Tree Nutrient Status and Nutrient Cycling in Tropical Forest—Lessons from Fertilization Experiments

E.J. Sayer and L.F. Banin

Abstract Highly productive tropical forests often occur on nutrient-poor soils. The apparent lack of a relationship between tree growth and site fertility has generated decades of research into which nutrients, if any, limit tropical forest productivity. This chapter looks at the lessons we have learned from several decades of fertilization experiments, which investigate nutrient limitation by measuring changes in growth and productivity in response to the addition of specific nutrients. The enormous diversity of tropical forest ecosystems often confounds attempts to measure a clear ecosystem response to fertilization because tree species' nutrient requirements differ according to life history strategy, adaptation to site fertility, and the life stage of the individuals under study. Importantly, other limiting resources, such as light and water, constrain individual responses to nutrient availability, whereas species interactions such as competition, herbivory, and symbioses can mask growth responses to nutrient amendments. Finally, fertilization changes the timing and balance of nutrient inputs to the forest, whereas litter manipulation studies demonstrate that the combined addition of many different nutrients and organic carbon minimizes nutrient losses. Most fertilization studies have investigated responses to nitrogen and phosphorus additions but there is still no general consensus on nutrient limitation in tropical forests. Future experiments will need to evaluate how the balance of multiple macro- and micronutrients affects tropical forest growth and ecosystem dynamics.

Keywords Belowground biomass · Ecosystem productivity · Life history strategy · Nitrogen fixation · Nutrient limitation · Soil chronosequence · Tree growth

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Nutrient Limitation of Ecosystem Productivity in Tropical Forests

Tropical forests are the most productive of all terrestrial ecosystems and yet large areas of tropical forest occur on nutrient-poor soils (Vitousek and Sanford 1986; Bruijnzeel 1991). Plant communities growing on highly nutrient-limited sites are likely to be well-adapted to nutrient shortage and large proportions of the nutrients available to plants are tied up in the living biomass and recycled with plant litter (e.g. Herrera et al. 1978). The maintenance of such high productivity in tropical forests on infertile soils can therefore be attributed to highly efficient cycling of nutrients in organic matter (e.g. Jordan 1985; Cuevas and Medina 1988) and nutrients from the decomposition of organic matter can make up a large proportion of the nutrients required for plant growth (Bruijnzeel 1991).

The relative infertility of tropical soils and the highly efficient recycling of nutrients in tropical forests have given rise to decades of research into which nutrients, if any, limit productivity in tropical forests (Dalling et al., this volume). The relationship between soil fertility and net primary productivity in tropical forests is uncertain; comparative studies have variously demonstrated that above-ground productivity can be positively (e.g. Quesada et al. 2012), negatively (Proctor 1983) or entirely unrelated to different measures of soil nutrient status (Jordan and Herrera 1981; Proctor 1983). On the one hand, this may be partly due to the challenges in quantifying plant-available nutrients in the soil and the ‘efficiency’ of nutrient cycling in tropical forests (Vitousek 1984; Vitousek and Sanford 1986), which decouples the simple relationship between soil fertility and plant nutrient acquisition. On the other hand, differences in biomass allocation and species composition can confound results in gradient studies; for example, tree growth was positively related to soil nutrient concentrations in Borneo because of the high density of a particular canopy emergent at the most fertile sites (Paoli et al. 2008).

Fertilization experiments are a useful tool to resolve some of these issues because nutrient limitation can be inferred from a change in the rate of an ecosystem process in response to the addition of a given nutrient (Tanner et al. 1998). Research on the nutrient regulation of plant productivity in the tropics has focused largely on the macronutrients nitrogen (N) and phosphorus (P). An adequate supply of N is essential for plant growth because it is a building block of amino acids, enzymes and nucleic acids (Santiago and Goldstein, this volume, Chap. 14). Phosphorus is also found in nucleic acids and it plays many vital roles in plants, including energy metabolism. Very few tropical studies have investigated the effects of fertilization with other plant macronutrients such as potassium (K), calcium (Ca) or magnesium (Mg), but any nutrient can be said to be ‘limiting’ when its availability constrains a biological or biochemical process (Tanner et al. 1998).

The concept of limiting nutrients was developed for individual plants or monoculture crops, whereas community- and ecosystem-level responses are likely to vary with species composition (Chapin et al. 1986). The high diversity of plants in tropical forests in particular makes pinpointing nutrient limitation at the ecosystem level especially challenging (Grubb 1989) because not all species are necessarily limited by the same nutrient, two or more nutrients can be co-limiting (Tanner et al. 1998), and apparent limitation by one nutrient may actually be limitation by a different nutrient in disguise, for example when uptake of N is limited by P-availability (Attiwill and Adams 1993). To complicate matters further, simultaneous limitation by different types of resources, such as light, water, or nutrients, is also often the rule (Bloom et al. 1985; Tanner et al. 1998).

During the search for the elusive ‘limiting nutrient’, fertilization experiments have provided a wealth of valuable information about tropical forest nutrient cycling, plant growth, and species interactions. In this chapter, we draw on the results of more than three decades of fertilization studies conducted in tropical forests to detect patterns in plant responses to altered nutrient supply and identify considerations and constraints for interpreting experimental results. Most of the evidence presented here concerns N- and P-dynamics, for which there is a large body of literature on tropical forests but the same general considerations are likely to apply to other nutrients.

Nutrients, soil development and the extraordinary case of Hawai’i—Theoretically, terrestrial ecosystems will experience a shift from N- to P-limitation over geological time. The primary source of P (and other base cations) in soils is the weathering of bedrock, so their concentrations decline progressively with soil age and development, mainly as a result of erosion and leaching (Walker and Syers 1976). In contrast, N accumulates in soil during the course of soil development, reaching maximum levels in middle-aged soils (Lambers et al. 2008).

