

Partitioning of understorey light and dry-season soil moisture gradients among seedlings of four rain-forest tree species in Madagascar

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Abstract: Resource partitioning has been hypothesized to play a role in the maintenance of tree diversity in tropical forests. We looked for evidence of light and soil moisture partitioning among seedlings of four native Malagasy tree species, the pioneer, gap-adapted species *Harungana madagascariensis* and the three shade-tolerant species *Ocotea cymosa*, *Stephanostegia capuronii* and *Uapaca ferruginea*. Four hundred and eighty seedlings were transplanted in experimental plots in the Tampolo coastal forest and grown for 2 y. Growth rates increased with increasing light availability for all species, and with increasing dry-season soil moisture for *H. madagascariensis*. With increasing light availability, survival increased for *H. madagascariensis*, *S. capuronii* and *U. ferruginea* but decreased for *O. cymosa*. While dry-season soil moisture did not influence the growth or survival of the shade-tolerant species, it interacted with understorey light in its effect on the performance of *H. madagascariensis*, which performed better in wet soils at high light than in dry soils in shade. Rank reversals in species performance suggested that three of the four tree species partition resource gradients as seedlings, mostly light and secondarily dry-season soil moisture. There was only partial agreement between the performance of transplanted seedlings and the distribution of natural seedlings of the same four species with respect to light and soil moisture, suggesting that the success of tropical tree regeneration can only be partly accounted for by seedling performance across resource gradients.

Key Words: drought, gradient, growth, *Harungana madagascariensis*, *Ocotea cymosa*, regeneration, RGR, *Stephanostegia capuronii*, survival, tropical forest, *Uapaca ferruginea*

INTRODUCTION

Studies of resource partitioning using a model of tropical tree seedling performance have traditionally focused on species responses to spatial variation in light availability (Dalling *et al.* 1998, Kobe 1999, Lieberman *et al.* 1995, Montgomery & Chazdon 2002), but even in wet tropical forests, soil water can also be a spatially heterogeneous and limiting resource during dry spells (Poorter 2005), especially for shallow-rooted tree seedlings (Bunker & Carson 2005). Ashton *et al.* (1995), Jackson *et al.* (1995) and Veenendaal *et al.* (1996) have suggested that heterogeneity in soil hydrology provides an additional axis of partitioning among tropical tree species, and Baraloto *et al.* (2006), Engelbrecht & Kursar (2003) and Poorter (2005) proposed that soil moisture availability may be one of the main factors other than light that influence species distribution in tropical forests. But perhaps because of the experimental complexity

required to do so, relatively few studies (but see Ashton *et al.* 2006, Bunker & Carson 2005, Sack & Grubb 2002) have investigated the combined effect of light and soil moisture availability on tropical tree seedling performance and distribution in the field (Palmiotto *et al.* 2004). Investigating the simultaneous effects of gradients of understorey light and soil moisture on seedling performance is necessary to detect any interaction the two environmental variables may have in shaping tropical forest regeneration dynamics.

The purpose of this study was to investigate whether four tree species native to the eastern rain forest of Madagascar exhibited patterns of partitioning of light and dry-season soil moisture gradients, and whether understorey light and soil moisture interacted in their effect on seedling performance. We assumed that if precipitation on the east coast of Madagascar is seasonal, lower soil moisture during the dry season could result in drought stress for the seedlings of some tree species since seedlings are rooted in only the uppermost soil horizons, which are most likely to desiccate during a dry spell (Tyree *et al.* 2003).

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The four native tree species used for this study are common in the Tampolo Forest area (Ratsirarson & Goodman 1998). *Harungana madagascariensis* Lam. ex Poir. (Clusiaceae) is a fast-growing, gap-adapted, medium-sized (15 m tall) tree species (Blaser *et al.* 1993). *Ocotea cymosa* (Nees) Palacky (Lauraceae) is a shade-tolerant emergent (25 m tall, taller than the surrounding forest canopy average height) tree. *Stephanostegia capuronii* Markgr. (Apocynaceae) and *Uapaca ferruginea* Baill. (Euphorbiaceae) are both classified as shade-tolerant canopy (20 m tall) species by Blaser *et al.* (1993). If there is resource partitioning among these tree species at Tampolo, we hypothesized that their seedlings should exhibit species-specific differences in performance across gradients of light and dry-season soil moisture manifested by performance rank reversals resulting in peaks of highest relative performance in different parts of the light-soil moisture resource continuum.

Specifically, we hypothesized that the shade-intolerant *H. madagascariensis* should perform better than other species at high irradiance and in moist soils, since soil moisture can become a limiting resource as light availability increases (Bunker & Carson 2005), especially for fast-growing pioneer species that typically sacrifice water use efficiency (WUE) to maximize growth (Engelbrecht *et al.* 2006, Poorter 2005). Emergent trees, on the other hand, typically exhibit high WUE, an important trait when crowns are exposed to desiccating wind and sun (Poorter 2005). High WUE has a respiratory cost (Baltzer *et al.* 2005), so we expected that seedlings of *O. cymosa* would be very slow-growing. They should also not respond to increasing light availability or to increasing dry-season soil moisture, since neither resource should be limiting for that shade-tolerant, water-conserving species. Seedlings of *S. capuronii* should exhibit similar responses to light and dry-season soil moisture gradients than seedlings of *O. cymosa*. Finally, seedlings of *U. ferruginea*, a moderately fast-growing shade-tolerant species that can benefit from canopy disturbance (Blaser *et al.* 1993), should respond positively to increased irradiance and to increased dry-season soil moisture in high light. Furthermore, if we found patterns of resource partitioning among transplanted seedlings, we hypothesized that the spatial distribution of wildlings (naturally occurring seedlings) of the same four species relative to light and soil moisture gradients should be consistent with the patterns of relative performance observed with transplanted seedlings.

