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Impacts of elevated atmospheric CO_2 on forest trees and forest ecosystems: knowledge gaps

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Abstract

Atmospheric CO_2 is rising rapidly, and options for slowing the CO_2 rise are politically charged as they largely require reductions in industrial CO_2 emissions for most developed countries. As forests cover some 43% of the Earth's surface, account for some 70% of terrestrial net primary production (NPP), and are being bartered for carbon mitigation, it is critically important that we continue to reduce the uncertainties about the impacts of elevated atmospheric CO_2 on forest tree growth, productivity, and forest ecosystem function. In this paper, I review knowledge gaps and research needs on the effects of elevated atmospheric CO_2 on forest above- and below-ground growth and productivity, carbon sequestration, nutrient cycling, water relations, wood quality, phenology, community dynamics and biodiversity, antioxidants and stress tolerance, interactions with air pollutants, heterotrophic interactions, and ecosystem functioning. Finally, I discuss research needs regarding modeling of the impacts of elevated atmospheric CO_2 on forests.

Even though there has been a tremendous amount of research done with elevated CO_2 and forest trees, it remains difficult to predict future forest growth and productivity under elevated atmospheric CO_2. Likewise, it is not easy to predict how forest ecosystem processes will respond to enriched CO_2. The more we study the impacts of increasing CO_2, the more we realize that tree and forest responses are yet largely uncertain due to differences in responsiveness by species, genotype, and functional group, and the complex interactions of elevated atmospheric CO_2 with soil fertility, drought, pests, and co-occurring atmospheric pollutants such as nitrogen deposition and O_3. Furthermore, it is impossible to predict ecosystem-level responses based on short-term studies of young trees grown without interacting stresses and in small spaces without the element of competition. Long-term studies using free-air CO_2 enrichment (FACE) technologies or forest stands around natural CO_2 vents are needed to increase the knowledge base on forest ecosystem responses to elevated atmospheric CO_2. In addition, new experimental protocols need to continue to be developed that will allow for mature trees to be examined in natural ecosystems. These studies should be closely linked to modeling efforts so that the inference capacity from these expensive and long-term studies can be maximized.

Keywords: Greenhouse gases; Climate change; Atmospheric CO_2; Research needs

1. Introduction

The Earth's atmospheric CO_2 concentration has risen to nearly 30% since the mid-1800s (Barnola et al., 1995; IPCC, 2001), an increase largely resulting from fossil fuel burning and forest clearing (Keeling et al., 1995). While thousands of papers have been published on the impacts of elevated atmospheric CO_2 on plants and plant communities (Mooney et al., 1991; Bazzaz and Fajer, 1992; Bowes, 1993; Curtis et al., 1994; Mooney and Koch, 1994; Drake et al., 1997), trees and forests have generally been underrepresented in the CO_2 literature (Ceulemans and Mousseau, 1994; Scarascia-Mugnozza et al., 2001). Nevertheless, a growing body of excellent reviews has been published in the past 8 years about the impacts of elevated atmospheric CO_2 on forest trees and forest ecosystems (Ceulemans and Mousseau, 1994; Curtis, 1996; Curtis and Wang, 1998; Saxe et al., 1998; Norby et al., 1999; Karnosky et al., 2001a). The growing interest in the impacts of elevated atmospheric CO_2 on forest trees and forest ecosystems is not surprising as forests cover some 43% of the Earth's surface (Melillo et al., 1993), account for some 70% of terrestrial net primary production (NPP) (Melillo et al., 1993), and are being bartered on world markets for carbon mitigation purposes (Nilsson, 1995). This paper will make no attempt to summarize previous research on elevated atmospheric

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CO_2 and forests (the reader is requested to see the above reviews). Rather, this paper will address areas where knowledge gaps remain and where additional research is needed.

