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REVIEW

Climate Warming Alters Nutrient Cycling and its Constraint on CO_2 Fertilization in Global Forests

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Abstract

Purpose of Review Climate warming affects both nutrient availability and plant nutrient requirements, with a potential alteration of nutrient limitation to the CO_2 fertilization effect on net primary productivity (NPP) and carbon (C) sinks, but the overall impact remains poorly understood. Based on a literature review, we synthesized the current understanding of climate warming-induced changes in (i) availability, (ii) demands, and (iii) limitation of the nutrients nitrogen (N) and phosphorus (P) in global forest biomes as well as (iv) how climate warming alters nutrient constraints on CO_2 fertilization.

Recent Findings Climate warming generally increases nutrient availability via accelerating nutrient cycling but this effect largely varies between different forest biomes, resulting in a considerable increase in N availability in temperate and boreal forests but a weak P availability increase in tropical forests due to a depleted soil P pool. Climate warming likely causes an increase of NPP and nutrient demands in thermal-limited boreal and temperate forests, but it can result in a reduction of growth and nutrient demand in forests with an exceedance of optimal growth temperatures (e.g. some of tropical forests) and/or warming-induced moisture deficiency. Overall, climate warming tends to alleviate N limitation in boreal and temperate forests to support NPP in response to rising CO_2 concentrations. In contrast, climate warming combined with CO_2 fertilization will likely strengthen P limitation in tropical forests.

Summary Warming-induced changes in nutrient limitation can lead to biome-specific responses of NPP to rising atmospheric CO_2 concentrations. Our review highlights the role of climate warming-induced changes in nutrient availability, demand, and limitation in constraining biogeochemical feedback to future CO_2 enrichment.

Keywords Nutrient availability · Nitrogen limitation · Phosphorus limitation · Nutrient limitation · Climate warming · Moisture deficiency · CO_2 fertilization

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Introduction

Global forests account for a major proportion of global land carbon (C) sinks and thus play a key role in the biogeochemical feedback to climate change [1]. Changes in future C sinks in global forests are largely driven by a CO_2 fertilization effect on net primary productivity (NPP), but the forecasted C sinks along with CO_2 enrichment remain controversial due to the potential constraint of nutrient limitation [2–4]. Especially the availability of the nutrients nitrogen (N) and phosphorus (P) widely limit plant growth in global terrestrial forests and thereby constrain the magnitude of NPP responses to rising CO_2 and climate warming [5–7]. Rapid climate warming has occurred in the past half-century and is projected to continue along with rising CO_2 concentrations [8]. Climate warming may significantly alter nutrient cycling and, thus, modify the nutrient constraint on future NPP and C sink capacity in response to future CO_2 enrichment (Fig. 1). However, the warming-mediated changes in nutrient availability, demand, and limitation as well as their effect on future C sinks in response to continuously rising CO_2 concentrations remain poorly understood.

Climate warming generally accelerates nutrient mineralization and consequently increases soil nutrient availability [9, 10]. Climate warming also stimulates NPP in regions with colder climates than the optimal temperature, thereby increasing nutrient requirements for faster plant growth. In contrast, climate warming may exert negative effects on forest growth attributable to enhanced thermal stress and water deficiency [11, 12]. Nutrient limitation, dependent on the balance of nutrient availability and plant nutrient requirements, may change in its strength and spatial distribution with climate warming, but such changes remain poorly understood in global forest biomes. Additionally, nutrient limitation varies across forest biomes and likely causes distinct constraints on future responses of NPP and C sinks to rising CO_2 concentrations [4, 5, 13]. Research efforts are therefore needed to gain a more in-depth understanding of the biome-specific effects of climate warming on nutrient limitation.

Covering one-third of the global land area, forests act as a large C sink (~ 3.5 Pg C yr^{-1}; [1]) that dominates global land C sinks and plays a key role in biogeochemical feedback to climate change. In this review, we synthesize literature to provide a perspective of shifting nutrient limitation in major forest biomes under climate warming, jointly determined by the changes in nutrient availability and nutrient demands by forests (Fig. 1). Furthermore, we discuss how the warming-induced changes in nutrient limitation affect the response of forest NPP and C sequestration to rising atmospheric CO_2 concentration across different forest biomes. Considering that N and P limitations are widespread in global terrestrial ecosystems [5], we limited our review to these primary and most essential nutrients for forest growth.

