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MORE EFFICIENT PLANTS: A Consequence of Rising Atmospheric CO_2?

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ABSTRACT

The primary effect of the response of plants to rising atmospheric CO_2 (C_a) is to increase resource use efficiency. Elevated C_a reduces stomatal conductance and transpiration and improves water use efficiency, and at the same time it stimulates higher rates of photosynthesis and increases light-use efficiency. Acclimation of photosynthesis during long-term exposure to elevated C_a reduces key enzymes of the photosynthetic carbon reduction cycle, and this increases nutrient use efficiency. Improved soil–water balance, increased carbon uptake in the shade, greater carbon to nitrogen ratio, and reduced nutrient quality for insect and animal grazers are all possibilities that have been observed in field studies of the effects of elevated C_a. These effects have major consequences for agriculture and native ecosystems in a world of rising atmospheric C_a and climate change.

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INTRODUCTION[1]

Several lines of evidence suggest that terrestrial ecosystems are responding to rising atmospheric carbon dioxide (C_a) (39, 80, 116). The terrestrial biosphere responds to this increase solely through the response of plants. Photosynthesis (133) and transpiration (95) have long been known to be sensitive to increase in C_a, and it is now evident that respiration will also be affected (85). These three processes appear to be the only mechanisms by which plants and ecosystems can sense and respond directly to rising C_a. Understanding how these processes are affected by increase in C_a is therefore fundamental to any sound prediction of future response of both natural and agricultural systems to human beings' influence on the composition of the atmosphere and on the climate system.

Many detailed and thorough reviews identify the long list of changes at the whole plant level to rising C_a (e.g. 21, 26, 72, 81), but few focus on these initial steps in perceiving rising C_a. Influential ecological discussions appear sometimes to have ignored a physiological understanding. A common view is that the impact of rising C_a through stimulation of photosynthesis will be short-lived because other factors, particularly nitrogen, will be limiting in most ecosystems (21, 146, 197). Yet this view may ignore evidence from physiology that elevated C_a allows increased efficiency of nitrogen use. Thus the key effect is not removal of a limitation but increase in efficiency. An analysis of the available evidence shows that relative stimulations of plants grown with low N averaged across several studies appear just as large as those for plants grown with high N (130).

In this review, current understanding of the effects of C_a on transpiration, photosynthesis, and respiration are examined to help explain why rising C_a

[1] Abbreviations: A, photosynthetic CO_2 assimilation; A_{sat}, light-saturated CO_2 assimilation; C_a, atmospheric CO_2 concentration; C_i, intercellular CO_2 concentration; Cyt, cytochrome pathway; Cytox, cytochrome-c-oxidase; ET, evapotranspiration; FACE, free-air carbon enrichment; g_s, stomatal conductance; HXK, hexokinase; KCN, potassium cyanide; LAI, leaf area index; LCP, light compensation point; LhcB, light-harvesting subunit; LUE, light-use efficiency; N, nitrogen; NEP, net ecosystem production; NUE, nitrogen use efficiency; Pa, pascal; PCO, photosynthetic carbon oxidation pathway; *RbcS,* Rubisco subunit gene; RH, relative humidity; RubP, Ribulose-1,5-bisphosphate; Rubisco, Ribulose-1,5-bisphosphate carboxylase/oxygenase; SDH succinate dehydrogenase; SHAM, salicylhydroxamic acid; S_r, Rubisco specificity; T, transpiration; T_{opt}, temperature optimum; TNC, total nonstructural carbohydrate; WUE, water use efficiency; $\varnothing$, photosynthetic light-use efficiency.

will increase resource-use efficiency and the implications of this increased efficiency. Each topic is introduced with a description of the mechanism by which elevated C_a has its effect, followed by a discussion of acclimation of the process to elevated C_a. Acclimation is defined as those physiological changes that occur when plants are grown in elevated C_a. We have summarized the most relevant literature to indicate the intensity of the responses for key aspects of each of the three processes we discuss. Current C_a is approximately 36 Pascals (Pa), although in many studies in our survey of the literature C_a was lower than this by as much as 1.5 Pa. Elevated C_a of the studies we reviewed varied considerably, from 55 Pa in the case of the Free Air Carbon Enrichment (FACE) studies to upward of 100 Pa in a few controlled environment studies. In most studies, however, the elevated C_a was approximately 70 Pa, a concentration that is expected sometime during the twenty-first century.

STOMATA

In contrast with the effects of C_a on photosynthetic CO_2 assimilation (A) and respiration, which are mediated by specific molecular targets, the mechanism by which stomata respond to C_a remains unclear (152), although it appears most probable that it is linked to malate synthesis, which is known to regulate anion channels in the guard cell plasma membrane (96). Stomata of most species close with increase in C_a as well as decrease in A and relative humidity (RH). For 41 observations covering 28 species, the average reduction of stomatal conductance was 20% (Table 1; see also 74). A recent analysis of responses in tree seedlings shows that the responses are highly variable, and in some species there is no response to elevated C_a (46). It is not clear, however, whether failure to respond to elevated C_a is due to a genetic trait or to acclimation of stomata to high humidity. For example, stomata of *Xanthium strumarium* grown in a greenhouse in high humidity failed to respond to elevated C_a until given a cycle of chilling stress (62). Reduction of stomatal aperture and conductance (g_s) explains the reduction in leaf transpiration observed in plants grown in elevated C_a (151). But does reduced g_s in elevated C_a limit photosynthesis in plants adapted to high C_a?

Stomatal Limitation of Photosynthesis

Two approaches to making a determination of the limitation of photosynthesis by g_s have been applied (193), and both are based on analysis of the dependence of A on the intercellular CO_2 concentration (C_i), the A/C_i curve. In plants grown in the present atmosphere, C_i is generally maintained at 0.7 C_a, even when C_a is varied. In many plants, the value of A at the operational C_i is commonly about 90% of what it would be without the epidermis as a barrier to water loss and CO_2 diffusion into the intercellular spaces (i.e. A at C_i is about 0.9A at C_a). Here we use C_i/C_a as an index of the limitation of photosynthesis. If C_i/C_a in elevated C_a is less than C_i/C_a in normal ambient C_a, then the g_s would have decreased to be more of a limitation to A in elevated than in normal ambient C_a. In the literature we examined, mean and range of C_i/C_a were nearly identical for both normal ambient and elevated C_a grown plants in 26 species and 33 observations (Table 1). In six field studies, C_i/C_a was also very close to 0.7 for both treatments (0.73, 0.74 for normal ambient and elevated C_a). Thus, although the stomatal conductance is reduced in elevated C_a, this by itself does not limit photosynthesis. Similarly, reduced g_s at the leaf level does not necessarily mean that stand transpiration will be lower because there could be a compensatory increase in leaf area index (LAI). But does failure to limit photosynthesis mean that stomata do not acclimate to elevated C_a?

