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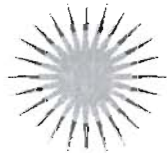
Photosynthetic responses of rice and soybean to elevated CO₂ and temperature

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ABSTRACT

Carbon dioxide and other 'greenhouse' gases continue to increase in the earth's atmosphere at a relatively rapid rate. Because of this, atmospheric general circulation models predict substantial increases in atmospheric temperature and changes in regional precipitation patterns by the later part of this century. Scientific evidence already indicates that the earth's near-surface temperature has increased about 0.6°C just over the past three decades. Both [CO₂] and temperature influence a myriad of biological processes in plants largely due to the effect they have on gas exchange and carbon metabolism. The interactive effects of these environmental factors on plant processes are quite complex and often vary among species. Agronomic crops that initially fix carbon by the C₃ photosynthetic pathway, are expected to be



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greatly effected by increases in atmospheric $[\text{CO}_2]$ and temperature. The following review mainly focuses on describing photosynthetic responses of two important C_3 crops, rice (*Oryza sativa* L.) and soybean (*Glycine max* L.), to elevated atmospheric $[\text{CO}_2]$ and high temperatures. These crops show interesting differences in how their photosynthetic processes adapt to rising CO_2 and temperature.

INTRODUCTION

Worldwide concern continues to grow over the increase of 'greenhouse' gases in the earth's atmosphere and the potential it poses for global climate change. Radiative forcing of the atmosphere caused by these gases leads to a warming of the earth's near-surface air temperatures [1]. Carbon dioxide is responsible for about 61% of global warming [2] and historically its rise has been coupled with increased temperatures [3]. Though there is considerable debate over the impact that rising atmospheric $[\text{CO}_2]$ will have on future climate change, there is little doubt that it is increasing at a rapid rate.

Evidence based on analysis of Antarctic ice cores reveals that 20 to 60 thousand years before present the earth's atmospheric $[\text{CO}_2]$ was as low as 180 to 200 $\mu\text{L CO}_2 \text{ L}^{-1}$ of air, and stabilized at about 280 $\mu\text{L L}^{-1}$ prior to the Industrial Age [3]. Since the 19th century atmospheric $[\text{CO}_2]$ has increased rapidly. Since 1958 the $[\text{CO}_2]$ has increased from 315 $\mu\text{L L}^{-1}$ to about 370 $\mu\text{L L}^{-1}$ at present, and is presently estimated to be increasing at a rate of 1.8 $\mu\text{L L}^{-1}$ per year [3, 4, 5]. With the atmospheric $[\text{CO}_2]$ expected to double within this century, various atmospheric general circulation models have predicted that the earth's near-surface temperatures could increase as much as 3 to 6°C [6, 7]. Stott *et al.* [1] estimate that just within the past three decades the earth's mean temperature has risen at a rate of 0.2°C per decade. Even small changes in average global temperatures may result in greater variability of geographic

temperature and precipitation patterns. Katz and Brown [8], by applying statistical models to climate change, estimate that extreme climatic events may be more frequent as mean global temperatures increase.

Episodes of extreme temperature and precipitation can be devastating to crop production. Agricultural productivity is expected to be sensitive to changes in global climate. Therefore, it is paramount to understand the interactive effects of elevated $[\text{CO}_2]$ and high temperature on physiological processes of plants to enable scientists and policy makers to more accurately predict future crop productivity in the face of a changing global climate. Inevitably, there will be the need to develop new crop management strategies and new genotypes that will be better adapted to such change.

Atmospheric $[\text{CO}_2]$ affects many plant processes, primarily through direct effects on photosynthesis and stomatal function [9, 10]. Present knowledge of photosynthetic carbon metabolism classifies terrestrial plants into three major photosynthetic categories: C_3 , C_4 , and crassulacean acid metabolism (CAM). Approximately 95% of all terrestrial plant species fix carbon by the C_3 photosynthetic pathway [10]. Current atmospheric $[\text{CO}_2]$, however, limits the photosynthetic capability, growth and productivity of many crop plants, among which the C_3 species show the greatest potential for response to rising $[\text{CO}_2]$ [11, 12, 13]. Cure and Acock [12] report an average 52% initial increase in photosynthesis among several C_3 species with short-term doubling of atmospheric $[\text{CO}_2]$. Despite an initial stimulation of photosynthesis by elevated $[\text{CO}_2]$, many C_3 species show a gradual decline when exposed to longer periods (i.e., weeks, months, or growing seasons) due to a down-regulation of the photosynthetic apparatus [9, 10, 14].

