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Reproductive size thresholds in tropical trees: variation among individuals, species and forests

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Abstract: Relative size at onset of maturity (RSOM) is defined as size at first reproduction divided by asymptotic maximal size. RSOM is remarkably constant among species within many higher clades of animals, but varies widely among tree species from the Pasoh Forest Reserve, Malaysia according to the work of S. C. Thomas. RSOM was examined for 16 mid-storey and canopy tree species from a second tropical forest at Barro Colorado Island (BCI), Panama. Interspecific variation in RSOM was equally large for BCI and Pasoh and was unrelated to gap dependence or life form for BCI species. The shape of the relationship between size and the proportion of individuals that were reproductive differed between forests, with an abrupt increase over a narrow range of sizes at Pasoh and a more gradual increase over a wider range of sizes at BCI. Both overtopping trees and heavy liana infestation reduced the probability that BCI trees were reproductive. This presumably reflects reduced availability of carbon for reproduction. We speculate that greater liana loads and a greater abundance of large, shade-casting trees at BCI may increase variation among individuals and contribute to the relatively wide range of sizes characterized by a mixture of sterile and fertile individuals observed for most BCI species.

Key Words: Barro Colorado Island, lianas, Pasoh Forest Reserve, reproductive size thresholds, tropical trees

INTRODUCTION

The life histories of most trees are characterized by a prolonged sterile stage (seeds, seedlings and saplings) followed by an initial flowering and then a prolonged fertile stage (adults). The transition from the sterile, juvenile stage to the fertile, adult stage is virtually unstudied for tropical trees despite its obvious importance for individual fitness, population growth rates and species coexistence and community diversity. To quantify the transition to reproductive maturity, relative size at the onset of maturity (RSOM) is expressed as size at first reproduction normalized by asymptotic maximal size (Charnov 1990, Thomas 1996). Size at first reproduction increases linearly with maximal size among related animal species with indeterminate growth such that RSOM is nearly invariant within clades (Charnov 1990, He & Stewart 2001). To our knowledge, RSOM has been documented just once for iteroparous plants. Interspecific variation in RSOM was much greater for trees from the Pasoh Forest Reserve, Malaysia, than for animals (Thomas 1996).

The observation that RSOM varies widely among tree species at Pasoh has broad implications for species composition and species coexistence. All else equal, a species that begins to produce seeds at a smaller size will produce more seeds over its lifetime and become more abundant than a second species that delays reproduction. More likely, early reproduction will incur costs including lower growth, seed production and/or survival in the future leading to a trade-off between early reproduction and lifetime seed production (Wesselingh *et al.* 1997).

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This trade-off could contribute to species coexistence in several ways. Greater reproductive capacity, which might be achieved in part through early reproduction, may allow small-stature, shade-tolerant tree species to coexist with larger and inherently superior competitors for light (Kohyama 1993). Gap-dependent species are also widely expected to reproduce at smaller sizes than are shade-tolerant species (Grubb 1977). More generally, RSOM will influence colonization ability and, where competition-colonization trade-offs contribute to species coexistence, species diversity. For these reasons, the single observation that RSOM varies unexpectedly widely among tropical tree species is intriguing.

This paper evaluates RSOM for mid-storey and upper canopy trees from a second tropical forest located at Barro Colorado Island (BCI), Panama. The methods pioneered by Thomas (1996) were adopted to facilitate comparison with Pasoh. The following questions are addressed:

(1) Is interspecific variation in RSOM similar at BCI and Pasoh?
(2) Are absolute values of RSOM similar at BCI and Pasoh?
(3) Does RSOM vary with gap-dependence and life form among BCI species?

Recent rates of resource acquisition influence the size at first reproduction for several temperate forest trees (Nakashizuka *et al.* 1997, Shibata & Tanaka 2002) and rates of carbon acquisition may be limited by shade cast by taller trees or by encroaching lianas. Thus, we also ask:

(4) Does crown exposure and/or liana infestation influence the size-dependent probability of reproduction?

Finally, if individual- or site-specific variation in resource availability does influence the probability of reproduction, then variation in RSOM may fall largely among individuals within species rather than among species with important implications for the mechanisms of species coexistence described above. This last possibility will be evaluated qualitatively by comparing patterns at BCI and Pasoh.

