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REVIEW

Nutrient limitation of eco-physiological processes in tropical trees

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Abstract
Key Message **Tropical forests play a disproportionately large role in the global climate system, yet the extent to which nutrients limit the potential for tropical trees to increase carbon gain as atmospheric carbon dioxide rises is unknown.**
Abstract This review focuses on what is known about tropical tree responses to experimental nutrient addition and how such information is critical for developing a more complete picture of the ability of tropical forest to respond to a changing world. Most of our knowledge of nutrient limitation of eco-physiological processes in tropical trees is derived from stand-scale nutrient addition experiments, in which physiological or growth responses signify limitation by that element. Our knowledge is further supplemented by fertilization studies of individual plants in pots. There is emerging evidence that fine root biomass decreases and maximum photosynthetic rates, water transport capacity and plant growth in tropical trees increase with nutrient addition, but the magnitude of response depends upon the successional status of the species, the size of the individual, light availability and the element in question. The sheer variation in responses of tropical trees to nutrient addition calls for a more complete evaluation across tropical environments.

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Introduction

Tropical forests harbor the greatest biodiversity, productivity and terrestrial carbon stocks of any biome and thus play a disproportionately large role in the global climate system (Beer et al. 2010; Saatchi et al. 2011). Thus, tropical forest responses to environmental change and subsequent feedbacks to the global climate system are likely to be large. One critical gap in our knowledge is the extent to which nutrients limit the concentration-carbon feedback, the ability of tropical trees to increase carbon gain as atmospheric CO_2 rises (Bonan and Levis 2010). In fact, modeling studies suggest that nutrient availability exerts a strong effect on gradients in productivity across the Amazon Basin, especially with regards to phosphorus (Mercado et al. 2011). More recent simulations of the resilience of tropical rainforests to CO_2-induced climate change further suggest that the largest uncertainties in how tropical forests might alter carbon stocks in response to climate change and atmospheric composition are associated with plant physiological responses (Huntingford et al. 2013). Therefore, tropical trees have the potential to drive ecosystem responses to environmental change, but what are their limitations? The literature is conflicting with some studies showing growth-nutrient relationships but others suggesting that additional factors limit growth, such as light. To address these and other questions, a growing number of recent studies specifically analyze physiological responses of tropical trees to nutrient addition (Bucci et al. 2006; Lovelock et al. 2006; Pasquini and Santiago 2012). This

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review focuses on what is known about tropical tree responses to nutrients and how such information is critical for developing a more complete picture of the ability of tropical forest to respond to a changing world.

Nutrient limitation is usually determined through nutrient addition experiments in which responses such as increased rates of physiological processes or growth relative to control treatments are interpreted as limitation by that nutrient. Otherwise, when nutrients are added and there is no response, the interpretation is that the added nutrient was not limiting (Vitousek 2004). The most comprehensive tropical nutrient addition experiments have occurred as stand-level fertilization with nitrogen (N), phosphorus (P), and/or potassium (K) in large (up to 40 × 40 m) plots (Tanner et al. 1992; Vitousek et al. 1993; Mirmanto et al. 1999; Newbery et al. 2002; Campo and Vázquez-Yanes 2004; Davidson et al. 2004; Lu et al. 2010; Wright et al. 2011; Álvarez-Clare et al. 2013; Fisher et al. 2013). These large experiments are especially valuable because they allow researchers to evaluate nutrient limitation at scales ranging from leaf-level physiology to whole-tree growth, as well as ecosystem-scale processes such as litterfall and nutrient cycling. Thus, in many cases, stand-level fertilization studies provide exactly the kind of information needed to determine how tropical forests will respond to environmental change. Other approaches to manipulating nutrient availability in tropical trees include litter removal and addition experiments (Sayer and Tanner 2010) or removal of vegetation to increase nutrient availability of target individuals. Although such manipulations of nutrient access do not directly reveal the identity of the key limiting element, in combination with foliar nutrient responses, some information on the relative importance of individual elements can be distilled (Lewis and Tanner 2000; Barberis and Tanner 2005). When fertilizer is added, researchers must ensure that responses are due to nutrients and not to other plant-soil interactions, such as changes in soil pH with N addition. At smaller scales, fertilizer has also been applied directly to individual plants in the field (e.g. Yavitt and Wright 2008), or in pots (Burslem 1996; Gunatilleke et al. 1997; Lawrence 2003; Cai et al. 2008). In small-scale fertilization experiments it is especially important to consider that roots can become pot-bound, and roots in the field can extend beyond the zone of nutrient addition. It is therefore useful to consider aboveground and belowground responses of trees to nutrient additions.

