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Global Climate Change and Tree Nutrition: Effects of Elevated CO₂ and Temperature.

Martin Lukac,^{1,5} Carlo Calfapietra,² Alessandra Lagomarsino³ and Francesco Loreto⁴

¹ *NERC Centre for Population Biology, Imperial College London, Ascot, SL5 7PY, UK*

² *Institute of Agro-Environmental & Forest Biology (IBAF), National Research Council (CNR), 05010 Porano (TR), Italy*

³ *Department of Forest Environment and Resources (DISAFRI), Università degli Studi della Tuscia, Via S. Camillo de Lellis, I-01100 Viterbo, Italy*

⁴ *Institute for Plant Protection (IPP), National Research Council (CNR), 50019 Sesto Fiorentino, Italy*

⁵ *Corresponding author (m.lukac@imperial.ac.uk)*

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 CO₂ 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 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 analyzing interactions between factors such as elevated CO₂, temperature or water availability .

1. Introduction

The cycling of nutrients between the soil and the 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 mineralisation, atmospheric deposition, weathering).

Forest trees are characterised by the C3 photosynthetic pathway (Ainsworth and Long 2005). As such, their productivity and demand for nutrients is greatly affected by atmospheric CO₂ concentration and temperature. Terrestrial ecosystems are already exposed to atmospheric CO₂ concentration higher than that encountered since the early Miocene (Pearson and Palmer 2000) and despite recent efforts to limit global CO₂ emissions, the atmospheric concentration of this greenhouse gas is likely to exceed the worst-case scenario considered by the 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 has been aimed at elucidating the responses of a wide range of plants to rising CO₂ and temperature. In general, a stimulation of biomass production with increasing CO₂ 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.

To date, most physiological observations on trees exposed to changing CO₂ 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 effects of elevated CO₂ 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 CO₂ 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 CO₂ 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.

2. Effects of elevated CO₂.

Photosynthetic carbon uptake by C₃ plants is enhanced by elevated CO₂ (Ainsworth and Rogers 2007) and has been shown to translate to a consistent stimulation of NPP in trees by about 23% (Norby et al. 2005). The increase in productivity expected from trees growing in elevated CO₂ 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 CO₂ 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 which have been fairly well investigated so far and the physiology and cycling of which is reasonably well understood in the frame of climate change.

2.1 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 future high CO₂ 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, depending on soil nutrient status and ecosystem type (Figure 2). Boreal forests, where most of 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 CO₂. 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 CO₂ enriched atmosphere (Ainsworth and Long 2005), but the initial stimulation decreases if photosynthetic acclimation takes place and foliar N content declines

(Ainsworth and Rogers 2007; Ellsworth et al. 2004). Foliar N content per unit leaf area often declines under elevated CO₂ (Ellsworth et al. 2004), an effect often amplified by denser canopies under elevated CO₂. Larger leaf biomass requires higher N investment 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 CO₂ assimilated per unit of foliar N is also increased in high CO₂, predominantly by enhanced CO₂ uptake rather than by N redistribution (Leakey et al. 2009; Liberloo et al. 2007). As atmospheric CO₂ continues to rise, further increases in PNUE would be necessary to sustain higher CO₂ uptake. The 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 CO₂ alters the relationship between photosynthesis or its component processes and foliar N content (increased PNUE). However, providing abundant N to trees grown under elevated CO₂ 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 CO₂ 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 CO₂ 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 CO₂ (Marinari et al. 2007; Tingey et al. 2003) 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 CO₂, resulting in a significant increase of Nitrogen Use Efficiency (NUE) under elevated CO₂ (Calfapietra et al. 2007). However, in other FACE sites the stimulation of biomass production due to elevated CO₂ 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) note 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 CO₂.

