CHAPTER THREE

Role of life-history trade-offs in the equalization and differentiation of tropical tree species

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Introduction

Early observations of the remarkable diversity in life-history and morphology exhibited by tropical plants have strongly influenced our views on how these species coexist. Initially plants were classified according to size and life form, and subsequently into ecological species groups that recognized the importance of variation in light availability associated with the forest growth cycle (Richards 1952; Swaine & Whitmore 1988; Burslem & Swaine 2002). These ecological species groups reflect the existence of adaptive strategies that trees adopt during regeneration, and are the consequence of unavoidable trade-offs among suites of traits influencing growth, survival and fecundity.

In tropical forests, light availability has typically been identified as the primary limiting condition to growth. Adaptive strategies influencing the colonization of canopy openings and the capture or use of light are manifested as combinations of traits influencing dispersal, germination, seedling establishment, and allocation of resources to growth, storage and defence (van Steenis 1958; Budowski 1965; Whitmore 1975; Bazzaz & Pickett 1980; Coley *et al.* 1985; Kitajima 1994). This review addresses two issues: first, the extent to which individual trade-offs linking these traits can lead to the differentiation of tree species accounting for interspecific differences in the requirements for light and other resources; and second, the extent to which the action of multiple opposing trade-offs has a contrary effect of equalizing overall recruitment success so that no particular trait combination provides a recruitment advantage.

Classical views of species coexistence are founded upon niche differentiation as the mechanism preventing competitive exclusion, with limiting similarity in niche requirements providing an upper bound on local species richness (Hutchinson 1959; MacArthur & Levins 1967; Grubb 1977). Interspecific competition for limiting resources might be expected to select for adaptations that

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maximize resource capture. However, specialized adaptations often invoke trade-offs. These may act by reducing the ability to acquire other potentially limiting resources, or may constrain the effectiveness of resource capture to particular environmental conditions. Trade-offs might therefore be expected to result in the partitioning of supply gradients of resources such as light and soil moisture (e.g. Denslow 1980; Smith & Huston 1989). Furthermore, selection affecting the acquisition of light versus moisture and nutrients may have particularly strong effects on niche differentiation as allocation to above- and below-ground resource capture may be in direct conflict (Tilman 1988).

Accumulating evidence from work on Barro Colorado Island (BCI), Panama, may be interpreted as showing that many tree species are similar in their shade-tolerance (Welden *et al.* 1991; Hubbell & Foster 1992), and that light gradient partitioning therefore plays a minor role in maintaining tree diversity (Hubbell *et al.* 1999). However, we caution against a premature rejection of the 'niche-differentiation' or 'niche-assembly' view for the structure of tropical tree communities based on these findings. Early acceptance of the paradigm that species coexisted through differences in light requirements precluded a more thorough examination of how species acquire and use other potentially limiting resources. Variation in supply rates of soil resources, and in the physical and biotic conditions required for seedling establishment, all contribute to variation in plant performance and may play a more important role than light availability in determining recruitment patterns, i.e. the spatial patterns of new individuals in the community.

However, in addition to the potential role played by performance-based trade-offs in aiding coexistence of species through the *differentiation* of regeneration requirements, life-history-based trade-offs may also operate with the paradoxical effect of *equalizing* the recruitment success of species. Equalizing trade-offs may arise when no recruitment advantage accrues from any particular trait combination, and may occur when fitness advantages of particular traits are balanced across life-history stages or habitat types. As a consequence, no species has an overall per-capita fitness advantage over any other (Levins 1968). Under this scenario, diversity is not maintained by niche partitioning in the face of competitive exclusion. Instead, exclusion is avoided by competitive equivalence.

Competitive equivalence among coexisting species is an underlying assumption of neutral theories of species coexistence based on demographic stochasticity (Hubbell 1979, 2001). In addition to the equalizing effects of life-history trade-offs, Hubbell and colleagues have also argued that equivalence may arise in diverse tropical forests as a consequence of restricted seed dispersal coupled with unpredictability in the biotic composition of local neighbourhoods. Under these conditions, opportunities for specialization to particular resource conditions may be limited and thus tree species may show convergent responses to long-term average environmental conditions (Hubbell & Foster 1986; Hubbell *et al.* 1999). Determining how and when competitive equivalence occurs is therefore a critical issue in ecology.

Here we examine the role that performance-based trade-offs play in the differentiation of species resource requirements, and the role that life-history-based trade-offs play in the equalization of species recruitment success. Much of the evidence we present is based on our own studies of the regeneration ecology of neotropical pioneer species. We start by reviewing the evidence that performance-based trade-offs contribute to the partitioning of resource gradients from germination to seedling growth. We concentrate initially on the role of light availability, and then examine the more limited evidence that differences in requirements for soil-borne resources contribute to species coexistence. We then address the equalizing role of trade-offs by focusing on the early establishment stages of plant life-histories, which play a critical role in determining species abundance and distribution (Grubb 1977; Swaine *et al.* 1997). We show how trade-offs couple dispersal, germination, emergence and seedling establishment leading to similar recruitment success for species with wide variation in seed mass.

Performance trade-offs affecting germination and emergence

The seeds of most tree species in seasonally moist and aseasonal tropical forests lack dormancy and germinate within a few months of dispersal, regardless of environmental conditions (Whitmore 1975; Garwood 1983). Nonetheless, most light-demanding species, and a few small-seeded shade-tolerant species, use a variety of environmental cues to detect the presence of canopy gaps and litter-free microsites on the forest floor (Vázquez-Yanes & Orozco-Segovia 1993; Metcalfe 1996). These cues include the spectral distribution of light (Vázquez-Yanes & Smith 1982) the amplitude of diurnal temperature fluctuations (Vázquez-Yanes & Orozco-Segovia 1982) and pulses in soil nitrate concentrations (Daws *et al.* 2002a). Here we show how differences in the effectiveness of these cues under varying environmental conditions may contribute to habitat partitioning among species.

