

Effects of elevated carbon dioxide concentration on wood structure and formation in trees

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Summary. The effects of elevated carbon dioxide concentration ($[CO_2]$) on the structure of xylem cells in trees have not yet been clarified, in spite of the importance of woody plants as large, long-term carbon sinks. We review recent studies that have investigated how elevated $[CO_2]$ affects growth ring features. In general, elevated $[CO_2]$ enhances radial growth, especially when sufficient nutrients are supplied. The mean density of growth rings also increased but sometimes it decreased or remained unchanged, depending on the extent of cell division, cell expansion and cell wall thickening under elevated $[CO_2]$.

Key words: Elevated CO_2 , Structure of growth ring, Wood formation, Woody plants

1. Introduction

Traits of a tree stem that are relevant to its role as a carbon sink are stability and longevity as compared with herbaceous species. Stems can hold carbon for a long time: not only when they are part of a living tree, but also after harvesting, as the wood components of buildings or as papers. Thus, carbon fixation by forest trees can be effective for centuries by virtue of the photosynthates accumulated in the xylem of the stem in trees.

Changes in the morphology of xylem cells under elevated $[CO_2]$ influence not only the physical properties of xylem cells, but also the extent to which the tree is a carbon sink. However, we have little knowledge of how rising atmospheric $[CO_2]$ affects cell division, cell expansion and the thickening of xylem cell walls in woody plants, in spite of the importance of woody plants. Here, we review previous researches and our studies on the structure and formation of wood in trees under elevated $[CO_2]$.

2. Changes in the growth ring features under elevated [CO₂]

2.1 Growth ring width

In experiments involving artificial exposure to CO₂, Curtis and Wang (1998) analyzed the effects of elevated [CO₂] on the growth and photosynthesis of woody species in more than 500 cases with a meta-analysis method, and they concluded that elevated [CO₂] stimulates tree growth in almost all cases, but that the response depends on the clone, species, growth stage and duration of elevated CO₂ exposure. These results raise the question: how does elevated [CO₂] alter the structure of a tree stem when they stimulate the growth of a tree? There have been several studies on the effects of elevated [CO₂] on tree ring width, density and cell dimensions (Table 1). Many studies reported that elevated [CO₂] resulted in the formation of wider tree rings in conifers (Atwell et al. 2003; Ceulemans et al. 2002; Conroy et al. 1990; Oren et al. 2001; Telewski et al. 1999; Yazaki et al. 2001) and hardwoods (Hättenschwiler et al. 1997; Norby et al. 2001). In contrast, some studies found no difference in growth ring width (Hättenschwiler et al. 1996; Kilpeläinen et al. 2003; Tognetti et al. 2000; Yazaki et al. 2004). In particular, sufficient nutrients were often required for the [CO₂]-induced enhancement of wood formation (e.g. Yazaki et al. 2001), but other times the growth-inducing effect of elevated [CO₂] depended less on nutrient supply (Hättenschwiler et al. 1996). These variations might depend on the differences in the relationship between growth stimulation and nutrient requirements among species or developmental stages.

As described above, growth rings tend, more or less, to become wider at elevated [CO₂] than at ambient [CO₂] when there are no limitations on other environmental factors. However, long-term exposure of CO₂ (> 10 years) results in a decline in the enhancement of radial growth induced by elevated [CO₂] due to some age-related factors and/or extent of the tree's acclimation to high [CO₂] (Adam et al. 2004; Tognetti et al. 2000). Thus, the response of seedlings to elevated [CO₂] should be applied cautiously to mature trees in the higher [CO₂] environment expected in the future (Norby et al. 2001).

2.2 Density of growth rings

Increases in wood density have been induced by elevated [CO₂] in some conifers (Table 1). However, in similar species, other studies indicate that there is little evidence of an increase in wood density under these conditions. For hardwoods, almost no change in wood density under elevated [CO₂] has been observed (Table 1), although hardwoods have been studied less than conifers. Furthermore, wood density in *Pinus taeda* grown at elevated [CO₂] is less than controls grown in ambient conditions, in Free-air-CO₂-enrichment (FACE) system (Oren et al. 2001). High nutrient levels can diminish wood density while high [CO₂] can increase it (Hättenschwiler et al. 1996). There may be negative interactions between the effects of [CO₂] and nutrient availability on wood formation because growth rings in conifers often have less wood density with higher rates of radial growth.

