INFLUENCE OF LIGHT LEVEL ON THE GROWTH AND MORPHOLOGY OF SAPLINGS IN A PANAMANIAN FOREST[1]

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Leaf spacing and aboveground growth were monitored in saplings of ten species in a range of light environments in a Panamanian lowland humid forest. One- to 2-m-tall individuals of the chosen species had intermediate to large leaves on stems with few or no branches. Saplings in high light environments grew faster in height and produced more biomass per unit leaf area than shaded saplings for all species. These growth responses involved morphological plasticity with greater extension per unit biomass increment increasing the height growth rate of gap-grown saplings and greater biomass allocation to leaves decreasing the whole plant light compensation point in shade. The relative performance of the species also varied across the light gradient and was related to differences in leaf lifespan and specific leaf mass. Light-demanding species grew as rapidly in shade as shade-tolerant species, but the shorter leaf lifespan of the former necessitates higher production rates to maintain a given leaf area, largely excluding light-demanders from shaded understory locations. Height growth rate was positively correlated with leaf spacing for each species, and differences between species in the height growth rate-internode length relationship were related to interspecific differences in specific leaf mass. Thus, sapling growth histories may be inferred from their morphologies.

The growth of plants is a self-feeding process whereby photosynthetic products are used to extend new leaves and roots that in turn acquire more carbon and nutrients for future extension. This process fuels exponential growth in favorable habitats, but barely permits a slow turnover of existing tissues in plants of marginal habitats. Phenotypic plasticity, involving changes in photosynthetic capacity (e.g., Bjorkman, 1981; Hogan, 1988), branch orientation (Steingraeber, 1982), and leaf vs. stem allocation (King, 1991a) enable many forest trees to both tolerate shade and respond vigorously to light gaps. Yet there are clear tradeoffs between shade- and sun-adapted species, with shade-tolerant herbs that grow poorly in the open at one extreme (Mulkey, 1986) and light-demanders that grow rapidly in gaps but cannot survive in shade at the other (Brokaw, 1987; Swaine and Whitmore, 1988). Segregation along light gradients theoretically permits different species to coexist (Denslow, 1987; Leigh, 1990), but only a small fraction of the tree species in the Forest Dynamics plot on Barro Colorado Island, Panama segregate according to light gap size (Welden et al., 1991).

Relative growth rate has often been used as the fundamental descriptor of growth. However, height growth and the whole plant compensation point (sensu Givnish, 1988) may be better attributes for characterizing the growth of field populations. Height growth is particularly important in the response of saplings to light gaps because it determines how long an individual can maintain itself in a high-light environment before being overtopped by its neighbors or closed out from above by gap-edge trees.

Recent work on the influence of plant geometry on extension growth (King, 1981, 1990; Givnish, 1984; Kohyama, 1987, 1991; Küppers, 1989) provides a basis for analyzing growth as a dynamic process in which the shoot not only supports the current foliage, but extends itself through space.

This paper develops a mechanistic approach for calculating growth in terms of biomass production and the efficiency with which it is used to extend the plant and replace senesced leaves. The growth analysis (restricted to the aboveground growth of field plants) was applied to saplings of a Panamanian moist lowland forest, including both shade-tolerant and light-demanding species in order to answer the following questions:

1. What is the minimum rate of biomass production required to maintain the current leaf area of a sapling?
2. How much height growth is achieved per unit of assimilate added to the sapling body?
3. Are there tradeoffs between maintenance of leaf area and efficiency of height growth that differentiate the regeneration patterns of different species?

In addressing these questions the study examines the relationship between the ecological and morphological characteristics of plants, and develops a number of growth descriptors that show how different aspects of plant form contribute to growth and survival.

MATERIALS AND METHODS

The study was carried out on Barro Colorado Island (BCI) (9°10'N, 79°51'W), Republic of Panama. BCI is part of a tropical moist forest reserve administered by the Smithsonian Tropical Research Institute. The island receives an average of 2.6 m of rain per year with a distinct dry season from late December to April (Leigh, Rand, and Windsor, 1982).

The species chosen for study had large leaves, making the inference of total foliage growth from leaf dimensional measurements feasible. However, the species differed taxonomically, in adult stature and light requirements, in-

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TABLE 1. Characteristics of the study species. Percent with branches refers to the percentage of saplings with at least one branch by the end of the study interval. The architectural characteristics are M = monopodial trunk (erect trunk bearing leaves or side branches), S = sympodial trunk (dividing into major branches supporting the crown). O = orthotropic branches (upward pointing branches with leaves arranged radially about each axis), P = plagiotropic branches (nearly horizontal branches bearing leaves in planes along each axis), - = no branches present.

Species	Family	Sample size	Percent with branches	Architecture (sample, adult)	Adult height (m)
Shade-tolerants					
Alseis blackiana	Rubiaceae	19	21%	M/-, M/O	15–25
Calophyllum longifolium	Guttiferae	16	6%	M/-, M/O	20–35
Coccoloba manzanillensis	Polygonaceae	10	10%	M/-, S/P	8–12
Herrania purpurea	Sterculiaceae	11	0	M/-, M/-	4–8
Protium panamense	Burseraceae	10	10%	M/-, M/O	10–15
Trichilia tuberculata	Meliaceae	11	82%	M/O, S/P	20–30
Tachigalia versicolor	Caesalpiniaceae	14	14%	M/-, M/O	25–30
Light-demanders					
Cecropia insignis	Cecropiaceae	12	0	M/-, M/O	20–30
Miconia argentea	Melastomaceae	15	20%	M/-, M/O	15–20
Palicourea guianensis	Rubiaceae	12	100%	M/P, M/O	4–8

cluding species characterized as light-demanding and shade-tolerant in other studies on BCI (e.g., Coley, 1983; Welden et al., 1991). For most of the ten chosen species, 1–2-m saplings bear their leaves on vertical, unbranched stems (Table 1). Saplings were first measured 23 August to 11 September 1990 and last measured 11 mo later, except for *Cecropia insignis,* which was followed over a 3-mo period, as it produces leaves continuously and most saplings grew too large to follow for a full year.

