Potential impacts of global elevated CO_2 concentrations on plants

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Early experiments investigating the effects of CO_2 enrichment on plants frequently showed photosynthetic stimulation and reduced stomatal aperture over short time periods. Work on the effects of elevated CO_2 has advanced in two major areas: by the extension of long-term and field experiments, and through investigations on the wide range of negative feedbacks affecting plant responses to CO_2. Downward photosynthetic acclimation in response to CO_2 enrichment is frequently observed over the short and long term, and indicates the activity of diverse feedback mechanisms. CO_2 is generally viewed as a limiting photosynthetic resource. However, recent work on stomatal development has shown that this view is simplistic: long- and short-distance signalling of CO_2 concentration are necessary components of normal plant development.

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Abbreviations

FACE	Free Air CO_2 Enrichment
ppm	parts per million

Introduction

Human activities have caused the concentration of atmospheric CO_2 to increase continuously from about 280 parts per million (ppm) at the beginning of the 19th century to 369 ppm at the beginning of the 21st century. Future projections of atmospheric CO_2 concentration range between about 450 and 600 ppm by the year 2050 and are strongly dependent on future scenarios of anthropogenic emissions. Carbon dioxide is a greenhouse gas and its increasing concentration in the atmosphere will cause global warming, indicating that the human race will increasingly be driving climatic change.

More than two decades of study on the effects of CO_2 enrichment on plants has provided a rich suite of data and understanding about a wide variety of plant responses. Initial short-term experiments demonstrated that elevated CO_2 concentrations partially alleviated the limitation of C3 (but not C4) photosynthesis by CO_2 supply and acted as a negative feedback on transpiration in both C3 and C4 species. Subsequent and often longer-term experiments have shown that photosynthesis could acclimate downwards in response to CO_2 enrichment, and there is now some evidence to suggest that photosynthesis is stimulated in C4 species in response to enrichment [1,2]. In species with the C3 photosynthetic pathway, high irradiance can lead to photoinhibition. Field studies have now demonstrated that CO_2 enrichment can reduce the severity of photoinhibition, although this effect is dependent on rubisco activity [3].

Initial emphases on photosynthesis and transpiration have expanded to accommodate the realisation that other metabolic and physiological pathways are intimately linked with the CO_2-exchange status of the plant. This greater depth of study has occurred in parallel with an increase in the number of studies investigating the long-term responses of plants to continued CO_2 enrichment under field conditions. This review investigates recent research that has sharpened our view of the impacts of CO_2 enrichment on plants, starting from long-term studies of whole plants before going on to look at work that has delved into interactions within the plant.

Long-term studies

Growth

Growing plants under different CO_2 concentrations for longer than a growing season requires techniques in which experimental artefacts are minimised. The 'Free Air CO_2 Enrichment' (FACE) method minimises experimental artefacts by allowing researchers to work in a field situation and provides the capacity to investigate the responses of trees, the life form that is globally most crucial for sequestering anthropogenic emissions of CO_2. For example, the net primary production of maturing loblolly pine (*Pinus taeda*), on a site of moderate soil fertility, increased by 25% in the two years following the onset of a 200 ppm CO_2 enrichment in a FACE experiment [4]. A parallel longer-term study produced a larger stimulation of tree growth of up to 34% over the first three years of enrichment [5••]. However, these high rates of growth were not sustained, and growth rates averaged only 6% above those of controls over the next four years. The early stimulation of tree growth was completely absent at another site that had infertile soil conditions [5••]. However, enhancing the nutrition of the infertile soil by adding nitrogen fertiliser produced a large and positive synergistic effect in combination with CO_2 enrichment. Trees treated with both nitrogen fertiliser and elevated CO_2 showed a three-fold increase in growth over controls. The photosynthetic rates of plant species within a grassland community also showed little positive response to CO_2 enrichment [6]. Again, this was accounted for by reductions in leaf nitrogen concentration occurring as a result of CO_2 enrichment in plants growing on a soil of limited nitrogen availability.