In C_3 plants, the binding of CO_2 to its primary acceptor, ribulose-1,5-bisphosphate (RuBP), is catalyzed by RuBP carboxylase/oxygenase (Rubisco), and the product of this carboxylation reaction, 3-

phosphoglycerate (PGA), is converted to other carbohydrates in the mesophyll cells. Rubisco also catalyzes an oxygenase reaction in which O₂ reacts with RuBP to give PGA and phosphoglycolate, a process known as photorespiration [15]. The oxygenase reaction and associated metabolism have an adverse effect on the efficiency of photosynthesis in C₃ plants, which results in a loss of carbon and energy [16]. In contrast, C₄ and CAM plants have developed anatomical, physiological and biochemical modifications to overcome the limitations of low atmospheric [CO₂] and photorespiration [17, 18]. Because of this, the photosynthesis of C₄ and CAM plants is presumably near saturation under present atmospheric [CO₂].

High temperatures can adversely effect photosynthesis, growth, and development of plants [19]. But it has been hypothesized that elevated atmospheric [CO₂] may alleviate some of the detrimental effects of high temperature [20]. Plants utilizing the C₃ photosynthetic pathway are expected to respond more greatly to rising atmospheric [CO₂] than C₄ and CAM species. However, few generalizations can be made about interactive effects of elevated [CO₂] and high temperatures on plant productivity, which are often complex and species dependent [19, 21].

The primary focus of this review is to compare and contrast the effects of rising atmospheric [CO₂] and temperature interactions on photosynthetic processes of two important C₃ agronomic crops, rice (*Oryza sativa* L.) and soybean (*Glycine max* L.). The physiological, biochemical, and molecular aspects of photosynthetic acclimation to elevated [CO₂] and interactive effects of both elevated [CO₂] and temperature on leaf photosynthesis will be discussed. In several instances comparisons are made to research conducted on other plant species.

PHOTOSYNTHETIC RESPONSES TO ELEVATED CO₂

The present low atmospheric [CO₂] limits

photosynthesis in C₃ plants primarily due to the oxygenase activity of Rubisco [22, 23, 24]. Currently, photorespiration accounts for about 25% or more loss of carbon in C₃ species [10]. Exposure of C₃ plants to elevated [CO₂] relieves this limitation resulting in stimulated photosynthesis [24]. A doubling of the present atmospheric [CO₂] could increase net photosynthesis in some C₃ crops by as much as 63%, and growth and yield up to 58% [11, 13, 25, 26]. Increased atmospheric [CO₂] also reduces stomatal conductance resulting in less transpiration and improved water-use efficiency [27] and may increase light use efficiency in some species [9].

Leaf and canopy photosynthesis of both rice and soybean are substantially enhanced by elevated [CO₂] [28, 29, 30, 31]. However, these two species differ in their photosynthetic responses when grown for long periods under high [CO₂]. Soybean grown under a range of atmospheric [CO₂] shows a continual increase in canopy photosynthesis from 160 up to 990 $\mu\text{L L}^{-1}$ [28]. This increase is primarily due to improvements in leaf area index, leaf photosynthesis, and quantum yield [32]. In contrast, canopy photosynthesis of rice grown long-term under the same range of atmospheric [CO₂] increases up to 500 $\mu\text{L L}^{-1}$ but then levels off at higher concentrations [33]. An atmospheric [CO₂] of 500 $\mu\text{L L}^{-1}$ is below that predicted for the later part of this century [2]. The dose-type response of rice canopy photosynthesis to increasing [CO₂] indicates acclimation [33].

With increasing light, canopy photosynthesis of high CO₂-grown soybean tends to respond hyperbolically [34], while that of rice increases linearly without a tendency towards saturation [33]. The difference in canopy photosynthetic light response between rice (linear) and soybean (hyperbolic) is likely due to the difference in architecture of the leaves in the canopy [34]. The erect leaf orientation of rice permits more sunlight penetration through the canopy,

especially as the solar elevation angle increases. This provides efficient light distribution and allows even lower leaves in the canopy to remain photosynthetically active throughout much of the day. Soybean leaves, in contrast, are much broader, and the upper canopy tends to shade lower leaves thus limiting their photosynthetic rates.

