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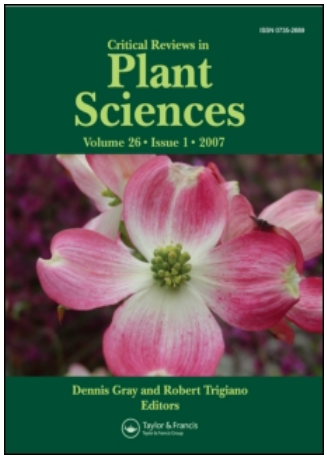

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Response of Forest Trees to Increased Atmospheric CO_2

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Response of Forest Trees to Increased Atmospheric CO_2

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The CO_2 fertilization hypothesis stipulates that rising atmospheric CO_2 has a positive effect on tree growth due to increasing availability of carbon. The objective of this paper is to compare the recent literature related to both field CO_2-enriched experiments with trees and empirical dendrochronological studies detecting CO_2 fertilization effects in tree-rings. This will allow evaluation of tree growth responses to atmospheric CO_2 enrichment by combining evidence from both ecophysiology and tree-ring research. Based on considerable experimental evidence of direct CO_2 fertilization effect (increased photosynthesis, water use efficiency, and above- and belowground biomass), and predications from the interactions of enriched CO_2 with temperature, nitrogen and drought, we propose that warm, moderately drought-stressed ecosystems with an ample nitrogen supply might be the most CO_2 responsive ecosystems. Empirical tree-ring studies took the following three viewpoints on detecting CO_2 fertilization effect in tree-rings: 1) finding evidence of CO_2 fertilization effect in tree-rings, 2) attributing growth enhancement to favorable climate rather than atmospheric CO_2 enrichment, and 3) considering that tree growth enhancement might be caused by synergistic effects of several factors such as favorable climate change, CO_2 fertilization, and anthropogenic atmospheric deposition (e.g., nitrogen). At temperature-limiting sites such as high elevations, nonfindings of CO_2 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 CO_2 response, 2) old trees past half of their maximum life expectancy and consequently only a small increase in biomass increment due to CO_2 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 CO_2-related trends in tree-rings, and 4) carbon partitioning and growth within a plant that is species-specific. Our review supports the atmospheric CO_2 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 CO_2 fertilization effect, CO_2 enrichment experiment, dendrochronology, ecophysiology, tree-rings, water use efficiency

I. INTRODUCTION

Atmospheric carbon dioxide (CO_2) is a substrate for plant photosynthesis. Increased atmospheric CO_2 concentration is believed to, therefore, increase photosynthesis rate by increasing CO_2 intake directly (Arp, 1991; Long and Drake, 1992; Koch and Mooney, 1996; Curtis, 1996; Mooney *et al*., 1999; Norby *et al*., 1999). Increased atmospheric CO_2might 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 CO_2-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, CO_2 has been the most important factor associated with a rise in temperature during recent decades (IPCC, 2007). A new simulation study under a doubled CO_2 concentration suggested that the positive feedbacks of CO_2 and CH4 might be important, i.e., higher temperatures may lead to increased releases (or reduced uptake) of CO_2 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 CO_2 enrichment on plants.

With continuously anthropogenic atmospheric CO_2 enrichment, it was hypothesized that CO_2 enhancement could enhance tree growth and change growth of forests through direct CO_2 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 CO_2 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 CO_2 fertilization effect or to indirect effect of enriched atmospheric CO_2 concentration.

The large size and long life spans of trees make it technically and economically challenging to measure and monitor their growth response to CO_2 enrichment. In practice, two kinds of approaches to detect the effects of atmospheric CO_2 enrichment on trees were used: 1) short-term field CO_2-enrichment experiments on seedlings or young trees, and 2) empirical dendrochronological studies. During the past decades, CO_2 enrichment experiments were conducted over five continents and the results showed that elevated CO_2 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 CO_2 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;

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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 CO_2-enriched experiments with trees and empirical dendrochronological studies detecting CO_2 fertilization effect in tree-rings in order to evaluate tree growth response to atmospheric CO_2 enrichment by combining congruent evidences from both ecophysiology and tree-ring research. Since some meta-analytical reviews on enriched-CO_2 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 CO_2 fertilization effect really occurs in tree-rings in natural forests. The text is structured as follows: 1) empirical evidence from CO_2 enrichment experiments, 2) empirical dendrochronological studies testing CO_2 fertilization effect in tree-rings, 3) evidence for CO_2 fertilization effect displayed in tree-rings in natural forests, and 4) conclusions.