Photoblastic species respond to shifts in the composition of light in the red and far-red spectra and are typically small-seeded (seed mass <2 mg; Pearson *et al.* 2002). Light is an appropriate germination cue for these species because it penetrates only a few millimetres through moist soil, coinciding with the maximum burial depth from which seedlings of these species can successfully emerge (Pearson *et al.* 2002, 2003a). In addition, red light is absorbed by dead leaves that may be present on the soil surface (Vázquez-Yanes *et al.* 1990), and that provide a significant barrier to successful emergence and establishment for species with minimal seed reserves (Molofsky & Augspurger 1992; Metcalfe & Grubb 1997).

In contrast, larger-seeded light-demanding species, with the capacity to emerge successfully through several centimetres of soil, typically lack a germination response to light (Pearson *et al.* 2002). The germination cues used by some of these species remain to be determined, but many are sensitive to temperature fluctuations (Vázquez-Yanes 1974; Vázquez-Yanes & Orozco-Segovia 1982; Pearson *et al.* 2002). Elevated diurnal temperatures can be recorded at depths of >10 cm below the soil surface in well illuminated gap microsites (Pearson *et al.* 2002). Elevated temperatures, however, only occur in gap microsites exposed to direct sun for long enough periods for soil warming to occur.

Constraints imposed by the effectiveness of these germination cues should result in predictable differences in the gap sites where light-demanding species can recruit. Large-seeded light-demanding species should germinate in large canopy gaps with open understorey allowing light penetration to soil level (Pearson *et al.* 2003b). In contrast, small-seeded species should successfully germinate across a range of gap sizes and may successfully colonize edges of gaps shaded from direct radiation. Furthermore, the capacity of photoblastic seeds to discriminate small differences in light availability from shifts in red:far-red ratios potentially allows for finer-scale niche partitioning among species with different minimum light requirements for seedling establishment and growth (Daws *et al.* 2002a). These constraints imposed by seed size on germination behaviour appear to be congruent with size-dependent constraints on post-germination recruitment success, as dessication risk is highest for small seedlings establishing from shallow-buried seeds in high-irradiance microsites (Engelbrecht *et al.* 2001; Daws 2002).

Performance trade-offs affecting establishment and growth

Trade-offs partitioning gradients of light availability

Initial observations that tropical trees could be classified into broad regeneration guilds according to their light requirements raised hopes among temperate and tropical ecologists that fine-scale partitioning of light gradients could be responsible for much of the differentiation and coexistence of species (Ricklefs 1977; Pickett 1980; Denslow 1980, 1987). Light gradient partitioning could be mediated by two alternate sets of trade-offs. Selection on suites of morphological and physiological traits that influence net carbon assimilation could result in narrow ranges of light conditions under which relative growth rate (RGR) is optimized. Different configurations of these traits among species could result in shifts in the ranking of species according to RGR along the light gradient (Latham 1992). If variation in RGR is sufficient to overcome the differences in initial seedling size and time of emergence among species, then recruitment patterns might vary predictably with light availability.

Alternatively, species may indirectly partition light gradients as a consequence of differing growth and mortality rates (Kitajima 1994; Kobe 1999). Competitive interactions among plants dictate that the successful colonization of high-light microsites in the forest requires rapid height growth. Once the limit of carbon fixation efficiency is reached this can only be achieved by preferentially investing resources into new leaf area and leaf support tissue at the expense of allocation to structural support and defence (so wood density is low and leaves are thin). In contrast, under low light conditions, where assimilation rates are low relative to the resources needed for new tissue construction, allocation to structural support and chemical defences that lower rates of damage from physical hazards, herbivores and pathogens should be favoured (Coley *et al.* 1985). These conflicting selective pressures predict that shade-adapted species lack competitive ability in high light conditions while sun-adapted species are unable to persist for long in the shade. This trade-off is most clearly manifested as a positive relationship across species between growth rate at high irradiance and mortality rate in the shade (Hubbell & Foster 1992; Kitajima 1994).

Even though seedlings of shade-tolerant trees are clearly limited in their growth by light availability in the forest understorey, there is little evidence that differences in light response contribute to their coexistence. While some differences in growth and mortality rates have been reported for seedlings of shade-tolerant trees (Zagt 1997; Montgomery & Chazdon 2002; Bloor & Grubb 2003), the only published community-level study showed that saplings of most tropical rain forest trees had uniformly low absolute growth and mortality rates in the shade (Welden *et al.* 1991). Small differences among species in physiological responses to light availability that can be detected in short-term controlled experiments may also be unlikely to influence the outcome of interspecific competition among variable-sized individuals in the dynamic light regime of forest understorey (Barker *et al.* 1997; Rose & Poorter 2003; Clark *et al.* 2003). Therefore, it remains to be determined whether the small absolute differences in the performance of tropical forest seedlings and saplings are important when integrated over the long time intervals that these plants persist in the shade.