Acclimation of g_s to Elevated C_a.

Because stomatal conductance is mediated by changes in photosynthesis, lower conductance in plants having a reduced photosynthetic capacity is to be expected. There is some evidence that growth in high C_a alters the gain in the feedback loop for regulation of stomatal conductance (195). However, apart

Table 1 The effect of growth in elevated C_a on acclimation of stomatal conductance (g_s), transpiration (T), the ratio of intercellular to ambient CO_2 concentration (C_i/C_a), and leaf area index (LAI) (field grown species only); and the numbers of species (Sp) and studies (n).[a]

Attribute	R	Sp, n	References
g_s	0.80[b,c]	28, 41	38, 43, 48, 66, 88, 89, 92, 107, 111, 140, 149, 160, 162, 181, 191, 192, 210, 217, 232, 241, 243
T	0.72[c]	35, 80	2, 3, 13, 35, 43, 55, 67, 76, 92, 105, 112, 113, 128, 160, 186, 188, 189, 191, 192, 203, 216, 234, 235
C_i/C_a	0.99	26, 33	15, 19, 20, 43, 48, 73, 88, 89, 107, 108, 140, 149, 160, 162, 170, 181, 191, 192, 210, 241, 243, 248, 249
LAI	1.03	8, 12	13, 92, 142, 165, 173, 187

[a] R is the mean of n observations in various species (Sp) of the ratio of the attribute in plants grown in elevated to that for plants grown in current ambient C_a.

[b] Means statistically different from 1.0 ($p < 0.01$) by Student's *t* test.

[c] Means statistically different from 1.0 ($p < 0.01$) by Mann-Whitney rank sum test for data that failed normality test.

from a single paper (195), there is little evidence that stomata acclimate to elevated C_a independently of acclimation of photosynthesis (65, 133, 193).

ACCLIMATION OF STOMATAL NUMBERS TO ELEVATED C_a An acclimatory decrease in stomatal numbers appears a common but not universal response to growth at elevated C_a. In the absence of variation in stomatal dimensions, stomatal density will determine the maximum g_s that a unit area of leaf could attain. One expectation at increased C_a is that fewer stomata are required because the rate of CO_2 diffusion into the leaf will be a decreasing limitation to photosynthesis as C_a rises. Reported changes in stomatal density with growth at elevated C_a include increases, decreases, and no change (90, 133). Long-term studies drawing on herbarium material and paleoecological evidence appear more conclusive, showing an inverse relation between variation in C_a and variation in stomatal numbers (22, 23, 239). However, in a detailed study of variation in stomatal density within leaves from a single tree, Poole et al (175) showed that variation within a single tree is of the order found in herbarium specimens covering a 200-year period and previously attributed to the change in C_a. The authors further demonstrate that uncertainties in the environment from which palaeobotanical specimens have been sampled could explain the variation attributed to past variation in C_a.

RISING C_a AND EVAPOTRANSPIRATION Will reduced leaf transpiration by elevated C_a also lead to reduced stand evapotranspiration (ET)? Whether elevated C_a reduces ET depends on the effects of elevated C_a on leaf area index (LAI) as well as on g_s. No savings in water can be expected in canopies where elevated C_a stimulates increase in LAI relatively more than it decreases g_s. However, our survey shows that LAI did not increase in any of the long-term field studies of the effects of elevated C_a, on crops or native species (Table 1). This survey included studies of wheat (*Triticum aestivum*) and cotton in Arizona where FACE was used to expose the plants to 55 Pa (173) as well as open top chamber studies of native species. Elevated C_a (>68 Pa) reduced ET compared with normal ambient in all the native species including the Maryland wetland (13), Kansas prairie (92), and the California grassland ecosystem (74). In the wetland ecosystem, ET was evaluated for a C_3-dominated and a C_4-dominated plant community (13). In these two communities, instantaneous values of ET averaged 5.5–6.5 for the C_3 and 7.5–8.7 mmol $H_20\ m^{-}2s^{-}1$ for the C_4 communities at present ambient C_a but at elevated C_a (68 Pa), ET was reduced 17–22% in the C_3 and 28–29% in the C_4 community, indicating the relatively greater effect of elevated C_a on g_s in the C_4 species. In the prairie ecosystem, cumulative ET over a 34-day period in midsummer was 180 kg $m^{-}2$ at present ambient C_a, whereas it was

20% less at elevated C_a. In the grassland ecosystem, elevated C_a reduced ET sufficiently that the availability of soil water was increased (74). A four-year study of the responses of native Australian grass to elevated C_a in a phytotron reported higher water content of soils (138).

STOMATAL CONDUCTANCE AND THE ENERGY BUDGET Reduced transpiration alters partitioning of energy between latent heat loss and convective exchange, potentially increasing leaf temperature (63). Elevating C_a to 55 Pa consistently decreased g_s and increased canopy temperature of cotton about 1°C (173).

SUMMARY Reduced stomatal conductance is expected to be a feature of plants exposed to ever increasing C_a. Stomata do not appear to limit photosynthesis with elevation of C_a any more than they do at normal ambient C_a, even though g_s is usually decreased. A pattern of decreased g_s coupled with maintenance of a constant C_i/C_a will mean that water use efficiency will rise substantially, and there is evidence that this means increased yield for crops with no additional penalty in water consumption. Elevated C_a does not stimulate increased leaf area index in field studies with both crops and native species. Thus, reduced g_s leads to reduced ET and increased soil water content. However, reduced ET also causes increased warming of the plant canopy and surrounding air. Evidence for acclimation of stomatal development to elevated C_a is conflicting, though there is good evidence for a response of g_s to the acclimation of photosynthesis. The following section examines this acclimation.

PHOTOSYNTHESIS

The evidence that elevated C_a stimulates increased photosynthesis is overwhelming. In our survey of 60 experiments, growth in elevated C_a increased photosynthesis 58% compared with the rate for plants grown in normal ambient C_a (Table 2). Acclimation of photosynthesis to elevated C_a clearly reduces photosynthetic capacity but rarely enough to completely compensate for the stimulation of the rate by high C_a. This section of the paper reviews the mechanism for the fundamental effects of C_a on photosynthesis and what is known about acclimation to rising C_a.