Soybean leaflet photosynthesis also increases with increasing growth $[\text{CO}_2]$, and hyperbolically with increasing solar irradiance. For both increasing light, and $[\text{CO}_2]$, leaves grown at $660 \mu\text{L L}^{-1} \text{CO}_2$ show greater initial slopes and saturated rates of photosynthesis than those developed at $330 \mu\text{L L}^{-1}$ [28, 36, 37]. Furthermore, light response curves show that high CO_2 -grown soybean leaves have a lower light compensation point, and higher apparent quantum yield than leaves developed at low $[\text{CO}_2]$. In contrast, rice leaves grown at 330 and $660 \mu\text{L L}^{-1} \text{CO}_2$ showed little difference in their response to either increasing light or $[\text{CO}_2]$ (Vu, unpublished data).

EFFECTS OF ELEVATED CO_2 AND HIGH TEMPERATURE

It is expected that as temperature increases so too will the responsiveness of the carbon balance of C_3 plants to increased $[\text{CO}_2]$ [19, 24]. This is primarily due to the interactive effects that elevated $[\text{CO}_2]$ and temperature have on Rubisco kinetics. Photorespiration increases with temperature [22]. This is largely because as temperature increases, the solubility of CO_2 relative to O_2 decreases, and the specificity of Rubisco for CO_2 and its activation are also reduced [23, 29, 38]. However, since increasing $[\text{CO}_2]$ partially depresses photorespiration, theoretically the enhancement of net photosynthesis is expected to increase with temperature at atmospheric CO_2 concentrations predicted for the future. This is illustrated by Long [23] who used a model of C_3 photosynthesis and Rubisco kinetics for wheat (*Triticum aestivum* L.) to show that

increasing $[\text{CO}_2]$ from 350 to $650 \mu\text{L L}^{-1}$ increases the temperature optimum for light saturated photosynthesis by 5°C . Additionally, the model predicts that the CO_2 -induced enhancement of photosynthesis should increase with temperature. Long [23] calculates that at ambient temperature of 10°C the enhancement would only be 14% but increases to 73% at 30°C .

High temperatures also lead to greater sink demand due to increased growth and respiration, thus resulting in a more rapid use of assimilates. This too is expected to enhance the stimulation of photosynthesis by elevated $[\text{CO}_2]$ at high temperatures. However, the data in this regard are limited and equivocal [39], and species-specific effects may be partly responsible for the differing results [19, 29]. This is especially apparent in studies that employ long-term growth of plants under elevated $[\text{CO}_2]$.

Vu *et al.* [29] grew rice and soybean in outdoor, sunlit, controlled-environment chambers at low ($330 \mu\text{L L}^{-1}$ for rice and $350 \mu\text{L L}^{-1}$ for soybean) and high $[\text{CO}_2]$ ($660 \mu\text{L L}^{-1}$ for rice and $700 \mu\text{L L}^{-1}$ for soybean) under a range of temperatures. Under both low and high $[\text{CO}_2]$ regimes, leaf photosynthetic rates were highest at midday temperatures of 32°C for soybean and 35°C for rice, but declined with higher or lower midday growth temperatures [29, 30]. As shown in Figure 1, there was a progressive CO_2 -induced enhancement of photosynthesis from 32 to 95% as temperature increased from 28 to 40°C , similar to the response predicted by Long [23] for an ideal C_3 leaf with a doubling of ambient $[\text{CO}_2]$. In contrast, the CO_2 -induced enhancement for rice was relatively constant at 60% from 32 to 38°C (Fig. 1). In this experiment neither elevated temperature or $[\text{CO}_2]$ altered the ratio of internal to external $[\text{CO}_2]$ of leaves, indicating that stomatal conductance was not a major limiting factor. Instead these differences were primarily attributed to the effect that high $[\text{CO}_2]$ and temperature had on "coarse" (i.e., altered enzyme protein content and total

activity) and "fine" (i.e., altered enzyme activation) control of Rubisco. Both elevated [CO₂] and temperature decreased Rubisco protein content, activity, and activation but the reduction by either environmental factor was much greater for rice than soybean [29]. In fact Vu et al. [30] showed that for soybean grown under elevated [CO₂] leaf Rubisco activity and protein content and sugar metabolism responded favorably to daytime temperatures as high as 40°C. Vegetative growth was fairly tolerant up to 44°C daytime temperature, although seed yield suffered greatly [40]. In general, we have found that soybean is more tolerant to high temperature than rice by about 4°C.