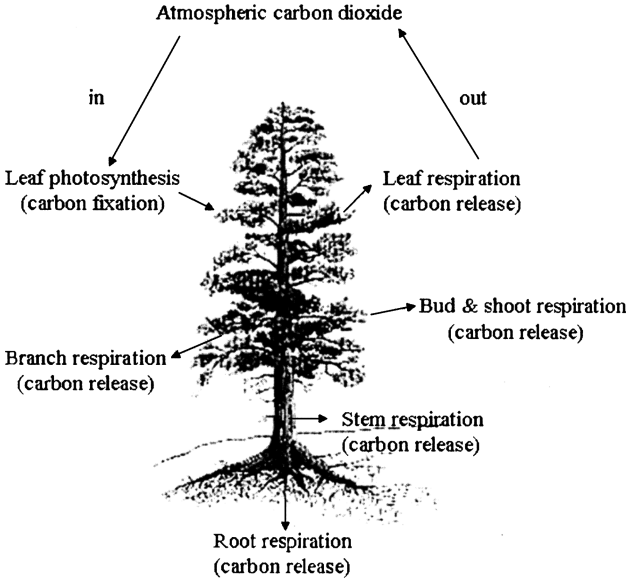

FIG. 1. Flow of carbon dioxide between atmosphere and tree.

II. EMPIRICAL EVIDENCE FROM CO_2 ENRICHMENT EXPERIMENTS

A. Physiological Response to CO_2

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 CO_2 enrichment. CO_2 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 CO_2 and other gases with the atmosphere mainly through the leaf stomata. Within the leaf, CO_2 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 CO_2 and O_2 in living cells, leaves, buds or shoots, branches, stems, and roots may consume some of the carbon and release it to the atmosphere as CO_2 (carbon release) (Norby *et al*., 1999; Beedlow *et al*., 2004) (Figure 1).

CO_2 partial pressure is an important limiting factor for photosynthesis (Aranjuelo *et al*., 2005). Net CO_2 assimilation rate per unit area of C_3 plants is affected by the ratio of atmospheric CO_2 concentration and O_2 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 CO_2, and carboxylation results in carbon fixation through the photosynthetic carbon reduction cycle (Morison and Lawlor, 1999). Higher CO_2 level hence increases the leaf internal CO_2 concentration and the CO_2:O_2 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 CO_2 concentration should be higher under warm conditions. Also, the ratio of carboxylation to oxygenation decreases with the CO_2 to O_2 ratio in the leaf. Drought also decreases the CO_2 concentration without affecting the O_2 concentration (Long, 1991). Increases in ambient CO_2 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 CO_2. 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

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several cases under enriched-CO_2 environment. A meta-analytical review of free-air CO_2 enrichment (FACE) experiments found that trees were more responsive than other function types to elevated CO_2 (Ainsworth and Long, 2005). In a review of short-term CO_2-enriched experiments (less than one season), Ceulemans and Mousseau (1994) found that photosynthesis of deciduous species was more sensitive to elevated CO_2 than that of conifers. However, evidence from long-term studies (more than one season) suggested that photosynthesis stimulation enhanced by elevated CO_2 was similar in unstressed 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 CO_2 between conifers and deciduous trees.

1. *CO_2 and Temperature*

When taking into account the interactive effects of increased CO_2 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 CO_2 concentration will favour photosynthesis over photorespiration (Long, 1991). With the elevation of CO_2 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 CO_2 uptake (A_{sat} μmol $m^{-2}s^{-1}$) 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 C_3 species (*Scrophularia desertorum* (Munz) R. Shaw, *Cardaria draba* Desv., *Populus fremontii* Wats.) (Sage and Sharkey, 1987). Long (1991) further pointed out that following from this interaction of CO_2 concentration and temperature, the temperature optimum (T_{opt}) of CO_2 uptake will increase, T_{opt} increases by 3 °C at CO_2 concentration = 500 μmol mol^{-1} and 5°C at CO_2 concentration = 650μmol mol^{-1} (Figure 2). Correspondingly, the predicted upper temperature at which positive CO_2 uptake may be maintained is also increased by 4 °C and 7°C, respectively (Long, 1991).

