Response of Forest Trees to Increased Atmospheric CO2

Jian-Guo Huang a, Yves Bergeron a, Bernhard Denneler a, Frank Berninger b, Jacques Tardif c

a Chaire industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, 445 boulevard de l'Université, Rouyn-Noranda, Québec, Canada
b Chaire du Canada en productivité forestière, Département des sciences biologiques, CP 8888 Succ Centre Ville, Université du Québec à Montréal, Québec, Canada
c Canada Research Chair in Dendrochronology, Centre for Forest Interdisciplinary Research (C-FIR), University of Winnipeg, Winnipeg, Manitoba, Canada

Online Publication Date: 01 September 2007

To cite this Article: Huang, Jian-Guo, Bergeron, Yves, Denneler, Bernhard, Berninger, Frank and Tardif, Jacques (2007) 'Response of Forest Trees to Increased Atmospheric CO2', Critical Reviews in Plant Sciences, 26:5, 265 - 283

To link to this article: DOI: 10.1080/07352680701626978
URL: http://dx.doi.org/10.1080/07352680701626978

Please scroll down for article

Full terms and conditions of use: http://www.informaworld.com/terms-and-conditions-of-access.pdf

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.
Response of Forest Trees to Increased Atmospheric CO₂

Jian-Guo Huang,¹ Yves Bergeron,¹ Bernhard Denneler,¹,² Frank Berninger,³ and Jacques Tardif⁴

¹Chaire industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, 445 boulevard de l’Université, Rouyn-Noranda, Québec, Canada, J9X 5E4
²Deceased on January 13th 2007
³Chaire du Canada en productivité forestière, Département des sciences biologiques, CP 8888 Succ Centre Ville, Université du Québec à Montréal, Québec, Canada, H3P 3P8
⁴Canada Research Chair in Dendrochronology, Centre for Forest Interdisciplinary Research (C-FIR), University of Winnipeg, 515 Avenue Portage, Winnipeg, Manitoba, Canada, R3B 2E9

Table of Contents

I. INTRODUCTION .................................................................................................................................266

II. EMPIRICAL EVIDENCE FROM CO₂ ENRICHMENT EXPERIMENTS .............................................267
   A. Physiological Response to CO₂ .........................................................................................................267
      1. CO₂ and Temperature .....................................................................................................................268
      2. CO₂ and N ..................................................................................................................................268
      3. CO₂ and Drought ..........................................................................................................................269
      4. Downregulation .............................................................................................................................269
   B. Growth Response to CO₂ ..................................................................................................................270
      1. Aboveground Growth .....................................................................................................................270
      2. Belowground Growth ......................................................................................................................271
      3. Interactions with Other Environmental Factors .............................................................................271
   C. Implications for Mature Trees in the Forests ....................................................................................271

III. EMPIRICAL DENDROCHRONOLOGICAL STUDIES TESTING CO₂ FERTILIZATION EFFECT IN TREE
     RINGS ..................................................................................................................................................272
   A. Finding Evidence of CO₂ Fertilization Effect in Tree Rings ............................................................274
   B. Growth Enhancement Caused by Favorable Climate Change .........................................................274
   C. Combined Effects of Several Factors Such as Favorable Climate Change, CO₂ Fertilization, and Anthropogenic
      Atmospheric Deposition ................................................................................................................275

IV. EVIDENCE FOR CO₂ FERTILIZATION EFFECT DISPLAYED IN TREE RINGS IN NATURAL FORESTS 275
   A. Occurrence of CO₂ Fertilization Effect in Drought-Stressed Environments .....................................275
   B. Underestimation for CO₂ Fertilization Effect ..................................................................................276
   C. Possible Occurrence for Synergistic Effects of Several Factors ......................................................277

V. CONCLUSIONS ...................................................................................................................................277

ACKNOWLEDGMENTS ..........................................................................................................................278

REFERENCES ........................................................................................................................................278

Address correspondence to Jian-Guo Huang, Chaire industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, 445 boulevard de l’Université, Rouyn-Noranda, Québec, Canada, J9X 5E4. E-mail: jianguo.huang@uqat.ca

265
The CO2 fertilization hypothesis stipulates that rising atmospheric CO2 has a positive effect on tree growth due to increasing availability of carbon. Our review supports the atmospheric CO2 fertilization effect by combining evidence from both ecophysiology and tree-ring research. Based on considerable experimental evidence of direct CO2 fertilization effects (increased photosynthesis, water use efficiency, and above- and belowground biomass), and predications from the interactions of enriched CO2 with temperature, nitrogen and drought, we propose that warm, moderately drought-stressed ecosystems with an ample nitrogen supply might be the most CO2 responsive ecosystems. Empirical tree-ring studies took the following three viewpoints on detecting CO2 fertilization effect in tree-rings: 1) finding evidence of CO2 fertilization effect in tree-rings, 2) attributing growth enhancement to favorable climate rather than atmospheric CO2 enrichment, and 3) considering that tree growth enhancement might be caused by synergistic effects of several factors such as favorable climate change, CO2 fertilization, and anthropogenic atmospheric deposition (e.g., nitrogen). At temperature-limiting sites such as high elevations, nonfindings of CO2 fertilization evidence could be ascribed to the following possibilities: 1) cold temperatures, a short season of cambial division, and nitrogen deficiency that preclude a direct CO2 response, 2) old trees past half of their maximum life expectancy and consequently only a small increase in biomass increment due to CO2 fertilization effect might be diminished, 3) the elimination of age/size-related trends by statistical detrending of tree-ring series that might remove some long-term CO2-related trends in tree-rings, and 4) carbon partitioning and growth within a plant that is species-specific. Our review supports the atmospheric CO2 fertilization effect hypothesis, at least in trees growing in semi-arid or arid conditions because the drought-stressed trees could benefit from increased water use efficiency to enhance growth.

Keywords CO2 fertilization effect, CO2 enrichment experiment, dendrochronology, ecophysiology, tree-rings, water use efficiency

1. INTRODUCTION

Atmospheric carbon dioxide (CO2) is a substrate for plant photosynthesis. Increased atmospheric CO2 concentration is believed to, therefore, increase photosynthesis rate by increasing CO2 intake directly (Arp, 1991; Long and Drake, 1992; Koch and Mooney, 1996; Curtis, 1996; Mooney et al., 1999; Norby et al., 1999). Increased atmospheric CO2 might induce a partial closure of stomata, reducing water loss by transpiration, which results in an increase in the ratio of carbon gain to water loss, i.e., water use efficiency (Farquhar et al., 1989; Bowes, 1993; Field et al., 1995; Drake et al., 1997; Farquhar, 1997; Körner, 2000). As a result, this effect can lengthen the duration of growing seasons in seasonally dry ecosystems, thus probably stimulating biomass accumulation (Ceulemans and Mousseau, 1994; Saxe et al., 1998), and enhancing ecosystem net primary productivity (Amthor, 1995; Loehle, 1995). This CO2-induced enhancement in primary productivity and water use efficiency is commonly referred to the direct ‘fertilization effect’ (Beedlow et al., 2004).

As one of the greenhouse gases, CO2 has been the most important factor associated with a rise in temperature during recent decades (IPCC, 2007). A new simulation study under a doubled CO2 concentration suggested that the positive feedbacks of CO2 and CH4 might be important, i.e., higher temperatures may lead to increased releases (or reduced uptake) of CO2 and/or CH4 by the ocean, forests, and soils (Torn and Harte, 2006; Scheffer et al., 2006). As a consequence, the greenhouse gases-induced temperature increases over the coming century might be able to reach 1.6–6.0°C (Torn and Harte, 2006) compared to 1.4–4.5°C predicted previously (IPCC, 2001). The increased temperature as well as the correspondingly increased precipitation over northern mid- to high latitudes could enhance growth of plants and change forest ecosystems. This is a so-called indirect effect of atmospheric CO2 enrichment on plants.

With continuously anthropogenic atmospheric CO2 enrichment, it was hypothesized that CO2 enhancement could enhance tree growth and change growth of forests through direct CO2 fertilization effect (LaMarche et al., 1984; Hari and Arovaara, 1988; Kienast and Luxmoore, 1988; Graumlich, 1991; Graybill and Idso, 1993). Interestingly, many tree-ring studies have reported an increase in radial growth of trees with the rise of atmospheric CO2 concentration (e.g., LaMarche et al., 1984; Payette et al., 1985, 1989; D’Arrigo et al., 1987; Hari and Arovaara, 1988; Kienast and Luxmoore, 1988; Archambault and Bergeron, 1992; Graybill and Idso, 1993; D’Arrigo and Jacoby, 1993; Becker et al., 1994; Nicolussi et al., 1995; Spiecker, 1996; Knapp et al., 2001; Zhang et al., 2003; Bunn et al., 2005; Wang et al., 2006; Huang and Zhang, 2007), although some other studies found no anomalous growth enhancement during recent decades (Schweingruber et al., 1993; Mielikäinen and Timonen, 1996; Mäkinen et al., 2000). However, it is still unclear whether increased growth of trees observed is attributed to direct CO2 fertilization effect or to indirect effect of enriched atmospheric CO2 concentration.