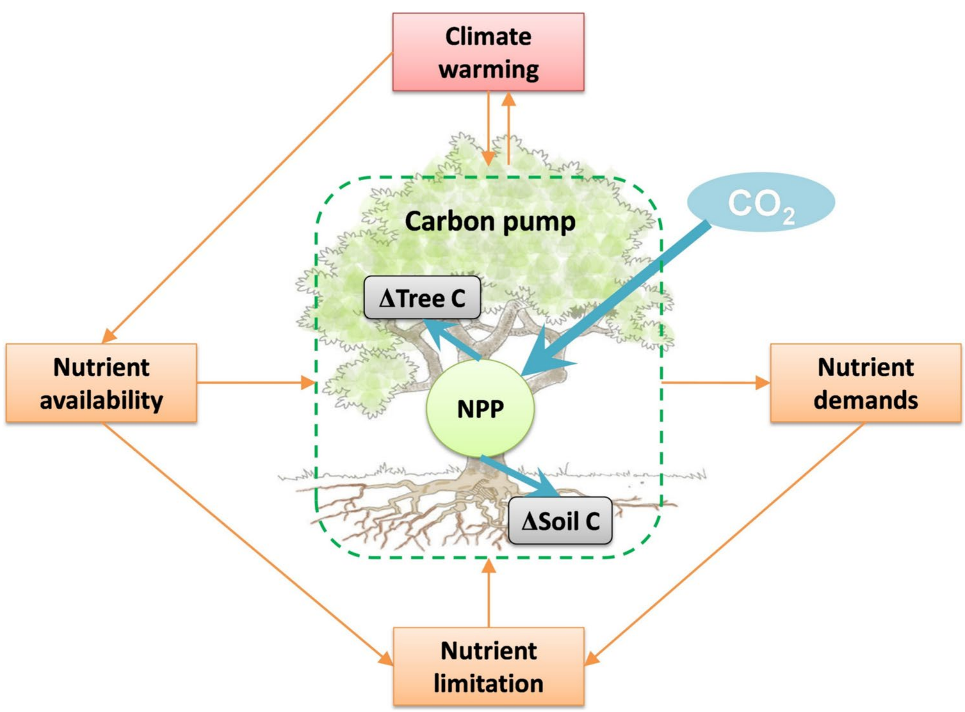

Fig. 1 A conceptual diagram summarizing the climate warming-induced changes in nutrient availability, demands and limitations and their potential effects on nutrient constraint on NPP and C sinks in response to CO_2 enrichment

Effects of Climate Warming on Nutrient Availability

Effects of Climate Warming on Nitrogen Availability

Available N in forest ecosystems comes from both external pathways (i.e., biological N fixation, N deposition, and weathering of N-containing bedrocks) and internal pathways (i.e., plant N resorption and soil mineralization) (Fig. 2a) [14–16]. Except for N deposition, climate warming can significantly alter four of these five pathways and, thus, change the amounts of soil available N for plant growth (Fig. 2b). Nitrogen deposition directly increases N availability in forest ecosystems and this effect is especially important in hotspot regions (e.g., eastern and southern China, Japan, Eastern U.S. and Europe) attributable to high levels of anthropogenic N emissions from agricultural activities and fossil fuel combustion [17–19]. The level of N deposition mainly depends on the amount of reactive N emissions, which are primarily determined by activities in the agricultural, industrial and transport sectors, although climate warming slightly enhances ammonia (NH_3) emissions [20].