Direct Effects of Rising C_a on Photosynthesis

Carbon dioxide has the potential to regulate at a number of points within the photosynthetic apparatus, including binding of Mn on the donor side of photosystem II (119), the quinone binding site on the acceptor side of photosystem II (86), and the activation of Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (178). While all these processes show a high affin-

Table 2 Acclimation of photosynthesis to elevated C_a determined as the ratio (R) of the value of the attribute for plants grown in elevated to that in normal ambient C_a (R)[a]

Attribute	R	Sp,n	References
A at growth C_a			
Large rv	1.58[b]	45, 59	15, 34, 37, 55, 89, 92, 107, 108, 141, 144, 170, 180, 187, 203, 207, 213–215, 219, 224, 241, 247, 248
Small rv	1.28[c]	28, 103	12, 19, 20, 29, 31, 38, 41, 43, 48, 53, 54, 56, 64, 66, 68, 71, 77, 79, 88, 98, 101, 110, 111, 115, 125, 140, 141, 149, 159, 162, 168, 181, 191, 192, 194, 196, 202, 205, 210, 221, 226, 234, 235, 238, 240, 243
High N supply	1.57[b]	8, 10	12, 49, 55, 111, 160, 214, 234, 235
Low N supply	1.23[b]	8,10	12, 49, 55, 111, 160, 214, 234, 235
A, $C_a \leq 35$			
	0.93	28, 33	15, 34, 37, 49, 108, 180, 203, 207, 213, 224, 248, 249
Large rv			
Small rv	0.80[c]	18, 53	19, 20, 29, 38, 43, 48, 54, 56, 68, 71, 79, 88, 97, 110, 111, 115, 125, 140, 149, 162, 191, 192, 194, 202, 210, 221, 226, 234, 235, 238
High N supply	0.80[c]	4, 6	49, 111, 234, 235
Low N supply	0.61[b]	4, 6	49, 111, 234, 235
Starch	2.62[c]	21, 77	1, 7, 20, 24, 36, 49, 50, 54, 68, 93, 94, 98, 103, 108, 115, 139–141, 144, 155, 156, 170, 171, 177, 196, 203, 210, 215, 221, 228, 235, 243, 244
Sucrose	1.60[b]	9, 38	1, 7, 24, 50, 68, 82, 93, 94, 98, 103, 104, 139, 141, 144, 156, 169, 177, 203, 221, 229, 243
Protein	0.86[b]	11,15	7, 34, 37, 56, 93, 94, 108, 200, 202–204, 220, 229
[Rubisco]	0.85[b]	11,8	4–6, 34, 56, 108, 187, 194, 200, 202, 215, 220
Rubisco activity	0.76[c]	11,13	4–7, 34, 37, 56, 93, 94, 97, 106, 108, 124, 125, 140, 144, 169, 187, 194, 200, 202, 203, 214, 215, 226, 228, 234, 237, 243
Leaf [N]			
High N supply	0.85[b]	8, 10	12, 42, 49, 58, 138, 143, 170, 172, 234
Low N supply	0.81[b]	22, 39	12, 40, 42, 48, 49, 58, 99, 138, 140, 143, 149, 150, 160, 170, 172, 182, 187, 190–192, 215, 224, 233, 234

[a] Rooting volume (rv) is either large (>10 L) or small (<10 L). Other details as in Table 1.
[b,c] See table 1.

ity for HCO_3^- or CO_2 and are saturated at the current C_a, Rubisco has a low affinity for CO_2 on carboxylation, and this reaction is not saturated at the current C_a. Therefore, the carboxylation of Rubisco will respond to rising C_a.

The kinetic properties of Rubisco appear to explain the short- and many of the long-term responses of photosynthesis to this change in the atmosphere. Rising C_a increases the net rate of CO_2 uptake for two reasons. First, Rubisco is not CO_2-saturated at the current C_a. Second, Rubisco catalyzes the oxygenation of Ribulose-1,5-bisphosphate (RubP), a reaction that is competitively inhibited by CO_2 (18). Oxygenation of RubP is the first step of the photosynthetic carbon oxidation or photorespiratory pathway (PCO), which decreases the net efficiency of photosynthesis by 20–50%, depending on temperature (245), by utilizing light energy and by releasing recently assimilated carbon as CO_2. CO_2 is a competitive inhibitor of the oxygenation reaction, such that a doubling of concentration at Rubisco will roughly halve the rate of oxygenation (131). This second effect on the PCO may be of greater importance, because an increase in net photosynthesis will result regardless of whether photosynthesis is Rubisco- or RubP-limited and regardless of where metabolic control lies. The increase in uptake resulting from suppression of the PCO requires no additional light, water, or nitrogen, making the leaf more efficient with respect to each.

RUBISCO SPECIFICITY Rubisco specificity (S_r) is the ratio of carboxylation to oxygenation activity when the concentrations of CO_2 and O_2 at Rubisco are equal. It determines directly the increase in efficiency of photosynthesis with rising C_a. This value is therefore of fundamental importance in predicting the direct responses of plants to rising C_a. S_r has been suggested to vary from 88–131 across a range of C_3 plants, with an average of about 100 (18). Terrestrial C_3 plants show both the highest and a fairly constant S_r in contrast with other photosynthetic groups such as C_4 plants and cyanophyta (26, 52, 225).

ELEVATED C_a AND TEMPERATURE As temperature increases, S_r declines dramatically for two reasons: decreased solubility of CO_2 relative to O_2 and decreased affinity of Rubisco for CO_2 relative to O_2 (133). About 68% of the decline in S_r is calculated to result from the binding affinity of the protein for CO_2 (27, 131). The effect of this decline in S_r with temperature is to produce a progressive increase in the stimulation of photosynthesis by elevated C_a with temperature. The minimum stimulation of RuBP-limited photosynthesis by increasing C_a from 35 to 70 Pa rises from 4% at 10°C to 35% at 30°C. It also follows from this interaction that the temperature optimum (T_{opt}) of light-saturated CO_2 assimilation (A_{sat}) must increase with C_a by 2, 5, and 6°C with increase in C_a to 45, 55, and 65 Pa, respectively (137). The upper temperature at which a positive A_{sat} may be maintained is similarly increased. The change in these characteristic temperatures underlies the importance of considering rise in C_a not just as a factor that increases photosynthetic rate, but also as one that strongly modifies the response to temperature. Because increasing C_a is predicted to increase leaf temperature, both directly by decreasing latent heat loss and indirectly through radiative forcing of the atmosphere, this interactive effect of CO_2 and temperature has profound importance to future photosynthesis. It also suggests a much greater stimulation of photosynthesis in hot versus cold climates (118, 135, 136).