Intraspecific variation in rice is found with respect to responses of photosynthesis, vegetative growth, and grain yield to increasing temperature under elevated [CO₂]. Recently, photosynthetic and growth processes in response to high temperature and elevated [CO₂] were compared between two contrasting ecotypes of rice. A tropical indica (IR-72) and temperate japonica (M-103) cultivar of rice were grown to maturity in outdoor, sunlit, controlled-environment chambers under 350 and 700 μL L⁻¹ CO₂ and midday growth temperatures ranging from 28 to 40°C [41].

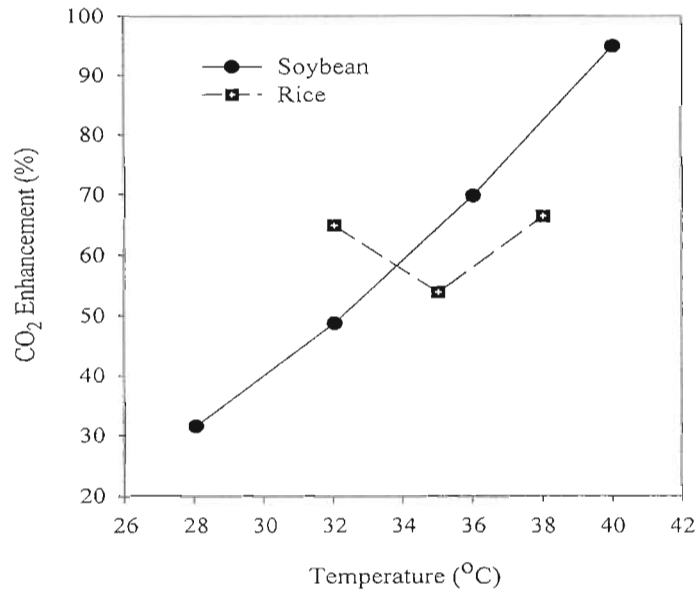


Figure 1. Percent enhancement of leaf photosynthesis by elevated [CO₂] and temperature for rice and soybean. Percent enhancement was calculated as $[(A_{high} - A_{amb}) / A_{amb}] \times 100$; A_{high} and A_{amb} = leaf CO₂ assimilation rates at elevated and ambient [CO₂], respectively. Adapted from Vu et al. [29].

Under elevated $[\text{CO}_2]$, the optimum temperature for flag leaf photosynthesis was 30 and 34°C for M-103 and IR-72, respectively. Significant temperature by cultivar interactions were found, with IR-72 exhibiting temperature optimums generally 1 to 4°C higher than M-103 for several growth characteristics [42]. Daytime temperatures above about 34°C caused gradual declines in photosynthesis and growth of both cultivars. However, at midday growth temperatures above 31°C, grain yield was substantially reduced and above 37°C both cultivars showed total failure. This occurred despite reasonable vegetative growth up to 40°C. Over the temperature range used in this study, elevated $[\text{CO}_2]$ significantly stimulated vegetative growth but not grain yield. A constant CO_2 -induced enhancement of photosynthesis with increasing temperature was found for IR-72, similar to Vu *et al.* [29], which on average was about 29% for leaves of plants grown at 28, 34, and 40°C. For M-103 there was a CO_2 enhancement of 23% at 28 and 34°C but at 40°C photosynthesis of high CO_2 -grown leaves was 25% less than that of their ambient CO_2 counterparts.

For rice, Baker and Allen [35] have reported that seed yield declines at a rate of about 10% for each 1°C rise in day/night temperature above 28/21°C. A similar trend has been reported for soybean [40, 43]. At high temperatures reduced seed yield may largely be due to floral sterility [44]. However, other complicating factors such as a shortening of life cycle and less biomass accumulation under high temperatures also contributed [19]. Further research on how high temperature and elevated $[\text{CO}_2]$ affect reproductive processes of plants is greatly needed.

PHOTOSYNTHETIC ACCLIMATION TO ELEVATED CO_2

Long-term exposure to elevated $[\text{CO}_2]$ leads to a variety of acclimation effects, including changes in the photosynthetic

biochemistry and stomatal physiology, and alterations in the morphology, anatomy, branching, tillering, biomass, timing of developmental events as well as life cycle completion [9, 10, 36, 45]. Many C_3 plants exhibit reduced photosynthetic capacity to long-term growth under elevated $[\text{CO}_2]$. This acclimation response is often associated with a decrease in Rubisco activity, protein content and activation [22, 29]. Plants responding to elevated $[\text{CO}_2]$ in this way sometimes have lower light-saturated photosynthetic rates than plants grown under ambient $[\text{CO}_2]$ when both are measured at a common $[\text{CO}_2]$ [46]. Since present day C_3 plants have evolved in a relatively low $[\text{CO}_2]$ atmosphere, they may not have the genetic capability to take full advantage of the high CO_2 concentrations that are predicted for the future [10, 47].