METHODS

Reproductive status, crown exposure and liana load were evaluated for 16 canopy and mid-storey tree species between January and April 1996 (Table 1). The 16 species include 15 genera and 14 families and, with the exception of the two congeners, will be referred to by genus only. Fifteen species were flowering heavily when evaluated as judged relative to long-term records of flower production captured by 200 0.5-m^2 traps over 15 y (Wright *et al.* 1999, 2005). *Prioria*, which is monoecious, was maturing fruit. *Cordia alliodora, Hyeronima, Jacaranda, Luehea, Miconia* and *Triplaris* are relatively light-demanding and require tree-fall gaps to regenerate. The 10 remaining species are relatively shade tolerant and survive and grow as seedlings in the shaded understory (Dalling *et al.* 1998, Wright *et al.* 2003).

All individuals larger than a species-specific minimum DBH (diameter measured at 1.3 m height) were evaluated for a fully enumerated 50-ha plot for 15 species and for six contiguous hectares for *Garcinia*, which was extremely abundant. The 50-ha plot is described elsewhere (Condit *et al.* 1996). The minimum DBH was based on estimates of the diameter at which BCI tree species become fully reproductive made by Robin B. Foster more than 20 y ago (henceforth the RBF thresholds). The initial minimum DBH equaled 67% of the species-specific RBF thresholds. When trees of this size were occasionally found to be reproductive, the minimum DBH was reduced to 50% of the RBF threshold (Table 1).

Tree crowns were evaluated from the ground using binoculars by SJW, MAJ and/or JP. Reproductive status was scored on a five-point scale. Sterile trees were scored zero. Trees with from one reproductive structure to 25% of the crown bearing reproductive structures were scored one. Trees with 26–50%, 51–75% and 76–100% of the crown bearing reproductive structures were scored two, three and four, respectively. Reproductive status was dichotomized for the analyses presented here; sterile trees lacked any reproductive structures while fertile trees had one or more reproductive structures. Liana load was scored on the same five-point scale. Liana load was also dichotomized for the analyses presented here and was either light (score ≤ 1) or heavy (score ≥ 2). Crown exposure was scored dichotomously in the field (shaded or exposed). Shaded crowns were overtopped by taller neighbours so that the entire crown was shaded when the sun was directly overhead. To determine the repeatability of these scores, 212 trees were evaluated independently by two investigators. Reproductive status, liana load and crown exposure were scored identically on dichotomous scales for 87%, 81% and 84% of these trees, respectively. A three-way contingency analysis was used to evaluate dependence among species identity, liana load and crown exposure.

Analyses of reproductive size thresholds

Logistic regression is commonly used to describe the relationship between a dichotomous variable (reproductive status) and a continuous variable (size). We estimated the probability (P) that a tree of size DBH was fertile using maximum likelihood methods and the following modified logistic function:

$$P = k/(1 + \exp(-a - b \times \ln(\mathrm{DBH})), \qquad (1)$$

Table 1. Sample sizes, reproductive size thresholds, and the reproductive consequences of crown exposure and liana load for 16 tree species from Barro Colorado Island, Panama. N_r and N_t are the number of flowering and the total number of individuals evaluated, respectively. Parameters a, b and k were fitted to Eqn 1 using maximum likelihood. a and b jointly determine the reproductive size threshold, DBH_{thr}. k is less than 1 when the probability of flowering is less than 1 for the largest individuals. Size thresholds refer to diameter at breast height (DBH). DBH_{thr} is the inflection point of equation 1. RBF is a qualitative estimate of the size at which trees become fully reproductive provided by Robin B. Foster. Min is the smallest tree evaluated. The hypotheses that crown exposure and liana load affect the probability that a tree is reproductive were evaluated by contrasting Eqns 1 and 2 with maximum likelihood methods, leading to likelihood ratio tests with two degrees of freedom. H_{max} is the asymptotic height in metres estimated from height-DBH relationships (see *Methods: Analyses of reproductive size thresholds*). RSOM is the dimensionless relative height at the onset of maturity. Significance levels reflect the sequential Bonferroni correction. Nomenclature follows D'Arcy (1987) as updated by Condit *et al.* (1996).