Climate warming directly increases N availability via accelerating internal N cycling via microbial N mineralization and external N inputs via biological N fixation and bedrock weathering (Fig. 2b). Specifically, warmer temperature generally accelerates the decomposition of soil organic matter and, thus, increases N availability from soil N mineralization [9, 10, 21]. Based on climate-controlled chamber experiments using rhizobial and actinorhizal associated N-fixing plants from temperate and tropical biomes, Bytnerowicz et al. have recently found that biological N fixation respond nonlinearly to warmer temperatures with a thermal optimum range varying between 29 °C to 37 °C across simulated temperate and tropical climates [22]. Additionally, there is an acclimation of optimal temperatures for biological N fixation to growing temperatures especially for the tropical symbioses (i.e., higher optimal temperatures at higher growing temperatures) [22]. Given a target of global warming by ~ 1.5 or 2 °C above pre-industrial levels, future climate warming is thus projected to increase the rates of biological N fixation in most forest biomes where ambient temperatures are lower than corresponding thermal optimums (Fig. 2b) [22–24]. However, a hypothesized thermal optimum of 25 °C is currently used in many terrestrial biosphere models and this likely leads to biased predictions of future changes (i.e., a decline) in biological N fixation in tropical regions with ambient temperature (> 25 °C) above the optimum [22, 23].

Although this process has been ignored for a long time, the weathering of N-containing parental materials is found to be an important external N source, especially in regions where soils form from highly N-containing bedrock [14]. The rate of weathering can be accelerated under climate warming (Fig. 2b) and this acceleration generally results in an increase in new N inputs from N-containing bedrocks into ecosystems [25]. Furthermore, climate warming-induced acceleration of biological N fixing and bedrock weathering may further enhance N mineralization over time [26]. Overall, the warming-induced available N increment from N mineralization is likely stronger than that from biological N fixation and bedrock weathering (Fig. 2b). In contrast, empirical evidence suggests that plant N resorption decreases significantly with warmer temperatures (Fig. 2b), likely due to a tradeoff in response to increasing ecosystem N availability under climate warming [27–29].

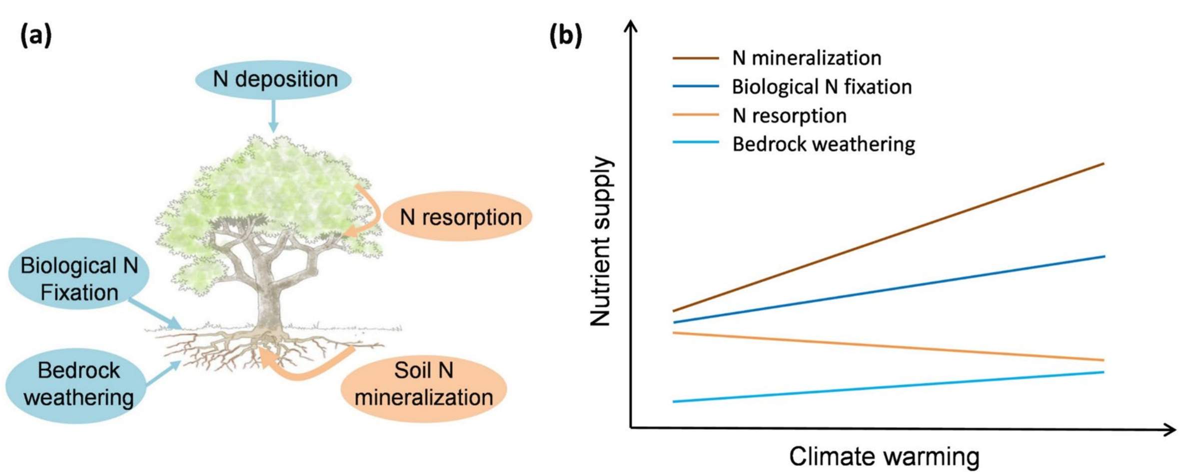

Fig. 2 External (biological N fixation, bedrock weathering, and N deposition) and recycled nitrogen (N) supply (soil N mineralization and plant N resorption) in forest ecosystems **a** and their potential responses to future climate warming **b**. See a more detailed description and relevant references in Section Effects of Climate Warming on Nitrogen Availability

Effects of Climate Warming on Phosphorus Availability

In contrast to N, other essential nutrients (e.g., P, K, Ca, Mg, and micronutrients) are mostly characterized by a sedimentary cycle in the absence of a stable gaseous form. These nutrients are externally supplied from bedrock weathering and atmospheric deposition and internally recycled via soil mineralization and plant resorption (Fig. 3a) [15, 30, 31]. Among these processes, climate warming can significantly alter the rates of bedrock weathering, soil mineralization and plant nutrient resorption except for atmospheric deposition (Fig. 3b).