The large size and long life spans of trees make it technically and economically challenging to measure and monitor their growth response to CO2 enrichment. In practice, two kinds of approaches to detect the effects of atmospheric CO2 enrichment on trees were used: 1) short-term field CO2-enrichment experiments on seedlings or young trees, and 2) empirical dendrochronological studies. During the past decades, CO2 enrichment experiments were conducted over five continents and the results showed that elevated CO2 concentration can have significant effects on growth of young trees or seedlings (e.g., Chidumayo, 1990; Sage, 1994; Amthor, 1995; Curtis, 1996; Eamus, 1996; Drake et al., 1997; Saxe et al., 1998; Curtis and Wang, 1998; Norby et al., 1999; Medlyn et al., 1999; Schlesinger and Lichter, 2001; Ainsworth and Long, 2005; Körner, 2006). In contrast, results from dendrochronological studies to detect atmospheric CO2 fertilization effect in tree-rings are controversial and still under debate (LaMarche et al., 1984; Hari and Arovaara, 1988; Kienast and Luxmoore, 1988; Graumlich, 1991; Briffa, 1991; D’Arrigo and Jacoby, 1993;
Graybill and Idso, 1993; Becker et al., 1994; Nicolussi et al., 1995; Spiecker, 1996; Rolland et al., 1998; Knapp et al., 2001; Bunn et al., 2005; Wang et al., 2006).

The objective of this paper is to compare the recent literature related to both field CO2-enriched experiments with trees and empirical dendrochronological studies detecting CO2 fertilization effect in tree-rings in order to evaluate tree growth response to atmospheric CO2 enrichment by combining congruent evidences from both ecophysiology and tree-ring research. Since some meta-analytical reviews on enriched-CO2 experimental studies already exist (e.g., Curtis and Wang, 1998; Norby et al., 1999; Ainsworth and Long, 2005; Wang, 2007), we will synthesize the results from the literature reviews and empirical dendrochronological studies to assess whether CO2 fertilization effect really occurs in tree-rings in natural forests. The text is structured as follows: 1) empirical evidence from CO2 enrichment experiments, 2) empirical dendrochronological studies testing CO2 fertilization effect in tree-rings, 3) evidence for CO2 fertilization effect displayed in tree-rings in natural forests, and 4) conclusions.

II. EMPIRICAL EVIDENCE FROM CO2 ENRICHMENT EXPERIMENTS

A. Physiological Response to CO2

The theoretical hypothesis suggests that plants growing in a higher temperature (Long, 1991; Drake et al., 1997), and higher nitrogen (N) availability environment (Luo et al., 2004; Norby and Iversen, 2006) with moderate drought (Beerling et al., 1996; Wullschleger et al., 2002; Morgan et al., 2004; Nowak et al., 2004) might have larger growth increases under atmospheric CO2 enrichment. CO2 and temperature dependencies of photosynthesis and temperature dependencies of dark respiration are metabolic pathways that produce ATP and reductants to meet energy demands for plant growth and maintenance (Berry and Björkman, 1980; Morison and Lawlor, 1999; Wang et al., 2001). Plants exchange CO2 and other gases with the atmosphere mainly through the leaf stomata. Within the leaf, CO2 reacts with the enzyme Ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) during photosynthesis to form carbohydrates (carbon fixation) that are allocated to different parts of trees, such as leaves, twigs, branches, stems, and roots (Jensen, 2000; Beedlow et al., 2004) (Figure 1). Concurrently, respiration that could oxidize the carbohydrate to CO2 and O2 in living cells, leaves, buds or shoots, branches, stems, and roots may consume some of the carbon and release it to the atmosphere as CO2 (carbon release) (Norby et al., 1999; Beedlow et al., 2004) (Figure 1).

CO2 partial pressure is an important limiting factor for photosynthesis (Aranjuelo et al., 2005). Net CO2 assimilation rate per unit area of C3 plants is affected by the ratio of atmospheric CO2 concentration and O2 concentration since they compete at the active site of the enzyme Rubisco for the primary acceptor, ribulose-1,5-bisphosphate (RuBP). Rubisco catalyzes both carboxylation and oxygenation of RuBP. Oxygenation results in respiratory loss of CO2, and carboxylation results in carbon fixation through the photosynthetic carbon reduction cycle (Morison and Lawlor, 1999). Higher CO2 level hence increases the leaf internal CO2 concentration and the CO2:O2 ratio at the Rubisco site, which favors carboxylation rather than oxygenation of RuBP (Andrews and Lorimer, 1987; Jensen, 2000), and thus suppresses respiration and enhances photosynthesis, consequently increasing net photosynthesis (Eamus, 1991; Stitt, 1991; Arp, 1991; Long and Drake, 1992; Saxe et al., 1998). The structure of the Rubisco-enzyme is highly conserved among plant groups (Yu et al., 2005) and plant physiologists expect that the behavior of Rubisco under different environmental conditions is predictable. The ratio of carboxylation over oxygenation decreases with temperature (Long, 1991). Based on calculations of enzyme kinetics the enhancement of photosynthesis by increases of the ambient CO2 concentration should be higher under warm conditions. Also, the ratio of carboxylation to oxygenation decreases with the CO2 to O2 ratio in the leaf. Drought also decreases the CO2 concentration without affecting the O2 concentration (Long, 1991). Increases in ambient CO2 concentration would therefore enhance more the photosynthesis of drought-stressed plants.

Körner (2006) summarized that stimulation of leaf photosynthesis was evidenced unequivocally in experiments when plants were exposed to enriched CO2. However, increases in the rates of photosynthesis varied with the duration of the experiment, the maturity stage of the trees, the plant N status, and the experimental exposure technique (Saxe et al., 1998; Ainsworth and Long, 2005). It also varied within canopy, seasonally, or between species (Norby et al., 1999). Norby et al. (1999) reported that photosynthesis was stimulated by 40–80% in most of the experiments with the exception of greater enhancement in
several cases under enriched-CO₂ environment. A meta-analytical review of free-air CO₂ enrichment (FACE) experiments found that trees were more responsive than other function types to elevated CO₂ (Ainsworth and Long, 2005). In a review of short-term CO₂-enriched experiments (less than one season), Ceulemans and Mousseau (1994) found that photosynthesis of deciduous species was more sensitive to elevated CO₂ than that of conifers. However, evidence from long-term studies (more than one season) suggested that photosynthesis stimulation enhanced by elevated CO₂ was similar in unstrressed conifers and deciduous trees, ranging from 50–60% (Norby et al., 1999). Gunderson and Wullschleger (1994) did not observe a significant difference in photosynthesis response under elevated CO₂ between conifers and deciduous trees.

1. CO₂ and Temperature

When taking into account the interactive effects of increased CO₂ concentration and temperature, based on the strong dependence of the ratio of carboxylation rates to oxygenation rates on temperature from theoretical calculations, Long (1991) suggested that with increases in temperature, the proportion of potential carbon uptake, lost due to photorespiration, will increase. Higher substomatal CO₂ concentration will favour photosynthesis over photorespiration (Long, 1991). With the elevation of CO₂ concentration from 350 to 650 μmol mol⁻¹, Long (1991) predicted (based on the so-called Farquhar model of photosynthesis (Farquhar et al., 1980)), that CO₂ uptake (Aₘₜₜ = μmol m⁻²s⁻¹) would increase by 14, 54, and 73% at leaf temperatures of 10, 20 and 30°C, respectively (Figure 2), which is similar to that in a study of three C₃ species (Scrophularia desertorum (Munz) R. Shaw, Cardaria draba Desv., Populus fremontii (Munz) (Sage and Sharkey, 1987). Long (1991) further pointed out that following from this interaction of CO₂ concentration and temperature, the temperature optimum (Tₜₐₜ) of CO₂ uptake will increase, Tₜₐₜ increases by 3 °C at CO₂ concentration = 500 μmol mol⁻¹ and 5°C at CO₂ concentration = 650μmol mol⁻¹ (Figure 2). Correspondingly, the predicted upper temperature at which positive CO₂ uptake may be maintained is also increased by 4 °C and 7°C, respectively (Long, 1991).