			Number of individuals		Fitted parameters			Size thresholds DBH (mm)			Consequences of			
											Exposure	Lianas		
Species	Family	Life form[1]	N_r	N_t	a	b	k	DBH_{thr}	RBF	Min	χ^2_2	χ^2_2	H_{max}	RSOM
Alchornea costaricensis	Euphorbiaceae	T	21	130	−13.0	3.28^{***}	0.55	430	200	134	2.46	0.52	31.9	0.63
Brosimum alicastrum	Moraceae	T	43	76	−13.0	3.41^{***}	0.92	376	300	200	0.00	8.42	39.8	0.64
Cordia alliodora	Boraginaceae	T	45	62	−9.0	3.24^{***}	0.90	133	200	100	7.38	4.80	36.5	0.42
Cordia bicolor	Boraginaceae	M	156	298	−12.8	4.24^{***}	0.95	183	160	108	14.92^{**}	1.38	23.7	0.71
Eugenia oerstedeana	Myrtaceae	M	24	91	−6.9	1.97	0.53	187	200	134	33.46^{***}	1.56	18.3	0.81
Garcinia intermedia	Clusiaceae	M	188	398	−5.6	2.61^{***}	0.94	61	100	50	0.60	37.00^{***}	20.0	0.37
Hyeronima alchorneoides	Euphorbiaceae	T	22	36	−11.9	3.17^{***}	1.00	347	300	150	n/a	n/a	36.9	0.64
Jacaranda copaia	Bignoniaceae	T	96	191	−13.3	3.52^{***}	0.78	367	300	200	†	22.80^{***}	35.7	0.70
Luehea seemannii	Tiliaceae	T	49	61	−18.3	5.42^{***}	1.00	270	300	200	0.02	1.54	NA	NA
Macrocnemum glabrescens	Rubiaceae	M	11	39	−11.5	3.56^{***}	1.00	213	80	54	n/a	n/a	NA	NA
Miconia argentea	Melastomataceae	M	61	177	−10.4	4.23^{***}	0.85^{***}	103	100	50	10.70^{*}	8.34	28.3	0.43
Ocotea whitei	Lauraceae	T	57	101	−13.5	3.71^{***}	0.85	326	300	200	13.30^{*}	1.12	41.0	0.63
Prioria copaifera	Caesalpinioideae	T	75[2]	136	−13.7	3.40^{***}	0.89	467	600	300	4.66	11.34^{*}	41.0	0.68
Simarouba amara	Simaroubaceae	T	69	176	−12.4	3.57^{***}	0.85	272	300	150	5.72	9.08	35.4	0.61
Trichilia pallida	Meliaceae	M	48	236	−6.4	2.23^{***}	0.59	115	80	40	6.62	10.42^{*}	NA	NA
Triplaris cumingiana	Polygonaceae	M	173	231	−11.7	4.60^{***}	1.00	116	200	100	2.98	20.96^{***}	NA	NA

[1] T and M represent upper canopy trees and mid-storey trees with maximum heights of approximately 20 m, respectively.

[2] Maturing fruit, not flowering when evaluated.

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$ Significance levels reflect the sequential Bonferroni correction.

n/a, sample size inadequate for analysis. † Zero shaded, reproductive individuals. NA, data not available.

where *a*, *b* and *k* are fitted constants determined for each species separately. Equation 1 is preferable to the standard logistic function (where DBH replaces ln[DBH]) because *P* approaches zero as DBH approaches zero for Eqn 1 but not for the logistic function (Thomas 1996). *b* quantifies the slope of the fertility–size relationship, and there is evidence for a threshold reproductive size when *b* is significantly greater than zero. *k* is the asymptotic probability that an individual is reproductive and is bounded between 0 and 1. Likelihood ratio tests were used to determine the significance of *b* and *k* (Hilborn & Mangel 1997) and to evaluate possible reproductive senescence at large DBH (using Eqn 6 in Thomas 1996).

To determine whether crown exposure or liana load influenced *P*, maximum likelihood methods were also used to fit the following function:

$$P = D/(1 + \exp(a_1 - b_1 \ln(\mathrm{DBH}))) + (1 - D)/(1 + \exp(a_0 - b_0 \ln(\mathrm{DBH}))), \quad (2)$$

where *D* is a dichotomous variable, which equaled 1 for trees with exposed crowns or heavy liana loads and zero for trees with shaded crowns or light liana loads and a_1, b_1, a_0 and b_0 are fitted constants. A likelihood ratio test was used to contrast equations 1 and 2 to determine whether crown exposure or liana load had a significant effect on *P*. The sequential Bonferroni procedure (Rice 1989) was used to correct significance levels for the maximum likelihood analyses, which were performed for 16 species.