The coupled nature of the carbon and nitrogen cycles feeds into whole-ecosystem processes. In a FACE study within a forest ecosystem, both litter fall and nutrient flux to the forest floor increased during the early period of CO_2 enrichment when net primary production was stimulated [7•]. However, the rates of litter decomposition, nitrogen mineralisation and nitrification did not change as a result of CO_2 enrichment. This imbalance between nitrogen supply and demand will increasingly limit the fertilisation effect of elevated CO_2 in this ecosystem, as appears to have been observed after at least three years of fumigation [5••]. The stimulation of carbon sequestration in the vegetation and litter of forest trees was paralleled in a grassland where CO_2 was enriched by 240 ppm over a six-year period [8]. As in the forest, the amount of carbon in vegetation and litter was stimulated by CO_2 enrichment of the grassland. The fraction of these short-lived carbon pools that move to longer-lived pools remains to be seen, but is likely to be small.

Transpiration

Early experiments demonstrated significant reductions in stomatal conductance under CO_2 enrichment. A two-year grassland study using the FACE technique, with a 192-ppm enrichment, demonstrated a 23% reduction in stomatal conductance for 13 perennial species [6]. In combination with the partial downregulation of photosynthetic rate as the plants acclimatised to elevated CO_2, the reduction in stomatal conductance led to a 40% increase in instantaneous water use efficiency. In contrast, during the early phase of the loblolly pine forest FACE experiment, there was no change in stomatal conductance or water use [9], but water use efficiency was increased as a result of photosynthetic stimulation. Analysis of 13 long-term (i.e. of duration of more than one year) field-based studies on tree species demonstrated an overall reduction of 21% in stomatal conductance [10]. The observation of reduced stomatal conductance was much more consistent in the longer-term than in the shorter-term studies.

Allocation and development

A meta-analysis of the responses of woody plants to CO_2 enrichment indicated no significant effect on biomass partitioning [11]. The six-year grassland study also demonstrated little change in shoot-to-root ratio in response to CO_2 enrichment [8]. It is particularly interesting, therefore, that carbon allocation to reproduction is strongly stimulated in loblolly pine after three years of CO_2 enrichment [12•]. After this period, trees growing in the enriched CO_2 were twice as likely to be reproductively mature, and produced three times as many cones and seeds, than control trees growing in ambient CO_2 concentrations. This surprising but robust result indicates that CO_2 enrichment hastens significantly the onset of seed production, a feature that may prove to be effective in tracking climatic change. In contrast, flowering and seed set in grasslands, where species may have deterministic life cycles, were unaffected [13], reduced [14] or stimulated [15•] under CO_2 enrichment. The species-specific nature of these responses indicates a strong potential for CO_2 enrichment to change the composition of plant communities.

Leaf thickness generally increases whereas specific leaf area decreases as a result of CO_2 enrichment [16]. A detailed analysis of leaf development in Scots Pine (*Pinus sylvestris*) after four years of exposure to CO_2 enrichment confirmed that leaf thickness was increased but also indicated reductions in stomatal density [17]. This stomatal-density response confirms observations of reduced stomatal conductance in Scots Pine made over a shorter period [18].

Mechanisms

Short-term detailed studies of plant responses to CO_2 enrichment have provided a wealth of detail about the range of processes involved. However, some of these experiments are barely relevant to the field situation because they are confounded by responses related to pot size and, more problematically, to large step changes in CO_2 concentration, as frequently seen in experiments in which CO_2 concentration is doubled. Recent long-term studies have identified three major types of plant response to CO_2 whose processes still require further investigation: nutrient limitation of plant CO_2 fluxes, the responses of stomatal development and opening, and impacts on plant development.

