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A search for predictive understanding of plant responses to elevated [CO_2]

YIQI LUO,* JAMES REYNOLDS,† YINGPING WANG‡ and DAVID WOLFE§
**Biological Sciences Center, Desert Research Institute, Reno, NV 89509, USA, †Duke University, Durham, North Carolina, USA, ‡CSIRO Division of Atmospheric Research, Aspendale, Victoria, Australia, §Cornell University, Ithaca, New York, USA*

Abstract

This paper reviews two decades of effort by the scientific community in a search for predictive understanding of plant responses to elevated [CO_2]. To evaluate the progress of research in leaf photosynthesis, plant respiration, root nutrient uptake, and carbon partitioning, we divided scientific activities into four phases: (I) initial assessments derived from our existing knowledge base to provide frameworks for experimental studies; (II) experimental tests of the initial assessments; (III) in cases where assessments were invalidated, synthesis of experimental results to stimulate alternative hypotheses and further experimentation; and (IV) formation of new knowledge. This paper suggests that photosynthetic research may have gone through all four phases, considering that (a) variable responses of photosynthesis to [CO_2] are generally explainable, (b) extrapolation of leaf-level studies to the global scale has been examined, and (c) molecular studies are under way. Investigation of plant respiratory responses to [CO_2] has reached the third phase: experimental results have been accumulated, and mechanistic approaches are being developed to examine alternative hypotheses in search for new concepts and/or new quantitative frameworks to understand respiratory responses to elevated [CO_2]. The study of nutrient uptake kinetics is still in the second phase: experimental evidence has contradicted some of the initial assessments, and more experimental studies need to be designed before generalizations can be made. It is quite unfortunate that we have not made much progress in understanding mechanisms of carbon partitioning during the past two decades. This is due in part to the fact that some of the holistic theories, such as functional balance and optimality, have not evolved into testable hypotheses to guide experimental studies. This paper urges modelers to play an increasing role in plant–CO_2 research by disassembling these existing theories into hypotheses and urges experimentalists to design experiments to examine these holistic concepts.

Keywords: acclimation, carbon dioxide, carbon partitioning, global change, nutrient uptake, photosynthesis, respiration, science philosophy.

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Introduction

It has been more than 20 years since the US Department of Energy (DOE) sponsored a workshop in Miami, Florida in 1977 which officially incorporated plants and terrestrial ecosystems into its Carbon Dioxide Research Program (Elliot & Machta 1979). Since the 1977 DOE workshop, predictive understanding of plant responses to rising atmospheric [CO_2] has been sought in order to help explain the past and to forecast future changes in global carbon cycling. The need for plant and ecosystem studies was stimulated largely by modelling results that had long suggested that the global carbon budget could not be balanced without storage of carbon in terrestrial ecosystems (Bacastow & Keeling 1973). Recently, more evidence has been presented to support the idea that terrestrial ecosystems play a critical role in modulating carbon balance in the earth system (Tans *et al.* 1990, 1993; Lloyd & Farquhar 1994; Ciais *et al.* 1995). To provide explanatory and predictive understanding of rising atmospheric [CO_2], the study of plant and ecosystem responses to elevated [CO_2] is necessary.

Stimulated by the global carbon cycling issue, signific-

Correspondence: Dr Yiqi Luo, tel +1/702-674-7562, fax +1/702-673-7485, e-mail yluo@dri.edu

ant research has been carried out by the international scientific community on many aspects of plant biology, including photosynthesis, respiration, nutrient uptake, and carbon partitioning. By 1993, ≈ 1500 papers had been published on plant responses to elevated [CO_2] (Körner 1993). In 1996 alone, nearly three hundred research papers were published in this area. Plant–CO_2 research is booming because atmospheric [CO_2] is increasing at an unprecedented rate and also because an increase in [CO_2] can stimulate horticultural and agronomic yields (Acock & Allen 1985) and alter plant and ecosystem function and structure in the earth system (Mooney *et al.* 1991). In addition, plant–CO_2 research in the past two decades has provided great opportunities to advance our understanding of many basic biological processes (Wardlaw 1990). As a result, many of the existing paradigms in plant biology have been re-examined and expanded in the context of global environmental change (Bazzaz 1990; Field *et al.* 1992).