2. Growth and productivity

A driving and largely unanswered question in the study of the effects of climate change on forest ecosystems is whether biomass production will be increased as a result of increasing atmospheric CO_2 concentrations (Medlyn et al., 2001a). While it is clear that photosynthesis is enhanced by elevated atmospheric CO_2 (Curtis, 1996; Eamus and Ceulemans, 2001) and that long-term down-regulation in photosynthesis may not occur (Norby et al., 1999, 2001a; Herrick and Thomas, 2001; Noormets et al., 2001a; Sôber et al., in press), it is far less certain what will happen with long-term growth and productivity under elevated atmospheric CO_2 (Körner, 2000; Scarascia-Mugnozza et al., 2001). This uncertainty arises for several reasons. First, most studies with trees have been with small trees, for short duration, and inside greenhouse or field chambers that modify the environmental conditions and do not allow for interactions with other natural stressors. Secondly, it is becoming increasingly clear that interactions with other factors such as soil fertility (Oren et al., 2001), atmospheric pollutants (Isebrands et al., 2001), and soil moisture (Chaves and Pereira, 1992) can offset the elevated atmospheric CO_2 “fertilization effect”, when trees are exposed under more natural forest conditions. Thirdly, almost all studies of elevated greenhouse gases on forest trees have either doubled the gas concentration or done a single large addition; thus, very little is known about the dose response and interactive effects of varying doses of greenhouse gases. With elevated CO_2, for example, little is known about how plants and plant communities will respond to the addition of 50–150 ppm above ambient. Similarly, little is known about the range of combinations of CO_2 and O_3, for example, where one pollutant or the other may dominate the response depending on the exposure doses.

2.1. Above-ground growth and productivity

The average enhancement of photosynthesis for trees exposed to elevated CO_2 has been about 60% (Norby et al., 1999). However, the responses vary considerably between species (Naumburg et al., 2001), by position in the crown (Takeuchi et al., 2001), by nitrogen fertility level (Sôber et al., in press), by season (Noormets et al., 2001a,b), and by co-occurring pollutant concentrations (Noormets et al., 2001a,b; Sôber et al., in press).

The enhanced photosynthesis has generally been followed by a similar, albeit a somewhat decreased magnitude, enhancement of above-ground growth. Growth enhancement for trees exposed to elevated CO_2 has been about 27% (Norby et al., 1999), with responses again varying with species (Karnosky et al., in press), soil fertility (Oren et al., 2001), O_3 levels (Isebrands et al., 2001), and year (Norby et al., 2001a). Whether or not the positive growth responses to elevated atmospheric CO_2 will be maintained through the life cycles of trees is not known. During the exponential growth phase, from planting to crown closure, trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.) growth enhancement under elevated atmospheric CO_2 has been maintained for 4 years (Isebrands et al., 2001; Karnosky et al., in press; Percy et al., 2002). However, with trees beyond the exponential growth stage, the picture is less clear. Growth enhancement of a 10-year-old loblolly pine (*Pinus taeda* L.) forest by elevated CO_2 resulted in a few years of growth stimulation (DeLucia et al., 1999). However, this was followed by sharply decreased growth after the third year of exposure (Oren et al., 2001), most likely because soil fertility became a limiting factor. A similar trend of early above-ground growth stimulation by elevated atmospheric CO_2, for a 15-year-old sweetgum (*Liquidambar styraciflua* L.) plantation, followed by a decreased annual response, has been reported by Norby et al. (2001a).

The longest study of continuous exposure of forest trees to elevated atmospheric CO_2 has occurred with forest patches of holm oak (*Quercus ilex* L.) growing for approximately 30 years in the vicinity of two natural CO_2 springs in Italy (Hättenschwiler et al., 1997). From this study, early growth enhancement included an almost doubling of annual growth ring size under elevated CO_2. However, a diminishing growth enhancement was noted over the study and at ages 25–30, there is no additional stimulation of annual growth rings, and the CO_2-enhanced trees are only marginally larger than controls. Interestingly, Tognetti et al. (2000) found no radial growth enhancement in their long-term study of five Mediterranean tree species growing near CO_2 vents.