METHODS

Study site

The littoral rain forest of eastern Madagascar is one of 12 tropical 'hot spots' of biodiversity in the world (Myers

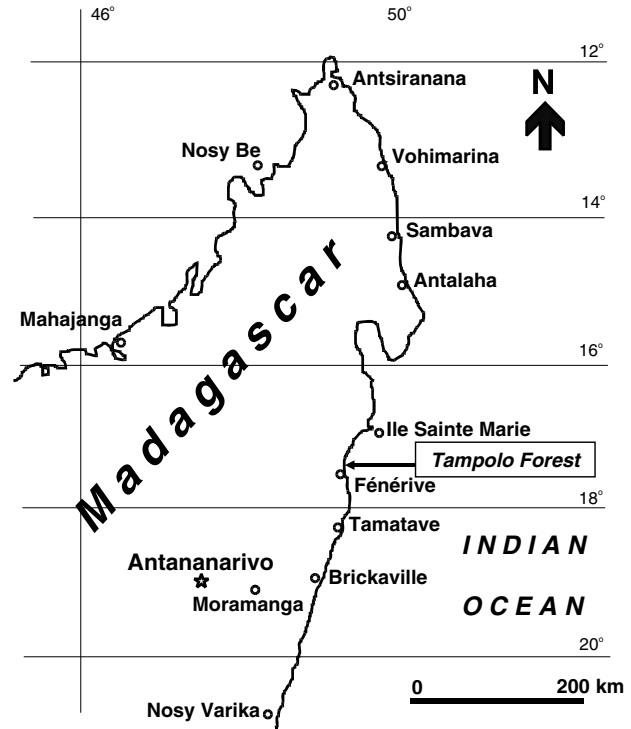


Figure 1. Location of the Tampolo Forest.

1988), yet little is known about its ecology. Because of rapid deforestation, it is one of the most threatened ecosystems of the world (Dumetz 1994, Green & Sussman 1990, Olson & Dinerstein 1998). Located along the Indian Ocean coastline 100 km north of the port city of Tamatave, the Tampolo Forest (17.3°S, 49.4°E) is an 800-ha protected fragment of this once-continuous rain forest (Figure 1).

Climate is humid tropical, with a mean precipitation of 3600 mm y^{-1} and a mean annual temperature of 24 °C. Our investigation of Ile Sainte Marie (45 km north-east of Tampolo; see Figure 1) 1978–1997 monthly weather records at the Madagascar Meteorology and Hydrology Office (DMH 1998) revealed that precipitation in that region of Madagascar, although not seasonal, is variable, occurring mostly from December to August, with less precipitation occurring from September to November (Figure 2). We henceforth refer to the September–November period as 'dry season' for convenience only, since a dry season is conventionally defined as occurring when mean monthly rainfall is less than 100 mm, which is not the case at Tampolo.

With winds of up to 300 km h^{-1} , Indian Ocean cyclones occasionally disturb coastal forests, creating spatial and temporal canopy heterogeneity, including large (> 0.5 ha) gaps (Chauvet 1972, de Gouvenain & Silander 2003, Donque 1972). Within the study site, soils are uniformly nutrient-poor acidic (pH ~ 4.5) sandy (~95% sand) Entisols (pseudopodzols) of Quaternary

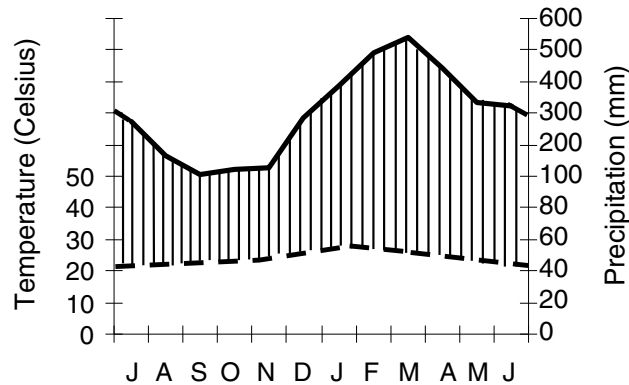


Figure 2. Climate diagram for Ile Sainte Marie, 45 km north-east of Tampolo, eastern Madagascar. Dashed line = temperature; solid line = precipitation.

dune origin (Rajoelison 1997). Topography is mostly flat with shallow ridges between 10 and 15 m asl.

Highlighting the importance of protecting littoral forest fragments to conserve Madagascar's biodiversity, a 1997 biological inventory of the Tampolo Forest (Ratsirarson & Goodman 1998) recorded 360 plant species, 90 species of ant, 56 bird species, 16 species of amphibian, 31 reptile species, three small-mammal species and six species of lemur.

Transplanted seedlings experiment

In the Tampolo Forest Station nursery, 480 bare-root seedlings (120 seedlings of each species) were grown for 3–6 mo, from either seeds (for *Stephanostegia* and *Uapaca*) or very small wildlings (for *Harungana* and *Ocotea*) collected in the Tampolo Forest. All seedlings were then transplanted in July 1998 into six transplanting plots (80 seedlings per plot) systematically on a grid, 1 m apart from each other, with seedlings of each species alternating along each row. Seedling mean height at transplant was different ($P < 0.05$) among species (*Harungana* = 9.7 cm; *Ocotea* = 9.5 cm; *Stephanostegia* = 14.1 cm; *Uapaca* = 6.6 cm).

The six 10 × 10-m transplanting plots (henceforth 'plots') were located within a 200 × 600-m area of littoral forest on uniformly nutrient-poor sandy soils, 500 m inland from the coastline. We took advantage of the heterogeneous forest canopy typical of the cyclone-disturbed coastal forests of Madagascar to locate the plots across a wide, continuous range of understorey photosynthetically active radiation (PAR) using a quantum sensor and a LI-1400 data logger (Li-Cor, Lincoln, Nebraska, USA). We searched for variation in PAR both among plots and within plots to avoid gaps in the overall PAR range. Plots were not set up as homogeneous treatments for discrete factor analysis

but merely as planting sites within which the light environment of each seedling was individually measured for continuous modelling. Approximate canopy gap size ranged from 400 m² to < 1 m². Although we later collected soil moisture data, the six plots were not located across any pre-measured variation in soil moisture.

All existing understorey vegetation was removed prior to planting seedlings and plots were weeded regularly during the 2-y experiment to prevent competition with the planted seedlings. Dead transplanted seedlings were not replaced. Although growth and mortality of natural seedlings can be influenced by neighbourhood effects such as host-specific disease and conspecific density-dependent feedback (Augsburger 1984, Hubbell *et al.* 2001, Webb & Peart 1999), we assumed that the 2-y performance of seedlings transplanted in weeded and maintained plots would be more strongly influenced by light and dry-season soil moisture than by neighbourhood effects associated with variation in the species composition of the surrounding forest.

Light availability was measured as instantaneous per cent transmittance, or %T (the per cent of PAR above the forest canopy that is reaching the forest understorey), with a quantum sensor held level 75 cm above the ground over each seedling (or immediately above the seedling when it grew taller than 75 cm), for approximately 5 s, three times during the experiment: immediately after transplant (census 0), after 12 mo (census 4) and after 24 mo (census 8); the three %T measurements were then averaged for each seedling. A base station data logger and quantum sensor recorded 'above-canopy PAR' in an open area synchronously with the 'seedling PAR' measurements, and %T was calculated from the ratio of the latter to the former using synchronous measurements. All %T measurements were made under diffuse light conditions during overcast days, as recommended by Nicotra *et al.* (1999) and Parent & Messier (1995), from mid-morning to mid-afternoon.