Even without experimentally adding nutrients, researchers have gained substantial information on physiology and nutritional status by evaluating patterns across environmental gradients that vary in soil nutrient availability (Vitousek et al. 1992; Santiago et al. 2004; Santiago and Mulkey 2005; Baltzer et al. 2008; Fyllas et al. 2009). In such studies, by determining how foliar nutrients or other physiological aspects vary with soil type one can infer nutrient limitation of physiological process and gain a greater understanding of which traits are better represented under particular ecological circumstances. For example, as mean annual precipitation increases in lowland tropical forest in Panama, there is gradual species replacement of dry-season deciduous canopy tree species with evergreen species, suggesting that evergreenness provides an advantage in leached soils at wetter sites by reducing the nutrient costs of leaf replacement (Santiago et al. 2005). Studies across environmental gradients are appropriate for revealing ecological patterns, yet the effects of soil and climate are often confounded and it can be difficult to pinpoint which element is most limiting to physiological function. Studies using foliar ratios suffer from the same limitations. Foliar ratios of nitrogen-to-phosphorus (N:P) have been employed to assess relative nutrient limitation of N versus P using the guideline that N:P ratios below 12 signify N-limitation, ratios above 16 signify P-limitation and values between 12 and 16 reflect co-limitation by N and P (Aerts and Chapin 2000). One recent refinement of this technique in tropical trees shows that stem, root, and older leaf N:P are more responsive indicators of soil nutrient availability than new leaf N:P, because new leaves appear to act as nutrient reservoirs during active growth, allowing maintenance of optimal N:P ratios in recently produced, physiologically active leaves (Schreeg et al. 2014). Therefore, observational approaches to understand nutrient limitation are limited in power to pinpoint key elements, but remain useful for generating hypotheses and identifying important patterns that can be further tested experimentally.

Because of recent tropical tree mortality due to El Niño-type drought (Condit et al. 1995; Slik 2004; Phillips et al. 2010; Feeley et al. 2011), tropical forests are now in the spotlight with regard to climate change. Nutrient limitation appears to be a deficiency in our ability to predict tropical forest responses and feedbacks to global change, so it is now more critical than ever to understand the basis of tropical tree nutrient limitation. Are there general principles that operate in all tropical forests across all levels of plant morphological complexity that have been revealed by nutrient addition experiments? To address this question, this review focuses on examples of tropical trees subjected to nutrient addition experiments—the most scientifically sound method for determining which elements limit which physiological processes. Consequently, fertilization studies on temperate trees, which in some cases react similarly to tropical trees, are not considered. Furthermore, experiments with herbaceous, epiphytic, or other non-woody growth forms, which provide relatively small but important contributions to tropical forest productivity are also not considered. I focus specifically on organismal processes

rather than ecosystem processes whose responses to nutrients have been reviewed elsewhere (Vitousek 2004; Cleveland et al. 2011). Finally, this review is organized along increasing levels of plant morphological complexity, first addressing leaves and roots, the characteristic resource-absorbing organs of higher plants, then moving to shoots, including the supply-and-demand coordination between stem and leaf water transport, and finally addressing the whole plant scale, where nutrient-driven responses are relatively well studied.