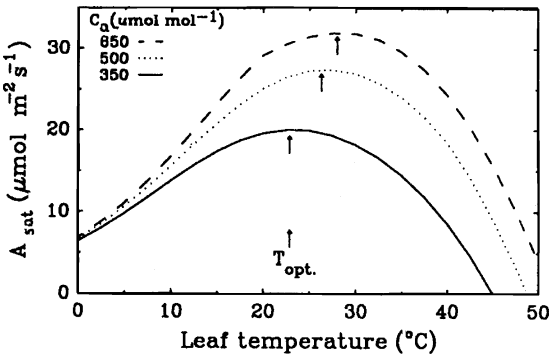

FIG. 2. Predicted light-saturation rates of leaf CO_2 uptake (A_{sat}) with leaf temperature for three atmospheric CO_2 concentrations (C_a μmol mol^{-1} of CO_2 in air). Arrows indicate T_{opt}, i.e., the temperature at which A_{sat} is maximal for each value of C_a (after Long, 1991).

Idso *et al*. (1992) found that at a mean leaf temperature of 31, 35, and 42 °C, the additional 300 ppmv of CO_2 in the CO_2-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 ambient-air enclosures, respectively, demonstrating that the upper-limiting temperature for growth was raised 7°C by the extra CO_2. The FACE experimental data showed that light-saturated CO_2 uptake of plants under elevated CO_2 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 CO_2 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 CO_2-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. *CO_2 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 CO_2-enriched environment. When plants are exposed to a CO_2-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 CO_2 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 CO_2-enriched atmosphere will sequester carbon and N in long-lived biomass and soil organic pools, thereby limiting available N and constraining the

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continued response of net primary productivity to elevated CO_2 concentration. Recent studies have provided partial evidence for the PNL (Hungate *et al*., 2006), or 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_2over 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

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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 CO_2

Currently, there are four methods of exposing tree foliage to elevated CO_2 in the field or under semi-field conditions, including the following: 1) Free Air CO_2 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 CO_2 concentration could have significant impacts on the above- and belowground growth of trees.

1. Aboveground Growth

Elevated CO_2 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 CO_2 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 CO_2 environment for subsequent four growing seasons when compared to ambient CO_2, respectively. Ceulemans *et al*. (1995) observed 8–18% leaf area increases for *Populus* clones under CO_2 enrichment. A meta-analysis found that trees had a 21% increase in leaf area index compared to less response of herbaceous C_3 grasses (Ainsworth and Long, 2005). Increase in leaf area of *Quercus alba* L. saplings in elevated CO_2 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 CO_2 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 CO_2 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).

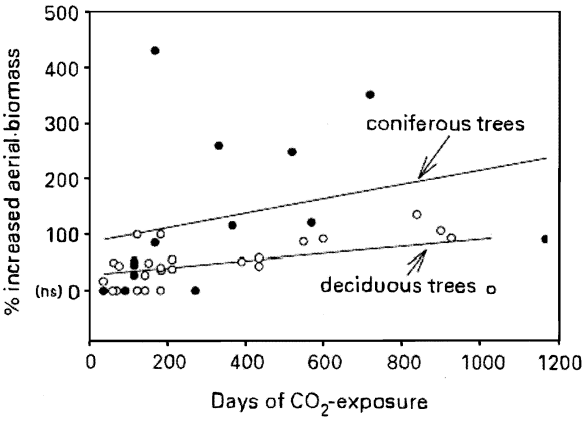

FIG. 3. Biomass enhancement of trees (. coniferous; ○ deciduous) under elevated CO_2 in experiments of variable exposure duration (after Saxe *et al*., 1998).

Elevated CO_2 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 CO_2 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 CO_2 enrichment than trees under ambient CO_2. Norby *et al*. (1992) showed that *L. tulipifera* trees grown in enriched CO_2 for 2.5 growing seasons had 27% more dry mass than trees grown in ambient CO_2. Saxe *et al*. (1998) reviewed the short-term CO_2-enriched experiments and summarized that, on average, elevated atmospheric CO_2 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 CO_2 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 C_3 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 CO_2 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.