The inflection point of the relationship between reproductive status and DBH will serve as a quantitative estimate of reproductive size thresholds. The inflection point ($\mathrm{DBH_{thr}}$) is determined by setting the second derivative of Eqn 1 equal to zero and solving for DBH (Thomas 1996). Linear regression was used to evaluate the relationship between $\mathrm{DBH_{thr}}$ and the RBF threshold for BCI species because we would like to be able to predict reproductive size thresholds for the many species for which just the RBF estimate is available.

Relative size at onset of maturity (RSOM) was estimated as follows:

$$\mathrm{RSOM} = \mathrm{H_{thr}}/\mathrm{H_{max}}, \quad (3)$$

where $\mathrm{H_{thr}}$ is the estimated height of a tree of size $\mathrm{DBH_{thr}}$ and $\mathrm{H_{max}}$ is asymptotic maximal height (Thomas 1996). Species-specific relationships between tree height (*H*) and DBH are available for 12 of the 16 species studied here (R. Condit, unpubl. data). These relationships take the following form:

$$H = H_{\max}(1 - e^{-cDBH^d})$$

where $H_{\max}$, *c* and *d* are fitted constants, and explain 75–99% of the intraspecific variation in *H*. Pooled variance t-tests were used to evaluate possible differences in RSOM for gap-dependent versus shade-tolerant species and for mid-storey versus canopy species from BCI.

Site comparisons were limited to species with maximum heights of 20 m or more ($\mathrm{H_{max}} \geq 20$ m). Species with $\mathrm{H_{max}} < 20$ m were excluded because there was just one shorter species for BCI and the slope of the relationship between $\mathrm{H_{thr}}$ and $\mathrm{H_{max}}$ changed at $\mathrm{H_{max}} \sim 20$ m for Pasoh (see Figure 2 in Thomas 1996). Species with non-significant *b*-values were also excluded because a reproductive size threshold had not been identified. Eleven Pasoh species from four genera met these criteria. Two Pasoh species met the criteria for two census years and the year with the larger number of individuals censused was used for the site comparison. The 11 Pasoh species were the largest representatives of genera that included many understorey and midstorey trees. Therefore, Pasoh species were compared with all BCI species and with just midstorey BCI species (identified in Table 1) to further control possible effects of tree stature on the site comparison. Results were robust to the subset of BCI species used and only results for all BCI species are reported.

Site differences in the variance of $\mathrm{DBH_{thr}}$ and RSOM were evaluated using Bartlett's homogeneity of variance test and overall site differences were then evaluated using the appropriate t-test. Standard major axis (SMA) or Model II regression was used to determine whether the $\mathrm{DBH_{thr}}$–$\mathrm{H_{max}}$ and $\mathrm{H_{thr}}$–$\mathrm{H_{max}}$ relationships differed between sites. The program (S)MATR (http://www.bio.mq.edu.au/ecology/SMATR) performs the Model II analogue of standard analyses of covariance, and, when a significant difference in slopes was not detected, shifts in intercepts and shifts along the common SMA were evaluated. All other analyses were performed with SYSTAT 10.0 (SPSS 2000).

RESULTS

Reproductive size thresholds

We scored 2439 trees (Table 1). More than 70% of the 10 largest trees were reproductive for all species except *Alchornea*. There was a significant reproductive size threshold (*b* significantly greater than zero; see Eqn 1) for all species except *Eugenia* (Table 1). The asymptotic probability of reproduction was less than one (*k* significantly less than one) for *Miconia* only (Table 1). There was no evidence for reproductive senescence or any other non-asymptotic relationship between reproductive status and DBH (analysis not shown).

There was a strong, positive relationship between $\mathrm{DBH_{thr}}$ and the RBF threshold ($r^2 = 0.59$, $P < 0.001$; data in Table 1). The intercept (37 ± 48; estimate ± 1 SE) and slope (0.79 ± 0.18) were indistinguishable from zero and one, respectively. *Alchornea* was an outlier; however and the low proportion of the largest ten

Alchornea that were reproductive (just 0.5) casts suspicion on the unexpectedly large value of DBH$_{\mathrm{thr}}$ (Table 1). The relationship between DBH$_{\mathrm{thr}}$ and the RBF threshold improved when *Alchornea* was excluded ($r^2 = 0.74$) and the intercept (9.9 ± 41) and slope (0.95 ± 0.16) approached zero and one, respectively.