Climate warming generally increases P availability by accelerating chemical weathering and thus P supply from soils [30, 32, 33] and enhancing soil P mineralization by an increase in decomposition rates and phosphatase enzyme activities [34]. Considering that weathering and mineralization depend on the amounts of mineral and organic P substrate, respectively, we expect that the stimulation of climate warming to additional P availability by bedrock weathering and soil P mineralization is likely weaker in tropical and subtropical forests than in temperate and boreal forests, due to highly weathered P-depleted soils [15]. Additionally, field studies also suggest that plant P resorption generally decreases with warmer temperatures as a tradeoff to accelerated P cycling (Fig. 3b) [35], while this negative effect of warmer temperatures on plant P resorption might be weak in tropical soils given a depletion in the P pool [15, 36].

Although most studies have been focused on N and P, the availability of other nutrients can also limit NPP in some cases. For example, potassium (K), calcium (Ca) and magnesium (Mg), all have been found to limit (to different extents) plant productivity in some terrestrial ecosystems and an acceleration of their cycling under climate warming likely increases the availability of these nutrients given a sufficient soil base cation nutrient pool [31, 37–39]. In contrast, soil K, Ca and Mg tend to deplete in humid and warm regions due to long-term leaching [38, 40] and, therefore, climate warming may have limited capacity to increase the availability of these nutrients in tropical regions. Future research efforts are needed to elucidate how the availability of nutrients, other than N and P, changes with climate warming and whether such changes will cause nutrient imbalance and shift in nutrient limitation to forest growth in the future.

Effects of Climate Warming on Plant Nutrient Demands

Direct Effects of Climate Warming on Plant Nutrient Demands

Climate warming can directly alter the rate of tree growth and thus change the requirements of forests for nutrients [10]. Plant nutrient demands may show an increase in accompany with a growth stimulation, a decrease in accompany with a growth decline or no change without a growth response to climate warming (Fig. 4). The effect of climate warming on tree growth largely depends on background temperature and water availability. Plant photosynthetic capacity and vegetation productivity increase with temperature up to an optimum temperature [41] and then decline. Consequently, tree growth response to climate warming shows strong spatial heterogeneity within and across terrestrial biomes [12, 42, 43].

Climate warming generally stimulates tree growth in colder parts of boreal forests (e.g., northeastern Siberia,

