Chapter 4

Nutrient limitation in global forests: current status and future trends

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Introduction

Nutrients are essential regulators of plant growth and species composition in natural ecosystems (Chapin, 1980; Maathuis, 2009; Seabloom et al., 2021). Nutrients show distinct concentrations in vascular plants and accordingly are grouped into macronutrients (e.g., nitrogen [N], phosphorus [P], potassium, calcium, magnesium, and sulfur) with relatively high concentrations and micronutrients (e.g., boron, chlorine, copper, iron, manganese, molybdenum, and zinc) with relatively low concentrations (Broyer & Stout, 1959; Welch & Shuman, 1995). These elements keep specific ranges of concentrations and ratios (i.e., stoichiometric homeostasis) to sustain plant growth and function (Sterner & Elser, 2002), and these ranges usually vary with functional type, climate, and soil conditions (Augusto, Achat, Jonard, Vidal, & Ringeval, 2017; Han, Fang, Reich, Ian Woodward, & Wang, 2011). Among these essential nutrients, N and P are considered to most widely limit plant growth in natural ecosystems, while deficiencies of other nutrients only occur in specific conditions or on local scales (Du et al., 2020; Elser et al., 2007; LeBauer & Treseder, 2008; Vitousek & Howarth, 1991).

Nutrients keep cycling within and between the biotic and abiotic pools. Nitrogen and P are characterized by a gaseous cycle and sedimentary cycle, respectively, and are distinct by their sources and fates. In terrestrial ecosystems, external N comes from the biological N fixation of atmospheric N_2, atmospheric N deposition, and bedrock weathering, while N losses mainly occur via leaching and gaseous pathways (Galloway et al., 2004; Houlton, Morford, & Dahlgren, 2018). In contrast, P is primarily from parental material weathering, and a significant proportion of P becomes lost over time by physical processes, such as leaching and sedimentation (Vitousek, Porder, Houlton, & Chadwick, 2010). Moreover, N and P are both internally cycled via plant uptake, litter production, immobilization, and mineralization in ecosystems (Vitousek et al., 2010). Overall, nutrient cycling sustains the nutrient supply for plant growth and thus fuels ecosystem carbon cycling (Du and de Vries, 2018).

Nutrient cycling can be altered by global change drivers, such as climate warming, rising atmospheric CO_2 concentration, and changing atmospheric N deposition. For instance, warmer temperature generally increases biological N fixation (Houlton, Wang, Vitousek, & Field, 2008) and accelerates N mineralization (Bai et al., 2013). Atmospheric CO_2 enrichment likely stimulates biological N fixation in terrestrial ecosystems (Hungate, Dijkstra, Johnson, Hinkle, & Drake, 1999) and also increases plant nutrient demand via a CO_2 fertilization effect (Norby et al., 2005). Nitrogen deposition generally increases N mineralization but inhibits biological N fixation in terrestrial ecosystems (Cusack, Silver, & McDowell, 2009; DeLuca, Zackrisson, Gundale, & Nilsson, 2008; Lu et al., 2011). Moreover, climate warming and rising atmospheric CO_2 concentrations may alter chemical weathering processes and thus change P release from parental materials (Kump, Brantley, & Arthur, 2000). As a result, these global change drivers are altering nutrient supplies for terrestrial plants and thus affecting the ecosystem structure and function over time.

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An increasing number of studies have suggested that N and P play a key role in constraining global terrestrial productivity and carbon sequestration in response to rising CO_2 concentrations and climate warming (e.g., Terrer et al., 2019; Wang et al., 2020; Wieder, Cleveland, Smith, & Todd-Brown, 2015). Therefore, understanding the spatial heterogeneity in N and P limitation and the future trends can provide insights into the future dynamics of forests and other terrestrial biomes. Based on current literature, here we (1) review the concept and mechanisms of nutrient limitation and how vascular plants adapt to nutrient limitation, (2) summarize the direct and indirect approaches to diagnose nutrient limitation, (3) synthesize the current understanding of global patterns of N and P limitation, and (4) discuss the future trends in N and P limitation in boreal, temperate, and tropical forests. This chapter focuses on forest biomes because they play a crucial role in global terrestrial carbon sinks and ecosystem services (Pan et al., 2011; Taye et al., 2021). Nutrients other than N and P are not considered in this chapter because they are not likely to limit terrestrial plant growth globally.