Many lowland tropical forest soils are old and highly weathered, particularly those on ancient Precambrian shield geology, and hence they have low availability of P, K and other cations (Grubb 1989; Banin et al. 2015). Conversely, tropical montane forests have low availability and mineralization rates of N (Grubb 1977; Vitousek 1984). Gradient studies also demonstrate that productivity is related to foliar P concentrations in lowland forests (Vitousek 1984) and to foliar N in montane forests (Tanner et al. 1998; Fisher et al. 2013). It is therefore widely accepted that tropical montane forests are more likely to be N-limited whereas lowland forests are more likely to be primarily limited by P (Vitousek and Sanford 1986; Tanner et al. 1998).

The Hawai’ian Long Substrate Age Gradient (LSAG) presents a unique opportunity to test these theories of nutrient availability during soil development in detail. The gradient comprises a chronosequence of primary forest succession at six sites ranging from 300 years to 4.1 million years of age; the relative availability of N is lower at the youngest sites whereas the relative availability of P is lower at the oldest sites (Crews et al. 1995). The sites along the gradient have comparable elevation, rainfall, parent material and species composition (Harrington et al. 2001), and the shift from N- to P-limitation along the gradient is reflected in foliar nutrient concentrations (Crews et al. 1995). Factorial +N and +P fertilization treatments at either end of the gradient have demonstrated N-limitation of forest productivity in the geologically youngest site and P-limitation at the oldest site (Vitousek and Farrington 1997). Unfortunately, another exceptional feature of the Hawaiian LSAG is that the forest is dominated by a single canopy tree species, and is therefore not necessarily representative of the highly diverse forests typical elsewhere in the tropics. Despite this potential limitation for extrapolating results to highly diverse tropical forests, dominance by only one species (in this case *Metrosideros polymorpha*) makes mechanistic studies possible (Cordell et al. 2001).

The evidence for N-limitation of productivity in tropical montane forests is strong; fertilization with +N increased tree diameter growth and/or litter production in Jamaica, Venezuela and Hawaii (reviewed by Tanner et al. 1998), Ecuador (Homeier et al. 2012), Panama (Adamek et al. 2009) and Peru (Fisher et al. 2013). In contrast, although the concept of P-limitation in lowland tropical forests is widely accepted, the collective results of fertilizer studies are far from conclusive.

Aboveground productivity—Large-scale fertilization experiments in lowland tropical forests have shown no effects of fertilization with +P alone on tree growth in Borneo (Mirmanto et al. 1999) or Cameroon (Newbery et al. 2002) despite very low soil P concentrations. After three years of fertilization in mature forest in Costa Rica, stem growth of small trees doubled with +P additions and a higher percentage of trees increased basal area in +P treatments than in control plots but there were no other community-level responses to fertilization with +N or +P (Alvarez-Clare et al. 2013). Tree growth in young and old Mexican dry forests increased with +P, +N and +NP fertilization; whereas +P and +NP treatments had a greater effect on trunk growth, only fertilization with +NP enhanced litter production (Campo and Vazquez-Yanes 2004). Interestingly, wood and leaf biomass of *Eucalyptus* trees in a Brazilian plantation were greatly enhanced by fertilization with +K and, to a lesser extent, sodium (+Na; Epron et al. 2011). Finally, a factorial fertilization experiment with +N, +P and +K in Panama demonstrated that the addition of each of these three macronutrients enhanced a different component of forest productivity: stem growth of saplings was enhanced by the addition of +NK, whereas seedling height growth increased with +K or +NP fertilization; litterfall increased with +P fertilization, plant investment in fruits and flowers increased with +N, and root biomass of trees and seedlings decreased in response to fertilization with +K or +NK (Kaspari et al. 2008; Yavitt et al. 2011; Wright et al. 2011; Santiago et al. 2012).

Belowground responses—It is possible that the variable responses in aboveground productivity are partly a result of changes in biomass allocation. In theory, plants adapted to nutrient-poor soils should allocate more biomass to roots to improve nutrient acquisition (Chapin 1980), whereas plants on fertile sites should invest a greater proportion of their biomass aboveground. Accordingly, stand-level root biomass should decrease when nutrient limitation is relieved by fertilization. On the other hand, fine roots can proliferate into hotspots of nutrient availability in nutrient-poor soils (St. John 1982), which creates microsites of high root biomass. This provides an alternative approach to assess the effects of fertilization by measuring root growth into microsites spiked with specific nutrients (Cuevas and Medina 1988). Using this method, ingrowth cores containing limiting nutrients represent nutrient hotspots and should therefore have higher root biomass than the surrounding soil (Raich et al. 1994).

A meta-analysis of root biomass responses to fertilization in 45 tropical montane and 52 lowland tropical forests showed that stand-level root production was enhanced by +N fertilization in tropical montane forests and by +P fertilization in lowland tropical forests, and the addition of +NP had a similar effect in both systems (Yuan and Chen 2012). Nonetheless, decreased root biomass has been observed in response to fertilization with +K and +NK in Panama (Wright et al. 2011), +P in Costa Rica (Gower 1987), +N in China (Zhu et al. 2013; Mo et al. 2008) and there were variable responses in root biomass and turnover in response to +N or +P at different sites in Hawai'i (Ostertag 2001).

Similarly, ingrowth core studies demonstrate increased root growth into cores supplemented with +N or +NP in montane forests (Stewart 2000; Graefe et al. 2010), whereas root proliferation into ingrowth cores has been observed in response to +N, +P, +K, +NP, +PK and +Ca fertilization in various lowland tropical forests (Cuevas and Medina 1988; Graefe et al. 2010). These results should be treated with caution because ingrowth cores are often filled with plant growth media made from expanded clays, which represent a source of cations such as K, Ca, or Mg (Raich et al. 1994) and have absorption sites that can interact with added ions (Stewart 2000). In addition, root proliferation into ingrowth cores could represent a response to greater instant availability of inorganic nutrients compared to the surrounding soil, rather than a clear indicator of nutrient limitation.

These contrasting and sometimes contradictory results on the nutrient limitation of above- and belowground productivity at the ecosystem level highlight a number of considerations for interpreting fertilization experiments. Importantly, stand-level responses to a sudden increase in nutrient availability are unlikely to be directly comparable to biomass distribution along natural fertility gradients because adaptation of plants to initial soil fertility affects ecosystem responses to fertilization (Ostertag 2001). Further, the life stage and life history strategies of individual plant species determine biomass allocation and internal demand for nutrients to a large extent. Consequently, several nutrient amendment experiments show highly variable responses of different tree species (Alvarez-Clare et al. 2013; Villagra et al. 2013) and size classes of trees (Wright et al. 2011; Alvarez-Clare et al. 2013). Hence, the interplay of many distinct site- and species characteristics influence the responses of highly diverse tropical forests to nutrient amendments.