Thirteen to 23 saplings per species were selected near trails, primarily in old forest, with initial heights of 0.7 to 2.2 m. An attempt was made to include similar numbers of saplings in gaps, understory, and intermediate conditions for each species. Mortality, severe herbivory, and other damage reduced the final sample size to ten to 19 saplings per species. Other marked species with smaller initial numbers and less than ten undamaged survivors were not included in the analysis.

Rings were painted on the stems and branches (if present) of each sapling so that their diameters could be measured repeatedly at the same points. The following data were recorded at least twice during the study for all saplings: length and width of each leaf blade, length and diameter (4 to 5 cm above the base) of any branches present along the stem, stem length and diameter at five or more regularly spaced points, and the distance from the top ring to the apex. Height growth was then defined as the increase in top ring-to-apex distance, as this increment can be precisely measured and the saplings' stems were vertical or nearly so. All diameters were measured to the nearest 0.05 mm in two perpendicular directions with a dial caliper. Terminal leaves were marked so that the production and spacing of new leaves could be measured subsequently. Three 1.34-cm-diameter discs were punched from mature leaves of each sapling (avoiding major veins) so that specific leaf mass could be estimated, as described below.

In order to estimate biomass from dimensional measurements, two to five other saplings per species of similar size were harvested from an adjacent mainland part of the forest reserve. Shade-tolerant species were taken from locations receiving somewhat more light than the closed understory, and light demanders were harvested from small gaps. Plant parts were measured as described above and then weighed after being oven dried at 60 C. Relationships between dry mass and dimensions of the form:

leaf area = b_1 × blade width × blade length

leaf biomass = b_2 × leaf disc specific mass

× leaf area

branch biomass = b_3 × branch length

× (basal diameter)^2

stem biomass = b_4 × Σ section length

× (section diameter)^2

where b_1, b_2, b_3 and b_4 are constants determined for each species (available from the author). Note that b_2 is the ratio of whole leaf specific mass to leaf disc specific mass, which is greater than one, due to the presence of a petiole and major veins in the leaf. These relationships were applied to the in situ saplings to estimate plant part biomass at the beginning and end of the study and total new aboveground biomass produced over the study period. The use of the specific mass of the leaf discs taken from each in situ sapling in the leaf biomass equations accounted for any differences in specific leaf mass between individuals of different light environments.

Light environments were estimated from hemispherical photographs taken above the apex of each sapling in November 1990. The video image analysis system of Becker, Erhart, and Smith (1989) was used to compute the indirect site factor, defined as the fraction of diffuse light penetrating the canopy openings above each sapling.

The height growth of a sapling depends on its production of aboveground biomass and on the extension achieved per unit of new biomass. The rate of aboveground biomass gain per unit leaf area was calculated for each sapling as:

$$G = \Delta M / (\overline{LA} \times \Delta T) \qquad (1)$$

where ΔM is the total production of aboveground biomass

TABLE 2. Parameters used to describe the growth of saplings.

Parameter	Definition	Units
G	Gross aboveground biomass production per unit leaf area	g m^{-2} yr^{-1}
Compensation G	Aboveground biomass production rate that just maintains the current sapling leaf area, including replacement of senescing leaves	g m^{-2} yr^{-1}
Compensation isf	Fraction of diffuse light or indirect site factor required to maintain a sapling at the compensation G	Dimensionless
HE	Height growth efficiency defined as the height growth achieved per unit of new aboveground biomass multiplied by sapling leaf area	m^3 g^{-1}
F	Fraction of newly produced aboveground biomass allocated to leaf growth	Dimensionless
LSE	Leaf support efficiency, defined as leaf area per unit cross-sectional woody biomass	m^3 g^{-1}
α	Allometric coefficient defining how woody biomass scales with total height in growing saplings (equations 7 and 8)	Dimensionless
RLA	Relative leaf area, defined as total sapling leaf area divided by the square of sapling height	Dimensionless

during the study, calculated as $\Delta M = M_f + M_{sl} - M_i$ where M_f and M_i are the standing biomasses at the final and initial census, respectively and M_{sl} is the biomass of shed leaves, $\overline{LA}$ is the geometric mean of the leaf areas measured at the beginning and end of the study, and ΔT is the study duration. G is similar to the unit leaf rate defined by Hunt (1982), except that the latter is computed in terms of the net aboveground plus belowground biomass increment.

A new growth parameter, the height growth efficiency (HE), was defined by N. M. Holbrook (Stanford University, personal communication) as

$$HE = LA \frac{dh}{dM} \qquad (2)$$

at any given time. Over the study period

$$HE = \Delta h \times \overline{LA}/\Delta M \qquad (3)$$

where Δh is sapling height growth during the period. The height growth efficiency is thus inversely proportional to the amount of new biomass required to extend a crown of given leaf area by a given height increment. The utility of this definition of height growth efficiency is that the height growth rate can then be written as the product of the biomass production per unit leaf area and HE, i.e.,

$$\frac{dh}{dt} = G \times HE \qquad (4)$$

The height growth efficiency can in turn be expressed as a function of biomass allocation between leaves and woody parts, sapling crown vs. stem proportions, and the

relationship between stem mass and sapling height (allometry). Thus, differences in height growth between species can be partitioned between differences in G and differences in sapling morphology.

This analysis of height growth is achieved by first defining the leaf support efficiency as

$$LSE = LA \times h/M_s \qquad (5)$$

where h is sapling height and M_s is the biomass of the stem and any branches. Because $M_s/h = \rho A_w$, where ρ is wood density (dry mass/fresh volume), and A_w is the mean cross-sectional area of the woody parts (averaged over height), the leaf support efficiency can also be expressed as

$$LSE = LA/\rho A_w \qquad (6)$$

i.e., LSE is the leaf area per unit woody cross-sectional biomass.