Baker *et al.* [33] tested for canopy photosynthetic acclimation in rice across several long-term growth $[\text{CO}_2]$ treatments ranging from 160 to 900 $\mu\text{L L}^{-1}$. This was done by comparing short-term canopy photosynthesis across all treatments at 160, 330, and 660 $\mu\text{L L}^{-1} \text{CO}_2$. It was consistently found that plants grown at 330 $\mu\text{L L}^{-1}$ or less photosynthetically outperformed those developed at 660 $\mu\text{L L}^{-1}$ and higher. Furthermore, rice leaves show a marked and linear decline in leaf Rubisco activity and protein content with increasing growth $[\text{CO}_2]$ [48]. Other agronomic plants such as cotton (*Gossypium hirsutum* L.) [49], bean (*Phaseolus vulgaris* L.) and potato (*Solanum tuberosum* L.) [46], winter wheat and barley (*Hordeum vulgare* L.) [50], and tomato (*Lycopersicon esculentum* L.) [51] also show reduced photosynthetic capacity to long-term growth under superambient levels of CO_2 . However, not all C_3 species show this response. Soybean for instance does not show reduced Rubisco activity or protein content with increasing growth $[\text{CO}_2]$ [28, 29, 30].

BIOCHEMICAL AND MOLECULAR BASIS OF PHOTOSYNTHETIC ACCLIMATION

An increase in soluble carbohydrates often accompanies photosynthetic acclimation to long-term growth under elevated [CO₂]. Long and Drake [52] report that across 32 studies involving plant growth under CO₂ enrichment, soluble carbohydrates increased by 52%, and across 62 studies starch content increased 160%. It has long been recognized that an accumulation of soluble carbohydrates can lead to a decline in photosynthesis [53]. Carbohydrate feedback inhibition of photosynthesis is often hypothesized as the most likely cause of photosynthetic acclimation in plants grown under elevated [CO₂] [9, 10, 14, 54, 55].

Feedback inhibition of photosynthesis to elevated [CO₂] may result from carbohydrate source-sink imbalances that develop when photosynthetic rate exceeds the export capacity or the capacity of sinks (e.g. growing tissues and storage organs) to utilize the photosynthate for growth [54]. This can result in the accumulation of soluble carbohydrates in photosynthetically active source tissues [39]. By a not yet fully understood mechanism (reviewed later), soluble carbohydrates are believed to signal the down-regulation of Rubisco synthesis, and in some instances other proteins of the photosynthetic apparatus [56].

Soybean, which typically does not show acclimation of photosynthetic capacity to elevated [CO₂], may do so by creating additional carbohydrate sinks to accommodate excess photosynthate. Baker et al. [43] showed that soybean exposed to elevated [CO₂] resulted in a greater number of seeds per plant. In an experiment directed at sink manipulation of soybean, Clough et al. [57] showed that by removing pods, plants grown under elevated [CO₂] exhibited photosynthetic acclimation. Conversely, rice, which tends to have more finite sink capacity [58], may be more susceptible to feedback

inhibition and hence photosynthetic acclimation.

Alternatively, the difference in photosynthetic acclimation response between rice and soybean to elevated [CO₂] may be related to their different mechanisms of partitioning excess photoassimilate. Soybean is a starch accumulator under high rates of photosynthesis associated with elevated [CO₂] and therefore its leaves tend to have a low abundance of soluble sugars [59]. Conversely, rice typically partitions more photoassimilate to sucrose than starch in response to growth under elevated [CO₂] [60]. Therefore, high CO₂-grown rice leaves tend to accumulate large amounts of soluble carbohydrates.