Differences among coexisting species in the architecture and allometry of seedlings and saplings provide an alternative perspective on the mechanism of differential species persistence in the shade over longer time scales (Kohyama 1987; King 1990; Kohyama & Hotta 1991; King 1994). Shade-tolerant species may be classified along a spectrum reflecting allocation to height growth versus lateral canopy development based on the allometric properties of individuals growing in the shade (Kohyama 1987). Species that grow quickly in height relative to their rate of canopy area development ('optimists' *sensu* Kohyama) will be at a competitive advantage in sites where irradiance increases rapidly with height and when canopy openness increases at the time of gap creation. In contrast, optimists are predicted to show a lesser ability to persist for long periods in the shade than species that invest in lateral spread of the canopy to maximize light capture and carbon gain (Kohyama's 'pessimists'). These predictions are supported by studies demonstrating positive correlations across species between maximum adult height and sapling height at a given diameter (Kohyama *et al.*

2003; Poorter *et al.* 2003). The recognition that species differ in architecture and allometry, however, does not provide direct evidence that these differences contribute to species coexistence. Further research may demonstrate that the trade-off between height growth and lateral canopy development in shade-tolerant species is another expression of the same trade-off between growth in sun versus persistence in the shade (Hubbell & Foster 1992).

A more restricted interpretation of light-gradient partitioning is that species coexist through differences in their recruitment success in gaps. The hypothesis proposes that species respond in different ways to gaps according to gap size or orientation, or according to microsites present within them (Denslow 1980, 1987; Pickett 1980; Orians 1982). The hypothesis has been tested by a number of long-term studies of seedling regeneration in natural and artificial gaps (e.g. Brokaw 1985; Uhl *et al.* 1988; Brown & Whitmore 1992), but fails to find support as a general mechanism of species coexistence among tropical forest trees (Brown & Jennings 1998; Hubbell *et al.* 1999; Brokaw & Busing 2000). Gap partitioning, however, may be more important as a mechanism that aids coexistence among the group of light-demanding species, defined according to their requirement for high-light microsites for germination or establishment (Brokaw 1987). These species represent a small proportion of overall tree diversity (10–20% of tree species; Dalling *et al.* 1998; Molino & Sabatier 2001), but recruit in microsites where resource availability is most variable. Total irradiance, the spectral composition of light, and the persistence of high irradiance conditions generally covary with the size of canopy disturbances (Barton *et al.* 1989; Brown 1993; van der Meer *et al.* 1994). Thus, if species are adapted to particular irradiance regimes then they might be expected to show differential recruitment success along a gradient of canopy gap sizes.

We have looked in detail at whether differences in light requirements contribute to species coexistence of light-demanding species at the Barro Colorado Island Nature Monument (BCNM), in central Panama. A pot experiment conducted with thirteen fast-growing species failed to show much evidence for rank shifts in RGR over the range of light conditions under which seedlings of these species are observed to recruit in the field (Dalling *et al.* 1999, 2004; Fig. 3.1). Furthermore, many of the most abundant light-demanding species had similar RGR and were rather unresponsive in growth to varying irradiance conditions. The fastest-growing species, *Cecropia*, *Cordia*, *Ochroma* and *Trema*, however, did show more variation in growth response.

In support of the growth–mortality trade-off hypothesis, our observations of the same species recruiting in natural (Dalling *et al.* 1998) and artificially created treefall gaps (Dalling & Hubbell 2002) show that growth rate is positively correlated with mortality rate, and that much of the variance in mortality could be attributed to differential susceptibility to browsing and stem-boring herbivores (Fig. 3.2). These observations suggest that a growth–mortality trade-off mediated by biotic enemies could result in gap-size partitioning among light-demanding

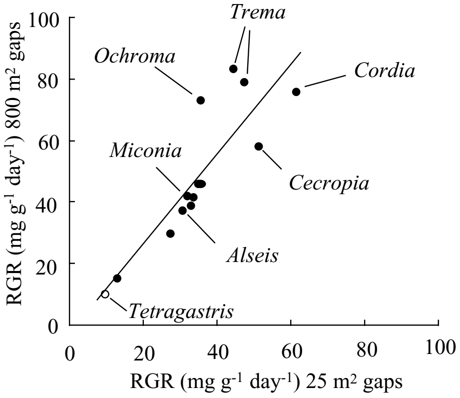

Figure 3.1 Correlation of mean relative growth rate (RGR) calculated for seedlings grown in pots in a shade house experiment simulating large (800 m^2) gaps and small (25 m^2) simulated gaps. Data are for thirteen light-demanding taxa (closed symbols) and one shade-tolerant species (open symbol) from Barro Colorado Nature Monument, Panama. For more details see Dalling *et al.* (2004).

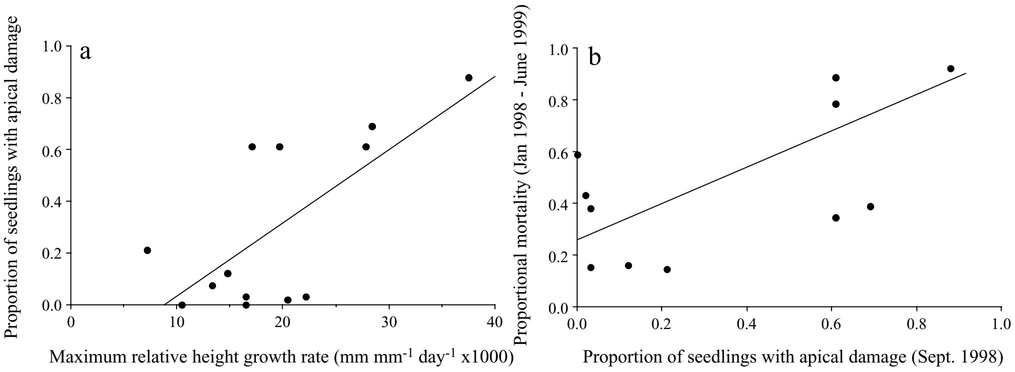

Figure 3.2 Proportional mortality of 1-year-old seedlings of pioneer species censused over 18 months in five artificially created gaps on Barro Colorado Island Panama, (a) regressed against the species-specific maximum relative height growth rate, and (b) the proportion of seedlings of each species exhibiting apical shoot damage (from stem-boring insects and mammalian browsers) and maximum relative height growth rate. Redrawn from Dalling & Hubbell (2002).