From studies to date, we know that the life-long above-ground growth response of forest trees in forest stands cannot be accurately predicted from short-term greenhouse or chamber studies (Norby et al., 1999) or from step increases in CO_2 concentrations of one age class of trees alone (Körner, 2000). Studies are needed under realistic forest conditions where trees are exposed to elevated CO_2 in competitive situations, under natural co-occurring stresses, and for the lifetime of the stand.

Long-term growth of forest trees under forest stand conditions, free of chamber effects, with realistic conditions of above- and below-ground competition, and with natural co-occurring stresses including other pollutants and insect disease pests are needed to reduce uncertainties related to impacts of elevated atmospheric CO_2. The two methods most likely to provide robust and repeatable results are free-air CO_2 enrichment (FACE) studies (Hendrey et al., 1999; McLeod and Long, 1999; Karnosky et al., 2001b) and studies using naturally occurring CO_2 vents surrounded by natural forest communities (Hättenschwiler et al., 1997;

Tognetti et al., 2000; Blaschke et al., 2001). While these studies also have limitations (e.g., blower effects and high costs of the FACE experiments and the co-occurrence of contaminating gases, difficulty of finding adequate replication and representative controls for the CO_2 vent studies), these types of studies are among the best options for addressing productivity and competitive effects on productivity under elevated CO_2.

2.2. Below-ground growth and productivity

Root systems comprise up to half the total tree biomass and below-ground net primary production may exceed 50% of total net primary production (Kubiske and Godbold, 2001). Because C allocation to roots is often favored over C allocation to shoots in plants grown under elevated atmospheric CO_2, below-ground function of forest ecosystems may change significantly (Pritchard et al., 2001).

Increased root growth of forest trees under elevated atmospheric CO_2 has been reported by several researchers (Matamala and Schlesinger, 2000; Pregitzer et al., 2000; King et al., 2001; Pritchard et al., 2001). Consistent findings show that the production and mortality of fine roots produced by trees growing under CO_2 enrichment are significantly increased (Matamala and Schlesinger, 2000; Pregitzer et al., 2000; King et al., 2001; Pritchard et al., 2001). Species differ in the responsiveness of their root systems to increased atmospheric CO_2, suggesting that differences in the ability of certain species to compete against others could be dramatically changed under elevated CO_2 (Pritchard et al., 2001). It is not clear what effect these increased rates of fine-root turnover will have on C storage in the soil (Pregitzer et al., 2000). In addition, little is known about CO_2 effects on the growth, development, and C storage capacity of large, structural roots (Kubiske and Godbold, 2001). Furthermore, more research is needed to determine if C allocation (i.e. root/shoot ratios) changes under elevated atmospheric CO_2 (Medlyn et al., 2001a).

3. Carbon sequestration

There is growing interest in the capacity of forest trees and forest ecosystems to sequester carbon. This very complex question has taken on a new level of importance with the advent of tree planting (Fearnside, 1999; Rotter and Danish, 2000; Van Kooten et al., 2000), improved forest management (DeJong et al., 2000; Pinard and Cropper, 2000) and forest conservation (Pfaff et al., 2000) for carbon emission credits are being publicly traded worldwide. Carbon sequestration is a complex process that is difficult to measure as growth, yield, net primary production, and C turnover are often confused with C sequestration (Körner, 1995). Carbon sequestration by forests can be quantified on the basis of their net ecosystem productivity (Jarvis, 1989; Malhi et al., 1999; Scarascia-Mugnozza et al., 2001). This is net primary productivity after subtracting the heterotrophic respiration caused by decomposition of above- and below-ground litter. Hence, the net ecosystem productivity is the amount of organic C immobilized in the forest ecosystem as living woody biomass and as soil organic matter over a given amount of time and per unit of land surface (Scarascia-Mugnozza et al., 2001). Few forest tree studies have as yet estimated impacts of elevated atmospheric CO_2 on carbon sequestration. However, observations at two FACE studies suggest that soil respiration rates are higher under elevated CO_2 (King et al., 2001; Schlesinger and Richter, 2001). Schlesinger and Richter (2001) suggest that a large portion of the additional C added to soils is likely returned to the atmosphere. They further point to the fact that they are not seeing C accumulation in deeper mineral soil layers in their loblolly pine stands exposed to elevated CO_2. Therefore, increased soil C sequestration of trees growing in elevated atmospheric CO_2 has not yet been demonstrated.

