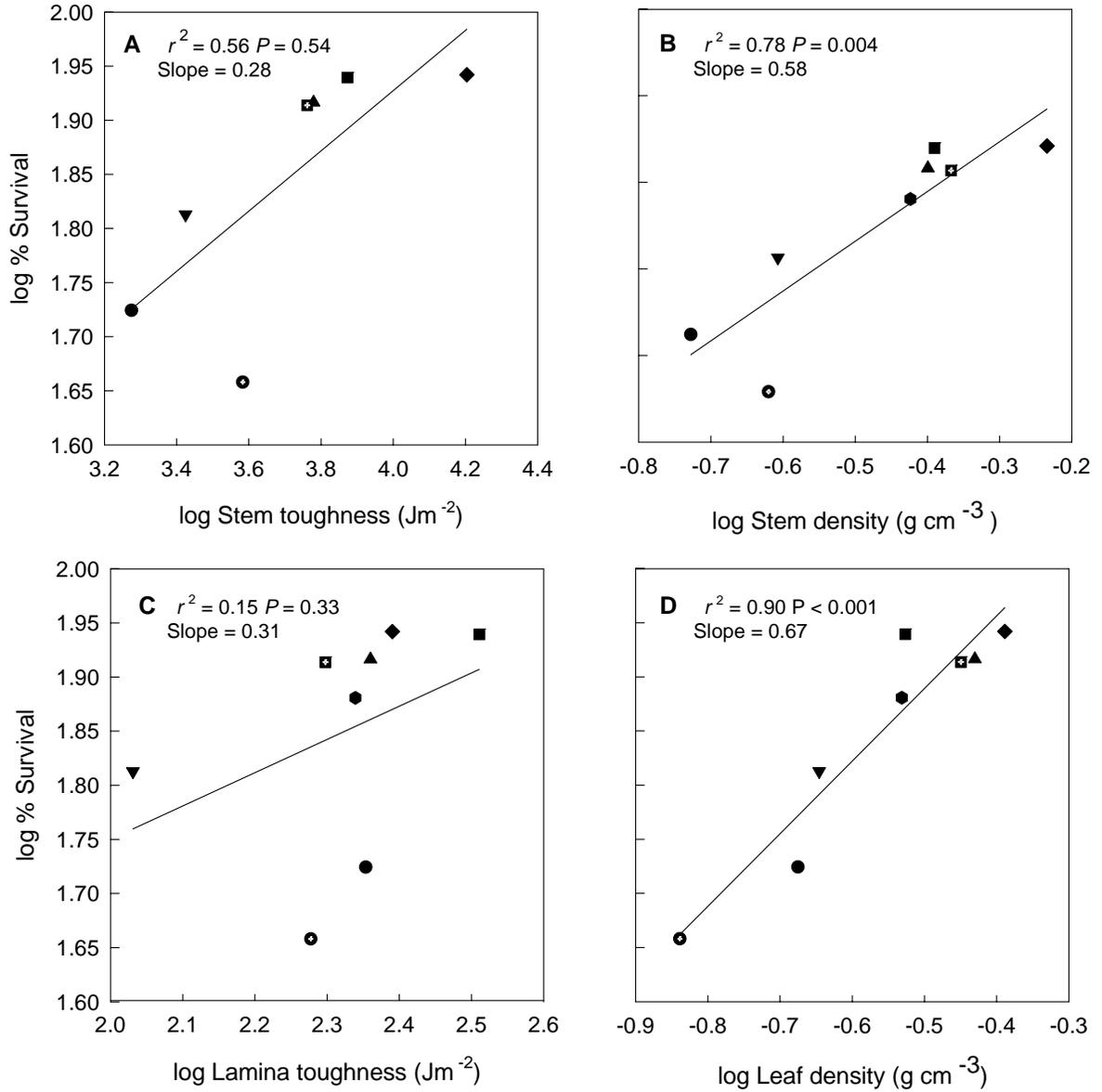
Figure 1-6. Log-log relationships between some biomechanical properties measured at 6 mos after first leaf expansion (T2), and % mean survival in shade for seedlings of eight tree species. A and B refer to stem traits, and C and D to leaf traits. Each point represents a species mean; symbols as in Figure 1-3.

CHAPTER 2
SPECIES DIFFERENCES IN SEEDLING SUSCEPTIBILITY TO BIOTIC AND
ABIOTIC HAZARDS IN THE FOREST UNDERSTORY

**Introduction**

For most plant species, mortality rates is highest during the seed and seedling

phases, thus early developmental stages are critical determinants of adult abundance and

distribution (Clark & Clark 1985, Condit, Hubbell & Foster 1995, Kitajima & Fenner

2000). Multiple mechanisms have been proposed to explain existing differences in

recruitment and survival across microsites in the forest understory, which lead to species-

specific distribution patterns and niche partitioning. For example, in the tropics

differential seedling survival in contrasting light environments has been related to

trade-offs involving growth, resource allocation, and defense (Kitajima 1994, Kobe 1999,

Montgomery & Chazdon 2002). Additionally, differences in seed size (Moles & Westoby

2004a,b), dispersal mechanisms (Howe & Schupp 1984, Chapman & Chapman 1996),

cotyledon function (Kitajima 1996, Ibarra-Manriquez, Martinez Ramos & Oyama 2001),

carbon allocation to storage (Canham *et al*. 1999, Myers 2005), and biomechanical

properties (Chapter 1) can all contribute to differential seedling survival across a light

gradient by allowing seedlings to avoid or respond to stresses in different ways.

A wide range of biotic and abiotic hazards resulting in physical damage can

seedling cause mortality. Numerous studies have addressed the importance of

invertebrate herbivory (Coley 1983, Aide & Zimmerman 1990, Benitez-Malvido,

Garcia-Guzman, & Kossmann-Ferraz 1999), pathogens (Auspurger 1983, 1984a),

vertebrate consumption and trampling (Osunkoya *et al*. 1992, Weltzin, Archer, &

Heitschmidt 1997, Gillman, Wright & Ogden 2002), and litterfall (Guariguata 1998,

Scariot 2000, Gillman *et al.* 2004) as mortality agents for seedlings. Mortality agents

such as disease, invertebrate herbivory, and vertebrate consumption are species-specific,

while mortality agents such as litterfall or vertebrate trampling affect seedlings from

different species indiscriminately. In other words, species vary in their susceptibility to

diseases or herbivores, but the chance of being trampled by animals or impacted by

falling litter is random. Additionally, all else being equal, species differences in mortality

due to severe mechanical hazards such as vertebrate trampling or large falling debris arise

mainly from their differential ability to respond and recuperate from damage, rather than

from the ability to evade it. In contrast, differential mortality among species due to

invertebrate herbivory, disease, or minor mechanical hazards (i.e., impact by small

litterfall) is also influenced by species differential ability to resist physical disturbances

by investing in strong materials and structures (Chapter 1). Species with high mechanical

strength in stems and leaves should 1) be affected less frequently by species-specific

damage agents such as herbivory and disease; 2) Suffer less and less intense mechanical

damage when affected by any mechanical damage agent; and, 3) die less frequently when

damaged by herbivores, disease, litterfall, and vertebrate trampling (Niklas 1992,

Chapter 1).

There are also differences in the types of damage inflicted on seedlings by damage

agents. Pathogens cause damping-off or tissue necrosis, while invertebrate herbivores,

vertebrate activity, and litterfall result in mechanical damage. Vertebrate activity often

results in bent, broken, uprooted or chewed stems, or in missing seedlings. Falling leaves

and branches can bend or break seedlings. Because seedlings face multiple stresses simultaneously or over short periods, it is difficult to determine the damage type resulting in the ultimate cause of mortality (Kitajima & Fenner 2000).

The main objective of my study was to describe first-year temporal patterns of seedling mortality, susceptibility to damage agents, and types of damage in eight species of tropical trees differing in their shade tolerance. Seedlings were transplanted to the forest understory and temporal patterns of damage susceptibility analyzed by constructing survivorship curves. Additionally, artificial seedlings constructed of plastic straws and wire, were "planted" with the real seedlings and monitored to assess susceptibility to damage agents from a community perspective. The artificial seedling approach has been frequently used to estimate potential damage by litterfall and vertebrate trampling (Clark & Clark 1989, McCarthy & Facelli 1990, Mack 1998, Scariot 2000, Roldan & Simonetti 2001, Drake & Pratt 2001, Gillman, Wright & Ogden 2002). Here, I further assess the efficacy of the artificial seedling method for predicting real seedling damage and mortality by comparing artificial and adjacent real seedlings that were transplanted to the forest understory.

## Materials and Methods

### Study Site and Species

This study was conducted in a seasonally moist tropical forest, on Barro Colorado Island (BCI), Panama (9º 10' N, 79º 51' W). Average annual precipitation is 2600 mm, 90% of which falls primarily between May and December (Windsor 1990). Ecological characteristics of BCI are well described in Croat (1978) and Leigh, Windsor & Rand (1982). The experiment took place in young forest (100-300 yrs, Foster & Brokaw 1982)

with abundant palms (mainly *Astrocarium standleyanum* and *Oenocarpus panamanus*) and evidence of frequent physical disturbances such as tree and branch falls.