Acclimation of Photosynthesis to Elevated C_a

There is abundant evidence that in the long term, photosynthesis acclimates to elevated C_a, i.e. the photosynthetic properties of leaves developed at elevated C_a differ from those developed at the current C_a (46, 90, 133, 230). The vast majority of studies in our and others' surveys show a decrease in A of plants grown in elevated C_a, relative to controls grown at normal ambient, when both are measured at the current ambient C_a (Table 2; see also 90, 136, 193). Acclimation of photosynthesis is accompanied by higher carbohydrate concentration, lower concentration of soluble proteins and Rubisco, and inhibition of photosynthetic capacity. When there is no rooting-volume limitation, as for example in our survey when the rooting volume exceeded 10L, significant reduction in A caused by growth in elevated C_a is the exception rather than the rule (Table 2, A at $C_a < 35$ Pa) while, exceptionally, an increase in photosynthetic capacity is observed (15, 91).

Two reasons for this acclimation are apparent. First, the plant may be unable to use all the additional carbohydrate that photosynthesis in elevated C_a can provide; therefore a decrease in source activity must result. Second, less Rubisco is required at elevated C_a. Our survey shows an average reduction in the amount of Rubisco of 15% in eight studies including 11 species and a reduction in Rubisco activity of about 24% (Table 2). As a protein that can constitute 25% of leaf N, these reductions are a major component of the lower tissue N observed in foliage (15–19%) (Table 2).

SOURCE/SINK BALANCE Arp (14) drew attention to the strong correlation between rooting volume and acclimation of photosynthesis of plants in elevated C_a. In small pots (i.e. <10 L), A of plants in elevated C_a was less than A of plants in normal ambient C_a. In Table 2 we separate the effects of elevated C_a on photosynthesis into the effects of small and large rooting volumes. In our survey of 163 studies, the stimulation of A was about 50% for large rooting volumes and field experiments but reduced by about half of this when the rooting volume is limited (Table 2). When there is no restriction of rooting volume, A_{sat} remains the same for plants grown in both elevated and ambient C_a. Similar conclusions are reported for tree seedlings (46). The effect of rooting volume on acclimation is probably confounded with effects of nutrient availability on photosynthesis.

NITROGEN-LIMITATION Other factors, such as available nutrients, also reduce the sink strength. In a small number of studies, reducing the available N had an effect on A that was the same as the effect of limiting the rooting volume: At high N, the stimulation of A by elevated C_a was about 50%, but this stimulation dropped to about 25% when available N was low. Acclimation of photosynthesis to elevated C_a has frequently been suggested to be more marked when N supply is limiting (26, 46). Rubisco and large subunit Rubisco RNA (*RbcS)* expression in *Pisum sativum* and *Triticum aestivum* were unaffected by growth in elevated C_a when N supply was abundant but showed marked decreases in response to elevated C_a when N was deficient (158, 185).

For plants such as wheat and pea, which are able to rapidly form additional sinks during early vegetative growth, sink limitation is unlikely, whereas other requirements are not limiting. However, growth of additional sinks would be limited if N supply is limiting. Because less Rubisco is required under elevated C_a, this redistribution of N would greatly increase the efficiency of N use.

Although acclimation in many early experiments was exaggerated by the artifact of rooting restriction, there is also clear evidence that acclimation can occur in the absence of any rooting restriction (46). In the Maryland wetland ecosystem where open top chambers have been used to study the effects of elevated C_a (68 Pa), Rubisco was reduced 30–58%, and photosynthetic capacity, measured at normal ambient C_a, was reduced 45–53% in the sedge (*Scirpus olneyi*) after seven years of exposure (108). Wheat grown with an adequate supply of N and water showed no acclimation of photosynthesis to C_a elevated to 55 Pa in FACE until completion of flag leaf development when there was a significant loss of Rubisco followed by other photosynthetic proteins, relative to controls (157).

HOW MUCH RUBISCO IS REQUIRED IN HIGH C_a? Rubisco can constitute 25% of leaf [N] in a C_3 leaf (18). Large quantities of this enzyme appear necessary to support light-saturated photosynthesis in present C_a (140). Calculations suggest that 35% of the Rubisco could be lost from the leaf before Rubisco will co-limit photosynthesis when C_a is increased to double the current concentration (133). *Nicotiana tabaccum* transformed with antisense *RbcS* to produce 13–18% less Rubisco showed lower rates of carbon gain and growth at the current C_a by comparison with the wild type from which they were derived. There was no difference in C gain or growth when both were grown at 80 Pa C_a (140), providing clear evidence of a decreased requirement for Rubisco at elevated C_a.

Woodrow (238) computed the amount of Rubisco required to maintain constant A as C_a increased from the present level to 100 Pa. At 25°C, the amount of Rubisco needed drops to 59% of present amount at 70 Pa, to 50% at 100 Pa (Figure 1). Because of the strong temperature dependence of S_r, the amount of Rubisco required will also decline strongly with increasing temperature. At 70 Pa and a leaf temperature of 35°C, only 42% of the Rubisco activity required at 35 Pa would be needed to maintain the same rate of photosynthesis. There would be a large need for Rubisco at low temperature, and this requirement changes very little as C_a rises (Figure 1). At 5°C, the requirement for Rubisco to maintain the same rate of photosynthesis at elevated C_a is 89% of that needed at normal ambient.