Table 1. Summary of changes in xylem anatomy in woody species grown at elevated [CO₂]

Species	RW	WD	CD	LD	CWT	FL	Reference
Conifers							
<i>Larix kaempferi</i>	0	0	+	0	0		n.a. Yazaki, K. et al. (2004)
<i>Larix sibirica</i>	+*	0	0	0	-*		n.a. Yazaki, K. et al. (2001)
<i>Picea abies</i>	0 (total) + (LW)	+	n.a.	n.a.	n.a.		n.a. Hättenschwiler et al. (1996)
	n.a.	0	n.a.	n.a.	n.a.		n.a. Beismann et al. (2002)
<i>Pinus ponderosa</i>	n.a.	0	0	n.a.	n.a.		n.a. Maherali and DeLucia (2000)
<i>Pinus radiata</i>	n.a.	n.a.	n.a.	0	0	0	Donaldson et al. (1987)
	+*	+	n.a.	0	+*	0	Conroy et al. (1990)
	+	+	n.a.	0 (area)	n.a.		n.a. Atwell et al. (2003)
<i>Pinus sylvestris</i>	+ (EW)	0	+	n.a.	n.a.		n.a. Ceulemans et al. (2002)
	0	+ (LW)	n.a.	n.a.	n.a.	0	Kilpeläinen et al. (2003)
<i>Pinus taeda</i>	+ (EW)	0 (soft x-ray)	n.a.	n.a.	n.a.		n.a. Telewski et al. (1999)
	+*	+ -	n.a.	n.a.	n.a.		n.a. Oren et al. (2001)
Hardwoods							
<i>Arbutus unedo</i>	0	n.a.	n.a.	n.a.	n.a.		n.a. Tognetti et al. (2000)
<i>Fraxinus ornus</i>							
<i>Quercus cerris</i>							
<i>Quercus ilex</i>							
<i>Quercus pubescens</i>							
<i>Fagus sylvatica</i>	n.a.	0	n.a.	n.a.	n.a.		n.a. Beismann et al. (2002)
<i>Liquidambar styraciflua</i>	+ (1st year)	0	n.a.	n.a.	n.a.		n.a. Norby et al. (2001)
	0 (2nd year)						
<i>Populus alba</i>	n.a.	0	n.a.	n.a.	n.a.		n.a. Calfapietra et al. (2003)
<i>Populus nigra</i>							
<i>Populus deltoides</i> x <i>P. nigra</i>							
<i>Populus tremuloides</i>	+	0	0 (vessel) 0 (fiber)	0 (vessel) 0 (fiber)	0 (vessel) 0 (fiber)		n.a. Kaakinen et al. (2004)
<i>Prunus avium</i> x <i>P. pseudocerasus</i>	n.a.	n.a.	n.a.	0	n.a.		n.a. Atkinson and Taylor (1996)
<i>Quercus ilex</i>	+	n.a.	n.a.	n.a.	n.a.		n.a. Hättenschwiler et al. (1997)
	n.a.	0	n.a.	+ (area)	n.a.		n.a. Gartner et al. (2003)
<i>Quercus robur</i>	n.a.	n.a.	n.a.	+	n.a.		n.a. Atkinson and Taylor (1996)

0, not significant difference; +, increase; -, decrease; n.a., not available.

RW, Radial growth or growth ring width; WD, Wood density or relative area of cell wall; CD, Cell diameter of tracheid (conifer) or vessel (hardwood); LD, Lumen diameter of tracheid (conifer) or vessel (hardwood); CWT, Cell wall thickness; FL, Fiber length.

*, effective only in combination with high levels of nutrients.

EW, effective mainly in earlywood; LW, effective mainly in latewood.

The effect of [CO₂] on wood density is more complicated than on growth ring width. For further clarification of this inconsistency, we need to turn to microscopic analysis because wood density is determined by cell dimensions (Yasue et al. 2000) (see below).

3. Variation in intra-ring cell dimensions under elevated [CO₂]

Growth ring structure depends on cambial activity and the development of xylem cells. Many environmental factors (temperature, water availability, nutrient supply, etc.) affect the development of xylem cells (e.g. Denne and Dodd 1981). It is possible that elevated [CO₂] also affects wood formation directly and/or indirectly (Pritchard et al. 1999).

Wood density is determined by growth ring structure, which is, itself, a consequence of changes in the dimensions of the cells in the different parts of the wood (Fig. 1). For example, the ratio of earlywood width to latewood width and/or the ratio of the amount of cell wall to inter- and intracellular spaces affect growth ring structure and wood density. Therefore, we need to divide the wood-forming effects of [CO₂] into those relevant to "cell division", to "cell expansion" and to the "deposition of cell wall" (Fig. 1).