Leaves and roots: nutrient limitation of resource-absorbing organs

One of the greatest expectations when adding nutrients to tropical trees is that photosynthetic capacity will increase. This expectation is based on the substantial increases in metabolically active elements in leaf tissue following alleviation of nutrient limitation (Cordell et al. 2001; Davidson et al. 2004; Laclau et al. 2009; Ostertag 2010; Wright et al. 2011; Pasquini and Santiago 2012; Santiago et al. 2012; Fisher et al. 2013). Alleviation of N limitation through N addition is expected to stimulate photosynthetic capacity because the proteins of the Calvin cycle and thylakoids make up the majority of N in leaves (Evans 1989), whereas P and K are expected to increase the efficiency of photosynthetic biochemistry (Evans and Sorger 1966; Marschner 1995). Therefore, N, P and K all have the potential to limit photosynthesis in tropical trees.

One landmark study on photosynthetic responses to alleviation of nutrient addition through stand-level fertilization addressed the effects of N and P addition on the canopy tree *Metrosideros polymorpha* at two sites in Hawaiian montane forest, one whose ecosystem productivity is N-limited and one whose ecosystem productivity is P-limited (Vitousek et al. 1993; Herbert and Fownes 1995). Photosynthetic measurements were undertaken to determine whether leaf scale photosynthetic rate was nutrient limited by the same elements as ecosystem productivity. At the N-limited site there was no change in foliar N concentration or maximum rates of net photosynthetic CO_2 assimilation (A_{max}; μmol of CO_2 per meter-squared of leaf area per second), but leaf life span decreased leading to reduced integrated photosynthetic nutrient-use efficiency. At the P-limited site foliar P concentration and A_{max}, increased with no change in leaf life span, also leading to reduced integrated photosynthetic nutrient-use efficiency (Cordell et al. 2001). These results highlight the importance of substrate in determining how nutrients limit physiological processes and emphasize that not all elements limit physiological processes in the same way (Pasquini and Santiago 2012). In an intertidal mangrove substrate, A_{max} in *Rhizophora mangle* increased in response to alleviation of P-limitation, but not in response to alleviation of N-limitation (Lovelock et al. 2006). On a denuded soil substrate following a landslide in montane forest in Puerto Rico, A_{max} of *Cecropia schreberiana* (pioneer tree) increased with N addition, but *Palicourea riparia* (gap and understory shrub), and *Manilkara bidentata* (nonpioneer canopy tree) were unaffected (Fetcher et al. 1996). Further examples of nutrient-driven stimulation of leaf-level physiology from pot studies or experimental common gardens include increases in A_{max} in *Cedrela odorata*, *Croton urucurana* and *Cariniana legalis* in response to combined N–P–K–Ca treatments (Carswell et al. 2000; de Oliveira et al. 2012), an increase in A_{max} in *Ficus insipida* in response to a combined N–P–K treatment (Cernusak et al. 2007), and increased A_{max} in response to N addition in one light-demanding tree species and one shade-tolerant liana species, but not in two light-demanding liana species (Cai et al. 2008). Thus, nutrient limitation of photosynthetic capacity in tropical trees is not uncommon, but the nature of limitation depends on the element in question, its availability in the environment and the successional status of the species.