A wide range of studies have reported decreases in Rubisco content and activity with growth in elevated C_a. In our survey of 18 studies of 12 species, Rubisco was reduced 15% (Table 2). Growth in elevated C_a commonly re-

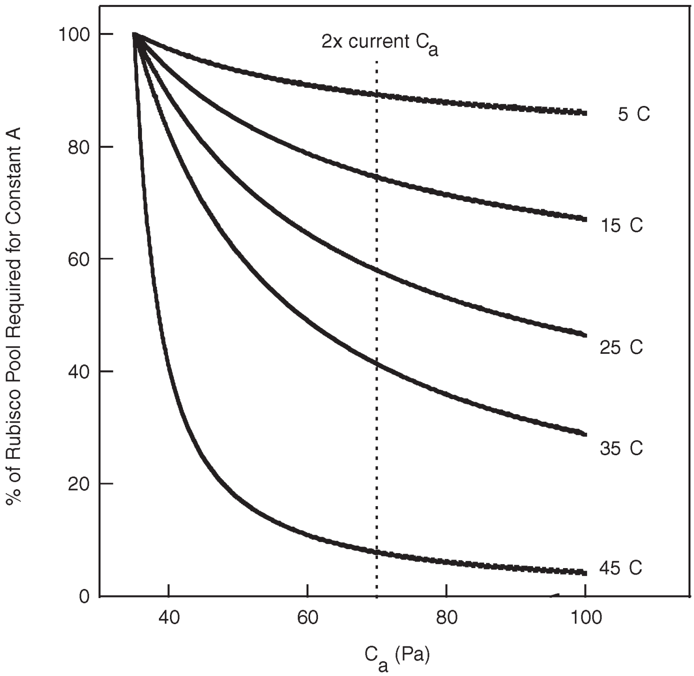

Figure 1 The proportion of Rubisco required to support the same rate of Rubisco-limited photosynthesis at 35 Pa as C_a increases at different leaf temperatures. (After 238.)

sults in decreased photosynthesis relative to controls when measured at the current atmospheric C_a, even though photosynthesis of the elevated grown leaves remains higher when they are measured at their elevated growth C_a. This could be explained by decreased in vivo Rubisco activity. In our survey of 13 studies and 11 species (Table 2), we indicate a reduction of Rubisco activity of 24%. Studies of *Phaseolus vulgaris* (194), *Pinus taeda* (215), and wheat (134) have shown A/C_i responses that indicate a selective loss of Rubisco activity in vivo without significant loss of capacity for regeneration of RuBP with growth at elevated C_a. A similar conclusion can be drawn from control analysis applied to *Helianthus annuus* (237).

THE MOLECULAR MECHANISM OF ACCLIMATION Decrease in Rubisco is commonly correlated with an increase in leaf nonstructural carbohydrates. In our survey we found that sucrose and starch increased 60 and 160% in elevated C_a (Table 2). Regulation of the expression of photosynthetic genes, via increased soluble carbohydrate concentration, may underlie acclimation to growth in elevated C_a (Figure 2; 199, 206, 230). Decreased expression of several photosynthetic genes has occurred when sugar concentrations have been increased by directly feeding mature leaves through the transpiration stream (121, 123, 222), by expression of yeast-derived invertase in transgenic tobacco plants that directs the gene product to the cell wall to interrupt export from source leaves (227), and by cooling the petiole to decrease the rate of phloem transport in intact tobacco plants (122). Using chimeric genes created by fusing maize photosynthetic gene promoters with reporter genes, seven promoters including those for the light harvesting subunit *(LhcB)* and *RbcS* were repressed by soluble carbohydrates. The low concentration of glucose required for this repression suggests that other sugars, in particular sucrose and fructose, may be effective via metabolism in the cell to glucose. How might glucose suppress gene expression in the nucleus? Based on glucose signaling in yeasts, a hypothetical scheme whereby hexokinase (HXK) associated with a glucose channel or transporter in the plasmalemma or tonoplast would release an effector in response to glucose has been proposed (Figure 2; 121, 199). The effector would then interact with the promoters of nuclear genes coding for chloroplast components. This system would allow sensing of both an accumulation of sucrose in the vacuole and in the leaf vascular tissue, indicating an imbalance in sink capacity relative to source activity. Repression is blocked by the HXK inhibitor mannoheptulose, providing evidence of the role of HXK in this signal transduction pathway (109). Where carbohydrate repression has been demonstrated it appears to involve both *RbcS,* coding for Rubisco, and genes that will affect capacity for RubP regeneration. Optimum use of resources would require a system that would allow decrease in

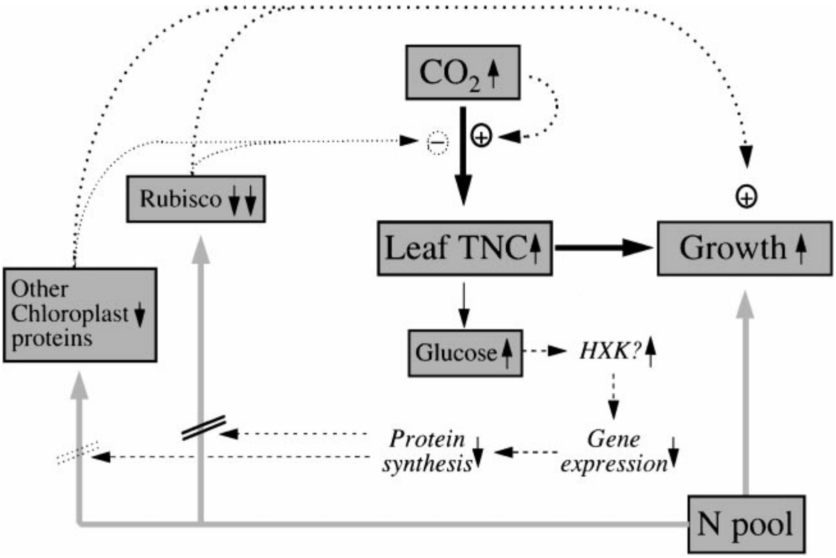

Figure 2 How rising C_a may support more growth when N is limiting. Elevated C_a ($CO_2\uparrow$) will stimulate photosynthesis and leaf total nonstructural carbohydrate (TNC) concentration, which in turn could support more growth of sink tissues. When growth is limited by N, TNC accumulation in the source leaves will be accentuated by elevated CO_2 concentration. Glucose, as a possible monitor of leaf TNC, represses expression of specific genes and in particular the *RbcS* gene coding for the small subunit of Rubisco. Glucose repression of nuclear gene expression is thought to occur via a hexokinase (*HXK*) signal transduction pathway. Decreased synthesis of Rubisco and to a lesser extent other chloroplast proteins will release a significant portion of the limiting supply of N.