The effect of allometry on height growth efficiency was analyzed by expressing woody biomass as a power function of sapling height, i.e.,

$$M_s = ah^\alpha \qquad (7)$$

where a and α are coefficients relating the woody biomass of a sapling to its height. The allometric coefficient α was defined for each sapling by logarithmically transforming equation 7, yielding

$$\ln M_s = \ln a + \alpha \ln h$$

Subtracting the initial from the final value of M_s then yields

$$\ln M_{sf} - \ln M_{si} = \alpha(\ln h_f - \ln h_i)$$

i.e.,

$$\alpha = \frac{\ln(M_{sf}/M_{si})}{\ln(h_f/h_i)} \qquad (8)$$

where the subscripts i and f refer to values at the beginning and end of the study interval, respectively. Given equation 7,

$$\frac{dM_s}{dh} = a\alpha h^{\alpha-1} = \alpha M_s/h,$$

i.e.,

$$\frac{dh}{dM_s} = h/\alpha M_s \qquad (9)$$

Substituting equation 5 into equation 9 and noting that

$$\frac{dh}{dM} = (1 - F)\frac{dh}{dM_s}$$

where F is the fraction of new aboveground biomass allocated to leaves, yields

$$\frac{dh}{dM} = (1 - F)LSE/\alpha LA$$

so equation 2 can be expressed as

$$HE = (1 - F)LSE/\alpha \qquad (10)$$

i.e., the height growth efficiency is directly proportional to LSE and inversely proportional to α for small growth increments. The latter relationship can be visualized by

noting that a sapling with a high α thickens its stem more per unit extension than a sapling with low α and hence attains less height growth per unit biomass production.

Substitution of equation 10 into equation 4 yields:

$$\frac{dh}{dt} = G(1 - F)LSE/\alpha \qquad (11)$$

so interspecific differences in height growth rate can be explained in terms of differences in G, allocation, leaf support efficiency, and allometry. Note that F refers to dynamic allocation (proportion of new biomass allocated to leaves) and not static allocation (proportion of standing biomass in leaves).

Other characters, including relative leaf area (RLA) defined as LA/h^2, were also estimated for each sapling. This definition of RLA normalizes leaf area so that saplings with similar ratios of crown width to sapling height and leaf area indices (leaf area/crown area) but different heights are assigned the same RLA value. The above growth parameters are summarized in Table 2.

Most of the above variates were significantly correlated with sapling light environment expressed as the fraction of diffuse light reaching the sapling, and were therefore regressed against this variable to describe the growth of each species. Both untransformed and logarithmically transformed regressions were applied as the latter substantially improved the fit for certain relationships, such as fractional allocation to leaf production. The method having the highest correlation for the majority of species was reported in the results unless there was little difference between the two, in which case the regression approach that yielded more reasonable values at the extremes was chosen. However, logarithmic transformation compresses deviations above the mean as compared to deviations below the mean, thus underestimating the mean. Estimates derived from logarithmic transformations were corrected for bias by multiplying the back-transformed y intercept by $\bar{y}/\hat{y}$, the ratio of observed to regression-predicted means, before correction (Snowdon, 1991).

One *Miconia argentea* and one *Cecropia insignis,* both in particularly large gaps, were excluded from the analysis because their height growth rates fell substantially below those predicted from regressions for the other saplings of these species. The exclusion of the above saplings is also justified by Loach's (1970) studies indicating that sapling height growth rates peak at one-third to one-half of full sunlight, and thus sapling height growth at these light levels departs from regressions for saplings of lower light levels.

To assess shade tolerance, the compensation G was derived as follows: for a shaded sapling that maintains an equilibrium leaf area by replacing senesced leaves with new ones, one can equate the loss and production of leaf biomass, expressed as

old leaf biomass loss rate = SLM × LA/lifespan   (12)

and

new leaf biomass production rate = G × LA × F   (13)

where SLM is specific leaf mass and lifespan is mean leaf longevity. Equating 12 and 13 then defines the compensation G of a sapling that produces just enough biomass
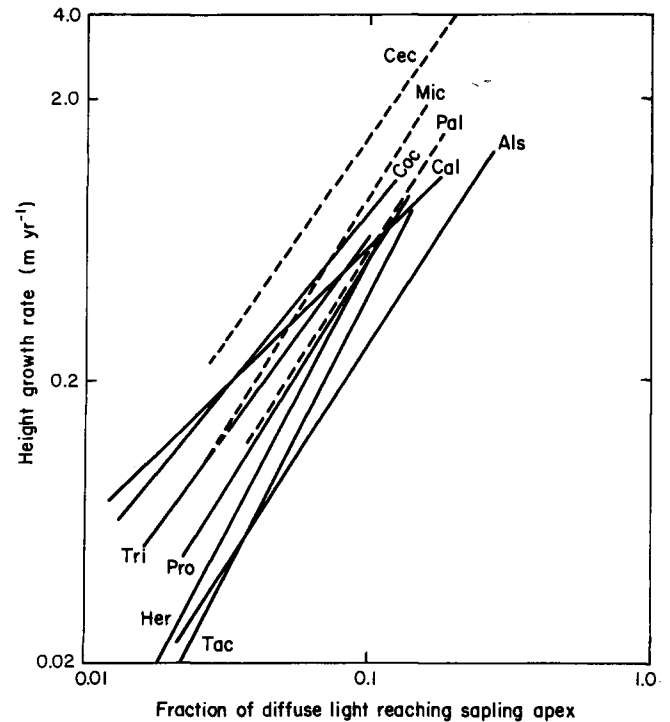

Fig. 1. Height growth rate vs. the fraction of diffuse light reaching the tops of saplings (indirect site factor) in a lowland humid Panamanian forest. The ranges shown in this and subsequent figures correspond to the range in observed values along the x-axis, except for those few cases where the full range would have passed beyond the figure boundary. Light-demanding species are indicated by dashed lines in this and subsequent figures.