These intensive studies of plant responses to elevated [CO_2] have rapidly broadened the scope of plant biology. The research scope presently ranges in scale from molecular response to [CO_2] (Griffin & Seemann 1996) to CO_2 impact on species diversity in ecosystem communities (Bazzaz 1990) and global biosphere fluxes (Melillo *et al.* 1993). Growth of plants in elevated [CO_2] usually results in accumulation of leaf starch and soluble sugars, and photosynthetic acclimation. Molecular studies have examined sugar-regulated gene expression as well as functions of encoded proteins and associated metabolic fluxes (Stitt 1991; Van Oosten *et al.* 1994). At the global scale, experimental results have been integrated into global biosphere models to predict potential changes in terrestrial ecosystems in the next century when atmospheric [CO_2] gradually increases to the elevated level (e.g. Polglase & Wang 1992).

While many aspects of CO_2 research have developed quickly, some fundamental plant processes are extremely variable in response to elevated [CO_2]. For example, the apparent respiration rate increases for some species and decreases for others during either short-term exposure to or long-term growth in elevated [CO_2] (Amthor 1997). Similarly, diverse responses of nitrogen uptake, stomatal conductance, carbon allocation (e.g. root/shoot ratio), and photosynthetic capacity to [CO_2] have been observed. Many of these diverse responses are presently not explicable, hindering utilization of experimental results and impeding integration of plant biology into global studies.

This paper will review the process of scientific investigation in plant–CO_2 research, focusing on activities playing critical roles in advancing our predictive understanding of plant responses to elevated [CO_2]. Toward that end, we distinguish four phases of scientific activities in knowledge advancement: (I) initial assessments derived from our existing knowledge base to provide frameworks for experimental studies; (II) experimentation to accept or reject the initial assessments; (III) in cases where assessments proved to be inaccurate, synthesis of experimental data to stimulate alternative hypotheses and further experimental studies; and (IV) formation of new knowledge. We will first provide an overview of the four phases and then discuss each phase in relation to studies of photosynthesis, respiration, nutrient uptake, and carbon partitioning in response to elevated [CO_2]. While this paper is primarily organized through the four phases, the evolution of research is described in three tables on individual processes of photosynthesis, respiration, and carbon partitioning. Research activities on other subjects (e.g. stomatal conductance and plant competition) can be similarly evaluated by the four-phase approach. In addition, this paper revolves around experimental studies leading to predictive understanding. Other aspects of CO_2 research have been extensively reviewed in other papers (e.g. Bazzaz 1990; Allen *et al.* 1992; Field *et al.* 1992; Körner 1995; Reynolds *et al.* 1996; Amthor 1997; Drake *et al.* 1997).

Overview of four phases of plant–CO_2 research

As in most scientific disciplines, research on plant responses to elevated [CO_2] has undergone four distinguishable phases of progress (Fig. 1). The core knowledge base from studies of plant responses to soil fertility (e.g. nitrogen and phosphorus) and light availability provides a starting point in the first phase. Initial assessments of possible responses of plants to elevated [CO_2] are imposed in order to frame experimental studies (Field *et al.* 1992). For example, a biochemically based model developed by Farquhar *et al.* (1980) that describes photosynthetic sensitivity to [CO_2] has been used to assess possible changes in photosynthetic capacity in response to elevated [CO_2] (Pearcy & Björkman 1983). Based on the colimitation concept in the model, it was inferred that plant growth in elevated [CO_2] should result in relative reduction of rubisco (ribulose-1,5-bisphosphate carboxylase-oxygenase) capacity and enhancement of RuBP (ribulose bisphosphate) regeneration (Sage 1990). To assess possible changes in carbon partitioning, a functional balance concept developed by Brouwer (1962) was used. Since nitrogen fertilization enhances root activities, leading to reduced root/shoot ratio (Wilson 1988), it seemed logical to expect that the root/shoot ratio would be increased in elevated [CO_2] because CO_2 enhances the shoot activities.