Rubisco, without loss of capacity for RubP regeneration. Nie et al (156) showed in wheat that elevated C_a can result in decreased expression of *RbcS* but not other Calvin cycle of chloroplast membrane genes. This is consistent with Figure 2 because several different promoters are involved that could have different sensitivities to carbohydrate concentrations (199). Is carbohydrate repression consistent with observations of plants grown in elevated C_a? Although as a general rule Rubisco decreases with growth in elevated C_a and soluble carbohydrates rise, there are important exceptions (156). This suggests that other possible regulatory elements need to be identified before the mechanisms of acclimation can be fully understood.

ACCLIMATION AND CANOPY PHOTOSYNTHESIS Our analysis of photosynthesis has only concerned the increase in leaf photosynthetic rates that result from growth in elevated C_a. If we consider a crop or natural canopy, carbon gain will only increase with increased leaf photosynthetic rates under elevated C_a in the absence of compensatory decreases in canopy size and architecture. If there is a compensatory decrease in canopy size, then gain at the leaf level might be offset by decrease at the canopy level. In Table 1 we show that for studies carried out in the field, canopy leaf area is not significantly increased or decreased by long-term growth in elevated C_a.

Considerable evidence supports the prediction that increase in CO_2 uptake will be greater in warm climates (131, 133, 145). Among the long-term experiments in which plants have grown under elevated CO_2 for successive seasons, most obvious is that in arctic tundra no sustained increase in net carbon gain was observed (163), whereas in warm temperate climates, e.g. the Maryland wetland ecosystem, stimulation of CO_2 uptake was observed for eight successive seasons (60). In two successive FACE experiments on the same site at Maricopa, Arizona, total daily canopy photosynthesis of *Gossypium hirsutum* in the middle of summer was increased by ca 40% in the canopy growing in 55 Pa. In wheat growing on the same site in the cooler temperatures of spring, canopy photosynthesis was increased by ca 10% (173). Relative stimulation of A by a doubled C_a in the evergreen *Pinus taeda* in the field was strongly correlated with seasonal variation in temperature (129).

Photosynthesis in the Shade

Photosynthesis is light limited for all leaves for part of the day, and for some leaves, those of the lower canopy, for all of the day. For a crop canopy, light-limited photosynthesis can account for half of total carbon gain, whereas photosynthesis of forest floor species might always be light limited. The initial slope of the response of photosynthesis to light defines the maximum quantum yield or photosynthetic light-use efficiency (∅) of a leaf and determines the rate of CO_2 uptake under strictly light-limiting conditions.

At a given C_a, ∅ has been shown to be remarkably constant in C_3 terrestrial plants regardless of their taxonomic and ecological origins (158). This may reflect the constancy of the photosynthetic mechanism across C_3 species. Even under light-limited conditions net photosynthesis is reduced by the PCO, which consumes absorbed light energy and releases CO_2. Inhibition of the PCO by elevated C_a will therefore increase light-limited photosynthesis. This increase may be closely predicted from the kinetic properties of Rubisco (133). Forest floor vegetation commonly exists close to the light compensation point (LCP) of photosynthesis. Any increase in ∅ could therefore result in large increases in net photosynthesis. These predictions are consistent with recent observations of more than two- to fourfold increases in net carbon gain by leaves of both forest floor herbs (CP Osborne, BG Drake & SP Long, unpublished data) and tree seedlings (126) grown in elevated C_a in situ. Calculated from the kinetic constants of Rubisco, the maximum quantum yield of photosynthesis at 24°C will increase by 24% when C_a is doubled. The LCP should decline reciprocally by 20% if mitochondrial respiration remains unchanged. In *S. olneyi* grown and measured in 70 Pa C_a, ∅ was 20% greater than that of plants grown and measured at 36 Pa, close to theoretical expectation (132). LCP, however, was decreased by 42%, almost double the theoretical expectation. A similar increase in maximum quantum yield was observed in the forest floor herb *Duchesnea indica,* but here LCP decreased by 60% (CP Osborne, BG Drake & SP Long, unpublished data). These greater-than-predicted decreases in LCP could only be explained by a decrease in leaf mitochondrial respiration rate. The next section considers the mechanisms and evidence for such a decrease in respiration rate.

SUMMARY Theory and experiments show that in rising C_a, photosynthesis will be stimulated in both light-limited and -saturated conditions and that the stimulation rises with temperature. Optimization theory suggests that substantial decreases in leaf Rubisco content could be sustained under elevated C_a while maintaining an increased rate of leaf photosynthesis, particularly at higher temperatures. Acclimation decreases Rubisco in response to elevated soluble carbohydrate levels. Higher quantum yield at elevated C_a reduces the light compensation point. Because of the temperature interaction between Rubisco activity and elevated C_a, we would expect higher rates of photosynthesis in tropical and subtropical species as well as shifts in the C:N for foliage.

MITOCHONDRIAL RESPIRATION The earliest reported findings of a direct inhibition of dark respiration by elevated C_a are those of Mangin from 1896 (quoted in 153), although the 5% level employed far exceeds the doubling of current ambient C_a. It has now been established that the specific rate of dark respiration, measured either by CO_2 efflux or by O_2 uptake, decreases about 20% when the current ambient C_a is doubled (Table 3, Direct effect; 8, 17, 30, 85, 87, 242). Two different effects of elevated C_a have been suggested (28): an effect that occurs because of the growth or acclimation of the plant in high C_a (e.g. 17) and a readily reversible effect (e.g. 9, 28). These two effects are now referred to as the indirect and direct effects of elevated C_a on respiration. Although the mechanism for the indirect effect is not yet clear, the direct effect appears to be caused by inhibition of the activity of two key enzymes of the mitochondrial electron transport chain, cytochrome *c* oxidase (Cytox) and succinate dehydrogenase

(85). We restrict our comments here to this emerging new direction in CO_2 effects research. For information on other aspects of the interaction of elevated C_a and respiration, we refer the reader to the numerous excellent reviews that have recently appeared (8, 16, 30, 70, 153, 176, 242).

Direct Effect of Elevated C_a on Dark Respiration

There are many reports of a decrease in respiration within minutes of increase in C_a (9, 28, 69, 87, 114, 166, 179, 183, 201). Respiration is reduced about 20% for a doubling of the atmospheric C_a (Table 3). This effect has been reported for many different kinds of tissues including leaves, roots, stems, and even soil bacteria, suggesting that whatever the basic mechanism, it involves a fundamental aspect of respiration.

