INVITED REVIEW: PART OF AN INVITED ISSUE ON TREE NUTRITION

Global climate change and tree nutrition: effects of elevated CO_2 and temperature

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Summary   Although tree nutrition has not been the primary focus of large climate change experiments on trees, we are beginning to understand its links to elevated atmospheric CO_2 and temperature changes. This review focuses on the major nutrients, namely N and P, and deals with the effects of climate change on the processes that alter their cycling and availability. Current knowledge regarding biotic and abiotic agents of weathering, mobilization and immobilization of these elements will be discussed. To date, controlled environment studies have identified possible effects of climate change on tree nutrition. Only some of these findings, however, were verified in ecosystem scale experiments. Moreover, to be able to predict future effects of climate change on tree nutrition at this scale, we need to progress from studying effects of single factors to analysing interactions between factors such as elevated CO_2, temperature or water availability.

Keywords: environmental change, nitrogen, nutrient cycle, nutrient uptake, phosphorus, tree species.

Introduction

The cycling of nutrients between the soil and plants is one of the defining aspects of ecosystem functioning. The availability of nutrients for plant uptake can limit the productivity and even the very survival of forest ecosystems (Rodin et al. 1967). Crucial for plant metabolism and growth, the accessibility of nutrients in the soil is the result of several biogeochemical processes, often involving complex feedbacks. While only 16 elements have been identified as essential to higher plants, a lack of any of these elements makes it impossible for plants to complete their life cycle (Chesworth 2008). According to the amount of each element required for normal plant growth, they are commonly classified as macronutrients and micronutrients (Allaway 1975). Macronutrients are required in large amounts and usually constitute more than 0.1% dry mass (C, H, O, N, P, K, Ca, Mg, S), while micronutrients are needed only in small quantities not exceeding 0.05% dry mass (Zn, Fe, Mn, Cu, Mo, B, Cl). Plants mostly take up C from the air, while the rest of the nutrients are acquired almost exclusively through plant root systems. The immediate availability of all soil nutrients is dependent on the rate of their uptake (e.g., by plant roots, fungi, microorganisms) and the rate of replacement (e.g., bacterial N fixation, organic matter mineralization, atmospheric deposition, weathering).

Forest trees are characterized by the C3 photosynthetic pathway (Ainsworth and Long 2005). As such, their productivity and demand for nutrients is greatly affected by atmospheric CO_2 concentration and temperature. Terrestrial ecosystems are already exposed to atmospheric CO_2 concentration higher than that encountered since the early Miocene (Pearson and Palmer 2000), and despite recent efforts to limit global CO_2 emissions, the atmospheric concentration of this greenhouse gas is likely to exceed the worst-case scenario considered by the Intergovernmental Panel on Climate Change (IPCC) (Raupach et al. 2007). Any further increase is likely to significantly impact on plant growth, both directly by stimulating photosynthesis (Drake et al. 1997) and indirectly by inducing planetary warming (IPCC 2007). A great number of studies have been aimed at elucidating the responses of a wide range of plants to rising CO_2 and temperature. In general, a stimulation of biomass production with increasing CO_2 concentration is observed, although its future extent is likely to be limited by nutrient availability. Further, stimulation of C metabolism processes such as photorespiration and mitochondrial respiration by increasing ambient temperature is likely to decrease net C uptake in the future (Atkin et al. 2000, Weston and Bauerle 2007). In a positive feedback loop, rising temperature may enhance organic matter mineralization and mineral weathering rates—thus alleviating, at least temporarily, some nutrient limitations.
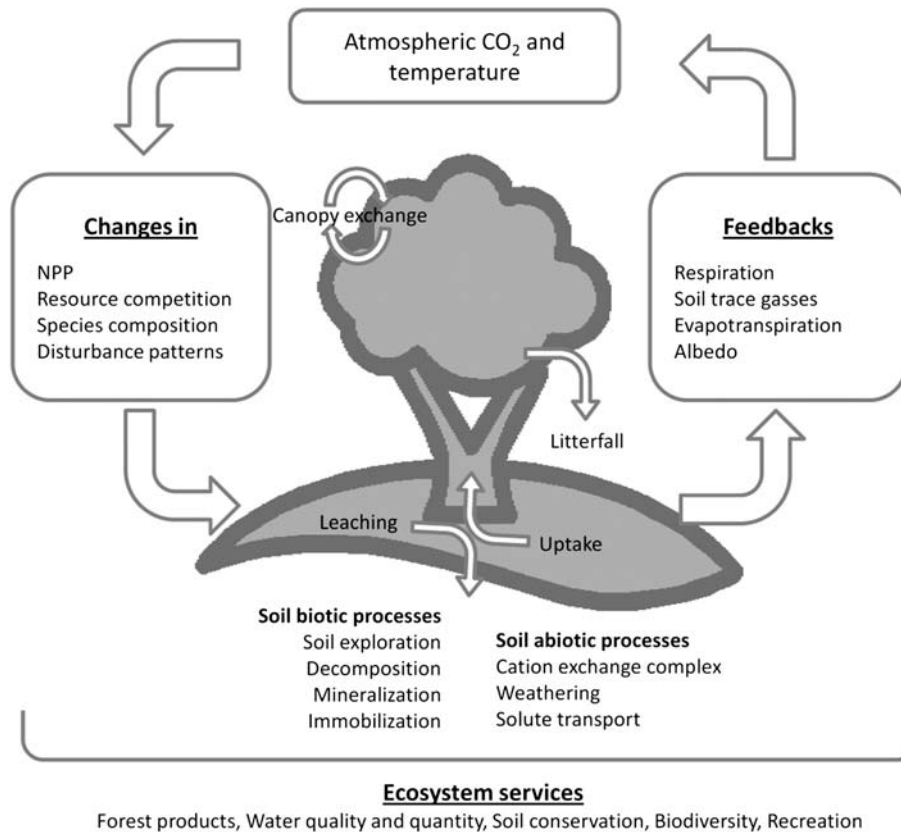
Figure 1. Schematic diagram showing the most important biogeochemical processes in forest ecosystems which will be affected by changes in atmospheric CO_2 concentration and ambient temperature. Present ecosystem service provision is also likely to be affected (adapted from Campbell et al. 2009).