Seeds of eight common tree species, that differ in ecological characteristics such as dispersal mode, cotyledon type, and seedling establishment probability (Table 1-1) were collected during the dry season of 2003 and germinated in a shade house. Seedlings from the eight species differed in time of germination (from approximately 5 days for *Aspidosperma cruenta* to 36 days for *Eugenia nesiotica*), number of leaves, and size (Table A-3). Species with the largest seedlings at germination were *Gustavia superba* and *Anacardium excelsum*, while the smallest was *Tabebuia rosea*. Species were selected based on seed availability during 2003 on BCI from a range of shade tolerance (K. Kitajima personal communication). Species ranged from shade-tolerant for an intermediate period (*T. rosea*) to shade-tolerant with slow growth in shade (*A. cruenta*) according to Augspurger (1984b). Additionally, according to a long-term study in BCI the study species differ dramatically in their recruitment index, which is a measure of a species ability to recruit seedlings that survive at least 1 yr relative to the number of seeds dispersed to the same microsite throughout that year (Wright *et al*. 2003, Table 1-1). The eight study species also varied substantially in the biomechanical properties of their stems and leaves (Chapter 1), which I expected to lead to differential susceptibilities and responses to mechanical damage.

**Experimental Design**

In June 2003, 755 seedlings from the eight study species were transplanted, at first leaf expansion, to 100 stations located randomly along a 9 km network of trails. The stations were at least 5 m away from the trail and separated by a minimum of 50 m. At each station, one seedling of each species was planted within a 1 m$^2$ area, and examined

every 1-2 wks for 8 mos and every 4 wks for four additional months, for a total of

22 censuses between June 2003 and May 2004. Because of limited seed availability,

*T. rosea* seedlings were transplanted to only 55 of 100 stations. During transplantation,

microsites were minimally altered (no litterfall or debris were removed). No evident

transplant shock (wilted or dried plants) was observed, presumably because abundant

rainfall during the transplanting period diminished the risk of desiccation.

In addition to the eight natural seedlings, two artificial seedlings made of plastic

and wire were "planted" at each station. The design of artificial seedlings followed Clark

& Clark (1989), but I used two sizes of artificial seedlings to evaluate the effect of

physical disturbance and mechanical damage on seedlings of different size classes. Each

large artificial seedling was made of two 200 mm-long transparent plastic straws oriented

in a cross and attached together with staples. A stiff, 3 mm-diameter x 100 mm-long wire

was inserted 20 mm into the vertical straw and the remaining 80 mm into the ground to

simulate a root (Figure 1 in Clark & Clark 1989). Small artificial seedlings were

constructed in the same way, except that they were made from 100 mm-long straws and

50 mm-long wire "root".

**Survival, Damage Agents, and Types of Mechanical Damage**

At each census, mortality, apparent damage agent, and damage types were

recorded. For real seedlings four main types of damage agents were recorded: vertebrate

activity, disease, litterfall, and missing without obvious indication of damage agent.

"Vertebrate activity" was characterized by plants that were uprooted, flattened, or having

damaged, broken, or chewed stems with no evidence of falling leaves or branches.

Although it was impossible to differentiate between vertebrate consumption and

trampling, chewed stems, missing cotyledons, and uprooted seedlings suggest that

vertebrate activity was mostly consumption-related. Seedlings were diagnosed as "diseased" when they exhibited necrotic tissue, or when they were severely wilted with at least one dry leaf. "Litterfall" was recorded when a seedling had a bent, damaged, or broken stem and there was direct evidence of litterfall or debris above it. "Missing" seedlings were those that could not be located and were presumed dead. This classification scheme underestimates litterfall damage and overestimates vertebrate activity, since all damaged stems without evidence of litterfall were considered as damaged by vertebrates. Likewise, missing seedlings within a relatively short census interval of 1-2 wks was likely to be caused by consumption of vertebrate browsers, also leading to an underestimation of vertebrate activity. A seedling was considered dead when it was completely dried, when the stem was cut in two and the lower portion uprooted, or when the whole seedling was missing. The four damage agents were not mutually exclusive. In fact, seedlings often died after being affected by two or more agents. It was not the intent of my study to determine the ultimate cause of mortality, but to describe the temporal patterns of these damage agents that may synergistically kill seedlings.

I also recorded the first occurrence of the four main types of mechanical damage that could be fatal: leaf damage, stem bent, stem broken, and seedling uprooted. A leaf was considered "damaged" if it was fractured, incomplete or had missing sections larger than 10% of the leaf area. A seedling with at least one damaged leaf was classified with "leaf damage". A stem was considered "bent" if it was curved or tilted at least 45º, and "broken" if it was fractured in two or more sections. A seedling was uprooted when it was completely pulled from the ground. Although the four types of mechanical damage

were not mutually exclusive, only the first type recorded on each plant was used for

calculation of "% damage fatality" at the end of the study. Furthermore, to be certain that

death (if it occurred) was caused by a particular damage agent, only plants affected by a

single damage type were considered. For each type of mechanical damage ($M_x$), I

calculated the likelihood of dying after receiving a given type of damage $P(D|M_x)$

expressed as the following formula (Gothelli & Ellison 2004):

$$P(D|M_x) = \frac{P\,(D \cap M_x)}{P\,(M_x)} \tag{2-1}$$

where $P(M_x)$ is the probability of receiving the damage type $M_x$, and $P(D)$ is the

probability of death. The conditional probability $P(D|M_x)$, multiplied by 100 and

expressed in %, was called "% damage fatality". I also evaluated the relationship between

material and structural stem properties and seedling susceptibility to mechanical damage,

by comparing species mean biomechanical traits measured in chapter 1 (Table 1-4) vs.

% damage fatality.

**Artificial Seedlings**

The artificial seedling method has been used in other studies to quantify damage

due to random disturbance agents such as litterfall and vertebrate trampling because

artificial seedlings are not susceptible to biotic species-specific agents of mortality such

as pathogens and herbivory. Here, artificial seedlings were censused simultaneously with

real seedlings to provide a comparison between real and artificial seedling damage and

mortality. An artificial seedling was considered damaged when it was bent such that at

least one of its arms was touching the ground, when it was flattened, cut, chewed, or

missing (Clark & Clark 1989). For comparison with previous studies, three standardized

categories of damage were recorded for artificial seedlings: vertebrate activity, litterfall,

and unknown. An artificial seedling was classified as damaged by "vertebrate activity" if it was flattened, chewed, cut, or missing with no evidence of litter or branch fall that could have caused the damage. If an artificial seedling was bent or flattened, with evidence of litterfall or debris above it, it was considered damaged by "litterfall". If a seedling was bent but there was no obvious cause, it was classified as "unknown". Therefore, the estimate of damage caused by litterfall is conservative, since it only reports artificial seedlings that were damaged by conspicuous litterfall and debris.

I compared the first occurrence of damage agents affecting real vs. artificial seedlings. Because missing artificial seedlings were included in the vertebrate activity category in previous studies (Gillman, Wright & Ogden 2002), I included missing real seedlings in the vertebrate activity category, such that when comparing artificial seedlings and real seedlings vertebrate activity refers to seedlings flattened, chewed, cut, or missing. In any case, it is likely that seedlings that suddenly disappeared (in an interval of one week) were eaten or uprooted by vertebrates. Additionally, when comparing real and artificial seedlings the "unknown" category was obtained from seedlings that were recorded as bent with no further evidence of damage; the "litterfall" category remained the same.

**Statistical Analyses**

Temporal patterns of the occurrence of seedling death and damage agents were analyzed using non-parametric Kaplan-Meier survival distribution functions (Collett 2003). Survival functions (also called hazard functions) describe the probability that an individual survives longer than a specified period, considering individuals at risk at the beginning of each interval and excluding censored values. An interval is defined as the lapse between two mortality events. Censors are individuals that "left" the study before

its conclusion (e.g., removed from the study) or individuals that were not dead at the time

of finalization of the experiment. In my study, censored plants were only those that were

alive at the end of the observation period. From the probability of hazard occurrence

during each census interval, survivorship curves throughout the entire period were drawn,

plotting the proportion of seedlings unaffected by the respective damage agent against

time. To observe each species behavior throughout different periods, additional

survivorship curves were drawn considering shorter intervals, of 0-2 mo, 2-6 mo, and

6-12 mo. The log-rank test and the Wilcoxon test (Pyke & Thompson 1986, Collett 2003)

were used to compare survival distribution functions for different species. The log-rank

test is more sensitive to differences in late survival times, while the Wilcoxon test is more

sensitive to differences in early survival times. However, here both tests had similar

outcomes, and therefore only results from log-rank tests are reported. For across-species

comparisons between survival proportions at the end of each period, Spearman rank

correlation coefficients were used. For interspecific comparison within types of damage,

likelihood chi-squared tests were used. Lastly, nonparametric Spearman correlation tests

were used to compare species mean biomechanical and ecological traits vs. % damage

fatality. For all analyses $\alpha = 0.05$ and all were performed JMP IN 4.0 (SAS Institute Inc.,

Cary, NC, USA).

## Results

**Seedling Survival**

Within the first 2 mos 59% of the transplanted seedlings died, and by the end of

1 yr 76% of transplanted seedlings were dead. The temporal pattern of mortality and

overall % mortality at the end of the first year differed among species (Figure 2-1).

Survival distribution functions varied among species for the entire 1 yr period (log-rank

$\chi^2 = 220.2$, d.f. = 7, $P < 0.001$; Figure 2-1D), and within each of shorter intervals

(0-2 mo: log-rank $\chi^2 = 220.2$, d.f. = 7, $P < 0.001$; 2-6 mo: log-rank $\chi^2 = 55.4$, d.f. = 7, $P <$

0.001; 6-12 mo: log-rank $\chi^2 = 49.6$, d.f. = 7, $P < 0.001$; Figures 2-1A to 2-1C). In

addition, species rankings of survival probability switched between intervals. Survival for

0-1 yr was determined mainly by survivorship during the first 2 mos, which differed from

survival in the following intervals. This is demonstrated by the high correlation between

the 0-2 mo period and the overall 1yr survival, and the lack of correlation between the

0-2 mo period with both the 2-6 mo and the 6-12 mo periods (Table 2-1).