The minimum light availability under which plants respond to nutrient availability varies substantially among species (Coomes and Grubb 2000), but some pot-grown tropical rainforest tree species increase growth in shade of <1 % daylight (Burslem 1996), indicating the possibility of nutrient limitation, even in highly-shaded conditions. In a stand-level factorial nutrient addition experiment in Panama, understory seedlings of *Alseis blackiana* increase A_{max} with N addition, and stomatal conductance with P and K addition, under light conditions ranging from <1 to 6.7 % canopy openness (Pasquini and Santiago 2012). In an experiment with a combined N–P–K nutrient treatment the understory in Sabah, Malaysia, seedlings of *Dryobalanops lanceolata* and *Shorea johorensis* increased photosynthetic induction time with nutrient addition, whereas only *S. johorensis* increased A_{max} with nutrient addition (Bungard et al. 2002). In upland rainforest in Queensland, Australia, seedlings of *Flindersia brayleyana*, an Australian tropical rainforest tree species with broad tolerance to sun and shade, increase A_{max} and the light level at which photosynthesis saturates, in response to a combined macro- and micro-nutrient addition treatment (Thompson et al. 1988). In a later pot study on four species from Queensland rainforests, nutrient addition caused an increase in A_{max} in seedlings of two out of three shade-tolerant tree species and one shade-intolerant tree species in low (30 μmol m^{-2} s^{-1}) light (Thompson et al. 1992). Furthermore, combined macro- and micro-nutrient addition treatment in low (25–35 μmol m^{-2} s^{-1}) light causes an increase in A_{max} in seedlings of two West African tree species, with the pioneer species, *Nauclea diderrichii* showing a greater response than the shade-tolerant species *Entandrophragma angolense* (Riddoch et al. 1991). Finally, two out of three understory species showed increasing A_{max} with N addition

in a subtropical forest in Dinghushan, China (Lu et al. 2007). Thus, there is growing evidence that even in low light, nutrients have the potential to limit photosynthetic capacity, consistent with the idea that plant allocation to carbon gain reflects total resource availability (Field 1991).

In contrast to leaves, resource acquisition by roots in response to nutrients has received less attention. Nonetheless, striking patterns exist across soil types. For example, across secondary forests in Costa Rica, fine root biomass is negatively correlated with soil fertility, mainly with regards to Mg, N and P (Powers and Pérez-Aviles 2013). In Borneo, fine root biomass, length and area growth are greater in poorer soils, especially in response to local supplies of N, P and K availability (Kochsiek et al. 2013). Furthermore, across tropical forests in Brazil, Costa Rica, Panama and Peru, root mass and length are negatively correlated with soil N and P, but arbuscular mycorrhizal fungi are not related to nutrients, root properties or aboveground biomass (Powers et al. 2005). The relationship between mycorrhizal fungi and soil nutrient availability is dynamic and complex. In one case, seedlings of *Clusia minor* and *Clusia multiflora* from P-limited montane forests in Miranda, Venezuela, produce greater root and shoot biomass, leaf area and height when inoculated with arbuscular mycorrhizal fungi than when grown with P fertilizer (Caceres and Cuenca 2006). In another example, mycorrhizal formation on seedlings of *D. lanceolata* increased with combined addition of N, P and K in a nursery in Sarawak, Malaysia (Irino et al. 2004). Experimental studies have taught us that fine root biomass decreases with nutrient addition, especially with K, in lowland tropical forest in Panama (Wright et al. 2011; Yavitt et al. 2011). Yet the most comprehensive experiment on the effects of nutrient availability on resource acquisition by roots is the study in Hawaiian montane forest, in which N addition increased root standing stock and extracellular phosphatase activity, and P addition reduced phosphatase activity, mycorrhizal colonization, root P uptake capacity, and increased root turnover rates (Ostertag 2001; Treseder and Vitousek 2001). The responses of roots to nutrient amendment is consistent with the idea that investment in acquisition of a nutrient is greatest when that nutrient is limiting to growth and when limitation is alleviated, plants allocate less resources to acquire previously limiting nutrients.