To date, most physiological observations on trees exposed to changing CO_2 or temperature have been carried out in controlled environments, providing a considerable amount of information about the likely responses of trees and their capacity to adapt to changing environment. However, due to the size of mature trees, much of this research has been done on seedlings or plant tissues removed from mature individuals, somehow limiting the predictive power of these experiments for natural conditions. Free-Air Carbon Dioxide Enrichment technology (FACE) was therefore developed to verify scientific findings on the effects of elevated CO_2 in open-air conditions (Lewin et al. 1994, Miglietta et al. 2001). Similarly, warming experiments were established in forests to test their reaction to rising temperature. Because of obvious technical challenges associated with warming of an entire forest canopy, such experiments have focused mainly on assessing the impacts on the soil (Bradford et al. 2008, Schindlbacher et al. 2008). Understanding the controls and processes that determine the cycling and the resulting availability of nutrients still remains a key challenge, chiefly because most of the studies focus only on the immediately available pools in soils and in plants. Nutrient availability is hugely variable, both in space and in time, and ultimately this variation can be more important for tree growth than the changes in tree physiology driven by climate (Salih et al.

2005). Since all major biogeochemical processes involved in nutrient cycling in forests will be impacted by changing CO_2 and temperature (Figure 1), only an integrative approach to studying nutrient cycles can provide reliable information necessary for predictions of future forest growth.

Currently, we have sufficient information relating to the availability of essential nutrients, their roles in plant metabolism and their cycles; the predicament we are facing now is that most of this information relates to impacts of single factors or to one nutrient at a time. To understand the full impact of climate change, we need information about multiple interacting factors, which at the moment is very scarce. To summarize present knowledge, we present known effects of elevated CO_2 and temperature on tree nutrition, focusing on the mobilization and immobilization processes rather than the pools. We identify existing gaps in knowledge and suggest research priorities for the near future.

Effects of elevated CO_2

Photosynthetic carbon uptake by C3 plants is enhanced by elevated CO_2 (Ainsworth and Rogers 2007) and has been shown to translate to a consistent stimulation of net primary productivity (NPP) in trees by about 23% (Norby et al. 2005).
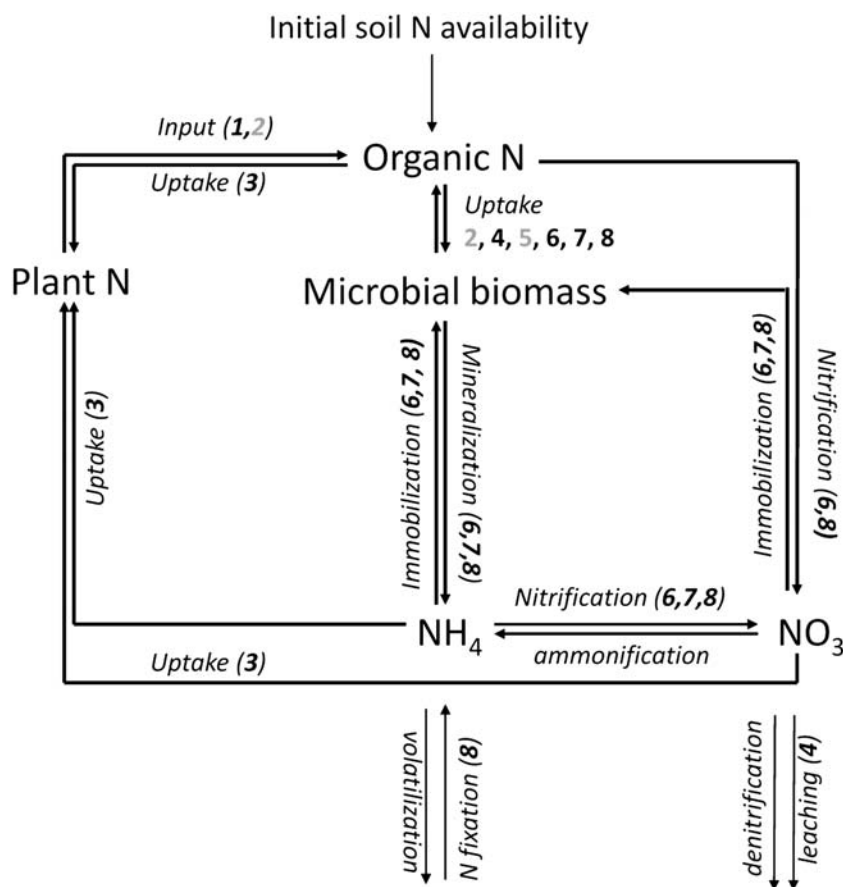
Figure 2. Conceptual scheme of soil N cycling. Factors affecting the N cycling are reported (grey numbers, those changed by elevated CO_2 only; black numbers, those changed by both elevated CO_2 and temperature): (1) N input; (2) input C/N ratio; (3) plant N requirement; (4) SOM turnover; (5) SOM decomposability; (6) microbial growth rates; (7) microbial turnover; (8) microbial composition.