species, as has been shown by Brokaw (1987). If fast-growing species are restricted to large canopy gaps by the assimilation rate needed to replace tissues lost to herbivores, then protection of seedlings from herbivores should result in a reduction in light requirements for growth and survival. We tested this hypothesis by transplanting seedlings of three light-demanding species inside and outside mosquito-netting exclosures in artificially created small (25 m^2) and large (225 m^2) gaps. The three species chosen differed in growth rate and minimum gap size requirements for sapling survival: *Miconia argentea* < *Cecropia insignis* < *Trema micrantha* (Brokaw 1987). We found that while the exclosures reduced foliar herbivory and increased leaf area growth of *Trema* and *Miconia*, they had no sustained effect on seedling survivorship (Fig. 3.3, Pearson *et al.* 2003b).

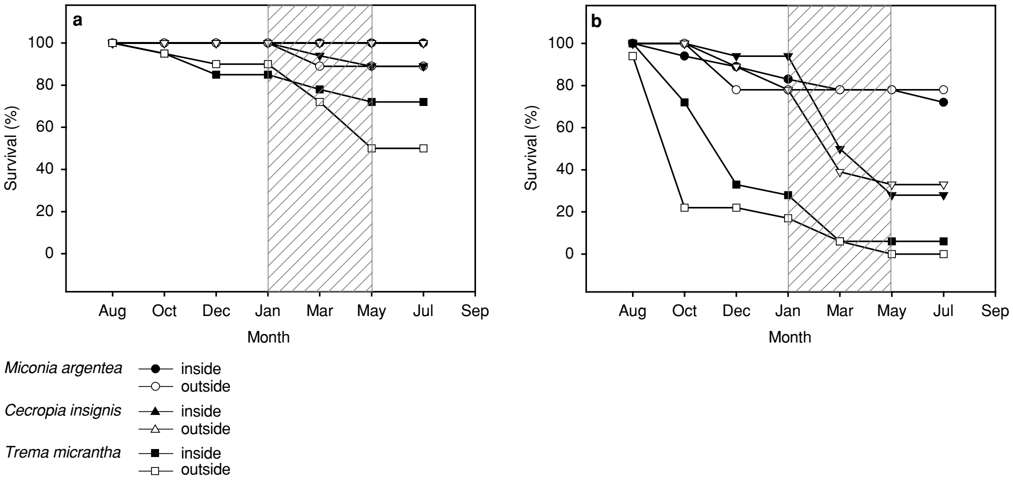

Figure 3.3 Percentage survival over time in large (a) and small (b) gaps for seedlings of *Miconia argentea*, *Cecropia insignis* and *Trema micrantha*. Filled synbols: seedlings inside enclosures; open symbols: seedlings outside enclosures. The experiment was conducted in secondary forest in the Barro Colorado National Monument, Panama. Hashed box indicates dry season. For more details see Pearson *et al.* (2003b).

In conclusion, light-demanding species show differences in growth and mortality rates, and in susceptibility to herbivores, but our field experiments in Panama fail to make a direct link between herbivory and variation in mortality rates in high and low light. The poor performance of the saplings of the fastest-growing species under relatively low light in the field may instead reflect the increased whole-plant light compensation point of larger plants with greater respiratory demands associated with higher growth rates, biomass allocation to support tissue, and tissue turnover rates (Givnish 1988; King 1994). These results emphasize the need for more long-term field experiments of growth performance to complement the short-term growing-house experiments that have mostly been used so far to characterize light requirements of different species.

Trade-offs partitioning gradients of nutrient availability

Species distributions in tropical forests may respond to variation in the availability of soil-borne resources as well as light. At landscape scales, variation in underlying geology and topography may generate gradients in both soil moisture and nutrient supply (Daws *et al.* 2002b; Baker *et al.* 2003). Analyses of tree distributions along transects and in large census plots using statistical techniques that account for spatial autocorrelation in recruitment have found that habitat associations with topographic or soils variables can be quite common (Harms *et al.* 2001; Debski *et al.* 2002; Phillips *et al.* 2003; Tuomisto *et al.* 2003). At more local scales, variation in nutrient availability may arise through disturbance, such as when sub-soils are exposed at the surface in tip-up mounds (Putz 1983) and on landslides (Dalling & Tanner 1995; Fetcher *et al.* 1996). A transient reduction in fine root density in canopy gaps may also impose heterogeneity in nutrient concentrations in soil solution (Vitousek & Denslow 1986; Uhl *et al.* 1988), while fine-scale heterogeneity in the amount and chemistry of litterfall may influence nutrient cycling and nutrient availability to plants that acquire nutrients directly from decomposing litter. Despite these patterns, however, the extent to which seedling growth and survival are limited by nutrients or water under field conditions remains poorly understood. Here we review evidence for resource partitioning resulting from trade-offs in response to below-ground resource availability.