Figure Abbreviations: Als, *Alseis blackiana;* Cal, *Calophyllum longifolium;* Cec, *Cecropia insignis;* Coc, *Coccoloba manzanillensis;* Her, *Herrania purpurea;* Mic, *Miconia argentea;* Pal, *Palicourea guianensis;* Pro, *Protium panamense;* Tac, *Tachigalia versicolor;* Tri, *Trichilia tuberculata.*

to maintain its current leaf area as

Compensation G = SLM/(F × lifespan)   (14)

The fractional leaf allocation F and specific leaf mass SLM in equation 14 were estimated for an indirect site factor of 0.03, corresponding to shaded understory conditions. For a suppressed sapling that produces new leaves at the same rate as senesced leaves are lost, thereby maintaining a constant number of leaves, the leaf lifespan is given by the total number of leaves divided by the leaf production or loss rate. However, if leaf production and loss are asynchronous, it is more accurate to estimate lifespan in terms of the means of the measured production and loss rates. Hence, leaf lifespan in equation 14 was calculated as:

$$\text{lifespan} = \frac{\text{mean number of live leaves}}{1/2(\text{leaf production rate} + \text{leaf loss rate})} \quad (15)$$

for each shaded sapling for which leaf loss and production did not differ by more than a factor of two, i.e., the saplings were not greatly out of equilibrium with respect to leaf turnover. The whole plant light compensation point can then be estimated from regressions of G vs. indirect site
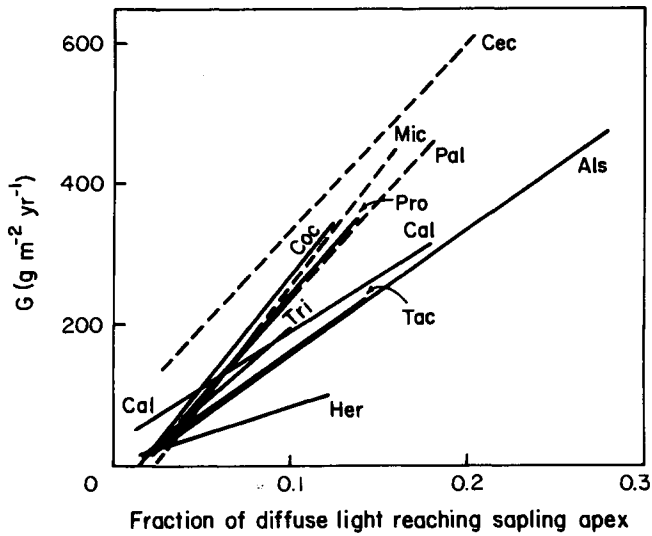
Fig. 2. Aboveground biomass production rate per unit leaf area (G) vs. the indirect site factor.

factor, as the light level for which G equals the compensation G for each species. This whole plant light compensation point is higher than the compensation point at which biomass production is zero (due to respiratory costs) because it also includes the cost of replacing senescing tissues (Givnish, 1988).

RESULTS

For clarity, the results are described in terms of patterns common to all species, differences between light-demanding and shade-tolerant species, and other interspecific patterns. Species are referred to by genus, as no two study species were of the same genus.
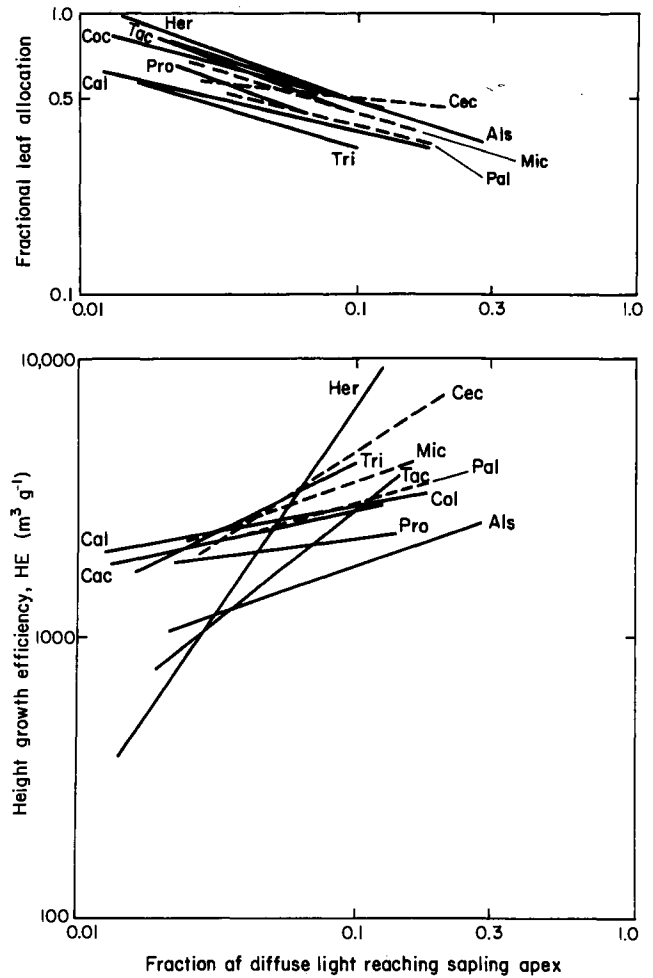

Fig. 3. Fraction of new aboveground biomass allocated to leaf growth (F) vs. the indirect site factor, and height growth efficiency (defined in Materials and Methods) vs. the indirect site factor.

TABLE 3. Height growth rate, aboveground biomass production per unit leaf area, height growth efficiency, fractional aboveground biomass allocation to new leaves, and leaf spacing estimated for an indirect site factor or diffuse light fraction of 0.06. Values for shade-tolerants within a column not sharing the same lowercase letter differ significantly (two-tailed $P < 0.05$) as determined by Duncan's multiple range test based on standard deviations from the expected values, derived from the regressions. Values for light-demanders denoted by > are significantly greater than corresponding mean values for shade-tolerants; those denoted by ≫ are significantly greater than values for all other species. Power function exponents denoted by * are significantly different from 0 ($P < 0.05$); those denoted by † are different from 0 at $P < 0.1$ but not $P < 0.05$.