**Damage Agents**

Vertebrate activity was the most common damage agent (Figure 2-2). Survival

functions differed significantly among damage agents calculated for all species combined

(log-rank $\chi^2 = 1496.9$, d.f. = 4, $P < 0.001$; Figure 2-2A). In addition, damage agents

affected species differentially. The percentage of seedlings affected by vertebrate activity

after 1 yr ranged from 31% for *Beilschmiedia pendula*, to 65% for *E. nesiotica* (log-rank

$\chi^2 = 56.0$, d.f. = 7, $P <0.001$; Figure 2-2B). However, there were more missing seedlings

of *B. pendula* than of the other species (log-rank $\chi^2 = 209.3$, d.f. = 7, $P <0.001$; Figure

2-2C) and most of these events happened in the first four weeks after transplant. In *B.

pendula*, 87% of the seedlings would have been affected by vertebrate activity if all

missing seedlings were included in the vertebrate activity category. *Tetragastris

panamensis, A. excelsum* and, *T. rosea* were the species most affected by disease.

Although, *T. rosea*, and *A. excelsum* were affected by disease mostly in the first 2 mos

after transplant, *T. panamensis* had a constant intensity of infection (log-rank $\chi^2 = 98.7$,

d.f. = 7, $P$ <0.001; Figure 2-2D). Only 4.1% of the seedlings were affected by litterfall, with no interspecific differences in damage agent distribution over time (log-rank $\chi^2$ = 13.7, d.f. = 7, $P$ >0.05).

**Types of Mechanical Damage**

Four types of mechanical damage were recorded during 1 yr: damaged leaves, bent stems, broken stems, and uprooted seedlings, caused by vertebrates, litterfall, or invertebrate herbivores (in the case of leaf damage). At the end of the study, 77% of seedlings showed some form of damage, of which leaf damage was the most frequent. After 1 yr, 30.6% exhibited leaf damage, 28.7% of the seedlings had broken stems, 23.9% had bent stems, and 25.6% had been uprooted (Table 2-2). These categories were not mutually exclusive. In fact, 45% of the damaged seedlings had two or more types of damage.

Species differed in their likelihood to die after suffering leaf damage or bent stems, but not after being uprooted or having their stem broken. Percent damage fatality (as defined by Formula 2-1) differed among species for leaf damage or bent stem (leaf damage: $\chi^2$ = 78.6, d.f. = 7, $P$ <0.001; stem bent: $\chi^2$ = 57.3, d.f. = 7, $P$ <0.001). In contrast, there was no interspecific difference in damage fatality for uprooted seedlings or those with broken stems (uprooted: $\chi^2$ = 14.0, d.f. = 7, $P$ = 0.052; stem broken: $\chi^2$ = 9.4, d.f. = 7, $P$ = 0.226). It should be pointed out that because of the low number of uprooted and broken seedlings in some species (cell $N$ < 5), results should be interpreted with caution. From all the biomechanical and ecological measurements tested (Table 1-4 in Chapter 1), only stem toughness, stem tissue density, and second moment of area were correlated with damage fatality (Table 2-3). Tougher, denser stems died less when their

stem was broken or bent than stems with weaker, less dense material. In contrast, species with larger stems (i.e., with large second moment of area) were more likely to die when their stem was broken.

**Artificial Seedlings**

After 1 yr, 9.5% of artificial seedlings were damaged by litterfall, 15.5% were damaged by vertebrate activity, and 22.5% were bent by unknown causes. Thus, damage levels on artificial seedlings were within the range of damage reported for other sites (Table 2-4). Overall, real seedlings were damaged more than artificial seedlings ($\chi^2 = 64.3$, d.f. = 1, $P$ <0.001; Figure 2-3) Artificial seedlings were damaged more by litterfall and by unknown causes, and less by vertebrate activity than each of the species of real seedlings. Large and small artificial seedlings did not differ in their damage frequencies ($\chi^2 = 6.0$, d.f. = 3, $P = 0.111$), and therefore they were averaged for comparisons with real seedlings and with previous studies.

Temporal patterns for each type of damage differed between artificial and real seedlings (Figure 2-4). Vertebrate activity damaged a much higher proportion of real than artificial seedlings, especially during the first 50 days. If missing seedlings were also considered to be affected by vertebrate activity, the difference became even stronger (log-rank $\chi^2 = 118.1$, d.f. =1, $P$ <0.001; Figure 2-4A). Real seedlings were particularly vulnerable to vertebrate activity during the first 2 mos after transplant, but artificial seedlings received a more constant rate of vertebrate damage. Litterfall damage was less than 10% for both artificial seedlings and real seedlings. Artificial seedlings were less affected during the first 6 mo, but the trend reversed during the subsequent period (log-rank $\chi^2 = 6.5$, d.f. =1, $P = 0.011$; Figure 2-4B). In addition, survival functions describing

the proportion of seedlings damaged by unknown causes, differed between artificial and real seedlings. Although real seedlings were more affected during the first 3 mo, the trend inverted and at the end of 1 yr, a larger proportion of artificial seedlings were affected by unknown causes (log-rank $\chi^2$ = 9.79, d.f. =1, $P$ = 0.002; Figure 2-4C).

## Discussion

### Survival, Damage Agents, and Types of Mechanical Damage

The combination of species-specific and indiscriminate damage agents, their temporal patterns, and the differential susceptibility to damage among species influences seedling performance in the forest understory. Consistent with other studies (Augspurger 1984a, Kitajima & Augspurger 1989, De Steven 1994), the proportion of seedlings dead after 2 mos was higher than in the 2-6 or 6-12 mo periods. Seedling mortality was highest during the first 2 mos after transplant, decreasing gradually and then becoming more constant over the remaining 8 mos (Figure 2-1). Although this was the trend for the eight species individually, the species mortality ranks during the 0-2 mo interval differed from the ranks during the 2-6 mo interval, or the 6-12 mo interval (Table 2-1). This observation suggests that mortality agents that had a greater effect during the first 2 mos became less important in the following 8 mo.

Vertebrates were the most common cause of damage overall, especially during the 0-2 mo period (Figure 2-2). Vertebrate activities included non-trophic interactions such as trampling, and trophic interactions including leaf herbivory and cotyledon consumption. During the initial 2 mo, low percentages of leaf herbivory (i.e., leaf damage) and high percentages of seedlings uprooted but left partially uneaten, with stems cut in half and cotyledons missing, suggest that cotyledon predation by vertebrates was the primary cause of mortality. Predation of large storage cotyledons has been recorded

as an important cause of mortality in previous studies (Sork 1987, Molofsky & Fisher 1993). Here, six of the eight study species have large-seeds (Table 1-1) and abundant cotyledon reserves that can attract vertebrate consumers, even months after germination (Smythe 1978). For example, *B. pendula,* an animal-dispersed species with large reserve cotyledons, suffered extremely high mortality during the first month after transplanting. Within the first week after transplanting 42% of the seedlings were missing, and by the end of the first month, 56% of the seedlings were missing and presumed dead. Cotyledon predation was potentially enhanced by soil disturbance during transplant, which could have attracted agoutis (*Dasyprocta punctata*). However, it has been shown that agoutis find buried seeds using predominantly olfactory cues (Smythe 1978). Thus, further investigations comparing cotyledon consumption in naturally germinated vs. transplanted seedlings are required to reach definitive conclusions.

Contrary to vertebrate damage, which affected almost 40% of seedlings during the first 2 mo, disease affected less than 10% of seedlings throughout the study. This observation differs from disease prevalence reported by Augspurger (1984a), who studied naturally germinated seedlings of nine wind-dispersed species on BCI. She found that the largest fraction of early seedling mortality under shaded conditions was due to pathogens. However, Augspurger (1984a) studied naturally germinated seedlings that were already established, diminishing the probability of recording early cotyledon predation, similar to that reported for *B. Pendula* here. Nevertheless, the two species (*A. cruenta* and *T. rosea*) overlapping between studies exhibited similar levels of mortality at the end of 2 mos. Mortality recorded for *A. cruenta* in Augspurger (1984a) and in my study was 20% and 27%, respectively. For *T. rosea* mortality was 65% in both studies.

Differences in survivorship between species reflected the interaction between likelihood of damage and the ability to tolerate damage-induced stress. Contrary to my expectation shade-tolerant species with stronger material properties (i.e., tougher stems and higher stem tissue density), did not differ from species with weaker material properties in the probability of suffering mechanical damage, but once damaged they were less likely to die than species with weaker stems (Table 2-2). Contrary to this pattern, *A.cruenta*, a shade-tolerant species with weak stems (Chapter 1), was the least likely to die after suffering mechanical damage, suggesting that other factors, such as carbohydrate storage reserves in stems and roots play an important role in the ability of seedlings to tolerate mechanical damage (Myers 2005). Additionally, the probability of survival after being damaged (measured as damage fatality) was different depending on the type of damage received. For example, seedlings that were uprooted or had broken stems usually died, while seedlings that suffered leaf damage or bent stems were more likely to survive. My results (and previous studies, Marquis & Braker 1994) suggest that leaf damage (caused by leaf herbivory) constitutes a less severe stress than stem bending and breakage.

Numerous studies have emphasized the benefits of having a large seed, resulting in a large seedling and increased survival (Paz & Martinez- Ramos 2003, Green & Juniper 2004, Moles & Westoby 2004b). In contrast, in my study there was no correlation between seed size and seedling survival, susceptibility to damage agents, or incidence of different types of damage (Table 1-4). One possible reason is that on BCI large seeded species face strong pressures from vertebrate cotyledon predators. Barro Colorado Island, due to the absence of top predators, supports high densities of medium sized mammals

(Glanz 1982) that can have a large effect on tree regeneration patterns through high predation rates on large seeded species before and after germination (Asquith, Wright & Clauss 1997). Additionally, the likelihood of death after stem breakage increased with stem size (Table 2-3), suggesting that large size is not always beneficial.

