Tap-root depth of tropical seedlings in relation to species-specific edaphic preferences

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Abstract: We compared seedlings of sandy-soil specialist species (*Dryobalanops aromatica* and *Scaphium borneense*) and clay-rich-soil specialist congeners (*D. lanceolata* and *S. longipetiolatum*) in a tropical rain forest in Lambir Hills National Park, Malaysia, to determine whether variations in belowground seedling architecture and allometry were related to edaphic specialization. A convergent trait that was phylogenetically independent across the two genera was the presence of a deeper tap-root at any height and any root biomass in sandy-soil specialists than in clay-rich-soil specialists. This trait was fixed independently of the edaphic conditions in which the trees actually grew. Finer-textured soils generally have better water-holding capacity; we concluded that seasonal water limitation would be more severe in sandy soils than in clay-rich soils, and that water limitation would provoke convergence in seedling root depth among species with the same edaphic preferences. All significant differences found in interspecific comparison within *Dryobalanops* were consistent with the water-availability hypothesis; the sandy-soil specialist had larger root biomass at any total biomass and had smaller leaf biomass at any root biomass than the clay-rich-soil specialist. However, for *Scaphium* this was not the case, suggesting that factors other than water-limitation may also underlie seedling allometric relationships.

Key Words: allometry, architecture, Dipterocarpaceae, *Dryobalanops aromatica*, *Dryobalanops lanceolata*, Lambir Hills National Park, *Scaphium borneense*, *Scaphium longipetiolatum*, Sterculiaceae, tropical rain forests

INTRODUCTION

Scientists have reported habitat niche differentiation among tree species in relation to edaphic conditions in species-rich tropical rain forests (Davies *et al.* 1998, Itoh *et al.* 2003, Lee *et al.* 2002, Palmiotto *et al.* 2004, Yamada *et al.* 2000a). One would therefore expect tree species to have developed numerous anatomical and physiological adaptations to specialized edaphic conditions in a niche where the species regenerate preferentially. Yamada *et al.* (2000b) documented an example of the modes of such adaptation using three congeneric species of *Scaphium*, which showed divergence in habitat niche promoted by the localized edaphic conditions in a Bornean tropical rain forest. The above-ground architectural and allometric differentiation of saplings of *Scaphium* species gave a

potential competitive advantage to each species over its congeners in stands where that species regenerated preferentially. However, there have been few studies of the adaptations of below-ground architecture to specialized edaphic conditions in tropical rain forests.

The roots of trees serve multiple functions, such as the uptake of water and nutrients, storage of energy and anchorage of the above-ground parts. Unsuberized fine roots play important roles in the uptake of water and nutrients. The effective deployment of these fine roots is of paramount importance in all trees. The availability of nutrients often varies inversely to that of water, because nutrients tend to lie close to the soil surface and, at least during dry periods, soil water availability typically increases with depth (Landsberg 1986). Therefore, deep tap-rooted species are advantaged in terms of water uptake, since they can deploy fine-roots in deeper parts of a soil. However, making a deep tap-root requires the use of energy at the expense of making fine roots close to the soil

Table 1. Edaphic preferences and sample sizes of species studied.

Species	Edaphic preference	Sample size (size range[1])	
		Clay-rich soils	Sandy soils
Dryobalanops aromatica Gaertn.	Sandy soils[2]	6 ($30 \leq Hs$ cm < 40)	24 ($20 \leq Hs$ cm < 50)
Dryobalanops lanceolata Burck	Clay-rich soils[2]	25 ($20 \leq Hs$ cm < 50)	11 ($30 \leq Hs$ cm < 40)
Scaphium borneense (Merr.) Kosterm.	Sandy soils[3]	0	33 ($10 \leq Hs$ cm < 50)
Scaphium longipetiolatum (Kosterm.) Kosterm.	Clay-rich soils[3]	29 ($10 \leq Hs$ cm < 50)	0

[1] *Hs* stands for stem height.
Data sources: [2] Itoh *et al.* (2003), [3] Yamada *et al.* (2000a).

surface for nutrient uptake and above-ground plant parts for assimilation. One would expect that root architecture and biomass allocation to roots would be subjected to the strong selective pressure in this trade-off, and that a tree species would strike an optimal balance that maximized the probability of its survival and regeneration in stands where it regenerated preferentially.