4. Mineral cycling

It has been well documented that the nitrogen level in the foliage of trees growing under elevated atmospheric CO_2 is generally decreased (Lindroth et al., 1993, 1997, 2001a). It is also decreased in the litter (Norby et al., 2001b). However, the quantity of litter increases 20–30% under elevated atmospheric CO_2 (DeLucia et al., 1999). Less certain is what is happening to nitrogen cycling (Zak et al., 2000; Johnson et al., 2001). Among the greatest uncertainties for nutrient cycling is whether or not nutrient mineralization rates will change due to the higher quantity of CO_2 in the soils (Ceulemans and Mousseau, 1994). It is also uncertain whether decomposition rates will be significantly impacted by elevated CO_2, although the bulk of literature in this area suggests that the decrease in leaf litter N, coupled with an increase in lignin concentration, results in a slower decomposition rate (Norby et al., 2001b).

5. Water balance

Given that some 70% of all water vapor emitted from terrestrial ecosystems passes through leaf stomata (Körner, 2000), there continues to be a great interest in how elevated atmospheric CO_2 affects stomatal conductance and forest stand-level transpiration. Long-term studies of forest trees have shown a significant 21% decrease in stomatal conductance (Medlyn et al., 2001b) with elevated CO_2. Because of the increased size of trees under elevated atmospheric CO_2, the question remains: 'Do trees use more water or less water even if stomatal conductance is decreased (Scarascia-Mugnozza et al., 2001)?'. Similarly, there is uncertainty whether water use efficiency will really be improved in forest stands, as has been suggested from instantaneous water use efficiency estimates from small and isolated trees (Scarascia-Mugnozza et al., 2001). Stand-level transpiration measurements for forest trees under elevated atmospheric CO_2 have only been made on a few species (Wullschleger and Norby, 2001); this remains an important research need. In conjunction with stand-level transpiration measurements, estimates of groundwater content should be made to complete the water balance picture.

6. Wood quality and chemical composition

Wood and pulp quality are known to be affected by factors such as wood density, early versus late wood amounts, juvenile wood, fiber length, branchiness, branch thickness, and wood chemical composition. Very little is yet known about the impacts of elevated atmospheric CO_2 on wood quality or chemical composition. Oren et al. (2001) reported a decrease in specific gravity from 0.52 to 0.48 g cm^{-3} for loblolly pine being grown under elevated CO_2. The decrease was similar in magnitude to what they reported for the same trees under fertilization. Karnosky et al. (in press) and Anttonen et al. (2001) reported no changes in lignin content, fiber length, hemicellulose content, or cellulose content in samples from young aspen trees exposed for 3 years to elevated CO_2. Similar results were reported for lignin by Blaschke et al. (2001). To the best of my knowledge, no one has tested pulp yields or pulping characteristics for forest trees growing under elevated atmospheric CO_2. Certainly, the impacts of elevated atmospheric CO_2 on wood quality and chemical composition for a cross-section of the major timber trees of the world is a high priority for the pulp and paper, and timber industries.

