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Seedling performance of four sympatric *Entandrophragma* species (Meliaceae) under simulated fertility and moisture regimes of a Central African rain forest

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Abstract: Relative densities of mahogany species vary across tropical Africa and correspond with changes in soil fertility and moisture status. Seedling growth of four co-occurring African mahoganies (*Entandrophragma* spp.) was studied in relation to soil nutrient and moisture status in a shade-house experiment. On naturally occurring forest soils, *E. cylindricum* and *E. utile* exhibited increased relative growth rate (RGR) and decreased root mass ratio (RMR) with an increase in soil fertility while *E. angolense* and *E. candollei* did not. Changes in leaf morphology with fertility did not correspond to changes in species performance. On moist, fertile soils, *E. angolense* outperformed congeners but *E. candollei* performed equally well on moist infertile soils. *Entandrophragma cylindricum* performed as well as *E. angolense* and *E. candollei* on two of three soil moisture stress treatments but *E. utile* consistently performed poorly. Comparative seedling performance fitted well with limited available data on the distribution of *Entandrophragma* spp. in relation to soil fertility and moisture gradients and suggests that within-forest microsite heterogeneity may help explain the distribution of *Entandrophragma* species within the Dzanga-Sangha Dense Forest Reserve, Central African Republic.

Key Words: African mahogany, Central African Republic, Dzanga-Sangha Dense Forest Reserve, *Entandrophragma*, performance, seedlings, soil fertility, soil moisture, species diversity, tropical forest

INTRODUCTION

Over the past two decades, significant progress has been made in understanding how tropical forests maintain diversity. While methods and approaches have varied, studies suggest that seedling and/or sapling response to amount of light (Ashton 1995, Ashton *et al*. 1995, Brandani *et al*. 1988, Brown *et al*. 1999, Denslow *et al*. 1990, Schnitzer & Carson 2001), moisture availability (Ashton *et al*. 1995, Poulsen 1996), and pathogens (Wills *et al*. 1997) all play roles in maintaining diversity. To a lesser extent, species-specific adaptations to edaphic gradients and/or habitat have also been invoked as an explanation as to how tropical forests maintain diversity (Clark *et al*. 1998, Davies *et al*. 1998, Gartlan *et al*. 1986, Palmiotto 1998, Webb & Peart 2000, but see Harms *et al*. 2001). As knowledge increases about tropical soils, it is becoming increasingly clear that these soils can be every bit as heterogeneous as temperate soils (Richter & Babbar 1991, Silver *et al*. 1994) and it stands to reason that habitat classes and topographic position may not be sufficient to describe the complexity of soil nutrient gradients (Clark *et al*. 1999). Some evidence suggests that dipterocarp seedlings only respond by changes in growth at very low nutrient levels (Turner *et al*. 1993) and that growth on highly leached tropical soils may be limited by base cations (Burslem *et al*. 1994, 1995; Gunatilleke *et al*. 1997). Thus it is possible that small-scale variation in the spatial distribution of varied nutrients may help determine the distribution of trees within tropical forests (Clark *et al*. 1999, Gunatilleke *et al*. 1996).

This study was undertaken to determine the extent to which the distribution of four species of sympatric *Entandrophragma* within a Central African forest may be explained by growth performance at the seedling stage. *Entandrophragma utile* (Dawe & Sprague) Sprague and *Entandrophragma candollei* Harms can be relatively abundant within a particular forest or region but are often found at much lower densities than either *Entandrophragma angolense* (Welw.) C. DC. or *Entandrophragma cylindricum* (Sprague) Sprague. For example in Ghana, Hall & Swaine (1981) found *E. utile* to be largely restricted to their north-west moist semi-deciduous forest type and they report *E. candollei* to be markedly more frequent in their upland evergreen forest stratum than elsewhere. In addition, while *E. candollei* is typically reported at lower densities than congeners (CTFT 1985, Eggelling 1947, Swaine & Hall 1988, van Rompaey 1993)

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it is more abundant than other *Entandrophragma* species in Odzala National Park in Congo (Dowsett-Lemaire 1996). The Ghanaian forests where *E. utile* is concentrated are relatively fertile with high total exchangeable bases (TEB, 9.2 meq 100 g^{-1}), high per cent base saturation of the cation exchange capacity (CEC; Hall & Swaine 1981) and approximately 15 ppm available phosphorus (Hall & Swaine 1976). In contrast, upland evergreen forest is reported by Hall & Swaine (1981) as one of the poorest forest-stratum soils with respect to TEB and soils of Odzala N. P. have both a low per cent base saturation of the CEC and very low values of exchangeable cations (FAO 1973). Both *E. angolense* and *E. cylindricum* are found across tropical Africa. However, in Ghana, *E. angolense* is relatively abundant in moist evergreen forest, a forest type that is reported to be clearly poorer in soil nutrients than those of semi-deciduous forest, while *E. cylindricum* is rare here (Hall & Swaine 1981).

The relationship between the regional patterns in distribution and relative abundance of *Entandrophragma* spp. with those of soil fertility suggest that soil fertility may be one factor important in determining the distribution of these species. As *Entandrophragma* spp. are also found along a gradient from wet to dry forest (Hall & Swaine 1981), adaptations to moisture stress may also be important in determining their distribution. Soil heterogeneity within a forest may provide sufficient microsites to favour regeneration of *Entandrophragma* spp. at different sites within the same forest. We suggest that, given the scale with which soils have been mapped within much of Central Africa, this heterogeneity may have heretofore been overlooked.

Because the seedling stage is critical to the establishment and ability of a species to occupy a given microsite (Grubb 1977), we used seedling performance at selected soil fertility and moisture levels in shade-house experiments to test the degree to which these resources may explain adult tree distributions. We specifically looked for differences in growth performance, biomass allocation and plasticity as a gauge of the importance of these gradients.

We hypothesized that response to different soil fertility conditions is a species-specific phenomenon within these four *Entandrophragma* species and that this differential performance will lead to a change in rank order in terms of which species performs best under a particular soil fertility and moisture combination. We first tested the hypothesis that each species responds to changes in soil fertility, with respect to levels of base cations and phosphorus, for soils found within the Dzanga-Sangha Dense Forest Reserve (Central African Republic) and those observed at a different site (Budongo Forest, Uganda) where *Entandrophragma* spp. are also found. We then tested the hypothesis that a shift in species rank occurs under different fertility conditions within a given moisture treatment. Finally, we tested the hypothesis that shifts in biomass allocation and leaf plasticity will reflect the abilities of species to respond to increased nutrients and changes in moisture regimes.

STUDY SITE AND SPECIES

This study was undertaken in Bayanga, within the Dzanga-Sangha Dense Forest Reserve, Central African Republic (2°55′0″N and 16°15′45″E), where the vegetation is a mosaic of mixed semi-deciduous and evergreen forest with swamp clearings. There is a pronounced dry season between early December and the end of March; average annual precipitation over a 12-y period was 1365 mm (Carroll 1997). Soils of the region are broadly classed as oxisols (Juo & Wilding 1996).