Most experimental tests of nutrient limitation of tropical tree growth have been conducted using seedlings grown in pots of amended forest soil, and are typically limited to a small number of species. One exception is the study by Huante *et al.* (1995), which examined the growth and allocation responses of 34 woody plant species from Mexican dry deciduous forest grown in sand containing high and low concentrations of N, P and K. This experiment failed to show any evidence for a direct trade-off among species in growth rates, as the relative growth rate (RGR) of seedlings growing in pots at low nutrient supply was positively correlated with RGR at high nutrient supply. However, species RGR in this experiment was negatively correlated with seed mass and positively correlated with specific leaf area in both nutrient treatments. This suggests that the 10-week growth period over which the experiment was run may have been too short to overcome initial differences in RGR that are constrained by seed mass and specific leaf area (Marañon & Grubb 1993; Grubb 1998).

A comparable but much longer (50-week) experiment, run by Metcalfe *et al.* (2002), gave rather different results. In this experiment, seedlings of six Australian rainforest tree species were grown in soil diluted to varying degrees with sand that contained low concentrations of N and P but relatively high concentrations of the major nutrient cations. Two of the six species that showed a significantly reduced growth rate in a medium containing only 5% soil compared with 50% soil were also two of the three species with the greatest dry mass increment in the 50% soil. In contrast, the species that was least responsive to soil dilution had the lowest growth rates in the richer soil mixes. These results provide some suggestion of cross-overs in species growth rates along a gradient of nutrient availability, but the role of trade-offs driving rank shifts in RGR in relation to nutrient supply remains unresolved, as it is for irradiance (Sack & Grubb 2001; Kitajima & Bolker 2003).

Studies of plant performance in pot experiments can perhaps be more readily interpreted when they are linked to species distributions along gradients of resource availability in the field (Lawrence 2003). Gunatilleke *et al.* (1997) compared eight species of *Shorea* section *Doona* (Dipterocarpaceae) that grow

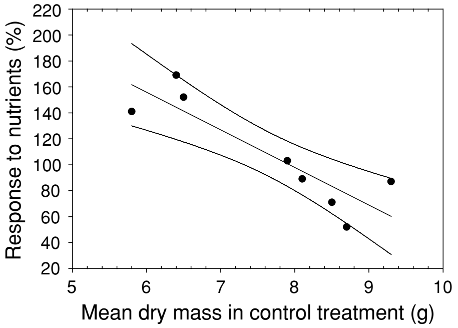

Figure 3.4 Relationship between mean dry mass (g) in an unfertilized control treatment and mean maximum dry mass yield (% of control) in response to nutrient addition for seedlings of eight species of *Shorea* section *Doona* grown in pots for 24 months at Sinharaja forest reserve, Sri Lanka. For more details see Gunatilleke *et al.* (1997).

sympatrically in lowland evergreen rain forest in Sri Lanka. They found that the four species with distributions biased towards relatively nutrient-rich soils on low slopes and valleys were more responsive to nutrient addition than the four species that occur naturally on less nutrient-rich soil. Responsiveness to nutrient addition (defined as the maximum increase in dry mass in response to nutrient addition as a percentage of the unfertilized control value) was also negatively correlated with mean dry mass in the control treatment across these eight species ($r = -0.881$; $P < 0.01$, Fig. 3.4). This 'trade-off', however, did not entirely reflect species distributions along the soil fertility gradient in the forest. Instead, a range of strategies for achieving a size advantage in response to nutrient addition were displayed among the four species of richer soil: large seed mass combined with fast relative growth rates (*S. megistophylla*), a high 'responsiveness' to nutrients (*S. trapezifolia* and *S. cordifolia*) and intermediate growth rate and responsiveness (*S. congestiflora*).

Shade-house evaluations of responses to soil resource gradients should, however, be interpreted with caution, as growth and allocation in pots may differ significantly from growth under similar mean light conditions in the field. This is largely because of variation in below-ground resource supply rates in the field, and consequent variation in patterns of seedling resource allocation (Burslem *et al.* 1994; Bloor 2003). Field manipulations of below-ground resource availability can be achieved by the removal of root competition by trenching. Although this is a robust method for testing the intensity of competition for nutrients and/or water imposed on seedlings by adult trees, it is a labour-intensive technique and most studies therefore test only a few species. Results of these studies typically support those of pot experiments, with positive growth responses for seedlings in relatively nutrient-poor oxisols or psamments (e.g. Whitmore 1966; Fox 1973; Coomes & Grubb 1998; Lewis & Tanner 2000), but not on the richer alfisols at La Selva, Costa Rica (Denslow *et al.* 1991; Ostertag 1998). Only one study, conducted by Coomes & Grubb (1998), has compared the responses of a significant number of species. They found that trenching had similar effects on the growth of saplings of 13 species growing in a nitrogen-limited caatinga forest in Venezuela.

Trade-offs partitioning gradients of soil moisture availability

Seasonality in rainfall and in the occurrence of unpredictable droughts, coupled with topographic and edaphic variation in moisture availability, also provide scope for fine-scale resource partitioning. Field and pot experiments have demonstrated that co-occurring species differ in survival and/or growth responses to water supply (e.g. Burslem *et al.* 1996; Poorter & Hayashida-Oliver 2000; Engelbrecht *et al.* 2000, 2002; Engelbrecht & Kursar 2003; Tyree *et al.* 2003), but only one study has compared the response of a sufficient sample of species to detect trade-offs that might partition species occurrence along gradients of soil moisture (Engelbrecht & Kursar 2003). In this study, the survival and leaf area change of 28 species of woody plants growing in the understorey of a semi-deciduous forest in Panama were compared between drought and irrigated treatments. The 28 species showed a continuum of response to drought that was manifested as differences in both survival and leaf area change, but growth–mortality trade-offs in treatments that varied water supply to the plants during the dry season were not observed. In some cases, species' differential response to drought predicted their local distribution along a gradient of soil water availability determined by topography on a 50-ha plot on nearby Barro Colorado Island (Becker *et al.* 1988; Harms *et al.* 2001; Daws *et al.* 2002b).