Stems: nutrient limitation of xylem hydraulic processes

A consistent water supply by stems is necessary to support photosynthetic activity of leaves, raising the question of whether tropical trees increase water transport capacity in coordination with greater photosynthetic capacity when nutrient limitation is alleviated. Increasing the supply of water to photosynthesizing leaves implies changes in wood anatomical properties such as xylem vessel diameter that lead to enhanced water transport capacity. Studies on the responses of tropical tree water relations parameters to nutrient addition are beginning to emerge. For example, in subtropical trees in Iguazú National Park, Argentina, stem-specific hydraulic conductivity (K_S; water transport capacity normalized per sapwood or stem cross-sectional area) and leaf area-specific hydraulic conductivity (K_L; water transport capacity normalized per distal leaf area) increased in two of six species, and decreased in one of six species, with three species showing no significant response to combined addition of N and P (Villagra et al. 2013). Furthermore, in an intertidal mangrove substrate, K_S in *R. mangle* increased in response to alleviation of P-limitation, but not in response to alleviation of N-limitation (Lovelock et al. 2006). In the seasonally dry Brazilian Cerrado, trees increased K_S, but K_L decreased because of increased leaf area per sapwood area (Bucci et al. 2006), indicating that changes in hydraulic architecture that accompany changes in water transport capacity can alter responses of K_L.

One of the major trade-offs in plant hydraulic strategies is the negative interspecific relationship between resistance to drought-induced xylem cavitation (P_{50}; the xylem pressure at which 50 % of water transport capacity is lost) and maximum K_S (Pockman and Sperry 2000). Therefore, one of the largest surprises of plant hydraulic responses to alleviation of nutrient limitation is that the responses of K_S and P_{50} appear to be uncoupled (Bucci et al. 2006; Goldstein et al. 2013; Villagra et al. 2013). Both Bucci et al. (2006) and Villagra et al. (2013) report increased K_S and decreased P_{50} following nutrient addition. This is counterintuitive because in many woody species, the increased vessel size required to increase K_S is also thought to increase the vulnerability to cavitation, which would lead to an *increase* in P_{50}. Yet, these results indicating that alleviation of nutrient limitation increases water transport capacity and makes trees less vulnerable to drought-induced xylem cavitation defies the trade-off between safety and efficiency of water transport. These results suggest that other xylem processes such as ion-mediated regulation of xylem flow (Zwieniecki et al. 2001), or pit membrane traits (Goldstein et al. 2013), rather than vessel diameter also contribute to changes in P_{50} when nutrient limitation is alleviated. Beyond tropical trees, responses of P_{50} to alleviation of nutrient limitation are equivocal; in hybrid poplar, vulnerability to xylem cavitation increases with N addition, decreases with P addition, and shows no response to K addition (Harvey and van den Driessche 1997, 1999). Therefore, nutrient limitation of P_{50} depends on the

limiting element and species identity, and there is not enough available data to predict responses of further species.

Nutrient limitation of whole plant processes

Growth is one of the most commonly measured responses of tropical trees to nutrient addition experiments, and can be measured as changes in height, diameter, biomass and leaf count or area. In the earliest studies to document mature tropical tree growth responses to nutrient addition at the stand scale in natural forest, N + P addition roughly doubled diameter growth of trees in Venezuelan montane forest (Tanner et al. 1992). Further studies showed that N addition increased tree diameter growth in N-limited sites, whereas P addition increased tree diameter growth in P-limited sites in Hawaiian montane forest (Vitousek et al. 1993; Herbert and Fownes 1995). In mature lowland tropical forest, no diameter growth stimulation of trees was observed in Kalimantan, Indonesia in response to N and P additions (Mirmanto et al. 1999), nor in Korop, Cameroon in response to P addition (Newbery et al. 2002). In lowland secondary forest near Paragominas, Brazil, tree biomass increased significantly with N addition or N and P, but not with P alone (Davidson et al. 2004). In lowland tropical forest in Costa Rica, P addition, but not N addition, doubled stem diameter growth rates in small trees, but had no effect on intermediate or large trees (Álvarez-Clare et al. 2013). Finally, in the most comprehensive stand level nutrient addition experiment in lowland tropical forest, N and K addition caused increased diameter growth in small and intermediate trees, but not large trees in Gigante, Panama after 11 years of factorial N–P–K fertilization (Wright et al. 2011). The Wright et al. (2011) study is the only nutrient addition experiment in tropical forest to find a response to K, yet it is also the only study to explicitly test for it, suggesting that K limitation could be more widespread (Tripler et al. 2006). The Wright et al. (2011) study, along with the Álvarez-Clare et al. (2013) study, also shows that smaller trees responded more than large trees, consistent with forestry trials showing that small trees have large increases in growth with nutrient addition that essentially accelerate their trajectory on the growth curve, whereas intermediate and large trees immobilize more added nutrients, making their growth responses more muted and more difficult to quantify (Miller 1981).