The four species chosen for this study are widely distributed across the semi-deciduous forest of West and Central Africa. All four *Entandrophragma* species studied are classified by Hawthorne (1995) as non-pioneer light demanders (NPLD) or species whose seedlings require shade for establishment and early growth but thereafter require release to escape mortality and continue development. They are canopy emergents with heights often reaching 50 m and diameters at breast height recorded well over 1.5 m in the Reserve (J. S. Hall, unpubl. data). Seeds are winged and similar in size and mass (Aubréville 1959, J. S. Hall, unpubl. data) and dispersal is wind aided (Medjibe & Hall 2003). Thus, they all apparently occupy the same ecological guild (see Hawthorne 1995).

METHODS

Shelter construction and soil preparation

Four nursery shelters were constructed for the experiment following the design of Ashton (1990) where shelters were covered and wrapped in plastic and neutral shade cloth to reduce light and exclude precipitation. An electric fence was erected to enclose nursery shelters and exclude elephants. Light was measured with Li 190S quantum sensors (LiCor Lincoln, Nebraska, USA) and found to be 26.9% full sunlight (12.8 mol m^{-2} d^{-1}) inside the shelters. The limited available data suggested this to be close to optimal light for growth of *E. angolense* (Riddoch *et al.* 1991), *E. cylindricum* (Pieters 1976), and *E. utile* (Agyeman *et al.* 1999). The average daily temperature inside the nursery shelters was 30.0 °C, slightly higher than the mean daily temperature of 28.7 °C recorded outside in the shade.

Prior to transplanting seedlings, two sites were identified with different levels of soil fertility (Table 1). Exchangeable base cations were determined by the barium chloride method following Sumner & Miller (1996) and available phosphorus was determined by the Bray (P-1)

Table 1. Nutrient status, pH and texture of soils used in nursery experiment (n = 4 for each soil). K, exchangeable potassium; Mg, exchangeable magnesium; Ca, exchangeable calcium; P, available phosphorus; SL, sandy loam. Superscript letters denote significant differences at $P < 0.05$; significance base on LS means in one-way ANOVA.

Soil	Texture	pH	K (meq 100 g^{-1} soil)	Mg (meq 100 g^{-1} soil)	Ca (meq 100 g^{-1} soil)	P (mg P kg^{-1} soil)
Time 0						
Kongana	SL	3.95^{a}	0.13^{a}	0.19^{b}	0.45^{a}	5.88^{a}
Massapoula	SL	4.33^{a}	0.14^{a}	0.46^{a}	0.93^{a}	13.2^{a}
1 year						
Dry						
Kongana	SL	–	0.09^{b}	0.16^{b}	0.24^{bc}	4.64^{c}
Massapoula	SL	–	0.12^{b}	0.43^{b}	1.17^{ab}	8.90^{b}
Nutrient	SL	–	0.63^{a}	1.14^{a}	2.08^{a}	22.3^{a}
Moist						
Kongana	SL	–	0.06^{ab}	0.15^{b}	0.20^{b}	4.15^{b}
Massapoula	SL	–	0.04^{b}	0.21^{ab}	0.71^{a}	4.32^{b}
Nutrient	SL	–	0.10^{a}	0.23^{a}	0.82^{a}	8.76^{a}

method (Bray & Kurtz 1954). Soils from Kongana, approximately 30 km south-east of Bayanga, and Massapoula, 3 km north of Bayanga, were used. Soil was taken from mixed forest, where large *Entandrophragma* spp. were found, from the upper 15 cm of the mineral soil and transported to Bayanga where it was sieved to remove coarse organic material.

Experimental design

The study was carried out between February 1999 and February 2000. Seedlings of *E. angolense*, *E. candollei*, *E. cylindricum* and *E. utile* were collected from the forest understorey and transplanted in a nursery between June and October 1998. Seedlings were collected below a minimum of three adult trees of each species, mixed together, and kept in approximately 5% full sunlight until enough seedlings of each species were available for the experiment. All seedlings were less than 1 y old and only individuals of one species, *E. utile*, had begun to put out compound leaves at the beginning of the experiment. All individuals were subsequently bare-root transplanted into sieved soil and given 6 wk to acclimate prior to the beginning of the experiment. Seedling sacks were each 20 litres in volume.

Seedlings were divided into three soil-fertility and two moisture treatments: infertile (Kongana soil), intermediate-fertility (Massapoula soil), and high-fertility (Massapoula soil with nutrient additions) treatments (Table 1). The level of nutrient addition was calculated to elevate soil fertility levels to those reported by Synnott (1975) for soil taken from mixed forest in Uganda where he undertook experiments with *E. utile* (exchangeable cations: K = 4.2 meq 100 g^{-1} soil, Mg = 2.7 meq 100 g^{-1} soil and Ca = 9.7 meq 100 g^{-1} soil). Nutrient additions of 0.144 g Ca (added as $CaCl_2$), 0.041 g Mg (added as $MgCl_2$), and 1.5 g 20-10-10 N-P-K added in aqueous solution were made monthly. The two moisture treatments applied were designed to replicate continually moist soils (moist) and those subjected to intermediate moisture stress (dry). In forests with similar precipitation patterns where *Entandrophragma* spp. occur in Ghana, Veenendaal *et al.* (1996*a*) measured soil matric potentials of −2 MPa during the dry season. Moisture treatments in this experiment were −0.05 MPa and −0.7 MPa for moist and dry treatments respectively. In moist treatments plants were watered every other day so that soil was saturated and allowed to drain freely. In dry treatments, 200 ml of water was added per sack twice a week. Moisture was monitored daily in each soil × moisture combination on four seedlings with gypsum blocks placed at 20 cm depth. Seedlings followed for moisture were mixed among blocks but were excluded from harvests. No significant differences between matric potentials were found within either moist or dry soils between fertility treatments.

Ten seedlings of each species were grown together in a randomized arrangement within each treatment (a total of 24 sub-blocks in the experiment). Each shelter or block contained one sub-block of each treatment (six sub-blocks per shelter). Thus, each shelter contained a moist and dry sub-block of each of three fertility treatments, with 40 seedlings (10 of each species) randomly arranged within each sub-block. Seedlings were spaced at approximately 50 cm between each nursery sack (90 cm between stems). Blocks were re-randomized after 6 mo to avoid possible effects of side shading by larger individuals.

Seedling processing

At time zero seedling height and root collar diameter of all seedlings were measured (Table 2) and 16 individuals of each species were harvested. Seedling stems and roots were air dried in the field and leaves were dried in plant presses over kerosene stoves at low heat. All harvested seedlings were subsequently transported to the United States where they were oven dried at 80 °C. Dry weights were taken for stems and leaves as well as fine and coarse roots. At the end of 1 y, seedling heights and root collar

Table 2. Initial height and root collar diameters of *Entandrophragma* spp. used in nursery experiment in Bayanga, Central African Republic (mean values and standard deviations presented; n = 40 individuals per species).