						Power function exponents for characters expressed as power functions of the indirect site factor			
Species	$\frac{dh}{dt}$ (m yr^{-1})	G (g m^{-2} yr^{-1})	HE (m^3 g^{-1})	F	Internode length (cm)	$\frac{dh}{dt}$	HE	F	Internode length
Shade-tolerants									
Alseis	0.12a	84b	1500a	0.57b	1.4a	1.56a*	0.35a	−0.32a*	0.95ab*
Calophyllum	0.36c	127bc	2700b	0.43a	8.2f	0.98a*	0.18a	−0.23a*	0.35a*
Coccoloba	0.41c	144c	2600b	0.56b	3.7cde	1.20a*	0.22a	−0.26a	0.50abt
Herrania	0.20abc	58a	3200b	0.58b	2.2b	1.92a*	1.48b*	−0.36a*	1.02b*
Protium	0.24abc	123c	2100ab	0.46ab	4.3de	1.60a*	0.13a	−0.35a*	0.65ab*
Trichilia	0.32bc	109bc	3300b	0.38a	5.1e	1.38a*	0.50a	−0.30a*	0.53ab*
Tachigalia	0.15ab	90bc	1900ab	0.53b	2.6bcd	1.97a*	0.80ab*	−0.37a*	0.97ab*
Light-demanders									
Cecropia	0.71≫	224≫	3300	0.53	5.2	1.43*	0.64*	−0.11>	0.89*
Miconia	0.39	122	3100	0.51	7.2>	1.63*	0.35	−0.25*	0.90*
Palicourea	0.26	107	2600	0.45	7.5>	1.59*	0.29	−0.30*	0.82†

TABLE 4. Summary of correlations between the parameters of Table 3 and isf and G. The minimum and maximum r^2 value per species is listed followed by the mean of the r^2 values for the ten species analyzed. The correlations apply to ln–ln transformed data except for G vs. isf.

	Range and mean of r^2 values from regressions of the dependent variable against:	
Dependent variable	Indirect site factor (isf)	Rate of aboveground biomass production per unit leaf area (G)
$\dfrac{dh}{dt}$	0.44–0.75, 0.59	0.55–0.98, 0.83
G	0.48–0.93, 0.75	—
HE	0.04–0.75, 0.25	0.10–0.53, 0.29
F	0.04–0.74, 0.43	0.21–0.86, 0.62
Internode length	0.30–0.79, 0.44	0.19–0.88, 0.64

General patterns—All species showed a large increase in height growth with increasing light (Fig. 1), due primarily to a linear increase in aboveground production per unit leaf area (G) (Fig. 2) and secondarily to a more gradual increase in height growth efficiency (HE) with increasing light (Fig. 3). Note that although the increase in HE was not often significant for individual species, it was observed for all species (Table 3). The height growth rate was proportional to the 1.5 power of the diffuse light fraction or indirect site factor (isf) used to assess sapling light environment, while HE was proportional to $isf^{0.5}$, averaged over all species. This increase in HE was mostly due to a decrease in fractional biomass allocation to foliage, proportional to $isf^{-0.3}$ (Table 3).

The spacing of leaves along the central stem increased with light level (Table 3), and the height growth rate was proportional to internode length raised to a power >1 for all species (Fig. 4). The latter relationship indicates that, for a given species, fast-growing saplings both space their leaves further apart and produce them at a faster rate than do slow-growing saplings. The internode length, height growth rate, and fractional allocation to foliage were more highly correlated with G than isf, the estimate of light level (Table 4). This pattern suggests that morphology is linked to plant carbon gain, which is in turn correlated
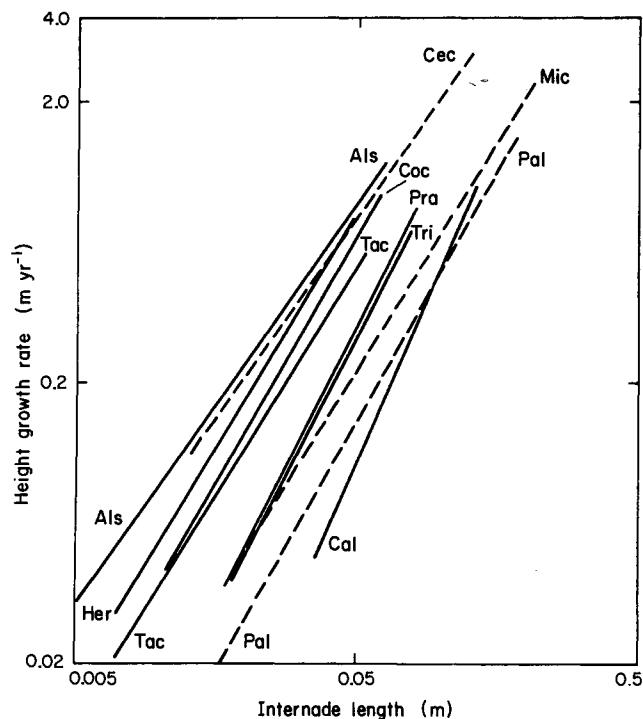

Fig. 4. Height growth rate vs. leaf internode length along main stem of saplings. The associated range of r^2 values for the log-transformed variates is 0.74–0.96.

with light. Specific leaf mass increased significantly with isf for all species except *Miconia* (Table 5).

Differences between light-demanding and shade-tolerant species—The height growth rates of the three light-demanding species were greater than or equal to the mean for the shade-tolerant species, compared at intermediate light levels (Fig. 1; Table 3). *Cecropia* grew significantly faster than any other species due to its very high G and high HE. *Cecropia* also differed from the other species in not showing a significant decline in fractional leaf allocation with increasing light (Fig. 3; Table 3). Nonetheless,

TABLE 5. Area per leaf, specific leaf mass, relative leaf area, leaf support efficiency, and allometric coefficient estimated for saplings with an indirect site factor of 0.06, and stem density determined from harvested saplings. Symbols following values are defined in Table 3. High-to-low-light-ratios are defined as the value for indirect site factor isf = 0.12 divided by the value for isf = 0.03. Ratios significantly different from 1 (two-tailed $P < 0.05$) are indicated by asterisks.