Fine roots of forest trees are, of course, not the only biomass pool increasingly competing for N under elevated CO₂. Symbiotic mycorrhizal fungi colonizing tree roots have been shown to significantly benefit from increased photosynthate availability under elevated CO₂ (Alberton et al. 2007; Treseder 2004). Nitrogen uptake by mycorrhizal networks is thought to be much more efficient and rapid than that of fine tree roots, largely due to 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 CO₂ needs further investigation as a stimulation of mycorrhizal growth under elevated CO₂ 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 CO₂ (Carney et al. 2007; Treseder 2004); 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- (AM) and ecto- mycorrhizae (EM) under elevated CO₂. Significantly, no studies reported negative effects on mycorrhizal colonisation or extraradical biomass. Fungi commonly have higher C/N ratios than soil bacteria, using smaller amounts of N to produce equivalent amount 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 CO₂ 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 will 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 CO₂ on this link, the few studies which focused on the impact of elevated CO₂ 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 inputs under elevated CO₂ are 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 NH₄) 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 mineralized N pool in the soil. Since elevated CO₂ alters 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 were reported on N cycling in forest ecosystems under elevated CO₂, probably reflecting different N status at the whole ecosystem scale. Nitrogen mineralization has been found to increase (when coupled to a correspondent increase in NH₄ immobilization) (Holmes et al. 2006), decrease (Billings and Ziegler 2005) and, most often, did not change (Austin et al. 2009; Finzi et al. 2006; Zak et al. 2003). 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 CO₂ 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 larger N uptake. Overall N availability under elevated CO₂ appears to be sensitive to forest ecosystem type, a factor which needs further investigation.

2.2 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 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 forms 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 CO₂ 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 CO₂ (Ineson et al. 1996; Lagomarsino et al. 2008)}, reflecting an increase of 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 CO₂ may lead to increased rates of P mineralization and release from soil mineral fraction.

There are not many observations on the effects of elevated CO₂ 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 CO₂ on P availability was shown, leading to a decrease in extractable P after five years (Johnson et al. 2003). In a sweetgum forest subjected to elevated CO₂, no effects of elevated CO₂ 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 CO₂ significantly changed the fractionation of P in the soil. Observed increase in tree growth under elevated CO₂ did not result in depletion of P pools in soils, but rather in 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 CO₂ 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 CO₂ on P uptake. Phosphorus nutrition of tree seedlings grown in unadulterated forest soils under elevated CO₂ 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.

2.3 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 CO₂ on nutrients other than N and P are almost exclusively based on crop plants. Such studies report a wide variation in effects of CO₂ 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 CO₂ 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 at a timescale of days, revealed that in young walnut seedlings grown in elevated CO₂ nutrient uptake rates of K⁺, Ca²⁺ and Mg²⁺ were proportional to CO₂ uptake rate, but that of 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 CO₂. They observed that the dilution of essential micronutrients in plant tissues harvested from high CO₂ treatment was less than that of non-essential ones. Alongside tree species and soil characteristics, the effect of elevated CO₂ 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 of some exchangeable base cations (Ca²⁺ and Mg²⁺) and a decrease of acid cations (Al³⁺ and Mn²⁺) in Scots pine grown in under elevated CO₂ 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 CO₂. At the same site, nutrient input of N, P, S, P, Ca, Mg, Cu and Zn to soil

through leaf litter under elevated CO₂ 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 CO₂. However, elevated CO₂ had no significant effect on availability of any measured nutrient in the soil, with the exception of the reduction of SO₄²⁻ and Ca²⁺ 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 CO₂. In a fast growing poplar plantation, an increase of base cation availability (Ca and Mg), together with an overall increase of CEC was found under elevated CO₂ (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 of CEC under elevated CO₂ can result from an increase of 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 CO₂ atmosphere might therefore be able to (indirectly) affect the soil's capacity for nutrient provision and thus regulate nutrient availability in the long term.

3. 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., (Watanabe et al. 2007; Wood et al. 2006)). Since soil and especially air temperature are more difficult to manipulate than atmospheric CO₂ at ecosystem level, our knowledge about the effects of increasing temperatures at this scale is currently limited and generally inferred from smaller scales or models.

3.1 Direct effects on trees

Changes in ambient temperature may induce a range of responses in trees and in forest ecosystems (Figure 3). Starting with the photosynthesis, the 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 O₂ is known to dissolve more efficiently than CO₂, which generates a better availability of O₂ 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, similarly to the effects of elevated CO₂, 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 impacts 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 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 of 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 signaling 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.