The increase in productivity expected from trees growing in elevated CO_2 is larger than the one estimated in crops, especially in the case of trees with indeterminate growth (Long et al. 2004). However, lasting increase in tree growth in elevated CO_2 can only be achieved if some combination of increased nutrient absorption and improved nutrient use efficiency is attained. Even though all macro- and micronutrients are essential for normal plant growth, apart from a few macronutrients, we only have very limited or no information about the interactions between the factors of climate change and tree physiology of nutrients. For the purpose of this review, we will therefore concentrate on the elements that have been fairly well investigated so far and the physiology and cycling of which is reasonably well understood in the frame of climate change.

Nitrogen

Due to the strong coupling between C and N cycles (Rastetter and Shaver 1992), N is the element most likely to limit tree growth in a future high-CO_2 world (Reich et al. 2006). The amount of N available for plant uptake in forests is determined by several processes, such as organic matter depolymerization and mineralization, microbial immobilization and competition between microbes and plants, and depends on soil nutrient status and ecosystem type (Figure 2). Boreal forests, where most N is locked up in undecomposed organic matter, are likely to have different gearing between C and N cycles than temperate forests where most N is in live biomass. Different forest types therefore need to be treated separately when considering present and future N limitation to their growth.

Increased N immobilization by plants and microbes (Holmes et al. 2006, Norby and Iversen 2006) and observed progressive N limitation (Luo et al. 2004) are all thought to decrease the amount of N accessible to trees, thus limiting any future NPP stimulation by elevated CO_2. Scarcity of N might be alleviated by predicted increases of atmospheric N deposition (Reay et al. 2008), but the exact extent of this phenomenon together with its interaction with increased C fixation is currently unknown at ecosystem scale. We know that light-saturated carbon uptake increases in trees grown in a CO_2-enriched atmosphere (Ainsworth and Long 2005), but the initial stimulation decreases if photosynthetic acclimation takes place and foliar N content declines (Ellsworth et al. 2004, Ainsworth and Rogers 2007). Foliar N content per unit leaf area often declines under elevated CO_2 (Ellsworth et al. 2004), an effect frequently amplified by denser canopies under elevated CO_2. Larger leaf biomass requires higher N in-

vestment into Rubisco, an enzyme driving photosynthesis in C3 plants and responsible for about 25% of foliar N content. Photosynthetic N use efficiency (PNUE), defined as the net amount of CO_2 assimilated per unit of foliar N, is also increased in high CO_2, predominantly by enhanced CO_2 uptake rather than by N redistribution (Liberloo et al. 2007, Leakey et al. 2009). As atmospheric CO_2 continues to rise, further increases in PNUE would be necessary to sustain higher CO_2 uptake. Photosynthetic activity and the growth rate can be stimulated by N addition in N-poor environments, but the response was found to be highly variable among clones of a single species, let alone different tree species (King et al. 2008). Similarly, long-term exposure to elevated CO_2 alters the relationship between photosynthesis or its component processes and foliar N content (increased PNUE). However, providing abundant N to trees grown under elevated CO_2 restores these relationships back to the status found under ambient conditions (Crous et al. 2008). These findings provide early evidence that increased carbon fixation in elevated CO_2 will only continue if sufficient N supply to tree foliage can be maintained. Nitrogen availability to metabolically important tissues can also be influenced by the movement of N within the plant. The process of N retranslocation from leaves before their abscission was shown to be slightly increased by elevated CO_2 in different poplar species, accompanied by more N immobilized in woody tissues (Calfapietra et al. 2007). Since woody tissues have substantially longer turnover times, N retranslocation could enhance N immobilization.

Nitrogen allocation in trees, as well as the total N uptake, is one of the main factors affecting foliar N concentration. In theory, trees optimize their N allocation for attaining maximum growth, thus allocating available N to organs with greatest benefit to net growth. The commonly observed decrease in foliar N content under elevated CO_2 (Tingey et al. 2003, Marinari et al. 2007) might be a result of either decreased N uptake per unit of biomass produced or preferential allocation of acquired N to other tissues (e.g., fine roots). Nitrogen uptake did not change in a short-rotation poplar plantation despite considerably increased biomass production under elevated CO_2, resulting in a significant increase in nitrogen use efficiency (NUE) under elevated CO_2 (Calfapietra et al. 2007). However, in other FACE sites, the stimulation of biomass production due to elevated CO_2 was supported by increased N uptake by trees, with negligible variation of NUE (Finzi et al. 2007). Analysing observations from two contrasting sites, Franklin et al. (2009) noted that soil N availability did not decline under an evergreen (*Pinus taeda*) forest, where a negative feedback between reduced soil N availability and uptake prevented N depletion. On the other hand, a broadleaf (*Liquidambar styraciflua*) stand achieved higher N uptake through increased production of fine roots—resulting in decreasing soil N availability. The authors used the investment in fine root systems to explain these contradictory responses of forests to elevated CO_2.