Idso et al. (1992) found that at a mean leaf temperature of 31, 35, and 42 °C, the additional 300 ppmv of CO₂ in the CO₂-enriched enclosures of sour orange trees (Citrus aurantium L.) increased net photosynthetic rates of leaves exposed to full sun by approximately 75, 100, and 200% over rates experienced by leaves in the atmosphere-air enclosures, respectively, demonstrating that the upper-limiting temperature for growth was raised 7°C by the extra CO₂. The FACE experimental data showed that light-saturated CO₂ uptake of plants under elevated CO₂ concentration was enhanced by 19% for the FACE experiments conducted below 25°C, and by 30% for those conducted above 25°C, respectively (Ainsworth and Long, 2005). Response of plant growth to elevated CO₂ concentration cannot be readily predicted from the response of photosynthesis alone (Morison and Lawlor, 1999). It involves not only the photosynthetic responses of leaves but also whole-plant respiration (Gifford, 1992). Since dark respiration is a temperature-dependent process, warmer temperatures hence increase the respiration rates of plants, which results in decreases of carbohydrate content in plants, and consequently limiting respiration and growth (Long, 1991; Rowland-Bamford et al., 1996). In a CO₂-enriched environment, additional carbohydrates as a result of increased photosynthesis could supply the demands of respiration on more energy at warmer conditions (Long, 1991).

2. CO₂ and N

As a most critical component of many important structural, genetic, and metabolic compounds in plant cells (for instance N compounds comprise 40 to 50% of the dry matter of protoplasm, i.e., the living substance of plant cells), N is required in relatively large quantities in connection with all growth processes in plants (Stitt and Krapp, 1999; Johnson, 2006), especially for plants growing in a CO₂-enriched environment. When plants are exposed to a CO₂-enriched environment, an increase in biomass of plant or soil organic matter (carbon fixation) will increase the N demand in plants and enhance sequestration of N into long-lived plant biomass and soil organic matter pools (Luo et al., 2004). Consequently, more N would be sequestered in organic matter (van Groenigen and van Kessel, 2002) because formation of organic matter requires N and other nutrients in relatively fixed proportions with carbon (Luo et al., 2004; Norby and Iversen, 2006). Over a longer time, N availability will progressively decline unless compensated by additional N supplies or reduced losses. Finally, long-term responses of plants to CO₂ could be limited since ecosystem productivity would become N limited (Comins and McMurtrie, 1993; Luo et al., 2004; Norby and Iversen, 2006). Based on the physiological and biogeochemical theory deductions discussed above, Luo et al. (2004) proposed the Progressive Nitrogen Limitation (PNL) hypothesis that ecosystems in a CO₂-enriched atmosphere will sequester carbon and N in long-lived biomass and soil organic pools, thereby limiting available N and constraining the

![Figure 2](image-url)
continued response of net primary productivity to elevated CO$_2$
concentration. Recent studies have provided partial evidence for the PNL (Hungate et al., 2006), but despite no evidence observed for the PNL, they claimed that it still could be possible to occur through time (Finzi et al., 2006; Norby and Iversen, 2006). For example, Norby and Iversen (2006) did not find any evidence for the PNL in a six-year record of N dynamics of a deciduous sweetgum (Liquidambar styraciflua L) stand exposed to elevated CO$_2$ concentration in the FACE experiment at Oak Ridge, Tennessee. However, the authors claimed that “we cannot, however, say that PNL will not start developing in this experimental forest some time in the future.” They observed two indications of the increasing deficit of N return in leaf litter and the greater reliance of CO$_2$-enriched trees on uptake rather than retranslocation to meet their N requirements, which might suggest a change in the N economy (Norby and Iversen, 2006). They attributed this change in N economy to the fact that N supply in soil may be sufficient to meet an increasing demand for available N (Johnson et al., 2004), especially as roots of CO$_2$-enriched trees develop deeper in the soil profile (Norby et al., 2004). A recent meta-analysis of FACE experiments also supports that there are positive interactions between CO$_2$ and N (Ainsworth and Long, 2005). Reich et al. (2006) pointed out that N limitation might progressively suppress the positive response of plant biomass to elevated CO$_2$ in sites with low or moderate soil N availability, but such limitation of the CO$_2$ fertilization effect by insufficient N may be weak or absent in N-rich sites. At the population and community levels, N status in the soil can also influence relative responsiveness to elevated CO$_2$ (Wang, 2007).

3. CO$_2$ and Drought

Increased atmospheric CO$_2$ concentration will increase the ratio of CO$_2$ to O$_2$ in the substomatal cavity. This will decrease carbon losses due to photorespiration. Drought induces stomatal closure and decreases partial pressure of CO$_2$ in the leaf. Increased CO$_2$ concentration may induce stomatal closure and could result in an increase in the ratio of carbon gain to water loss, i.e., water use efficiency, at the leaf and whole stand level, and higher plant biomass (Farquhar et al., 1989; Field et al., 1995; Picon et al., 1996; Drake et al., 1997; Centritto et al., 1999; Körner, 2000; Wullschleger et al., 2002; Morgan et al., 2004). Also increased allocation of carbon to root growth (e.g., increased fine roots, root surface area and volume) and osmotic adjustment in plants exposed to enriched CO$_2$ may, for example, enable plants to exploit soil water in a deeper and larger range of soil (Wullschleger et al., 2002). In addition, altering developmental processes including root and shoot architecture (Berntson and Woodward, 1992; Miao et al., 1992) and leaf morphology (Thomas and Harvey, 1983) under enriched CO$_2$ concentration might affect water relations and plant response to drought. Consequently, these responses could increase water uptake and improve water balance in plants, hence ameliorating the negative effects of water stress and better adapting to a water-limited environment (Wullschleger et al., 2002; Morgan et al., 2004). A review article pointed out that although the cause and effect relationships between growth, gas exchange, anatomy, and plant water relations were rarely established in many conducted experimental CO$_2$-enriched studies, it would be probable that plants could benefit from increased root-shoot ratio or fine-root proliferation to better adapt to a water-limited environment (Wullschleger et al., 2002). In a FACE experiment on a closed-canopy, deciduous sweetgum forest, Norby et al. (2004) observed the CO$_2$-induced increase in fine-root standing crop (total length of root visible) in summer, which might be an important mechanism for conferring increased resistance to late-season drought. Morgan et al. (2004) suggested that the effect of enriched CO$_2$ induced increases in water use efficiency and thus plant biomass enhancement might be especially important in drier ecosystems.

4. Downregulation

Long-term exposure to elevated CO$_2$ over periods of several weeks or longer often leads to a reduction of the photosynthetic capacity of plants (Arp, 1991; Gunderson and Wullschleger, 1994; Loehle, 1995; Ainsworth et al., 2004). Usually downregulation is due to a reduction of the capacity of dark reactions to process CO$_2$ (Drake et al., 1997; Ainsworth et al., 2004). Decreased photosynthetic efficiency could be caused by 1) reduced light capture (PSII activity), which results from inhibition due to the accumulation of inactive PSII reaction centers and the decrease in light harvesting complexes, and/or 2) decreased carboxylation of RuBP catalyzed by Rubisco (Long et al., 2004; Aranjuelo et al., 2005). Rubisco, which constitutes about 30% of the total protein in a plant leaf, is a major sink for plant N and is widely accepted as the ultimate rate-limiting step in photosynthetic carbon fixation (Jensen, 2000). Decreased efficiency of Rubisco might be due to a reduction of leaf N concentration and photosynthetic N-use efficiency (Stitt and Krapp, 1999; Medlyn et al., 1999; Nowak et al., 2004). Past studies frequently reported some downregulation of photosynthesis and biomass (e.g., Eamus and Jarvis, 1989; Sage, 1994; Gunderson and Wullschleger, 1994; Vivin et al., 1995; Miglietta et al., 1998; Saurer et al., 2003; Ellsworth et al., 2004). In a meta-analysis that summarized effects of long-term CO$_2$ increase on photosynthetic model parameters obtained from 15 field-based elevated CO$_2$ experiments on European tree species, Medlyn et al. (1999) observed a 10–15% reduction in photosynthesis when measured at the same CO$_2$ concentration. Adam et al. (2004) found that after 14 years of exposure to elevated CO$_2$ concentration, CO$_2$-induced enhancement of photosynthesis has declined and this decline was strongly correlated with the decrease in the aboveground wood biomass enhancement ratio reported by Idso and Kimball (2001).

In addition, elevated CO$_2$ concentration could reduce the light compensation point for net photosynthesis and increase maximum quantum efficiency by reducing respiration, which is of significance for survival and growth of tree seedlings in deeper shade (Körner, 2006), with possible implications on interspecific interactions.
competition and forest regeneration (Saxe et al., 1998). Reduced stomatal conductance, enhanced photosynthesis, or both factors combined could enhance leaf water use efficiency and, hence, improve drought tolerance of plants (Eamus, 1991; Saxe et al., 1998; Wullschleger et al., 2002; Morgan et al., 2004). Increases in both net photosynthesis and water use efficiency enhance assimilation of carbon available for growth of plants.