Gravimetric mineral soil per cent moisture was measured for groups of nine (3 × 3) seedlings in systematically replicated locations within each plot every 3 mo (census 0 to 8) at 10 cm depth, the root depth of the newly transplanted seedlings, using a ThetaProbe (Delta-T Devices, Cambridge, UK). Soil moisture data were corrected using a calibration equation calculated from three randomly located soil samples with known moisture content following the Delta-T Devices protocol. We assumed that if soil water content exhibited significant seasonal variation, soil water availability to plants would be more spatially heterogeneous during the dry season than during the rest of the year when precipitation is abundant. We also assumed that variation in gravimetric soil moisture during the dry season in the top soil horizons would correspond to comparable variation in soil water availability to shallow-rooted seedlings. Furthermore,

since growth and mortality differences among seedlings of different species are typically more apparent in drier soils (Ashton *et al.* 2006), we inferred that any drought stress that could affect seedling growth and/or survival would best be measured during the dry season.

Height of each seedling was measured to the highest apical bud immediately following transplanting (census 0) and every 3 mo thereafter for 24 mo, up to census 8. Mortality (including missing seedlings) was also recorded at each census.

Wilding density

Two parallel, 100-m transects were systematically established 20 m apart from each other to traverse groups of adult seed trees at each of four regeneration sites where at least one of the four focal species occurred as both adult trees and seedlings. Along each transect, all wildings < 25 cm tall of the four focal species were inventoried, four instantaneous PAR measurements were made at 75 cm above ground with a LI-1400 data logger and a levelled quantum sensor (Li-Cor, Lincoln, Nebraska, USA), and three mineral soil moisture measurements were made at a depth of 10 cm using a Delta-T Probe (Delta-T Devices, Cambridge, UK) within each of 20 contiguous 5 × 5-m quadrats (40 quadrats total per regeneration site). Per cent T was calculated from the PAR data with synchronous PAR measurement from an LI-1400 base station. Soil moisture measurements were made during consecutive days to minimize variations among regeneration sites, and calibrated using data collected on three randomly located soil samples of known moisture content using the Delta-T Devices protocol.

Data analysis – performance of transplanted seedlings

From the original 480 transplanted seedlings, 17 were excluded because of obvious human-caused mortality and 30 others because they died within 3 mo of planting, possibly from transplant shock. For each remaining seedling, a 2-y mean %T was calculated from three yearly %T measurements. We investigated whether soil moisture in the Tampolo Forest co-varied with the seasonal precipitation pattern (Figure 2) by comparing the quarterly soil moisture measurements (February, May, July, November) over the 2-y study period using ANOVA and Tukey's post hoc multiple comparisons test with SPSS (SPSS, Chicago, Illinois, USA).

For each species, growth rate in height was measured as relative growth rate (RGR), defined as the increase in plant height per unit of height per unit time, using the formula from Hunt (1982). RGR was then modelled as a function of both %T and dry-season soil

moisture using generalized least-squares modelling in S-Plus (MathSoft, Seattle, USA), specifying a maximum likelihood parameter optimization method. We tested four different functional forms for each species and compared model fit to data using likelihood ratio test (LRT) or Akaike information criterion (AIC) (Hilborn & Mangel 1997).

First, the linear model is:

$$\text{RGR} = a + b(\%T) + c(\text{H}_2\text{O}) \quad (1)$$

Where a is the intercept, b is the light (%T) coefficient and c is the dry-season soil moisture (H_2O) coefficient.

Second, we fitted a Michaelis–Menten function with respect to light and an additive linear term to characterize the effects of dry-season soil moisture on RGR:

$$\text{RGR} = (a \times \%T) / \left(\left(\frac{a}{b} \right) + \%T \right) + (c \times \text{H}_2\text{O}) \quad (2)$$

Third, we fitted a saturating function with respect to light and an additive linear term to characterize the effects of dry-season soil moisture on RGR:

$$\text{RGR} = a \times \left(1 - \exp \left(- \left(\frac{b}{a} \right) \times \%T \right) \right) + (c \times \text{H}_2\text{O}) \quad (3)$$

Models (Eqn 2) and (Eqn 3) have been used in previous studies (without the soil moisture term) to fit tree growth functions in Costa Rica (Kobe 1999) and the north-eastern USA (Pacala *et al.* 1994).

Survival analysis and maximum likelihood methods were used to develop species-specific models of mortality as a function of light and dry-season soil moisture. We generally followed the methods of Kobe *et al.* (2002), using an exponential distribution of survival time and specifying the hazard function (or instantaneous mortality rate) in terms of light and soil moisture. For each species, four nested models were tested.

First, a saturated model was tested, which includes both %T and dry-season soil moisture (H_2O) as predictors:

$$\text{P}(\text{mort}) = 1 - \exp(-t \times a \times \exp(-(b \times \%T + c \times \text{H}_2\text{O}))) \quad (4)$$

where $\text{P}(\text{mort})$ = a seedling's probability of mortality over time interval t (mo), and a , b and c are parameters estimated from the data. We set $t = 21$ mo, from census 1 (3 mo after transplant) to census 8 (24 mo after transplant).

Second, two univariate models were fitted to data to test for the significance of light or dry-season soil moisture in predicting mortality:

$$\text{P}(\text{mort}) = 1 - \exp(-t \times a \times \exp(-(0 \times \%T + c \times \text{H}_2\text{O}))) \quad (5)$$

$$\text{P}(\text{mort}) = 1 - \exp(-t \times a \times \exp(-(b \times \%T + 0 \times \text{H}_2\text{O}))) \quad (6)$$

where b or c are set = 0 to discount the effect of light or soil moisture on mortality probability, respectively.

Third, a null model (constant mortality rate) was fitted to data to test the significance of the univariate models (Eqn 5 and 6):

$$P(\text{mort}) = 1 - \exp(-t \times a) \quad (7)$$

where mortality is constant over measured variation in light and soil moisture.

Finally, we defined seedling survival = 1 - P(mort).

RGR and survival surfaces were combined (as functions of %T and dry-season soil moisture) into one performance surface for each species using array multiplication in MATLAB (The MathWorks, Natick, Massachusetts, USA). We assessed evidence of resource partitioning by identifying rank reversals of the performance surfaces of the four species when combined into one graph.