Species	Height (cm)	Root collar (mm)
E. angolense	9.8 ± 2.9	3.1 ± 0.7
E. candollei	14.2 ± 4.0	3.2 ± 0.7
E. cylindricum	8.9 ± 2.8	2.1 ± 0.7
E. utile	18.4 ± 6.1	4.7 ± 1.3

diameters were measured. Four individuals of each species were harvested from each treatment within each block. Fresh and dry weights were taken for plant parts as above. Leaf area was measured for all leaves and leaflets of each from the 16 individuals harvested per species per treatment using a Li 3100 Area Meter (LiCor Lincoln, Nebraska).

Data analysis

The moisture treatments were designed to assess growth under conditions that seedlings would be expected to experience during different seasons and not at different places within the forest during the same season. The marked differences in moisture resulted in the error variance not being constant across moisture treatments thus prohibiting analysis of moist and dry treatments in the same analysis of variance (ANOVA). Within moisture treatments, data were analysed as a randomized complete block design with a two-way factorial structure and with sub-sampling. An analysis of variance where fertility and species were factors was completed in SAS 6.12 (SAS Institute, Cary, North Carolina, USA). F ratios were calculated by dividing the treatment mean square by the three-way interaction term mean square (Soil × Species × Block; Sokal & Rohlf 1995, Steel & Torrie 1960). Because no block × factor interactions were significant, they were excluded from the model to increase the power of tests of treatment effects.

Statistically significant interactions between factors make comparisons where both species and soil vary of questionable value. However, in terms of plant performance in this experiment, the primary interest is to assess differences in plant growth among species within a given soil type and/or among soils for a given species. These are termed simple main effects and, in experiments with factorial structure, are appropriately assessed by unfolding the design and expressing main and interaction effects as sets of contrasts of cell means (Schabenberger *et al.* 2000). Simple main effects were compared using the Slice command in SAS to determine significant interactions and subsequently using the LS means command in the two-way ANOVA model for pairwise comparisons of simple main effects (Schabenberger *et al.* 2000).

Analyses were completed for relative growth rates (RGR) of total mass, relative height and root-collar growth rates, Leaf Area Ratio (LAR), Specific Leaf Area (SLA), Leaf Mass Ratio (LMR), Root Mass Ratio (RMR) and Stem Mass Ratio (SMR). RGR was calculated following Fisher (1921) where

$$\mathrm{RGR} = \frac{\log W_2 - \log W_1}{t_2 - t_1}$$

and where W_1 and W_2 represent mass, height or diameter at time t_1 and t_2 respectively.

RESULTS

Relative growth rates

In moist soils, significant differences were found within soil fertility treatments and between species for RGR; however, only *E. cylindricum* and *E. utile* exhibited significant differences between moist soil treatments (Table 3). Similar patterns emerged for relative height and diameter growth rates and are not discussed further. *Entandrophragma angolense* performed significantly better than congeners on high-fertility-status soils (Massapoula and Massapoula soil with nutrient addition; Figure 1). On infertile (Kongana) soil, *E. candollei* performed as well as *E. angolense* and both of these species performed significantly better than *E. cylindricum* and *E. utile*.

On moisture-stressed soils, only *E. utile* did not exhibit significantly higher RGR between Kongana and nutrient-addition soils (Table 4). *Entandrophragma angolense* ranked consistently among the species with the highest RGR while *E. utile* consistently performed poorly in relation to congeners here (Figure 1).

Biomass allocation

Both *E. cylindricum* and *E. utile* had significantly higher root mass ratios (RMR) on moist Kongana soil than on the Massapoula soil but all four species had significantly lower RMR on nutrient-addition soil as compared with Kongana soil (Figure 2, Table 3). *Entandrophragma cylindricum* and *E. utile* exhibited significantly higher RMR on Kongana soil than *E. angolense* and *E. candollei*. However, on Massapoula and nutrient addition soils, *E. cylindricum* had significantly lower allocation to roots than congeners.

Entandrophragma candollei and *E. cylindricum* exhibited significant increase in LMR between moist soils (Figure 2, Table 3). Three of the four species showed significant differences in stem mass ratio (SMR) between soils but only *E. cylindricum* and *E. utile* showed significant changes in pair-wise comparisons between soils where the former had significantly lower stem allocation

Table 3. F values and significance (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant) for analysis of variance of Total Mass Relative Growth Rate (RGR), Root Mass Ratio, Stem Mass Ratio, Leaf Mass Ratio, Specific Leaf Area (SLA), and Leaf Area Ratio (LAR) in nursery experiments with *Entandrophragma* spp. in Bayanga, Central African Republic. Analysis was completed as a two-factor, random block design in moist soil for soil and species.

	Degrees of freedom	Total Mass RGR	Root Mass Ratio	Stem Mass Ratio	Leaf Mass Ratio	SLA	LAR
Block	3	0.24ns	0.56ns	2.07ns	1.23ns	1.55ns	0.31ns
Soil	2	7.37**	59.80***	0.25ns	24.50***	5.15*	24.59***
Species	3	23.78***	11.41***	1.14ns	5.02**	20.83***	4.37*
Soil × Species	6	2.77*	7.14***	5.67***	5.45***	2.05ns	6.33***
Simple Main Effects							
Soil × Species							
E. angolense	2	2.48ns	20.95***	3.97*	2.83ns	0.77ns	1.00ns
E. candollei	2	1.03ns	3.72*	0.64ns	4.54*	4.60*	9.02***
E. cylindricum	2	9.84***	53.55***	8.53**	35.24***	4.78*	34.19***
E. utile	2	4.31*	13.04***	4.13*	0.56ns	0.15ns	0.90ns
Kongana	3	12.61***	6.25**	1.70ns	2.20ns	5.91**	1.44ns
Massapoula	3	5.43**	10.37***	2.54ns	1.64ns	7.86***	2.88ns
Nutrient Addition	3	11.67***	9.36***	8.32***	12.13***	12.14***	13.57***