RSOM-values did not differ between gap-dependent and shade-tolerant species ($t = 1.05$, $P > 0.32$) nor between mid-storey and canopy species ($t = -0.45$, $P = 0.66$). Three BCI species had unusually low RSOM-values, including a light-demanding canopy tree (*Cordia alliodora*), a light-demanding mid-storey tree (*Miconia*) and a shade-tolerant mid-storey tree (*Garcinia*) (Table 1).

Lianas and crown exposure

All two-way interactions among species identity, liana load and crown exposure were significant ($P < 0.001$). Heavy liana loads afflicted 44.6 and 33.9% of trees with exposed and shaded crowns, respectively ($\chi^2_1 = 29.7$ for the liana-exposure interaction). Rapid growth of lianas in exposed crowns is likely to explain this association. Heavy liana loads characterized *Alchornea*, *Cordia bicolor* and *Ocotea* while light liana loads characterized *Jacaranda* ($|\text{standardized deviates}| > 3$) ($\chi^2_{15} = 375.0$ for the liana-species interaction). Putz (1984) reviews reasons why tree species vary in susceptibility to liana infestation on BCI. Finally, as expected, exposed crowns were underrepresented among mid-storey tree species (identified in Table 1) with the exceptions of *Miconia* and *Triplaris*, which are characterized by light-dependent regeneration ($\chi^2_{15} = 1006$ for the exposure–species interaction).

Liana load and crown exposure had significant effects on relationships between reproductive status and size for five and four BCI species, respectively (Table 1). Heavy liana loads reduced the probability of reproduction for all five species (Figure 1). Being overtopped by a taller tree consistently reduced the probability of reproduction for *Miconia, Ocotea* and *Cordia bicolor* (Figure 2). For *Eugenia*, which was the smallest species examined, the probability of reproduction was greater for small individuals with exposed crowns and for large individuals with shaded crowns (data not shown). This interaction among reproductive status, size and crown exposure contributed to the absence of a significant reproductive size threshold (*b*-value) when all *Eugenia* were pooled without regard to crown exposure.

BCI and Pasoh compared

DBH$_{\mathrm{thr}}$, which is the inflection point of the reproductive status-DBH relationship, had both significantly greater

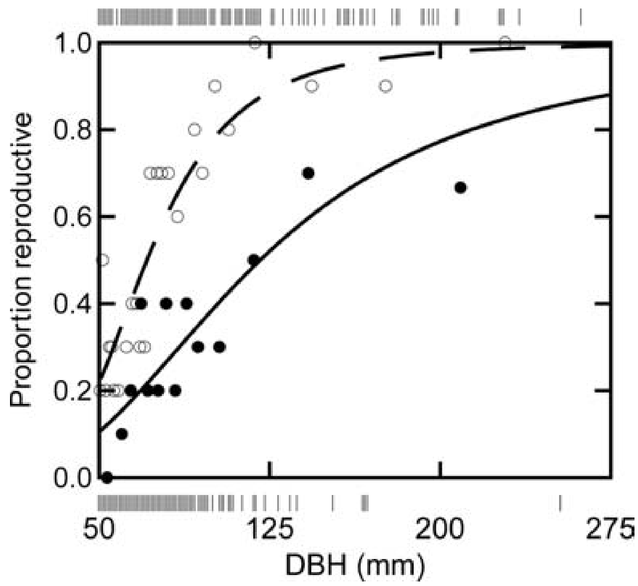

Figure 1. The impact of liana load on the probability of reproduction for the mid-storey tree *Garcinia intermedia* on Barro Colorado Island, Panama. Open circles and the dashed line represent individuals with light liana loads (0–25% of the crown infested). Solid circles and the solid line represent individuals with heavy liana loads (26–100%). Circles represent the proportion of individuals that were fertile and mean diameter at breast height (DBH) for groups of 10 individuals binned together by ranked DBH. The curved lines represent the maximum likelihood fit of equation 2. Vertical lines just above and below the figure represent fertile and sterile individuals, respectively.