Seedling growth responses to nutrient addition have also been evaluated. In field based studies, seedlings of *S. johorensis*, but not *D. lanceolata* increased plant biomass in response to combined N–P–K addition, in the understory in Sabah, Malaysia (Bungard et al. 2002), and seedlings of *F. brayleyana* increased plant biomass in medium and high light, but not in low light in response to combined nutrient treatments in Australian rainforest (Thompson et al. 1988). Naturally established seedlings of one liana and two tree seedlings also showed positive increases in height growth, but not leaf count, in response to combined nutrient additions on Barro Colorado Island, Panama (Yavitt and Wright 2008). In addition, naturally established seedlings of five species increased relative growth rate of height in response to K addition and with N and P in combination, whereas relative growth rate of leaf count only trended 8.5 % higher with K addition (Santiago et al. 2012). Finally, two studies now demonstrate that combined nutrient additions enhanced the growth response to elevated atmospheric CO_2 (Carswell et al. 2000; de Oliveira et al. 2012), offering support for nutrient limitation of the concentration-carbon feedback. Thus it is clear from the available data that the growth responses of field grown tropical tree seedlings to nutrient addition depend on light availability, the element that limits growth and local soil conditions.

Responses of tropical tree seedlings to nutrient addition have also been demonstrated in pots. Burslem et al. (1996) showed that height and leaf area growth of two out of three tree seedlings from tropical forest in Singapore were enhanced with addition of Mg and macronutrients. Similarly, Gunatilleke et al. (1997) showed that plant dry mass of seedlings in six out of eight tropical tree species from Sri Lanka increased with additions of Mg, P and Mg + P. Finally, in a meta analysis of tropical tree seedling responses to nutrient addition, 73 % of light-demanding species and 60 % of shade-tolerant species showed a positive growth response to added N or P (Lawrence 2003). The data of Lawrence (2003) also indicate that the magnitude of the growth response of light-demanding species to nutrient addition was more than twice that of shade-tolerant species, demonstrating how forest responses to changes in nutrient supply depend heavily on successional status.

Besides growth, another whole plant process that has been shown to respond to nutrients is water use, and especially, water-use efficiency, productivity per unit water transpired. Although interactions between nutrient availability and water-use efficiency have been studied since the seventeenth century (Woodward 1699), and are well studied in the herbaceous agricultural literature (Walker and Richards 1985; Lips et al. 1990; Lösch et al. 1992; Raven et al. 2004), the mechanistic bases of many of these interactions are poorly understood, and even less is known regarding these processes in field-grown wild plants. Raven et al. (2004) summarized the results of mostly agricultural studies evaluating the effects of fertilization on water-use efficiency, and found that only three out of 31 species showed no effect of relief of

nutrient deficiency on water-use efficiency, whereas the remaining 28 species showed an increase in water-use efficiency with nutrient addition. Twenty-one species were tested with N, five with K, three with P, and two with micronutrients. These compiled data overwhelmingly demonstrate an increase in water-use efficiency with increasing nutrient availability. There is recent evidence suggesting that the benefit of increased transpiration and therefore reduced water-use efficiency in nutrient deficient plants is the potential to increase nutrient uptake rates through mass flow (Cramer et al. 2008). In tropical trees, few data are available, but N addition increased leaf scale water-use efficiency and whole plant transpiration efficiency in pot-grown *F. insipida* saplings from Central Panama (Cernusak et al. 2007), suggesting that this response could be more widespread.