CO_2 fluxes

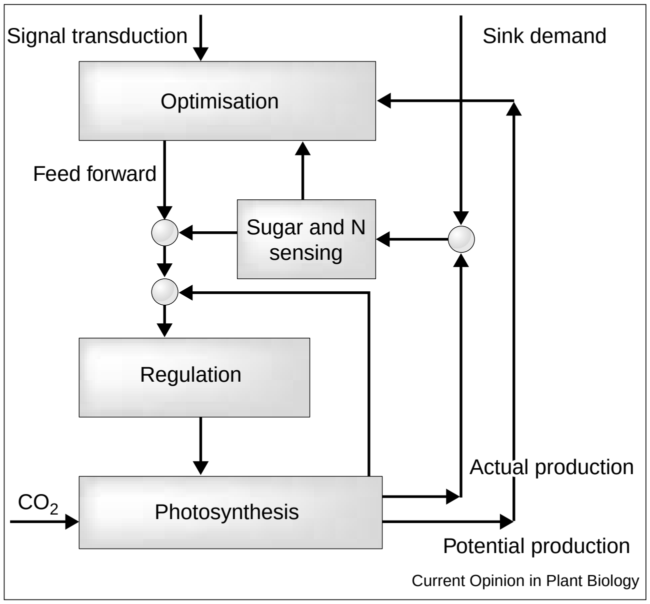
CO_2 enrichment may impact on CO_2 fluxes by causing a downward regulation, or acclimation, of both photosynthesis [19,20] and respiration [21,22]. In this context, downward regulation is defined as a reduction in photosynthetic or respiratory capacity, which also indicates a time component. It is interesting to note that the CO_2 sensitivity of stomatal conductance in field-grown scrub oak also shows a downward acclimation [23]. Long-term field experiments indicate that downward regulation of photosynthesis is generally incomplete and that leaf photosynthesis is stimulated by a CO_2 enrichment of about 200 ppm. However, the extent of photosynthetic stimulation varies over a wide range for C3 species, from 7% for legume herbs [6] to 98% for *Pinus radiata* [24]. Similarly, respiration rates have been observed to decline [25,26] or remain unchanged [25] with CO_2 enrichment, again depending on the species.

The causes of photosynthetic downregulation have been variously ascribed to a reduction in carbohydrate sink strength [24], a limited capacity to sequester carbon in a storage form [27], changes in nitrogen allocation [28,29•] and a reduction of rubisco concentration [30]. These responses indicate not only a decreased expression of photosynthetic genes [31] but also a co-ordination of the carbon to nitrogen balance. For example, nitrate and ammonium uptake, and nitrate reductase activity are sensitive to CO_2 [32]. These co-ordinating activities match photosynthetic capacity with the capacities for growth and carbon storage [29•].

Rates of dark respiration are directly correlated with leaf nitrogen content [25]. Therefore, when CO_2 enrichment leads to a reduction in leaf nitrogen concentration, respiration also declines [26]. Surprisingly, CO_2 enrichment increases the average number of mitochondria in each cell [33••], even though leaf respiration rate decreases in response to elevated CO_2 across a diverse selection of plant species. This response may be indicative of a shift in plant metabolism and the increased energy demand resulting from higher photosynthetic rates under CO_2 enrichment.

The responses of CO_2 exchange to CO_2 enrichment indicate the operation of a range of feedback controls on process rates. These controls must be supported by signal transduction pathways that sense a variety of demands at sinks and products at sources [31]. Figure 1 provides a schematic representation of likely components of the feedback controls affecting photosynthesis that have particular relevance for responses to CO_2 enrichment [34]. In essence, photosynthesis has a potential rate of carbohydrate production that exceeds the actual rate. This is readily demonstrated by the fact that photosynthetic capacity when resources are not limiting is two- to three-fold greater than typical observed rates [35]. The over-capacity allows for a significant range of regulatory pathways to operate in determining the actual photosynthetic rate. The plant determines setpoints for photosynthetic rates, which are carefully modulated by sugar and nitrogen sensors [36] and by sink demand, and which are based on the difference between potential and actual capacity. Photosynthetic rate may be limited by the regulation of the expression of genes encoding photosynthetic components or by the reduction of rubisco activity. Alternatively, sugar content may be restricted by the stimulation of starch synthesis when photosynthetic production exceeds sugar utilisation [31]. The central nature of the sugar- and nitrogen-sensing component indicates that these processes can override other signals [37,38]. These other signals indicate environmental and internal metabolic challenges on the photosynthetic pathway, and may be mediated, for example, through changes in stomatal conductance and the supply of plant hormones [39,40]. These challenges are optimised and provide a feed-forward control of the setpoint for photosynthesis. The setpoint is further adjusted by sugar and nitrogen signalling, and then serves to regulate photosynthesis. This regulation may involve the rapid transcriptional control of particular photosynthetic genes or more extensive controls of leaf development or senescence [31].