Data analysis – wilding density

To measure the spatial autocorrelation often associated with data collected along transects (Fortin & Gurevitch 2001), we computed the Mantel statistic r (Mantel 1967) with the Mantel module of the R-Package (University of Montreal, <http://www.bio.umontreal.ca/casgrain/en/labo/R/>) after transforming wilding density (Y) data using $Y' = \ln(Y + 1)$ and computing Euclidean distance matrices. Our transect data being spatially autocorrelated ($P < 0.05$), seedling density data were analysed in two steps. First, we assessed the patch size (Cain *et al.* 1995) of wilding density with Moran’s I autocorrelograms using the GS+ software (Gamma Design Software, Plainwell, Michigan, USA). This patch size was then used to perform Markov chain Monte Carlo (MCMC) regression analyses (Brooks 1998) with the program WinBUGS (MRC Biostatistics Unit, Cambridge, UK). A conditional autoregressive (CAR) prior distribution on the random error term (ε) was specified to explicitly model the spatially autocorrelated variance in the data by setting the CAR to match the patch size from Moran’s I autocorrelograms. Wilding density was predicted as following a Poisson distribution with expected density:

$$E(Y) = \beta_0 + \beta_1(\%T) + \beta_2(H_2O) + \beta_3(\%T \times H_2O) + \varepsilon[\text{CAR}] \quad (8)$$

where $E(Y)$ is the expected seedling density, ε [CAR] is the random error with spatially explicit, conditional autoregressive prior distribution:

$$\tau \frac{R}{2} \exp \left[-\frac{\tau}{2} \sum_i \sum_{j \in \text{Neigh}[i]} w_{ij} (\varepsilon_i - \varepsilon_j)^2 \right]$$

where R is the dimension of the spatial random effect ε , w_{ij} is the weight defined by patch size from Moran’s I autocorrelogram and $\tau = 1/\text{var}$ is the precision parameter.

We measured the significance of the regression coefficients with credible intervals (Lee 1997) and assessed the convergence of the MCMC models using the Raftery & Lewis Convergence Diagnostic (Raftery & Lewis 1992) routine of the Bayesian Output Analysis Program (University of Iowa, <http://www.public-health.uiowa.edu/boa/>).

RESULTS

Soil moisture and understorey light

For all six plots combined, 2-y soil per cent moisture means for the November census (21.2%) and for the February census (24.5%) were not significantly different ($P > 0.05$) from each other but were significantly lower ($P < 0.001$) than 2-y soil per cent moisture means for May (38.2%) or August census (44.1%) (Figure 3), suggesting that November and February soil moisture data reflected the effect of lower September–November precipitation (Figure 2) with a 2-mo lag. We therefore used both November and February measurements (from 1998 to 2000) in calculating an average dry-season soil moisture for each seedling, which ranged from 10% to 50% among plots (Figure 4a). Average dry-season soil moisture measurements were correlated between the 1998–1999 and the 1999–2000 dry seasons ($r = 0.106$, $P < 0.05$). Understorey light (%T) ranged from 2% to 60%

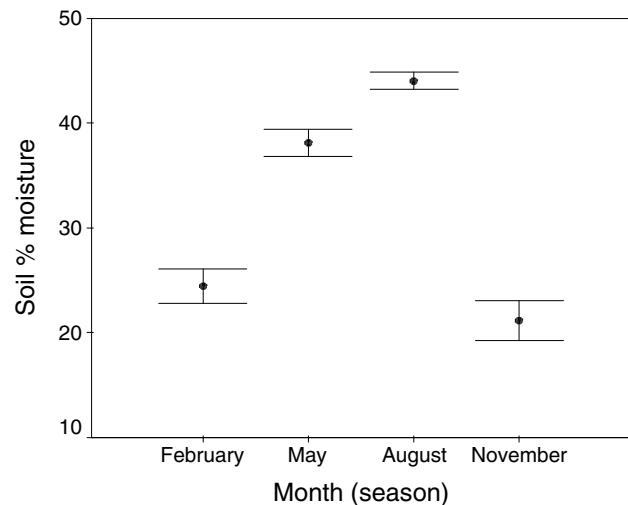


Figure 3. Soil % moisture as a function of census month (season), all years combined for each season. February, May, November 1998 and 1999 (n = 102 for each season), August 1998, 1999 and 2000 (n = 153); bars and whiskers represent 1 SE from the mean (dot).

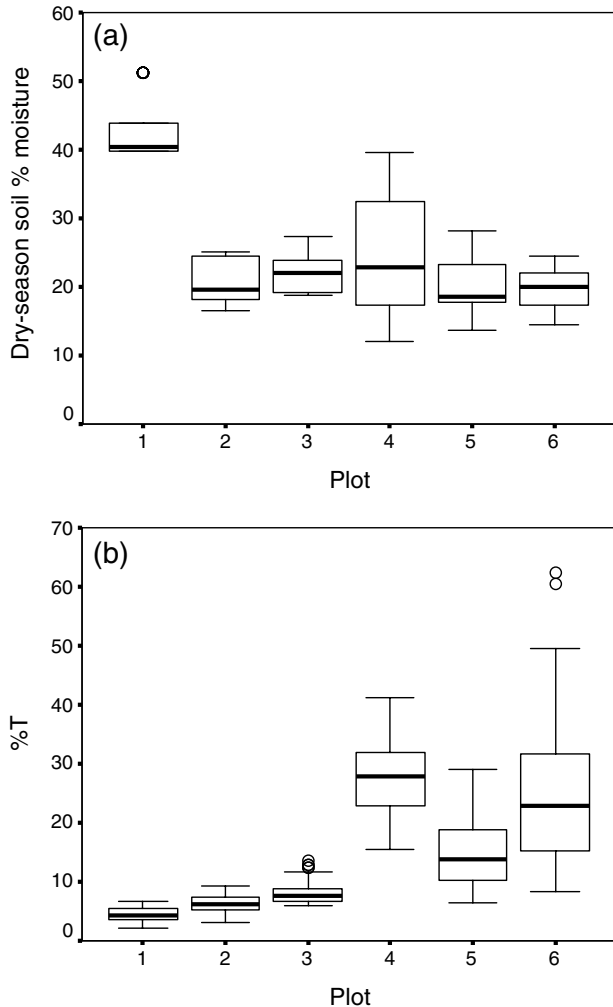


Figure 4. Range in dry-season soil moisture (a) and %T (b) for each of the six seedling transplant plots. Bottom and top of each box represent first and third quartiles, respectively. Thick horizontal line within each box represents the median, and bottom and top whiskers are minimum and maximum, respectively, except in presence of outliers (open circles). Boxplots without whiskers indicate small variance.

(Figure 4b). Among census periods 0, 4 and 8, seedling %T measurements were correlated (r in range of 0.5–0.71, $P < 0.001$).