3.1 Cell division

For conifers, the increase in the width of growth rings under elevated [CO₂] (compared with ambient [CO₂]) mainly results from a higher number of tracheids along the radius (Yazaki et al. 2001). This increase in the number of cells is brought about by two mechanisms: (1) an increase in the rate of cell division and (2) a prolongation of the cell division period. Shoot development affects the duration of cambial activity via changes in levels of endogenous plant growth regulators in cambial regions (Funada et al. 2001;

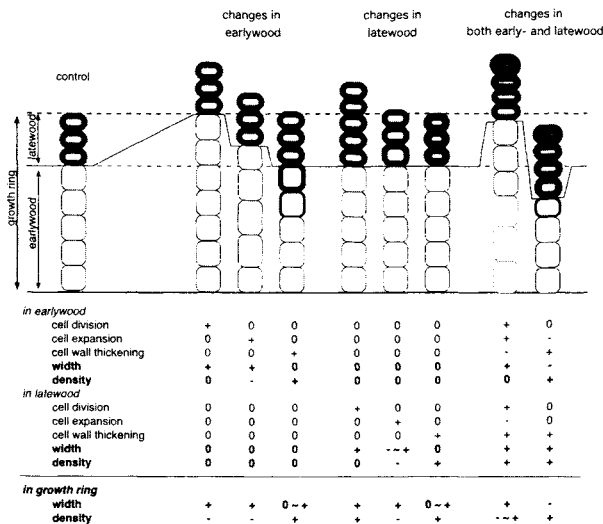


Fig. 1. A schematic representation of the changes in cell development and wood properties compared to control wood. 0, no change; +, increase; -, decrease.

Pritchard et al. 1999). The period of shoot elongation or radial growth could be prolonged for some species by elevated [CO₂] (Koike et al. 1996; Peltola et al. 2002). However, shorter periods of shoot elongation in response to elevated [CO₂] was also reported, in connection with accelerated leaf senescence and bud formation (Centritto et al. 1999; Sigurdsson 2001), and some studies found no differences in the timing of shoot growth cessation among various [CO₂] treatments (Calfapietra et al. 2003; Koike et al. 1995; Roberntz 1999). Thus, the increase in the number of cells at elevated [CO₂] is not always associated with specific changes in the duration of shoot elongation.

Elevated [CO₂] can shorten the time required for each cell division in the apical meristem of a shoot of *Dactylis glomerata*, a herbaceous species (Kinsman et al. 1996). For woody species, a CO₂-induced increase in relative growth rate was observed especially early in the growing season (Jach and Ceulemans 1999, Yazaki et al. 2001, 2004), implying an increase in the rate of cell division under elevated [CO₂]. Therefore, it is possible that elevated [CO₂] enhances the rate of cambial activity, although there have been very few estimates of both the response of vascular cambium to elevated [CO₂] and the influence of rising [CO₂] on growth regulators in woody plants.

3.2 Cell development - cell expansion and cell wall thickening

In conifers, wood properties are determined mainly by the dimensions and arrangement of tracheids in growth rings (Fig. 1). With sufficient nutrients, tracheids of *Pinus radiata* seedlings under elevated [CO₂] had cell walls that were 43 % thicker compared to those of control specimens, while tracheid lumen diameter was unaffected (Conroy et al. 1990). On the other hand, tracheid diameter (lumen diameter + two times the cell wall thickness) was 16 - 24 % higher at elevated [CO₂] than at ambient [CO₂] in *Pinus sylvestris* (Ceulemans et al. 2002). In contrast, no obvious change was found in the cell dimensions in *Pinus radiata* (Atwell et al. 2003; Donaldson et al. 1987) and *Larix kaempferi* (Yazaki et al. 2004) treated with elevated [CO₂]. Although, in *Larix sibirica*, tracheids tended to have a 10 % larger lumen diameter and a 16 % smaller cell wall thickness compared with specimens exposed to ambient [CO₂] where all trees received sufficient nutrients (Yazaki et al. 2001).

In some cases, the increase in growth ring width at elevated [CO₂] was due to a significant increase in earlywood (Ceulemans et al. 2002; Telewski et al. 1999; Table 1), implying an increase in cell expansion rate and/or a delay of thick cell wall deposition under elevated [CO₂]. In *Larix sibirica*, Yazaki et al. (2001) suggested that elevated [CO₂] had major effects on cell division and cell expansion rather than cell wall thickening, especially early in the growing season. According to this, wood density was lower in elevated [CO₂] than in ambient [CO₂] conditions.

In contrast, an increase in the growth ring width or density of latewood was also observed at elevated [CO₂], without significant changes in the structure of earlywood (Hätenschwiler et al. 1996; Kilpeläinen et al. 2003). Changes in latewood structure depend on the ratio of cell wall thickening to cell expansion, the first component of which can be altered by (1) prolongation of cambial activity and (2) increase in the duration or amount of secondary cell wall deposition (Denne and Dodd 1981; Funada et al. 1990; Fig. 1). However, as described previously, duration of activity of the cambium under elevated [CO₂] is variable and inconsistent among studies. On the other hand, the increase in wood density might be a consequence of the larger accumulation of total non-structural carbo-

hydrates (TNC), produced in current or previous growing seasons (Hättenschwiler et al. 1996; Telewski et al. 1999). When we are able to estimate the relationship between the quantity of photosynthesis products and TNC and the process of cell wall deposition, the effects of elevated $[\text{CO}_2]$ on latewood formation will become clear.