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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 CO_2 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 CO_2 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 CO_2 concentration. Saxe *et al*. (1998) reported that, if the leaf development is hastened under elevated CO_2 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 CO_2 effect on flowering and fruiting (Saxe *et al*., 1998). LaDeau and Clark (2001) have done an experiment study exposing 19-year-old *P. taeda* to 4 years of CO_2 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 CO_2 concentration. This indicates that a higher carbon allocation to reproduction under enriched CO_2 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 CO_2 and seeds germinated much earlier, with more than three times germination success compared to the ambient seed source (Hussain *et al*., 2001). A CO_2-enriched study on reproduction of hardwood trees (*Q. myrtifolia* Willd., *Q. chapmanii* Sarg., and *Q. geminate* Small) in a natural scrub-oak forest of Florida suggested that the number of acorns produced under elevated CO_2 was significantly higher than in ambient CO_2 (Stiling *et al*., 2004).

2. *Belowground Growth*

The responses of roots to CO_2 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 CO_2 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 CO_2 conditions (Oechel and Strain, 1985). By reviewing plant root and rhizosphere response to elevated CO_2, Rogers *et al*. (1994) found that root dry weight increased in all studies under elevated CO_2. However, a few destructive harvest multi-year studies of trees in elevated CO_2 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. (Rey and Jarvis, 1997), *P. taeda* (Tissue *et al*., 1997), *P. ponderosa* Dougl. (Walker *et al*., 1997), or *F. excelsior* L.,*Q. petraea* Liebl. and *P. sylvestris* (Crookshanks *et al*., 1998). In a FACE experiment of *P. taeda* forest of North Carolina, Allen *et al*. (2000) found that elevated CO_2 caused significant increases in loblolly pine fine root increment after two growing seasons. Lukac *et al*. (2003) revealed that elevated CO_2 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 CO_2 compared with plots in ambient CO_2 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 CO_2 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 CO_2. However, they did not confirm any positive interactions between drought and CO_2 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 CO_2-enriched experiments showed that elevated CO_2 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 CO_2 fertilization effect. But those CO_2-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 CO_2 with time (i.e., acclimation) (Loehle, 1995).

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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 CO_2 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 CO_2 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 CO_2 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 CO_2 environment, thus magnifying the effect of rising CO_2 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 CO_2 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 CO_2 and a nearby control site in Tuscany, Italy, Tognetti *et al*. (2000) found that CO_2 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 CO_2 under drought stress, or to the acclimation of trees to high CO_2.

Taken together, there is an ample body of evidence from short- to medium-term CO_2 enrichment studies to suggest that trees may be able to increase their photosynthesis and growth under elevated CO_2. 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 CO_2 values in chambers of FACE experiments that might potentially affect photosynthetic production and growth. Despite all these weaknesses enrichment experiments provide valuable information to allow prediction of which ecosystems might be most responsive to CO_2. We propose that warm, moderately drought-stressed ecosystems with an ample N supply might be the most CO_2 responsive ecosystems.

III. EMPIRICAL DENDROCHRONOLOGICAL STUDIES TESTING CO_2 FERTILIZATION EFFECT IN TREE RINGS

Trees provide long-term records of growth and, hence, are a natural archive for documenting environmental information. In dendrochronology, growth series for an individual tree can be translated into an aggregate of environmental factors from both human and natural origins that affected growth over time (Fritts, 1976; Schweingruber, 1996). Cook (1987) suggested that radial growth (ring width) in any one year (t) is a function of an aggregate of all factors. In order to understand environment impacting factors on trees, age/size-related growth detrending is required. However, an obvious problem is that growth decline with age/size is difficult to model and the detrending processes commonly used in dendroclimatology might eliminate somehow high and/or low frequency variations in tree-ring time series. Traditional detrending assumes that ring growth can be decomposed into different effects as follows (Cook, 1987, 1990):

$$R_t = A_t + C_t + \delta D1_t + \delta D2_t + E_{CO2t} + e_t$$

in which:

- R_t – the observed ring width in the year of t,
- A_t –the age/size related growth trend due to normal physiological aging processes,
- C_t – the climate effects that affected tree growth in the year of t,
- $D1_t$ – the occurrence of disturbance factors within the forest stand (e.g. a blow down of trees),
- $D2_t$ – the occurrence of disturbance factors from outside the forest stand (e.g. an insect outbreak that defoliates the trees),
- E_{CO2t} – the CO_2 fertilization effect,
- et – random processes not accounted by those above processes,
- δ – either a '0' for absence or '1' for presence of the disturbance signal.