In Phase II of plant–CO_2 research, experiments are designed to test the hypotheses derived from the initial assessments. Based on experimental results, some of these assessments are accepted and some are rejected. For

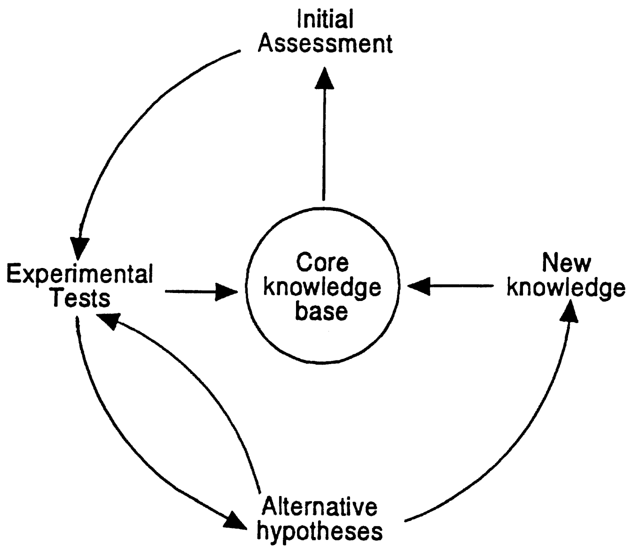

Fig. 1 Evolution of scientific knowledge in reference to research on plant responses to elevated [CO_2]. The research process can be divided into four phases: I, initial assessment derived from existing knowledge base leading to new experimental hypotheses; II, collection of experimental evidence to either support prior knowledge or reject it; III, if the initial hypotheses are rejected, alternative hypotheses are proposed to stimulate more experiments (this hypothesis-experiment cycle may repeat several times); IV, new knowledge (concepts, theory, and/or models) is developed and then added to the core knowledge base.

example, the construction cost of leaf tissue for plants grown in elevated [CO_2] was largely predictable from tissue chemical composition (Poorter *et al.* 1997). That was generally consistent with the concept established by research of plant responses to nitrogen supply (Penning de Vries *et al.* 1974). When the initial assessment was confirmed experimentally, it was generally safe to say that our existing knowledge was applicable to plant responses to growth in elevated [CO_2]. However, many hypotheses resulting from the initial assessments have been rejected. Specific nutrient uptake rate, for example, has been demonstrated to either increase or decrease in elevated [CO_2], depending on types of nutrients, plant species, and growth environments (Bassirirad *et al.* 1996a,b; Jackson & Reynolds 1996). That result was contradictory to the general expectation based on existing knowledge that increased nutrient demand in elevated [CO_2] would stimulate nutrient uptake. When the hypotheses resulting from the initial assessments are rejected, assumptions upon which the assessments are based need to be reexamined or the knowledge base from which the assessments are derived may need to be expanded.

When the initial assessments are not confirmed, experimental results have to be synthesized in phase III, and alternative hypotheses are formed. Since some of the plant responses to elevated [CO_2] have been found to vary widely, a search for predictive understanding of the variable responses has been undertaken through data synthesis. Many synthetic papers have been written on plant responses to elevated [CO_2] (e.g. Kimball 1983; Poorter 1993; Gunderson & Wullschleger 1994; Rogers *et al.* 1994; Sage 1994; Curtis 1996). Curtis (1996) recently introduced a meta-analysis method to provide statistically unbiased estimates of mean responses of experimental data from multiple projects. Synthesis, direct experimental evidence, or both may lead to alternative hypotheses. On photosynthetic acclimation to elevated [CO_2], for instance, at least several hypotheses have been proposed (e.g. disruption of chloroplast, end-product inhibition through sugar accumulation, and increased mesophyll growth). These hypotheses stimulate more experimental studies.

The hypothesis–experiment cycle may be iterated several times. Eventually in Phase IV, this scientific process leads to development of new knowledge regarding plant responses to elevated [CO_2]. For example, the canopy productivity index (i.e. the annual production of wood per unit of leaf area) has been found to be similar across several broadleaf tree species despite the fact that CO_2 stimulation of tree biomass growth is extremely variable (Norby 1996). Molecular studies have recently led to the conclusion that the accumulation of leaf hexoses initiates a chain of molecular and biochemical responses that may be directly related to acclimative changes in rubisco activities and mRNA transcripts when plants are exposed to elevated [CO_2] (Sheen 1994; Van Oosten & Besford 1994).

Initial assessments

As discussed, initial assessments are made from the existing knowledge base. The core knowledge base is generally organized by various frameworks which influence our thinking (i.e. schools of thought). The knowledge base of plant biology is fairly rich and consists of many schools of thought including: (i) plant functional balance (Brouwer 1962; Reynolds & Thornley 1982; Wilson 1988); (ii) resource balance (Field *et al.* 1992); (iii) plant functional types (Chapin 1991); (iv) ontogenetic drift (Coleman *et al.* 1993); (v) growth analysis (Bazzaz 1993); (vi) nitrogen productivity (Ågren 1985; Ågren & Ingestad 1987); (vii) source-sink regulation (Stitt 1991); and (viii) optimality (Bloom *et al.* 1985; Hilbert 1990). For example, the growth analysis approach separates plant growth rate into several components, including net assimilation rate per unit of leaf area, leaf area ratio, and specific leaf area. These components have been used to assess the impact of global change on plant growth and allocation (Bazzaz 1993). These schools of thought identified above are not mutually exclusive. Each has its own features and differentially influences the thinking of various research groups, though.

