

Woody Plant Growth and Development under Elevated CO₂

Subjects: Plant Sciences

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Climate change is mainly driven by the accumulation of carbon dioxide (CO₂) in the atmosphere in the last century. Plant growth is constantly challenged by environmental fluctuations including heat waves, severe drought and salinity, along with ozone accumulation in the atmosphere. The effects of the predicted environment scenario of elevated CO₂ concentration (e[CO₂]) and more severe abiotic stresses have been scarcely investigated in woody plants, and an integrated view involving physiological, biochemical and molecular data is missing.

Keywords: climate change ; multiple stresses ; trees

1. Effect on Leaf Photosynthesis

Atmospheric e[CO₂] usually stimulates the source activity of woody plants, but the response varies with species and exposure time. Initially, photosynthesis can be enhanced by the higher CO₂ availability surrounding ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco). Under these conditions, the carboxylation role of Rubisco is favored to the detriment of its oxygenation activity, increasing photosynthetic efficiency and the production of sugars. However, in some species, after an acclimation period, these reactions slow down or decrease when compared to the initial levels, mostly as a consequence of stomatal closure and/or soluble sugar accumulation in the mesophyll cells ^{[1][2]}. According to the FvCB model, photosynthesis can be limited biochemically by Rubisco activity, RuBP regeneration or triose phosphate utilization (TPU) ^{[3][4][5]}. Hence, as Rubisco's substrate CO₂ increases, a gradual decrease in photosynthesis by RuBP regeneration or TPU restrictions is expected ^[6]. Afterwards, the rise of internal CO₂ partial pressure (C_i) and the accumulation of specific metabolites can culminate in a series of negative feedback regulations, such as a decrease in stomatal conductance (g_s) and stomatal density and the inhibition of photosynthesis-related proteins ^{[7][8]}.

However, many studies over the decades have shown that the behavior of g_s on e[CO₂] is contradictory and species-specific. Ainsworth and Rogers (2007) reported in a meta-analysis study from FACE (free-air concentration enrichment) experiments that e[CO₂] decreased g_s in all plant groups, but to less extent in trees compared to grasses and herbaceous crops ^[1]. In a previous meta-analysis work, specific to woody plants, Medlyn et al. (2001) found no reduction in g_s after a short-term e[CO₂] exposure (less than 1 year), while under long-term exposure (more than 1 year), g_s decreased 23% ^[9]. Additionally, they reported that conifers are less sensitive to e[CO₂] than deciduous and evergreen broadleaf species. Notably, some studies reported that particular coniferous trees (*Pinus taeda* and *Pinus densiflora*) have guard cells insensitive to e[CO₂] ^{[10][11]}. This response corroborates the finding that g_s-[CO₂] sensitivity increased as tree species evolved (gymnosperms < deciduous angiosperms < evergreen angiosperms) due to atmospheric CO₂ level changes over the years ^[12]. Purcell et al. (2018), using in situ measurements of 51 woody plants, demonstrate that g_s can be increased in response to e[CO₂] in specific weather conditions (high temperature and low humidity) depending on water availability ^[13]. Therefore, the downregulation of g_s under e[CO₂] in some studies might be more related to methodological artefacts involving differences in the climatic and/or measurements conditions, water status and/or nutrients and signal-to-noise ratio of g_s ^[14] than an increase of C_i itself in the mesophyll and guard cells.

Stomatal size and density are other traits that could interfere with photosynthetic activity, but there is no clear evidence of this in woody plants in response to CO₂ enrichment ^{[1][15]}. In *Coffea* exposed to long-term e[CO₂], stomatal density and size showed dichotomous behavior, decreasing and increasing, respectively, without significant negative impacts on g_s and CO₂ assimilation ^[15]. An increase in leaf area index (LAI) is observed in growing season trees, which can offset any downregulation of g_s on CO₂ assimilation ^[16]. Nevertheless, after archive maturity, LAI tends to decrease in the upper layer of the canopy, reducing the shade effect and favoring light capture and photosynthesis in the whole shoot ^{[16][17]}. The coordination between g_s and the photosynthetic rate was described in many plant species grown in several environmental

conditions [18]. It is clear that the stomatal aperture should maximize CO₂ uptake while minimizing water loss to increase photosynthesis and water use efficiency. However, the connection between g_s and CO₂ assimilation is diverse in woody plants, and while stomatal conductance does not seem to acclimate, photosynthesis does under e[CO₂] [9].