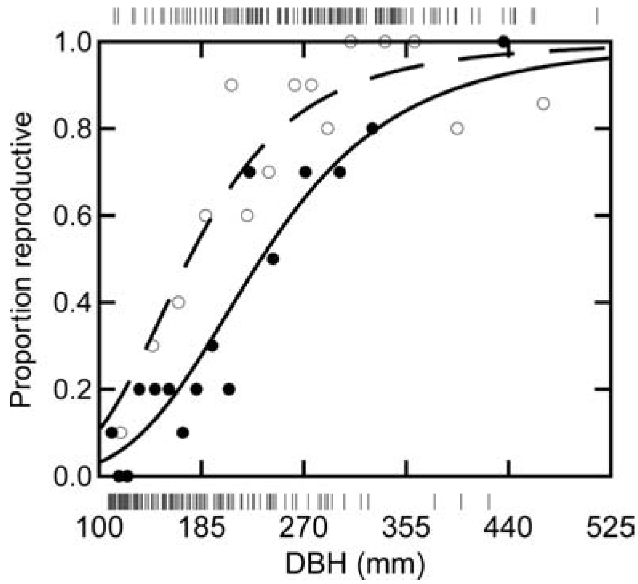

Figure 2. The impact of crown exposure on the probability of reproduction for the mid-storey tree *Cordia bicolor* on Barro Colorado Island, Panama. Open circles and the dashed line represent individuals with crowns exposed to the sun. Solid circles and the solid line represent individuals with crowns completely shaded by taller neighbours. The caption to Figure 1 provides further explanation.

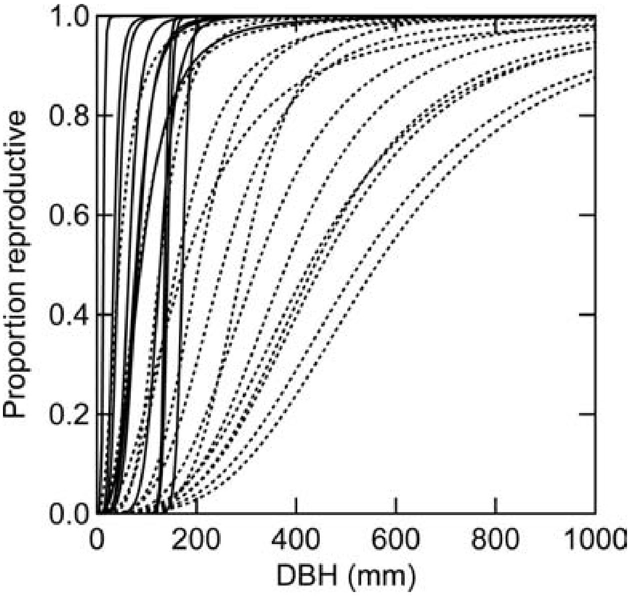

Figure 3. The proportion of individuals that are reproductive increases more slowly with size (quantified by DBH or diameter at breast height) for tree species from Barro Colorado Island, Panama (dashed lines) than from the Pasoh Forest Reserve, Malaysia (solid lines). The relationship also varies more among species in Panama. Each line represents one species. All species have maximum heights of 20 m or more.

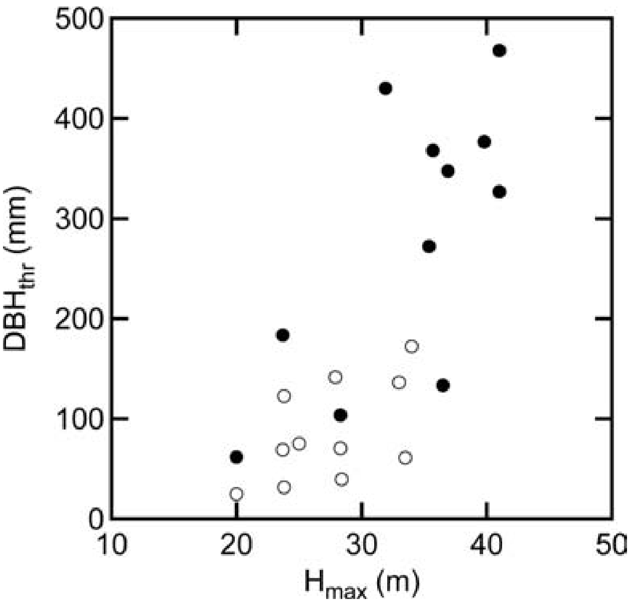

Figure 4. The relationship between asymptotic maximal height (H_{max}) and diameter at breast height at reproductive maturity (DBH_{thr}) for tree species from Barro Colorado Island, Panama (solid circles) and the Pasoh Forest Reserve, Malaysia (open circles). All species have maximum heights of 20 m or more.