Fine roots of forest trees are, of course, not the only biomass pool increasingly competing for N under elevated CO_2.

Symbiotic mycorrhizal fungi colonizing tree roots have been shown to significantly benefit from increased photosynthate availability under elevated CO_2 (Treseder 2004, Alberton et al. 2007). Nitrogen uptake by mycorrhizal networks is thought to be much more efficient and rapid than that of fine tree roots, largely due to a greater degree of soil exploitation and enzymatic depolymerization of organic compounds containing N (Lindahl et al. 2002, Read and Perez-Moreno 2003). However, the interaction between mycorrhizal symbiosis and elevated CO_2 needs further investigation as stimulation of mycorrhizal growth under elevated CO_2 was shown to be negatively correlated with tree shoot N content and overall plant N uptake (Alberton et al. 2007). One possible explanation of such contradictory observations of N uptake is a frequently observed increase in fungal abundance or an increase in fungi/bacteria ratio in soils under elevated CO_2 (Treseder 2004, Carney et al. 2007) and/or an increase in the proliferation of mycorrhizal fungi (Parrent et al. 2006). In a recent review, Hu et al. (2006) report that about two-thirds of 135 experiments on trees and herbaceous plants observed an increase in the infection and external fungal hyphae of both arbuscular mycorrhizae (AM) and ecto-mycorrhizae (EM) under elevated CO_2. Significantly, no studies reported negative effects on mycorrhizal colonization or extraradical biomass. Fungi commonly have higher C/N ratios than soil bacteria, using smaller amounts of N to produce equivalent amounts of biomass. Moreover, the translocation of C and N within fungal mycelium might explain the low mineralization rates and, hence, lower N availability in fungal dominated ecosystems (Boberg et al. 2010). Positive effects of elevated CO_2 on mycorrhizal activity (Lukac et al. 2003, Pritchard et al. 2008) and turnover (Godbold et al. 2006) may enhance tree N nutrition in the future but only if mycorrhizal fungi proliferate at the expense of bacteria or other fungal groups.

Immediate N availability in the soil is driven by several N release and uptake processes, the relative importance of which is dependent on the overall soil N status. Focusing on organic N uptake, N mineralization in N-poor ecosystems such as boreal forests should be of lesser importance than microbial depolymerization (Schimel and Bennett 2004). There are currently no direct observations of effects of elevated CO_2 on this link; the few studies that focused on the impact of elevated CO_2 on organic N uptake by plants reported no changes in temperate forest (Hofmockel et al. 2007) or increased uptake of both mineral and organic substrates in desert shrubs (Jin and Evans 2010).

Increased C input under elevated CO_2 is reported to stimulate either microbial N immobilization (Zak et al. 2000) or mineralization (priming effect; Blagodatskaya and Kuzyakov (2008)), depending on the prevalence of N or C limitation in microbial communities and on the C/N ratio of the substrate being decomposed (Hodge et al. 2000). When decomposing substrates with high C/N ratio, microorganisms will retain more inorganic N (mainly as NH_4) during decomposition, thus reducing the availability of this N pool to plants. Conversely, if the C/N ratio of the substrate is lower than that of

the decomposers, microorganisms will increase the size of the mineralized N pool in the soil. Since elevated CO_2 alters the C/N ratio of plant litter (Cotrufo et al. 2005), we need to know how the interaction of these two factors will affect N cycling and eventually soil N availability. To date, contrasting results have been reported on N cycling in forest ecosystems under elevated CO_2, probably reflecting different N status on the whole ecosystem scale. Nitrogen mineralization has been found to increase (when coupled to a correspondent increase in NH_4 immobilization) (Holmes et al. 2006), decrease (Billings and Ziegler 2005) and, most often, not change (Zak et al. 2003, Finzi et al. 2006, Austin et al. 2009). Nitrification, which usually is the greatest component of soil N mineralization, has been reported either to increase (Carnol et al. 2002), decrease (Lagomarsino et al. 2008) or not change (Austin et al. 2009).

Current data thus indicate that elevated CO_2 will significantly affect soil N availability by stimulating net growth, at least initially. This stimulation may or may not last in the long term, depending on the gearing between C and N cycles, existence of physiological limits to increases in NUE, and whether external N inputs will be able to keep pace with greater N uptake. Overall N availability under elevated CO_2 appears to be sensitive to forest ecosystem type, a factor that needs further investigation.

Phosphorus

Phosphorus is used in energy storage and transfer (Tisdale et al. 1985) and is an important structural component of nucleic acids, coenzymes, nucleotides, phosphoproteins, phospholipids and sugar phosphates (Schachtman et al. 1998). While the physiological importance of P and its use in plant metabolism are fairly well understood, the knowledge of P biogeochemistry and cycling in forest soils is lagging. Largely due to the complexity of the processes involved, we are only now starting to uncover the effects of climate change on P nutrition. Phosphorus is found in inorganic mineral forms and in organic forms resulting from plant and microbial biomass turnover. Both inorganic and organic P form a continuum of compounds in equilibrium with each other, ranging from the readily plant-available P dissolved in the soil solution to poorly available P held in stable compounds (Larsen 1967). In forest soils, geochemical processes determine the long-term distribution of P, and biological processes influence P distribution in the short term, as most of the plant-available P is derived from soil organic matter (Ballard 1980). Any effects of elevated CO_2 on P availability in forests are therefore likely to be indirect and mediated by the response of the biotic part of the ecosystem.