Trade-offs resulting from interactions between above- and below-ground resource acquisition

To evaluate trade-offs in resource requirements as a mechanism generating fine-scale partitioning of habitats, we require stronger experimental evidence from studies that assess interactions among potentially limiting resources. For example, when controlled independently, shade and drought have contrasting effects on the allocation of dry mass above- or below-ground. These effects might be expected to result in a growth–survival trade-off in environments that vary in both irradiance and water supply (Smith & Huston 1989). This trade-off might arise if expansion of leaf area and specific leaf area in shade occurs at the cost of reduced allocation to roots, so that more shaded plants are predicted to suffer greater mortality to drought.

Experiments conducted at BCI, Panama, in which seedlings of six pioneer species were transplanted into gaps in seasonally moist forest yielded results that are consistent with this prediction. Seedlings of the three species that maintained the highest RGR in the wet season had the lowest dry-season survival. A seasonal decline in survivorship was particularly marked for *Cecropia insignis*, the species with the highest biomass fraction allocated to leaf area when grown under similar irradiance conditions in a pot experiment (Pearson *et al.* 2003b; c; Dalling *et al.* 2004). Similar results were obtained when seedlings of two light-demanding species were transplanted to gap, edge and forest understorey sites in seasonally moist forest in Ghana (Veenendaal *et al.* 1996). Whereas seedlings survived equally well in all sites during the wet season, survival dropped to low levels in the understorey in the dry season but was unchanged in the gap. In contrast, Fisher *et al.* (1991) found no differences in survival among treatments for yearling seedlings of the shade-tolerant tree *Virola surinamensis* transplanted to gap and understorey sites on BCI, Panama, and irrigated during the dry season. However, seedlings in the understorey only showed positive growth rates when irrigated.

The strategies that plants adopt to acquire water and nutrients under limiting conditions may involve adjustments that are unrelated to plasticity in allocation of above- versus below-ground dry mass (such as changes in root form without a change in root mass). Thus it may be overly simplistic to anticipate an allocation-based growth−survival trade-off for tropical tree seedlings exposed to variable light and water regimes (Sack & Grubb 2002). Unfortunately, the diversity of mechanisms that tropical forest plants have evolved to tolerate combinations of limiting supply rates of light, nutrients and water remains poorly explored. New research in this area is important because independent effects of different resources on tree seedling growth and survival would increase the scope for fine-scale niche partitioning along multiple gradients of limiting soil-borne resources.

Life-history trade-offs equalizing recruitment success

The seed number/seedling survival trade-off

Trade-offs in plant performance resulting from specialized resource requirements may be less prevalent than expected because limited seed production and dispersal greatly reduce the probability that individuals encounter the microsites to which they are best adapted. Increased seed production can partially offset the effects of dispersal limitation, but constraints imposed by the finite resources available for reproduction invoke a new set of trade-offs. These life-history trade-offs arise from a negative correlation between seed mass and colonization success, which is balanced by a positive correlation between seed mass and seedling survival (described as a seed number/seedling survival trade-off by Coomes & Grubb 2003). The consequence of this trade-off is to equalize recruitment success among species with similar habitat requirements but divergent life-history characters.

The seed size/seedling survival trade-off is usually viewed as mediated by seed-size-dependent variation in colonization and competitive ability (e.g. Horn & MacArthur 1972; Tilman 1994). However, interspecific interactions among establishing seedlings still dependent upon their seed reserves are likely to be weak in forest understoreys because plant density is insufficient to permit strong direct competition for light and soil resources, and because most resources are acquired by canopy vegetation rather than by neighbouring seedlings (Wright 2002). Size-dependent seedling survival may be mediated instead by size-dependent tolerance of low overall availability of resources (Boot 1996), and to common sources of mortality affecting emerging and establishing seedlings. These include shading and physical damage from falling litter (Clark & Clark 1991), uprooting disturbance by animals (Theimer & Gehring 1999), insect seed and seedling predation (Dalling *et al.* 1997a; Harms *et al.* 1997), and shoot browsing by mammals (Harms & Dalling 1997). Whether these mortality hazards provide a sufficient recruitment advantage to large-seeded shade-tolerant species to balance their reduced reproductive output compared with small-seeded shade-tolerators remains unclear. Nonetheless, available evidence does indicate that seedling mortality scales with seed size over a wide range of seed masses (Silman 1996; Muller-Landau 2001).

Interspecific competition among recruiting seedlings might be expected to be more important in gaps than in the forest understorey. In addition to recruits from seed rain, gaps are filled by seedlings emerging from the seed bank, which can be stocked at densities of >3000 individuals per m^2 (Garwood 1989). However, only a small fraction of seed-bank individuals emerge following gap formation. In a study tracking seedling recruitment in artificially created gaps, Dalling and Hubbell (2002) found that, on average, only 6% of seeds present in the top 3 cm of soil emerged in litter-free microsites. Natural litter cover within these gaps further reduced seedling emergence success three-fold. Moreover, small initial seedling size for most light-demanding species coupled with high mortality in the first weeks following emergence greatly reduces opportunities for direct competition during seedling establishment.