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 CO_2 fertilization effects (E_{CO2t}) in tree-rings through the removal of other factors in tree-ring growth. The trend of CO_2 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 ($D1_t$) and exogenous ($D2_t$) factors were minimized (e.g., Nicolussi *et al*., 1995; Soulé and Knapp, 2006), CO_2 fertilization effect was assessed either by analyzing trends in basal area increment (BAI) or by comparing growth trends among age classes or

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TABLE 1
Empirical dendrochronological studies detecting CO_2 fertilization effect in tree-rings

Results	Study region	Species	Detrending (Yes/No)	Analysis Methods	Authors
I	Semiarid, western USA	*P. aristata* *P. longaeva*	Yes	Comparisons of growth	LaMarche *et al*., 1984
	Semiarid, western USA	*P. flexilis*	Yes	Comparisons of growth	Graybill, 1987
	Semiarid, high elevations western NA	*P. aristata* *P. longaeva*	Yes	Comparisons of growth	Graybill and Idso, 1993
	Subalpine, central Alps	*P. cembra*	No	Age classes	Nicolussi *et al*., 1995
	Semi-arid, CO_2 springs Mediterranean, Italy	*Q. ilex*	Yes	Growth comparisons with CO_2 data	Hättenschwiler *et al*., 1997
	Arid Oregon	*J. occidentalis*	Yes	Detecting trends in residuals	Knapp *et al*., 2001
	Arid Oregon	*P. ponderosa*	Yes	Comparisons with drought years	Soulé and Knapp, 2006
	Southeast Missouri	*Q. velutina* *Q. coccinea* *P. echinata*	Yes	Comparisons of growth trends	Voelker *et al*., 2006
	Dry environment, southwestern Manitoba	*P. glauca*	Yes	Comparisons between young trees and old trees	Wang *et al*., 2006
II	Tree line, NA		Yes	Detecting trends in residuals	Jacoby and D'Arrigo, 1989
	Northeastern France	*A. alba*	Yes	Analysis of residuals	Becker, 1989
	Southwestern USA	subalpine conifers	Yes	Response surface	Graumlich, 1991
	Tree line, northern NA	*P. glauca*	Yes	Detecting trends in residuals	D'Arrigo and Jacoby, 1993
	Semiarid mountain, western NA	*P. balfouriana* *P. longaeva* *P. albicaulis* *P. occidentalis* *P. flexilis*	Yes	Comparisons	Bunn *et al*., 2005
III	Finland	*P. sylvestris*	Yes	A four component model	Hari *et al*., 1984
	Finland	*P. sylvestris*	Yes	Comparisons of time series models	Arovaara *et al*., 1984
	Finland	*P. sylvestris*	Yes	A four component model	Hari and Arovaara, 1988
	Northern hemisphere	*Pinus, Picea, Abies, Cedrus, Pseudotsuga*	Yes	ß factor	Kienast and Luxmoore, 1988
	Northeastern France	*Q. petraea* *Q. robur*	No	Basal area increment	Becker *et al*., 1994
	European	European species	No	Basal area increment	Briffa *et al*., 1998b
	Tree-line French Alps	*P. abies* *L. decidua* *P. cembra* *P. uncinata*	Yes	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	Rolland *et al*., 1998

I: finding evidence of CO_2 fertilization effect in tree-rings; II: growth enhancement caused by favorable climate change; III: combined effects of several factors such as favorable climate change, CO_2 fertilization effect, anthropogenic atmospheric deposition (e.g., N); NA-northern America). Dentrending methods include some conservative methods such as negative exponential, regression line or straight line.

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between old trees and young trees or by computing the biotic growth factor (ß factor, which is a parameter used for comparing responses of various species to CO_2 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 CO_2 fertilization effect are various, although LaMarche *et al*. (1984) first claimed a possible CO_2 fertilization effect in tree-rings. After an extensive survey of the pertinent literature, three viewpoints on detecting CO_2 fertilization effect in tree-rings were found:

A. Finding Evidence of CO_2 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 CO_2 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 CO_2 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 CO_2. 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 CO_2 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 CO_2 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 (Soulé and Knapp, 2006). Wang *et al*. (2006) compared the growth of young *Picea glauca* (Moench) Voss trees that are currently exposed to high atmospheric CO_2 to the early growth period of older trees that were exposed to low atmospheric CO_2 in a dry environment of southwestern Manitoba, Canada, and the results provided circumstantial evidence that atmospheric CO_2 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* Muenchh.) and coniferous (*P. echinata* Mill.) species increased in stem growth coincidently with increases in atmospheric CO_2 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 CO_2 increase.