The proportion of organic P in forest soils varies widely (Newbery et al. 1997), its availability driven by the action of ectoenzymes produced by roots, mycorrhizal hyphae and soil microorganisms (Read et al. 2004). Production of such enzymes, which forms a significant proportion of rhizodeposition, has been shown to increase under elevated atmospheric CO_2 (Ineson et al. 1996, Lagomarsino et al. 2008), reflecting an increase in microbial and/or plant demand for P. In addition, the contribution of tree roots and mycorrhizas to mineral weathering and subsequent release of P is well known (Dijkstra et al. 2003). Put together, increases in belowground availability of C under elevated CO_2 may lead to increased rates of P mineralization and release from the soil mineral fraction.

There are not many observations on the effects of elevated CO_2 on P availability and uptake in trees. In one of such studies, Johnson et al. (2000) investigated a fire-regenerated Florida scrub oak ecosystem. During the first year after the fire, a negative effect of CO_2 on P availability was shown, later leading to a decrease in extractable P after 5 years (Johnson et al. 2003). In a sweetgum forest subjected to elevated CO_2, no effects of elevated CO_2 on P cycling were shown after 2 years of enrichment (Johnson et al. 2004). However, Khan et al. (2008) found that growing poplar under elevated CO_2 significantly changed the fractionation of P in the soil. Observed increase in tree growth under elevated CO_2 did not result in depletion of P pools in soils but rather increased storage of P in the rooting zone. In the fast-growing poplar plantation, the biogenically driven weathering of primary minerals in the rooting zone was sufficient to maintain the replenishment of plant-available inorganic P.

Since P cycling in forests is much more efficient and its recovery by trees more complete than that of N, it is likely that any effect of CO_2 on the P cycle will be driven by changes in C uptake, tree growth and litter production. Particularly noteworthy is the potential role of mycorrhizas in the mediation of effects of elevated CO_2 on P uptake. Phosphorus nutrition of tree seedlings grown in unadulterated forest soils under elevated CO_2 was shown to improve when grown in the presence of mycorrhiza (Choi et al. 2009). Such findings highlight the need to investigate nutrient cycling in natural conditions with all major fluxes, feedbacks and interactions present and largely undisturbed.

Other nutrients

As already mentioned, we are only now starting to uncover the effects of climate change on tree nutrition; our knowledge of the full range of nutrients is very limited. For obvious reasons related to human nutrition, published studies of effects of elevated CO_2 on nutrients other than N and P are almost exclusively based on crop plants. Such studies report a wide variation in effects of CO_2 enrichment on plant nutrition; the direction and the size of observed effects varies greatly depending on plant species and soil nutrient availability. In general, however, elevated CO_2 is expected to significantly alter the elemental composition of plants and to lower the micronutrient concentration in plant tissues (Loladze 2002). An investigation of immediate nutrient uptake, carried out on a timescale of days, revealed that in young walnut seedlings grown in elevated CO_2, nutrient uptake rates of K^+, Ca^{2+} and Mg^{2+} were proportional to CO_2 uptake rate, but that of
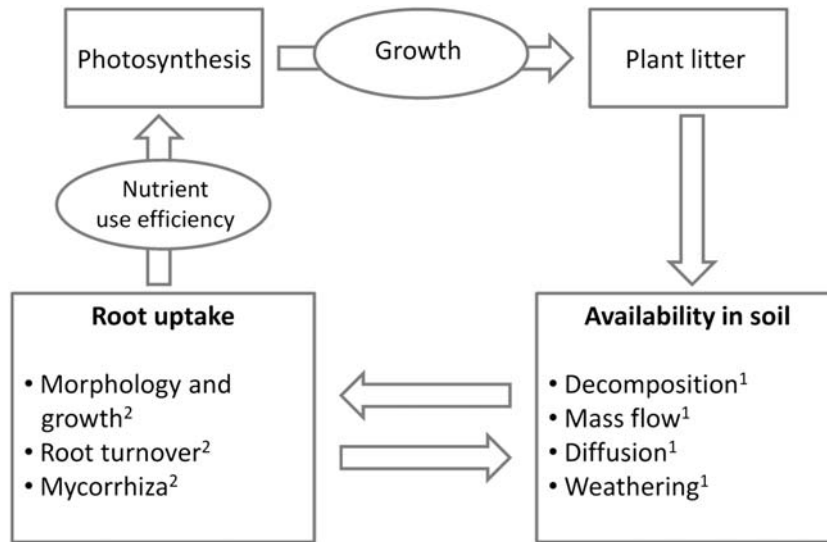
Figure 3. Component processes of ecosystem nutrient cycle, directly (1) and indirectly (2) affected by increasing temperature (adapted from BassiriRad 2000).