Seedling growth and survival

Understorey light influenced the growth of all four species but soil moisture was a significant predictor of growth only for *H. madagascariensis* (Table 1, Figure 5a). For all species, increasing PAR up to %T = 20% was always associated with increases in RGR. Above %T = 20%, RGR increased little if at all, except for *O. cymosa* seedlings which nevertheless had the lowest RGR at %T in range 2–50%. Of the three shade-tolerant species, *O. cymosa* seedlings exhibited the highest RGR at %T < 2%, but they did not survive above %T = 50%. The pioneer species *H. madagascariensis* had the highest RGR of all four species in all light and dry-season soil moisture levels, but more so in high soil moisture conditions, where it grew nearly twice as fast as in dry soil conditions (Figure 5a). Except within %T in range 2–4%, RGR for *U. ferruginea* was always lower than for *S. capuronii*.

Survival of *H. madagascariensis* seedlings was affected by both light and soil moisture, being highest in high light on dry soils and lowest in shade on moist soils (Table 1, Figure 5b). Survival of *O. cymosa* seedlings was not affected by variation in dry-season soil moisture but diminished with increasing light levels, dropping from nearly 80% survival at %T < 2% to 0% survival at %T = 60%. *Stephanostegia capuronii* and *U. ferruginea* seedlings had constant survival (87% and 81%, respectively) across both light and dry-season soil moisture gradients (Figure 5b).

Seedling performance model

The combination of survival and RGR into a model of relative performance revealed that at very low (%T < 2%)

Table 1. RGR and mortality models as functions of light (%T) and dry-season soil per cent moisture (H₂O) from seedling transplant experiment.

Species	Model
Relative height growth rate (RGR)	
<i>Harungana madagascariensis</i>	$RGR = 0.12 \times (1 - \exp(-(0.01/0.12) \times \%T)) + (0.002 \times H_2O)$
<i>Ocotea cymosa</i>	$RGR = 0.02 + (0.001 \times \%T)$
<i>Stephanostegia capuronii</i>	$RGR = (0.12 \times \%T) / ((0.12/0.01) + \%T)$
<i>Uapaca ferruginea</i>	$RGR = 0.07 \times (1 - \exp(-(0.01/0.07) \times \%T))$
Mortality	
<i>Harungana madagascariensis</i>	$P(\text{mort}) = 1 - \exp(-21 \times 0.02 \times \exp(-(0.11 \times \%T - 0.06 \times H_2O)))$
<i>Ocotea cymosa</i>	$P(\text{mort}) = 1 - \exp(-21 \times 0.01 \times \exp(-(-0.05 \times \%T)))$
<i>Stephanostegia capuronii</i>	$P(\text{mort}) = 1 - \exp(-21 \times 0.004)$
<i>Uapaca ferruginea</i>	$P(\text{mort}) = 1 - \exp(-21 \times 0.01)$

Note: $\exp(a) = e^a$.

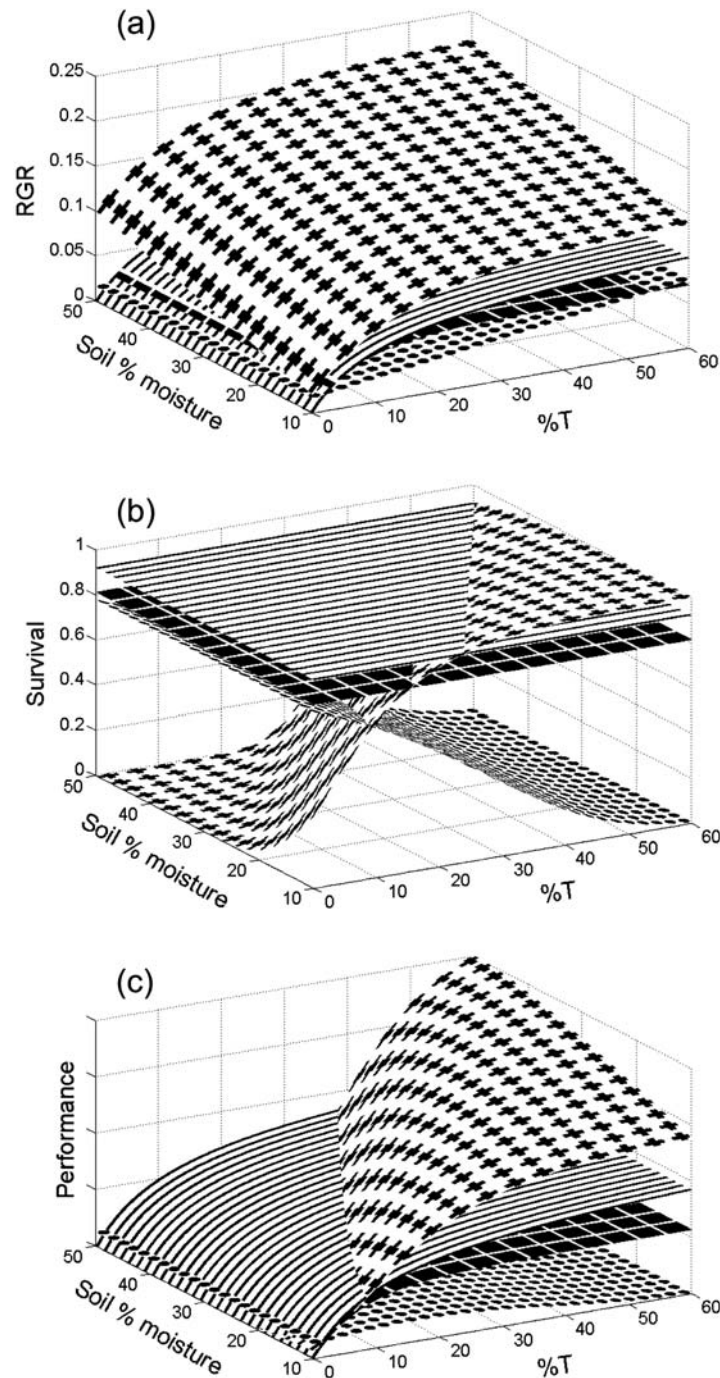


Figure 5. Response surfaces of transplanted seedlings of the four focal species as a function of understorey light (%T) and dry-season soil % moisture. (a) Relative height growth rate (RGR, in $\text{cm cm}^{-1} \text{mo}^{-1}$). (b) Survival probability. (c) Performance (RGR \times survival; no units). Cross pattern = *Harungana madagascariensis*; dot pattern = *Ocotea cymosa*; line pattern = *Stephanostegia capuronii*; square pattern = *Uapaca ferruginea*.

light, *O. cymosa* seedlings outperformed the other three species, suggesting that *O. cymosa* is an extremely shade-tolerant species that can maintain a positive carbon balance even at very low light under closed forest canopies (Figure 5c). However, increased mortality at higher light levels cancelled out the concomitant increase in RGR, thereby making performance of *O. cymosa* seedlings

constant across light gradients up to %T = 30%. Within the %T range 30–50%, performance of *O. cymosa* declined to nil due to high mortality.