We investigated inter- and intraspecific differences in biomass allocation and plant architecture, with particular reference to tap-root depth and species-specific edaphic preferences, in tropical seedlings growing under field conditions. The excavation of whole root systems, including fine roots, under field conditions is time consuming and difficult, because roots of different trees can be entwined with each other and are vulnerable to breakage during excavation. It was therefore not realistic for us to examine the fine roots of many trees, so we carefully excavated only the tap-roots and focused on their potential function of water uptake; deeper tap-rooted species would be able to deploy fine-roots in deeper parts of a soil and thus be more effective in water uptake during droughts than shallower tap-rooted species. We aimed to answer the following two questions. First, are there differences in tap-root depth and biomass allocation to roots between closely related species with different edaphic preferences? Second, if so, are these traits fixed independently of the edaphic conditions in which the trees actually grew or plastically changed with changes in the edaphic conditions?

METHODS

Study sites and species

The study was performed in an equatorial foothill forest in Lambir Hills National Park, East Malaysia (3°12′N, 114°00′E). Annual rainfall averages around 320 cm. At the site the climate is fairly aseasonal but is not drought free (Nakagawa *et al.* 2000). Details of the climate, soils, vegetation and physiography are provided by Watson (1985) and Yamakura *et al.* (1996).

We conducted interspecific comparisons of biomass allocation and plant architecture, but only within the same genus. This was for two reasons. First, the co-existence of closely related species with similar ecological and physiological characteristics is central to our understanding of the maintenance of biodiversity in tropical rain forests (Ashton 1988). The second reason is phylogenic constraint. A hierarchically structured phylogeny undermines the comparison of two phenotypes across two higher taxa, and this often leads to serious statistical problems (Felsenstein 1985). Interspecific comparisons within a genus are more likely to weaken this phylogenic constraint.

We examined two species of *Scaphium* (Sterculiaceae) and *Dryobalanops* (Dipterocarpaceae) which occur at Lambir Hills National Park (Table 1). *Scaphium* is a small genus of large, briefly deciduous trees, and *Dryobalanops* is a small genus of huge evergreen emergents (Itoh *et al.* 2003, Yamada *et al.* 2000a). *Scaphium borneense* and *D. aromatica* occur primarily on sites covered by sandy soils, whereas *S. longipetiolatum* and *D. lanceolata* prefer sites with clay-rich soils. *Dryobalanops aromatica* was the most abundant canopy species in a 52-ha study plot in Lambir Hills National Park (n = 8940); the others were common canopy or emergent species found to number 954 (*D. lanceolata*), 1135 (*S. borneense*) and 63 (*S. longipetiolatum*) in the same plot (Itoh *et al.* 2003, Yamada *et al.* 2000a).

Field methods

Seedlings under closed canopy that were of sound appearance and with no evidence of stem breakage or root death were chosen. About 30 seedlings per species, with heights ranging from 10–50 cm, were sampled from a stand on the soil preferred by each species (Table 1). Seedlings of *Dryobalanops* species were sometimes distributed on soils on which the species was not normally found. Six and 11 seedlings of *D. aromatica* and *D. lanceolata*, respectively, ranging in height from 30–40 cm were sampled from these stands. In September 2001 we carefully excavated the tap-roots of the sample seedlings and then measured stem height (*Hs*, cm) and tap-root length (*Lr*, cm). The sample plants were dried at 80 °C for 1 wk in an electric oven, and the following

oven-dry masses were measured: leaf dry mass (Wl, g), root dry mass (Wr, g) and total dry mass (W, g).

Analysis of interspecific differences in allometry

We analysed interspecific differences in the allometric relationships between a sandy-soil specialist and a clay-rich-soil specialist congener using samples from a stand on the soil preferred by each species. It is well known that the allometric relationships between two parts of an organism, x and y, often satisfy the following power function:

$$\ln y = b_0 + b_1 \ln x,$$

where b_0 and b_1 are parameters obtained by linear regression of natural logarithm-transformed variables. Many researchers have pointed out that the standard regression method is unsuitable for calculating allometric relationships where both variables are covariant and/or are subject to error, and alternative regression methods for bivariant data have been recommended (LaBarbera 1989, Niklas 1994). We used the reduced major axis (RMA) method to determine the parameters. Four allometric pairs related to Wr or Lr were examined (Table 2). Significant correlations were found for all relationships examined ($R^2 > 0.293$, $P < 0.05$ for all cases). For the interspecific comparison of the allometric line, the differences in the slope of the allometric line, b_1 were tested first (i.e. test for homogeneity of slopes). If there was no difference in slope (test for homogeneity, $P > 0.05$), a common slope, $b_{1\text{common}}$ between the species was determined. The tests for homogeneity of slopes and calculation of the common slopes followed Warton & Weber (2002). Then the difference in the intercept of the allometric line, b_0 with the common slope was tested by Student's t-test of group mean y', where y' is y-transformed as $\ln y - b_{1\text{common}} \ln x$ for each species. That is, these analyses used an RMA analogue of standard ANCOVA. These tests were performed using (S)MATR (Version 1,

http://www.bio.mq.edu.au/ecology/SMATR). Species with a larger slope show a greater increase of y per increment of x, and species with a larger intercept have a larger y at any particular value of x.