**Artificial Seedlings**

The comparison between artificial vs. real seedlings revealed that on BCI damage agents affecting artificial seedlings were not good predictors of damage agents affecting the real seedling community (Figure 2-3). Moreover, artificial seedling damage was not a good predictor of mortality for transplanted seedlings because real seedlings were more affected by vertebrate consumption than artificial seedlings, especially during the first 2 mos. However, artificial seedlings were more affected by litterfall, in terms of cumulative damage, after 1 yr. Consistent with my results, Gillman, Wright & Ogden (2002) found that artificial seedling damage was not a good predictor of mortality of naturally germinated seedlings in five evergreen temperate forests in New Zealand. Because artificial seedlings are not significantly consumed by vertebrates, they would be accurate predictors of mechanical damage, only in environments where indiscriminate, non-trophic damage agents (e.g., litterfall, vertebrate trampling) are more frequent than trophic interactions.

Temporal patterns of mechanical damage also differed between real and artificial seedlings. Real seedlings were severely affected by vertebrate activity during the first 2 mos with a rapid decline afterwards, while artificial seedlings experienced a relatively constant rate of damage (Figure 2-4). This difference suggests that damage agents that affect seedlings indiscriminately (e.g., litterfall) became important after the early establishment period when seedlings suffer heavily from vertebrate consumers.

The total percentage of artificial seedlings damaged on BCI after 1 yr, was within

the range reported in other studies (Table 2-4). However, the percentage ($9.5 \pm 2.1\%$ $yr^{-1}$)

of artificial seedlings damaged by litterfall on BCI was lower than the percentage

reported in most other tropical forests, possibly due to differences in rainfall, canopy

composition, and topography (Van Der Meer & Bongers 1996,Gillman *et al*. 2004).

Seedlings in the old secondary forest on BCI suffered an intermediate frequency of

mechanical damage. La Selva, Costa Rica (Clark & Clark 1989) exhibited the highest

percentage of damaged artificial seedlings ($82.4\%$ $yr^{-1}$), and the intensive hunted forest in

Beni, Bolivia (Roldán & Simonetti 2000) the lowest ($25\%$ $yr^{-1}$). However, in the Bolivian

study, litterfall damage was not considered. The large variation between studies suggests

that either the probability of being affected by mechanical damage differs widely across

forest communities, or researchers used different criteria to classify agents of mechanical

damage. Interestingly, the most frequent agent of mechanical damage reported in each

study, was usually the focal agent of interest for each author.

**Conclusions**

Survivorship analyses revealed that diverse ecological pressures, such as

vertebrate predation and disease affect seedlings differentially through time and among

species. For example, seedlings from *T. panamensis* suffered little seedling mortality due

to vertebrate predation during the initial 2 mo, but became more susceptible to disease in

the following period. In contrast, seedlings from *E. nesiotica* and *B. pendula* were

severely damaged by vertebrate predation in the initial 2 mo, but attained high survival

rates if they escaped predation. Furthermore, species such as *A. cruenta* that suffered little

mechanical damage overall can be limited by other factors, such as seed production and

dispersal (Augspurger 1984a). Additionally, differences among damage agents affecting

real and artificial seedlings indicate that litterfall can become an important cause of damage after the early establishment period. Although there was no relationship between shade tolerance and the types of mechanical damage affecting each species, shade-tolerant species with stronger stems survived more often after damage, suggesting that investment in strong stems is beneficial for seedling performance. The combined effects of species-specific and indiscriminate damage agents, and species differences in the responses to damage determine seedling performance. The resulting differences in survival allow different species to succeed under different ecological conditions, ultimately contributing to plant diversity in tropical forests.

Table 2-1. Relationships among species rankings of survival probability during the specified interval for seedlings of eight tree species.

|         | 0-2 mo          | 2-6 mo          | 6-12 mo         |
| ------- | --------------- | --------------- | --------------- |
| 2-6 mo  | 0.50 (0.207)    |                 |                 |
| 6-12 mo | 0.55 (0.160)    | **0.90 (0.002)** |                |
| 0-12 mo | **0.90 (0.002)** | **0.79 (0.021)** | **0.83 (0.010)** |

Order of species codes listed in Fig 2-1 A-C. Shown are Spearman correlation coefficients with their corresponding $P$ values in parentheses and significant correlations in bold.

Table 2-2. Percent damage fatality of four types of mechanical damage on eight tree species during 1 yr in the forest understory.

| Sp. code | Leaf damage | | Stem bent | | Stem broken | | Uprooted | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | $N$ | % Fatality | $N$ | % Fatality | $N$ | % Fatality | $N$ | % Fatality |
| TABR | 20 | 100.0 | 20 | 100.0 | 4 | 100.0 | 22 | 95.5 |
| ANAE | 37 | 97.3 | 39 | 100.0 | 36 | 100.0 | 36 | 100.0 |
| CASE | 45 | 64.4 | 17 | 76.5 | 31 | 100.0 | 16 | 100.0 |
| BEIP | 7 | 100.0 | 9 | 88.9 | 22 | 100.0 | 16 | 100.0 |
| GUSS | 47 | 44.7 | 25 | 48.0 | 36 | 94.4 | 35 | 85.7 |
| TETP | 35 | 48.6 | 19 | 57.9 | 19 | 94.7 | 9 | 100.0 |
| EUGN | 9 | 22.2 | 28 | 57.1 | 44 | 93.2 | 41 | 97.6 |
| ASPC | 31 | 32.3 | 23 | 47.8 | 25 | 92.0 | 18 | 88.9 |
| Total | 231 | 61.5 | 180 | 72.2 | 217 | 96.3 | 193 | 95.3 |

$N$ = total number of seedlings affected by each damage type. Damage types are not mutually exclusive. For species codes refer to Table 1-1.

Table 2-3. Relationships among stem biomechanical traits and % damage fatality for seedlings of eight tree species.

| Biomechanical properties | Types of mechanical damage | |
|---|---|---|
| | Stem broken | Stem bent |
| Modulus of elasticity | -0.36 (0.388) | - 0.61 (0.108) |
| Stem toughness | **-0.77 (0.044)** | **- 0.82 (0.024)** |
| Stem density | **-0.79 (0.019)** | **-0.71 (0.048)** |
| % NDF | -0.406 (0.318) | -0.69 (0.056) |
| Second moment of area of stem | **0.79 (0.019)** | 0.61 (0.108) |
| Flexural stiffness | 0.61 (0.109) | 0.54 (0.169) |

Shown are Spearman correlation coefficients for tests performed on species means ($N = 8$) with $P$ values in parentheses and significant correlations in bold; % NDF = percent non-detergent fiber.

Table 2-4. Percentage of artificial seedlings affected by specified damage agents in this and other published studies in different forest communities. Means (yr$^{-1}$) $\pm$ 1 SD when applicable.

| Forest type | Site | Study length | $N$ | Litterfall | Vertebrate activity | Unknown | Undamaged | Study |
|---|---|---|---|---|---|---|---|---|
| Tropical wet forest | La Selva, Costa Rica | 1 yr | 500 | 19.2 | 21.0 | 42.2 | 17.6 | Clark & Clark (1989) |
| Tropical wet forest | Crater Mountain, Papua New Guinea | 1 yr | 418 | 13.8 | 7.0 | 11.0 | 65.3 | Mack (1998)[a] |
| Seasonal tropical forest | BDFFP, Manaus, Brazil | 1 yr | 100 | 21.7 | 9.7 | 8.6 | 60 | Scariot (2000)[b] |
| **Seasonal tropical forest** | **BCI, Panama** | **1 yr** | **100** | **9.5 $\pm$ 2.1** | **15.5 $\pm$ 4.9** | **22.5 $\pm$ 4.9** | **52.5 $\pm$ 6.4** | **This study[c]** |
| Tropical *terra firme* forest | OHF Beni, Bolivia | 6 mo | 500 | — | 80 | 5 | 15 | Roldán & Simonetti (2000)[d] |
| | IHF Beni, Bolivia | | 500 | — | 13 | 12 | 75 | |
| Montane tropical forest | (+ Pigs) Mauna Loa, Hawaii | 1 yr | 150 | 15.3 | 4.7 | 11.3 | 68.7 | Drake & Pratt (2001)[e] |
| | (- Pigs) Mauna Loa, Hawaii | | 150 | 20 | 0 | 0 | 80 | |
| Evergreen temperate forest | North Island, New Zealand | 2 yr | 200 | 6.1 $\pm$ 5.8 | 2.8 $\pm$ 2.2 | — | — | Gillman, Wright & Ogden (2002)[f] |
| Temperate forest | New Jersey, USA | 10 mo | 200 | 2 | 39 | 13 | 44 | McCarthy & Facelli (1990)[g] |