These schools of thought have not equally influenced research into plant responses to elevated [CO_2]. In the history of CO_2 research, the knowledge base related to growth analysis has been one of the most influential in directing experimental studies. Based on the fact that rising atmospheric [CO_2] will directly increase photosynthetic carbon fixation and reduce water loss through transpiration, Strain & Cure (1985) proposed three-level (primary, secondary, and tertiary) effects of elevated [CO_2] on plants. The primary effects are those of [CO_2] on photosynthesis, transpiration, and stomatal conductance. These physiological processes are directly responsive to changes in ambient [CO_2]. The secondary effects are on primary productivity, growth, and carbon partitioning which are influenced by [CO_2] through altered carbohydrate availability and plant water status. The tertiary effects are on secondary chemical compounds that regulate herbivory and then community dynamics. Influenced by this framework, a considerable fraction of the plant-CO_2 research has focused on biomass and gas exchange, providing a rich array of data for developing plant growth models (Reynolds *et al.* 1996). Other influential frameworks include those derived from the concept of source–sink regulation by Stitt (1991) and Farrar & Williams (1991) as well as the resource-based approach and plant functional types by Mooney *et al.* (1991). The source–sink framework is particularly useful in guiding molecular and biochemical studies of plant responses to [CO_2]. The resource-based approach provides a research framework in relation to an array of ecosystem types ordinated by two axes of drought stress and nutrient availability. This framework is presently influencing ecosystem-scale studies using Free-Air CO_2 Enrichment (FACE) facilities and open-top chambers.

Initial assessments become useful in guiding experimental studies only if testable hypotheses can be derived from the core knowledge. For example, the paper by Stitt (1991) disassembled the source–sink concept into a variety of testable hypotheses. The paper by Mooney *et al.* (1991) placed the resource balance and functional type concepts in a context of different ecosystem types. In contrast, other concepts such as optimality, nitrogen productivity, and functional balance have not become major frameworks in influencing experimental studies. These concepts have been integrated into modelling studies (Reynolds & Thornley 1982; Ågren & Ingestad 1987; Hilbert & Reynolds 1991) and have proved useful in interpreting whole-plant responses to environmental factors (Bloom *et al.* 1985). These holistic approaches have, unfortunately, not been well disseminated as testable hypotheses that experimentalists can easily test. It is the future responsibility of the CO_2 research community to explore how to design experiments to measure, for example, marginal cost vs. marginal benefit associated with environmental changes.

Experimental tests of initial assessments

Many of the initial assessments of physiological processes in response to elevated [CO_2] have not been confirmed by experimental evidence. For example, the speculation in the early 1980s that photosynthetic capacity should decrease in elevated [CO_2] (Pearcy & Björkman 1983) was gradually challenged by experimental data (Table 1). The photosynthetic capacity of plants grown in elevated [CO_2] has been experimentally shown to increase, decrease, or not change depending on species and growth environments (Campbell *et al.* 1988; Sage *et al.* 1989). For example, a comparative study with five species conducted by Sage *et al.* (1989) demonstrated that growth in elevated [CO_2] led to either an increase or decrease in maximal values as well as initial slopes of A/C_i (assimilation/intercellular [CO_2]) responses.

The experimental evidence has also challenged some of the existing assumptions on respiratory responses to elevated [CO_2]. According to the respiratory control theory, the rate of respiration is primarily regulated by consumption of respiratory products (e.g. ATP, NAD(P)H, carbon skeleton intermediates) (Palmer 1984; ap Rees 1990; Amthor 1991). Since the consumption of respiratory products is associated primarily with growth and maintenance processes, CO_2-enhanced plant growth should require more respiratory products, leading to a higher respiration rate. However, experimental results suggest that apparent respiration rates can either decrease (Amthor *et al.* 1992; Bunce 1990; Thomas & Griffin 1994) or increase (Ryle *et al.* 1992a,b; Ziska & Bunce 1994) during short-term CO_2 increases. Long-term growth of plants in elevated [CO_2] also leads to variable responses of respiration (Poorter *et al.* 1992; Thomas & Griffin 1994; Wullschleger *et al.* 1994; Amthor 1997). The variable, long-term responses of respiration may still be consistent with the control theory because of the interactive effects of increased growth and decreased tissue nitrogen concentration on respiration (Amthor 1997). However, the mechanisms of short-term effects of [CO_2] on respiration are unclear and may be related to inhibition of cytochrome *c* oxidase activity (Gonzàlez-Meler *et al.* 1996) (Table 2).