To test whether an accumulation of soluble carbohydrates can lead to photosynthetic acclimation in rice, Gesch et al. [31] used a non-intrusive approach to modify source-sink balance of plants. In this experiment rice was grown in a series of four outdoor, sunlit, controlled-environment chambers. Two chambers of plants were grown at daytime atmospheric [CO₂] of 350 μL L⁻¹ (ambient CO₂) and the other two were grown at 700 μL L⁻¹ (high CO₂). At the late vegetative stage of development a cross-switching of growth [CO₂] was performed. For plants growing at ambient CO₂, one chamber was switched to high CO₂ and the other was maintained at ambient CO₂, and for the high CO₂-grown rice, one chamber was switched to ambient while the other was maintained at 700 μL L⁻¹ CO₂. If photosynthetic acclimation to elevated [CO₂] results from carbohydrate feedback inhibition, then switching growth [CO₂] from high to ambient should cause a shift from sink to source limited photosynthesis, thus alleviating feedback effects and the opposite should be true for switching from ambient to high CO₂.

Figure 2 shows results of Rubisco activity and protein content for expanding rice leaves of plants before and after switching from ambient to high CO₂ (Fig. 2A

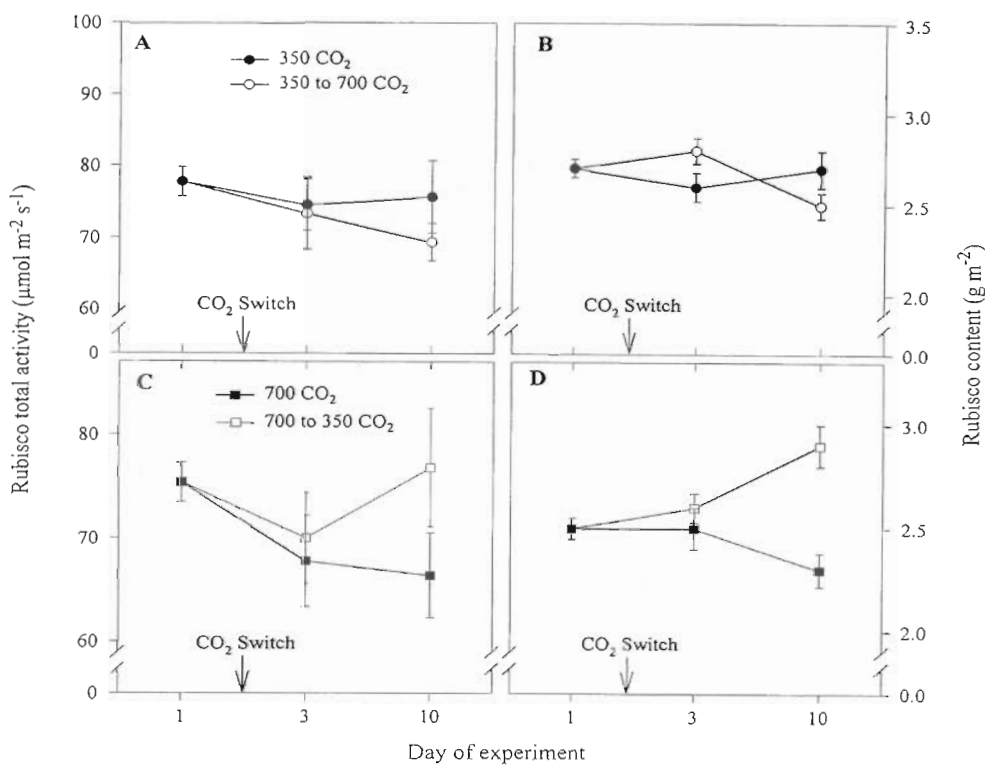


Figure 2. Rubisco total activity (A & C) and protein content (B & D) for expanding rice leaves on day 1, 3, and 10 of the experiment. The switch was made at day 2 as denoted by the arrows. Graphs A and B are the results for switching from ambient to high CO₂, while graphs C and D show results of switching from high to ambient CO₂. Adapted from Gesch *et al.* [31].

& B) and switching from high to ambient CO₂ (Fig. 2C & D), including their respective controls. Throughout the study, leaves of plants maintained at high CO₂ had lower Rubisco activity and content than those of plants maintained under ambient CO₂ (Fig. 2), thus proving acclimation at the biochemical level. Additionally, leaves of plants kept at high CO₂ showed significantly higher levels of hexoses and sucrose than ambient CO₂ controls [31]. Despite Rubisco down-regulation in leaves of rice kept at high CO₂, they still showed photosynthetic rates that ranged from 20 to 30% greater than ambient CO₂ plants.