CO_2 springs, i.e., places where CO_2 is emitted naturally from the soil, are places that permit us to study the effects of CO_2 enrichment on tree growth without the problems associated with climatic trends that are superimposed on CO_2concentration trends. Hättenschwiler *et al*. (1997) and Tognetti *et al*. (2000) used these natural CO_2 springs (including the Bossoleto CO_2 spring and the Laiatico CO_2 spring, Italy) for dendrochronological studies. Hättenschwiler *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 CO_2 interacts with water stress. Tognetti *et al*. (2000) were unable to extend Hättenschwilers' 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 ^{14}C measurements, they found that CO_2 concentration (or the contribution of CO_2 spring to ambient CO_2 concentration) seemed to decrease with tree age. Changes in the ^{13}C discrimination and the oxygen isotopes indicated a progressive downscaling of photosynthesis with plant age, confirming Hättenschwilers' initial conclusions. All these studies (except Tognetti *et al*., 2000) support the hypothesis that elevated atmospheric CO_2 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 CO_2 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 CO_2 (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 CO_2 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 tree-ring record, but CO_2 fertilization was not detectable as a major factor influencing growth on these sites. Bunn *et al*. (2005) in-

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vestigated some 1000-year chronologies of five high-elevation conifers (*P. balfouriana* Balf., *P. longaeva, 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 CO_2 fertilization effect.

C. Combined Effects of Several Factors Such as Favorable Climate Change, CO_2 Fertilization, and Anthropogenic Atmospheric Deposition

It is not easy to clearly separate the direct CO_2 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 CO_2 or nutrient deposition (Hari *et al*., 1984; Arovaara *et al*., 1984; Hari and Arovaara, 1988). Kienast 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 CO_2 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, CO_2 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 CO_2 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 CO_2 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, CO_2 fertilization effect, and anthropogenic atmospheric deposition of nutrients, particularly of N.

IV. EVIDENCE FOR CO_2 FERTILIZATION EFFECT DISPLAYED IN TREE RINGS IN NATURAL FORESTS

In natural forests, anthropogenic-caused increases in atmospheric CO_2 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 CO_2 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 CO_2 Fertilization Effect in Drought-Stressed Environments

Of three viewpoints, it is very likely that direct CO_2 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 CO_2 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 CO_2 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 ($^{13}C/^{12}C$) and oxygen ($^{18}O/^{16}O$) 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

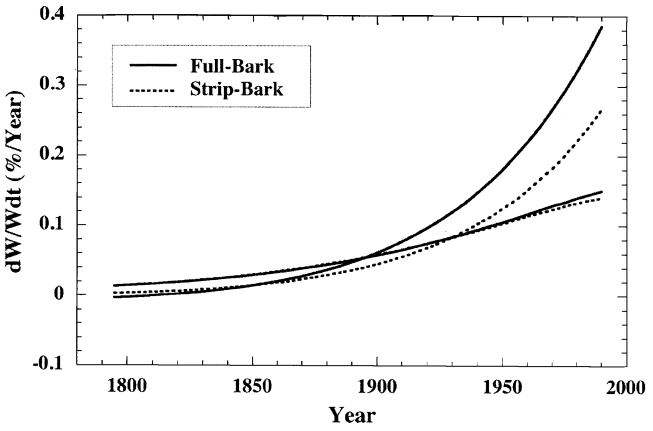

FIG. 4. The relative rate of change in water-use efficiency (% per year) for the full-bark (solid lines) and strip-bark (dashed lines) bristlecone pine trees on Sheep Mountain of the White Mountains, California (after Tang *et al*., 1999).

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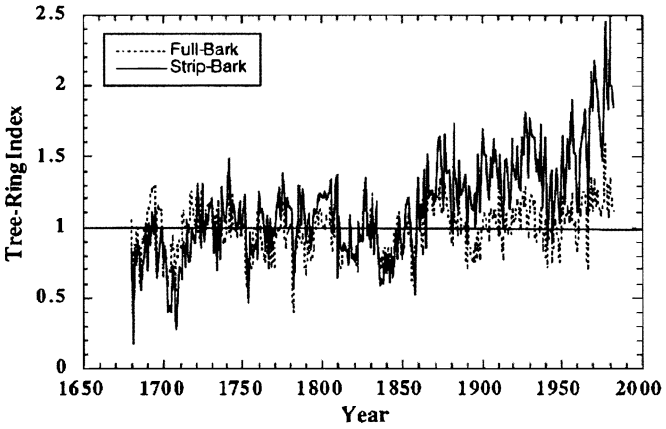

FIG. 5. Bristlecone pine tree-ring index chronologies of full-bark (dashed line) and strip-bark (solid line) growth forms from Sheep Mountain, California (after Graybill and Idso, 1993).