4. The relationship between anatomical features and physiological responses under elevated $[\text{CO}_2]$

4.1 Photosynthetic down-regulation and xylem structure under elevated $[\text{CO}_2]$

$[\text{CO}_2]$ -induced increased rates of photosynthesis often decrease within several months, even if trees grow without any limitation of root growth or nutrient supply (e.g. Adam et al. 2004, Eguchi et al. 2004). With this reduction of photosynthetic capacity, the growth rate of the stem, which have been stimulated by elevated $[\text{CO}_2]$ early in the growing season, decreases less than that of trees exposed to ambient $[\text{CO}_2]$, and little difference is seen in growth ring width between $[\text{CO}_2]$ treatments (Yazaki et al. 2004). Although a direct relationship between photosynthetic properties and the development of xylem has not been established, structure of growth rings might change when a CO_2 -induced increase in photosynthesis rate is depressed by a plant's acclimation to higher ambient $[\text{CO}_2]$ over time (e.g., over 3 weeks, over 1 year, etc.).

4.2 Water balance and vessel dimensions

The reduction of stomatal conductance and the increased water-use efficiency that are induced by elevated $[\text{CO}_2]$ are well known phenomena (e.g. Wullschlegler et al. 2002). Leaf water potential is also maintained at high levels by elevated $[\text{CO}_2]$ owing to stomatal closure, increases in whole-plant hydraulic conductance and perhaps osmotic adjustment (Wullschlegler et al. 2002).

In general, diameter of vessel elements tends to increase with xylem water potential if there are no limiting environmental factors (e.g. Doley and Leyton 1968). Thus, it is possible that the structure and dimensions of conductive cells may alter if CO_2 -induced changes in the efficiency of water use by trees. It has been reported that mean vessel area increases by about 1.6-fold under conditions of elevated $[\text{CO}_2]$ in seedlings of *Quercus robur* (ring-porous hardwood) but does not change in seedlings of *Prunus avium* x *pseudocerasus* (diffuse-porous hardwood) (Atkinson and Taylor 1996). In contrast, our observations show no obvious difference in the mean vessel area of earlywood in seedlings of *Fraxinus mandshurica* var. *japonica* (ring-porous hardwood) and *Betula platyphylla* (diffuse-porous hardwood; Fig. 2) under various $[\text{CO}_2]$ regimes. At high $[\text{CO}_2]$, larger sized vessels is found in *Betula platyphylla* planted only in large pots. A close relationship between the efficiency of water use and the dimensions of the conducting cells might be expected when elevated $[\text{CO}_2]$ affects the water balance of hardwoods, owing to resulting enhancement of leaf and root production.

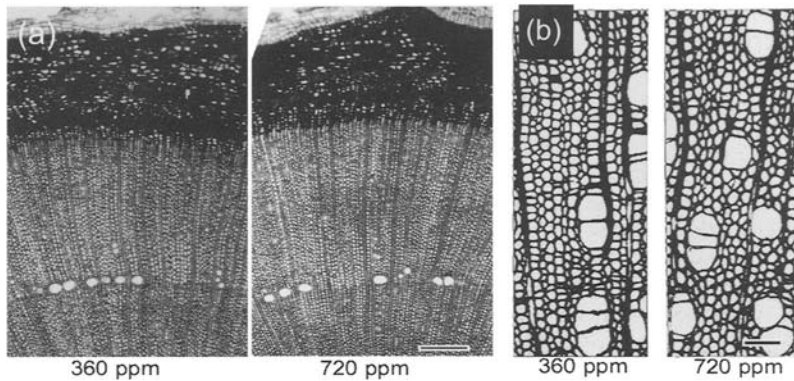


Fig. 2. Transverse sections of (a) *Fraxinus mandshurica* var. *japonica* and (b) *Betula platyphylla* at an ambient (360 ppm) or elevated (720 ppm) CO₂. Bars indicate 250 μm (a) and (b) 50 μm, respectively (Yazaki and Ishida unpublished data).

5. Conclusion

To sum up, according to recent studies, rising [CO₂] has a less drastic effect on wood anatomical features than physiological properties of trees. In addition, the effect that elevated [CO₂] does have on growth ring structure depends on species, clone, tree age and environmental factors. For the assessment of wood properties in the future, we need to investigate the response of mature trees to rising [CO₂], focusing on the phenological, physiological and chemical pathways by which [CO₂] affects wood formation with respect to a whole tree (Pritchard et al. 1999). The structure of a growth ring reflects the growth pattern of a tree. To better understand wood formation at elevated [CO₂], we need to investigate the detailed process of cell development in growth rings and the variations in cell dimensions in the intra-growth ring at elevated [CO₂] in many species and developmental stages.

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