[a] Total shown adds to 99.1% seedlings, and the remaining 02.9% artificial seedlings were damaged by water erosion. [b] data for continuous forest averaged for the three study sites. BDFFP = Biological Dynamics of Forest Fragments Project. [c] Average from large and small artificial seedlings damaged ($\pm$ 1 SD). BCI = Barro Colorado Island. See text for methodological details. [d] OHF = Occasionally Hunted Forest, IHF = Intensively Hunted Forest; approximate damages were taken from Figure 2, since exact numbers were not shown in the study. Authors did not record % litterfall damage. [e] Half of the artificial seedlings were fenced to exclude pigs (- pigs). [f] Shown are averages ($\pm$ 1 SD) from five sites included in the study. Only non-trophic vertebrate activity was recorded. Undamaged or unknown fractions were not reported. [g] Only forest habitat data are shown. Total adds to 98% seedlings, the remaining 2% AS were damaged by "frost heaving".
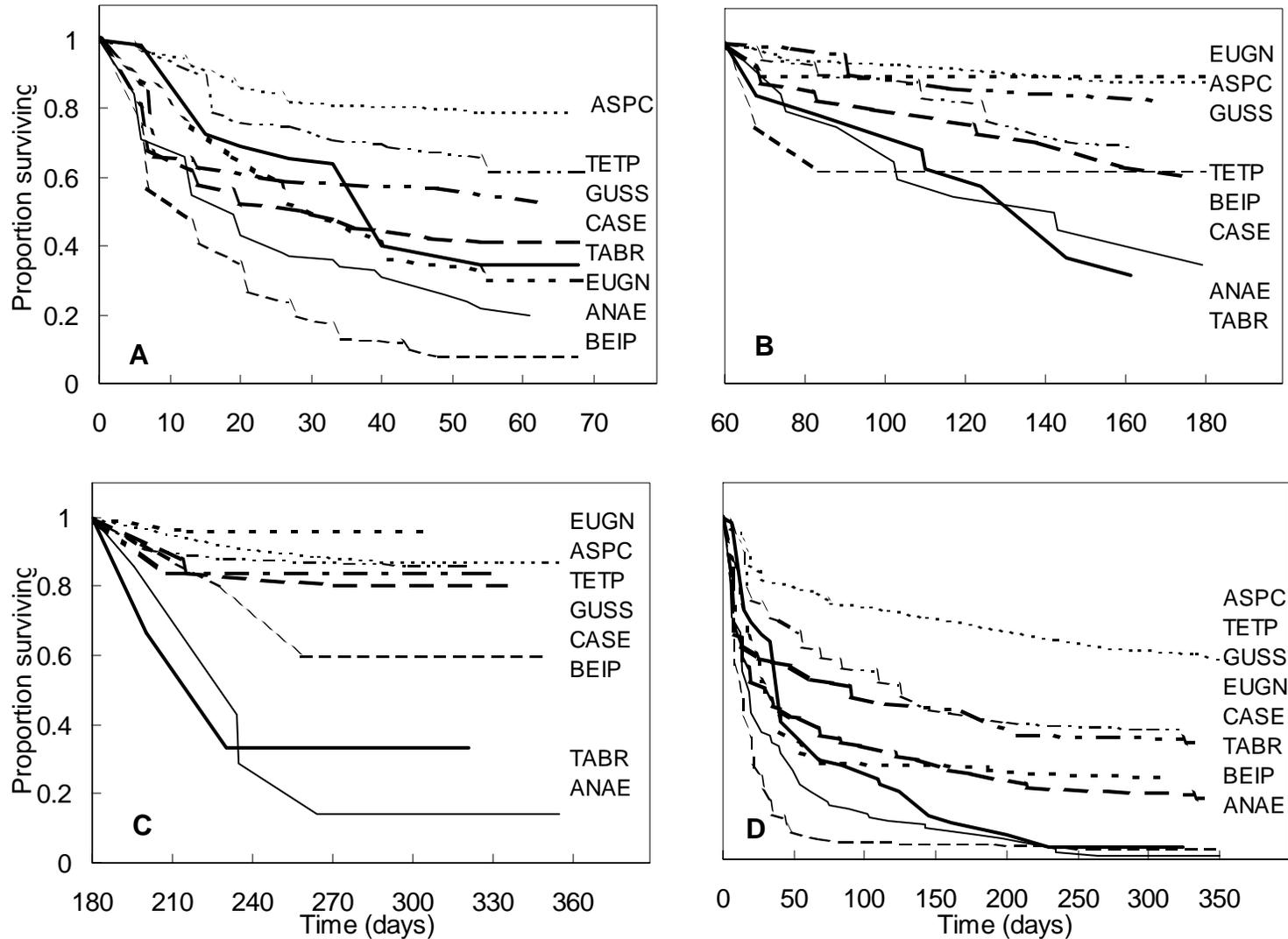
Figure 2-1. Kaplan-Meier survivorship curves for seedlings of eight tree species transplanted to the forest understory. Survivorship is relative to the number of seedlings alive at the beginning of each period; A) 0-2 mo, B) 2-6 mo, C) 6-12 mo, and D) total study period (0-12 mo). For species codes refer to Table 1-1.
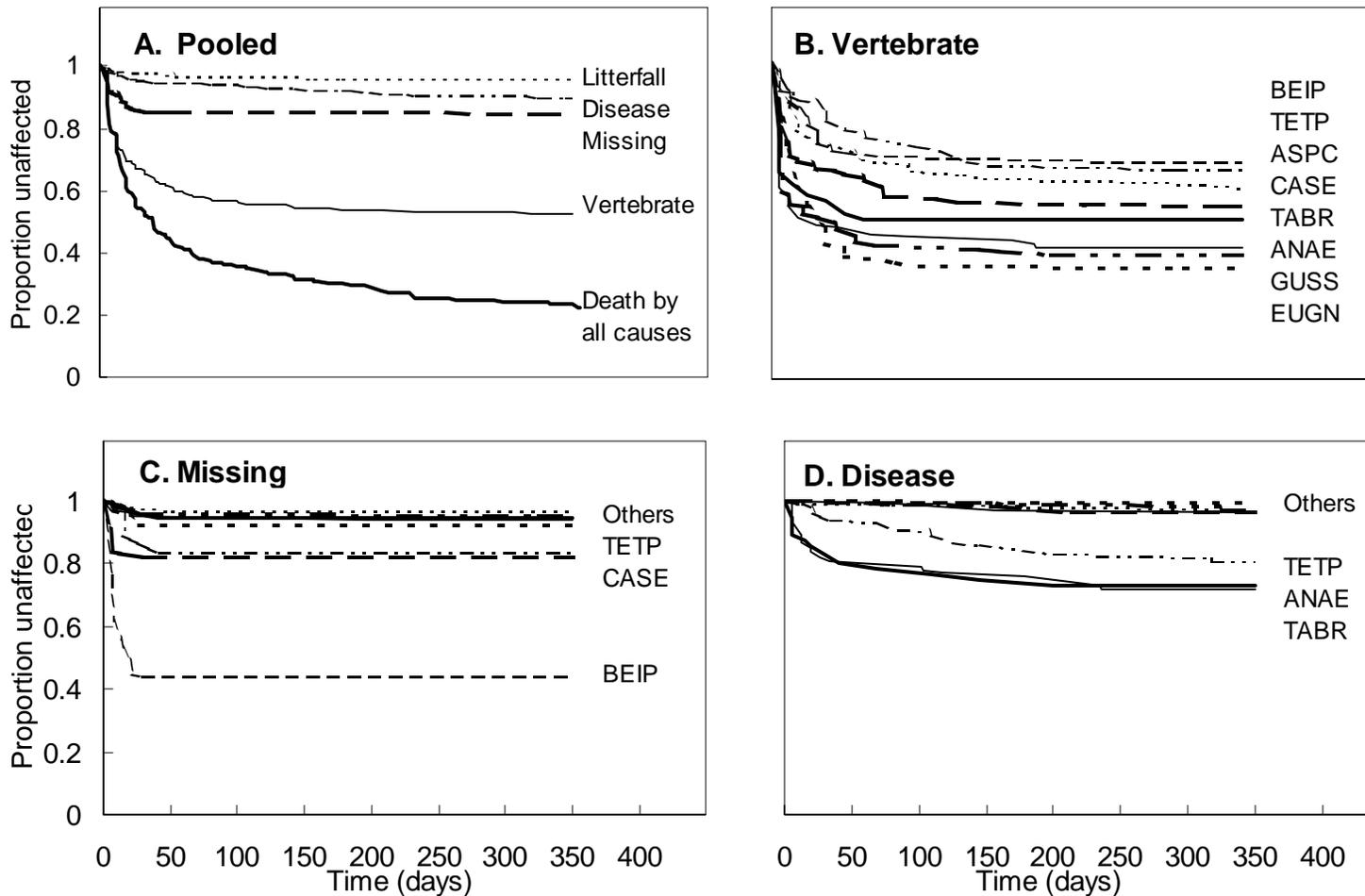
Figure 2-2. Kaplan-Meier survivorship curves (proportion of seedlings yet to be hit by specified damage agents plotted against time) for seedlings of eight tree species transplanted to the forest understory. A) Comparison of agents of mechanical damage for the pooled data of the eight study species. B) Vertebrate activity on each species (uprooted, flattened, chewed or broken stems; see methods). C) Seedlings missing most likely due to consumption by vertebrates and presumed dead. D) Disease. For species codes refer to Table 1-1.
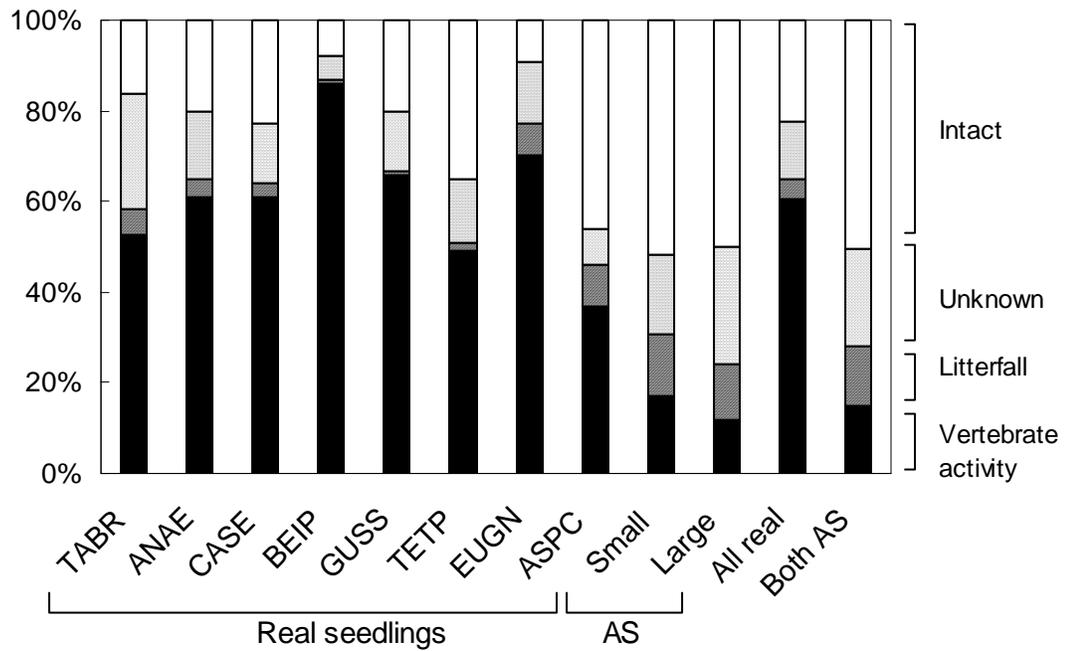
Figure 2-3. Percent of real and artificial seedlings (AS) damaged during 1 yr in the forest understory by specific damage agent. Small and large artificial seedlings were pooled as "both AS" ($N = 200$), and real seedlings were pooled as "all real" ($N = 755$). Categories are mutually exclusive, as each seedling was assigned only to the first damage agent it experienced. For species codes refer to Table 1-1.
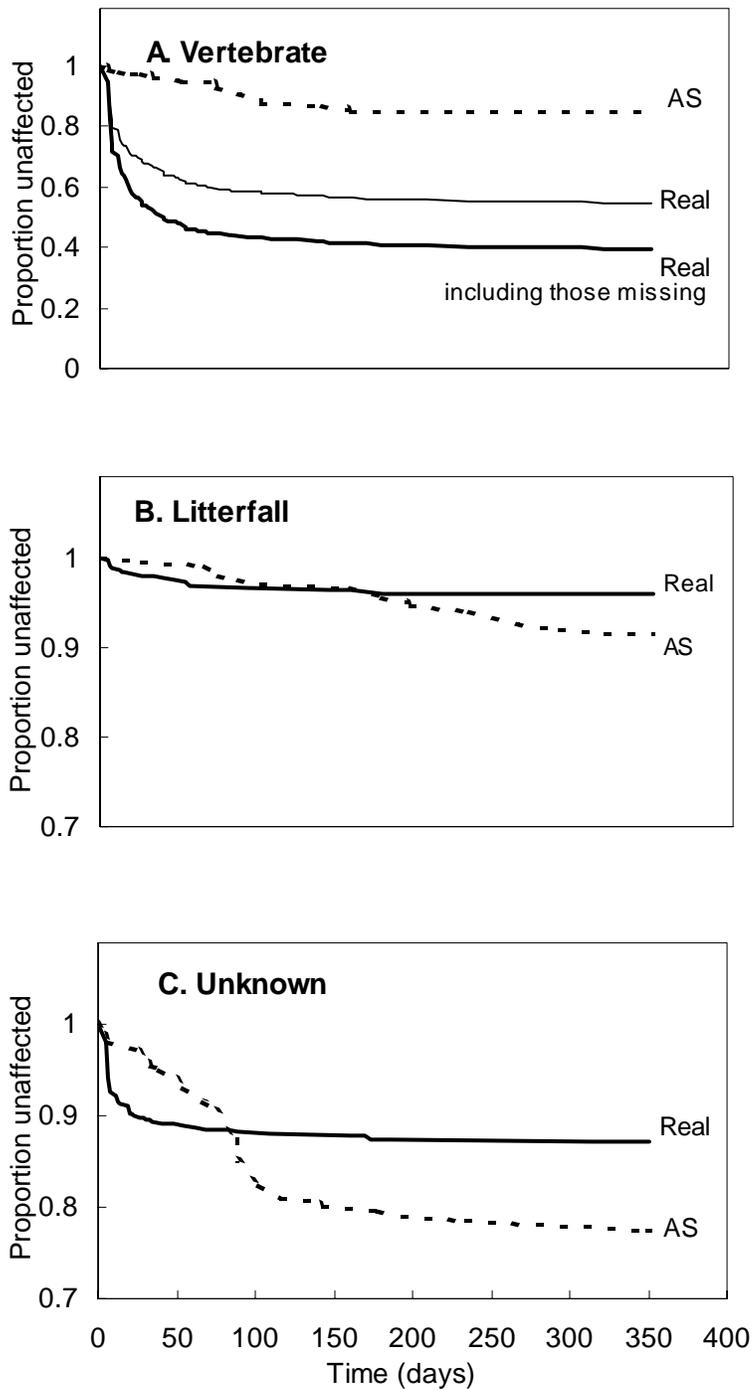
Figure 2-4. Kaplan-Meier survivorship curves for mechanical damage experienced by
            artificial (AS) and real seedlings during 1 yr in the forest understory.
            A) Vertebrate activity (estimated excluding missing seedlings and assuming
            those missing seedlings were all due to vertebrate consumption). B) Litterfall
            damage. C) Bent by unknown causes. For real seedlings, the average from
            eight species is shown. Notice the different scales in y-axes.