Finally, because plants store resources that can be later used for reproduction, nutrient supply has important consequences for reproductive yield in tropical trees. The relationship between nutrition and yield has long been established based on two of the most commonly cultivated subtropical tree species in the world, *Persea americana* (avocado) and *Citrus* × *sinensis* (Orange and other citrus) (Lynch et al. 1954; Reese and Koo 1975). Within these agricultural, subtropical tree crops, N, P and K have all been found to enhance yield in some circumstances, with both citrus and avocado generally being most responsive to N addition (Lynch et al. 1954; Reuveni et al. 1990; Nath and Mohan 1995; Lovatt 2001). In natural systems it is considerably more difficult to track the effects of nutrients on fruit yield and reproductive output, yet there is evidence that nutrient availability has the potential to limit overall reproductive output and the phenomenon of mass fruiting as well. In one study on the tropical tree *Ipomoea wolcottiana* from a Mexican dry forest, P addition increased the number of inflorescences and flowers by 200 %, and the initiation of fruits by 400 %, but there was no response for mature fruits (Parra-Tabla and Bullock 1998). In a detailed study of the dynamics of mineral nutrient storage for mast reproduction in the tropical emergent tree *Dryobalanops aromatica*, stored P accounted for 67.7 % of the total P requirements for reproduction, but stored N accounted for only 19.7 %, and contributions of stored potassium were negligible (Ichie and Nakagawa 2013). Finally, in the stand-level factorial fertilization experiment in Gigante, Panama, reproductive litterfall increased with P addition over the course of 11 years (Wright et al. 2011). Thus soil nutrient supply, as well as the accumulation of key elements in storage tissue, can be decisive factors in reproductive output and therefore fitness of tropical trees, especially on poor soils occurring in many locations in the tropics.

Summary

The results of nutrient addition studies in tropical trees suggest that most species converge on particular responses, yet there are also several processes, which have been shown to increase or decrease with nutrient addition (Fig. 1). Whereas not all elements are associated with all responses, N, P, K or combined nutrient treatments have been implicated in all of the responses outlined in Fig. 1. In the short term, increases in foliar nutrient concentration are often the first response documented, and are associated with increased A_{max}, and to a lesser degree increases in stomatal conductance (g_s) and transpiration (E), leading to an increase in water-use efficiency (WUE). In the long term, numerous other responses have been observed and are thought to support increased growth and yield.

Conclusions and future directions

Overall, the results of tropical tree responses to nutrients offer several important lessons for understanding the magnitude of nutrient limitation of tropical tree responses to environmental changes. First, multiple limiting nutrients appear to be the rule rather than the exception whenever experiments allow analysis by element. Whereas at one time, the multiple limiting nutrients hypothesis was juxtaposed against Liebig's Law of the minimum, in which only the most limiting element produces a response when added, it now appears that different physiological processes, such as A_{max} versus stomatal conductance, or different ecosystem compartments, such as tree size classes, can be limited by different elements.

Second, much of the available data on tropical tree responses to nutrient addition indicate that responses depend on the element in question, its availability in the environment and the successional status of the species. Not all elements promote physiological processes in the same way, thus the biochemical nature of nutrient limitation is highly dependent on the process and the chemistry of the metabolites involved. The greater propensity for early successional species to exploit increases in nutrient availability is also an important consideration, but leads to further questions. For example, do we expect forests that undergo N deposition to gradually shift community composition towards more early successional fast-growing species? If so, such differences in how species respond to nutrient addition may have important implications for the future of tropical forests, as disturbed, degraded, and fragmented tropical forests are dominated by species at the early successional side of the spectrum. Furthermore, availability of other resources can mediate the ability of