The concept, mechanisms, and adaptation to nutrient limitation

The concept of nutrient limitation

The concept of nutrient limitation originates from Sprengel–Liebig's Law of the Minimum, a principle first developed in agricultural science by Carl Sprengel and later popularized by Justus von Liebig in the 1840s (Van der Ploeg, Böhm, & Kirkham, 1999). It states that the minimum resource (limiting factor) relative to the requirement limits crop yields. Sprengel–Liebig's Law of the Minimum predicts monolimitation of plant productivity by a single nutrient in agricultural monocultures. The yield of monoculture generally increases with the availability of a limiting nutrient until a certain threshold amount of nutrient supply is exceeded (Fig. 4.1A). Chapin, Vitousek, and Van Cleve (1986) expanded the concept of nutrient limitation in wild plant communities that consist of diverse species with distinct nutrient use strategies (Fig. 4.1B). In contrast to simplified crop systems, the magnitude of community-level nutrient limitation depends on the limiting strength weighted by each plant species.

Different from the conventional view that plants are generally limited by one nutrient at a time (Fig. 4.2A), increasing evidence suggests there is a smooth transition between limiting nutrients with shifting nutrient supply ratios (Ågren, Wetterstedt, & Billberger, 2012; Bracken et al., 2015; Elser et al., 2007; Harpole et al., 2011). For example, within a specific range of N:P supply ratios (e.g., r_1–r_2) (Fig. 4.2B), an increase in either nutrient will increase plant productivity. This leads to the concept of colimitation by multiple nutrients (Fig. 4.2B).When the N:P supply ratio deviates from this range ($<r_1$ or $>r_2$), it generally follows Sprengel–Liebig's Law of the Minimum, and a single nutrient limits plant growth ($<r_1$ for N limitation and $>r_2$ for P limitation) (Fig. 4.2B).

Mechanisms of nutrient limitation

Nutrient limitation occurs when nutrient supply is insufficient to support the nutrient demand to achieve the potential of net primary productivity. Generally, nutrient limitation frequently occurs due to limited external nutrient inputs, demand-independent nutrient losses, and multiple nutrient utilization barriers (Vitousek et al., 2010). Specifically, N limitation is often caused by low biological N fixation and N mineralization, both strongly constrained by low temperature, moisture, and/or soil pH (Vitousek et al., 2010). Nitrogen limitation can also be progressively intensified along with long-term N accumulation in plant biomass and litter during forest development (Johnson, 2006; Wardle, Walker, & Bardgett, 2004). Phosphorus limitation is generally associated with low P availability due to depleted soil P pools,

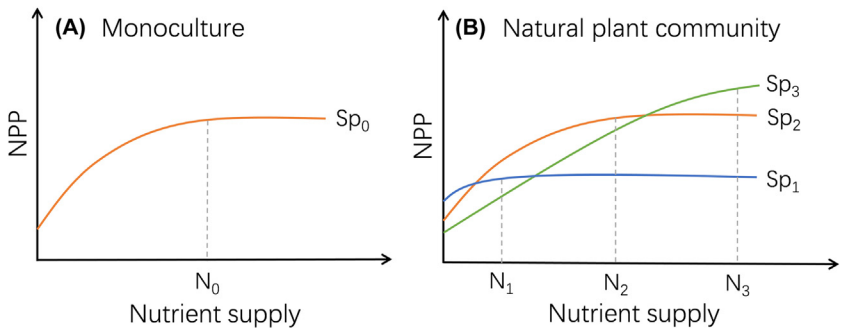

FIGURE 4.1 Plant growth response to nutrient supply in monoculture (A) and natural plant community (B). N_0, N_1, N_2, N_3, thresholds of nutrient supply for maximum NPP for different species; NPP, net primary productivity; Sp, species.