							High-to-low-light-ratios of				
Species	Area per leaf (cm²)	SLM (g m⁻²)	RLA (m² m⁻²)	LSE (m³ g⁻¹)	α	Stem density (g cm⁻³)	Area per leaf	SLM	RLA	LSE	α
Shade-tolerants											
Alseis	160a	30a	0.10a	9,000a	2.7b	0.48b	0.88	1.47*	1.30*	1.26	1.03
Calophyllum	220b	95e	0.14b	11,000abc	2.2b	0.51b	1.26	1.33*	0.96	1.08	1.05
Coccoloba	420c	79d	0.20cd	9,000a	1.4a	0.52b	1.50	1.33*	1.53	1.28	1.59
Herrania	700d	43b	0.31cd	15,000c	2.0ab	0.37a	0.86	1.36*	1.99	2.75*	0.77
Protium	620d	76d	0.18bc	10,000abc	2.7b	0.48b	1.23	1.36*	1.11	0.86	1.00
Trichilia	230ab	80d	0.17bc	10,000ab	2.1ab	0.64c	0.72	1.34*	1.23	1.29	0.98
Tachigalia	780d	58c	0.32d	8,000a	1.9ab	0.58bc	1.18	1.34*	0.89	1.31	0.92
Light-demanders											
Cecropia	340	40<	0.09<	19,000>	2.3	0.15≪	3.32*	1.36*	2.52*	2.25*	1.21*
Miconia	230	61	0.11<	11,000	1.8	0.44	1.91*	1.12	3.17*	1.85*	1.42*
Palicourea	150<	34<	0.28	13,000	2.8	0.29<	1.01	1.12*	1.96*	1.49	0.98

TABLE 6. Compensation aboveground production rate (that which just replaces senescing leaves) as compared to the aboveground production rate for an indirect site factor of 0.03 (shaded understory). Symbols following values are defined in Table 3. The asterisk indicates that G (isf = 0.03) is significantly less than the compensation G for *Miconia*. The compensation isf, or whole plant light compensation point was estimated from the G vs. isf relationship of Fig. 2 as the isf value yielding the compensation G.

Species	Compensation G (g m^{-2} yr^{-1})	G for isf = 0.03 (g m^{-2} yr^{-1})	Compensation isf	Leaf lifespan (mo)
Shade-tolerants				
Alseis	39a	31a	0.034	11a
Calophyllum	46a	80a	0.009	44d
Coccoloba	45a	50a	0.028	29bcd
Herrania	36a	37a	0.029	17b
Protium	36a	38a	0.029	38bcd
Trichilia	40a	45a	0.028	45d
Tachigalia	34a	38a	0.028	26c
Light-demanders				
Cecropia	172≫	143	0.041	4.4<
Miconia	94>	23*	0.052	12<
Palicourea	56	41	0.037	13<

HE increased significantly with light for *Cecropia*, due to a large increase in leaf support efficiency (LSE), which was in turn associated with an increase in relative leaf area (RLA = LA/h^2) with increasing light (Table 5).

The generally high LSE of *Cecropia* was associated with a very low stem density defined as dry mass/(total stem volume, including the hollow center) (Table 5). Unlike the case for the shade-tolerants, RLA also increased substantially with light for the other light-demanders. For the two light-demanders that seldom branched before reaching 2-m heights (*Cecropia* and *Miconia*) this increase in RLA was associated with an increase in leaf size (Table 5). The RLAs of these two species were significantly less than the mean for the shade-tolerants at intermediate light levels (Table 5), and particularly small for low-light-grown saplings.

The light-demanding species all had higher compensation Gs and higher whole plant light compensation points than the shade-tolerant species (Table 6), due to their short leaf lifespan and hence greater leaf replacement requirements. Some of the shade-tolerant species had very high fractional leaf allocation under low light (Fig. 3), i.e., their leaves were replaced with very little diversion of biomass to stem growth, thereby decreasing their compensation Gs. A comparison of the compensation G estimated for isf = 0.03 (understory conditions) indicates that the light-demanders cannot maintain current leaf area at this light level while the shade-tolerants can (Table 6). This inference of lower shade tolerance in the light-demanders was supported by the observation that eight of 55 light-demanding saplings died over a period of 11 months for *Miconia* and *Palicourea* and 6 months for *Cecropia*, while only two of 115 shade-tolerant saplings died in 11 months. A mean isf of 0.036 was determined for the dead light-demanders, all of whom decreased in leaf area before dying.

Other interspecific patterns—The shade-tolerant species exhibited three- to fourfold differences in leaf lifespan, SLM, and height growth rate and two-fold differences in

G and HE at intermediate light levels (Tables 3, 5, 6). More significant differences between species were observed for the leaf characteristics than for the growth rates and efficiencies, as the relative errors associated with the latter whole plant characteristics were larger. The shade-tolerant species were quite distinctive in SLM (Table 5), but because leaf lifespan was highly correlated with SLM (Table 7) there was little difference in the compensation Gs of these species (Table 6).

An intriguing difference occurred between the species that placed their leaves in close-packed rosettes about the apex when shaded (*Herrania*, *Tachigalia*, and especially, *Alseis*) and the other shade-tolerants with deeper crowns. The former three species each had lower intermediate-light-level height growth rates, Gs, SLMs, and leaf lifespans than any of the other shade-tolerants, although these differences were not always significant (Tables 3, 5, 6). The above three species also had the lowest HEs at low light levels (Fig. 3), as would be expected given their minimal extension per new leaf in shade.

These differences among the shade-tolerants may also be expressed as correlations between the growth variables for each species and SLM (Table 7). For intermediate light levels, the height growth rate and G were highly correlated with SLM, while the fractional leaf allocation F was negatively correlated with SLM. Furthermore, the exponents in the power functions relating height growth and F to light level were also related to SLM, although these correlations were only weakly significant (Table 7). Thus, at intermediate light levels, species whose leaves weighed more per unit area grew faster in height and weight, while investing a lower proportion of their total growth increment in leaves.

Differences between species in the relationship between height growth rate and leaf internode length (Fig. 4) were also related to interspecific differences in SLM (Table 7). In this comparison, the internode lengths of the opposite leaved species (*Alseis*, *Calophyllum*, and *Miconia*) were halved to express them as distance per single leaf. In general, leaf spacing increased with increasing specific leaf mass and decreasing fractional allocation to leaf growth. Thus, fast growing saplings in high light with low allocation to leaf growth and somewhat higher values of SLM spaced their leaves more widely than slow-growing shaded saplings, and interspecific differences in the height growth-internode length relationship were related to interspecific differences in SLM and F.