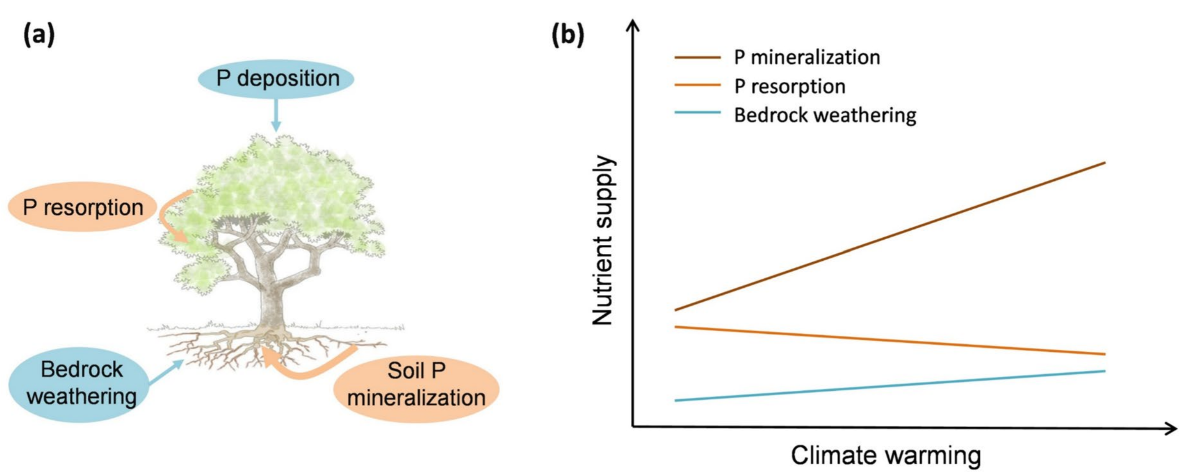

Fig. 3 External (bedrock weathering and P deposition) and recycled phosphorus (P) supply (soil P mineralization and plant P resorption) in forest ecosystems **a** and their potential responses to climate warming **b**. See a more detailed description and relevant references in Section Effects of Climate Warming on Phosphorus Availability

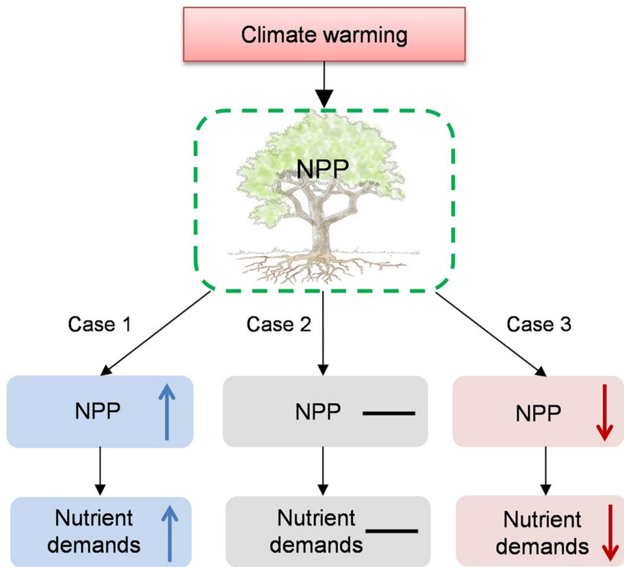

Fig. 4 Direct effects of climate warming on net primary productivity (NPP) and consequent changes in plant nutrient demands in forest ecosystems. There are three possible cases depending on the responses of NPP to warmer temperatures

Alaska, northeastern Canada, and coastal Scandinavia) and alpine forests (e.g., Alps and Tibet) by alleviating cold temperature limitation and lengthening the growing season [42–44]. Accordingly, accelerated tree growth and biomass production increase the biological demands of all essential nutrients (e.g., N, P, S, K, Ca, Mg and micronutrients) in these forests [45]. Since nutrients are stoichiometrically coupled in plants to maintain optimal growth and adapt to changing environmental conditions [46, 47], the stimulating effect of climate warming on forest biomass production may further strengthen nutrient coupling among these nutrients. In response to increasing nutrient requirements for growth, plants may also improve nutrient use efficiency via stoichiometric and allometric adjustments [46].

Warmer temperatures may lead to a decline in tree growth when exceeding the thermal optimal threshold for photosynthetic production [41, 48]. One would thus expect lower or even negative impacts of climate warming going from boreal towards tropical regions but optimum air temperatures of vegetation productivity also increase in this direction, as demonstrated by a combination of in situ eddy covariance measurements and satellite-derived proxies [41]. Particularly, the optimal growing-season air temperature of gross primary productivity was estimated to be on average 20, 22 and 30 °C in boreal, temperate and tropical forests [41]. Air temperatures in global tropical and subtropical forests are currently close to the optimum values [49] and are projected to exceed them under all climate scenarios, thus likely causing widespread negative effects on forest growth, while the exceedance of optimal temperature will less likely occur in boreal and temperate forests [41].