7. Phenology

Elevated atmospheric CO_2 concentrations affect the phenology of bud break and bud set, flowering time, length of time to seed set, leaf senescence and drop, and branch and shoot development rates (Jach et al., 2001). The most thoroughly studied phenological events have been spring bud break and autumn bud set. Bud break is either delayed (Murray et al., 1994; Repo et al., 1996) or advanced (Repo et al., 1996) under elevated atmospheric CO_2. Similarly, the date of bud set in the autumn can either be advanced (Mousseau and Enoch, 1989; Murray et al., 1994) or delayed (Karnosky et al., in press). Both timing of bud break and bud set are important in determining frost and winter hardiness of northern trees species (Repo et al., 1996; Lutze et al., 1998; Wayne et al., 1998). Increased frost injury (Repo et al., 1996; Lutze et al., 1998) and increased winter dieback (Isebrands et al., 2001) have both been described for trees growing under elevated atmospheric CO_2 in northern regions. Others have described a possible increased cold hardiness for some trees growing under elevated atmospheric CO_2 due to the buildup of soluble sugars that may act as cryoprotectants (Ögren et al., 1997). This variation in CO_2-induced phenology responses suggests that species differences play an important role and that additional study is needed to determine major trends in CO_2 effects on phenology.

8. Antioxidants and stress tolerance

Because of its capability to impact primary plant metabolism, increasing atmospheric CO_2 has been predicted to have profound and far-reaching consequences for the delicate equilibrium between pro-oxidants and antioxidants within the plant cell (Podila et al., 2001). Increasing CO_2 could potentially reduce the basal rate of O_2 activation and reactive oxygen species formation within several plant cell compartments through enhancing the pCO_2/pO_2 ratio at the sites of photo-reduction, and also by progressively suppressing photo-respiration in C_3 plants (Podila et al., 2001). In the long term, this could lead to a depressed antioxidant status in plants with as yet undetermined impacts for overall stress tolerance, which in large part are attributable to antioxidants. Research is only beginning to show the complexity of CO_2 impacts on antioxidant production. For example, both CO_2-driven down-regulation (Polle, 1996; Schwanz and Polle, 1998; Karnosky et al., 1998; Niewiadomska et al., 1999; Wustman et al., 2001) and up-regulation (Niewiadomska and Miszalski, 1995) of antioxidants have been demonstrated.

As with the antioxidant data, the story developing with CO_2 impacts on stress tolerance is also complex. The literature has examples of both enriched CO_2-induced increased (Wayne et al., 1998; Schwanz and Polle, 2001a,b) and decreased (Kull et al., 1996; Karnosky et al., 1998; Wustman et al., 2001) oxidative stress tolerance. Again, these responses are complex because of species and genotypic differences (Badiani et al., 1998, 1999) and because there is such a wide array of antioxidants produced by plants (Podila et al., 2001). This is an area needing additional research attention. With the advent of modern molecular methods, significant progress has been made in isolating antioxidant genes (Akkapeddi et al., 1999) and in producing transgenic trees silenced or enhanced for specific antioxidant genes (Barnes et al., 1999; Grover et al., 1999). These transgenic trees could now serve to better test hypotheses about up or down-regulation of specific antioxidant activities by elevated atmospheric CO_2.

9. Pollutant interactions

While it is well known that atmospheric CO_2 is increasing globally (Keeling et al., 1995; IPCC, 2001), large areas of future forests will concurrently be exposed to other anthropogenic atmospheric pollutants (Reilly et al., 1999). These are rising at similar rates and include both nitrogen oxides (Norby, 1998; Fowler et al., 1998, 1999a) and tropospheric ozone (O_3) (Fowler et al., 1999b; IPCC, 2001). Although low levels of nitrogen deposition may stimulate the usual growth enhancement by CO_2 fertilization, particularly if the forest is growing on nutrient-poor soils, excess nitrogen deposition can (a) erode leaf surface waxes, (b) cause luxuriant autumn growth and lack of proper winter hardening in conifers predisposing them to early fall frosts and winter dieback, (c) induce leaching of nutrients from foliage and soils, (d) alter nutrient and toxic ion mobilization in the soil, and (e) alter soil pH (Norby, 1998). Furthermore, the nitrogen status of foliage is vital in plant–pest interactions. Little is known about how forests will react to elevated nitrogen deposition concurrently with elevated atmospheric CO_2 (Norby, 1998; Norby et al., 1999).