Another notable pattern involved the allometric exponent α, expressing wood biomass as a power of sapling height in equation 7. For branchless saplings, of given stem taper, wood biomass is proportional to hd^2, implying that stem diameter d is proportional to h$^{(\alpha-1)/2}$. Thus, the fact that α was less than 3 for all species (Table 5) indicates that the ratio of diameter to height decreased somewhat over the study period for the saplings. King (1990) observed similar allometric relationships between 1- and 6-m-tall saplings for *Alseis* and *Trichilia*, although diameter increases as a higher power of height in larger trees, thereby maintaining mechanical stability (McMahon, 1973).

The low value of α for *Coccoloba* (Table 5) indicates that diameter increases only slightly as saplings grow in height. This low α may be associated with a change in

TABLE 7. Interspecific relationships for the study species. Dependent variables were estimated for an indirect site factor of 0.06.

Interspecific relationship	r^2	P	N	Species used
Leaf support efficiency (m³ g⁻¹) vs. stem density (g cm⁻¹)				
LSE = 21,000 − 21,000ρ	0.81	0.0004	10	All
Specific leaf mass (g m⁻²) vs. leaf lifespan (mo)				
SLM = 27.3 + 1.35lifespan	0.78	0.0007	10	All
Relative leaf area vs. area per leaf (m²)				
RLA = 0.03 + 3.5A	0.80	0.0026	8	All but *Trichilia* and *Palicourea*[a]
Height growth rate (m yr⁻¹) vs. specific leaf mass (g m⁻²)				
$\dfrac{dh}{dt} = 0.00045SLM^{0.965}$	0.74	0.012	7	Shade-tolerants[b]
G (g m⁻² yr⁻¹) vs. specific leaf mass				
G = 36.2 + 1.04SLM	0.67	0.025	7	Shade-tolerants[b]
Fractional leaf allocation vs. specific leaf mass				
F = 0.67 − 0.0025SLM	0.57	0.051	7	Shade-tolerants[b]
Exponent b in power function relationship between height growth rate and the indirect site factor vs. SLM				
b = 2.24 − 0.0110SLM	0.50	0.08	7	Shade-tolerants[b]
Exponent c in power function relationship between fractional leaf allocation and the indirect site factor vs. SLM				
c = −0.40 + 0.0014SLM	0.37	0.15	7	Shade-tolerants[b]
Height growth rate at given internode length[c] vs. specific leaf mass				
$\dfrac{dh}{dt} = 223SLM^{-1.641}$	0.76	0.002	9	All but *Palicourea*[d]
Exponent d in power function relationship between height growth rate and internode length vs. SLM				
d = 0.99 + 0.0122SLM	0.82	0.0007	9	All but *Palicourea*[d]

[a] Excluded because saplings of these two species were usually branched, with multiple apices, and therefore bore greater leaf area than unbranched saplings of similar leaf size.

[b] Restricted to shade-tolerants to determine if differences in the growth parameters for these species, estimated at a given light level, are related to specific leaf mass.

[c] Internode length is 3 cm for alternative-leaved species and 6 cm for opposite-leaved species, i.e., the spacing is 3 cm per individual leaf.

[d] Excluded because most of the leaf area produced during the study was borne on branches for this species, resulting in a different relationship between leaf spacing, biomass partitioning and height growth.

architecture from an erect unbranched stem with a radially symmetric leaf arrangement to an arching, bilaterally symmetric branched form (the Troll model of Hallé, Oldeman, and Tomlinson, 1978) occurring as saplings grow above the study sapling height range. Thus, the limited secondary thickening associated with an α of 1.4 (Table 5) may result in saplings arching over and shifting in leaf orientation about the stem as they extend. The low α results in a higher HE than would otherwise be the case, but limits the height growth possible before the onset of mechanical instability (McMahon, 1973; King, 1987). Mature *Coccoloba* trees have thicker stems supporting sprawling planar crowns in the understory (King, personal observation). However, such increases in height growth efficiency may be more limited in other species of the Troll form because they begin branching and arching over at a lower height than does *Coccoloba*.

Herrania exhibited an extremely high HE at high light levels, compensating for its particularly low G and resulting in an intermediate height growth rate as compared to other shade-tolerants in gaps. (Figs. 1–3; Table 3). This high HE is associated with a low α and stem density and high RLA (Table 5).

DISCUSSION

Saplings of all study species increased biomass production and height growth with increasing ambient light, but their relative performances across a light-gradient varied. The analysis of height growth as the product of biomass production per unit leaf area and height growth

efficiency indicated both phenotypic plasticity within species and differences between species in their morphological responses to light. Thus, most species can regenerate in a wide range of microhabitats, but their ability to outgrow competitors may vary with habitat.

The observed morphological shifts in response to increased ambient light included an increase in specific leaf mass and an increase in leaf support efficiency and allocation to stem vs. leaves that produced an increase in height growth efficiency. As the light saturated photosynthetic rate and specific leaf mass both increase with ambient light (Fetcher et al., 1987), the observed linear increase in aboveground production per unit leaf area (G) was probably due in part to differences in the morphology and physiology of sun vs. shade leaves (Bjorkman, 1981), in addition to the increase in photosynthesis with increasing light expected for a given leaf. Because both G and height growth efficiency (HE) increased with ambient light, the height growth rate (equal to HE × G) increased more rapidly than either HE or G. Thus, morphological plasticity results in plants having higher height growth rates in gaps, but lower whole plant light compensation points when grown in shade, than would be the case for plants with fixed morphologies. However, the observed morphological shifts apply only to saplings growing with competing vegetation in sites receiving from 2% to 10%–25% of above-canopy light, and should not be extrapolated to plants in more open conditions. Studies of uncrowded saplings grown in higher light suggest that height growth efficiency declines as ambient light increases from 30% to 100% of above-canopy light (Loach, 1970).
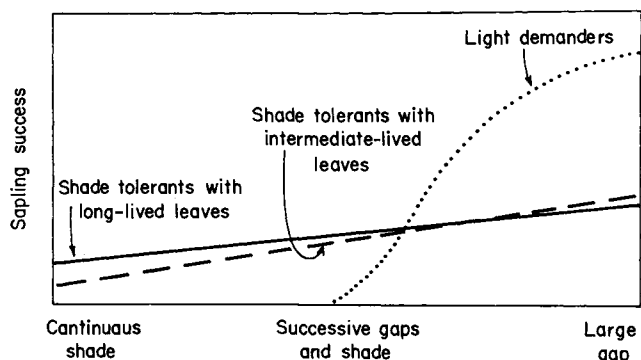
Fig. 5. Hypothesized success of passing through the sapling stage as a function of light environment for three functional groups, based on the results of this study.