Furthermore, empirical studies also suggest an acclimation of plant photosynthesis and growth to climate warming with a shift in the optimum temperature [50–53]. Based on multiple datasets of satellite-derived productivity and model simulations, a recent study indicates that optimal temperature for vegetation productivity has increased significantly during the past four decades and will show a further increase until the end of the twenty-first century [54]. Given an acclimation of photosynthesis and a shift of optimum temperature with warmer temperatures, boreal trees are found to maintain C uptake under simulated climate warming but negative effects are prevailing for tropical forests [41, 55]. Nevertheless, future research efforts are needed to better understand how optimal temperatures for vegetation productivity will change under future climate warming and determine the growth response to climate warming.

Regardless of temperature limitation, climate warming is found to exert negative effects on plant growth when moisture deficiency simultaneously increases with warmer temperatures [12, 42, 43]. For instance, a global analysis of tree growth response to climate change indicates that in cold and dry regions climate warming generally exerts negative effects on tree growth and water deficiency is becoming increasingly limiting in boreal forests [42]. As a result, the area of temperature-limited forests has been shrinking in the context of continuing climate warming [42]. Moreover, the effect of climate warming on tree growth in the Eurasian boreal forest has been found to shift from positive in the northern part to negative in the southern part due to increased stress of water deficiency and the area with the negative effect of climate warming is expected to expand northward and upward in this century [12]. In tropical forests, the temperature-associated increase in atmospheric vapour pressure deficit may cause a reduction in photosynthesis and productivity [56, 57]. Overall, this climate-induced increase, or decrease, in productivity implies simultaneous changes in nutrient demands in these forest ecosystems.

Indirect Effects of Climate Warming on Plant Nutrient Demands

Co-occurring plant species in a community generally have distinct strategies for nutrient utilization and different required amounts of nutrients [58]. Shifts in species composition under climate warming may thus alter the nutrient demands on an ecosystem scale. Climate change has been found to change the distribution of plant species and shift the species composition of forest biomes, as evidenced by an upward and poleward shift in plant distributions [59–61]. For instance, warmer temperatures can lead to a shift in species composition with different root-associated microbial symbionts, including a decrease in ectomycorrhizal trees and an increase in arbuscular mycorrhizal and N-fixer symbiotic trees [62]. However, it remains poorly understood how such climate-induced changes in plant community structure alter the biomass production and nutrient requirement on an ecosystem scale. Future research efforts are needed to combine manipulated warming experiments and field investigations across transects of forest ecotones (e.g., temperate-boreal forest ecotone) to improve our understanding of this critical topic.

Effects of Climate Warming on Nitrogen and Phosphorus Limitation

Changing Strength of Nitrogen and Phosphorus Limitation Under Climate Warming

Global patterns of N and P limitation have been a research topic of focus for decades [5, 63–65]. Conventionally, N and P limitations are thought to occur widely in various terrestrial ecosystems and N limitation is thought to prevail over P limitation on a global scale [63–65]. However, a quantitative assessment of global terrestrial N and P limitation has been lacking for decades. Meta-analyses of N and P addition experiments can theoretically quantify the global pattern of N and P limitation [63, 64, 66], but such approaches imply considerable uncertainties by using non-isometric growth indicators (e.g., diameter at breast height, basal area, tree biomass carbon storage, and NPP) and/or using effect-size metrics not standardized by the level of nutrient addition [67]. Based on the stoichiometric homeostasis theory and Liebig's 'Law of the Minimum', Du et al. [5] assessed terrestrial N and P limitation using a new indicator, i.e., the ratio of plant leaf N and P resorption efficiencies and concluded that P limitation is more prevailing than N limitation in global terrestrial ecosystems. Moreover, N limitation shifts towards P limitation at higher temperatures across broad climate gradients [5]. Specifically, N limitation generally occurs in boreal forests and temperate coniferous forests, while P limitation prevails in tropical forests, subtropical forests and warm temperate broadleaved forests characterized by highly weathered soils [5].