APPENDIX
SPECIES MEANS AND STANDARD DEVIATIONS FOR BIOMECHANICAL
MEASUREMENTS, FIBER ANALYSIS, AND BIOMASS

Table A-1. Biomechanical measurements of seedling stems from eight tree species at T1 and T2 (1 and 6 mos after first leaf expansion, respectively). Shown are means ($\pm$ 1 SD) and $N$ = number of individuals. For species codes refer to Table 1-1.

| | | | T1 | | | T2 | |
|---|---|---|---|---|---|---|---|
| Modulus of elasticity | Species | N | Mean | SD | N | Mean | SD |
| (MN m$^2$) | ANAE | 14 | 255.06 | 90.66 | 15 | 451.10 | 108.15 |
| | ASPC | 14 | 356.16 | 126.64 | 14 | 768.01 | 289.30 |
| | BEIP | 15 | 507.93 | 102.44 | 15 | 944.71 | 488.98 |
| | CASE | 14 | 336.08 | 110.51 | 14 | 779.27 | 255.60 |
| | EUGN | 15 | 3590.92 | 768.37 | 9 | 5265.72 | 1215.35 |
| | GUSS | 15 | 916.04 | 178.94 | 7 | 1244.89 | 354.93 |
| | TABR | 15 | 171.72 | 107.84 | 14 | 331.35 | 193.40 |
| | TETP | 15 | 1674.51 | 402.98 | 10 | 2269.71 | 538.67 |
| Fracture toughness | | | | | | | |
| (J m$^{-2}$) | ANAE | 14 | 1551.82 | 414.41 | 2 | 1883.80 | 560.45 |
| | ASPC | 15 | 2476.14 | 709.15 | 9 | 7471.83 | 2466.70 |
| | BEIP | 15 | 3430.16 | 636.75 | 15 | 6015.59 | 1760.58 |
| | CASE | 15 | 1325.15 | 353.23 | 0 | 2657.60 | 842.52 |
| | EUGN | 15 | 5433.04 | 1064.57 | 9 | 16004.96 | 2914.35 |
| | GUSS | 5 | 5463.60 | 953.86 | — | — | — |
| | TABR | 13 | 1135.16 | 672.99 | 16 | 3831.43 | 1774.03 |
| | TETP | 15 | 5692.55 | 869.12 | 10 | 5778.97 | 2245.26 |
| Density (g cm$^{-3}$) | | | | | | | |
| | ANAE | 45 | 0.15 | 0.03 | 24 | 0.19 | 0.04 |
| | ASPC | 45 | 0.52 | 0.14 | 27 | 0.39 | 0.07 |
| | BEIP | 44 | 0.35 | 0.09 | 25 | 0.40 | 0.10 |
| | CASE | 43 | 0.14 | 0.04 | 26 | 0.25 | 0.05 |
| | EUGN | 44 | 0.47 | 0.13 | 20 | 0.58 | 0.14 |
| | GUSS | 46 | 0.29 | 0.04 | 21 | 0.38 | 0.07 |
| | TABR | 25 | 0.13 | 0.03 | 19 | 0.24 | 0.10 |
| | TETP | 45 | 0.44 | 0.06 | 24 | 0.43 | 0.07 |
| Flexural stiffness | | | | | | | |
| (N cm$^2$) | ANAE | 13 | 23.85 | 12.96 | 15 | 52.11 | 29.23 |
| | ASPC | 14 | 3.38 | 1.30 | 14 | 12.19 | 9.25 |
| | BEIP | 15 | 7.76 | 3.25 | 14 | 16.38 | 7.73 |
| | CASE | 14 | 4.22 | 1.69 | 13 | 13.79 | 6.73 |
| | EUGN | 15 | 1.43 | 0.96 | 9 | 7.69 | 2.38 |
| | GUSS | 15 | 36.15 | 11.75 | 7 | 84.46 | 41.12 |
| | TABR | 15 | 0.24 | 0.23 | 13 | 2.80 | 2.17 |
| | TETP | 15 | 3.96 | 1.21 | 10 | 10.16 | 4.85 |