B. Growth Response to CO2

Currently, there are four methods of exposing tree foliage to elevated CO2 in the field or under semi-field conditions, including the following: 1) Free Air CO2 Enrichment (FACE) (e.g., Hendrey et al., 1993; Ellsworth et al., 1995; Miglietta et al., 2001; Hättenschwiler et al., 2002; Pepin and Körner, 2002), 2) Open-top chamber experiments (e.g., Ashenden et al., 1992; Whitehead et al., 1995; Norby et al., 1997; Körner et al., 2005), 3) Closed-top chamber experiments (e.g., Tingey et al., 1996; Beerling and Woodward, 1996), and 4) Branch-bag experiments (e.g. Barton et al., 1993). In spite of existing advantages and disadvantages in each technique (Saxe et al., 1998; Ainsworth and Long, 2005; Körner, 2006), a large body of field studies conducted in tropical, temperate, and boreal forests showed that elevated atmospheric CO2 concentration could have significant impacts on the above- and belowground growth of trees.

1. Aboveground Growth

Elevated CO2 persistently increases leaf area index, leaf number, branches, thus positively changing canopy structure under optimal conditions (e.g., Idso and Kimball, 1994; Norby et al., 1995; Griffin et al., 1995; Epron et al., 1995; Ceulemans et al., 1996; Tingey et al., 1996; Tissue et al., 1997; Arp et al., 1998). Open-top chamber experiments usually showed an increase in leaf area of seedlings and saplings with CO2 enrichment (Norby et al., 1999). For example, Tissue et al. (1997) reported a 217, 80, 58, and 41% increase in leaf area of loblolly pine (Pinus taeda L.) growing in elevated CO2 environment for subsequent four growing seasons when compared to ambient CO2, respectively. Ceulemans et al. (1995) observed 8–18% leaf area increases for Populus clones under CO2 enrichment. A meta-analysis found that trees had a 21% increase in leaf area index compared to less response of herbaceous C3 grasses (Ainsworth and Long, 2005). Increase in leaf area of Quercus alba L. saplings in elevated CO2 also can be ascribed to increased leaf number, leaf size and, more or less, changed leaf shape (Gregory, 1996). By modifying leaf area, number and size, as well as tree height, elevated CO2 concentration could influence branching patterns (Gunderson and Wullschleger, 1994) and, consequently, change canopy structure (Saxe et al., 1998). Past studies on Liriodendron tulipifera L. (Murray and Ceulemans, 1996), P. taeda (Tissue et al., 1997), and Alnus glutinosa L., Fraxinus angustifolia Vahl. and Q. robur L. (Bucher et al., 1997) found that elevated CO2 significantly increased the number of branches (Saxe et al., 1998), which resulted in changes in crown size and structure (Bazzaz et al., 1993). A 25% increase in branch number summarized from six species at three FACE sites was reported (Ainsworth and Long, 2005).

Elevated CO2 concentration generally increases stem biomass (Curtis et al., 1998; Saxe et al., 1998; Ainsworth and Long, 2005). An increase in seedling dry matter production of P. radiata D. and P. virginiana Mill. was observed under low nutrient conditions exposed in CO2 enrichment for 22 and 16 weeks, respectively (Conroy et al., 1986; Luxmoore et al., 1986). Idso and Kimball (1992) found that C. aurantium trees had approximately 160% more trunk and branch volume under CO2 enrichment than trees under ambient CO2. Norby et al. (1992) showed that L. tulipifera trees grown in enriched CO2 for 2.5 growing seasons had 27% more dry mass than trees grown in ambient CO2. Saxe et al. (1998) reviewed the short-term CO2-enriched experiments and summarized that, on average, elevated atmospheric CO2 significantly enhanced tree biomass with increasing exposure time. Under the mean exposure duration of 338 days, conifers increased their biomass by 130%, whereas deciduous trees exposed during 329 days increased by only 49% (Figure 3, Saxe et al., 1998). Based on meta-analysis on the FACE experiments, Ainsworth and Long (2005) reported that elevated CO2 resulted in taller plants with larger stem diameter, and plant height enhancement in the third growing season was greater than in the first and second. They further pointed out that shrubs and trees showed more height increases than C3 crops, and trees exhibited the largest response (28%) in dry matter production. Norby et al. (2005) observed a growth increase of 23% in a synthesis analysis of four FACE studies on dominant trees in multi-species forests. Wang (2007) quantitatively evaluated the responses of aboveground biomass of woody species to enriched CO2 by meta-analysis and observed an increase of 31% and 23% at the population and community levels, respectively. In addition, other reviews (e.g., Ceulemans and Mousseau, 1994; Lloyd and Farquhar, 1996; Curtis and Wang, 1998; Norby et al., 1999) showed an increase in stem growth and dry biomass, although the increased rates of growth were different among the studies.
Norby et al. (1999) ascribed these differences to the growth rate or growth potential of different species, effects of environmental interactions, or differences in experimental protocol.

Elevated CO₂ might also affect phenology such as sprouting, periodicity of leafing, flowering, and fruiting through changes in tree biochemistry and physiology (Jach and Ceulemans, 1999), and through warming effect. Changes in starch or hormonal concentrations may alter dormancy status and growth patterns by shifting timing and duration of the vegetative season (Saxe et al., 1998; Norby et al., 1999). In a two-year open-top chamber experiment on three-year-old *P. sylvestris* L., elevated CO₂ significantly advanced date of bud burst in both the first and second years of the experiment (Jach and Ceulemans, 1999). Repo et al. (1996) observed that dehardening in *P. sylvestris* seedlings grown at increased temperatures proceeded significantly faster if concurrently exposed to elevated CO₂ concentration. Saxe et al. (1998) reported that, if the leaf development is hastened under elevated CO₂ in the spring, trees could potentially benefit from an earlier onset of carbon assimilation at the start of growing seasons. They further pointed out that this could be an important factor to influence expansion of tree populations into areas currently too cold for their growth. Since most of the work is done with immature plants (seedlings and young trees), little is known about the CO₂ effect on flowering and fruiting (Saxe et al., 1998). LaDeau and Clark (2001) have done an experiment exposing 19-year-old *P. taeda* to 4 years of CO₂ enrichment in an intact forest of North Carolina, and found that trees were twice as likely to be reproductively mature and produced three times as many cones and seeds as trees at ambient CO₂ concentration. This indicates that a higher carbon allocation to reproduction under enriched CO₂ results in trees reaching maturity sooner and at a smaller size (LaDeau and Clark, 2001). Further study demonstrated that seed weight increased by 91% in elevated CO₂ and seeds germinated much earlier, with more than three times germination success compared to the ambient seed source (Hussain et al., 2001). A CO₂-enriched study on reproduction of hardwood trees (*Q. myrtifolia* Willd., *Q. chapmanii* Sarg., and *Q. geminata* Small) in a natural scrub-oak forest of Florida suggested that the number of acorns produced under elevated CO₂ was significantly higher than in ambient CO₂ (Stiling et al., 2004).

2. **Belowground Growth**

The responses of roots to CO₂ are dependent on experimental conditions (Ceulemans and Mousseau, 1994). Low nutrition and water availability tend to increase the ratio of root to shoot in response to CO₂ enhancement (Stulen and den Hertog, 1993; Saxe et al., 1998), allowing plants growing on poor and dry sites to explore a greater soil volume to acquire water and nutrients (Day et al., 1996; Norby et al., 2004; Phillips et al., 2006; Norby and Iversen, 2006). Earlier studies on responses of potted tree seedlings growing in low nutrient conditions generally concluded that the ratio of root mass to shoot mass increased in elevated CO₂ conditions (Oechel and Strain, 1985). By reviewing plant root and rhizosphere response to elevated CO₂, Rogers et al. (1994) found that root dry weight increased in all studies under elevated CO₂. However, a few destructive harvest multi-year studies of trees in elevated CO₂ showed no significant effect on root-to-shoot ratio in *L. tulipifera* (Norby et al., 1992), *Q. alba* (Norby et al., 1995), *Betula pendula* Roth. (Ry and Jarvis, 1997), *P. taeda* (Tissue et al., 1997), *P. ponderosa* Doug. (Walker et al., 1997), or *F. excelsior* L.*. petraea* Liebl. and *P. sylvestris* (Crockshanks et al., 1998). In a FACE experiment of *P. taeda* forest of North Carolina, Allen et al. (2000) found that elevated CO₂ caused significant increases in lobolly pine fine root increment after two growing seasons. Lukac et al. (2003) revealed that elevated CO₂ increased belowground allocation of biomass in three *populus* species investigated (*P. alba* L., *P. nigra* L., and *P. x euramericana* Dode (Guinier)), and standing root biomass enhanced by 47–76% as a result of FACE treatment. Norby et al. (2004) reported that annual production of fine roots was more than doubled in plots with 550 ppm CO₂ compared with plots in ambient CO₂ in a FACE experiment on a closed-canopy, deciduous sweetgum forest.