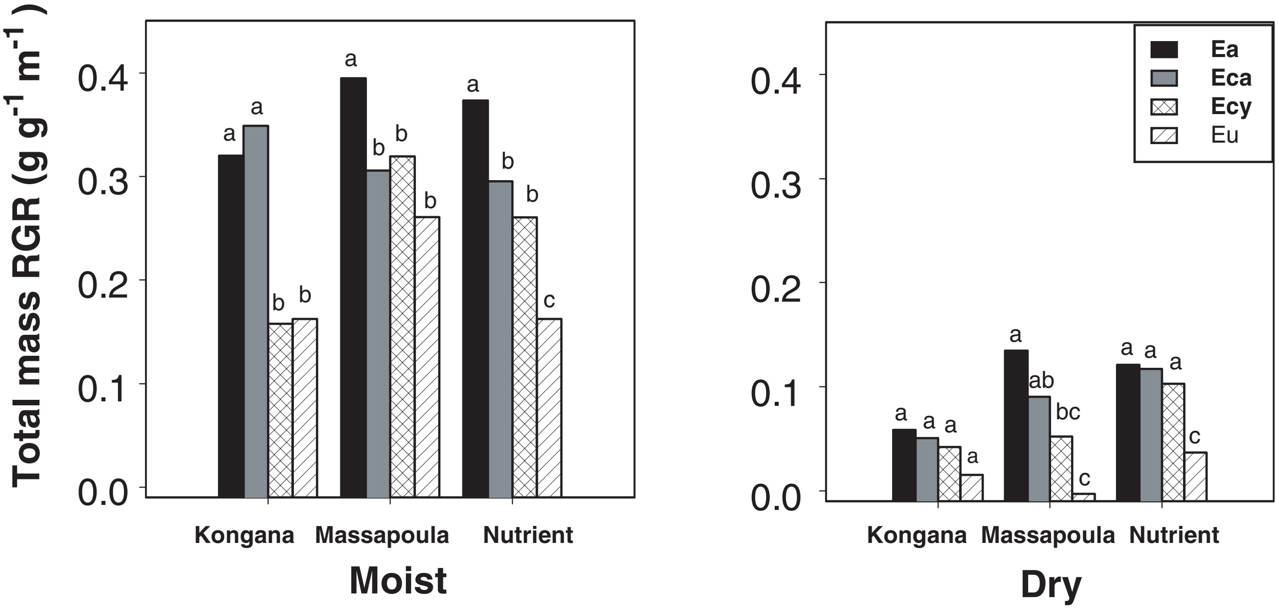

Figure 1. Total mass relative growth rates (RGR) for *Entandrophragma* spp. within soil fertility and moisture treatments (Ea, *E. angolense*; Eca, *E. candollei*; Ecy, *E. cylindricum*; Eu, *E. utile*; letters denote significant differences between species and within soil-fertility/moisture treatment; significance determined by LS means in SAS and significant at $P < 0.05$, df = 33).

on nutrient-addition soil and the latter had significantly higher allocation (Figure 2).

In pair-wise comparisons on moist soils, both *E. candollei* and *E. cylindricum* had significantly higher Leaf Area Ratios (LAR) in the nutrient-addition treatment than in Kongana soil and both of these species had significantly higher LARs than the other two species on nutrient-addition soils (Figure 3). Within species, a similar pattern was observed in Specific Leaf Area (SLA) as the pattern detected for change in LAR. Within the Kongana soil treatment, *E. cylindricum* and *E. utile* had significantly higher SLA than *E. angolense* and *E. candollei* (Figure 3, Table 3). This trend remained consistent with increased fertility with the exception being that *E. candollei* was among the species with the highest SLA on nutrient-addition soils.

Few differences were observed within species and between soil treatments for RMR on dry soils; however, *E. utile* was always among the species with the highest allocation to roots when species were compared within soils (Figure 2, Table 4). As with moist soils, LMR was the inverse to RMR; however, *E. angolense* allocated significantly less biomass to leaves on both Kongana and nutrient-addition soils than on Massapoula soil while *E. cylindricum* significantly increased allocation to leaves at the expense of stem allocation on nutrient-addition soils (Figure 2).

Both *E. angolense* and *E. cylindricum* exhibited

Table 4. F values and significance (* P < 0.05; ** P < 0.01; *** P < 0.001; ns, not significant) for analysis of variance of Total Mass Relative Growth Rate (RGR), Root Mass Ratio, Stem Mass Ratio, Leaf Mass Ratio, Specific Leaf Area (SLA) and Leaf Area Ratio (LAR) in nursery experiments with *Entandrophragma* spp. in Bayanga, Central African Republic. Analysis was completed as a two-factor, random block design in dry soil for soil and species.

	Degrees of freedom	Total Mass RGR	Root Mass Ratio	Stem Mass Ratio	Leaf Mass Ratio	SLA	LAR
Block	3	0.15ns	0.20ns	0.32ns	1.93ns	1.56ns	1.43ns
Soil	2	13.26***	1.08ns	1.47ns	0.10ns	2.38ns	0.20ns
Species	3	25.35***	7.86***	11.91***	21.49***	9.98***	23.78***
Soil × Species	6	3.09*	1.58ns	2.08ns	5.11***	4.59**	6.39***
Simple Main Effect Soil × Species							
E. angolense	2	10.22***	3.72*	1.70ns	5.96**	1.08ns	4.20*
E. candollei	2	3.97*	0.96ns	2.54ns	0.66ns	1.07ns	1.61ns
E. cylindricum	2	6.83**	0.44ns	8.32***	5.95**	1.14ns	10.72***
E. utile	2	1.89ns	0.53ns	3.97*	3.10ns	13.47***	3.38*
Kongana	3	1.80ns	1.26ns	0.64ns	1.23ns	0.94ns	1.21ns
Massapoula	3	21.00***	7.57***	8.53**	15.86***	15.15***	14.74***
Nutrient Addition	3	9.09***	2.49ns	4.13*	14.35***	4.05*	20.42***

significantly lower LARs on Kongana soil than more fertile soil for pairwise comparisons of simple main effects on dry soils. While no significant differences were observed for *E. candollei* here, *E. utile* exhibited significantly lower LAR on Massapoula than on Kongana soil. Few significant differences were observed in SLA on dry soil (Figure 3, Table 4).

DISCUSSION

Soil fertility

This study found important differences in RGR and patterns of allocation between *Entandrophragma* spp. seedlings grown on different fertility-status soils under both moist and dry conditions. In a strict sense, differences in soil fertility between Kongana and Massapoula soil amounted to differences in exchangeable magnesium (Table 1). Therefore, these data are consistent with assertions by Burslem *et al.* (1994, 1995) that, for mycorrhizal and/or shade-tolerant plants, limitations to growth by major base cations may prove more significant than limitation by phosphorus in tropical forests. It is important to note that even the relatively fertile Massapoula soil represents a soil with low levels of exchangeable calcium and magnesium, even within this region (J. S. Hall, unpubl. data). The less-pronounced response of RGR between Massapoula soil and Massapoula soil with nutrient addition is similar to those findings of Turner *et al.* (1993) who found dipterocarp seedlings only respond to fertilizer addition when grown under very low nutrient availabilities. While it is possible that the general lack of response to nutrient addition could be due to leaching of nutrients, given that the moist nutrient-addition soils had significantly higher levels of exchangeable potassium and available phosphorus at the end of the experiment, this seems unlikely (Table 1).