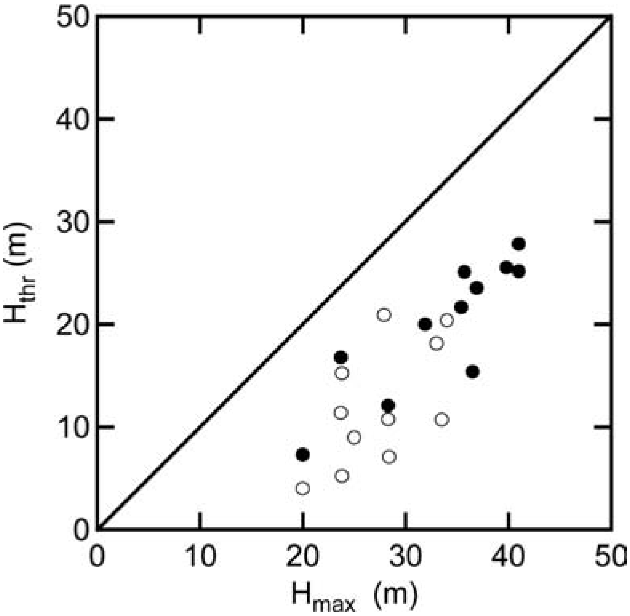

Figure 5. The relationship between asymptotic maximal heights (H_{max}) and height at reproductive maturity (H_{thr}) for tree species from Barro Colorado Island, Panama (solid circles) and the Pasoh Forest Reserve, Malaysia (open circles). The solid line represents $H_{thr} = H_{max}$. All species have maximum heights of 20 m or more.

variance among species (Bartlett's $\chi^2{}_1 = 21.0$, $P < 0.001$) and significantly greater values (separate variance $t = 4.01$, $P < 0.01$) for BCI than for Pasoh (Figure 3). Figure 4 presents the relationship between DBH_{thr} and asymptotic maximal heights (H_{max}). The standard major axis (SMA) slopes were not significantly different; however, there were significant shifts in intercepts ($F_{1,20} = 8.00$, $P < 0.01$) and along the common SMA slope ($F_{1,20} = 14.6$, $P < 0.001$). Both shifts contributed to the significant site differences observed for DBH_{thr}. BCI tree species tended to be larger (shift along the common SMA slope) and to have larger DBH_{thr} for a given maximal height (shift in intercepts).

Relative heights at the onset of maturity (RSOM) had indistinguishable variance (Bartlett's $\chi^2{}_1 = 1.53$, $P > 0.2$) but marginally significantly greater values (pooled variance $t = 2.01$, $P = 0.032$) for BCI than for Pasoh (data in Table 1 for BCI and in Table 1 of Thomas 1996 for Pasoh). Figure 5 presents the relationship between the components of RSOM for both sites (Eqn 3). The SMA slopes (permutation test, $P = 0.355$) and intercepts ($F_{1,20} = 0.83$, $P = 0.37$) were not significantly different. This brings the marginally significant site difference in RSOM-values into question. There was a significant shift along the common SMA slope ($F_{1,20} = 8.66$, $P < 0.01$), with taller tree species at BCI than at Pasoh even when comparisons were limited to species with $H_{max} \geq 20$ m. This latter shift cannot have contributed to the site difference in RSOM-values because the common SMA slope was virtually identical to one (common SMA slope = 1.008; lower and upper confidence intervals = 0.730 and 1.387, respectively). We conclude that the marginally significant site difference in RSOM-values should be discounted.

DISCUSSION

Reproductive size thresholds (DBH_{thr}) of BCI trees

Reproductive size thresholds were first quantified as the inflection point of the relationship between DBH and the probability that an individual was reproductive (DBH_{thr}; Figures 1–3). The close match between these values and reproductive size thresholds guesstimated by Robin B. Foster (Table 1) suggests that experienced field botanists may be able to provide reliable estimates of reproductive size thresholds for the many tropical tree species whose life histories remain unstudied.

The probability that an individual was reproductive increased very gradually with DBH for most BCI tree species (Figures 1–3). For these species, individuals from a wide range of DBH centred on DBH_{thr} had probability of being fertile between zero and one. The number of individuals declines exponentially as DBH increases for most BCI tree species, particularly shade-tolerant species (Wright *et al.* 2003). If the decline in number of individuals is more rapid than the increase in the probability of reproduction, there may actually be more reproductive trees below than above the reproductive size threshold. There were, however, very few reproductive trees with DBH less than 50–67% of DBH_{thr} (Figures 1 and 2). These smaller size thresholds should be used whenever it is important to identify all reproductive individuals (e.g. for analyses of paternity or seed dispersal; Muller-Landau *et al.* 2002).