Life-History Strategies and Adaptation to Multiple Limiting Resources

A large number of experiments have measured seedling responses to nutrient amendments, which can be conducted on a small scale under controlled conditions. Studies using multiple species have observed highly variable responses to nutrient amendments; although the vast majority of species increased biomass in response to nutrient addition, a much smaller proportion increased relative growth rates (Lawrence 2003). In general, light-demanding species are more likely to increase growth and/or biomass in response to nutrient additions, whereas a larger number of shade-tolerant species increase foliar N and P concentrations (Lawrence 2003; Cai et al. 2008; Tripathi and Raghubanshi 2014). These patterns are fairly clear for pot experiments, whereas field studies with transplanted or naturally occurring seedlings have shown fewer or smaller growth and biomass responses to fertilization (Denslow et al. 1987; Turner et al. 1993). These differences among species and types of experiments highlight the importance of considering other limiting resources and their interactions with nutrient availability.

Light limitation in the understorey—Plants adapted to low-resource environments often have low potential for resource acquisition, invest heavily in defense and storage, and grow slowly even when resources are increased (e.g. Huante et al. 1995). For seedlings growing in the understorey of tropical forests, light availability can be more important than nutrient availability. Adaptation to low light levels often includes greater allocation to leaves, smaller root biomass and low relative growth rates (Cai et al. 2008). Slow-growing, shade-tolerant species have low nutrient requirements when light is limiting (Burslem et al. 1996), so they may not exhibit a strong response to nutrient amendments during the lifetime of an experimental study (Dalling and Tanner 1995). In addition, seedlings grown in low-light conditions invest primarily in increasing leaf area and leaf longevity while reducing biomass allocation to roots; this can preclude a rapid or strong growth response to a sudden increase in nutrient availability (Gunatilleke et al. 1997). Due consideration of species-specific responses to light conditions is also important for designing pot-based studies and interpreting their results: whereas some shade-tolerant understorey species can exhibit a strong positive growth response to nutrient amendments when light limitation is removed (Burslem et al. 1995), others may become photo-inhibited under high light conditions (Fetcher et al. 1996).

Changes in growth or biomass in response to nutrient addition are often minimal or completely absent when seedlings are grown under low-light conditions; instead a strong increase of nutrient concentrations in foliage (Campo and Dirzo 2003; Lawrence 2003) and other plant parts (Raaimakers and Lambers 1996) is observed. Nutrient uptake in excess of requirement is regarded as 'luxury consumption' (e.g. Ostertag 2010; Tripathi and Raghubanshi 2014) but these nutrient stores can enable rapid growth once plants are no longer constrained by light availability, for example when a new gap is created by a treefall (Raaimakers and Lambers 1996). Tropical tree seedlings growing in the understorey are able to respond to very brief increases in light levels such as sunflecks, so higher foliar concentrations of N, P and K in particular could allow understorey plants to maximize photosynthesis even when increased light availability is very sporadic (Pasquini and Santiago 2012). These trade-offs between nutrient-use strategies and light availability can determine competitive outcomes along gap-understorey gradients (Cai et al. 2008), because nutrient storage under low light provides an advantage when the light limitation is removed, whereas fast growth rates are beneficial for competition under high light (Raaimakers and Lambers 1996).

Water stress—Many lowland tropical forests experience periods of low rainfall or drought each year, and there are multiple lines of evidence for important interactions between water and nutrient availability. The relative mobility of different nutrients and the activity of extracellular enzymes vary strongly with soil water content, which for example affects N mineralization rates and the diffusion of nutrients to root surfaces (Cavelier et al. 2000; Cernusak et al. 2010). Adaptation to drought stress can also include greater biomass allocation belowground, which could make plants more responsive to nutrient additions when water availability is low or once drought conditions are alleviated. Hence, total root biomass and root biomass allocation would only decrease in response to increased nutrient supply if the water supply were adequate (Hall et al. 2003). Despite this, few experiments report responses of tropical trees or seedlings to nutrient amendments under drought stress (but see Hall et al. 2003; Burslem et al. 1996).

Nutrient addition can affect the drought resistance of trees by modifying their hydraulic architecture. Rapid growth in response to fertilization was thought to increase the risk of drought-induced embolism as a consequence of lower wood density and larger total leaf surface area, which would result in larger transport vessels and higher rates of transpiration (Goldstein et al. 2013). Surprisingly, an experiment with six species of saplings showed the opposite: growth rates and resistance to drought-induced embolism increased in response to fertilization because changes in wood anatomy and wood density in response to increased leaf surface area and transpiration appear to have mitigated the risk of cavitation (Villagra et al. 2013). Shade-tolerant species in particular were able to increase growth in response to +N and +P fertilization without increasing their vulnerability to drought because they have lower specific leaf conductivity than light-demanding species (Villagra et al. 2013).

Fertilization can reduce transpiration rates in tropical tree seedlings (Winter et al. 2001). An experiment with different species of tree and liana seedlings showed that water use efficiency was positively related to foliar N and negatively related to foliar P concentrations (Cernusak et al. 2010). It is possible that increased water-use efficiency at higher foliar N concentrations decreases transpiration rates, and hence weakens the pressure gradient that transports solutes to root surfaces by mass flow, resulting in lower P uptake (Cernusak et al. 2010). These results are intriguing, because greater water-use efficiency at higher foliar N concentrations may help to explain why many species of tropical trees and seedlings exhibit luxury consumption and storage of N.

Species Interactions

Tropical tree communities are often strongly affiliated with soil type; particular species show strong local associations with certain soils because strong competition excludes species growing in non-optimal habitats (e.g. Russo et al. 2005). Aside from inter- and intraspecific competition for different resources, plant responses to altered nutrient supply can modify or be modified by herbivory and symbioses with mycorrhizal fungi or N-fixing bacteria.