Although the spatial variations in N and P limitation across climate gradients have been well investigated, it remains poorly understood how climate warming will affect the strength and type of nutrient limitation over time [67]. Climate warming alters both the availability and demands of multiple nutrients [68], likely causing distinct trends in the strength of nutrient limitation to forest biomes [67]. In N-limited forests (e.g., boreal forests), the strength of N limitation will be likely alleviated by climate warming since the potential increase in demand will likely be compensated by the accelerated N cycling and increased N availability [69, 70]. In contrast, tropical soils are typically depleted in the P pool and climate warming combined with atmospheric CO_2 fertilization will likely strengthen P limitation in tropical forests since the demand will likely increase while the availability is hardly affected [15, 71]. Such predictions of changes in nutrient limitation under climate warming across different forest biomes need to be further underpinned with additional empirical evidence.

Shifting From Nitrogen to Phosphorus Limitation Under Climate Warming

In addition to a change in the strength of nutrient limitation, climate warming may also result in a shift in the limiting nutrients. Experimental results indicate that climate warming significantly increased leaf N:P ratio [68, 72, 73], implying that warmer temperature tends to shift ecosystems from N limitation toward P limitation over time. In some regions where forest is weakly limited by N availability (e.g., southern temperate forest), climate warming may result in a shift from N limitation to P limitation over time. Such effects may lead to a poleward or upward of the boundary for P limitation in future. Assessments in European forests also indicate an overall increase in P limitation by a higher leaf N:P ratio over the past three decades [74–76] because a warming and CO_2-driven increase in N demand is likely compensated by a higher N availability from accelerated N mineralization and considerable N deposition, while the increase in P supply is relatively limited.

Warming-Induced Changes in Nutrient Constraint on CO_2 Fertilization Effect

CO_2 Fertilization Effect as Regulated by Nutrient Limitation

Woody plants, characterized by a C3 photosynthetic pathway, theoretically benefit from continuously rising atmospheric CO_2 concentrations [77]. Accordingly, previous studies based on experimental and modelling approaches have shown that forest biomass production and consequent C sinks increase significantly in response to CO_2 enrichment [7, 78, 79]. The fertilization effect of rising CO_2 concentrations is a key mechanism that drives an increase in future C sinks as a premise to achieve C neutrality and migrate climate change [80].

Free air CO_2 enrichment experiments (FACE) in temperate forests indicate that the stimulation of forest growth by elevated CO_2 concentrations diminishes over time, possibly attributed to progressive N limitation [81, 82]. Accordingly, the CO_2 fertilization effect on global vegetation productivity has been found to decline over the past three decades, partially attributable to a constraint by N and P limitation [3]. These findings challenge the conventional views that forest C sinks will grow continuously and indefinitely with rising air CO_2 concentrations.

Furthermore, free air CO_2 enrichment experiments in tropical forests have shown that the NPP and C sinks showed a weak response to CO_2 enrichment mainly attributable to strong P limitation [83–85]. However, simulations using dynamic global vegetation models (DGVMs) indicate that productivity and C sinks of tropical ecosystems have the highest sensitivity to CO_2 fertilization among terrestrial biomes [79]. Additionally, intercomparison between experimental results and P-enabled models suggests that the magnitude of the CO_2 fertilization effect on C sequestration is overestimated in current land surface models [86]. These contrasting results suggest that dynamic global vegetation models have not adequately accounted for the role of nutrient limitation.

As driven by atmospheric CO_2 enrichment, plant nutrient concentrations have been found to decrease in many terrestrial ecosystems, implying a trend of oligotrophication [75, 87–89]. Model simulations have suggested that the expected increase in future NPP and C storage would be largely reduced over time when considering, among other things, the role of N and/or P limitation [4, 13, 78, 90]. Particularly, tropical forests, currently holding the largest C sinks among all forest biomes, will likely play a less important role in future C sequestration and climate feedback than previously assumed [90]. The nutrient constraint on global land C sinks remains the largest uncertainty of future biogeochemical feedback to climate change.