Analysis of intraspecific differences

Intraspecific differences in architecture and biomass allocation were analysed between seedlings inhabiting preferred and unpreferred habitats. In most allometric relationships of seedlings inhabiting unpreferred habitats, there were no significant correlations between two parts of each organism owing to the small sample sizes and size ranges. Therefore, the RMA analogue of standard ANCOVA was not appropriate. Instead, we compared the means of Hr, W, Wl and Wr in the seedling size range of $30\,\text{cm} \leq Hs < 40\,\text{cm}$ using Student's t-test with sequential Bonferroni corrections (Rice 1989).

RESULTS

Interspecific differences

In the allometry of W-Lr, a significant difference was found only in intercept in both cases of *Dryobalanops* and *Scaphium* (Table 2); sandy-soil specialists had significantly deeper tap-roots than clay-rich-soil specialists at the same total biomass (Figure 1a, b). In the allometry of Wr-Lr, a significant difference was found only in intercept in the case of *Scaphium* (Table 2); a sandy-soil specialist had significantly deeper tap-root than a congeneric clay-rich-soil specialist at the same root biomass (Figure 1d). In the case of *Dryobalanops*, a significant difference was found in slope (Table 2). But in the size range studied, the regression line for a sandy-soil specialist was always above that for a clay-rich-soil specialist (Figure 1c), suggesting that a sandy-soil specialist had deeper tap-root than a congeneric clay-rich-soil specialist at any root biomass,

Table 2. Result of regression analysis of the allometric relationship, $\ln y = b_0 + b_1 \ln x$ between selected pairs (x, y) of dimensions by using RMA (reduced major axis) method for sandy-soil and clay-rich-soil specialists of *Dryobalanops* and *Scaphium* species. Interspecific differences in the allometric relationship were analysed using a RMA analogue of standard ANCOVA test. The results of the test are also shown.