Mycorrhizal associations—The interplay between soil nutrient availability and root symbioses is well established. In tropical forests, plants associated with ecto- and arbuscular mycorrhizal fungi are highly competitive for P (Högberg 1986), so it is particularly striking that mycorrhizal plants rarely respond to experimental additions of P (Denslow et al. 1987; Newbery et al. 2002; Burslem et al. 1995), although the results of some studies suggest that mycorrhizal species may be limited by K, Ca or Mg (Burslem et al. 1995, 1996; Hall et al. 2003).

Although fertilization with inorganic +N and +P can have a negative (Treseder and Vitousek 2001) or no effect on mycorrhizal colonization (Turner et al. 1993; Brearley et al. 2007), mycorrhizas can improve tropical seedling growth by accessing nutrients directly from decomposing litter (Hodge et al. 2001; Brearley et al. 2003). Arbuscular mycorrhizal colonization and growth has been associated with patches of nutrient-rich organic matter in tropical forests (St. John 1982); it is hence conceivable that mycorrhizas are better adapted to access nutrients in organic matter and nutrients added as inorganic fertilizers may not have the same effect (Brearley et al. 2003).

Legumes and N-fixation—Di-nitrogen (N_2) fixation by plants can constitute an important input of N to terrestrial ecosystems when N-availability is low but it is regarded as a 'costly' N-acquisition strategy to plants (Gutschick 1981). The high prevalence of potentially N-fixing leguminous trees in tropical forests, where N is not thought to be limiting, has therefore fueled scientific debate about the ecological and evolutionary advantages of N-fixation (see review by Hedin et al. 2009). N-fixation requires a sufficient supply of P and could therefore be constrained in lowland tropical forests (Vitousek and Howarth 1991; Batterman et al. 2013). Fertilization experiments have contributed evidence to support or refute various hypotheses about how trade-offs between N and P acquisition or investment may explain the abundance of N-fixing plants (henceforth: fixers) in lowland tropical forests. One such theory is that N-fixation occurs in response to low availability of soil N but is down-regulated when N is abundant (e.g. Hedin et al. 2009; Batterman et al. 2013), and experiments show that non-legumes respond more strongly to +N fertilization than legumes when available soil N is low (Tripathi and Raghubanshi 2014). Another theory postulates that N-fixers are able to invest additional N in the production of extracellular phosphatases to acquire P (Houlton et al. 2008; Baribault et al. 2012). However, experimental evidence suggests that plants cannot overcome severe P-limitation by investing N in enzyme production alone (Batterman et al. 2013) and even N-fixing mycorrhizal species can be poor competitors for P (Högberg 1986).

Herbivory—Herbivory can substantially affect the outcome of fertilization experiments. Leaves with higher nutrient concentrations and lower investment in secondary plant compounds or structural carbon are thought to be more susceptible to herbivore attack (Coley and Barone 1996). Consequently, there are trade-offs between increasing growth or photosynthetic capacity in response to fertilization and maintaining defenses against herbivory: firstly, photosynthetic capacity increases with foliar N concentrations (Evans 1989) but higher foliar N also make leaves more palatable to herbivores; secondly, rapid growth in response to fertilization may preclude high investment in chemical or structural defenses (Coley and Barone 1996).

Several experiments have noted that increased herbivory probably masked growth responses to +N fertilization (Andersen et al. 2010), as well as +P and +K (Santiago et al. 2012). Herbivore damage was particularly noticeable in pioneer vegetation (Campo and Dirzo 2003) and fast-growing light-demanding species (Villagra et al. 2013), which invest fewer resources in structural defenses, as well as legumes (Campo and Dirzo 2003) and species associated with more fertile soils (Andersen et al. 2010), which have higher leaf nutrient concentrations. Increased risk of herbivory may also exert selective pressure against luxury consumption of N (Ostertag 2010). This risk could be offset by greater investment in plant chemical defenses but to our knowledge, only a single study has measured increases in phenolic compounds with addition of specific nutrients and found no consistent patterns across light-demanding and shade tolerant species (Denslow et al. 1987).

Life Stages

We would expect large growth responses to fertilization in young forests due to the predominance of fast-growing pioneer vegetation and because tree growth during the years prior to canopy closure (when light availability is high) is very dependent on soil nutrient concentrations (Miller 1981). A study of 10-year and 60-year old stands of secondary tropical dry forest showed that growth rates and litter production were higher in the 10-year old forest compared to the 60-year old stand and greater increases in tree growth and litterfall were also measured in the young forest in response to fertilization (Campo and Vazquez-Yanes 2004).

Strong responses of secondary forest regrowth to nutrient amendments can also be attributed to low soil nutrient availability after land-use for pasture or agricultural crops (Davidson et al. 2004). Accordingly, the productivity of regenerating secondary tropical forests can increase substantially with fertilization: an 85 % increase in annual net primary productivity was observed in plots treated with a complete fertilizer during four years of forest reestablishment (Giardina et al. 2003) and the rates of tree biomass accumulation in a six-year old forest almost doubled after only three years of +N and +NP fertilization, although +P fertilization alone had little effect (Davidson et al. 2004). Similar results were obtained in young dry forest in Mexico, where trunk growth increased substantially after three years of +N or +P fertilization and litterfall increased in response to +NP (Campo and Vazquez-Yanes 2004).

By contrast, the effects of nutrient amendments in mature forests are harder to determine, as they are dominated by slow-growing, shade-tolerant species. Tree size influences individual- and stand-level responses to nutrient amendments because large trees are less likely to be light-limited than smaller trees in the subcanopy (Wright et al. 2011). Species-specific responses of mature tropical trees to nutrient amendments are also expected but this is difficult to test experimentally because of the high diversity of tropical forest trees and the relatively low densities of individuals of the same species. In addition, disturbance (e.g. gap formation) creates areas of forest at different stages of regeneration and as a result, nutrient requirements are likely to be patchy throughout the forest. Seedling experiments are thought to be useful to address this, because the regeneration phase is most likely to influence adult abundance and distribution (Grubb 1977). However, seedlings are subject to very different conditions and constraints than adult trees and hence their responses may not be representative of later life stages.