Table A-1. Continued

| | Species | | T1 | | | T2 | |
|---|---|---|---|---|---|---|---|
| | | N | Mean | SD | N | Mean | SD |
| Whole stem flexibility (Radians/N) | ANAE | 10 | 0.034 | 0.015 | 10 | 0.014 | 0.004 |
| | ASPC | 15 | 0.062 | 0.017 | 12 | 0.018 | 0.008 |
| | BEIP | 14 | 0.024 | 0.008 | 10 | 0.016 | 0.005 |
| | CASE | 15 | 0.061 | 0.041 | 11 | 0.03 | 0.021 |
| | EUGN | 10 | 0.15 | 0.035 | 12 | 0.092 | 0.052 |
| | GUSS | 15 | 0.009 | 0.003 | 11 | 0.007 | 0.002 |
| | TABR | — | — | — | 4 | 0.087 | 0.076 |
| | TETP | 15 | 0.069 | 0.036 | 8 | 0.055 | 0.023 |
| Work to bend (J) | | | | | | | |
| | ANAE | 13 | 0.0034 | 0.0016 | — | — | — |
| | ASPC | 10 | 0.0008 | 0.0005 | — | — | — |
| | BEIP | 9 | 0.0019 | 0.0008 | — | — | — |
| | CASE | 7 | 0.0010 | 0.0006 | — | — | — |
| | EUGN | 9 | 0.0007 | 0.0004 | — | — | — |
| | GUSS | 11 | 0.0041 | 0.0012 | — | — | — |
| | TABR | — | — | — | — | — | — |
| | TETP | 9 | 0.0016 | 0.0006 | — | — | — |
| % Critical height | | | | | | | |
| | ANAE | 14 | 28.36 | 6.03 | 14 | 23.35 | 4.53 |
| | ASPC | 15 | 22.31 | 2.71 | 10 | 16.93 | 2.43 |
| | BEIP | 13 | 21.05 | 3.35 | 14 | 16.62 | 3.80 |
| | CASE | 15 | 20.69 | 4.35 | 14 | 19.78 | 4.82 |
| | EUGN | 15 | 14.49 | 2.60 | 14 | 14.99 | 1.97 |
| | GUSS | 14 | 13.68 | 1.90 | 9 | 14.31 | 3.21 |
| | TABR | 14 | 18.46 | 2.84 | 15 | 16.66 | 6.18 |
| | TETP | 15 | 17.87 | 2.21 | 7 | 14.44 | 1.95 |

Table A-2. Biomechanical measurements of seedling leaves from eight tree species at T1 and T2 (1 and 6 mos after first leaf expansion, respectively). Shown are means (± 1 SD) and *N* = number of individuals. For species codes refer to Table 1-1.

| | | | T1 | | | T2 | |
|---|---|---|---|---|---|---|---|
| Lamina fracture toughness ($J m^{-2}$) | Species | N | Mean | SD | N | Mean | SD |
| | ANAE | 15 | 274.12 | 75.12 | 13 | 225.73 | 71.25 |
| | ASPC | 14 | 371.28 | 92.76 | 14 | 324.28 | 59.60 |
| | BEIP | 15 | 130.34 | 60.45 | 15 | 229.19 | 51.23 |
| | CASE | 15 | 71.29 | 39.63 | 6 | 107.40 | 35.21 |
| | EUGN | 15 | 191.55 | 59.37 | 8 | 245.71 | 32.90 |
| | GUSS | 16 | 395.43 | 150.29 | 9 | 218.39 | 58.59 |
| | TABR | 4 | 117.78 | 90.17 | 18 | 189.49 | 46.37 |
| | TETP | 14 | 339.27 | 135.27 | 10 | 198.51 | 71.58 |
| Midvein fracture toughness ($J m^{-2}$) | ANAE | 15 | 2198.47 | 419.80 | 12 | 2532.61 | 360.55 |
| | ASPC | 15 | 2370.67 | 455.09 | 14 | 2545.19 | 403.04 |
| | BEIP | 15 | 1405.83 | 494.77 | 15 | 2271.53 | 477.84 |
| | CASE | 13 | 984.15 | 183.35 | 6 | 1001.03 | 185.94 |
| | EUGN | 15 | 1609.67 | 461.49 | 8 | 2417.33 | 501.64 |
| | GUSS | 16 | 3124.26 | 426.99 | 9 | 2906.78 | 582.72 |
| | TABR | 4 | 1521.65 | 387.46 | 17 | 2194.12 | 427.60 |
| | TETP | 14 | 2217.99 | 348.91 | 10 | 3475.15 | 666.77 |
| Force of fracture (N) | ANAE | 15 | 43.27 | 15.85 | 13 | 40.58 | 14.92 |
| | ASPC | 14 | 74.52 | 19.97 | 14 | 63.89 | 13.64 |
| | BEIP | 15 | 38.45 | 18.34 | 15 | 32.23 | 6.84 |
| | CASE | 15 | 12.41 | 8.00 | 6 | 11.84 | 4.73 |
| | EUGN | 15 | 20.71 | 8.36 | 8 | 20.04 | 3.72 |
| | GUSS | 16 | 56.81 | 20.53 | 9 | 30.54 | 8.93 |
| | TABR | 4 | 15.93 | 12.08 | 18 | 28.67 | 10.54 |
| | TETP | 14 | 41.53 | 12.72 | 10 | 25.49 | 8.80 |
| Density ($g cm^{-3}$) | ANAE | 15 | 0.25 | 0.04 | 12 | 0.30 | 0.04 |
| | ASPC | 14 | 0.29 | 0.02 | 14 | 0.34 | 0.02 |
| | BEIP | 12 | 0.20 | 0.03 | 15 | 0.48 | 0.07 |
| | CASE | 15 | 0.20 | 0.03 | 6 | 0.28 | 0.04 |
| | EUGN | 15 | 0.33 | 0.04 | 8 | 0.45 | 0.04 |
| | GUSS | 15 | 0.30 | 0.02 | 9 | 0.35 | 0.03 |
| | TABR | 4 | 0.21 | 0.06 | 18 | 0.23 | 0.05 |
| | TETP | 13 | 0.36 | 0.06 | 10 | 0.42 | 0.04 |

Table A-2. Continued

| Specific leaf area ($cm^2\,g^{-1}$) | Species | N | Mean | SD | N | Mean | SD |
|---|---|---|---|---|---|---|---|
| | | | T1 | | | T2 | |
| | ANAE | 15 | 317.02 | 36.46 | 13 | 257.89 | 28.66 |
| | ASPC | 15 | 193.95 | 14.78 | 14 | 172.03 | 8.88 |
| | BEIP | 13 | 248.38 | 47.50 | 15 | 196.52 | 29.83 |
| | CASE | 15 | 486.00 | 83.97 | 6 | 427.39 | 102.53 |
| | EUGN | 15 | 360.38 | 24.02 | 8 | 305.14 | 36.79 |
| | GUSS | 16 | 281.02 | 19.03 | 9 | 248.32 | 28.84 |
| | TABR | 4 | 478.64 | 130.97 | 18 | 501.46 | 90.48 |
| | TETP | 13 | 287.33 | 26.60 | 10 | 231.80 | 27.27 |

Table A-3. Fiber fractions of seedling stems from eight tree species at T1 and T2 (1 and 6 mos after first leaf expansion, respectively). Shown are means ($\pm$ 1 SD) and $N$ = number of samples (each sample composed of 5-15 seedlings); percent NDF = Non detergent fiber. For species codes refer to Table 1-1.

|  |  | T1 | | | T2 | | |
|---|---|---|---|---|---|---|---|
| % NDF | Species | N | Mean | SD | N | Mean | SD |
|  | ANAE | 3 | 48.60 | 2.49 | 3 | 48.43 | 1.31 |
|  | ASPC | 3 | 51.33 | 1.60 | 3 | 55.28 | 3.20 |
|  | BEIP | 3 | 66.83 | 1.40 | 3 | 63.57 | 1.68 |
|  | CASE | 3 | 52.95 | 3.20 | 3 | 57.13 | 3.03 |
|  | EUGN | 3 | 76.36 | 1.04 | 3 | 74.41 | 3.46 |
|  | GUSS | 3 | 62.29 | 0.88 | 3 | 62.43 | 0.42 |
|  | TABR | 1 | 48.38 | — | 2 | 53.01 | 8.57 |
|  | TETP | 3 | 67.90 | 1.24 | 3 | 64.46 | 2.19 |
| % Hemicellulose |  |  |  |  |  |  |  |
|  | ANAE | 3 | 8.54 | 1.00 | 3 | 10.28 | 0.66 |
|  | ASPC | 3 | 13.95 | 0.82 | 3 | 15.93 | 0.54 |
|  | BEIP | 3 | 11.98 | 0.43 | 3 | 14.71 | 1.54 |
|  | CASE | 3 | 13.71 | 0.82 | 3 | 18.82 | 1.57 |
|  | EUGN | 3 | 14.34 | 0.09 | 3 | 14.39 | 2.65 |
|  | GUSS | 3 | 14.89 | 0.60 | 3 | 13.47 | 0.60 |
|  | TABR | 1 | 10.12 | — | 2 | 11.58 | 2.13 |
|  | TETP | 3 | 13.09 | 0.22 | 3 | 13.20 | 0.47 |
| % Cellulose |  |  |  |  |  |  |  |
|  | ANAE | 3 | 27.94 | 1.13 | 3 | 26.18 | 1.01 |
|  | ASPC | 3 | 26.52 | 0.70 | 3 | 27.80 | 2.78 |
|  | BEIP | 3 | 29.22 | 1.76 | 3 | 28.54 | 0.98 |
|  | CASE | 3 | 27.01 | 0.54 | 3 | 26.66 | 0.40 |
|  | EUGN | 3 | 37.32 | 0.32 | 3 | 37.59 | 5.54 |
|  | GUSS | 3 | 34.19 | 1.23 | 3 | 34.11 | 0.54 |
|  | TABR | 1 | 25.33 | — | 2 | 30.58 | 5.17 |
|  | TETP | 3 | 40.22 | 1.90 | 3 | 37.21 | 2.51 |
| % Lignin |  |  |  |  |  |  |  |
|  | ANAE | 3 | 12.12 | 0.44 | 3 | 11.97 | 0.36 |
|  | ASPC | 3 | 10.85 | 0.60 | 3 | 11.55 | 1.13 |
|  | BEIP | 3 | 25.63 | 1.59 | 3 | 20.33 | 2.31 |
|  | CASE | 3 | 12.23 | 3.04 | 3 | 11.65 | 2.24 |
|  | EUGN | 3 | 24.71 | 0.73 | 3 | 22.43 | 1.03 |
|  | GUSS | 3 | 13.21 | 0.94 | 3 | 14.85 | 1.08 |
|  | TABR | 1 | 12.93 | — | 2 | 10.85 | 1.27 |
|  | TETP | 3 | 14.59 | 3.06 | 3 | 14.06 | 0.44 |