Warming-Mediated Nutrient Constraint on CO_2 Fertilization Effect

The pathway that climate warming alters nutrient cycling and thereby the strength of nutrient limitation will likely play a key role in regulating the future C response to rising air CO_2 concentrations. In view of distinct nutrient status across different forest biomes [5], climate warming will likely cause spatially divergent nutrient-mediated effects on the response of NPP and C sequestration to rising air CO_2 concentrations. Experimental results indicate no significant stimulation of CO_2 enrichment on NPP (warming leads also to increased autotrophic respiration) and C sinks in tropical forests mainly attributable to strong P limitation [84, 85]. Future climate warming will not likely alleviate the P limitation to sustain the CO_2 fertilization effect in tropical forests (Fig. 5). In contrast, climate warming is expected to improve N availability in N-limited forests (e.g., boreal forests and temperate forests) via accelerating N mineralization and biological N fixation and this alleviation of N limitation will likely sustain a significant increase in future CO_2 fertilization effect (Fig. 5). Moreover, the warming-mediated response of NPP to rising CO_2 concentrations is predicted to be stronger in boreal forest compared with temperate and tropical forests given increased available nutrients from an acceleration of decomposition and mineralization of the accumulated litters and soil organic matter (Fig. 5).

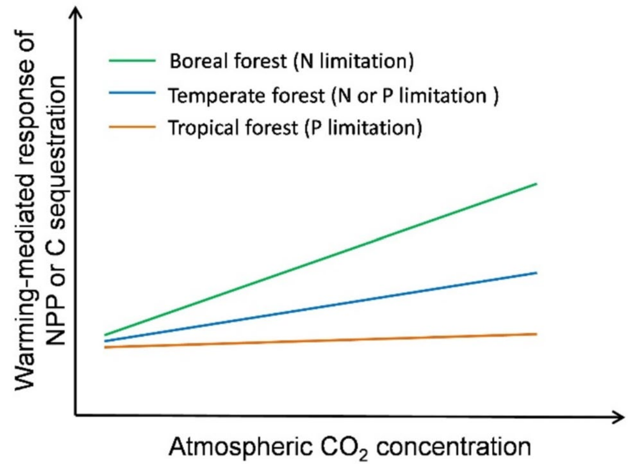

Fig. 5 Hypothesized responses of NPP and C sequestration to future increase in air CO_2 concentration as mediated by warming-induced changes in nutrient limitation in boreal, temperate and tropical forest biomes. See a more detailed description and discussion in Section Warming-Mediated Nutrient Constraint on CO 2 Fertilization Effect

Accordingly, a recent study of model simulations demonstrated a stronger response of gross primary productivity to the future rise of atmospheric CO_2 concentrations in boreal zone compared with the tropics [91]. However, there are only a small number of earth system models including both N and P cycling and only one was included in the Sixth Phase of the Coupled Model Intercomparison Project (CMIP6) [92–95]. The inclusion of C, N and P cycles in earth system models is crucial since model simulations generally predict a reduction of future land C sinks by 25–50% when accounting for N and P limitation [4, 95]. Future research efforts are further needed to better account for N and P cycling processes in earth system models to constrain future C sinks in response to future CO_2 enrichment and climate change.

Conclusions and Outlook

Rising air CO_2 concentration is a key driver of the projected increase in land C sinks. However, increasingly more evidence suggests that nutrient limitation (especially N and P) constrains the CO_2 fertilization effect. Based on a literature synthesis, here we provide a perspective that N and P limitations in major forest biomes can shift in strength under continuing climate warming as a result of changes in nutrient availability and plant nutrient requirements. Our review suggests that climate warming causes a considerable increase in N availability of generally N-limited boreal and temperate forests but a weak increase in P availability in generally P-limited tropical forests. Climate warming tends to alleviate N limitation in boreal and temperate forests but it will not likely alleviate P limitation in tropical forests given a depleted P pool. We further highlight that warming-induced changes in nutrient cycling and availability will play an important role in regulating future C sinks in biome-specific response to rising CO_2 concentrations. Empirical and modelling research efforts both are needed to further improve our understanding of this pathway to reduce uncertainties in future C sink projection.

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Author Contributions E.D. and W.D. proposed the outline of the review. E.D wrote the manuscript and prepared all figures. E.D., W.D., A.C., and A.D. reviewed and revised the manuscript.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Ethical Approval Not applicable as no human or animal subjects were used.

Competing Interests The authors declare no competing interests.

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