For %T in the range 2–10% in drier soils, and for %T in the range 2–30% in wetter soils, *S. capuronii* seedlings outperformed the other three species. Above %T = 20%, performance of *S. capuronii* did not increase substantially.

For %T above 10% or 30%, depending on dry-season soil moisture levels, *H. madagascariensis* seedlings outperformed the other three species, more so on wetter soils in high (%T > 45%) light. At intermediate light levels (%T = 10–30%), *H. madagascariensis* seedlings growing on drier soils performed better than *H. madagascariensis* seedlings growing in wet soils (Figure 5c). Thus across a light gradient, our study revealed two rank reversals in performance, one between *O. cymosa* and *S. capuronii* at low light, and another between *S. capuronii* and *H. madagascariensis* at intermediate light levels, secondarily influenced by soil moisture (Figure 5c).

The increase in performance of *H. madagascariensis* with increasing light on wet soils was steeper than the corresponding increase on drier soils, suggesting an interaction of light and soil moisture on *H. madagascariensis* performance (Figure 5c). Thus while dry-season soil moisture was limiting at high (%T > 45) light for *H. madagascariensis*, it was less limiting at lower light levels. Indeed higher dry-season soil moisture had negative effects on the performance of *H. madagascariensis* in shade, because of lower survival (Figure 5b). This differential performance of *H. madagascariensis* across a dry-season soil moisture gradient resulted in a rank reversal in performance between it and *S. capuronii* across that gradient, which modified the above-mentioned rank reversal between these two species along a light gradient. In all combinations of light and soil moisture, seedlings of *U. ferruginea* were outperformed by the three other species.

Wilding density

The variation in density of wildings of the four focal species across light and soil moisture gradients partly supported our seedling performance model (Table 2; Figure 5c). In agreement with that model, *H. madagascariensis* wilding density was positively associated with light and soil moisture, *O. cymosa* wilding density was negatively associated with light and was not influenced by soil moisture in regeneration site 4, *S. capuronii* and *U. ferruginea* wilding densities were not associated with

soil moisture in regeneration site 4, and *U. ferruginea* wilding density was not associated with light levels (which matches our performance model for %T > 20%, above which performance of *U. ferruginea* seedlings was constant). However, the positive and negative associations, respectively, of *O. cymosa* and *S. capuronii* wilding densities with soil moisture in some regeneration sites, and the lack of significant association (for *O. cymosa*) or the negative association (for *S. capuronii*) of wilding density with light in regeneration sites 2, 3 and 4 were not expected based on our performance model (Figure 5c). Overall, 7 out of 12 (58%, or nearly what one would expect by chance) of the pairwise associations of wilding density with either light or soil moisture matched our expectations based on our seedling performance model (Table 2).

DISCUSSION

Of the four species we studied, two (*O. cymosa* and *H. madagascariensis*) performed in accordance with our hypotheses. The emergent species *O. cymosa* was the slowest-growing and most shade-tolerant, and did not respond to increased understorey light or dry-season soil moisture. The pioneer species *H. madagascariensis* was the fastest-growing but most shade-intolerant. It outperformed the other three species only at high light, especially on moist soils. The interaction of light and dry-season soil moisture on the performance of *H. madagascariensis* is likely the result of soil moisture becoming limiting at high light. On Barro Colorado Island, Bunker & Carson (2005) observed that dry-season mortality of 3000 wildings comprising 130 tree species (including *Trichilia tuberculata* and *Prionostemma aspera*) was higher than wet-season mortality in high light but not in low light, suggesting a similar interaction.

Contrary to our expectations and unlike *O. cymosa*, the slow-growing shade-tolerant canopy species *S. capuronii* responded positively to increased irradiance, especially in the low-to-intermediate light range typical of disturbed forests, where it outperformed the other species, especially on wetter soils because of reduced performance of *H. madagascariensis*. *Uapaca ferruginea* did not respond to either increasing light or dry-season soil moisture as we hypothesized, performing instead similarly to *S. capuronii* but with a lower overall performance, outperformed by one or more of the three other species at all combinations of light and soil moisture. Yet its common occurrence in the Tampolo Forest suggests that other resource gradients or processes important for regeneration (see Dalling *et al.* 1998, Hall *et al.* 2003), which we did not measure, provide opportunities for *U. ferruginea* to outperform other species.

The rank reversals in performance among *O. cymosa*, *S. capuronii* and *H. madagascariensis* suggest that some

Table 2. Association of natural seedling density with light (%T) and soil per cent moisture (H₂O) for the four focal species. + = positive association; – = negative association; ns = non-significant model (no association) at a 0.05 significance level. § indicates agreement with performance model from seedling transplant experiment.

Species	Regeneration site	%T	H ₂ O
<i>Harungana madagascariensis</i>	1	+ §	+ §
<i>Ocotea cymosa</i>	2	ns	+
	4	– §	ns §
<i>Stephanostegia capuronii</i>	3	–	–
	4	ns	ns §
<i>Uapaca ferruginea</i>	4	ns §	ns §

native tree species of the Tampolo Forest exhibit patterns of light partitioning, and to a lesser extent dry-season soil moisture partitioning. These rank reversals could be due to a performance trade-off of the type observed in other tropical forest regeneration studies (Ashton *et al.* 2006, Baraloto *et al.* 2005). Dalling & Burslem (2005) remark that several studies of tropical tree seedling regeneration fail to show light gradient partitioning among shade-tolerant species. Our study suggests that while some shade-tolerant species (e.g. *S. capuronii* and *U. ferruginea*) do not exhibit rank reversal in performance across light gradients, and could thus be considered ecologically equivalent in terms of performance, very slow-growing and extremely shade-tolerant species (e.g. *O. cymosa*) exhibit some degree of rank reversal in performance relative to other shade-tolerant species at very low (%T in range 0–3%) light levels. Montgomery & Chazdon (2002) also found evidence of light partitioning in a narrow gradient of low (%T in range 0.2–6.5%) light among seedlings of shade-tolerant species in Costa Rica.