P ion was not. This indicates that despite the nutrient storage capacities previously observed in young trees, nutrient uptake by roots is strongly coupled to carbon uptake (Delaire et al. 2005). In a more long-term analysis of trace metal concentration in forest trees grown under FACE treatment, Natali et al. (2009) found an additional factor guiding element uptake in elevated CO_2. They observed that the dilution of essential micronutrients in plant tissues harvested from high CO_2 treatment was less than that of non-essential ones. Alongside tree species and soil characteristics, the effect of elevated CO_2 in this study was mediated by the fact whether the particular metal element is essential to plant growth or not.

Carnol et al. (2002) found an increase in some exchangeable base cations (Ca^{2+} and Mg^{2+}) and a decrease in acid cations (Al^{3+} and Mn^{2+}) in Scots pine grown under elevated CO_2 in open top chambers. Liu et al. (2007) reported a decrease in N, S and B concentrations, increase in K and P concentrations and no effects on other elements (Mg, Ca, Mn, Cu, Zn) in aspen and birch leaf litter under elevated CO_2. At the same site, nutrient input of N, P, S, P, Ca, Mg, Cu and Zn to soil through leaf litter under elevated CO_2 increased, but the return of Mn was reduced. Johnson et al. (2004) in a sweetgum plantation found increased uptake of N, K and Mg and significant increases in the requirement of N, K, Ca and Mg under elevated CO_2. However, elevated CO_2 had no significant effect on availability of any measured nutrient in the soil, with the exception of the reduction in SO_4^{2-} and Ca^{2+} in soil solution.

Nutrient availability in soil relies on the presence of cation exchange capacity (CEC), an inherent soil property which may be strongly affected by elevated CO_2. In a fast-growing poplar plantation, an increase in base cation availability (Ca and Mg), together with an overall increase in CEC, was found under elevated CO_2 (Lagomarsino et al. 2006). A corresponding increase in the concentration of foliar Mg

was also observed but was limited to the beginning of the growing season (Marinari et al. 2007). An increase in CEC under elevated CO_2 can result from an increase in organic matter content, roots and mycorrhizal biomass and exudation (Mareschal et al. 2010) and soil aggregation status (Hoosbeek et al. 2006). Trees growing in elevated CO_2 atmosphere might therefore be able to (indirectly) affect the soil's capacity for nutrient provision and thus regulate nutrient availability in the long term.

Effects of elevated temperature

Global temperatures are forecasted to increase during the course of this century and beyond, bringing about a change in tree functional biology and nutrient demands, chiefly because tree species distribution is unlikely to be able to keep pace with climatic changes. The magnitude and the speed of nutrient cycles in forests differ greatly due to the degree of biological control and the origin of the elements. Elements with primarily biologically controlled cycles (such as C and N) might show different reaction to changing temperature than elements with cycles controlled both by biological and geological processes (such as P, S and K) or elements with predominantly geologically controlled cycles (such as K, Ca, Mg, S or micronutrients, e.g., Wood et al. 2006, Watanabe et al. 2007). Since soil and especially air temperature are more difficult to manipulate than atmospheric CO_2 at ecosystem level, our knowledge about the effects of increasing temperatures on this scale is currently limited and generally inferred from smaller scales or models.

Direct effects on trees

Changes in ambient temperature may induce a range of responses in trees and in forest ecosystems (Figure 3). Starting

with photosynthesis, optimal Rubisco activity is considered to be at around 25 °C, and therefore the highest rates of photosynthesis should be recorded at this temperature. However, Rubisco is known to acclimate to temperature (Bernacchi et al. 2002), and at high temperatures O_2 is known to dissolve more efficiently than CO_2, which leads to higher availability of O_2 at the Rubisco sites in the chloroplasts. Hence, a higher rate of photorespiration reduces the efficiency of photosynthesis with increasing temperatures. As a consequence, it is extremely difficult to define an optimal temperature range for trees. If the acclimation processes are not considered, it could be surmised that global warming may improve the photosynthetic efficiency of boreal forests by allowing them to operate closer to the thermal optimum of Rubisco. At the same time, the opposite would be true for the Mediterranean forests which already experience temperatures above the physiological optimum for most of the year.

The implications in terms of tree nutrition could be far reaching and, similar to the effects of elevated CO_2, are probably dependent on the differential responses of nutrient supply and demand. If an increase in boreal forest productivity due to higher temperatures is to be maintained in the long run, it will have to be accompanied by an increase in weathering or deposition. Increased mineralization and turnover rates of organic matter might initially supply sufficient nutrients to support higher growth, but any nutrients currently held in undecomposed organic matter would eventually be locked up in larger biomass. Conversely, if tree growth in arid and semi-arid regions will not be stimulated by further increases in temperature, forests in this environment are unlikely to become nutrient limited—especially since existing climate scenarios forecast a concomitant increase in drought.

Soil heating experiments have shown that the stimulation of tree growth by increasing temperature is species specific (Farnsworth et al. 1995, King et al. 1999, Prieto et al. 2009), thus highlighting the potential impact of changing species composition and altered natural distribution of tree species in the future (Saxe et al. 2001). Nutrient uptake by trees, an active process supported by enzyme activity, is highly temperature dependent (Rennenberg et al. 2006). The direct effect of increasing soil temperature on this process is difficult to quantify in field conditions, largely because it is confounded by co-occurring drought. Several authors claim that nutrient uptake increases with rising temperature (Bassirirad 2000, Dong et al. 2001, Weih and Karlsson 2002), but, just like other enzymatic processes, the rate of uptake increases only until a threshold temperature is reached. Gessler et al. (1998) measured ammonium uptake in spruce and found maximum uptake at 20 °C, followed by a decrease at higher temperatures. Given that forest soil temperatures are much lower than the expected critical threshold, such limitation of nutrient uptake is unlikely to be reached in field conditions—at least not under a closed canopy forest.