As expected, soluble carbohydrate content in rice leaves declined rapidly after switching plants from high to ambient CO₂ [31]. This was followed by a slow up-regulation of Rubisco activity and content as compared to the high CO₂ controls, evident by eight days after making the switch (Fig. 2C & D, day 10). Switching from ambient to high CO₂ led to a slight down-regulation of Rubisco activity and content by day 10 of the experiment (Fig. 2A & B). However, the extent of the response was not as great as that due to the opposite switch. Furthermore, upon switching to high CO₂ there was not a rapid increase in soluble carbohydrates [31].

Increased export of carbohydrate from leaves switched to high CO₂ may have prevented accumulation. Recently, we found that switching from ambient to high CO₂ results in a rapid up-regulation of sucrose-phosphate synthase (SPS) activity in mature source leaves of rice, thus partitioning assimilate to sucrose for export (Gesch, unpublished data). Indeed, much of the photosynthate derived soon after switching rice to high CO₂ appears to have been exported from source leaves to stem and sheath tissues, which are primary sinks during vegetative growth, thus perhaps delaying acclimation of Rubisco. For leaves of rice grown under elevated [CO₂] Hussain et al. [61] report increased SPS activity and sucrose production concomitant with a down-regulation of Rubisco. They postulate that plant resources may be diverted away from Rubisco synthesis to up-regulate sucrose production and export, thus optimizing the capacity for carbon utilization and export in rice.

During the past decade several studies have shown that modifying levels of certain

soluble carbohydrates in plant cells can lead to altered expression of a host of genes, many of which are integral to photosynthesis [56, 62, 63]. Using a transient expression system in maize (*Zea mays* L.) protoplasts, Sheen [64] showed that the transcription of seven different maize photosynthetic gene promoters, including that of the small subunit gene of Rubisco (*rbcS*), was repressed by the addition of soluble sugars, especially glucose and sucrose. Transcript levels for *rbcS*, Rubisco activase (*rca*), and the chlorophyll a/b binding complex (*cab*), all nuclear encoded genes, were shown to be repressed in tomato leaves grown under elevated [CO₂] [65], and the response could be mimicked by feeding glucose or sucrose to detached leaves. In contrast, the expression of some genes, especially those involved in carbohydrate metabolism, can be activated by glucose and/or sucrose [62]. In addition to rice and soybean [30, 31, 66], a variety of other crop species show reduced Rubisco gene expression to growth under elevated [CO₂] [67, 68, 69, 70].

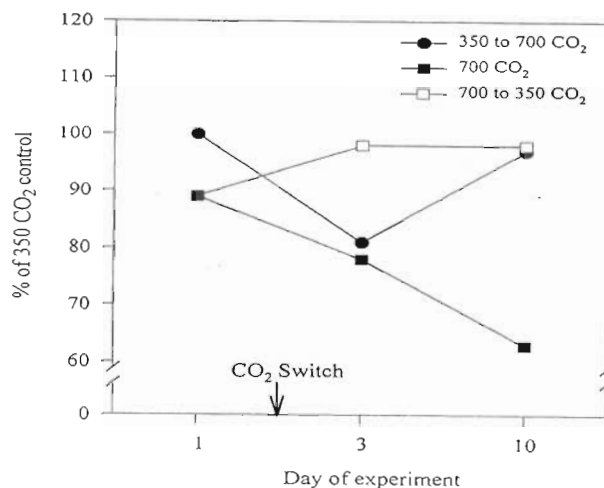


Figure 3. Abundance of *rbcS* mRNA in expanding rice leaves at days 1, 3, and 10 of the experiment. Values are the percent of the 350 (ambient) CO₂ control. The switching of [CO₂] was done at day 2 of the experiment. Adapted from Gesch et al. [31].

The CO₂-switching experiment previously described [31] was used to test the hypothesis of whether an accumulation of soluble carbohydrates might signal the repression of *rbcS* in rice leaves. As shown in Figure 3, within 24-h of switching from ambient to high CO₂, there was a repression of *rbcS* transcript abundance, while switching from high to ambient CO₂ caused an increase in *rbcS* mRNA. This was one of the first examples to show that changes in growth [CO₂] could cause rapid changes in *rbcS* expression for plants grown under field-like conditions. Although transcript levels for the switch to ambient CO₂ correlated with a rapid decrease in hexose and sucrose, there was not a correlation between repressed *rbcS* mRNA and soluble sugars for the switch to high CO₂. Therefore, it was concluded that soluble carbohydrate pool sizes alone could not explain the adjustments in *rbcS* that were observed, at least within the first 24-h.