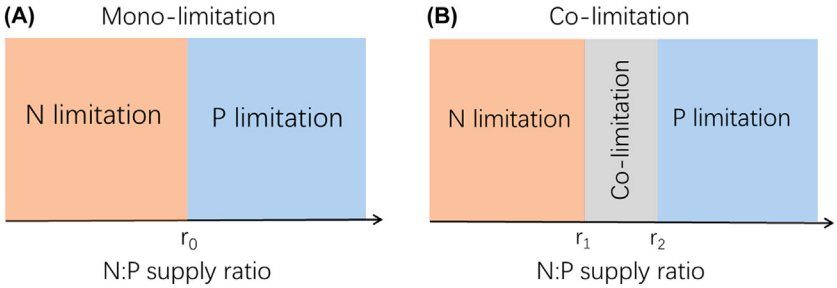

FIGURE 4.2 Shifts in N limitation toward P limitation with increasing ratios of N and P supplies in the diagrams of monolimitation (A) and colimitation (B). Note that r_0, r_1, and r_2 indicate certain thresholds of the N:P supply ratio for the shifts in nutrient limitation.

low-P parent materials, and accumulating biomass P pools (Vitousek et al., 2010). Moreover, anthropogenic enhancement of N deposition also likely leads to or strengthens P limitation in some regions (Crowley et al., 2012; Du et al., 2016), but it does not likely have a significant effect on a global scale (Du et al., 2020).

Plant adaptation to nutrient limitation

Plants have evolved strategies to adapt to low nutrient availability (Chapin, 1980). For instance, legumes establish a symbiotic relationship with nitrogen-fixing rhizobia, bacteria that convert atmospheric N_2 into ammonia, an inorganic form that can be directly utilized by host plants (Ferguson et al., 2019). Perennial plants can internally conserve nutrients for growth via resorbing a large proportion of nutrients from senescing leaves (Rennenberg & Schmidt, 2010). Moreover, plants can strengthen external nutrient uptake by increasing root biomass allocation, modifying root morphology, and/or maintaining mycorrhizal associations (Hodge, 2004). Mycorrhizal associations between roots and fungi (e.g., the ectomycorrhizas and the vesicular−arbuscular mycorrhizas) are common in infertile soil conditions. Plant nutrition can be improved directly by mycorrhizal fungi that take up and deliver nutrients or indirectly by ectoenzymes that provide host plants with the potential to access organic N and P forms (Marschner & Dell, 1994). Although these strategies help plants adapt to nutrient-poor conditions, the potential plant productivity is widely limited by nutrients in natural ecosystems because many of these strategies are at a considerable cost of carbohydrates.

Methodologies to assess nutrient limitation

Direct test via nutrient addition experiments

There are a variety of approaches to test nutrient limitation in natural ecosystems (Sullivan et al., 2014; Van Sundert et al., 2020). A straightforward method is to test the response of plant growth or net primary productivity via nutrient additions that are sufficient to saturate chemical and microbial immobilization processes and still meet plant nutrient requirements (Augusto et al., 2017; Chapin et al., 1986). If adding a specific nutrient stimulates the net primary productivity, the plant community is then recognized to be limited by that nutrient. The experimental approach gives the most accurate measurement of nutrient limitation, but it is costly and labor-intensive, especially when applied in forest ecosystems. A unique example of large-scale applications of this approach is the Nutrient Network (https://nutnet.org/), which consists of coordinated nutrient addition experiments across more than 130 grassland sites worldwide. Fay et al. (2015) conducted a large-scale analysis of nutrient limitation in grasslands based on this platform. Although regional networks of nutrient addition experiments exist in forest ecosystems (e.g., Du et al., 2013), a well-coordinated network is lacking in global forests.

Many studies have tried to assess the patterns of N and P limitation based on meta-analyses of nutrient addition experiments and have concluded that N and P limitation occurred globally in terrestrial ecosystems (Elser et al., 2007; Hou et al., 2020; LeBauer & Treseder, 2008). However, these studies are inconclusive, identifying different environmental factors as the main drivers of N and P limitation. This uncertainty is potentially attributable to combining nonisometric growth indicators (e.g., diameter at breast height, basal area, tree biomass, carbon storage, and net primary productivity) and/or using effect-size metrics not standardized by the level of nutrient addition (Du et al., 2020).