Table A-4. Fiber fractions of seedling leaves from eight tree species at T1 and T2 (1 and 6 mos after first leaf expansion, respectively). Shown are means ($\pm$ 1 SD) and $N$ = number of samples (each sample composed of 5-15 seedlings); percent NDF = Non detergent fiber. For species codes refer to Table 1-1.

| | | | T1 | | | T2 | |
|---|---|---|---|---|---|---|---|
| % NDF | Species | N | Mean | SD | N | Mean | SD |
| | ANAE | 3 | 42.08 | 1.16 | 3 | 43.11 | 1.58 |
| | ASPC | 3 | 52.32 | 1.87 | 3 | 54.23 | 4.12 |
| | BEIP | 3 | 54.87 | 1.95 | 3 | 55.87 | 0.31 |
| | CASE | 3 | 51.84 | 0.81 | 3 | 44.83 | 10.05 |
| | EUGN | 3 | 56.93 | 4.59 | 3 | 50.28 | 6.60 |
| | GUSS | 3 | 54.77 | 0.89 | 3 | 52.67 | 0.67 |
| | TABR | 1 | 43.83 | — | 2 | 50.82 | 0.16 |
| | TETP | 3 | 54.73 | 1.85 | 3 | 45.86 | 6.90 |
| % Hemicellulose | | | | | | | |
| | ANAE | 3 | 7.77 | 1.15 | 3 | 8.68 | 2.35 |
| | ASPC | 3 | 14.21 | 0.58 | 3 | 14.29 | 2.10 |
| | BEIP | 3 | 9.68 | 0.55 | 3 | 10.34 | 1.51 |
| | CASE | 3 | 20.43 | 0.47 | 3 | 18.27 | 2.54 |
| | EUGN | 3 | 19.05 | 2.12 | 3 | 16.99 | 2.31 |
| | GUSS | 3 | 16.37 | 0.95 | 3 | 17.58 | 1.22 |
| | TABR | 1 | 10.78 | — | 2 | 12.24 | 0.50 |
| | TETP | 3 | 12.63 | 0.18 | 3 | 11.84 | 1.58 |
| % Cellulose | | | | | | | |
| | ANAE | 3 | 18.43 | 1.16 | 3 | 19.85 | 0.88 |
| | ASPC | 3 | 20.62 | 1.03 | 3 | 22.11 | 2.45 |
| | BEIP | 3 | 16.96 | 0.48 | 3 | 17.98 | 0.97 |
| | CASE | 3 | 16.73 | 1.34 | 3 | 16.51 | 5.29 |
| | EUGN | 3 | 17.45 | 0.30 | 3 | 16.18 | 0.91 |
| | GUSS | 3 | 22.65 | 0.30 | 3 | 20.48 | 1.01 |
| | TABR | 1 | 14.51 | — | 2 | 18.98 | 0.31 |
| | TETP | 3 | 24.18 | 1.14 | 3 | 20.23 | 3.38 |
| % Lignin | | | | | | | |
| | ANAE | 3 | 15.87 | 0.82 | 3 | 14.58 | 1.20 |
| | ASPC | 3 | 17.48 | 0.56 | 3 | 17.83 | 1.02 |
| | BEIP | 3 | 28.23 | 1.21 | 3 | 27.55 | 1.50 |
| | CASE | 3 | 14.67 | 1.76 | 3 | 10.05 | 2.84 |
| | EUGN | 3 | 20.43 | 2.24 | 3 | 17.11 | 3.69 |
| | GUSS | 3 | 15.75 | 0.20 | 3 | 14.61 | 0.86 |
| | TABR | 1 | 18.54 | — | 2 | 19.60 | 0.35 |
| | TETP | 3 | 17.91 | 1.38 | 3 | 13.80 | 2.17 |

Table A-5. Biomass measurements of seedling stems and leaves from eight tree species at
　　　T1 and T2 (1 and 6 mos after first leaf expansion, respectively). Shown are
　　　means ($\pm$ 1 SD) and $N$ = number of individuals. For species codes refer to
　　　Table 1-1.

| | | | T1 | | | T2 | |
|---|---|---|---|---|---|---|---|
| Stem height (mm) | Species | N | Mean | SD | N | Mean | SD |
| | ANAE | 45 | 238.2 | 35.4 | 24 | 253.4 | 40.7 |
| | ASPC | 45 | 140.7 | 19.6 | 27 | 154.8 | 26.9 |
| | BEIP | 44 | 165.3 | 36.9 | 25 | 162.8 | 35.0 |
| | CASE | 43 | 140.1 | 34.5 | 26 | 173.3 | 32.7 |
| | EUGN | 44 | 140.3 | 27.7 | 20 | 182.5 | 25.0 |
| | GUSS | 46 | 176.7 | 29.8 | 21 | 196.3 | 50.2 |
| | TABR | 25 | 64.1 | 12.6 | 19 | 115.9 | 39.4 |
| | TETP | 45 | 154.5 | 19.0 | 24 | 162.7 | 21.8 |
| Leaf area (cm$^2$) | | | | | | | |
| | ANAE | 45 | 112.78 | 41.03 | 25 | 125.42 | 57.70 |
| | ASPC | 45 | 35.40 | 8.26 | 28 | 55.98 | 20.29 |
| | BEIP | 45 | 67.70 | 34.61 | 25 | 67.94 | 25.32 |
| | CASE | 44 | 66.24 | 42.23 | 26 | 122.44 | 80.94 |
| | EUGN | 30 | 13.89 | 5.97 | 21 | 34.32 | 9.23 |
| | GUSS | 45 | 138.05 | 41.97 | 21 | 171.96 | 55.02 |
| | TABR | 23 | 6.54 | 6.52 | 18 | 52.09 | 16.84 |
| | TETP | 45 | 28.22 | 6.52 | 24 | 41.82 | 16.84 |
| Leaf thickness (mm) | | | | | | | |
| | ANAE | 15 | 0.16 | 0.03 | 13 | 0.18 | 0.05 |
| | ASPC | 14 | 0.20 | 0.01 | 14 | 0.20 | 0.01 |
| | BEIP | 15 | 0.29 | 0.04 | 15 | 0.14 | 0.01 |
| | CASE | 15 | 0.17 | 0.04 | 6 | 0.11 | 0.02 |
| | EUGN | 15 | 0.11 | 0.02 | 8 | 0.08 | 0.01 |
| | GUSS | 16 | 0.15 | 0.02 | 9 | 0.14 | 0.01 |
| | TABR | 4 | 0.14 | 0.03 | 18 | 0.15 | 0.05 |
| | TETP | 14 | 0.13 | 0.03 | 9 | 0.13 | 0.02 |
| Plant biomass (g) | | | | | | | |
| | ANAE | 45 | 0.8066 | 0.2689 | 25 | 1.1550 | 0.4724 |
| | ASPC | 45 | 0.5446 | 0.1265 | 28 | 0.7385 | 0.2422 |
| | BEIP | 43 | 1.8675 | 0.5233 | 25 | 0.9564 | 0.4232 |
| | CASE | 44 | 0.3022 | 0.2076 | 26 | 0.6178 | 0.3901 |
| | EUGN | 30 | 0.3990 | 0.1743 | 21 | 0.3508 | 0.2056 |
| | GUSS | 46 | 3.6938 | 1.3287 | 21 | 2.5911 | 0.8554 |
| | TABR | 23 | 0.0459 | 0.0240 | 19 | 0.2540 | 0.2180 |
| | TETP | 44 | 0.2467 | 0.0543 | 24 | 0.3735 | 0.1564 |

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BIOGRAPHICAL SKETCH

Silvia Alvarez-Clare was born in San José, Costa Rica in September 1977. She attended Saint Francis High School where she was inspired to become a biologist. Silvia earned her bachelor's degree in biology at the Universidad de Costa Rica (UCR) in July 2001. During her undergraduate studies at UCR, she became interested in plant ecophyisiology and conservation partly because she had many opportunities to work in diverse tropical ecosystems throughout Costa Rica. She also worked as a research assistant in the Centro de Investigación en Biología Celular y Molecular at Universidad de Costa Rica (CIBCM) and at the university herbarium. Silvia was also a naturalist guide in the Monteverde cloud forest, an experience that reinforced her love of nature and her desire to continue her studies. When she finished her undergraduate studies, Silvia taught biology for a year in the International Baccalaureate program at Lincoln High School in San José. She then came to the University of Florida where she obtained her master's degree in Botany with a minor in Statistics in May 2005. Silvia will continue her education toward her doctoral degree in interdisciplinary ecology under the guidance of Dr. Michelle Mack at the University of Florida. For her dissertation research she plans to study tropical forest regeneration, restoration, and nutrient cycling in Costa Rica.