Heavy liana loads and taller neighbouring trees both tended to reduce the probability that shaded trees were reproductive and hence to increase DBH_{thr} (Table 1, Figures 1 and 2). The full impact of lianas and taller neighbours was probably underestimated here because reproductive status, liana loads and crown exposure were each scored dichotomously. Lianas and shade have quantitative effects on carbon acquisition and hence reproduction. The leaves of lianas displace leaves of their host plants on a one-to-one mass basis (Kira & Ogawa 1971). Seasonal, inter-annual and experimentally induced variation in light levels all influence levels of carbon gain and reproduction in Panamanian trees (Graham *et al.* 2003, Wright & van Schaik 1994, Wright *et al.* 1999). The true impact of lianas and overtopping trees on reproduction by shaded trees is likely to be even greater than is apparent here once the three variables are quantified rather than dichotomized.

BCI and Pasoh compared

Interspecific variation in relative size at the onset of maturity (RSOM) was indistinguishable for large trees ($H_{max} > 20$ m) from BCI and Pasoh. The slope and intercept of the relationship between the components of RSOM were also indistinguishable (Figure 5). The similar RSOM-values observed at BCI and Pasoh mask one striking site difference.

The probability that an individual was reproductive increased much more slowly for BCI species than for Pasoh species (Figure 3). It is unlikely that this site difference was related to general flowering in which many Pasoh species flower only at irregular multi-year intervals because Thomas (1996) selected Pasoh species that reproduce annually as do most BCI species and made measurements during three non-general flowering years and just one general flowering year. Several possible explanations of the strong site difference in the abruptness of the reproduction-size relationship remain.

Forest structure and liana loads differ between BCI and Pasoh and may influence tree reproduction. The difference in forest structure concerns very large trees (DBH > 400 mm), which are 26.3% more abundant at BCI relative to Pasoh (Condit *et al.* 1999). We speculate that the greater abundance of very large trees at BCI may increase the proportion of smaller trees that are overtopped and shaded. The density of large lianas (DBH ≥ 20 mm) is 27.3% greater at BCI than at Pasoh (429 versus 337 lianas ha^{-1}, respectively, Putz 1984, Gardette 1998). We speculate that greater proportions of trees with infesting lianas and shaded crowns will both introduce greater variation in the conditions that favour reproduction among individual trees on BCI. Greater variation in the conditions that favour reproduction could, in turn, contribute to the wide range of DBH characterized by a mixture of sterile and fertile individuals observed for most BCI species.

Implications for species coexistence

The species composition of tropical forests is changing in response to a wide range of anthropogenic pressures (Laurance *et al.* 2004). For example, the basal area of large lianas (> 100 mm DBH) increased by 100% over the past 20 y in western Amazonian forests (Phillips *et al.* 2002) and total liana leaf mass increased by 50% over the same period on BCI (Wright *et al.* 2004). This widespread increase in the importance of lianas is already likely to have caused reductions in seed production by infested trees in many Neotropical forests (e.g. Figures 1 and 2). Interspecific variation in levels of seed production largely determines interspecific variation in the number of sites seeds reach among tropical forest trees (Dalling *et al.* 2002, Hubbell *et al.* 1999, Muller-Landau *et al.* 2002). If life history trade-offs involving colonization ability contribute to the coexistence of tropical tree species (reviewed by Wright 2002), then the increasing importance of lianas and the differential susceptibility of tree species to liana infestation are likely to combine to alter the diversity and species composition of tropical tree communities in the future.

Interspecific variation in RSOM is much greater for tropical trees at both BCI and Pasoh than for animal species from several major taxa (reviewed by Thomas 1996, also see He & Stewart 2001). Life history trade-offs involving interspecific variation in RSOM could contribute to species coexistence through several different mechanisms (reviewed by Thomas 1996). The large interspecific variation in RSOM observed for two tropical tree communities suggests that these life history trade-offs may make important contributions to the maintenance of species diversity in tropical tree communities. However, the wide range of sizes characterized by a mixture of sterile and fertile individuals observed for most BCI species suggests that broad intraspecific variation might limit these potential contributions. Quantification of RSOM for additional species and, in particular, for additional plant communities will be necessary to explore these possibilities.

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