Detailed studies of seed dispersal and seed-bank dynamics in the 50-ha plot on BCI, and of recruitment patterns in artificially created gaps in the Dalling and Hubbell (2002) study allow us to ask, at least for light-demanding species, whether seed-size-dependent differences in seedling recruitment probabilities are sufficient alone to equalize species differences in reproductive output. In the artificial gaps study, recruitment success from the soil seed bank to first-year survival was positively correlated with seed mass and effectively balanced size-dependent variation in seed abundance in the surface 0–6 cm of the soil (Fig. 3.5). As a consequence, observed first-year recruit densities were uncorrelated with seed masses ($r^2 = 0.01$). Using data on seed captures to mesh traps in the BCI 50-ha plot, Dalling *et al.* (2002) used a maximum likelihood approach to estimate fecundity parameters (seed production per unit basal area) for 11 light-demanding species. Estimated fecundity was found to scale with seed mass as a power relationship with slope of -0.92. Seed-bank densities measured for the same species at 192 sample locations in the plot also scaled with seed mass, with a somewhat shallower slope of -0.76, but slopes were not significantly different (t-test $\mathrm{df}_{2,18} = 0.63$, $p > 0.05$; Fig. 3.6). This suggests that probabilities of seed incorporation into the soil are largely invariant with respect to seed mass.

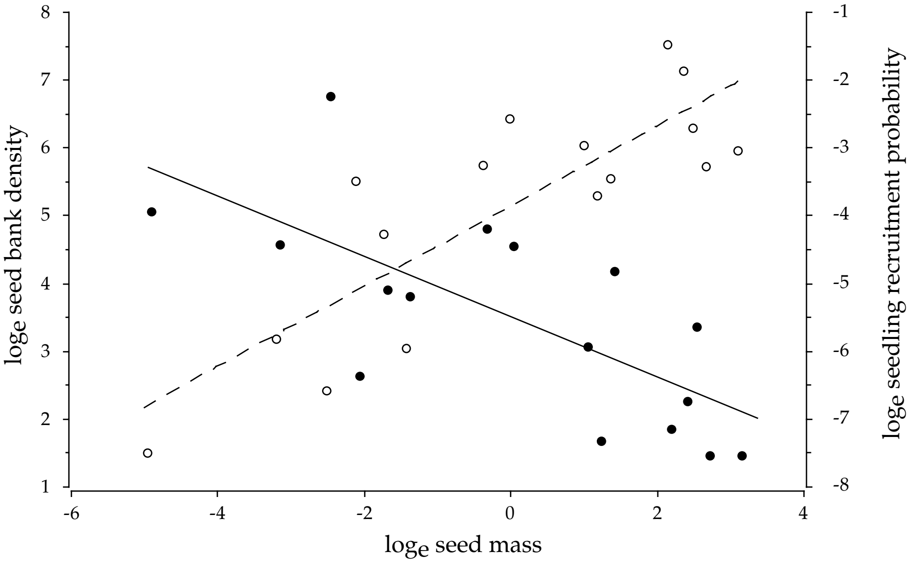

Figure 3.5 Relationship between seed mass (mg) and and soil seed bank density (seeds m^{-2}; closed symbols), and between seed mass and seedling recruitment probability (probability of successfully emerging from the seed bank and surviving one wet and dry season). Data are for sixteen light-demanding taxa recruiting into artificially created gaps in secondary forest on the Barro Colorado Nature Monument, Panama. For more details see Dalling and Hubbell (2002).

A seed size/seed persistence trade-off?

Conventional views of the relationship between seed mass and seed persistence in the soil are based on studies of weed seeds in temperate grasslands (Thompson & Grime 1979; Rees 1993; Thompson *et al.* 1993; Funes *et al.* 1999). These show that small seeds are more readily incorporated into the soil (Peart 1984), and are more likely to persist because burial provides an escape from predation by ants, beetles and rodents that forage primarily on the soil surface (Thompson 1987). Adaptive arguments have also been made that lead to the expectation of a negative relationship between size and persistence, as these traits incur a fitness cost associated with reduced reproductive output and increased generation time, respectively. To avoid incurring both these fitness costs, plants should therefore produce either small seeds that persist between unfavourable periods or large seeds that tolerate unfavourable conditions (Venable & Brown 1988).

Our observations of variation in seed persistence among light-demanding species in Panama, however, fail to support this prediction. Instead, we find the opposite pattern, whereby long-term seed persistence appears to be limited to the larger-seeded species (>3 mg seed mass). Small-seeded species (<1 mg) that we have examined in detail typically lose viability within one year of burial (Dalling *et al.* 1997b), with mortality attributable to seed-infecting fungi (Dalling