RGR and biomass allocation in moist treatments

Two of the four *Entandrophragma* species studied exhibited significant responses in RGR to soil fertility under moist conditions. All four species had significantly higher RMRs on Kongana soil than on nutrient-addition soil. High allocation to roots under low soil-fertility conditions follow descriptions of Chapin (1980) and predictions of Tilman (1988) and has also been found by Kolb *et al.* (1990) for northern red oak (*Quercus rubra* L.) and Minotta & Pinzauti (1996) for beech (*Fagus sylvatica* L.) seedling growth. *Entandrophragma angolense* significantly outperformed congeners on Massapoula and nutrient-addition soils. However, *E. candollei* performed as well as *E. angolense* on Kongana soil (Figures 1 and 2).

The patterns in change in RGR and root allocation suggest a threshold below which two of the species perform extremely poorly with respect to congeners. For example, both *E. cylindricum* and *E. utile* almost doubled their RGR between Kongana and Massapoula soil. They exhibited similarly pronounced changes in allocation to roots. In contrast, *E. angolense* and *E. candollei* did not exhibit significant changes in RGR or root allocation patterns with this increase in fertility. However, neither *E. cylindricum* nor *E. utile* maintained a continued increase in growth rate with nutrient addition, even though fertilizer addition represented a ten-fold increase in total exchangeable bases and an approximately three-fold increase in available phosphorus. In fact, *E. utile* actually showed a significant decline in RGR, perhaps reflecting a narrow range within which this species is able to respond to changes in fertility.

RGR and biomass allocation in dry treatments

Overall, there were fewer statistically significant differences within dry soils than moist soils; however, this may

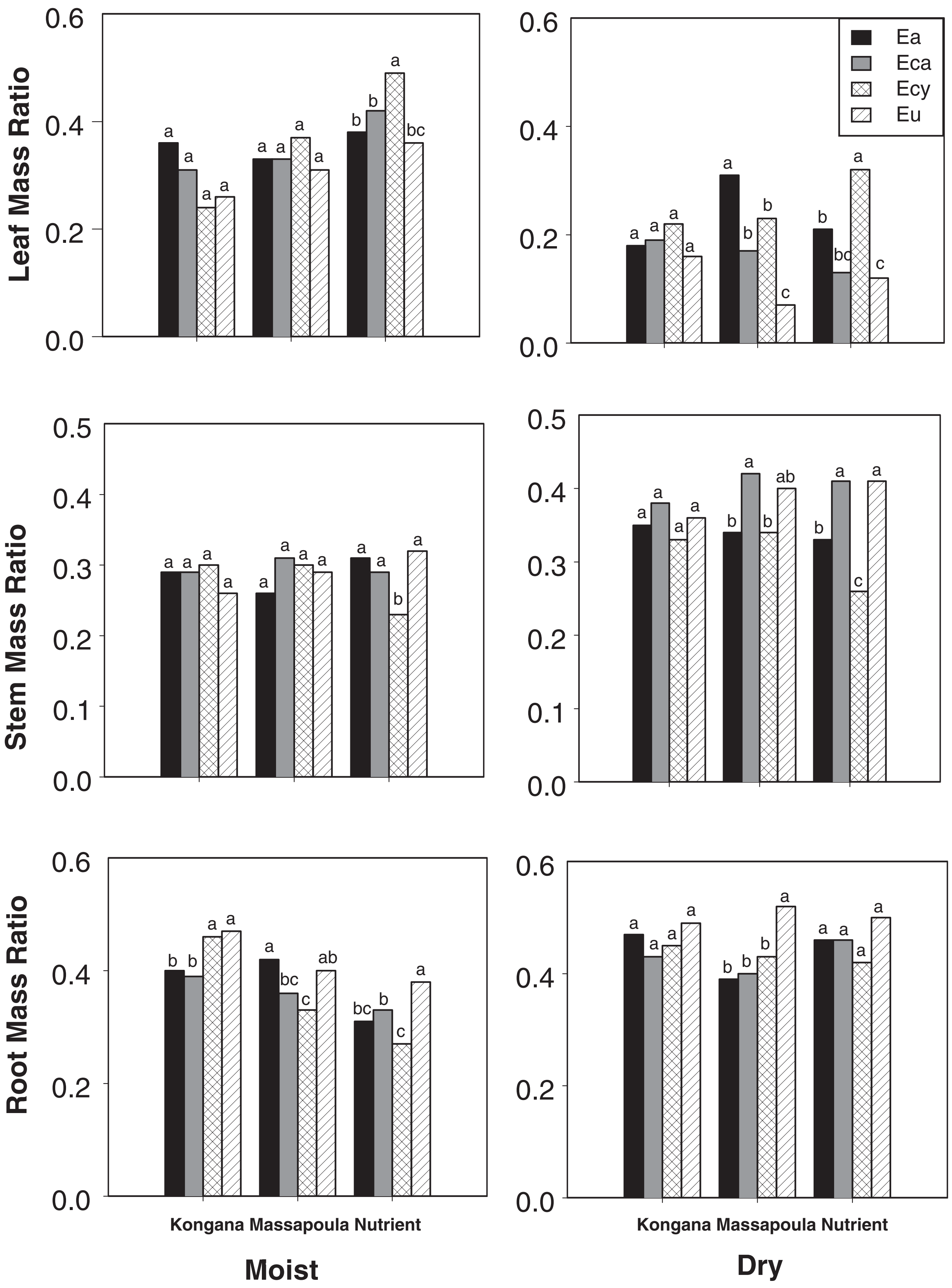

Figure 2. Leaf, stem, and root mass ratios for *Entandrophragma* spp. within soil fertility and moisture treatments (Ea, *E. angolense*; Eca, *E. candollei*; Ecy, *E. cylindricum*; Eu, *E. utile*; letters denote significant differences between species and within soil-fertility/moisture treatment; significance determined by LS means in SAS and significant at $P < 0.05$, df = 33).