3. **Interactions with Other Environmental Factors**

Körner (2006) proposed, based on a meta-analysis of FACE experiments, that CO₂ enrichment effects are only transitory in established ecosystems with closed nutrient cycles and fully developed canopies. Nutrient limitations are, according to Körner, strong enough to limit long-term increases in tree growth. Altogether, Körner (2006) claimed that there are only low long-term increases in growth and no increases in leaf area index. On the other hand, Nowak et al. (2004) insisted that there are increases in growth which persist over time in most FACE experiments. The results confirmed that increases in belowground activity will be higher than aboveground growth. Furthermore, the results confirmed that increases in soil fertility and N additions interact positively with CO₂. However, they did not confirm any positive interactions between drought and CO₂ enrichment. Forest ecosystems from areas with high precipitation had higher growth increases than dry ecosystems.

C. **Implications for Mature Trees in the Forests**

Most field CO₂-enriched experiments showed that elevated CO₂ concentration directly enhanced growth of young trees or seedlings regardless of growth conditions (e.g., Ceulemans and Mousseau, 1994; Curtis and Wang, 1998; Norby et al., 1999, 2001; Ainsworth and Long, 2005; Körner, 2006), providing strong evidence to support the direct CO₂ fertilization effect. But those CO₂-enriched experiments were conducted in the field for only hours, weeks, or a few growing seasons. When exposed for longer time periods, photosynthesis and biomass accumulation could be lower than predicted from the initial growth response (Sage, 1994; Gunderson and Wullschleger, 1994; Vivin et al., 1995; Miglietta et al., 1998; Saurer et al., 2003; Ellsworth et al., 2004) because trees might adjust to development under elevated CO₂ with time (i.e., acclimation) (Loehle, 1995).
Hypothetically, if downregulation of photosynthesis does not occur, tree growth rate might still not increase proportionally with increase in photosynthesis (Norby et al., 1999; Hungate et al., 2003; Berninger et al., 2004). Because when trees are exposed to CO₂ enrichment, other limiting factors may become more important, thus limiting the ability of trees to increase their growth rates in response to further increases in CO₂ concentration, particularly in natural ecosystems (Norby et al., 1999; Körner, 2003; Hungate et al., 2003; Berninger et al., 2004). Investigating growth of *P. sylvestris* trees using a combination of process-based models and dendroecological approaches, Berninger et al. (2004) postulated that the growth rate of trees at the northern tree-line can not parallel the increase in photosynthesis although photosynthesis is enhanced under elevated CO₂ concentration. They ascribed this asynchrony to the reason that potential growth rate is limited directly by temperature. Using carbon isotopes, Tardif et al. (in press) also showed that both tree-ring formation and carbon uptake in tree-ring cellulose were limited by cool summer temperatures.

Seedlings or young trees usually grow much more rapidly than mature trees when exposed to increased CO₂ environment, thus magnifying the effect of rising CO₂ on growth of mature trees (Saxe et al., 1998; Norby et al., 1999; Körner, 2006; Wang, 2007). In addition, the response of experimental trees exposed to an abrupt increased CO₂ concentration (typically 600–700 ppm) in experimental studies may be different from the response of trees under the much smaller natural increase (Wang et al., 2006). By comparing the ring widths of five Mediterranean forest tree species (*Arbutus unedo* L., *F. ornus* L., *Q.cerris* L., *Q. ilex* L., and *Q. pubescens* Willd.) growing close to a natural source of CO₂ and a nearby control site in Tuscany, Italy, Tognetti et al. (2000) found that CO₂ enrichment did not lead to a significant enhancement of radial increment. They attributed the result to the counteracted effect from other resource limitations, such as low nutrient availability with the positive effect of elevated CO₂ under drought stress, or to the acclimation of trees to high CO₂.

Taken together, there is an ample body of evidence from short- to medium-term CO₂ enrichment studies to suggest that trees may be able to increase their photosynthesis and growth under elevated CO₂. Apart from a few long-term FACE studies (e.g., Hättenschwiler et al., 2002; Rasse et al., 2005; Handa et al., 2005; Asshoff et al., 2006), most studies are associated with the problems of a short duration of the experiments. Also, all chamber experiments alter the environment of trees. Another potential problem is the constancy of CO₂ values in chambers of chamber experiments altering the environment of trees. Another important, thus limiting the ability of trees to increase their growth rate with further increases in CO₂ concentration, particularly in natural ecosystems (Norby et al., 1999; Körner, 2003; Hungate et al., 2003; Berninger et al., 2004). Investigating growth of *P. sylvestris* trees using a combination of process-based models and dendroecological approaches, Berninger et al. (2004) postulated that the growth rate of trees at the northern tree-line can not parallel the increase in photosynthesis although photosynthesis is enhanced under elevated CO₂ concentration. They ascribed this asynchrony to the reason that potential growth rate is limited directly by temperature. Using carbon isotopes, Tardif et al. (in press) also showed that both tree-ring formation and carbon uptake in tree-ring cellulose were limited by cool summer temperatures.

Seeds or young trees usually grow much more rapidly than mature trees when exposed to increased CO₂ environment, thus magnifying the effect of rising CO₂ on growth of mature trees (Saxe et al., 1998; Norby et al., 1999; Körner, 2006; Wang, 2007). In addition, the response of experimental trees exposed to an abrupt increased CO₂ concentration (typically 600–700 ppm) in experimental studies may be different from the response of trees under the much smaller natural increase (Wang et al., 2006). By comparing the ring widths of five Mediterranean forest tree species (*Arbutus unedo* L., *F. ornus* L., *Q. cerasus* L., *Q. ilex* L., and *Q. pubescens* Willd.) growing close to a natural source of CO₂ and a nearby control site in Tuscany, Italy, Tognetti et al. (2000) found that CO₂ enrichment did not lead to a significant enhancement of radial increment. They attributed the result to the counteracted effect from other resource limitations, such as low nutrient availability with the positive effect of elevated CO₂ under drought stress, or to the acclimation of trees to high CO₂.

Seeds or young trees usually grow much more rapidly than mature trees when exposed to increased CO₂ environment, thus magnifying the effect of rising CO₂ on growth of mature trees (Saxe et al., 1998; Norby et al., 1999; Körner, 2006; Wang, 2007). In addition, the response of experimental trees exposed to an abrupt increased CO₂ concentration (typically 600–700 ppm) in experimental studies may be different from the response of trees under the much smaller natural increase (Wang et al., 2006). By comparing the ring widths of five Mediterranean forest tree species (*Arbutus unedo* L., *F. ornus* L., *Q. cerasus* L., *Q. ilex* L., and *Q. pubescens* Willd.) growing close to a natural source of CO₂ and a nearby control site in Tuscany, Italy, Tognetti et al. (2000) found that CO₂ enrichment did not lead to a significant enhancement of radial increment. They attributed the result to the counteracted effect from other resource limitations, such as low nutrient availability with the positive effect of elevated CO₂ under drought stress, or to the acclimation of trees to high CO₂.

An additional problem is that this separation of different signals must be done in absence of detailed information of stand history, since our ability to infer past disturbances from scars, stumps or snags are limited, especially for disturbances occurred a long time ago or less obviously.

Empirical dendrochronological studies test CO₂ fertilization effects (*E_{CO_2}* in tree-rings through the removal of other factors in tree-ring growth. The trend of CO₂ fertilization effect could thus be detectable in residuals of the growth-climate models (e.g., Jacoby and D’Arrigo, 1989; Graumlich, 1991; D’Arrigo and Jacoby, 1993; Knapp et al., 2001) (Table 1). By selecting good sampling sites in which the influences of indigenous (*D_1*) and exogenous (*D_2*) factors were minimized (e.g., Nicolussi et al., 1995; Soulé and Knapp, 2006), CO₂ fertilization effect was assessed either by analyzing trends in basal area increment (BAI) or by comparing growth trends among age classes or
### TABLE 1
Empirical dendrochronological studies detecting CO₂ fertilization effect in tree-rings