Many of the existing notions on nutrient uptake can not be supported by experimental results to date, either. Plant nutrient acquisition is expected to be enhanced when nutrient demand associated with growth is accelerated in elevated [CO_2]. Measured phosphorus uptake, however, did not show an increase in either the uptake rate or root fraction (Bassirirad *et al.* 1996a). Similarly, physiological rates of ammonium uptake were unchanged

Table 1 Evolution of the research on photosynthetic responses to elevated [CO_2] characterized by four phases: Phase I is the initial assessment of photosynthetic responses to elevated [CO_2]; Phase II is experimental tests of the initial assessments; Phase III is generation of alternative hypotheses; and Phase IV is the formation of new knowledge. (See text for more description of the phases.)

Phase	Description	References
I	1. Photosynthetic rate will be increased.	Pearcy & Bjorkman (1983)
	2. Photosynthetic capacity will be decreased (i.e. downregulation).	
II	Experimental data confirmed the increase in photosynthetic rate but rejected the speculation that photosynthetic capacity is always decreased.	Sage *et al.* (1989)
III	Hypotheses to explain responses of photosynthetic capacity to [CO_2] include:	
	1. Chloroplast breakdown;	DeLucia *et al.* (1985)
	2. N redistribution;	Sage (1994)
	3. Source-sink regulation;	Stitt (1991)
	4. End-product inhibition;	Long (1991)
	5. Starch accumulation;	Long & Drake (1992)
	6. Morphological growth;	Vu *et al.* (1989)
	7. Compensatory changes in N dilution and mesophyll growth.	Luo *et al.* (1994)
IV	1. The balance between biochemical downregulation and morphological upregulation explains both up- and down-regulation of photosynthetic capacity.	Luo *et al.* (1994)
	2. The accumulation of leaf hexoses initiates a signal-response mechanism that represses transcription of many photosynthetic genes.	Jang & Sheen (1994)
	3. Photosynthetic sensitivity is scaleable to the globe but the acclimative changes are not.	Luo *et al.* (1996)

Table 2. Evolution of the research on respiratory responses to elevated [CO_2] characterized by four phases. (See Table 1 and text for description of the four phases.)

Phase	Description	References
I	1. Whole-plant growth and maintenance respiration will increase because of more growth and large plants.	Amthor (1991)
	2. Growth cost and specific maintenance respiration rate may decrease if tissue composition changes.	
	3. No prediction prior to experiments was made on short-term CO_2 effect.	
II	1. Experimental data generally confirmed that whole-plant growth and maintenance respiration increases and growth cost and specific maintenance respiration rates decrease.	Amthor (1997) Gonzàlez-Meler *et al.* (1996)
	2. Experiments demonstrated a short-term effect that respiration decreases as measurement [CO_2] increases.	Amthor *et al.* (1992)
III	Hypotheses to explain the short-term CO_2 effect on respiration include:	
	1. Measurement error with leaking chambers;	Amthor (1997)
	2. Inhibition of enzymatic activities;	Gonzàlez-Meler *et al.* (1996)
	3. Dark CO_2 fixation;	Amthor (1995)
	4. Substrate stimulation of alternative pathway.	Palet *et al.* (1992)
IV	1. The long-term CO_2 effects on whole-plant growth and maintenance respiration, growth cost, and specific maintenance respiration are conceptually explicable and yet to be evaluated quantitatively.	Amthor (1997) Gonzàlez-Meler *et al.* (1996)
	2. Inhibition of cytochrome *c* oxidase activity may be partly responsible for the short-term CO_2 effects.	Azcón-Bieto *et al.* (1994)

with elevated [CO_2] and rates of nitrate uptake decreased in a study of six species in California grasslands (Jackson & Reynolds 1996). Opposite to that finding are the nutrient uptake rates by field-grown loblolly pine saplings: [CO_2] enrichment enhanced the root uptake capacity for nitrate but not for ammonium (Bassirirad *et al.* 1996b). Yet the additional nutrient demand can be balanced by increasing root uptake areas (Jackson & Reynolds 1996) and/or reduced tissue nutrient concentration in elevated [CO_2].