Current knowledge of sensing and signaling of sugar-mediated gene expression suggests that the fluctuation of soluble carbohydrate pools and metabolic cycling of carbon are more vital to regulation, than pool sizes themselves [71, 72]. Perhaps the most widely accepted mechanism for explaining sugar-sensitive gene regulation is a signal transduction pathway involving hexokinase as a carbon flux sensor [71]. According to this hypothesis, the carbon flux through hexose pools is sensed by their phosphorylation via hexokinase. The precise effector sent to the nucleus to regulate transcription has not yet been identified.

The hydrolysis of sucrose by acid soluble invertase, and the proposed 'futile cycling' of sucrose (i.e., the synthesis and hydrolysis of sucrose as it moves back and forth across the tonoplast), may amplify the hexokinase-mediated response [56, 69]. Moore et al. [69] tested 16 different plant species grown under elevated [CO₂] and found a relatively good correlation between high acid soluble invertase activity and reduced Rubisco protein content. Recently, it

has been shown that there may also be other signal transduction pathway(s) for sugar-mediated gene responses that do not involve hexokinase. Chiou and Bush [73] report convincing evidence that sucrose acts as a signaling molecule in a signal-transduction pathway that regulates the activity of a plasma membrane-bound proton-sucrose symporter from leaf cells.

In addition to transcription, other factors such as transcript stability, translation and turnover of Rubisco may be affected by long-term elevated [CO₂][55]. To date, research concerning these issues is lacking. As Gesch et al. [31] and others [69] have noted, there is not always a good correlation between mRNA transcript abundance of the large and small subunit of Rubisco and the content of Rubisco protein measured in leaf cells.

CONCLUDING REMARKS

Terrestrial plants have evolved to relatively low atmospheric [CO₂] over the past several thousand years but now may be forced to adapt rather rapidly to increasing concentrations along with potentially rising temperatures. For most C₃ crops, elevated [CO₂] in the absence of high temperatures enhances photosynthesis and generally leads to greater biomass and seed yield. However, long-term exposure, for many C₃ plants such as rice, can lead to a down-regulation of photosynthetic processes. Though photosynthetic acclimation may be a mechanism to increase resource use efficiency under high assimilation rates [9, 61], it still means that some species may not be able to take full advantage of the increased CO₂ levels projected for the later part of this century.

Temperatures above the optimum for growth and development of plant species can be detrimental. Although high temperatures generally stimulate plant growth, they also speed up development thus shortening the life cycle. This means that tissues and organs have less time to acquire photoassimilates,

which can result in fewer and/or smaller organs leading to less biomass accumulation.

Reproductive development and maturity of rice and soybean are more greatly influenced by temperature than elevated [CO₂] [35, 40, 42]. Although these processes are hastened by increasing temperatures, both species begin to show delays when daytime temperatures exceed about 35°C [40, 42].

Photosynthetic processes of rice and soybean are negatively affected by high temperatures but to a lesser extent than reproductive development. Elevated [CO₂] can compensate for some of the negative affects of high temperatures. But in this regard, there is considerable variation among C₃ species. Soybean for instance shows a continued CO₂-enhancement of photosynthesis with increasing temperature, while rice does not. To a large extent this may be due to the greater degree of photosynthetic acclimation in rice and differences in carbohydrate source-sink balance. These and other species-specific differences in response to global climate change factors will likely impact future plant interactions and biodiversity in both agricultural and natural ecosystems. For instance, species that do not photosynthetically acclimate to elevated [CO₂] may out compete those that do. Undoubtedly, this will have greater consequences for natural systems than intensively managed agricultural systems. However, Morison and Lawlor [19] upon reviewing several studies note that the effects of elevated [CO₂] and temperature on growth and biomass accumulation cannot be precisely determined by photosynthetic processes alone.

Additionally, though it is not the scope of this review to discuss, we must also realize that other environmental growth limiting factors such as nutrition, light, and water can significantly influence the response of plants to elevated [CO₂] and temperature. Advancements towards our understanding of the effects of elevated

[CO₂] and temperature on plant photosynthesis and productivity will require further study of the integration of these other environmental factors.

In the future, agricultural practices and genotype selection may have to be modified to adapt to global climate change factors. Higher temperatures may require modifying planting dates for rice and soybean, or growing alternative crops with greater heat tolerance. Rice and soybean production may intensify at higher latitudes. In the case of soybean, this may require designing cultivars that are less sensitive to photoperiod. Finally, there will also be a need to select for crop genotypes with improved heat and drought tolerance, and that can utilize fixed carbon more efficiently for seed production.

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