<table>
<thead>
<tr>
<th>Results</th>
<th>Study region</th>
<th>Species</th>
<th>Detrending (Yes/No)</th>
<th>Analysis Methods</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Semiarid, western USA</td>
<td><em>P. aristata</em></td>
<td>Yes</td>
<td>Comparisons of growth</td>
<td>LaMarche <em>et al.</em>, 1984</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>P. longaeva</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Semiarid, western USA</td>
<td><em>P. flexilis</em></td>
<td>Yes</td>
<td>Comparisons of growth</td>
<td>Graybill, 1987</td>
</tr>
<tr>
<td></td>
<td>Semiarid, high elevations western NA</td>
<td><em>P. aristata</em>, <em>P. longaeva</em></td>
<td>Yes</td>
<td>Comparisons of growth</td>
<td>Graybill and Idso, 1993</td>
</tr>
<tr>
<td></td>
<td>Subalpine, central Alps</td>
<td><em>P. cembra</em></td>
<td>No</td>
<td>Age classes</td>
<td>Nicolussi <em>et al.</em>, 1995</td>
</tr>
<tr>
<td></td>
<td>Semi-arid, CO₂ springs Mediterranean, Italy</td>
<td><em>Q. ilex</em></td>
<td>Yes</td>
<td>Growth comparisons with CO₂ data</td>
<td>Hättenschwiler <em>et al.</em>, 1997</td>
</tr>
<tr>
<td></td>
<td>Arid Oregon</td>
<td><em>J. occidentalis</em></td>
<td>Yes</td>
<td>Detecting trends in residuals</td>
<td>Knapp <em>et al.</em>, 2001</td>
</tr>
<tr>
<td></td>
<td>Arid Oregon</td>
<td><em>P. ponderosa</em></td>
<td>Yes</td>
<td>Comparisons with drought years</td>
<td>Soulé and Knapp, 2006</td>
</tr>
<tr>
<td></td>
<td>Southeast Missouri</td>
<td><em>Q. velutina</em>, <em>Q. coccinea</em>, <em>P. echinata</em></td>
<td>Yes</td>
<td>Comparisons of growth trends</td>
<td>Voelker <em>et al.</em>, 2006</td>
</tr>
<tr>
<td></td>
<td>Dry environment, southwestern Manitoba</td>
<td><em>P. glauca</em></td>
<td>Yes</td>
<td>Comparisons between young trees and old trees</td>
<td>Wang <em>et al.</em>, 2006</td>
</tr>
<tr>
<td>II</td>
<td>Tree line, NA</td>
<td><em>A. alba</em></td>
<td>Yes</td>
<td>Detecting trends in residuals</td>
<td>Jacoby and D’Arrigo, 1989</td>
</tr>
<tr>
<td></td>
<td>Northeastern France</td>
<td><em>subalpine conifers</em></td>
<td>Yes</td>
<td>Analysis of residuals</td>
<td>Becker, 1989</td>
</tr>
<tr>
<td></td>
<td>Southwestern USA</td>
<td><em>P. glauca</em></td>
<td>Yes</td>
<td>Response surface</td>
<td>Graumlich, 1991</td>
</tr>
<tr>
<td></td>
<td>Tree line, northern NA</td>
<td><em>P. balfouriana</em></td>
<td>Yes</td>
<td>Detecting trends in residuals</td>
<td>D’Arrigo and Jacoby, 1993</td>
</tr>
<tr>
<td></td>
<td>Semiarid mountain, western NA</td>
<td><em>P. sylvestris</em>, <em>P. longaeva</em>, <em>P. albicaulis</em>, <em>P. occidentalis</em>, <em>P. flexilis</em></td>
<td>Yes</td>
<td>Comparisons</td>
<td>Bunn <em>et al.</em>, 2005</td>
</tr>
<tr>
<td>III</td>
<td>Finland</td>
<td><em>P. sylvestris</em></td>
<td>Yes</td>
<td>A four component model</td>
<td>Hari <em>et al.</em>, 1984</td>
</tr>
<tr>
<td></td>
<td>Finland</td>
<td><em>P. sylvestris</em></td>
<td>Yes</td>
<td>Comparisons of time series models</td>
<td>Arovaara <em>et al.</em>, 1984</td>
</tr>
<tr>
<td></td>
<td>Finland</td>
<td><em>P. sylvestris</em></td>
<td>Yes</td>
<td>A four component model</td>
<td>Hari and Arovaara, 1988</td>
</tr>
<tr>
<td></td>
<td>Northern hemisphere</td>
<td><em>Pinus, Picea, Abies, Cedrus, Pseudotsuga</em></td>
<td>Yes</td>
<td>β factor</td>
<td>Kienast and Luxmoore, 1988</td>
</tr>
<tr>
<td></td>
<td>Northeastern France</td>
<td><em>Q. petraea</em>, <em>Q. robur</em></td>
<td>No</td>
<td>Basal area increment</td>
<td>Becker <em>et al.</em>, 1994</td>
</tr>
<tr>
<td></td>
<td>European</td>
<td>European species</td>
<td>No</td>
<td>Basal area increment</td>
<td>Briffa <em>et al.</em>, 1998b</td>
</tr>
<tr>
<td></td>
<td>Tree-line French Alps</td>
<td><em>P. abies</em>, <em>L. decidua</em>, <em>P. cembra</em>, <em>P. uncinata</em></td>
<td>Yes</td>
<td>Average growth trend curve as a function of tree age; plotting ring-width as a function of the year of ring formation for cambial ages</td>
<td>Rolland <em>et al.</em>, 1998</td>
</tr>
</tbody>
</table>

I: finding evidence of CO₂ fertilization effect in tree-rings; II: growth enhancement caused by favorable climate change; III: combined effects of several factors such as favorable climate change, CO₂ fertilization effect, anthropogenic atmospheric deposition (e.g., N); NA-northern America. Detrending methods include some conservative methods such as negative exponential, regression line or straight line.
between old trees and young trees or by computing the biotic growth factor (β factor, which is a parameter used for comparing responses of various species to CO2 enrichment (Bacastow and Keeling, 1973)) (Table 1). Because of discrepancies in site conditions (mesic, semi-arid, arid, subalpine, alpine, treeline, etc.), tree species, data treatments among different studies (Table 1), the conclusions related to detecting CO2 fertilization effect are various, although LaMarche et al. (1984) first claimed a possible CO2 fertilization effect in tree-rings. After an extensive survey of the pertinent literature, three viewpoints on detecting CO2 fertilization effect in tree-rings were found:

A. Finding Evidence of CO2 Fertilization Effect in Tree Rings

LaMarche et al. (1984) and Graybill (1987) first observed increased radial growth of P. aristata Engelm., P. longaeva Bailey, and P. flexilis James in semiarid regions of the western United States and claimed that it was evidence of a possible CO2 fertilization effect in subalpine tree-rings. After modeling of the growth-climate relationships in regression analysis and comparison with other dendroclimatic reconstructions for western Northern America, Graybill and Idso (1993) also detected CO2 fertilization effect in tree-rings of high-elevation bristlecone pine (P. aristata and P. longaeva) characterized by a strip bark morphology (partial cambial dieback). Nicolussi et al. (1995) associated the 25% increase in ring width of subalpine P. cembra L. from the central Alps, which occurred since the middle of the nineteenth century, with an increase in atmospheric CO2. Based on the analyses of growth-climate associations of Juniperus occidentalis Hook, in arid Oregon using multiple regression models, Knapp et al. (2001) provided evidence for atmospheric CO2 fertilization effect on the radial growth rates, especially during drought stress. A study of P. ponderosa carried out in the same region also showed evidence of CO2 fertilization effect, i.e., significant increases in radial growth rates occurred post-1950, particularly during drought years, with the greatest increases generally found at the most-water-limited sites (Soule and Knapp, 2006). Wang et al. (2006) compared the growth of young Picea glauca (Moench) Voss trees that are currently exposed to high atmospheric CO2 to the early growth period of older trees that were exposed to low atmospheric CO2 in a dry environment of southwestern Manitoba, Canada, and the results provided circumstantial evidence that atmospheric CO2 fertilization increased radial growth in this dry environment. However, the authors could not exclude that atmospheric deposition of N contributed to the observed increase in growth. Another study from the Ozark Mountains in Missouri revealed that both hardwood (Q. velutina Lam. and Q. coccinea Muench.) and coniferous (P. echinata Mill.) species increased in stem growth coincidently with increases in atmospheric CO2 over the past 150 years (Voelker et al., 2006). Other studies (see Spiecker, 1996) also found some indications of enhanced tree growth and attributed it, in some cases, to atmospheric CO2 increase.

CO2 springs, i.e., places where CO2 is emitted naturally from the soil, are places that permit us to study the effects of CO2 enrichment on tree growth without the problems associated with climatic trends that are superimposed on CO2 concentration trends. Hältenschwiler et al. (1997) and Tognetti et al. (2000) used these natural CO2 springs (including the Bossoleto CO2 spring and the Laiatico CO2 spring, Italy) for dendrochronological studies. Hältenschwiler et al. (1997) found that radial stem width of Q. ilex was, indeed, initially enhanced but differences in growth rates flattened out when trees got older. Enhancement of radial growth was especially pronounced in years with a dry spring, indicating that CO2 interacts with water stress. Tognetti et al. (2000) were unable to extend Hältenschwiler’s results to four other species (A. unedo, F. ornus, Q. pubescens, and Q. cerris). They attributed the differences to the discrepancies in control sites, stand history, sampling methods, and sample replications (Tognetti et al., 2000). Saurer et al. 2003 used isotopic methods to understand the changes that occurred in these trees. Based on 14C measurements, they found that CO2 concentration (or the contribution of CO2 spring to ambient CO2 concentration) seemed to decrease with tree age. Changes in the 13C discrimination and the oxygen isotopes indicated a progressive downscaling of photosynthesis with plant age, confirming Hältenschwiler’s initial conclusions. All these studies (except Tognetti et al., 2000) support the hypothesis that elevated atmospheric CO2 concentration could enhance tree growth.