Rigorous experimental tests of existing concepts on carbon partitioning have rarely been conducted (but see Chu *et al.* 1992) although many experiments observed simple indices such as root/shoot ratio and leaf area ratio (Rogers *et al.* 1994) (Table 3). These simple indices do not

Table 3 Evolution of the research on carbon partitioning responses to elevated [CO_2] characterized by four phases. (See Table 1 and text for description of the four phases.)

Phase	Description	References
I	Root/shoot ratio is speculated to increase because of enhancement in shoot activity	Wilson (1988)
II	Experimental data indicate root/shoot ratio increases for some species and decreases for others, rejecting the initial hypothesis.	Rogers *et al.* (1994)
III	Hypotheses that possibly explain the diverse carbon partitioning include:	
	1. Optimality;	Hilbert (1990)
	2. Growth/photosynthesis balance;	Luo *et al.* (1994)
	3. Ontogenetic drift;	Coleman *et al.* (1993)
	4. Functional balance;	Reynolds & Thornley (1982)
	5. Coordination;	Reynolds & Chen (1996)
	6. Source–sink relationship.	Stitt (1991)
IV	Variation in root/shoot ratio may be explicable by increased nitrogen productivity and reduced carbon use efficiency for carbon fixation and nutrient uptake. Critical datasets are required to test the above hypotheses.	

reveal much about the mechanisms of carbon partitioning. To test the functional balance concept, for example, specific shoot and root activities (i.e. mass-based, whole-shoot photosynthetic rate and whole-root nutrient or water uptake rates) and shoot and root biomass should be simultaneously measured (Wilson 1988). To the best of our knowledge, no single experiment has been undertaken to measure these components in order to test the functional balance concept in elevated [CO_2]. The root/shoot ratio alone can not validate or falsify the concept because the balance between shoot with root functioning also depends on specific root and shoot activities. These activities have been shown to vary with elevated [CO_2]. In addition, a modelling study by Luo *et al.* (1994) has demonstrated that two partitioning schemes (nitrogen productivity and functional balance) lead to contradictory predictions on the effects of nitrogen on the root/shoot ratio. A model formulation based on nitrogen productivity suggests root/shoot ratio should increase in elevated [CO_2] with decreased plant nitrogen concentration. The opposite is suggested by the functional balance. It remains a challenge for experimentalists to design tests of these concepts.

Synthesis and alternative hypothesis

A great amount of experimental data have been accumulated since 1977. Because experimental results have proven to be highly variable and often species- and condition-specific, synthesizing experimental results across species and growth environments has become a very effective approach to generalizing plant responses to elevated [CO_2]. The synthetic papers can be grouped into two types: (i) single variable and (ii) multiple variables with a central theme. For example, papers by Kimball (1983), Poorter (1993), Gunderson & Wullschleger (1994), and Amthor (1997) synthesized published data of crop yield, biomass growth, photosynthesis, and respiration in response to elevated [CO_2], respectively. One of the primary goals of these synthetic papers has been to provide mean responses and variability, usually associated with different types of plants (e.g. C3 vs. C4 plants). The synthetic papers dealing with multiple variables generally attempt to explain observed phenomena by integrating several underlying processes having variable responses (e.g. Long 1991; McMurtrie & Wang 1993; Luo *et al.* 1994; Poorter *et al.* 1997). For example, Long (1991) synthesized the responses of starch content, soluble sugar, transpiration, and rubisco content to elevated [CO_2] and incorporated them into a model to predict photosynthetic responses to elevated [CO_2]. Poorter *et al.* (1997) integrated the leaf chemical composition of 27 species in an attempt to understand CO_2 effects on tissue construction costs and growth respiration. In order to explain nonlinear photosynthetic response to [CO_2], Luo *et al.* (1998) have examined relationships among [CO_2], photosynthesis, nitrogen, and specific leaf area by synthesizing data from several CO_2 projects.