Our study shows no evidence of soil moisture gradient partitioning among shade-tolerant species. However, fast-growing pioneer tree species such as *H. madagascariensis* are more responsive to resource availability than slow-growing shade-tolerant species (Baker *et al.* 2003). For instance, in seedling trials of five tropical tree species from India, Khurana & Singh (2004) observed that performance of slow-growing species was less affected by experimental water stress than the performance of fast-growing species. This may explain the difference in performance variability we observed between the two functional groups relative to dry-season soil moisture at Tampolo.

The lack of robust agreement between transplanted seedling performance and natural seedling density suggests that natural tree regeneration at Tampolo is a complex process that integrates other outcomes besides seedling performance. Limitations on seed dispersal and germination also influence the successful regeneration of tropical tree species (Janzen 1970, Levey & Byrne 1993, Marod *et al.* 2002), and while performance of established seedlings may be limited by light more than by soil moisture, the latter may, for instance, influence seed germination (Khurana & Singh 2004). Thus for some species such as *O. cymosa*, wetter soils could yield higher natural seedling densities than could be accounted for solely by performance models from transplanted seedlings, as observed in this study.

Notwithstanding their negative effect on the survival of *O. cymosa* seedlings, higher light levels had a positive effect on the growth of all four species we studied, whether shade-intolerant or shade-tolerant. So while *O. cymosa* seedlings suffered lower survival in high light, seedlings that survived in moderate light grew faster than seedlings growing in low light. This decoupling of the effect of light

on *O. cymosa* mortality and growth suggests that, for some tree species, linking mortality probability to growth rate (see Pacala *et al.* 1996) may be inappropriate to model forest dynamics.

Evidence for resource partitioning is insufficient to demonstrate that niche differentiation has occurred among a suite of sympatric species (Brown & Jennings 1996). Indeed niche differentiation may well be impossible to prove unambiguously (Barker *et al.* 1997). However, resource partitioning mediated by differential survivorship and growth across resource gradients may provide a basis for niche differentiation among sympatric tree species, both in temperate (Nakashizuka 2001) and tropical (Barker *et al.* 1997, Kobe 1999) forests. Although measurements of gravimetric soil moisture may not accurately gauge soil water availability to plants (Kursar *et al.* 2005), thus calling for caution in interpreting the results of our study, the patterns of resource partitioning we observed among transplanted seedlings suggest that niche differentiation processes at the seedling stage may have had a role in generating the diversity of tree species found in the Tampolo Forest. However, patterns of wilding densities suggest that tropical forest regeneration and diversity are influenced by other processes besides differential seedling performance. Experimental seed dispersal and germination studies would help advance our understanding of tree regeneration dynamics in the eastern coastal forests of Madagascar.

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LITERATURE CITED

- 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.
- ASHTON, M. S., SINGHAKUMARA, B. M. P. & GAMAGE, H. K. 2006. Interaction between light and drought affect performance of Asian tropical tree species that have differing topographic affinities. *Forest Ecology and Management* 221:42–51.

- AUGSPURGER, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705–1712.
- BAKER, T. R., SWAINE, M. D. & BURSLEM, D. F. R. P. 2003. Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. *Perspectives in Plant Ecology, Evolution and Systematics* 6:21–36.
- BALTZER, J. L., THOMAS, S. C., NILUS, R. & BURSLEM, D. F. R. P. 2005. Edaphic specialization in tropical trees: physiological correlates and responses to reciprocal transplantation. *Ecology* 86:3063–3077.
- BARALOTO, C., GOLDBERG, D. E. & BONAL, D. 2005. Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology* 86:2461–2472.
- BARALOTO, C., BONAL, D. & GOLDBERG, D. E. 2006. Differential seedling growth response to soil resource availability among nine neotropical tree species. *Journal of Tropical Ecology* 22:487–497.
- BARKER, M. G., PRESS, M. C. & BROWN, N. D. 1997. Photosynthetic characteristics of dipterocarp seedlings in three tropical rain forest light environments: a basis for niche partitioning? *Oecologia* 112:453–463.
- BLASER, J., RAJOELISON, G., TSIZA, G., RAJEMISON, M., RABEVOHITRA, R., RANDRIANANJAFY, H., RAZAFINDRIANILANA, N., RAKOTOVAO, G. & COMTET, S. 1993. *Choix des essences pour la sylviculture à Madagascar*. Département des Eaux et Forêts de l'E.S.S.A. Antananarivo, Madagascar. 166 pp.
- BROOKS, S. P. 1998. Markov chain Monte Carlo method and its application. *The Statistician* 47:69–100.
- BROWN, N. D. & JENNINGS, S. 1996. Gap-size niche differentiation by tropical rainforest trees: a testable hypothesis or a broken-down bandwagon? Pp. 79–94 in Newbery, D. M., Prins, H. H. T. & Brown, N. D. (eds.). *Dynamics of tropical communities*. Blackwell Science, Oxford.
- BUNKER, D. E. & CARSON, W. P. 2005. Drought stress and tropical forest woody seedlings: effect on community structure and composition. *Journal of Ecology* 93:794–806.
- CAIN, M. L., PACALA, S. W., SILANDER, J. A. & FORTIN, M.-J. 1995. Neighbourhood models of clonal growth in the white clover *Trifolium repens*. *American Naturalist* 145:888–917.
- CHAUVET, B. 1972. The forests of Madagascar. Pp. 191–199 in Battistini, R. & Richard-Vindard, G. (eds.). *Biogeography and ecology of Madagascar*. W. Junk, The Hague.
- DALLING, J. W. & BURSLEM, D. F. R. P. 2005. Role of life-history trade-offs in the equalization and differentiation of tropical tree species. Pp. 65–88 in Burslem, D. F. R. P., Pinard, M. & Hartley, S. E. (eds.). *Biotic interactions in the tropics: their role in the maintenance of species diversity*. Cambridge University Press, Cambridge.
- DALLING, J. W., HUBBELL, S. P. & SILVERA, K. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology* 86:674–689.
- DE GOUVENAIN, R. C. & SILANDER, J. A. 2003. Littoral forest. Pp. 103–111 in Goodman, S. M. & Benstead, J. (eds.). *The natural history of Madagascar*. Field Museum of Natural History, Chicago.
- DMH (Direction de la Météorologie et de l'Hydrologie). 1998. Weather Records. Antananarivo, Madagascar.
- DONQUE, G. 1972. The climatology of Madagascar. Pp. 87–144 in Battistini, R. & Richard-Vindard, G. (eds.). *Biogeography and ecology of Madagascar*. W. Junk, The Hague.
- DUMETZ, N. 1994. Sur les traces d'une forêt tropicale en voie d'extinction à Madagascar (l'ancienne forêt à *Humbertia madagascariensis*). *Comptes Rendus de l'Académie des Sciences, série IIa* 318:1009–1014.
- ENGELBRECHT, B. M. J. & KURSAR, T. A. 2003. Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia* 136:383–393.
- ENGELBRECHT, B. M. J., DALLING, J. W., PEARSON, R. H., WOLF, D. A. G., KOEHLER, T., TYREE, M. T. & KURSAR, T. A. 2006. Short dry spells in the wet season increase mortality of tropical pioneer seedlings. *Oecologia* 148:258–269.
- FORTIN, M.-J. & GUREVITICH, J. 2001. Mantel tests: spatial structure in field experiments. Pp. 308–326 in Scheiner, S. M. & Gurevitch, J. (eds.). *Design and analysis of ecological experiments*. (Second edition). Oxford University Press, Oxford.
- GREEN, G. M. & SUSSMAN, R. W. 1990. Deforestation history of the eastern rain forests of Madagascar from satellite images. *Science* 248:212–215.
- HALL, J. S., ASHTON, M. S. & BERLYN, J. P. 2003. Seedling performance of four sympatric *Entandrophragma* species (Meliaceae) under simulated fertility and moisture regimes of a Central African rain forest. *Journal of Tropical Ecology* 19:55–66.
- HILBORN, R. & MANGEL, M. 1997. *The ecological detective*. Princeton University Press, Princeton. 330 pp.
- HUBBELL, S. P., AHUMADA, J. A., CONDIT, R. & FOSTER, R. B. 2001. Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research* 16:859–875.
- HUNT, R. 1982. *Plant growth curves – the functional approach to plant growth analysis*. Edward Arnold, London. 256 pp.
- JACKSON, P. C., CAVELIER, J., GOLDSTEIN, G., MEINZER, F. C. & HOLBROOK, N. M. 1995. Partitioning of water-resources among plants of a lowland tropical forest. *Oecologia* 101:197–203.
- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forest. *American Naturalist* 104:501–528.
- KHURANA, E. & SINGH, J. S. 2004. Germination and seedling growth of five tree species from tropical dry forest in relation to water stress: impact of seed size. *Journal of Tropical Ecology* 20:385–396.
- KOBE, R. K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80:187–201.
- KOBE, R. K., LIKENS, G. E. & EAGAR, C. 2002. Tree seedling growth and mortality responses to manipulations of calcium and aluminium in a northern hardwood forest. *Canadian Journal of Forest Research* 32:954–966.
- KURSAR, T. A., ENGELBRECHT, B. M. J. & TYREE, M. T. 2005. A comparison of methods for determining soil water availability in two sites in Panama with similar rainfall but distinct tree communities. *Journal of Tropical Ecology* 21:297–305.
- LEE, P. M. 1997. *Bayesian statistics: an introduction*. John Wiley & Sons, New York. 368 pp.
- LEVEY, D. J. & BYRNE, M. M. 1993. Complex ant plant interactions – rain-forest ants as secondary dispersers and postdispersal seed predators. *Ecology* 74:1802–1812.