Indirect diagnosis via leaf nutrient stoichiometry

Direct nutrient limitation tests are time-consuming, labor-intensive, and costly, so indirect approaches are used frequently. For decades, the diagnostic analysis of leaf nutrients has been a common approach to understanding plant

nutritional status (Holford, 1968; Melsted, Motto, & Peck, 1969). Indirect approaches have been proposed to diagnose nutrient limitation based on the ecological stoichiometry theory. Mass ratios of leaf N and P have been used to indicate N and P limitation (Güsewell, 2004; Koerselman & Meuleman, 1996; Tessier & Raynal, 2003). Based on an analysis of the leaf N:P ratio in comparison with the results of nutrient addition experiments, Koerselman and Meuleman (1996) proposed the threshold leaf N:P ratios of 14:1 and 16:1 to indicate N (<14:1) and P limitation (>16:1), respectively. However, the threshold leaf N:P ratios have been found to vary across various ecosystems, and other ecologists have also proposed different thresholds (e.g., <10:1 for N limitation, >20:1 for P limitation) (Güsewell, 2004). Although this approach has been widely used in literature, an assessment of large datasets on leaf N:P thresholds and nutrient addition experiments indicates relatively significant uncertainties (Yan, Tian, Han, Tang, & Fang, 2017). Due to a lack of theoretical support for valid thresholds, the nutrient stoichiometry approach is unlikely to make a reliable assessment of nutrient limitation on regional and/or global scales.

Indirect diagnosis via the ratio of nutrient resorption efficiencies

Nutrient resorption from senescent leaves is one essential strategy for perennial plants to adapt to low nutrient availability. Leaf resorption efficiencies of N and P generally decline with increasing leaf concentrations of respective nutrients (Kobe, Lepczyk, & Iyer, 2005) and in response to respective nutrient fertilization (Yuan & Chen, 2015), implying a trade-off between leaf nutrient resorption and external nutrient availability. Some earlier studies tried to link leaf N and P resorption efficiencies to plant nutrient limitation (Han, Tang, Chen, & Fang, 2013; Reed, Townsend, Davidson, & Cleveland, 2012; Vergutz, Manzoni, Porporato, Novais, & Jackson, 2012), but a theoretical framework was still lacking.

Based on the stoichiometric homeostasis theory (Sterner & Elser, 2002) and Sprengel–Liebig's Law of the Minimum (Hooker, 1917), Du et al. (2020) proposed a new framework to test nutrient limitation based on the ratio of plant leaf N and P resorption efficiencies (Fig. 4.3). At an ecosystem scale, the ratio of average leaf N resorption efficiency (NRE) to P resorption efficiency (PRE) weighted by the leaf mass of all species was demonstrated a theoretical indicator of N (NRE/PRE >1) or P limitation (NRE/PRE <1) (see more details in Du et al., 2020). In their global analysis, they used the ratio of averaged NRE to average PRE of dominant species as an approximation because species-specific leaf mass is rarely reported together with NRE and PRE in literature.

The ecosystem-level indicator can be derived by measuring plant species composition and foliar resorption efficiencies of N and P (Fig. 4.4). It can be further validated by well-designed experiments using N and P fertilizers (Fig. 4.4). However, it is time-consuming to simultaneously measure species-specific nutrient resorption efficiencies and leaf mass in natural ecosystems that comprise of highly diverse plant species. An approximation is to use the ratio of averaged NRE to averaged PRE of the dominant species (Du et al., 2020). Overall, it provides an easy-to-use approach to assess N and P limitation in various ecosystems.

Current patterns of N and P limitation

General patterns of terrestrial N and P limitation

Du et al. (2020) assessed the global patterns of N and P limitation in terrestrial ecosystems based on the ratio of site-averaged leaf N and P resorption efficiencies of the dominant species. The results indicate a shift from relative P to N

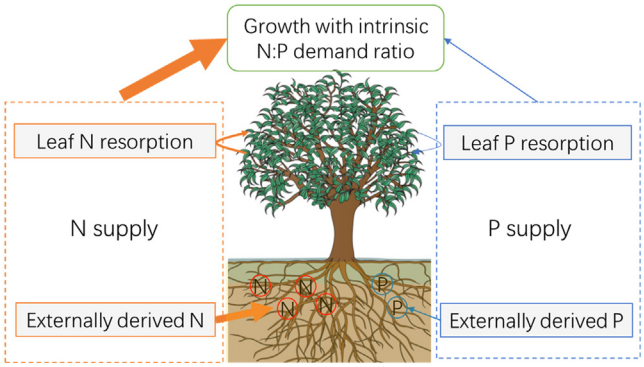

FIGURE 4.3 The scheme of internal and external supply of N and P for perennial plants.