Experimental results and/or their synthesis often lead to alternative hypotheses and further experimentation. In searching for mechanisms to explain the diverse photosynthetic responses to long-term growth in elevated [CO_2], for example, several hypotheses have been proposed (Table 1). Among them are (i) source-sink limitation (Farrar & Williams 1991; Stitt 1991), (ii) chloroplast breakdown by oversized starch grains (Delucia *et al.* 1985), (iii) starch accumulation inhibition (Long & Drake 1992), (iv) phosphorus limitation (Sage 1990, 1994; Harley *et al.* 1992), (v) pot-size effect (Arp 1991; Thomas & Strain 1991), (vi) morphological changes, (Vu *et al.* 1989; Sims *et al.* 1998), and (vii) balance between biochemical downregulation and morphological upregulation (Luo *et al.* 1994, 1998). Chloroplast breakdown has not been observed in many subsequent experiments. An increase in leaf soluble carbohydrate has been consistently observed in many plants grown at elevated [CO_2] (Long & Drake 1992), but the increase is not always well correlated with changes in photosynthetic capacity (Baxter *et al.* 1995; Jacob *et al.* 1995). End-product inhibition, phosphorus limitation, and source-sink regulation have been modelled (Hilbert *et al.* 1991; Long 1991; Harley *et al.* 1992) and found to partly explain the downregulation but not the upregulation. Luo *et al.* (1994) evaluated various hypotheses in a quantitative framework and concluded that a balance between biochemical downregulation and morphological upregulation can account for most of the observed variability in photosynthetic acclimation to elevated [CO_2]. The biochemical downregulation encompasses various processes including CO_2-induced inorganic phosphorus limitation, end-product inhibition through nonstructural carbohydrate (e.g. sugar), depressed gene expression, and reduced rubisco amount and/or activity. These biochemical processes generally result in lower photosynthetic rate and capacity (i.e. downregulation). The morphological upregulation is CO_2-stimulated mesophyll tissue growth, possibly including expanded cell volumes and cell layers in a leaf. The balance hypothesis was tested by manipulative experiments in the field (Jackson *et al.* 1995) and in a controlled environment (D.A. Sims and Y. Luo, unpubl. data).

Respiration in response to both short-term exposure or long-term growth in elevated [CO_2] has also been extensively studied (Bunce 1990; Poorter *et al.* 1992; Wullschleger *et al.* 1994; Amthor 1995). The review by Poorter *et al.* (1992), for example, found that apparent leaf respiration rates increased by an average of 16% on a leaf area basis but decreased by an average of 14% on a leaf mass basis for plants grown in elevated [CO_2]. Alternative hypotheses on the variable, long-term effects of [CO_2] on respiration include reduction in mitochondrial enzyme activities and concentration (Azcón-Bieto *et al.* 1994), regulation of respiration by tissue carbohydrate concentration (Farrar & Williams 1991), changes associated with increased photosynthesis and growth (Amthor 1997). While those hypotheses seem adequate to explain and predict respiratory responses to long-term exposure to elevated [CO_2], a quantitative evaluation against concomitant measurements of growth, tissue chemical composition, and respiration is urgently needed to provide insights into respiratory physiology.

A short-term increase in [CO_2] from $\approx$ 350 to 700 ppm (in the dark) has been found to reduce leaf respiration by 10–30% across 37 species (Amthor 1997). Several hypotheses have been proposed to identify the possible mechanisms causing this short-term response (Table 2). Gonzàlez-Meler *et al.* (1996) suggests that inhibition of cytochrome *c* oxidase and succinate dehydrogenase may be a mechanism of the short-term depression. Other possible mechanisms causing the short-term reduction in respiration include dark [CO_2] fixation by several nonphotosynthetic carboxylases (Amthor 1995), instrumental inaccuracy (Amthor 1997), and substrate stimulation of alternative pathway (Palet *et al.* 1992). Tests of these hypotheses are under way and will duly advance our understanding of the basic mechanisms of respiratory response to elevated [CO_2].

Only a few studies have been reported on the kinetics of root nutrient uptake with respect to elevated [CO_2] (Bassirirad *et al.* 1996a,b; Jackson & Reynolds 1996). The general trend of nutrient uptake in response to elevated [CO_2] will not be clear until more experiments are completed involving a variety of species. Although many data are available on plant growth components, it is not easy to assemble the data sets necessary for testing hypotheses on carbon partitioning, largely because the data were not collected under guidance of synthetic frameworks. Nonetheless, the extremely large database accumulated in the past 20 years on many aspects of plant responses to elevated [CO_2] may provide an opportunity for further synthetic studies and modelling integration. Modelling studies, in combination with data synthesis and hypothesis testing, may become a very fruitful approach to improved understanding of the CO_2 effects.