Ozone, a regional pollutant that occurs down wind of metropolitan areas around the world, is generated as a secondary pollutant from reactions of nitrogen oxides and volatile organic compounds in the presence of sunlight. Highly toxic to plants, O_3 alters leaf cuticle waxes, destroys chlorophyll, breaks down rubisco, causes premature foliar senescence, alters root–shoot ratios, impacts host–pest interactions, and decreases growth and productivity (Chappelka and Samuelson, 1998; Bortier et al., 2000).

Since pre-industrial times, background O_3 levels have risen about 36% (IPCC, 2001). Nearly one quarter of the Earth's forests is now subjected to O_3 concentrations that exceed 60 ppb, and it is likely that nearly one-half of the Earth's forests (17×10^6 km^2) will be subjected to similar damaging concentrations by 2100 (Fowler et al., 1999a,b). Thus, large areas of the world's forests will eventually be exposed concomitantly to elevated atmospheric CO_2 and O_3 (Barnes and Wellburn, 1998; Saxe et al., 1998). Since these two gases generally induce opposite sets of physiological responses, there is considerable uncertainty as to how tree growth and productivity and forest ecosystem functions will be affected by these two interacting pollutants (Barnes and Wellburn, 1998; Saxe et al., 1998). The few studies done for multiple years with trees planted in the ground have largely shown that O_3 offsets the growth enhancement of elevated atmospheric CO_2 both for hardwood trees (Broadmeadow and Jackson, 2000; Isebrands et al., 2001) and conifers (Broadmeadow and Jackson, 2000; Utriainen et al., 2000). The magnitude of the O_3 offset depends on the O_3 sensitivity of the species (Broadmeadow and Jackson, 2000; Karnosky et al., in press) and the concentrations of each pollutant, although research needs to be done with tree species to characterize dose responses.

In the only open-air exposure system in the world exposing forest stands to interacting atmospheric CO_2 and O_3, researchers at the Aspen FACE project found that $1.5 \times$ ambient O_3 offset the growth enhancement of $+200$ ppm CO_2 for trembling aspen and paper birch (Isebrands et al., 2001; Karnosky et al., in press). Interestingly, this study has shown consistent offsetting effects for a suite of host responses including leaf surface wax production (Mankovska et al., 1998; Karnosky et al., 1999), stress gene activation (Wustman et al., 2001), gas exchange (Karnosky et al., in press; Noormets et al., 2001a,b; Sôber et al., in press), foliar chemistry (Lindroth et al., 2001), foliar retention (Karnosky et al., in press), fine-root biomass production, and fine-root turnover (King et al., 2001).

Initial evidence for ecosystem-level O_3 offsets in net primary production, litter decomposition, water use efficiency, microbial enzymes, and microbial biomass is also noted (Karnosky et al., in press). Certainly, there is a need to study more species and more ecosystems under interaction of CO_2 and O_3. There is also a need to carry on these FACE studies to see if some of these O_3 offsets continue or even increase as these stands end their exponential phase of growth and attain sexual maturity.

10. Heterotrophic interactions

Elevated atmospheric CO_2 can substantially alter plant chemistry and leaf surface properties. These, in turn, can alter host/pest interactions. For example, it is well documented that levels of foliar N decline for trees growing under elevated atmospheric CO_2 (Cotrufo et al., 1998; Norby et al., 2000; Lindroth et al., 2002). Elevated CO_2 also alters C-based secondary metabolites, such as tannins and phenolic glycosides (Lindroth et al., 2001). Furthermore, elevated CO_2, alone or in combination with O_3, can significantly alter leaf surface wax chemical composition, structure, and wettability (Mankovska et al., 1998; Karnosky et al., 1999, 2002a). These alterations to leaves and leaf surfaces, for trees exposed to elevated atmospheric CO_2, impact host–pest interactions with changes in frequency of occurrence and/or feeding behavior in aphids (*Hamamelistes spinosus*), aspen blotch miner (*Phyllonorycter tremuloidiella*), forest tent caterpillar (*Malacosoma disstria*), and the wood borer (*Oberea schaumii*) (Karnosky et al., in press).