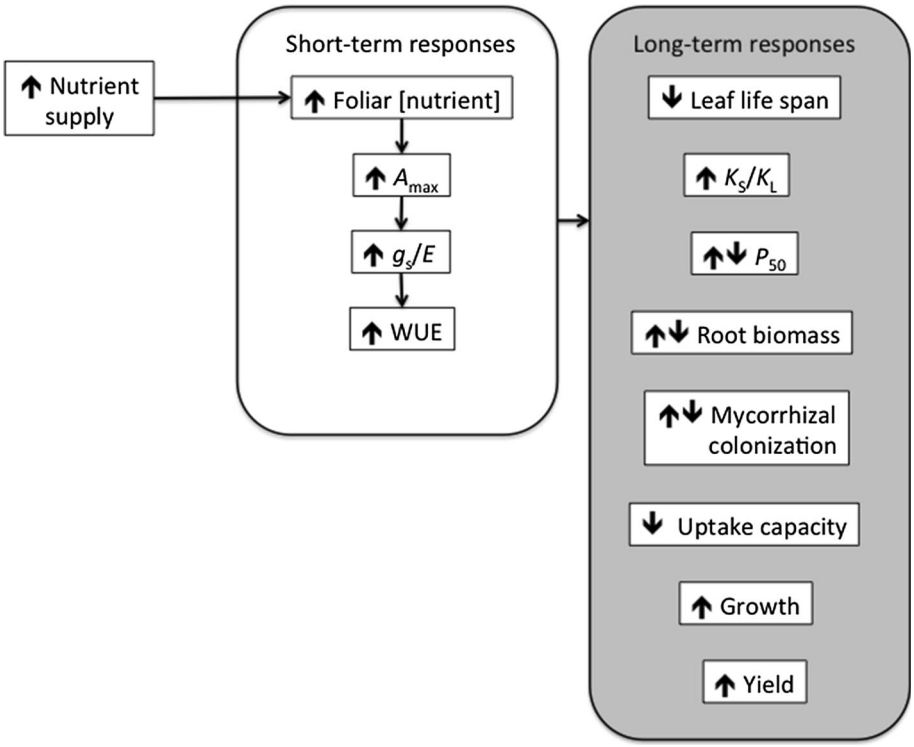

Fig. 1 Major tropical tree responses to increases in nutrient supply. These responses are grouped into short-term responses and long-term responses. Maximum photosynthetic rate (A_{max}), stomatal conductance (g_s), transpiration (E), water-use efficiency (WUE), stem-specific hydraulic conductivity (K_S), leaf area-specific hydraulic conductivity (K_L), xylem water potential at 50 % loss of hydraulic conductivity (P_{50})

plants to exploit increases in nutrient availability. For example, understory tree seedlings can show greater growth responses to nutrient addition with increased light availability (Thompson et al. 1988), as well as with increased water availability (Yavitt and Wright 2008). Less is known about how salinity in mangrove ecosystems or occasional frost in subtropical forests interacts with nutrient limitation.

Finally, whereas some results of tropical tree responses to nutrient addition appear to be context-specific, many patterns cut across study sites and elements. For example, reduced root biomass following nutrient addition is observed in a variety of sites, species and elements, and allows us to begin asking general questions, such as whether reduced root biomass could make plants more susceptible to climate change-type drought in the future. Ultimately researchers search for cross-cutting patterns that uncover fundamental mechanisms and allow predictions for other sites. In order to move towards this, it is imperative that researchers measure actual physiological processes to understand the mechanisms of the common ecosystem processes that are often measured in stand-level fertilization experiments. Furthermore, because physiological measurements can be detailed and time consuming, it is also vital that researchers find ways to evaluate the responses of many species in order to characterize the diversity of responses in tropical forests. Finally, the sheer variation in responses of tropical trees to nutrient addition calls for more studies in more places to capture the variation in tropical forests and to distinguish between unique natural history stories and fundamental mechanisms that shape the responses of all plants. Only through focused and intentional studies can we determine the limits of tropical trees to drive ecosystem responses to environmental change.

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Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

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