Unless the ambient temperature is already at the photosynthetic threshold, as in the aforementioned example of Mediterranean forests, any increase in temperature due to climatic change should favour tree growth. In turn, better growth conditions should increase within-tree nutrient allocation to tissues most likely to take advantage of the new environment. Domisch et al. (2002) observed increased nutrient allocation to shoots of Scots pine seedlings and Fotelli et al. (2005) have shown higher N allocation to beech leaves when the trees were grown at higher air and soil temperatures. An important point to consider is the nature of temperature increases, whether it is a small and gradual increase in mean annual temperature or a severe hot spell in the middle of the growing season. A period of very high seasonal maximum is likely to disturb normal nutrient uptake patterns, not least because of its interaction with drought. Due to their longevity, trees have developed physiological mechanisms to deal with such disruption and are able to store and re-mobilize nutrients (Grassi et al. 2003). However, repeated seasonal stress might exhaust this capacity for nutrient storage, with detrimental effects for tree health in the long run. Most nutrients, with the notable exceptions of Ca and Bo (Epstein 1973), can be transported both upwards (xylem flow) and downwards (phloem flow) within a tree. This cycle of nutrients is thought to act as a buffer against minute nutrient shortages (Gessler et al. 1998) and is probably involved in metabolic signalling and growth regulation in trees (Nordin et al. 2001). Sardans et al. (2008b) have shown strong effects of heat and drought on aboveground biomass accumulation of some elements. Such direct effects of temperature on tree physiology and metabolism are likely to be species and element specific.

Indirect effects of temperature

Increasing temperature is likely to affect nutrient availability in the soil through the stimulation of organic matter decomposition and mineralization of soil nutrients (Jarvis and Linder 2000). Available studies on the influence of warming on N cycling in soils report highly variable responses across a range of ecosystems (Rustad et al. 2001, Beier et al. 2008). In particular, observed effects appear to be very seasonal, with the highest increase in enzyme activities related to N cycling during the winter when temperature is limiting or in the spring during the period of maximum plant and microbial activity (Beier et al. 2008, Sardans et al. 2008a). These authors also report a different pattern for NH_4 and NO_3 availability in soil, the former decreasing in spring in concomitance with the increase in N uptake by plants, with the latter increasing at the same time, probably due to an increase in nitrification activity.

Several studies have shown that soil warming can increase soil N mineralization and possibly nitrate leaching (see review by Pendall et al. (2004)). In a meta-analysis of 32 research sites, Rustad et al. (2001) found a significant increase in soil N mineralization at higher temperatures, with beneficial effects on plant growth. However, Beier et al. (2008) reported that nitrogen mineralization was relatively insensitive to the temperature increase across a range of ecosys-

tems and was mainly affected by changes in soil moisture. Moreover, the authors reported an asymmetric response of C and N mineralization to warming, with C, but not N, mineralization following the Q_{10} relationship, leading them to hypothesize progressive nitrogen limitation and thereby acclimation of plant production. Litter decomposition was predicted to increase by 4–7% relative to the present rate following an increase in temperature and precipitation estimated from a double atmospheric CO_2 scenario (Moore et al. 1999), with important implications for nutrient availability to the soil. Higher enzyme activities related to N cycling in soil in response to warming have been reported for shrubland (Sardans et al. 2008a) and fir forest (Feng et al. 2007) in the absence of moisture limitations. Enzyme activities are temperature-sensitive processes, generally following the Q_{10} relationship, as is the case in respiration (Davidson and Janssens 2006) where even a slight temperature increase can produce a significant enhancement of activity (Kuzyakov et al. 2007).

On the whole, despite observed differences in responses to higher temperature, an increase in N mineralization in soil can be predicted under favourable moisture conditions and substrate availability, mainly in those ecosystems where temperature is a limiting factor. An increase in N mineralization under increasing temperature is reported in a recent review by Hyvonen et al. (2007). In a negative feedback loop, this normally leads to increased NPP, increased N demand and ultimately to decreased N availability in the soil.

Interactions and feedbacks

As the presented current knowledge makes clear, we have information about effects of singular factors of climate change on tree nutrition, mostly in seedlings or young trees. We know little about interactions of multiple factors or about long-term effects on mature trees. Having said that, certain interactions between the effects of elevated CO_2 and increasing temperature on tree physiology are fairly well described and understood. For instance, photosynthetic rate increases substantially with elevated CO_2, and the effect is more pronounced at temperatures around 20 °C than at 10 °C (Sigurdsson et al. 2002). However, it is likely that forest trees will be subjected to several vectors of climate change at the same time, in addition to CO_2 concentration and warming. Use of fully factorial experiments to investigate such interactions is advisable; however, as Norby and Luo (2004) point out, their results are often confusing and difficult to interpret. The trade-off between the number of factors and the replication rate due to financial and/or space constraints must be carefully considered to maximize the information value of every such experiment.