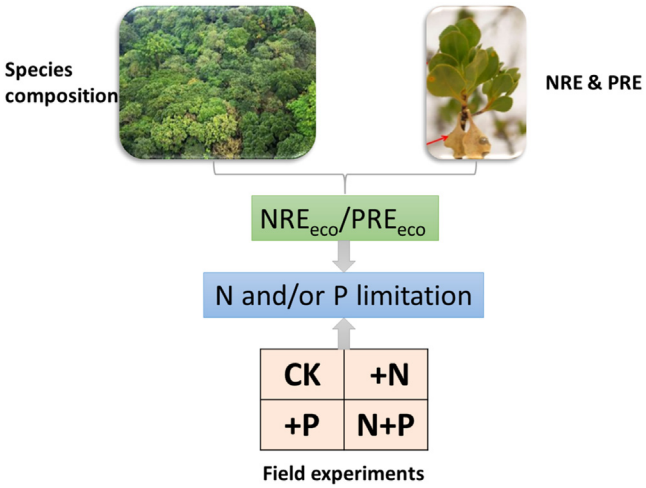

FIGURE 4.4 Combining paired field measurements and fertilization experiments to evaluate ecosystem nutrient limitation. NRE_{eco} and PRE_{eco} indicate ecosystem-level N and P resorption efficiencies, respectively.

limitation toward higher latitudes on a global scale and higher elevations on a regional (or local) scale. The poleward increase of N limitation is likely due to a decrease in biological N fixation and N mineralization toward higher latitudes (Deng et al., 2018; Houlton et al., 2008; Menge et al., 2017). However, the opposite trend of P limitation is likely shaped by a decrease in P sources from geologically young Arctic and boreal soils to old tropical soils with lower "weatherable" P and stronger P occlusion under acidic soil conditions (Vitousek et al., 2010; Walker & Syers, 1976). On a global scale, N deposition is an unimportant factor affecting the spatial patterns of N and P limitation (Du et al., 2020). Nitrogen deposition may, however, significantly impact N or P limitation at regional and local scales (Crowley et al., 2012).

In contrast to the conventional view that N limitation is prevailing in global terrestrial biomes (LeBauer & Treseder, 2008; Vitousek & Howarth, 1991), Du et al. (2020) revealed that P limitation dominated a larger natural terrestrial land area than N limitation did with 18% of Earth's land area (excluding cropland, urban, and glacial areas) being strongly limited by N alone. By comparison, 43% of Earth's land area is P-limited alone (Du et al., 2020). The remaining 39% of natural terrestrial land area could be colimited by N and P or weakly limited by either nutrient alone. These findings have provided a more quantitative view of N and P limitation in global terrestrial ecosystems that might help to understand current and future ecosystem responses to elevated CO_2 concentrations and climate change.

Nitrogen and P limitation in global forest biomes

On a global scale, N and P limitation shift across forest biomes. Specifically, N limitation occurs more frequently in boreal and temperate coniferous forests, while P limitation is more common in tropical, subtropical, temperate broadleaf, and temperate mixed forests (Fig. 4.5; Du et al., 2020). Within each forest biome, nutrient limitation also likely shifts in strength or type. Specifically, Du et al. (2020) estimated that P limitation dominated 91% of global tropical and subtropical forests on an area basis, while the other 9% was colimited by N and P or weakly limited by either nutrient alone. In temperate broadleaved and mixed forests, P and N limitation occurred in 30% and 2% of the biome area, respectively. In contrast, N limitation affected 35% of the temperate conifer forests, while P limitation occurred in 11% of the biome area. In boreal forests, N limitation occurred in 48% of the total area, while the other 52% was colimited by N and P or weakly limited by either nutrient alone (Du et al., 2020). Overall, N limitation occurs in an increasing fraction of the area from tropical to boreal forests, and P limitation shows an opposite trend.