MECHANISM OF DIRECT EFFECT OF C_a ON DARK RESPIRATION A plausible mechanism underlying the direct effect is the inhibition of enzymes of the mitochondrial electron transport system. Experiments with enzymes in vitro showed that elevated C_a reduces the activity of both Cytox and succinate dehydrogenase (85, 166, 184a). Under experimental conditions in which Cytox controlled the overall rate of respiration in isolated mitochondria (148), O_2 uptake was inhibited by about 15% (85). Experiments with the enzymes in vitro indicated a direct inhibition by elevated C_a on their activity of about 20% for a doubling of the current ambient C_a (85; Figure 3). Measurements of O_2 consumption on isolated soybean mitochondria that were fully activated (State 3 conditions, i.e. sufficient ADP) and in which the respiration inhibitor salicylhydroxamic acid (SHAM) was used to inhibit the alternative pathway showed that doubling C_a inhibited the cytochrome (Cyt) pathway approximately 10–22% (85). By blocking the Cyt pathway with potassium cyanide (KCN) and using either succinate

Table 3 Respiration of shoots and leaves in elevated C_a[a]

Respiration	R	Sp, n	References
Direct Effect	0.82[b]	23, 53	9, 28, 32, 33, 45, 51, 57, 75, 78, 102, 114, 147, 191, 192, 208, 209, 212, 221, 223, 246
Indirect Effect	0.95	17, 37	17, 28, 32, 57, 103, 117, 120, 147, 154, 191, 192, 203, 221, 231, 246

[a] The direct effect refers to the ratio (R) of rates of dark respiration in the same samples when C_a is increased from the current ambient to the elevated level. The indirect effect refers to the ratio of rate of dark respiration of plants grown in elevated to the rate of plants grown in current ambient C_a when measured at the same background of C_a. Other details as in Table 1.

[b] Significantly different from 1.0 ($p < 0.05$) by Students' *t* test.

or NADH as electron donors, it was shown that the succinate dehydrogenase (SDH) in vivo was also inhibited by doubling C_a (85). The activity of the alternative pathway has been shown to be unaffected directly by changing the level of C_a (85, 184a). What is the specific mechanism for inhibition of Cytox by elevated C_a? Because the effect is time dependent (85; Figure 3) and appears to be dependent on CO_2 and not HCO_3 (166), one possibility is a carbamylation reaction. The structure of Cytox contains lysine residues (218), necessary for the proposed carbamylation.

Another proposed mechanism for the apparent inhibition of respiration is that elevated C_a stimulates dark CO_2 fixation (8). Measurements of the respiratory quotient (consumption of O_2/emission of CO_2) show that this is not a viable possibility because reduced CO_2 evolution is balanced by an equal reduction of O_2 uptake in elevated C_a (184).

The possibility that CO_2 inhibition of these enzymes mediates the direct effect of C_a on respiration in plants is supported by measurements on different types of plant organelles and tissues. Doubling present atmospheric C_a re-

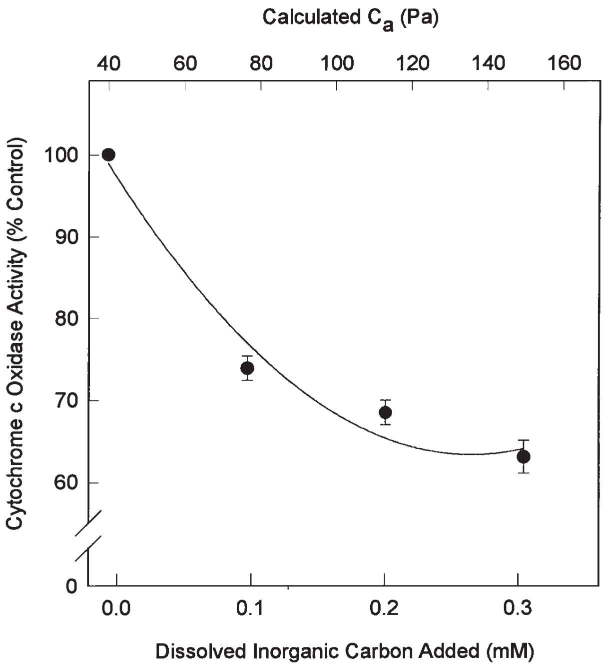

Figure 3 The inhibition of bovine heart Cytochrome *c* oxidase activity in vitro by elevated C_a (85).

duced in vivo O_2 uptake by soybean mitochondria, and by extracts from excised shoots of the sedge *S. olneyi* (84, 85). Experiments in which CO_2 efflux was used to measure dark respiration showed that doubling C_a reduced respiration in excised shoots removed from the field to the lab and from intact stands in which respiration was determined in the field on the C_3 sedge, *S. olneyi* (58). The importance of this effect for carbon balance of plants and ecosystems is that it apparently occurs at the most fundamental level of organization of the mitochondrial electron transport. Thus all respiring tissues are subject to this effect.

Acclimation of Respiration to Elevated C_a

Over days to months, the rate of dark respiration of foliage declines. This occurs in parallel with tissue declines in N concentration or protein content that is energetically costly (25), indicating that this decline reflects decreased demand for energy to sustain growth and/or maintenance. Plants grown in elevated C_a typically have lower protein and nitrogen concentrations (Table 2). Several reviews indicate the considerable potential for rising C_a to reduce respiration through effects on tissue composition (8, 46, 242). We reviewed data on measurements of respiration on leaves of 17 species grown in current ambient and elevated C_a. Acclimation of dark respiration was determined by comparison of the rate of CO_2 efflux or O_2 consumption measured on samples of tissue grown in current ambient or elevated C_a at a common background C_a (Table 3, Indirect effect). In our survey of the literature we found no overall difference between the specific rates of respiration of shoots and leaves grown in elevated or ambient C_a (Table 3).

However, some C_3—but not C_4—species do show the effects of acclimation to high C_a. Acclimation of the rate of respiration in the C_3 plants, *S. olneyi, Lindera benzoin,* and wheat, was due to reduction in activity of enzymatic complexes of the mitochondrial electron transport chain (Cytox and Complex III), which resulted in diminished capacity of tissue respiration (11, 17). Reduction of the activity of these enzymes was not found in the C_4 species *Spartina patens* (11).