- LIEBERMAN, M., LIEBERMAN, D., PERALTA, R. & HARTSHORN, G. S. 1995. Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. *Journal of Tropical Ecology* 11:161–178.
- MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209–220.
- MAROD, D., KUTINTARA, U., TANAKA, H. & NAKASHIZUKA, T. 2002. The effects of drought and fire on seed and seedling dynamics in a tropical seasonal forest in Thailand. *Plant Ecology* 161:41–57.
- MONTGOMERY, R. A. & CHAZDON, R. L. 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia* 131:165–174.
- MYERS, N. 1988. Threatened biotas: “hotspots” in tropical forests. *Environmentalist* 8:1–20.
- NAKASHIZUKA, T. 2001. Species coexistence in temperate, mixed deciduous forests. *Trends in Ecology and Evolution* 16:205–210.
- NICOTRA, A. B., CHAZDON, R. L. & IRIARTE, S. V. B. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80:1908–1926.
- OLSON, D. M. & DINERSTEIN, E. 1998. The Global 200: a representation approach to conserving the Earth’s most biologically valuable ecoregions. *Conservation Biology* 12:502–515.
- PACALA, S. W., CANHAM, C. D., SILANDER, J. A. & KOBE, R. K. 1994. Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research* 24:2172–2183.
- PACALA, S. W., CANHAM, C. D., SAPONARA, J., SILANDER, J. A., KOBE, R. K. & RIBBENS, E. 1996. Forest models defined by field measurements: estimation, error analysis, and dynamics. *Ecological Monographs* 66:1–43.
- PALMIOTTO, P. A., DAVIES, S. J., VOGT, K. A., ASHTON, M. S., VOGT, D. J. & ASHTON, P. S. 2004. Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. *Journal of Ecology* 92:609–623.
- PARENT, S. & MESSIER, C. 1995. A simple and efficient method to estimate microsite light availability under a forest canopy. *Canadian Journal of Forest Research* 26:151–154.
- POORTER, L. 2005. Resource capture and use by tropical forest tree seedlings and their consequences for competition. Pp. 35–64 in Burslem, D. F. R. P., Pinard, M. & Hartley, S. E. (eds.). *Biotic interactions in the Tropics: their role in the maintenance of species diversity*. Cambridge University Press, Cambridge.
- RAFTERY, A. L. & LEWIS, S. 1992. Comment: one long run with diagnostics: implementation strategies for Markov chain Monte Carlo. *Statistical Science* 7:493–497.
- RAJOELISON, L. G. 1997. *Etude sylvicole de la forêt tropicale humide Malagasy. Exemple de la forêt littorale exploitée de Tampolo (Fenoarivo-Atsinanana) – Côte est de Madagascar*. Série du Département des Eaux et Forêts No. 4. Université d’Antananarivo, Ecole Supérieure des Sciences Agronomiques, Antananarivo. 138 pp.
- RATSIRARSON, J. & GOODMAN, S. M. 1998. *Inventaire biologique de la forêt littorale de Tampolo (Fenoarivo Atsinanana)*. Centre d’Information et de Documentation Scientifique et Technique, Antananarivo. 261 pp.
- SACK, L. & GRUBB, P. J. 2002. The combined impacts of deep shade and drought on the growth and biomass allocation of shade-tolerant woody seedlings. *Oecologia* 131:175–185.
- TYREE, M. T., ENGELBRECHT, B. M. J., VARGAS, G. & KURSAR, T. A. 2003. Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance. *Plant Physiology* 132:1439–1447.
- VEENENDAAL, E. M., SWAINE, M. D., AGYEMAN, V. K., BLAY, D., ABEBRESE, I. K. & MULLINS, C. E. 1996. 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* 84:83–90.
- WEBB, C. O. & PEART, D. R. 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* 80:2006–2017.