Future trends of nutrient limitation in global forests

Future trends of global change drivers

Future changes in atmospheric CO_2 concentration and climate are key drivers of the shift in spatial patterns of terrestrial N and P limitation on a global scale. As driven by emissions from fossil fuel combustion and land-use changes, atmospheric CO_2 concentration has increased by approximately 50% since the Industrial Revolution and passed 410 ppm in 2020 (Friedlingstein et al., 2020; https://gml.noaa.gov/ccgg/trends/global.html). Atmospheric CO_2 concentration will

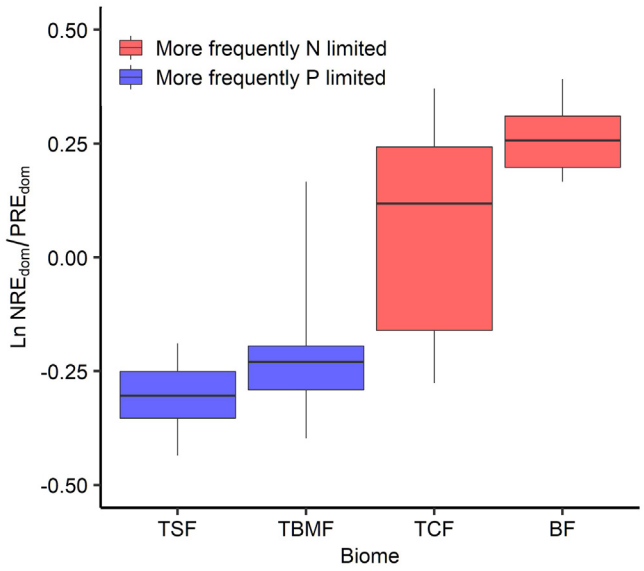

FIGURE 4.5 Prevailing nutrient limitation across global forest biomes. The boxplot shows the mean, 95th, 75th, 25th, and 5th percentiles of nutrient limitation strength (Ln-transformed $NRE_{dom}/PRE_{dom} < 0$ indicates P limitation; Ln-transformed $NRE_{dom}/PRE_{dom} > 0$ indicates N limitation) for 1×1 km pixels in each biome. NRE_{dom} and PRE_{dom} indicate N and P resorption efficiencies of dominant species, respectively. Abbreviations: BF, boreal forest; TBMF, temperate broadleaved and mixed forests; TCF, temperate conifer forests; TSF, tropical and subtropical forest. Data were from Du et al. (2020).

continue to increase unless the global carbon-neutral target is achieved. By the end of this century, atmospheric CO_2 concentration is projected to range from 446 ppm for the low-emission scenario (SSP1-2.6) to 1135 ppm for the highest-emission scenario (SSP5-8.5) (Meinshausen et al., 2020). Climate model projections show that the global mean surface temperature will increase by 2°C by 2100 (using a 1900 baseline) under the low-emission scenario (SSP1-2.6) and to 5°C using the highest-emission scenario (SSP5-8.5) (Ribes, Qasmi, & Gillett, 2021). Meanwhile, mean annual precipitation on land is projected to increase but with large spatial heterogeneity (Chen et al., 2020). In addition, N deposition, as a local and/or regional regulator of nutrient limitation (Du et al., 2016), will continue to show distinct trends across regions (Ackerman, Millet, & Chen, 2019), such as an increase in many developing countries and a decrease in developed countries due to the implementation of N emission reduction policies (Du, 2022).

Nitrogen and P limitation in future forests

Experimental results suggest that rising atmospheric CO_2 concentration generally stimulates terrestrial net primary productivity and consequently causes or aggravates nutrient limitation due to increasing nutrient demands for plant growth (Norby et al., 2005). Accordingly, assessments of long-term change in plant leaf N concentration and isotope ratio reveal regional and global N oligotrophication of terrestrial ecosystems (Craine et al., 2018; Groffman et al., 2018; Mason et al., 2022). Regional trend analyses of long-term monitoring datasets revealed an overall decrease in leaf N and P concentrations in European forests over recent decades (Jonard et al., 2015; Peñuelas et al., 2020). Based on plot-level trend analyses of leaf N:P ratios compared with threshold leaf N:P ratios for specific tree species, Du, van Doorn, and de Vries (2021) concluded that P limitation occurred in an increasing proportion of European forests during the past two decades. In contrast, only a minor proportion of the plots showed a shift toward N limitation, and this trend was most significant in plots with a more substantial decrease in N deposition (Du et al., 2021). Given the projected increasing levels of atmospheric CO_2 concentration in the future (Friedlingstein et al., 2020; Meinshausen et al., 2020), these recent trends of N and P limitation will likely continue to occur.