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 sites as strip-bark trees did not exhibit anomalous growth trends to support the CO_2-fertilization hypothesis (Graumlich, 1991; Jacoby and D'Arrigo, 1997; Bunn *et al*., 2003). All in all, there is increasing evidence to support the hypothesis of direct CO_2 fertilization effect in arid or sub-arid regions as based on studies of precipitation-limited *J. occidentalis* (Knapp *et al*., 2001) and *P. ponderosa* (Soulé and Knapp, 2006) in arid central Oregon, as well as *P. glauca* growing on dry sites in southwestern Manitoba, Canada (Wang *et al*., 2006).

B. Underestimation for CO_2 Fertilization Effect

The second viewpoint attributes growth enhancements to climate warming rather than CO_2 fertilization. Long-term increases in tree growth during the last century were detected in many tree-ring studies (e.g. Payette *et al*., 1985; Jacoby and D'Arrigo, 1989; Luckman, 1989; Graumlich, 1991; Archambault 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 $0.6^{\circ}C \pm 0.2^{\circ}C$ 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 CO_2 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 CO_2 fertilization effect to the following possible reasons: 1) There exists a threshold of CO_2 level that trees may need to be reached, but current CO_2 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 CO_2 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 CO_2 uptake at any given CO_2 partial pressure in plants from high altitudes (Körner and Diemer, 1987; Körner *et al*., 1991; Handa *et al*., 2005), suggesting potentially greater sensitivity to CO_2 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 CO_2 fertilization effect might be diminished. Therefore, Voelker *et al*. (2006) proposed to consider the purported CO_2 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 CO_2-related long-term trends in tree-ring growth. In addition, translation of a photosynthetic CO_2 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 CO_2-fertilization evidence from many CO_2-enriched experiments and increasing tree-ring studies, it is possible that the studies

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ascribing growth increase solely to climate change underestimate direct atmospheric CO_2 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, CO_2 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; Wilmking *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 CO_2 and N interactive experiment on *Q*. *robur* seedlings showed a significantly higher growth (139%) in the elevated CO_2/high-N environment compared to the elevated CO_2/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 CO_2 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 CO_2 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 CO_2 fertilization and anthropogenic atmospheric deposition (e.g., N). To clearly separate CO_2 fertilization and N fertilization effects on tree growth in tree-ring studies, it will be necessary to establish CO_2/N-fertilization experiments in natural forests, while precluding N fertilization.

V. CONCLUSIONS

The CO_2 fertilization effect hypothesis, i.e., rising atmospheric CO_2 has a positive effect on tree growth due to increasing availability of carbon, was extensively tested by CO_2 enrichment experiments and empirical dendrochronological studies. In this paper, we compared and synthesized the literature from both CO_2 enrichment experiments on seedlings or young trees and empirical tree-ring studies detecting CO_2 fertilization effect to assess whether CO_2 fertilization effect occurs in tree-rings in natural forests. Considerable CO_2 enriched experiments demonstrated significantly positive physiological and growth responses of trees to CO_2, providing strong evidence to support the direct CO_2 fertilization effect (increased photosynthesis, water use efficiency, above- and belowground growth) and thus allowing predication of which ecosystems might be most responsive to CO_2. We propose that warm, moderately drought-stressed ecosystems with an ample nitrogen supply might be the most CO_2 responsive ecosystems. Empirical tree-ring studies took the following three viewpoints on detecting CO_2 fertilization effect in tree-rings: 1) finding evidence of CO_2 fertilization effect in tree-rings, 2) attributing growth enhancement to favorable climate change rather than CO_2 fertilization, and 3) considering that tree growth enhancement might be caused by synergistic effects of several factors such as favorable climate change, CO_2 fertilization, and anthropogenic atmospheric deposition, especially of nitrogen. Correspondingly, we interpreted these three viewpoints as 1) occurrence of CO_2 fertilization effect in drought-stressed environments, 2) underestimation for CO_2 fertilization effect, and 3) possible occurrence for synergistic effects of several factors, respectively. Our review supports the atmospheric CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 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

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more CO_2 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 CO_2 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 CO_2 concentration.

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