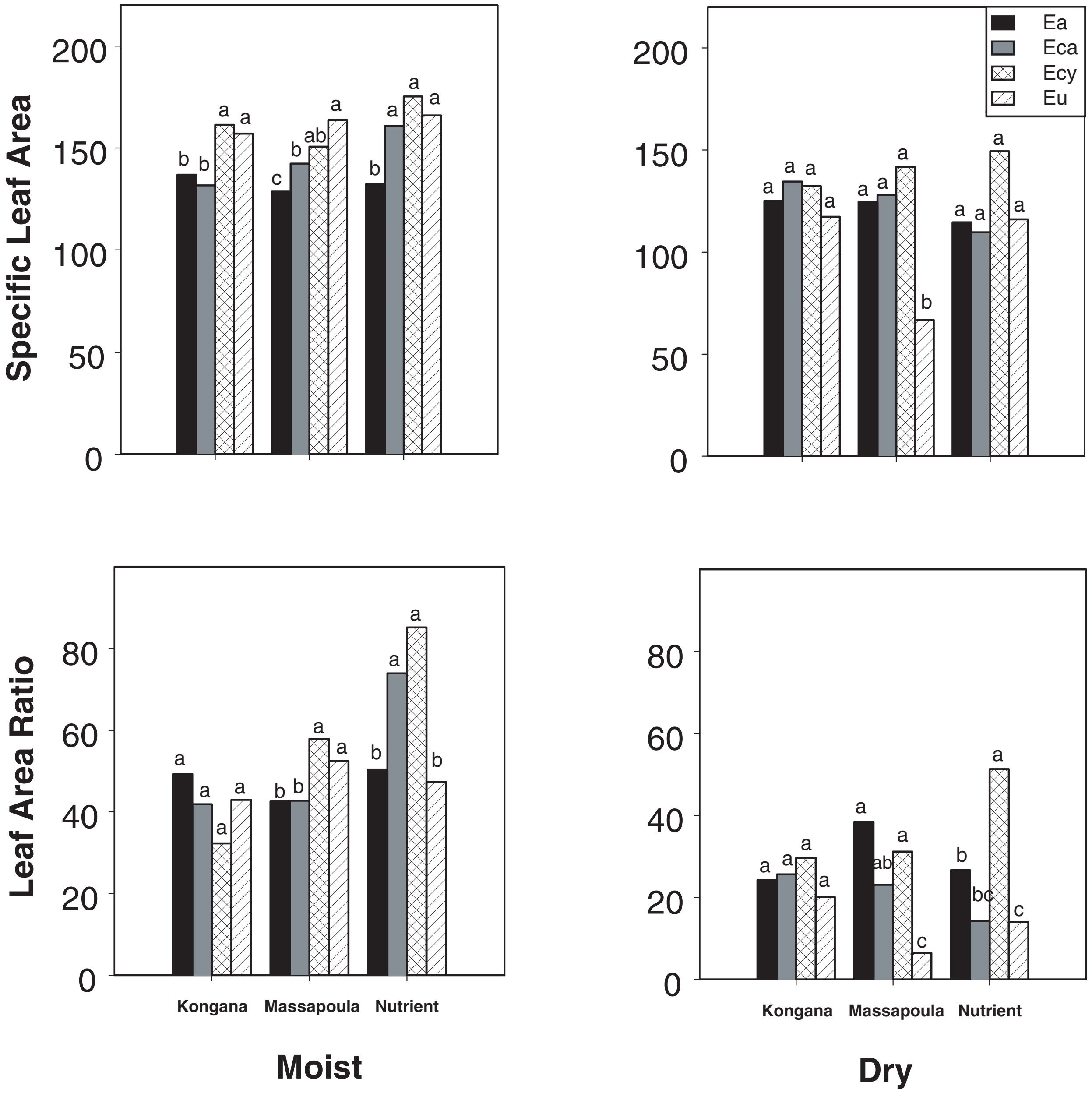

Figure 3. Specific leaf area (cm^2 g^{-1}) and leaf area ratios for *Entandrophragma* spp. within soil fertility and moisture treatments (Ea, *E. angolense*; Eca, *E. candollei*; Ecy, *E. cylindricum*; Eu, *E. utile*; letters denote significant differences between species and within soil-fertility/moisture treatment; significance determined by LS means in SAS and significant at $P < 0.05$, df = 33).

be an artifact of both small sample size and very low RGR under these conditions (Figure 1). Nevertheless, three of the four species exhibited significantly higher RGR on nutrient-addition than on Kongana soil. Within soils on both Kongana and nutrient-addition soils, *E. angolense*, *E. candollei* and *E. cylindricum* had indistinguishable RGRs suggesting that no one species gains a marked advantage over the other two at this level of moisture stress on these soils.

Leaf plasticity as a predictor of RGR under varied fertility conditions

LAR is a significant component of RGR and can be broken down into SLA and LMR (Hunt 1982, Lambers *et al.* 1998). Both SLA and LMR have been linked to declines in RGR with nutrient limitation (Poorter *et al.* 1995, Van Arendonk *et al.* 1997). On moist soils, there were significant increases in LAR with increased soil fertility for two of the four species studied here. These same two species, *E. candollei* and *E. cylindricum*, also showed significant increase in both SLA and LMR with increased fertility (Figure 3, Table 3). *Entandrophragma angolense E. cylindricum* and *E. utile* all showed significant responses in LAR to increased soil fertility on dry soils (Figure 3, Table 4); however, the response of *E. angolense* and *E. utile* are difficult to interpret and *E. cylindricum* only responded with addition of fertilizer.

Veenendaal *et al.* (1996*b*) report a reduction in LAR and SLA on infertile soils for a non-pioneer light demander (NPLD) showing significant differences in RGR between fertility treatments. Our results are therefore consistent with those of Veenendaal *et al.* (1996*b*) for species exhibiting leaf plasticity with respect to soil fertility. However, *E. candollei* did not show a significant response in RGR to changes in soil fertility in moist treatments while *E. utile*, a species that did exhibit significant differences in RGR on moist soils with changes in soil fertility, did not show changes in either SLA or LAR. The lack of a consistent response in leaf morphology on both moist and dry soils to increased fertility suggests that this parameter is not a good indicator of species response to changes in fertility within the NPLD guild. However, it is possible that these results reflect inconsistencies due to measuring leaf area on leaves dried in the field.

Relative performance and the distribution of *Entandrophragma* spp.

Results from our nursery trials are consistent with the limited data available from other nursery trials and the distribution of these *Entandrophragma* species. Swaine *et al.* (1997) found a similar trend to ours for *E. utile* planted within gaps created in forest reserves of apparently different soil fertility status. However, Synnott (1975) was unable to show a response to growth with fertilizer addition to *E. utile* in a nursery experiment conducted in Budongo Forest, Uganda. In that study, nutrients were added to soil that had almost twice the level of TEB than the higher fertility site of Swaine *et al.* (1997, Hall & Swaine 1981). Thus, it is conceivable that our nutrient-addition treatment and both the control and nutrient-addition treatments reported by Synnott (1975) were beyond the range of fertility where *E. utile* responds with increased RGR. Both our Massapoula and the higher-fertility site of Swaine *et al.* (1997) appear to be within the optimum range of performance of *E. utile*. Finally, the site of relatively high growth of *E. utile* in the experiment discussed by Swaine *et al.* (1997) is within the zone where *E. utile* is concentrated (Hall & Swaine 1981).

The results from these growth trials for *E. angolense*, *E. candollei* and *E. cylindricum* are also consistent with the limited distribution data available for these species. *Entandrophragma angolense* performed as well or better than congeners over a range of fertility and moisture conditions. This species is widely distributed throughout the forests of Ghana (Hall & Swaine 1981), with peaks of abundance in moist evergreen and moist semi-deciduous forest. These forests also span a broad range of soil fertility and moisture conditions (Hall & Swaine 1981). *Entandrophragma candollei* performed particularly well in relation to congeners on moist Kongana soil. This too is consistent with the fact that its peak abundance in Ghana is within a forest type (upland evergreen) of particularly low TEB (Hall & Swaine 1981) and that it is more abundant than congeners on soils with low TEB in Odzala N.P., Congo (Dowsett-Lemaire 1996, FAO 1973). The peak abundance of *E. cylindricum* in Ghana is within moist semi-deciduous forest, a stratum with soils of high values for TEB (Hall & Swaine 1981). This fits with its pronounced growth response to changes in fertility between Kongana and Massapoula soil on moist treatments. If deciduosity is linked to moisture availability, this may also reflect its ability to perform well relative to congeners on drier sites.