SUMMARY Exposure of plants to elevated C_a usually results in a lower rate of dark respiration. Efflux of CO_2 from stands in the field; from excised leaves, roots, and stems; and from O_2 consumption of isolated mitochondria, suspensions of cells, and pieces of tissues are reduced about 20% for a doubling of current C_a. This effect appears to be caused mainly by the direct inhibition of the activity of the respiratory enzymes, cytox, and succinate dehydrogenase by

CO_2. Although acclimation of plants to elevated C_a has been reported to lower the rate of dark respiration, this correlates with reduced activity of respiratory enzymes.

CONCLUSION

Are plants more efficient when grown in elevated C_a? Different definitions apply to efficiency for water, nitrogen, and light, the three main environmental factors we consider here. However, in each case, greater carbon assimilation per unit of water lost, per unit nitrogen content, or per unit absorbed light is consistently found in plants exposed to elevated C_a.

WATER USE EFFICIENCY Water use efficiency (WUE) means here the ratio of A to T per unit leaf area. Reduced g_s in elevated C_a improves WUE by reducing water loss, whether or not photosynthesis is stimulated. In a study of subambient CO_2 effects on oats, mustard, and two cultivars of wheat, WUE increased 40–100% as the ambient CO_2 was increased from about 15 to 35 Pa (174). In a FACE study in wheat, C_a elevated to 55 Pa increased WUE by 76% and 86% in cotton crops, averaged over two full growing seasons (173). Increased C_a also increased WUE in both C_3 and C_4 wetland species (13). The greater decrease in stomatal conductance on the upper than on the lower epidermis of leaves in response to elevated C_a could further decrease WUE under conditions of natural convection (167).

NITROGEN USE EFFICIENCY Rubisco, the primary carboxylase of C_3 photosynthesis, is the most abundant protein in plant leaves and in the biosphere with an estimated 10 kg per capita (10). Acclimation of photosynthesis to a world with higher C_a will mean that less nitrogen will be needed to meet the requirement for this enzyme, leading to reduction in leaf N concentration and increased C:N (44, 47, 99, 161, 164, 236). By the definition of nitrogen use efficiency (NUE) we apply here, the rate of carbon assimilation per unit of N in the foliage, elevated C_a clearly increases NUE. Reduction in [N] is not entirely due to dilution but also represents lower concentration of photosynthetic proteins. In our survey, we found that tissue N is reduced 15–20% depending on N availability (Table 2). In a four-year study of a native Australian grass, NUE increased irrespective of the availability of N in the soil, and this was accompanied by accumulation of carbon in the microcosm (138). In a long-term study of a Maryland wetland ecosystem, [N] was reduced an average of 18% in *S. olneyi* throughout eight years of elevated C_a exposure (61) during which time the elevated C_a treatment stimulated net ecosystem production (NEP). However, while reduction in foliage [N] has the benefit of increasing NUE, it also has the consequence that it may reduce quality or palatability for grazers. The sedge, *S. olneyi*, grown in elevated C_a, was less often the target for egg deposition and larval grazing than in those in current ambient C_a (211). Growth in elevated C_a increased phenolics and tannins as well as toughness of the tissues in *Eucalyptus* sp., and the beetle *Chrysophthartus flaveola* fed this material did poorly: The low nutritional status resulted in lower body weight, reduced digestive efficiencies, and increased mortality (127). Protein content of wheat grain was reduced in elevated C_a (99, 100), although it is not clear how this is related to acclimation of photosynthesis and Rubisco to elevated C_a.

LIGHT USE EFFICIENCY Despite the many studies of plant growth in elevated C_a, few have actually analyzed light use efficiency (LUE; dry matter production per unit intercepted light) at the stand level. In a microcosm study of wheat, LUE increased to a maximum at anthesis and declined thereafter (86). Similarly, Pinter et al (173) found that cotton crops grown under FACE at 55 Pa showed a highly significant increase in LUE of 20% and 22% in consecutive years, regardless of whether the crops were grown with full irrigation or only 50% of the optimal water supply.

Even with acclimation of photosynthesis to elevated C_a, in the sedge, *S. olneyi*, elevated C_a stimulated ecosystem carbon uptake (60). In four out of five studies of native ecosystems in which NEP was measured by gas exchange, long-term elevated C_a exposure stimulated carbon assimilation (55, 59, 60, 74, 92, 163). The exception was the arctic tussock tundra in which there was no net increase in NEP in response to elevated C_a after three weeks (163). Photosynthesis in the dominant species in this system, *Eriophorum vaginatum*, rapidly adjusted to elevated C_a in controlled environment studies (213). This appears to be one of the few species in which one can demonstrate complete loss of initial increase in photosynthesis resulting from increase in C_a.

One of the most important findings of the past ten years of work in elevated C_a is that all but one of the field studies in both crops and native species photosynthesis per unit of ground area was stimulated. Most of the extra carbon from this stimulation must reside in storage tissues such as wood or roots since there is clear evidence that it does not stimulate the increase in foliage. The major consequence of this is that we can expect additional carbon to be accumulated in terrestrial ecosystems as C_a continues to increase.

Improved efficiency generally leads to increased carbon assimilation. Nevertheless, there are a number of consequences that deserve careful study because they may not result in positive outcomes for climate, for yield of crops, or for plant/insect/animal interactions. Reduced stomatal conductance results in greater WUE and reduced ET, and it may increase soil water content. However, reduced transpiration also alters canopy energy balance and shifts some heat loss from transpiration to convective heat loss. This effect has important consequences for climate. Incorporating a model of stomatal response to elevated C_a into a coupled biosphere-atmosphere model (SiB2-GCM) showed that decreased g_s and latent heat transfer will cause a warming of the order of 1–2°C over the continents (198) in addition to warming from the CO_2 greenhouse effect. Implicit in this development is that any loss of photosynthetic capacity, through acclimation, would lead to further decreased g_s (198). These studies emphasize the need for an improved mechanistic understanding of stomatal response to atmospheric change.

Whereas the effects of CO_2 on these separate physiological processes occur via independent mechanisms, there are interactions among all three of them. Acclimation of photosynthesis reduces tissue [N], which may reduce the demand for energy generated by respiration. Reduction of g_s improves water balance, which delays the onset of midday water stress and extends the period of most active photosynthesis; reduced ET increases soil water content and leads to increased N mineralization.

There are problems in moving across scales in the interpretation of processes on a global scale based upon effects at the molecular level. Yet the reduction of stomatal conductance, the improvement in the efficiency of photosynthesis, and the inhibition of the activity of respiratory enzymes are primary mechanisms by which terrestrial ecosystems will respond to rising atmospheric carbon dioxide.

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