Figure 1



Schematic of the feedback controls on photosynthesis in response to CO_2 concentration. Boxes indicate processes; small circles are setpoints of operation. Photosynthesis is considered as a potential unconstrained production and a lesser constrained production. The production is constrained at less than potential by negative feedback because of sink demand for carbohydrates, which is determined by sensors such as those for sugars and nitrogen. The external environment is sensed by a range of mechanisms; these influence, for example, stomatal development and activity, the supply of water and nutrients from roots, and the allocation of photosynthate to organ development. These different signals interact with the sugar- and nitrogen-sensing components to feed forward a predicted setpoint for photosynthesis. This setpoint is compared with the current photosynthetic potential and can then influence gene expression or the activity of photosynthetic components. The rate of photosynthesis at any particular time is significantly less than potential, because it is dynamically controlled by multiple pathways of both photosynthate demand and environmental response.

Stomatal development and opening

Recent work has identified a gene *HIC* (*HI*gh *C*arbon dioxide) whose disruption leads to large increases in the number of stomata initiated in response to CO_2 enrichment [41]. This response contrasts with the typical, but not universal, decrease in stomatal initiation under CO_2 enrichment [42]. The *HIC* gene encodes an enzyme involved in the synthesis of those long-chain fatty acids that are typically found in the cuticle of leaves. Changes in these fatty acids may influence the cell-to-cell signalling of stomatal development.

The short-distance cell-to-cell signalling of stomatal development is complimented by longer distance systemic signalling of stomatal development [43•]. The systemic signal allows the development of stomata in immature leaves to be controlled after CO_2 concentration is detected by mature leaves. Work with mutants of *Arabidopsis* indicates that abscisic acid, ethylene and jasmonates are involved in the signalling process, with independent controls for the adaxial and abaxial leaf surfaces [44].

Plant development

Many short-term experiments have revealed changes in plant development in response to changes in CO_2 concentration, but these appear to be less significant in longer-term experiments [8,11]. Reproductive responses have been studied infrequently, but species-specific effects of CO_2 on reproduction in grasses have been identified [13]. The early flowering of pine in a long-term FACE experiment [12•] offers the intriguing possibility of precocious flowering in trees as atmospheric CO_2 concentration continues to rise. The enhanced sink size resulting from increased fruit production as CO_2 concentration rises may also serve to maintain photosynthetic stimulation under CO_2 enrichment. In sour orange, a CO_2 enrichment of 300 ppm stimulated total orange production and hastened the onset of fruit production by about one year [45]. It is most interesting to note that the timing of flowering in citrus is considerably enhanced after juvenile trees are transformed to constitutively express the *Arabidopsis* genes *LEAFY* and *APETALA1* [46••]. These genes are involved in the timing of flowering in *Arabidopsis*. Flowering occurs a remarkable 4–5 years earlier in the transgenic citrus than in wildtype citrus, but flowering is still induced by environmental stimuli such as temperature or drought. The interactions with CO_2 concentration remain to be investigated.

Conclusions

This review is concerned with a few important aspects of the impact of CO_2 enrichment on plants. Other areas are emerging that are likely to attract further attention. These include the protective effects of CO_2 enrichment against pollutants such as ozone [47] and the enhanced frost sensitivity of plants under CO_2 enrichment [48•]. Work on CO_2 signalling indicates that plants are able to detect CO_2 concentration. The mechanism or mechanisms of CO_2 signalling are poorly understood but there are pointers to a diversity of mechanisms [49–51].

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