A direct comparison of tree and seedling responses to fertilization—We are not aware of any direct comparisons of the responses of seedlings and adult trees of the same species to fertilization treatments, but there are legitimate biological reasons to assume that species' responses to nutrient additions will vary according to life stage. We used published data on foliar nutrient concentrations in naturally occurring seedlings and adult trees in a long-term experiment in Panama to examine the responses of three common tropical tree species to fertilization with +N, +P, and +NP (Santiago et al. 2012; Mayor et al. 2013, 2014). The three species included a small subcanopy tree *Heisteria concinna* (Standl.), a medium-sized pioneer tree *Alseis blackiana* (Hemsl.), and a large canopy tree *Tetragastris panamensis* (Engl. Kuntze); all three species have shade-tolerant seedlings that can persist in the understorey (Santiago et al. 2012).

First, we investigated the relationships between seedling and adult foliar nutrients in control plots. We then calculated the proportional response to experimental treatments as log response ratios (Eq. 1) to standardize effect size across species and groups:

$$\mathrm{RR} = \ln(\mathrm{Rx}/\mathrm{Rc}) \tag{1}$$

where Rx is the measured value of the response variable in a given treatment and Rc is the corresponding control value (Santiago and Goldstein, this volume); a response ratio of zero indicates no change in response to a treatment, whereas values greater than or less than zero represent positive and negative responses, respectively (Hedges et al. 1999). The effects of fertilization treatment, species and life stage were determined using linear mixed-effects models in R version 3.1.3. (nlme package; Pinheiro et al. 2015; Development Core Team R 2014) with block as a random effect. Significance of each term was determined by comparing nested models using likelihood ratio tests and AICs to check for model improvement (Pinheiro and Bates 2000).

In unfertilized plots, foliar N and N:P ratios were higher in adults than in seedlings (Fig. 1). Individuals of *Alseis* had the highest foliar concentrations of both nutrients and *Tetragastris* had the lowest. Foliar P concentrations varied little among species but were higher in seedlings than in adults, especially in individuals of *Tetragastris* (Fig. 1).

Although there was no significant overall effect of fertilization with +N, +P or +NP on foliar N concentrations, the response of *Heisteria* seedlings was more positive and more variable than that of adult trees, whereas the other two species showed no notable response. In contrast, foliar P significantly increased in +P and +NP treatments (Fig. 2). Although the interaction terms were not significant in the

Fig. 1 Boxplots of foliar N and P concentrations of adult trees (*dark shading*) and seedlings (*light shading*) of three common tree species in the control plots of a fertilization experiment in lowland tropical forest in Panama, Central America; species are *Alseis blackiana*, *Heisteria concinna* and *Tetragastris Panamensis*

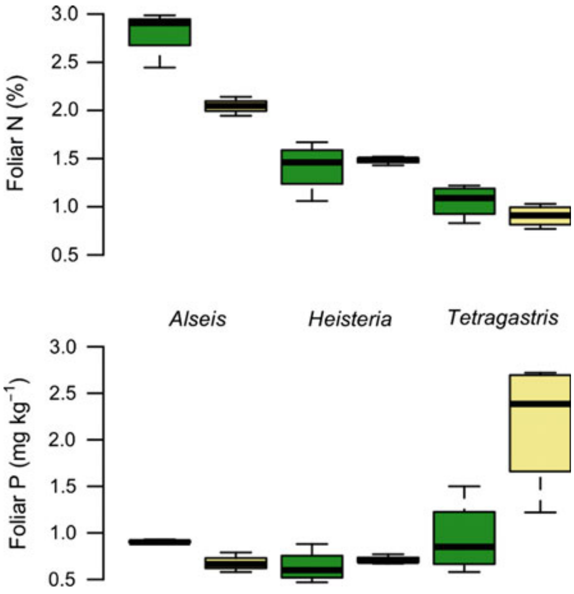
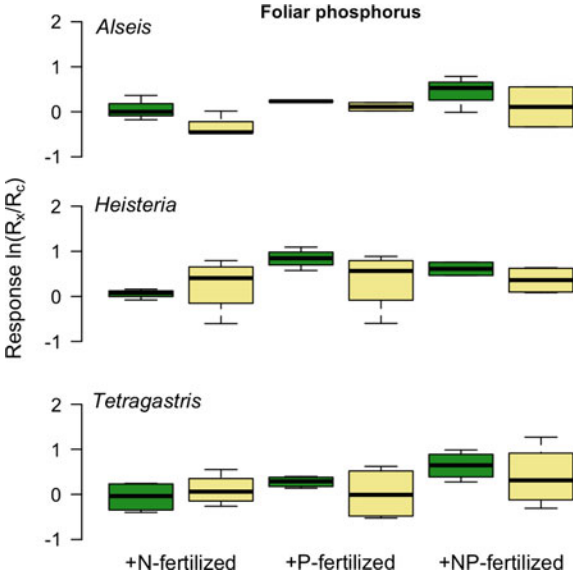
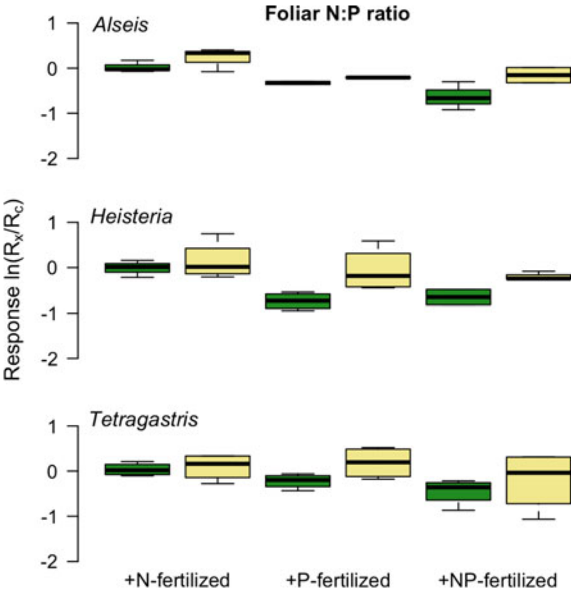


Fig. 2 Boxplots of foliar P concentrations of adult trees (*dark shading*) and seedlings (*light shading*) of three common tree species in a fertilization experiment in lowland tropical forest in Panama, Central America, where +N, +P and +NP are treatments fertilized with nitrogen, phosphorus or both nutrients, respectively; species names are as given in Fig. 1



models, the response to fertilization differed slightly among species and life stages: foliar P varied more amongst seedlings than adult trees and individuals of *Heisteria* displayed the strongest response to fertilization (Fig. 2), whereas foliar N:P ratios tended to decrease in response to +P and +NP fertilization and the fertilization effect was slightly lower in seedlings than in adult trees, especially in individuals of *Heisteria* (Fig. 3).