3.2 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 (Beier et al. 2008; Rustad et al. 2001). In particular, observed effects appear to be very seasonal, with the highest increase of 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, while 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 on soil N mineralization at higher temperatures, with beneficial effects on plant growth. However, Beier et al. (2008) reported nitrogen mineralization was relatively insensitive to the temperature increase across a range of ecosystems 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 nutrients 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 difference in responses to higher temperature, an increase of N mineralization in soil can be predicted under favourable moisture conditions and substrates availability, mainly in those ecosystems where temperature is a limiting factor. An increase of 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 Net Primary Productivity (NPP), increased N demand and ultimately to decreased N availability in the soil.

4. 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 CO₂ and increasing temperature on tree physiology are fairly well described and understood. For instance photosynthetic rate increases substantially with elevated CO₂ 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 CO₂ 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 CO₂ is expected to directly influence tree physiology, compounding the changes affected by alterations of ambient temperature and rainfall (both amounts and patterns) – with 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 CO₂ is not thought to have a direct effect on weathering, larger supply of photosynthate to mycorrhizal fungi has been shown to occur under elevated CO₂ (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 future elevated CO₂ 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 CO₂ alters litter quality (Cotrufo et al. 2005; Cotrufo et al. 1998), with significant decreases in its nutrient content. Less nutrients per unit weight, coupled with slower litter decomposition under elevated CO₂ (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), 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 CO₂ 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 CO₂ and temperature on enzyme activities were more significant

than those of elevated CO₂ or temperature alone. Such positive feedbacks between elevated CO₂ and temperature are to be expected, as both factors have a generally positive effect on enzyme activity. The first through an increase of 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 CO₂ 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.

5. 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 CO₂ 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 as to be able to make reliable forecasts.

To close this gap in knowledge, CO₂ and temperature manipulation studies should proceed from studying the responses of seedling or young trees to evaluating impacts on mature trees and to work at 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 CO₂ enrichment experiments on forest ecosystems due to obvious funding constraints. To get around such limitations, experiments which 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 into forest vegetation dynamics models.

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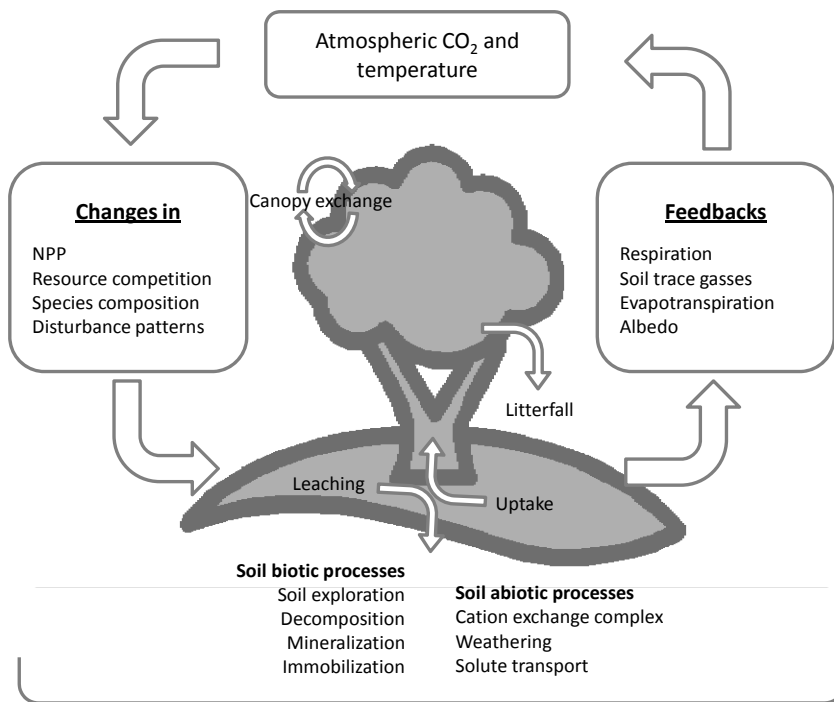
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Ecosystem services

Forest products, Water quality and quantity, Soil conservation, Biodiversity, Recreation