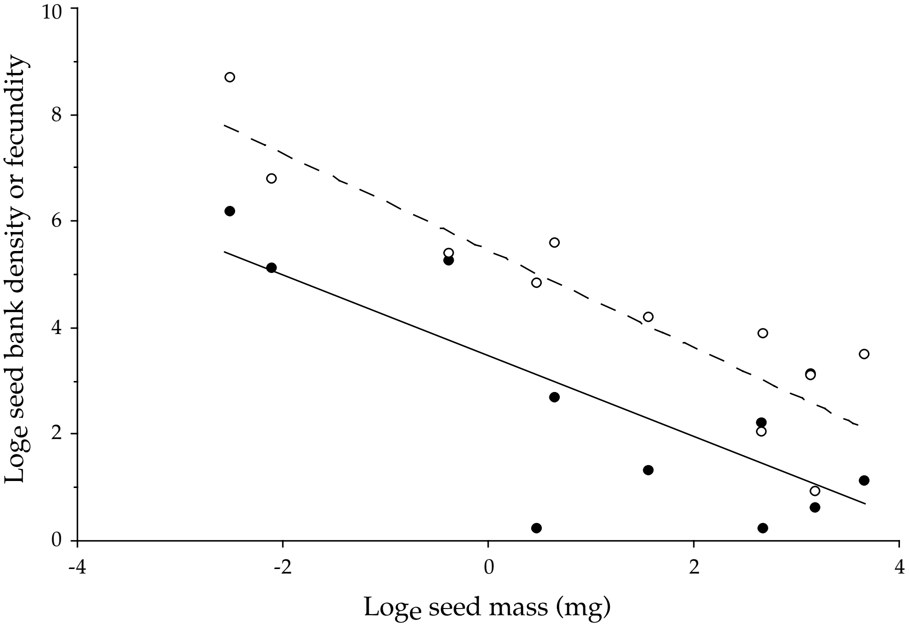

Figure 3.6 Relationship between predicted reproductive output (seeds per cm^2 basal area) and seed mass (open symbols, dashed regression line), and between soil seed-bank density and seed mass (closed symbols, solid regression line) for eleven light-demanding taxa. Reproductive output was calculated using maximum likelihood parameter estimation based on data obtained from seed traps arrayed in the 50-ha forest dynamics plot on BCI (Dalling *et al.* 2002). Seed-bank density was measured for the top 3 cm of soil in 192 soil samples collected in May 1993 in the BCI 50-ha plot (Dalling *et al.* 1997b).

et al. 1998; R. Gallery & J. W. Dalling, unpublished data). In contrast, larger-seeded species with thick seed coats appear to be resistant to pathogens, and may be too hard for many soil invertebrates to penetrate (cf. O'Dowd & Hay 1980). Direct ageing of the endocarps of viable seeds collected from the field on BCI using accelerator mass spectrometry of ^{14}C (cf. Moriuchi *et al.* 2000) has shown that seeds of several of these species are capable of extraordinary persistence. Seeds of *Trema micrantha*, *Hyeronima laxiflora*, *Zanthoxylum eckmannii* and *Croton bilbergianus* buried <3 cm below the soil surface can be >30 years old (J. W. Dalling & T. A. Brown, unpublished data).

These results, based on relatively few species, suggest therefore that in tropical moist forests, seed size and persistence are positively related for pioneer species. Under these conditions seed persistence becomes an important trait that could further offset the fecundity advantage associated with small seed mass, and for light-demanding species may be a significant component of the equalizing trade-offs that permit coexistence of species varying in seed mass. Long-term seed persistence may be particularly advantageous in tropical forests where disturbances providing recruitment opportunities for light-demanding species are infrequent and where community-level dispersal limitation is high (Murray 1998; Dalling *et al.* 2002).

Conclusions

In this chapter we have provided evidence for the view that trade-offs act both to equalize recruitment success and to differentiate habitat requirements among tropical tree species. The equalizing role is apparent early in ontogeny, and is manifested primarily as a dispersal–establishment trade-off that hinges on seed mass. At present, this trade-off is best documented for light-demanding species, but a similar relationship can also be described for shade-tolerators (Muller-Landau 2001; Daws 2002). In the absence of niche differentiation, it might be argued that the dispersal–establishment trade-off is alone sufficient to maintain tree diversity in both regeneration guilds. Evidence for declining mortality rates through ontogeny suggest that species abundance and distribution patterns are largely determined by differences in survivorship during early establishment. Equalization of recruitment success would then imply that relative abundance is determined primarily by random drift, and that community-wide dynamics are consistent with the neutral model (Hubbell 2001; Chave *et al.* 2002).

In contrast, trade-offs that result in partitioning of regeneration niches should act to stabilize the relative abundances of in the face of random drift, according to the availability of suitable habitat (Chesson 2000). However, initial suggestions that species finely partition gradients of light availability appear to be unfounded. An unfortunate consequence of these suggestions has been a failure adequately to test for partitioning in the acquisition and use of other potentially limiting resources. In part, this may be because ecologists have assumed that life-history traits that influence the capture of secondary resources covary with shade tolerance (Bazzaz & Pickett 1980; Hubbell 2001). However, there is no *a priori* reason to predict that this assumption is justified: in tropical forest environments the availability of nutrients and water varies at multiple spatial scales independently of the availability of light, and over time in response to seasonality and interannual variation in rainfall and the climatic drivers of evapotranspiration (e.g. Daws *et al.* 2002b; Baker *et al.* 2003). Thus gaps of a particular size in a wet year might not provide the same regeneration environment as gaps of the same size in a dry year. We suggest that trade-offs imposed by the conflicting demands for maximizing fitness in response to multiple limiting resources might play a much more important role in determining recruitment success than current evidence suggests. These trade-offs will only become apparent, however, once ecologists have better described spatial patterns of variation in below-ground resource supply rates as well as plant responses to them.

The future resolution of the role of equalizing versus stabilizing forces in structuring tropical tree communities is only likely to emerge from comparative studies among sites. Comparisons of relative abundances of species in tropical forests at a range of spatial scales (Pitman *et al.* 1999, 2001; Terborgh *et al.* 1996), over decadal scales during recovery from large-scale disturbance (Burslem *et al.* 2000) and in temperate forests over the past 10 000 years (Clark & McLachlan 2003), make a persuasive case for stable species assemblages in which relative abundance distributions are conserved. Once a stronger mechanistic framework has been established to determine how seed and seedling traits influence resource capture, we will also be able to assess the extent to which trait composition varies among tree communities found on sites varying in resource supply rates. Concurrent shifts in the trait composition of communities along resource gradients may provide the strongest evidence that tropical forests are structured through niche partitioning.

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