Work linking the distribution of these species to soil fertility and moisture gradients on a 100-ha plot is currently under way at our study site, but the naturally occurring forest soils used in this experiment are well within the fertility ranges found on our plot (J. S. Hall, unpubl. data). In the absence of these results, we can only draw tentative conclusions as to how seedling response to soil moisture and fertility regimes relates to adult tree distribution within our forest. However, several points are unequivocal. Under moist conditions, both *E. cylindricum* and *E. utile* respond with increased RGR to increased soil fertility between Kongana and Massapoula soil while *E. angolense* and *E. candollei* do not. *Entandrophragma angolense* outperforms congeners on both Massapoula and nutrient-addition moist soils in our shade-house experiments. *Entandrophragma candollei* performs as well as *E. angolense* and both perform significantly better than *E. cylindricum* and *E. utile* on Kongana moist soils. On drought-stressed soils, there are fewer significant differences in growth parameters between species. Here *E. cylindricum* performed as well as both *E. angolense* and *E. candollei* on both Kongana and nutrient-addition soils.

Soil fertility within an area of tropical forest can be highly variable, as evidenced by Silver *et al.* (1994) in Puerto Rico, Gunatilleke *et al.* (1996) in Sri Lanka, Palmiotto (1998) in Sarawak, Clark *et al.* (1998) in Costa Rica, and our study site (J. S. Hall, unpubl. data). We did not observe a shift in performance rank in RGR as soil fertility changed within a moisture treatment as might be expected should soil fertility and/or moisture be exclusively responsible for the distributions of species within the forest. However, the relationship suggested by the limited available data on the distribution and abundance of

Entandrophragma spp. in relation to soil fertility and/or moisture status was reinforced by seedling performance in this study and therefore may be an important factor in helping to maintain a diversity of *Entandrophragma* species within the forest of our study site.

Little distinction has heretofore been made in separating *Entandrophragma* spp. along resource gradients (see Hawthorne 1995 for summary of silvics). Coomes & Grubb (2000) have highlighted the need to better understand the importance of below-ground competition for moisture and nutrients and how regeneration niches of species may be influenced by their rooting systems. This study provides compelling evidence linking seedling performance of *Entandrophragma* to soil fertility and moisture gradients. Given the emerging picture of increased heterogeneity of soil moisture and fertility at relatively small scales, we suggest that the availability of these below-ground resources may be an important factor in maintaining species diversity within tropical forests.

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LITERATURE CITED

AGYEMAN, V. K., SWAINE, M. D. & THOMPSON, J. 1999. Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology* 87:815–827.

ASHTON, P. M. S. 1990. *Seedling response of* Shorea *species across moisture and light regimes in a Sri Lankan rain forest*. Ph.D. thesis, Yale University, New Haven, CT.

ASHTON, P. M. S. 1995. Seedling growth of co-occurring *Shorea* species in the simulated light environments of a rain forest. *Forest Ecology and Management* 72:1–12.

ASHTON, P. M. S., GUNATILLEKE, C. V. S. & GUNATILLEKE, I. A. U. N. 1995. Seedling survival and growth of four *Shorea* species in a Sri Lankan rainforest. *Journal of Tropical Ecology* 11:263–279.

AUBRÉVILLE, A. 1959. *La flore forestière de la Côte d'Ivoire*. Centre Technique Forestier Tropicale, Nogent-Sur-Marne, France. 341 pp.

BRANDANI, A., HARTSHORN, G. S. & ORIANS, G. H. 1988. Internal heterogeneity of gaps and species richness in a Costa Rican tropical wet forest. *Journal of Tropical Ecology* 4:99–119.

BRAY, R. H. & KURTZ, L. T. 1954. Determination of total, organic, and available forms of phosphorus in soils. *Soil Science* 59:39–45.

BROWN, N., PRESS, M. & BEBBER, D. 1999. Growth and survivorship of dipterocarp seedlings: differences in shade persistence create a special case of dispersal limitation. *Philosophical Transactions of the Royal Society of London B* 354:1847–1855.

BURSLEM, D. F. R. P., TURNER, I. M. & GRUBB, P. J. 1994. Mineral nutrient status of coastal hill dipterocarp forest and adinandra belukar in Singapore: bioassays of nutrient limitation. *Journal of Tropical Ecology* 10:579–599.

BURSLEM, D. F. R. P., GRUBB, P. J. & TURNER, I. M. 1995. Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical rain forest in Singapore. *Journal of Ecology* 83:113–122.

CARROLL, R. W. 1997. *Feeding ecology of the western lowland gorilla (*Gorilla gorilla gorilla*) in the Central African Republic*. Ph.D. thesis, Yale University, New Haven, CT.

CHAPIN, F. S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:233–260.

CLARK, D. B., CLARK, D. A. & READ, J. M. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *Journal of Ecology* 86:101–112.

CLARK, D. B., PALMER, M. W. & CLARK, D. A. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* 80:2662–2675.

COOMES, D. A. & GRUBB, P. J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs* 70:171–207.

CTFT. 1985. *Inventaire des resources forestières du Sud Cameroun*. Centre Technique Forestier Tropicale, Département Forestier du CIRAD, Nogent-sur-Marne.

DAVIES, S. J., PALMIOTTO, P. A., ASHTON, P. S., LEE, H. S. & LAFRANKIE, J. V. 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology* 86:662–673.

DENSLOW, J. S., SCHULTZ, J. C., VITOUSEK, P. M. & STRAIN, B. R. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71:165–179.

DOWSETT-LEMAIRE, F. 1996. Composition et evolution de la vegetation forestière au Parc national d'Odzala, Congo. *Bulletin du Jardin Botanique National de Belgique* 65:253–292.

EGGELLING, W. J. 1947. Observations on the ecology of the Budongo rain forest, Uganda. *Journal of Ecology* 34:20–87.

FAO 1973. *Soil map of the world*. FAO and UNESCO, Rome.

FISHER, R. A. 1921. Some remarks on the methods formulated in a recent article on 'the quantitative analysis of plant growth'. *Annals of Applied Biology* 7:367–372.

GARTLAN, S., NEWBERY, D. M., THOMAS, D. W. & WATERMAN, P. G. 1986. The influence of topography and soil phosphorus on the vegetation of Korup Forest Reserve, Cameroon. *Vegetatio* 65:131–148.

GRUBB, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52:107–145.

GUNATILLEKE, C. V. S., GUNATILLEKE, I. A. U. N., PERERA, G. A. D., BURSLEM, D. F. R. P., ASHTON, P. M. S. & ASHTON, P. S. 1997. Responses to nutrient addition among seedlings of eight closely related species of *Shorea* in Sri Lanka. *Journal of Ecology* 85:301–311.