2. Effect on Source–Sink Relationship and Nitrogen Metabolism

Photosynthetic downregulation after a long period of e[CO₂] exposure has been termed CO₂ acclimation, which was demonstrated in some species [19][20]. This response might be associated with the negative regulation of photosynthesis-related proteins, especially Rubisco, as in many cases reductions in V_{max} (*in vivo* Rubisco maximum carboxylation rate) are observed [20]. One hypothesis for this photosynthesis acclimation is the unbalance between source and sink activity. The accumulation of carbohydrates in source leaves (photosynthetic active) by the low utilization in sink tissues (non-photosynthetic) downregulates photosynthesis owing to negative feedback, decreasing the amount and activity of photosynthetic proteins [2][21][22]. The stimulation of photosynthesis by higher sink activity (root biomass) was observed in cassava (*Manihot esculenta* Crantz.) after e[CO₂] acclimation [23]. Indeed, the export of photosynthates might increase to sink tissues by e[CO₂] as plant growth increase and the expression/activity of sugar metabolism-related enzymes change [23][24][25].

A second hypothesis is related to nutrient dilution/acquisition, mainly nitrogen (N) and phosphorus (P), as a consequence of the rapid growth and/or allocation in sink tissues [26][27][28]. Rubisco is the most abundant protein in plants; then, a strong N-sink and reductions in its amount can be a common symptom of N deficiency and/or remobilization to other pathways, directly decreasing CO₂ assimilation. Feng et al. (2015) reported a negative correlation between e[CO₂] and plant N concentration in different ecosystems, including croplands, grasslands and forests. In this study, N limitation was more associated with the negative effects of e[CO₂] on plant N uptake by unknown mechanisms rather than growth dilution [29]. The C/N unbalanced ratio seems to be related to the inhibition of photorespiration in plants exposed to e[CO₂], as it was observed in a metabolic model that the levels of glycine and serine are correlated with *de novo* N assimilation [30]. However, the mechanisms underlying how e[CO₂] limits N acquisition and if it is a cause or a consequence of photosynthesis acclimation are still open questions.

Actually, photosynthesis acclimation after e[CO₂] exposure can be found in many plant species, especially in non-woody crops [22][31]. Nevertheless, it is a rare event in woody plants growing in normal conditions with no limitations of root growth space, water and nutrients [12][16]. For instance, tree species from northeast Asia grown under FACE conditions in infertile and immature volcanic ash (VA) and fertile brown forest (BF) soils for 2 years had different photosynthetic responses [32]. The photosynthesis of *Betula platyphylla* was downregulated in both soils, while in *Betula maximowicziana*, this response happened only in VA soil, probably due to the reduced N and Rubisco content. In contrast, a negative regulation in *Alnus hirsute* was observed only in BF soil, which might be related to higher amounts of starch in the leaves [32]. In many other studies, the photosynthetic rate in woody plants does not seem to acclimate, neither presenting any down-regulation nor even up-regulation [33][34][35][36].

High CO₂ enhanced overall photosynthesis and Rubisco-specific activity, even with decreases in Rubisco content and photochemical parameters in *Betula pendula* [37][38]. A study with aspen tree (*Populus tremuloides*) exposed to e[CO₂] revealed an increase in photosynthesis, despite the downregulation of many transcripts involved with chloroplast biosynthesis and function, including the photosynthetic protein genes Rubisco and Rubisco activase, proteins from photosystem I and II, light harvest complex and chlorophyll biosynthesis [39][40]. This transcriptional level pattern might be related to negative feedback triggered by the accumulation of sugars in leaves [40].

The carbohydrate level in source tissues is controlled by sink pathways (growth rate, respiration and storage/compartimentalization in certain organs), which tend to increase in high CO₂-acclimated trees to keep a metabolic balance between synthesis and consumption. Respiration rate also responds in different ways according to the species and environmental conditions, and there is no immediate effect of high CO₂ on mitochondrial respiration rate [41][42]. This process has been strongly increased in *Eucalyptus saligna*, while in *Coffea* spp. it has not been affected under e[CO₂] [43][43]. Additionally, it has been demonstrated that leaf mitochondrial respiration could be unaffected by e[CO₂], especially at night-time under mild temperatures, but the overall rate might be higher considering the whole plant leaf area, which usually increases in those conditions [43][44]. Some studies noticed a stimulation of gene expression and metabolite alterations of the TCA (tricarboxylic acid) cycle, such as citric, succinic, fumaric and malate acid in e[CO₂]-enriched leaves [45][46].

In fact, the respiratory process in leaves should be slightly affected considering the photosynthetic stimulation in elevated CO₂-exposed plants, as these are opposite reactions and strictly regulated. It is hypothesized that leaf respiration might

be stimulated due to the higher concentration of non-structural carbohydrates (respiratory substrate), whereas the N dilution induced by elevated CO₂ might reduce protein turnover and the demand for respiratory energy [43][47]. However, what has been reported to e[CO₂] acclimated forest is an increase in fine root growth and rhizosphere respiration, indicating the export of photosynthates and utilization of heterotrophic respiration [48][49].