Fig. 3 Boxplots of foliar NP concentrations of adult trees (*dark shading*) and seedlings (*light shading*) of three common tree species in a fertilization experiment in lowland tropical forest in Panama, Central America, where +N, +P and +NP are treatments fertilized with nitrogen, phosphorus or both nutrients, respectively; species names are as given in Fig. 1



We demonstrate here that the responses of plants to nutrient amendments also vary with life stage, at least for these three common tropical tree species. Overall, seedling responses to a given fertilization treatment were more variable, which suggests stronger constraints on seedling nutrient uptake and storage, e.g. because of light limitation (see Sect. Light limitation in the understorey), distinct internal demands for nutrients, less developed root networks, or because seedlings are outcompeted by adults (Tanner and Barberis 2007). The foliar nutrient concentrations of adult trees used in our analysis were from canopy leaves, which were fully exposed to sunlight (Mayor et al. 2014), whereas the seedlings experienced light levels of only *c.* 1 % in the understorey (E.J. Sayer, unpublished data). This alone could account for the large differences between adult trees and seedlings. However, it is noteworthy that *Heisteria* displayed the greatest fertilization responses and the largest differences between seedlings and adult trees, even though subcanopy trees are often strongly light-limited. This suggests that distinct nutrient demands at different life stages and by functionally different species may also play a role in determining foliar nutrient concentrations and the balance of carbon and nutrients.

Litter Manipulation Experiments

Litter manipulation treatments involve the regular removal or addition of the litter standing crop and fine litterfall (leaves, fruits, flowers and small branches) to disrupt or enhance the natural forest nutrient cycle (Sayer 2006). Unlike fertilization experiments, litter manipulation studies do not aim to identify limiting nutrient elements but instead investigate the importance of nutrient cycling via organic matter (Sayer et al. 2012) and are accordingly discussed separately here. It is important to note that litter manipulation treatments affect several important soil properties, such as soil water content, soil temperature, and habitat space for decomposer organisms (reviewed in Sayer 2006). Furthermore, many of the previously described constraints and interactions affecting plant responses to nutrient amendments will also apply to litter manipulation studies.

Although litter addition can also be regarded as a nutrient addition treatment, two important features distinguish it from fertilization: (1) litter addition treatments supply multiple nutrients in approximate stoichiometric balance, and (2) nutrients are added in combination with organic carbon. This second point is important, because the forest is adapted to cycling nutrients from organic matter and the slow release of many nutrients from decomposing litter minimizes losses from the system (Qualls et al. 1991; Sayer et al. 2012). Litter removal treatments have no parallel in fertilization studies because they effectively disrupt the forests' natural nutrient cycle. This disruption allows us to identify different nutrient cycling strategies. For instance, rapid decreases in the concentrations of N in soil and leaves in response to litter removal could suggest that decomposing organic matter is the principal source of N for plant growth (Sayer and Tanner 2010). On the other hand, it also indicates an inefficient N-cycle, characterized by a lack of mechanisms to mitigate large losses from the system, such as through retranslocation of nutrients before leaf abscission.

Although there are now a number of litter manipulation experiments across the tropics, most have focused on seedling establishment, soil biogeochemistry or decomposition processes. The few experiments investigating tree responses or ecosystem productivity have demonstrated rapid responses to litter addition treatments, including increased stem growth of individual tree species (Villalobos-Vega et al. 2011; see also Sect. The effects of litter manipulation on plant growth.), increased litterfall (Wood et al. 2009; Sayer and Tanner 2010) and changes in foliar nutrient concentrations or nutrient return in litterfall (Tutua et al. 2008; Wood et al. 2009; Sayer and Tanner 2010). Litter removal treatments have had little effect on productivity, possibly because tropical forest adaptation to infertile soils includes efficient nutrient retention mechanisms. Nonetheless, litter removal affected the cycling of N and/or K in most experiments with at least four years of treatments (Tutua et al. 2008; Vasconcelos et al. 2008; Sayer and Tanner 2010), demonstrating the key role of organic matter in minimizing losses of the more mobile nutrient elements.

The effects of litter manipulation on plant growth—Tropical tree seedling responses to litter manipulation have mostly focused on germination, establishment and survival in the field. Litter addition influences seedling establishment by forming a physical barrier and providing a favorable habitat and microclimate for pathogens and herbivores (Sayer 2006), so it is hard to evaluate the effect of litter-derived nutrients on seedling growth in these experiments. Nevertheless, a greenhouse experiment showed that litter addition enhanced seedling growth and biomass via direct uptake of nutrients by mycorrhizal fungi (Brearley et al. 2003).

Few litter manipulation studies to date are sufficiently long-term to assess the effects of treatments on the growth of mature tropical trees (but see Villalobos-Vega et al. 2011). There was no discernable effect of litter manipulation on stand-level tree growth after 4 years of treatments in a lowland tropical forest in Panama (Sayer and Tanner 2010), so we used additional data from the same experiment to explore the individual growth responses of four common tree species to six years of litter removal (L−) and litter addition (L+) treatments. The focal species were *Heisteria concinna* (Standl.) and *Tetragastris panamensis* (Engl. Kuntze), as described in Sect. The effects of litter manipulation on plant growth, and *Simarouba amara* (Aubl.), a fast-growing tree associated with forest gaps, and *Virola sebifera* (Aubl.), a shade-tolerant canopy tree. Experimental treatments began in 2003 and changes in diameter at breast height (dbh) were recorded using dendrometers from 2004 to 2009; all stems had a dbh between 10 and 40 cm at the start of measurements. We produced a linear mixed effects model with relative growth rate as the response variable, treatment and species as fixed effects, and plot and year as random effects. We used the same model simplification approach as described in Sect. 5.1. and the model with the best fit included species, treatment and their interaction term.