Leaf lifespan influenced the growth response to light through its impact on the compensation G, the production rate required to just maintain current leaf area. Saplings of light-demanding species were largely excluded from typical understory sites, not because of lower G in shade than other species or necessarily higher photosynthetic compensation points (Fetcher et al., 1987), but because their short leaf lifespans necessitate higher production rates to maintain their canopies. High rates of herbivory on light-demanders, associated with lower investments in lignins, cellulose, and tannins for defense also make them vulnerable in low light environments where losses to herbivores cannot be offset by rapid growth (Coley, 1983, 1988). Leaf lifespan has been linked with sets of morphological and ecological characteristics both within and between ecosystems (Coley, 1983, 1988; Reich et al., 1991; Reich, Walters, and Ellsworth, 1992) with SLM and leaf toughness increasing and leaf nitrogen concentration and maximum net photosynthetic rate decreasing with increasing leaf longevity.

Cecropia insignis had both the highest compensation G and the highest height growth rate of any study species and is more dependent on large light gaps for regeneration than most other light-demanding species on BCI (Brokaw, 1987; Welden et al., 1991). The height growth efficiency of *Cecropia* was among the highest of the study species because of its high leaf support efficiency (LSE), which was twice that of the shade-tolerant species (Table 5). The high LSE of *Cecropia* is associated with a hollow stem produced by a particularly wide apex, resulting in saplings having an obconic (widest at the top) form with thin-walled upper sections that are later thickened by secondary growth. This tubular construction (with cross walls at leaf nodes) places proportionately more wood at the periphery where it aids most in increasing stem rigidity. By reducing mechanical support *Cecropia* increases its height growth per unit biomass added to the stem, but runs greater risk of damage from falling debris and mammalian herbivores.

The results presented here support the conclusions of others that long leaf lifespans and high aboveground allocation to leaf growth allow shade-tolerant species to survive in low-light environments (Williams, Field, and Mooney, 1989; King, 1991a). The shade-tolerant species had quite similar compensation Gs because interspecific differences in leaf lifespan were largely matched by cor-

responding differences in SLM. However, the shade-tolerant species with high SLM and long-lived leaves (e.g., *Calophyllum* and *Trichilia*) grew faster in height at low and intermediate light levels than thinner-leaved shade tolerants (e.g., *Alseis* and *Herrania*), with little difference between the two groups at high light levels (Fig. 1). This difference suggests that there may be differences between the regeneration patterns of shade-tolerant species, particularly when temporal variation in light is considered, as outlined in Fig. 5. Because they cannot maintain their canopies in the understory, light-demanding species must establish in tree-fall gaps where they compete with each other and with established shade-tolerant saplings. The results indicate that established shade-tolerant saplings of differing SLM grow at similar rates in gaps, although low SLM species may respond more quickly to newly opened gaps because they are able to produce more new leaf area per unit new biomass and thus shift more rapidly from shade- to sun-grown foliage. However, in understory locations with decades of low illumination levels, the regeneration of high SLM shade-tolerants would be favored. Because shade-tolerants with high SLM have longer crowns than those with low SLM (when grown in shade) these two groups may also differ in their ability to intercept side vs. vertical light. However, this postulated relationship between the growth of shade-tolerants and SLM is necessarily tentative, as it is based on seven species in a single forest.

The greater height growth rates of shade tolerants with high SLM in low light was primarily due to their greater G in low light. This difference in G could be caused by differences in photosynthetic response, respiration, or root vs. shoot allocation. An intriguing possibility is that saplings with thick, long-lived leaves require lower nutrient uptake rates to replace nutrients lost in senesced leaves and therefore require lower belowground allocation. Long leaf lifespans have been suggested as a means of conserving nutrients (Chabot and Hicks, 1982) as well as enduring shade (Coley, Bryant, and Chapin, 1985). As nutrient concentration per unit leaf area is not correlated with leaf lifespan in tropical species (Reich et al., 1991), the nutrient uptake rate required to maintain a given leaf area should be inversely proportional to leaf longevity. Studies of root growth and nutrient retranslocation are needed to test the hypothesis that nutrient use efficiency plays a role in differential responses of shade-tolerant species.

Tropical trees exhibit a wide range of branching patterns that have been classified into 23 different growth models by Hallé, Oldeman, and Tomlinson (1978) based on differences in axis orientation and timing of growth. Because my study focused on large-leaved, unbranched saplings of a limited size range, it provides only a partial description of sapling morphology and growth response to light. Other allometric studies indicate that the positive correlation between leaf size and total leaf area noted for unbranched saplings is reversed for branched saplings, where small-leaved species support wider crowns (King, 1991b). As all the unbranched study saplings eventually branch (except for *Herrania*), differences in crown allometry may be related to height of first branching, which ranges from 0.1 to >10 m in dicotyledonous species on BCI, and appears to be correlated with leaf size (White, 1983). Tropical forests exhibit greater diversity of first

branching height and sapling leaf size and lifespan than temperate deciduous forests where leaf lifespan is usually restricted to half a year by cold winters. Restrictions on leaf lifespan may also limit temperate species diversity, in addition to other suggested limits to diversity (Leigh, 1990).

The relationships between height growth rate and leaf internode length of Fig. 4 may be useful in assessing the growth histories of trees. King (1993) found that old leaf scars were still visible on mature trunks of *Pourouma aspera* (Cecropiaceae) in Costa Rica and used internode relationships derived from marked saplings to reconstruct the growth histories of a population of trees. Because interspecific differences in the height growth-internode length relationship were highly correlated with specific leaf mass (Table 7), the relations determined here could be extended to species not included in the study. (Note, however, that the derived relationships apply only to the lower unbranched portion of the stem, as they were determined from saplings that had not yet begun to branch.) The ability to determine growth histories would be useful in assessing the past environments of study plants, aging light gaps (Martínez-Ramos et al., 1988), and conducting demographic studies.

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