B. Growth Enhancement Caused by Favorable Climate Change

Jacoby and D’Arrigo (1997) pointed out that the analyses of LaMarche et al. (1984) and Graybill (1987) did not exclude possible contribution of favorable climatic change to growth increase. If non-climatic factors such as CO2 significantly influence tree growth, the residuals of growth-climate models should show some trends (Graumlich, 1991; Jacoby and D’Arrigo, 1997). Jacoby and D’Arrigo (1989) did not detect significant trends of the residuals since 1973 for temperature-sensitive chronologies averaged for tree-line sites across North America. Through dendroecological investigation of Abies alba Miller in the Vosges mountains of northeastern France, Becker (1989) suggested that indirect effects of CO2 (increases in temperature and precipitation) may play a major role in changing radial growth. By using response surface models to account for the effects of interactions between climate variables on tree growth in the southwestern United States, Graumlich (1991) did not find any evidence for CO2 fertilization effect as a cause for enhanced growth among subalpine conifers in Sierra Nevada. D’Arrigo and Jacoby (1993) tested residual trends of growth-climate models of P. glauca at the northern boreal tree-line of North America, and reported that an equal or faster growth rate occurred since the mid-1800s than the prior period of treering record, but CO2 fertilization was not detectable as a major factor influencing growth on these sites. Bunn et al. (2005) in-
investigated some 1000-year chronologies of five high-elevation conifers (P. balfouriana Balf., P. longeva, J. occidentalis, P. flexilis, and P. albicaulis Engelm.) in western North America, and found that their growth rates during the last half of the twentieth century differed from that any time during the past 1,000 years, indicating a distinct biological signature of global climate change (mainly unprecedented warming). These studies attributed growth enhancements to favorable climate condition rather than to the CO₂ fertilization effect.

C. Combined Effects of Several Factors Such as Favorable Climate Change, CO₂ Fertilization, and Anthropogenic Atmospheric Deposition

It is not easy to clearly separate the direct CO₂ fertilization effect on vegetation from its effect as a greenhouse gas, which is its more or less important role in modifying the climate (Wigley and Jones, 1981). Several studies on P. sylvestris at the northern treeline in Finland showed that several environmental factors were changing simultaneously and results were inconclusive despite suggesting a possible CO₂ or nutrient deposition (Hari et al., 1984; Arovaara et al., 1984; Hari and Arovaara, 1988). Kiennast and Luxmoore (1988) found that 8 out of 34 chronologies showed increases in ring width in the post-1950, and attributed the increases to favorable climatic conditions and to factors other than CO₂ such as the better availability of nutrients due to atmospheric deposition. Briffa (1991) speculated that N fertilization could stimulate tree growth in some areas of Europe exposed to industrial pollution. In a dendroecological study of northeastern France, Becker et al. (1994) observed a 64% increase in radial growth of Q. petraea during the period 1888–1987 and 40% in Q. robur. The authors interpreted these growth increases as the effects of climate, CO₂ enrichment, and other factors such as anthropogenic atmospheric depositions, especially of N. Briffa et al. (1998b) reported that the BAI of a group of European tree species has steadily increased over recent centuries, and inferred that greater twentieth-century tree growth might be driven by a combination of factors such as warmer temperatures, rising CO₂ levels, and distant transport of nitrates. Rolland et al. (1998) observed increased radial growth of four conifer species (P. abies L., Larix decidua Mill., P. cembra, and P. uncinata Mill.) during the last two centuries in the French Alps near the upper treeline and ascribed these growth increases to climatic warming (especially minimum temperature) and some other factors such as atmospheric CO₂ enrichment, N deposition and human impact. Thus, these studies indicate that tree growth enhancements might be caused by the combined effects of several factors such as favorable climate change, CO₂ fertilization effect, and anthropogenic atmospheric deposition of nutrients, particularly of N.

IV. EVIDENCE FOR CO₂ FERTILIZATION EFFECT DISPLAYED IN TREE RINGS IN NATURAL FORESTS

In natural forests, anthropogenic-caused increases in atmospheric CO₂ concentration might enhance forest growth in the following two ways: 1) through favorable climatic change associated with increasing greenhouse gas concentration, and/or 2) via direct CO₂ or other nutrient fertilization such as nitrate (D’Arrigo and Jacoby, 1993). As for the observed radial growth enhancements in natural forests attributing to three viewpoints that were summarized in the above section, correspondingly we have three different interpretations as follows:

A. Occurrence of CO₂ Fertilization Effect in Drought-Stressed Environments

Of three viewpoints, it is very likely that direct CO₂ fertilization effect does occur in trees growing in drought-stressed environments, as shown by most studies in the first viewpoint (LaMarche et al., 1984; Graybill, 1987; Knapp et al., 2001; Hättenschwiler et al. 1997; Wang et al., 2006; Soulé and Knapp, 2006). Drought-stressed trees might benefit from increased water use efficiency under elevated atmospheric CO₂ concentration and thus alleviate drought stress, which in turn delays the onset of reduced photosynthesis caused by stomata closure (Owensby et al., 1999), allowing trees to have an extended growing season (Knapp et al., 2001). Many field experiments have strongly suggested an increase in water use efficiency of trees under CO₂ enrichment (e.g., Ceulemans and Mousseau, 1994; Lloyd and Farquhar, 1996; Curtis and Wang, 1998; Norby et al., 1999; Schlesinger and Lichter, 2001). Since stable carbon (¹³C/¹²C) and oxygen (¹⁸O/¹⁶O) isotopes analysis has been an important tool to study water use efficiency and climate influences (Bert et al., 1997; Berninger et al. 2000; Helle and Schleser, 2004; Tardif et al., in press), several carbon isotope studies in natural forests have already discovered increased water use efficiency for the study period of the past 100–200 years (Duquesnay et al., 1998; Feng, 1998, 1999; Liu et al., 2007). Increased water use efficiency was also revealed in P. aristata, showing full-bark and strip-bark morphology in arid White Mountains of California, but no significant differences between the two growth forms.
were observed (Tang et al., 1999) (Figure 4). Graybill and Idso (1993) showed an enhanced growth trend of both strip-bark and full-bark trees over the past 150 years, but the growth rate increased more for strip-bark trees than for full-bark trees (Figure 5). It was supposed that the strip-bark trees are more sensitive to climate changes than trees with more complete cambial tissue (D’Arrigo and Jacoby, 1993), and more likely than full-bark trees to allocate any additional carbon to cambial production of stem tissue (Graybill and Idso, 1993). The discrepancy between the same rate of increased water use efficiency and different rates of cambial growth of two different tree forms was explained in the following ways: 1) carbon allocation to different parts of a tree differs in spite of increases in biomass in both tree forms, and 2) biomass may increase without any corresponding change in water use efficiency of plants (Tang et al., 1999). In contrast, trees with entire bark collected from similar bault and Bergeron, 1992; D’Arrigo and Jacoby, 1992; Cook D’Arrigo, 1989; Luckman, 1989; Graumlich, 1991; Archambeau and Bergeron, 1992; D’Arrigo and Jacoby, 1992; Cook et al., 1991, 1992; Rolland, 1996; Zhang et al., 2003; Huang and Zhang, 2007). This trend was supposed to be associated mostly with greenhouse-induced temperature or precipitation increases during that period. IPCC (2001) reported that within the twentieth century a 0.6°C ± 0.2°C rise of mean global surface temperature and an increase of precipitation by 0.5 to 1% per decade over most mid- and high latitudes of the Northern Hemisphere were observed with the increase of atmospheric CO2 from 295 ppm to 350 ppm between 1900 and 1990 (Keeling and Wort, 1994). Lloyd and Farquhar (1996) commented that both ring-width and temperature data are auto correlated and need to be prewhitened (a procedure that removes the potentially differing level of serial correlation between climate data and climate-sensitive tree-ring series, such as temporal autocorrelation, Cook et al., 1999) to remove underlying trends, otherwise one could find correlations between unrelated parameters. However, most previous studies (D’Arrigo and Jacoby, 1993; Jacoby and D’Arrigo, 1989; Graumlich, 1991) did not prewhiten climate data and the results may thus be questionable (Lloyd and Farquhar, 1996). D’Arrigo and Jacoby (1993) ascribed their failure to detect CO2 fertilization effect to the following possible reasons: 1) There exists a threshold of CO2 level that trees may need to be reached, but current CO2 level may not yet be reached for trees at the temperature-limiting sites such as northern tree-line and high elevations, and 2) Close to the boreal tree-line, cold temperatures, short growing seasons, and N shortage could preclude a direct CO2 growth response (Jacoby and D’Arrigo, 1997). Their first hypothetical explanation lacks a theoretical basis and is not supported by any experimental evidence. Berninger et al. (2004) and Tardif et al. (in press) have partially supported their second explanation for the tree-line. In contrast, several high-elevation or tree-line studies provided clear evidence for greater efficiency of CO2 uptake at any given CO2 partial pressure in plants from high altitudes (Körner and Diemer, 1987; Körner et al., 1991; Handa et al., 2005), suggesting potentially greater sensitivity to CO2 enrichment compared to plants from lower altitudes (Hättenschwiler et al., 2002). Without a critical and convincing comparison with Mann et al. (1999), in which they found that the twentieth-century warming was abrupt and truly exceptional, Bunn et al. (2005) conclusion that recent growth enhancement might be caused by global climate change (mainly unprecedented warming) was doubted (McIntyre, 2005). Since dendroclimatological studies focus on old trees past half of their maximum life expectancy, the small increase in biomass increment due to CO2 fertilization effect might be diminished. Therefore, Voelker et al. (2006) proposed to consider the purported CO2 effect relative to age by species. Recently, researchers such as Cherubini et al. (1998) and D’Arrigo et al. (2007) recognized the potential problem in age-related detrending methods, which could also remove some CO2-related long-term trends in tree-ring growth. In addition, translation of a photosynthetic CO2 response into a growth response is not a 1:1 ratio (Körner, 2006). Furthermore, carbon partitioning and growth within a plant is species specific (Körner et al., 2005). In any case, with increasing CO2-fertilization evidence from many CO2-enriched experiments and increasing tree-ring studies, it is possible that the studies...
ascribing growth increase solely to climate change underestimate direct atmospheric CO2 fertilization effect.