Species responded very differently to the treatments. Growth rates of *Simarouba* and *Virola* were highest in the L+ and lowest in the L− plots, and this was most marked in later years (Fig. 4), which suggests that these species have increased growth in response to the nutrients added with the litter. In contrast, the highest growth rates of *Tetragastris* and *Heisteria* were observed in L− treatments and the lowest in control plots (Fig. 4); these counterintuitive results could indicate that these shade-tolerant species are better competitors for fluctuating resources under disturbed conditions.

Our analyses are restricted to these four species because they were sufficiently common in the study forest. Nonetheless, these findings demonstrate non-uniform responses among species to litter and nutrient addition, which perhaps reflect the complexities of life history traits and competitive interactions that occur in diverse, mixed-aged natural forests.

Comparing litter manipulation and inorganic fertilization experiments—The only formal comparison of litter manipulation and fertilization treatments in tropical forest to date suggests that there are substantial differences in the way nutrients are cycled, depending on whether they are added as inorganic fertilizers or in organic material (Sayer et al. 2012). In particular, the dynamics of the most mobile macronutrients N and K differed substantially between experiments at the same study site, even though the fertilization and litter treatments added or removed similar amounts of these nutrients each year. The L+ treatment resulted in much greater availability of inorganic N in the soil and higher N concentrations in litterfall compared to +N fertilization, whereas K concentrations in litterfall decreased more in the L− treatments than they increased with +K fertilization (Sayer et al. 2012). Although the P added with litter in the L+ treatment was only *c*. 12 % of the amount added in the +P-fertilization treatments, most of the P added as fertilizer remained in the soil (*c*. 81 %; Yavitt et al. 2011), whereas increased litterfall in the

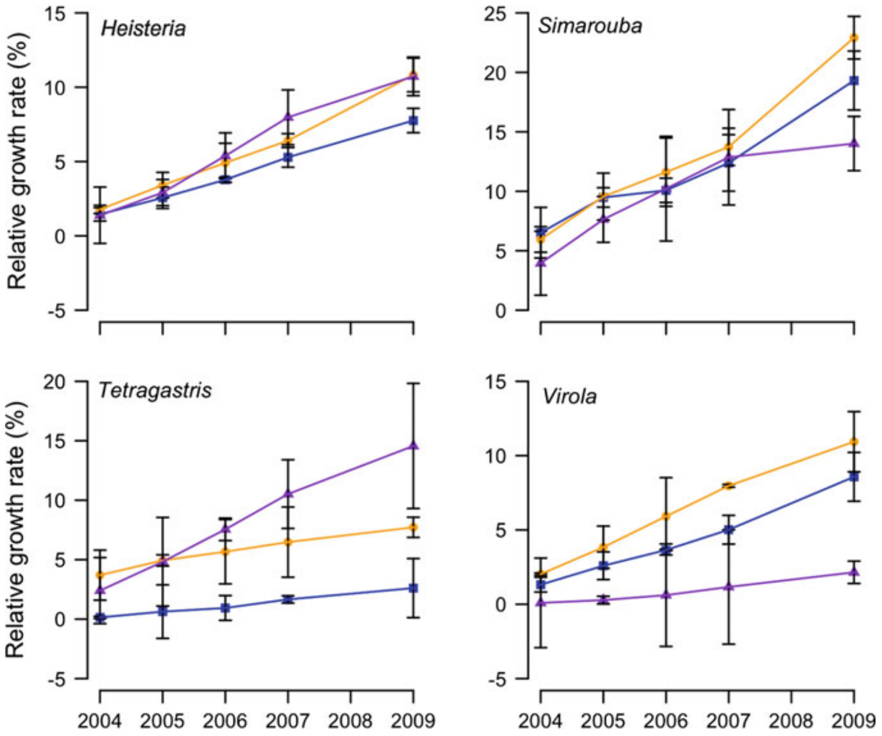


Fig. 4 Relative growth of three common tree species in a litter manipulation experiment in lowland tropical forest in Panama, Central America, showing means and standard errors for $n = 5$ per treatment and species; square symbols denote controls, circles denote litter removal and triangles denote litter addition; species are *Heisteria concinna, Simarouba amara, Tetragastris panamensis* and *Virola sebifera*

L+ treatment accounted for *c*. 85 % of the P added with litter (Sayer and Tanner 2010; Sayer et al. 2012).

Changes in root biomass distribution were also revealing: whereas root biomass in the uppermost soil horizons decreased in +K and +N fertilized plots (Wright et al. 2011; Yavitt et al. 2011), the distribution of fine roots in L+ plots shifted towards the litter layer and soil surface, probably to take advantage of the greater concentration of nutrients in the forest floor (Sayer 2006). Direct uptake of different nutrients by roots and mycorrhizal hyphae from decomposing litter has been demonstrated clearly by experiments using labeled substrates (Stark and Jordan 1978; Brearley et al. 2003) and a large proportion of the nutrients required for growth may be taken up directly from organic matter on the forest floor (Herrera et al. 1978). Compounds in litter leachate can also increase the availability of nutrients to plants, by limiting sorption of P to clay minerals (Schreeg et al. 2013). Collectively, these results suggest that decomposing litter constitutes an important source of nutrients for plant growth that needs to be considered in studies of nutrient cycling and limitation in tropical forests.

Experimental Limitations

We have demonstrated that differences in life history strategies, species-specific responses to light conditions, water availability, competition, and mutualistic associations need to be taken into account when interpreting the responses of plants to nutrient amendments. The topics we have addressed in this chapter also help us pinpoint the limitations of fertilizer experiments in tropical forests. To explain some discrepancies between pot- and field-based studies, we also need to consider specific ‘pot effects’, the differences in the mobility of nutrient elements, and the balance and timing of nutrient inputs.