| | | Regression for | | | | | | Intercept with common slope for | | |
| | | Sandy-soil specialist | | Clay-rich-soil specialist | | P for homogeneity of slopes | Common slope | Sandy-soil specialist | Clay-rich-soil specialist | P for intercept comparison |
Genus	x-y	b_1	b_0	b_1	b_0					
Dryobalanops	W-Lr	0.25	2.83	0.43	2.29	0.059	0.27	2.79	2.40	< 0.001
Dryobalanops	Wr-Lr	0.26	3.12	0.56	3.02	0.006	–	–	–	–
Dryobalanops	W-Wr	0.97	−1.11	0.80	−1.21	0.132	0.92	−1.07	−1.31	0.001
Dryobalanops	Wr-Wl	1.15	0.03	1.46	0.41	0.152	1.24	0.04	0.28	< 0.001
Scaphium	W-Lr	0.47	2.57	0.42	2.27	0.533	0.44	2.61	2.23	< 0.001
Scaphium	Wr-Lr	0.55	3.23	0.40	2.92	0.059	0.46	3.22	2.92	< 0.001
Scaphium	W-Wr	0.86	−1.20	1.07	−1.65	0.006	–	–	–	–
Scaphium	Wr-Wl	1.31	0.46	0.82	0.39	0.001	–	–	–	–
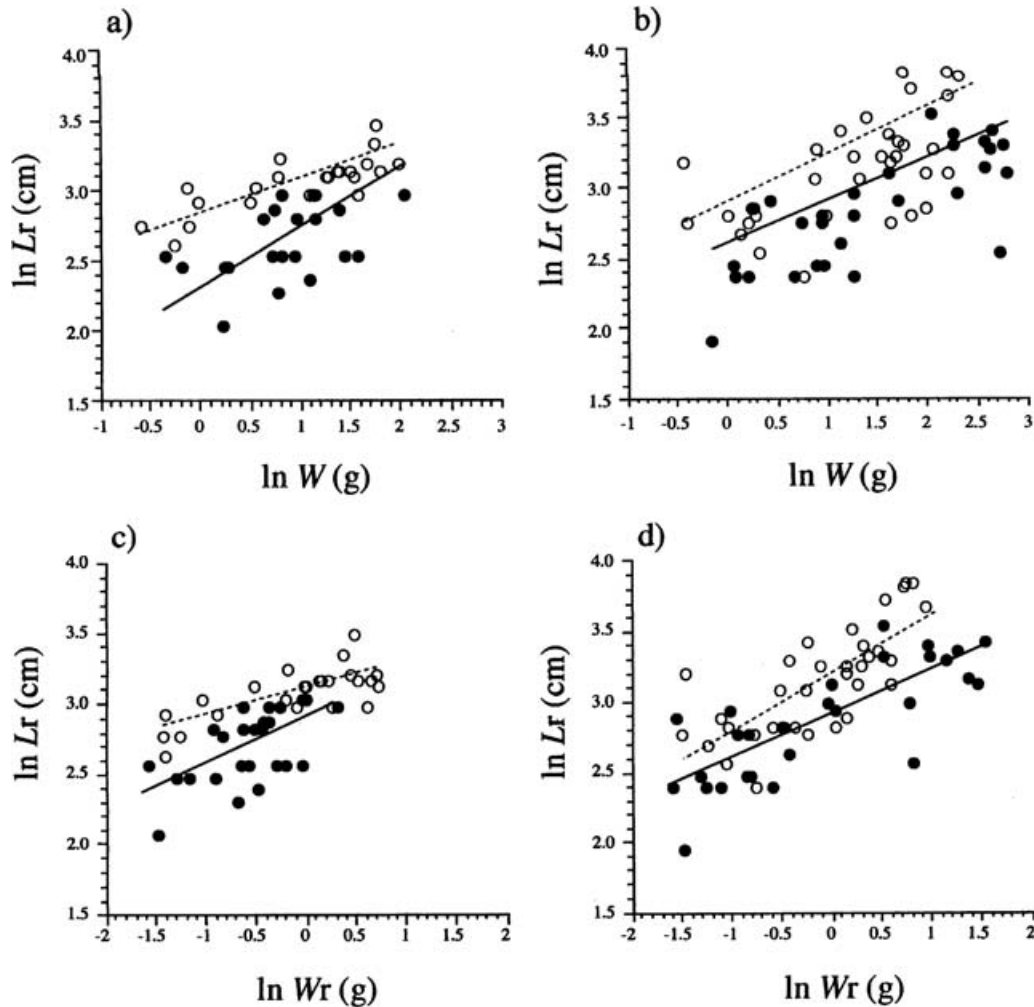
Figure 1. Relationships between total dry mass (*W*) and tap-root length (*Lr*) (parts a and b) and between root mass (*Wr*) and tap-root length (*Lr*) (parts c and d) for *Dryobalanops* (parts a and c) and *Scaphium* (parts b and d). ○, sandy-soil specialists (*D. aromatica* and *S. borneense*); and ●, clay-rich-soil specialists (*D. lanceolata* and *S. longipetiolatum*). Regression lines for sandy-soil specialists and clay-rich-soil specialists are shown by dotted and solid lines, respectively, which were determined by the reduced major axis method.

the same tendency as the case of *Scaphium*. The results of the interspecific comparison of allometries of *W-Wr* and *Wr-Wl* differed between the genera examined. In the case of *Dryobalanops*, a significant difference was found in intercept of both allometric relationships; the sandy-soil specialist had larger root biomass at the same total biomass and had smaller leaf biomass at the same root biomass than clay-rich-soil specialist congener (Table 2). In the case of *Scaphium*, a significant difference was found in slope of both allometric relationships; the sandy-soil specialist had significantly smaller and larger slope in *W-Wr* and *Wr-Wl* relationships, respectively, than the clay-rich-soil specialist (Table 2).

Intraspecific differences

Student's t-tests showed no significant intraspecific differences between seedlings inhabiting sandy or clay-

rich soils for both *D. aromatica* and *D. lanceolata*, suggesting that within these species the architecture and allometry of all of the dimensions measured remain the same regardless of the soil type.

DISCUSSION

Considerable differences in the allometries in relation to tap-root dimensions were found among the closely related species in this study (Table 2). Kohyama & Grubb (1994), who compared allometries of root dimensions among 14 species for which seed mass covered four orders of magnitude in a Japanese warm-temperate rain forest, found that seed mass had an influence on tap-root depth; larger seeds gave rise to deeper tap-rooted seedlings and smaller seeds to shallower tap-rooted seedlings. The species examined in this study produce similar-sized seeds of

2–3 g in dry mass. The interspecific difference in seed mass is thus unlikely to explain the interspecific differences in the allometries in relation to tap-root dimensions.