C. Possible Occurrence for Synergistic Effects of Several Factors

The third viewpoint insists that the long-term increase of tree growth could be attributed to the combined effects of several factors such as favorable climate change, CO2 fertilization effect, and anthropogenic atmospheric deposition of nutrients (e.g., N). Tree growth is a complex process and influenced by multiple factors (Fritts, 1976; Schweingruber, 1996). Recent studies showed that associations between tree growth and climate are changing. Tree growth at high latitudes may be less sensitive to variations in temperature today than in the past (Briffa et al., 1998a, 1998b; Barber et al., 2000; Jacoby et al., 2000; Wilson and Luckman, 2003; Wilnking et al., 2004, 2005; Büntgen et al., 2006; D’Arrigo et al., 2007). Climate variability alone seems to be insufficient to explain trends observed in trees like Q. petraea (Becker et al., 1994). With N deposition from urban-industrial pollution during the last several decades (Kauppi et al., 1992), tree growth might also benefit from N fertilization, especially in nutrient-limited soil. Previous studies did not find any N fertilization effect in natural forests (Miller et al., 1991), but a CO2 and N interactive experiment on Q. robur seedlings showed a significantly higher growth (139%) in the elevated CO2/high-N environment compared to the elevated CO2/low-N treatment (Maillard et al., 2001). On the other hand, studies (Tognetti et al., 2000; Saurer et al. 2003) in a semi-arid, N-limited Mediterranean ecosystem (Cherubini et al., 2003) failed to discover long-term significant growth enhancements in several species close to natural CO2 springs, providing inverse evidence for N fertilization effect in natural forests. In other words, if soil N is sufficient in this ecosystem, these species might have shown significant growth enhancements as a result of CO2 and N fertilization effects. Therefore, while the residuals of growth-climate models show obvious trends (Wang et al., 2006), it is very likely that tree growth is influenced by complex and synergistic effects due to several factors, including CO2 fertilization and anthropogenic atmospheric deposition (e.g., N).

To clearly separate CO2 fertilization and N fertilization effects on tree growth in tree-ring studies, it will be necessary to establish CO2/N-fertilization experiments in natural forests, while precluding N fertilization.

V. CONCLUSIONS

The CO2 fertilization effect hypothesis, i.e., rising atmospheric CO2 has a positive effect on tree growth due to increasing availability of carbon, was extensively tested by CO2 enrichment experiments and empirical dendrochronological studies. In this paper, we compared and synthesized the literature from both CO2 enrichment experiments on seedlings or young trees and empirical tree-ring studies detecting CO2 fertilization effect to assess whether CO2 fertilization effect occurs in tree-rings in natural forests. Considerable CO2 enriched experiments demonstrated significantly positive physiological and growth responses of trees to CO2, providing strong evidence to support the direct CO2 fertilization effect (increased photosynthesis, water use efficiency, above- and belowground growth) and thus allowing predication of which ecosystems might be most responsive to CO2. We propose that warm, moderately drought-stressed ecosystems with ample nitrogen supply might be the most CO2 responsive ecosystems. Empirical tree-ring studies took the following three viewpoints on detecting CO2 fertilization effect in tree-rings: 1) finding evidence of CO2 fertilization effect in tree-rings, 2) attributing growth enhancement to favorable climate change rather than CO2 fertilization, and 3) considering that tree growth enhancement might be caused by synergistic effects of several factors such as favorable climate change, CO2 fertilization, and anthropogenic atmospheric deposition, especially of nitrogen. Correspondingly, we interpreted these three viewpoints as 1) occurrence of CO2 fertilization effect in drought-stressed environments, 2) underestimation for CO2 fertilization effect, and 3) possible occurrence for synergistic effects of several factors, respectively. Our review supports the atmospheric CO2 fertilization effect hypothesis, at least in trees growing in semi-arid or arid conditions because the drought-stressed trees could benefit from increased water use efficiency to enhance growth. However, a CO2 spring study in a semi-arid (mean total precipitation during dry summer (May–August) from 1918–1982 below 200 mm in the study region), N-limited Mediterranean ecosystem did not observe significant growth enhancements in several species, even in extremely dry years (Tognetti et al. 2000). In addition, Nowak et al. (2004) did not find strong evidence to support greater response of productivity to elevated CO2 concentration in drier ecosystems or in dry years within an ecosystem. Rather, they suggested that it would occur at some intermediate precipitation (annual precipitation between 300 mm and 500 mm from the empirical results). This indicates that there might exist extreme drought thresholds that could limit CO2 fertilization effect in semi-arid and arid environments. Hence questions on how to define it in dry environments will need to be considered.

In contrast, studies in cold, arid Chaidamu basin with relatively fertile loess (annual mean total precipitation from 1958-2000 around 200 mm, with 80% dropped between May and August in the study area) of the Qinghai-Xizang Plateau (also referred to the Tibetan Plateau (Huang et al., 2007)) showed significant growth enhancements (Zhang et al., 2003; Shao et al., 2005; Liang et al., 2006; Huang and Zhang, 2007; Zhang and Qiu, 2007) as well as increased water use efficiency (24.7% and 33.6% for each species, respectively) (Liu et al., 2007) in Qilian juniper (Sabina przewalskii Kom.) and Qinghai spruce (P. crassifolia Kom.) since the 1850s. These contrasting results suggest that the thresholds of extreme drought that could limit CO2 fertilization effect might be related to the interactions among temperature, N, and drought, as well as to site- and species-specific conditions. To clarify this, however, will need
more CO₂ fertilization effect studies focusing on site conditions (fertility, drought, and temperature) and growth increases of different species in semi-arid and arid environments in the future. Further extensive research on CO₂ fertilization effects in semi-arid and arid environments will certainly contribute to better understanding of global carbon sinks and modification of the current global carbon cycle models, as well as adjustment of long-term reforestation policy in semi-arid and arid regions, which could potentially mitigate the continuing increases in atmospheric CO₂ concentration.

ACKNOWLEDGMENTS

We thank Dr. Feng Xiahong for providing figure 4, Blackwell Publishing for the granted permission to reproduce figure 2 and figure 5, New Phytologist for the granted permission to reproduce figure 3. Venceslas Goudiaby for formatting the manuscript, and Dr. Young-In Park for his helpful comments on the early draft. Particular thanks are due to Dr. Paolo Cherubini (WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Switzerland), Dr. Martin Lechowicz (Mcgill University, Canada), Dr. Xianzhong Wang (Indiana University-Purdue University Indianapolis, USA), and editor Dr. Dennis J. Gray for their critical and valuable comments and suggestions on the early manuscript. This work was funded by the Canada Chair in Forest Ecology and Management hold by Dr. Yves Bergeron at the University of Quebec at Abitibi-Témiscamingue, Quebec, Canada.

REFERENCES


RESPONSE OF FOREST TREES TO INCREASED ATMOSPHERIC CO₂