Pot size effects—Although it is certainly possible to use pot experiments to infer plant performance in the field, the influence of pot size is a well-known issue in greenhouse studies. The size of the pot not only determines the amount of water and nutrients available to plants, but the available rooting volume often decides the duration of the study. The ‘pot-size effect’ is particularly important for fertilization experiments because the different relative mobilities of nitrate and phosphate ions cause a shift from P- to N-limitation during the course of the study, which is determined by the ratio between the soil volume and the length of absorptive roots (Cornforth 1968; Burslem et al. 1995). The highly mobile nitrate ion is delivered to the root surface by diffusion or water flow (Ostertag 2010), whereas the relative immobility of phosphate ions requires roots to forage for P (Yavitt et al. 2011). Consequently, P is more likely to be limiting at the start of a study when root biomass is low, and will become increasingly available as roots grow and access more of the soil in the pot. In contrast, most of the N in the soil is available to plants at the start of the study and it becomes progressively more limiting during the experiment as soil N reserves are depleted. The combination of pot size effects and restricted rooting space could also explain why many fertilization experiments with potted seedlings have not observed the expected changes in plant root:shoot ratios in response to nutrient additions.

Balance and timing of nutrient additions—Differences in the mobility and uptake of nutrient elements also present a problem for field experiments. Substantial losses of mobile elements can occur as soon as supply exceeds demand, even for a short period of time (Vitousek et al. 2010). When added as fertilizer, a large proportion of N in particular can be lost from the system through gas emissions or leaching, rather than taken up by plants (Sayer et al. 2012). Substantial losses of N have been measured in long-term fertilization experiments in montane and lowland tropical forests (Hall and Matson 2003; Koehler et al. 2009; Corre et al. 2010) and as supply continues to exceed demand, the system becomes increasingly ‘leaky’ (Koehler et al. 2009). In contrast, phosphate is not only immobile in the soil but is also easily sorbed to clay minerals. Hence, many fertilizer experiments often apply large amounts of inorganic P to saturate binding sites and increase the availability of P to plants (Ostertag 2010; Wright et al. 2011). These changes in the ratios of different nutrients can substantially influence the forest nutrient cycle and outcome of an experiment.

Biological stoichiometry is the balance of energy and nutrient elements in living systems. The stoichiometry of C:N:P in particular plays a critical role in a large number of ecosystem properties and processes (Elser et al. 2000 and references therein). Plant growth rates are thought to be related to the balance of N and P, because fast-growing organisms require more P to support protein synthesis relative to N content (termed 'the growth rate hypothesis'; Elser et al. 2000; Matzek and Vitousek 2009). In addition, the decomposition of organic matter is strongly constrained by the stoichiometric requirements of decomposer organisms, which in turn influence the dynamics of carbon and nutrients (Manzoni et al. 2010).

The C:N:P ratios of plant tissues are at least partly determined by physiological constraints and adaptation to nutrient limitation, resulting in a distinct C:N:P ratio within a given forest ecosystem (McGroddy et al. 2004); pulses of fertilizer application or large inputs of specific nutrients not only upset this balance but also alter the timing of nutrient availability, which may be a critical mechanism for maintaining productivity in nutrient-poor tropical forests (Lodge et al. 1994). The potential effects of altering the timing and balance of nutrient inputs is summed up nicely by Newbery et al. (2002): "Forests… are complex, long-lived and highly interconnected systems in which short-term adjustment responses and time lags are to be expected. Adding large quantities of fertilizer to such a presumably near-equilibrium system (in terms of nutrient cycling) is tantamount to a major disturbance."

Conclusions

This chapter contributes to the growing body of evidence for multiple nutrient limitations in tropical forests by demonstrating that plant nutrient demands, and hence response to fertilization, are strongly influenced by life history strategy, life stage, water stress, light availability, mutualistic associations, competition and herbivory, all of which are site- and species-specific.

The interpretation of nutrient amendment experiments also requires due consideration of how different nutrients are transported, stored and cycled. Differential soil availability and internal demand for nutrients by plants can translate into distinct uptake strategies for each nutrient (Ostertag 2001), whereas cost-benefit trade-offs largely determine luxury consumption and storage. The dissimilarities in the biogeochemistry of N and P, combined with plant life-history strategies and adaptation to soil nutrient status could even mean that 'limitation' and 'availability' are qualitatively different for N and P (Harrington et al. 2001; Ostertag 2010).

Plants require at least 17 mineral elements throughout their life cycle (Watanabe et al. 2007) and several fertilizer experiments and physiological studies have demonstrated the importance of other nutrients besides N and P in tropical forest productivity, in particular the macronutrients K and Mg (e.g. Burslem et al. 1995, 1996; Hall et al. 2003; Wright et al. 2011; Santiago et al. 2012). Our understanding of other macro- and micronutrients in tropical ecosystem processes is much less well developed, even though their respective roles in plant physiology and enzyme production are clear. Tropical soils can contain critically low concentrations of many micronutrients (Sobrado 2013) but we lack the experiments to evaluate how this affects tropical forest growth and ecosystem dynamics.

Finally, organic matter plays a crucial role in tropical nutrient cycling, which is underestimated by studies applying inorganic fertilizers and measuring responses in the mineral soil. Aside from being a direct source of nutrients for plant growth, the forest floor helps retain highly mobile elements. Indeed, mineral soil reserves may contribute less than 10 % to a forest's annual N cycle and less than 20 % to annual P cycling (Attiwill and Adams 1993), so nutrients in litter and organic matter may represent a better measure of site fertility than stocks in the mineral soil (Vitousek and Sanford 1986; Tanner et al. 1998).

The accumulation and balance of energy and nutrients in plants underpins the productivity and diversity of ecosystems (Grime 2001). In tropical forests, the high plant diversity and heterogeneity of the ecosystem make it difficult to assess nutrient limitation of tropical forest productivity but fertilizer experiments have nevertheless taught us some valuable lessons about tropical forest nutrient cycling and forest functioning.

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