Climate is the most important factor affecting spatial patterns of N and P limitation on a global scale (Du et al., 2020). Specifically, there is a shift from relative N to P limitation for higher mean annual temperature and mean annual precipitation (Du et al., 2020). On a global scale, P limitation will likely be strengthened in tropical forests and P-limited temperate forests, while N limitation will likely be partially alleviated (e.g., in boreal forests) or shift toward P limitation (e.g., in some temperate forests) given the continuing climate warming and the projected increase of precipitation on land (Chen et al., 2020; Ribes et al., 2021). As joint driven by rising CO_2 concentrations and climate change, a recent assessment found a shift toward P limitation in European forests. This shift was more substantial in plots of broadleaf forests with higher mean annual temperatures (Du et al., 2021).

Based on the observational and experimental studies discussed above, future N and P limitation trends are predicted theoretically in global forest biomes (Fig. 4.6). In boreal and some N-limited temperate forests, N availability will likely

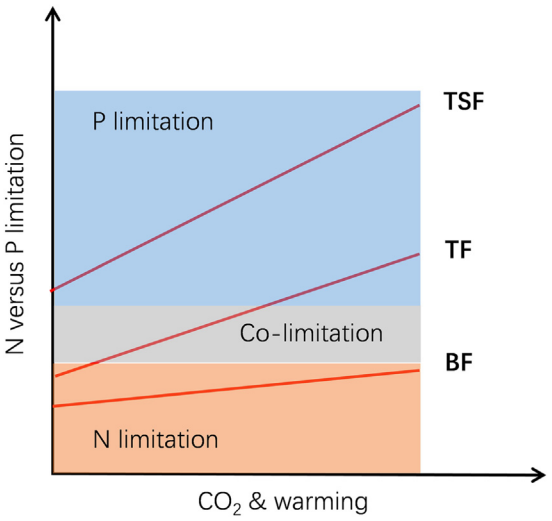

FIGURE 4.6 Future trends in N and P limitation in response to rising CO_2 and climate warming in global forest biomes. Abbreviations: BF, Boreal forest; TF, temperate forest; TSF, tropical and subtropical forest.

increase due to accelerated N mineralization and biological N fixation with global warming and rising atmospheric CO_2 concentration. The predicted increase in N availability may partially alleviate N limitation in these forests. However, unlike a significant N replenishment via biological N fixation over time, external P inputs mainly depend on parental material weathering (Vitousek et al., 2010). In tropical, subtropical, and some P-limited temperate forests, P limitation will be further aggravated due to increased P demand driven by CO_2 fertilization compared to limited external P inputs. As a result, N-limited forests will likely experience weaker N limitation or shift from N limitation to P limitation. In contrast, forests that are currently N and P colimited or P-limited will likely be subject to further P limitation. Overall, the area of P limitation in global forests will likely expand with a poleward shift in the boundary. In turn, the increase of P limitation in area and magnitude will likely constrain forest growth in response to the future rise of atmospheric CO_2 concentrations.

Conclusion

This chapter synthesized our current understanding of the spatiotemporal patterns of N and P limitation in global forest biomes. Generally, there is a shift from P limitation in tropical forests to N limitation in boreal forests. On a global scale, P limitation dominates a larger area than N limitation does. Forests currently N-limited may decrease in N limitation strength or shift towards P limitation. In contrast, forests that are currently N and P colimited or P-limited will likely experience further P limitation, resulting in an increasing area of P-limited forests given the continuing increase of atmospheric CO_2 concentration and climate warming. More observational, experimental, and modeling efforts are needed to better understand the consequences of changing nutrient status on the structure and function of future forests.

Acknowledgments

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