Certainly, there remain many knowledge gaps of host/pest interactions under increasing atmospheric CO_2. What will happen to host–pest dynamics as global warming accompanies elevated atmospheric CO_2 so that pest ranges expand to the north (Lincoln, 1993) into forests that have not previously been exposed to such pests and as additional life cycles of some insect pests increase their abundance? Kurz and Apps (1999) believe that increasing disturbance from insects, diseases, and fire in the Canadian boreal forest has resulted in this large region changing from a carbon sink to a carbon source in the past few decades. Certainly, more work is needed to verify Kurz and Apps' hypothesis and to better understand insect and disease dynamics under elevated atmospheric CO_2.

11. Community dynamics, biodiversity, and ecosystem function

Constrained plant shoot and root architecture and, thus, light, nutrient, and water captured in a competitive situation is normal for forest trees and, hence, should be considered as a prerequisite for realistic tree responses to CO_2 enrichment (Körner, 1995). Furthermore, there is no doubt that plant species respond in rather different ways depending on their age, neighbors, microbial partners, soil resources, and atmospheric conditions so that the experimental negation of these interactions and dependencies is wasteful or even worse, creating a biased picture of the world (Körner, 1995). As mentioned previously, two ways to escape the risks of artifacts are: FACE systems over large forest stands or in situ experimentation in natural forest communities around CO_2 springs.

Effects of CO_2 enrichment on forest tree competition, understory soil productivity and biodiversity, and ecosystem function are largely unknown. Few studies have been conducted on a large enough scale and for a long enough period of time to detect these effects, which are among the most important for ecosystem function but also among the most difficult to detect. Clearly, this area remains as high-priority research for the future.

12. Modelling and scaling

Since the majority of physiological, gene expression, and growth studies have been done with small trees growing without competition, there is a need for more measurements of CO_2 enriched trees at the whole-tree level with larger trees and at the canopy level with forest stands (Eamus and Ceulemans, 2001). Several factors require careful consideration when extrapolating data from studies of isolated small trees to forests (Ceulemans et al., 1999; Norby et al., 1999; Eamus and Ceulemans, 2001). These include (Norby et al., 1999):

- Seedlings or saplings do not respond in the same way as mature trees.
- Competition between trees for light and nutrients is normal in forests but rare in studies of individual trees.
- Patterns of allocation between root, stem, and leaf differ between immature and mature trees.
- The architecture of mature trees differs from that of immature trees.
- Species composition, tree density and leaf area distribution in space and time may change in response to CO_2 enrichment, and all of these factors influence gas exchange in the canopy.
- There have been few successful attempts to relate plant functional type to response functions to CO_2 enrichment. Consequently, modeling ecosystem response is limited to either dealing with mono-specific plantations or assigning average responses to a mix of species.

Process growth models, based on our best understanding of basic physiological processes, stand out as the best available tools to predict the impacts of elevated atmospheric CO_2 concentrations on forest trees and forest ecosystems (Magnani and Matteucci, 2001), when time scales and spatial scales preclude routine measurements at all scales needed. For these process models to be useful, additional research is needed for several key processes that still escape our understanding. Stomatal conductance, canopy-level conductance, water balances in trees, tissue, and soil respiration, and resource allocation patterns among forest trees growing in closed canopy stands can only be represented in a very empirical way (Magnani and Matteucci, 2001), as are nutrient uptake, tissue mortality, and flowering and seed production (Luo et al., 1999; Scarascia-Mugnozza et al., 2001).

On an ecosystem and landscape level, models need to incorporate respiration as a major determinant of the carbon balance (Valentini et al., 2000). Another modeling need on this level and above is to include elevated O_3 as a concomitant stress in the next century. No major global model of terrestrial net primary productivity includes O_3 as a co-occurring greenhouse gas (Karnosky et al., in press).

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