GUNATILLEKE, C. V. S., PERERA, G. A. D., ASHTON, P. M. S., ASHTON, P. S. & GUNATILLEKE, I. A. U. N. 1996. Seedling growth of *Shorea* section *Doona* (Dipterocarpaceae) in soils from topographically different sites of Sinharaja rain forest in Sri Lanka. Pp. 245–265 in Swaine M. D. (ed.). *Tropical tree seedling ecology*. UNESCO/Parthenon, Paris.

HALL, J. B. & SWAINE, M. D. 1976. Classification and ecology of closed-canopy forest in Ghana. *Journal of Ecology* 64:913–951.

HALL, J. B. & SWAINE, M. D. 1981. *Distribution and ecology of vascular plants in a tropical rain forest: forest vegetation in Ghana*. Dr W. Junk, The Hague. 383 pp.

HARMS, K. E., CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89:947–959.

HAWTHORNE, W. D. 1995. *Ecological profiles of Ghanaian forest trees*. Tropical Forestry Papers 29, Oxford Forestry Institute, Oxford. 319 pp.

HUNT, R. 1982. *Plant growth curves: the functional approach to plant growth analysis*. Edward Arnold, London. 240 pp.

JUO, A. S. R. & WILDING, L. P. 1996. Soils of the lowland forests of West and Central Africa. *Proceedings of the Royal Society of Edinburgh* 104B:15–29.

KOLB, T. E., STEINER, K. C., MCCORMICK, L. H. & BOWERSOX, T. W. 1990. Growth response of northern red-oak and yellow-poplar seedlings to light, soil moisture, and nutrients in relation to ecological strategy. *Forest Ecology and Management* 38:65–78.

LAMBERS, H., CHAPIN, F. S. & PONS, T. L. 1998. *Plant physiological ecology*. Springer-Verlag, New York. 540 pp.

MEDJIBE, V. & HALL, J. S. 2003. Seed dispersal and its implications for silviculture of African mahogany (*Entandrophragma* spp.) in undisturbed forest in the Central African Republic. *Forest Ecology and Management* 170:249–257.

MINOTTA, G. & PINZAUTI, S. 1996. Effects of light and soil fertility on growth, leaf chlorophyll content and nutrient use efficiency of beech (*Fagus sylvatica* L.) seedlings. *Forest Ecology and Management* 86:61–71.

PALMIOTTO, P. A. 1998. *The role of specialization in nutrient-use efficiency as a mechanism driving species diversity in a tropical rain forest*. Ph.D. thesis, Yale University, New Haven, CT.

PIETERS, A. 1976. Etude de l'influence du milieu sur la germination et la croissance dans le jeune age d'*Entandrophragma cylindricum*. Pp. 551–566 in *International Union of Forestry Research Organizations, 16th Congress*. Norwegian IUFRO Congress Committee, Norway.

POORTER, H., VAN DE VIJVER, C. A. D. M., BOOT, R. G. A. & LAMBERS, H. 1995. Growth and carbon economy of a fast-growing and a slow-growing grass species as dependent on nitrate supply. *Plant and Soil* 171:217–227.

POULSEN, A. D. 1996. Species richness and density of ground herbs within a plot of lowland rainforest in north-west Borneo. *Journal of Tropical Ecology* 12:177–190.

RICHTER, D. D. & BABBAR, L. I. 1991. Soil diversity in the tropics. *Advances in Ecological Research* 21:315–389.

RIDDOCH, I., LEHTO, T. & GRACE, J. 1991. Photosynthesis of tropical tree seedlings in relation to light and nutrient supply. *New Phytologist* 119:137–147.

SCHABENBERGER, O. S., GREGOIRE, T. G. & KONG, F. 2000. Collections of simple effects and their relationship to main effects and interactions in factorials. *The American Statistician* 54:210–214.

SCHNITZER, S. A. & CARSON, W. P. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82:913–919.

SILVER, W. L., SCATENA, F. N., JOHNSON, A. H., SICCAMA, T. G. & SANCHEZ, M. J. 1994. Nutrient availability in montane wet tropical forest: spatial patterns and methodological considerations. *Plant and Soil* 164:129–145.

SOKAL, R. R. & ROHLF, F. J. 1995. *Biometry*. W. H. Freeman and Company, New York. 887 pp.

STEEL, R. G. D. & TORRIE, J. H. 1960. *Principles and procedures in statistics*. McGraw-Hill, New York. 633 pp.

SUMNER, M. E. & MILLER, W. P. 1996. Chapter 40: Cation exchange capacity and exchange coefficients. Pp. 1201–1229 in Sparks, D. L. (ed.). *Methods of soil analysis part 3. Chemical Method.* Soil Science Society of America and American Society of Agronomy, Madison.

SWAINE, M. D. & HALL, J. B. 1988. The mosaic theory of forest regeneration and the determination of forest composition in Ghana. *Journal of Tropical Ecology* 3:331–345.

SWAINE, M. D., AGYEMAN, V. K., KYEREH, B., ORGLE, T. K., THOMPSON, J. & VEENENDAAL, E. M. 1997. *Ecology of forest trees in Ghana*. ODA Forestry Series No. 7., University of Aberdeen, Aberdeen.

SYNNOTT, T. J. 1975. *Factors affecting the regeneration and growth of seedlings of* Entandrophragma utile *(Dawe & Sprague) Sprague*. Ph.D. thesis, Makerere University, Kampala, Uganda.

TILMAN, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton. 360 pp.

TURNER, I. M., BROWN, N. D. & NEWTON, A. C. 1993. The effect of fertilizer application on dipterocarp seedling growth and mycorrhizal infection. *Forest Ecology and Management* 57:329–337.

VAN ARENDONK, J. J. C. M., NIEMANN, G. J., BOON, J. J. & LAMBERS, H. 1997. Effects of nitrogen supply on the anatomy and chemical composition of leaves of four grass species belonging to the genus *Poa*, as determined by image-processing analysis and pyrolysis-mass spectrometry. *Plant, Cell and Environment* 20:881–897.

VAN ROMPAEY, R. S. A. R. 1993. *Forest gradients in West Africa: a spatial analysis*. Wageningen Agricultural University, Wageningen.

VEENENDAAL, E. M., SWAINE, M. D., AGYEMAN, V. K., BLAY, D., ABEBRESE, I. K. & MULLINS, C. E. 1996*a*. Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology* 83:83–90.

VEENENDAAL, E. M., SWAINE, M. D., LECHA, R. T., WALSH, M. F., ABEBRESE, I. K. & OWUSU-AFRIYIE, K. 1996*b*. Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology* 10:501–511.

WEBB, C. O. & PEART, D. R. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* 88:464–478.

WILLS, C., CONDIT, R., FOSTER, R. & HUBBELL, S. P. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences USA* 94:1252–1257.