Elevated atmospheric CO_2 is expected to directly influence tree physiology, compounding the changes affected by alterations of ambient temperature and rainfall (both amounts and patterns)—with the complex interactions and feedbacks such

changes bring. Moreover, any direct effects on ecosystem functioning brought about by climate change will certainly have indirect effects on nutrient availability and cycling. Due to the dearth of experiments investigating multiple factors, we know relatively little about such phenomena. Any change in nutrient availability, utilization or cycling in an ecosystem component such as soil, plant biomass or soil water will affect nutrient status of other components, causing a potential cascade of effects (Campbell et al. 2009). For instance, it has been shown that future increases in temperature may increase root mortality more in N-rich soils in temperate forests than in N-poor soils in boreal forests, with important implications for the N cycling between plant and soil (Hyvonen et al. 2007).

Mineral weathering, together with atmospheric deposition, is the most important source of plant nutrients other than C, H, O and N. The process of weathering can be best described as a concerted attack of several soil formation processes on mineral structures found within the rooting zone or wider soil. The rate of weathering is strongly dependent on soil temperature and soil moisture (White et al. 1999), both of which will be affected by climate change. Increasing temperature will speed up the release of nutrients locked up in the mineral soil fraction, while decreasing soil moisture may limit this process. Higher rates of weathering of nutrient-rich rocks generally lead to higher base saturation of the soil and maintain higher soil pH—both characteristics favourable to plant growth. While elevated CO_2 is not thought to have a direct effect on weathering, larger supply of photosynthate to mycorrhizal fungi has been shown to occur under elevated CO_2 (Treseder 2004). Since mycorrhizas are directly implicated in mineral weathering through the release of organic acids (van Breemen et al. 2000), their proliferation may potentially increase ecosystem nutrient availability. There is some evidence of a direct transport of nutrients from soil minerals to trees via mycorrhizal hyphae (Kohler et al. 2000), providing a direct link between increased C fixation and tree nutrition. The implication of these findings is that the nutrition of forest trees might be maintained at higher levels of NPP in a future elevated CO_2 atmosphere; however, we do not have any information to confirm or refute the long-term viability or the scale of such processes.

Despite the fact that most nutrients necessary for tree growth ultimately originate from mineral weathering or from atmospheric deposition, the bulk of nutrient uptake comes from the recycling of organic matter deposited to the soil. Nutrients are released into the soil solution during the decomposition of litter and are quickly taken up and recycled for the production of new organic matter. Climate change is likely to have a very significant effect on this process as nearly all organisms involved will be affected, both directly and indirectly. Litter quality, temperature and soil moisture are known to control the rate of decomposition and subsequent release of nutrients. Elevated CO_2 alters litter quality (Cotrufo et al. 1998, 2005), with significant decreases in its nutrient content. Less nutrients per unit weight, coupled with slower litter de-

composition under elevated CO_2 (Parsons et al. 2008), are therefore likely to reduce nutrient availability in the long run. Working in the opposite direction, as several soil warming experiments have shown (Robinson et al. 1995, Verburg et al. 1999), a 3–5 °C rise in soil temperature strongly increases the rate of decomposition. All of these effects appear to be tree species specific and are probably also influenced by soil properties.

Interactions between elevated CO_2 and temperature may greatly affect soil enzyme activity via changes in soil microbial community and plant growth. Feng et al. (2007) found that the compound effects of elevated CO_2 and temperature on enzyme activities were more significant than those of elevated CO_2 or temperature alone. Such positive feedback between elevated CO_2 and temperature is to be expected, as both factors have a generally positive effect on enzyme activity, the first through an increase in substrate availability and the second through an enhancement of activity rates. In N-limited ecosystems, warming may make more N available for increased plant uptake under elevated CO_2 by increasing N mineralization (Shaver et al. 2000), but the immediate availability of N is likely to be moderated by temperature, moisture, labile C and N input, soil pH and texture (Reich et al. 1997)—all characteristics likely to be altered by climate change.

Future research

Scientific evidence gathered so far indicates that climate change is likely to have a significant impact on tree nutrient uptake, allocation and cycling. More specifically, elevated CO_2 and temperature reviewed in this article have the potential to change both tree physiology and the long-term availability of nutrients. To date, however, we do not possess sufficient breadth of information relating to tree nutrition to be able to make reliable forecasts.

To close this gap in knowledge, CO_2 and temperature manipulation studies should proceed from studying the responses of seedling or young trees to evaluating impacts on mature trees and to work on an ecosystem scale, thus taking into account interactions and feedbacks between plants and soil (Calfapietra et al. 2010). Future studies should focus on simultaneous investigation of multiple factors in order to uncover and study interactions and feedback mechanisms that drive nutrient cycles in forest ecosystems. Although clearly needed, it will be difficult to initiate large-scale warming and/or CO_2 enrichment experiments on forest ecosystems due to obvious funding constraints. To get around such limitations, experiments that make use of existing climatic and soil gradients should be established to test the response of the dominant forest tree species to alterations in nutrient availability. An important avenue of research, somewhat unrepresented at the moment, is the development of dedicated nutrient cycle models to assess and predict the response of forests to climate change and to include these in forest vegetation dynamics models.

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