Therefore, the increase of belowground biomass and soil respiration might be a reason to support higher CO₂ assimilation in trees fertilized with e[CO₂] under non-stressful conditions, allowing a narrow connection between photosynthesis and ecosystem respiration [48][49]. The up-regulation expression of respiratory genes triggered by e[CO₂] has been reported in leaves of non-woody plants [47][50]. However, the effect of e[CO₂] focused on the respiration process at the transcriptional level of tree species is poorly investigated, particularly in roots.

Certainly, the behavior of source activity will depend on sink strength and how the whole plant metabolism will be adjusted to grow with the available resources. It is clear in the literature that woody plants will cope with e[CO₂] by remodeling their metabolism to decrease the expression of key photosynthetic proteins, adjust nutrient distribution between the tissues and increase CO₂ assimilatory capacity.

3. Growth and Developmental Stage-Dependent Regulation

The pattern of growth and establishment of woody plants exposed to e[CO₂] will also depend on a wide range of factors—ultimately on species, genotype, developmental stage and environment. Studies linking physiological and molecular data are better documented in *Populus* genera, which is considered a model tree genus, than in other species [39][40][51][52][53][54][55]. In general, these works report photosynthesis and above-ground biomass stimulation with increases in stem wood density in high CO₂-fertilized *Populus*, except for the triploid white poplar, which had lower photosynthesis but a higher stem diameter. The enhancement of shoot growth by e[CO₂] was also observed in *Pinus radiata* [56], *Pinus sylvestris* [57], *Acacia karroo* and *Acacia nilotica* [33] and *Aulonemia aristulata* [36]. Along with this physiological response, the expression of genes from different categories in leaves and stems was strongly changed in *P. deltoides* [53]. In this work, stems showed more CO₂-responsive transcripts than leaves (2.5-fold upregulated and 6.5-fold down-regulated in stems compared to leaves), and most of them were related to metabolism. The main enhanced genes in leaves were those involved with storage proteins and wall expansion, whereas in stems, they were more related to lignin biosynthesis (enzymes responsible for lignin formation and polymerisation and ethylene response factors), cell wall formation and cell growth, corroborating the growth stimulation response.

The effects of e[CO₂] in plant metabolism also rely on the developmental stage of each species [39][58][59]. The gene expression pattern was dependent on leaf age in elevated CO₂-acclimated *Populus* [39]. While in young leaves, the most differentially expressed genes were upregulated, in semimature leaves, were downregulated under e[CO₂]. This environmental condition upregulated 16-photosynthetic gene transcripts, including Rubisco small subunit, in young leaves compared to older leaves [39]. Certainly, the predicted elevated CO₂ atmosphere concentration will change the carbon (C) status in plants. Some studies have suggested that the leaf development pattern is likely to be accelerated by e[CO₂], as gene expression related to photosynthesis, cell-wall loss and synthesis (xyloglucan endotransglycosylase) and calcium-signaling (CPK2) were up-regulated in young leaves [39][60]. These findings support the hypothesis of growth promotion and sucrose-cleaving and synthesizing enzyme activity modifications by CPKs under e[CO₂] [61][62]. Moreover, in mature leaves, the C flux can be redirected to the glycolysis pathway once the transcripts for adenylate kinase are upregulated [39].

A commonly raised question would be whether leaf senescence is intensified in woody CO₂-fertilized plants, once growth and LAI are generally increased. Different groups demonstrated that senescence-related gene (β -amylase and metallothioneins) expression and proteins were lower and, consequently, leaf longevity was augmented in e[CO₂]-acclimated plants [39][40][52][59]. Moreover, a transcriptome study in *Populus* demonstrated that delayed senescence was correlated with the up-regulation of glycolysis and secondary metabolism genes, including anthocyanin biosynthesis-related genes (leucoanthocyanidin dioxygenase—LDOX, and dihydroflavonol reductase—DFR) [54].

Therefore, despite the limited studies, the findings obtained so far with woody species suggest that e[CO₂] will increase plant growth through modifications in C allocation to different pathways (secondary metabolism) and organs (stem) and will also affect the ecosystem of soil microorganisms by enhancing respiratory substrates (fine roots turnover) [39][52][53][54]. Besides this, lignin accumulation in stems could contribute to pathogen resistance but may negatively impact the wood quality for both timber and paper production [53]. Hence, CO₂-fertilized trees may not act directly to C sequestration, and

the metabolic pathway changes may not be desired by agriculture. To better understand how $e[\text{CO}_2]$ will affect woody plant metabolism, more studies are needed, especially under the projected climate change scenarios.

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