Our first research question – are there differences in tap-root depth and root biomass allocation between species with different edaphic preferences? – was answered affirmatively by our data. One convergent trait that was phylogenetically independent across the two genera was the fact that the sandy-soil specialists had deeper tap-roots than the clay-rich-soil specialists (Table 2, Figure 1). A question arises as to why sandy-soil specialists would have deeper tap-roots than clay-rich-soil specialists. In general, finer-textured soils such as clay-rich soils have better water-holding capacity than sandy soils. Although northern Borneo lies in the aseasonal tropics, moderately severe droughts are frequent and severe droughts occur occasionally, especially in El Niño Southern Oscillation periods (Bebber *et al.* 2002, Cao 2000, Nakagawa *et al.* 2000). During these drought periods, water stress would be more severe in sandy soils than in clay-rich soils. Soil water availability typically increases with soil depth during rainless periods (Landsberg 1986). Sandy-soil specialists must therefore develop deeper tap-roots than clay-rich-soil specialists for the effective uptake of water. Paz (2003) found that seedlings' roots were deeper in the site with the longer dry season. An alternative explanation in the climate under consideration is that the clay-rich soils are frequently anoxic at depth, and lethal to young roots. Therefore, tap-root depth convergence among species with the same edaphic preferences would confer a competitive advantage over other congeners with different edaphic preferences in stands growing on soils that the former preferred.

All significant differences found in interspecific comparison within *Dryobalanops* were consistent with the water-availability hypothesis; a sandy-soil specialist had larger root biomass at the same total biomass and had smaller leaf biomass at the same root biomass than clay-rich-soil specialist congener (Table 2). But for *Scaphium* this was not the case. For example, allocation to leaves versus root increased more rapidly in a sandy-soil specialist, and root allocation increased more rapidly with total biomass in the clay-rich soil specialist (Table 2). Both results would not support the water-availability hypothesis. Other factors than water-limitation, such as the difference in understorey irradiances and soil nutrients related to edaphic conditions may also underlie seedlings' allometric relationships.

Besides water stress, soil nutrient conditions also differ between sandy and clay-rich soils (Palmiotto *et al.* 2004); the udult soils (roughly similar to clay-rich soils) had significantly higher concentrations of total N, P, K, Ca and Mg than the humult soils (roughly similar to sandy soils). Any one or a combination of these differences may explain the soil effects on root architecture and biomass.

For example, a community-level study revealed that soil nitrogen concentration was significantly correlated with fine-root biomass among various forest types in Australian tropical forests (Maycock & Congdon 2000). However, these nutrient differences would have a more critical effect on the biomass of the fine roots than on the biomass of the tap-root. In addition, a nursery experiment has led to a conclusion that the differences in soil water availability between the udult and humult soils are more important than those in nutrient availability in influencing species' growth and spatial distributions in Lambir Hills National Park (Palmiotto *et al.* 2004). Hence, water limitation is likely to have more severe influence on seedlings' tap-root dimensions than nutrient limitation in Lambir Hills National Park.

The answer to our second question – do architectural and allometric traits change with changes in edaphic conditions? – was negative. There were no differences in architecture or biomass allocation between seedlings of the same species on sandy and clay-rich soils, suggesting that their architecture and biomass allocation traits are fixed. This is in accordance with the results of a nursery experiment by Palmiotto *et al.* (2004). They conducted intraspecific comparison of the biomass allocation, specific leaf area and leaf area ratio between seedlings grown on humult and udult soils using *D. aromatica* and *D. lanceolata*. One of the results of the nursery experiment showed that if seedlings were grown under a shaded condition, which is the same condition as this study, there was no significant intraspecific difference in biomass allocation, specific leaf area and leaf area ratio between seedlings on udult and humult soils.

We showed an example of convergence pattern; sandy-soil specialists had deeper tap-roots than clay-rich-soil specialists, but only using two genera. A phylogenic independent contrast (PIC) design with two genera has no statistical power to test an underlying hypothesis. Hence, here we can only present a hypothesis that sandy-soil specialists have deeper tap-root than clay-rich-soil specialists, which should be re-examined by a robust PIC design dealing with many species groups and having sufficient statistical power to test.

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