New knowledge

New knowledge can be evaluated using several criteria including (i) phenomenological consistency of plant responses, (ii) explanatory power of observed phenomena, (iii) mechanistic understanding of plant processes, and (iv) scalability of our knowledge across spatial and temporal scales. One notable consistency is that the majority of plant processes in response to elevated [CO_2] are extremely variable, increasing for some species grown in certain environments but decreasing for other species grown in different environments. Consistent responses to elevated [CO_2] include increased photosynthetic rate (Gunderson & Wullschleger 1994; Curtis 1996), increased nonstructural carbohydrate concentration (Long 1991), increased nitrogen and water-use efficiency (Field *et al.* 1995; Drake *et al.* 1997), and decreased leaf and plant nutrient concentration (Luo *et al.* 1994). While there are some exceptions, it appears to be the pattern that respiration rates increase for crop species and decrease for perennial native species grown in high [CO_2] (Gonzàlez-Meler *et al.* 1996).

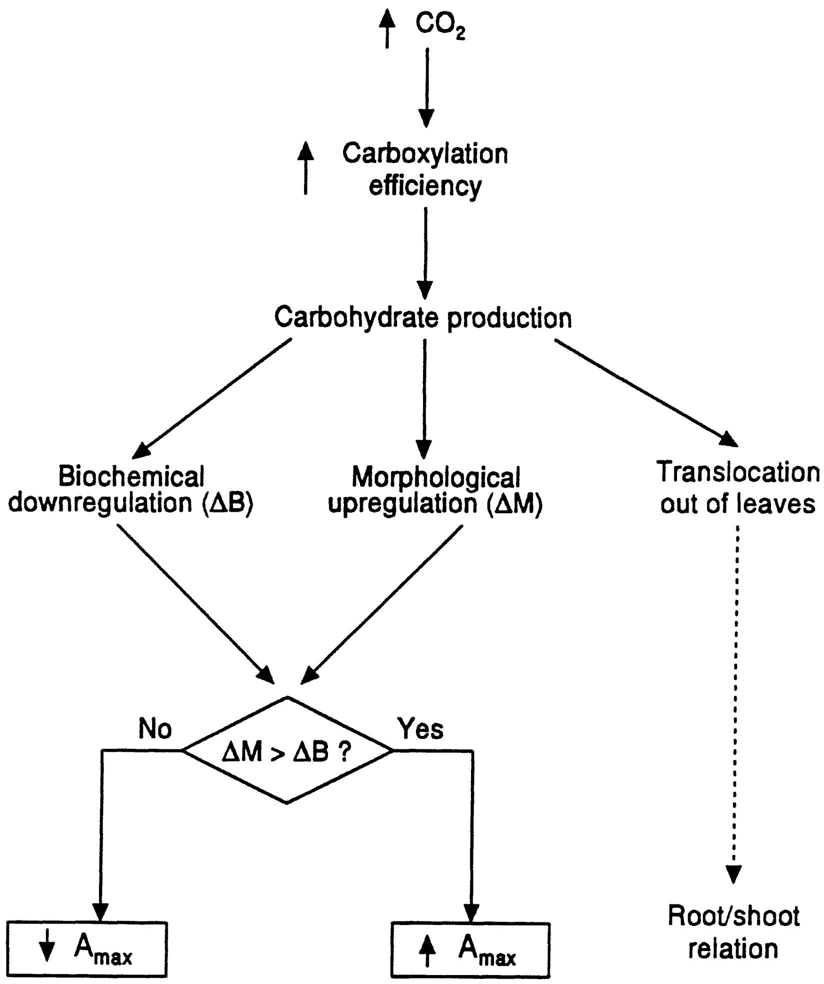

Fig. 2 Proposed mechanisms for responses of photosynthesis to elevated [CO_2]. Photosynthetic capacity (A_{max}) increases in elevated [CO_2] only when the additional leaf mesophyll growth more than compensates for the effect of nitrogen dilution on A_{max} (modified from Luo *et al.* 1994).

The explanatory power of observed phenomena lies in providing causal relationships between the phenomenon in question and underlying processes. Variable responses of photosynthetic capacity to elevated [CO_2] can be explained largely by a balance of biochemical downregulation and morphological upregulation (Luo *et al.* 1994; 1998) (Fig. 2). When growth at elevated [CO_2] leads to morphological upregulation that is larger than decreases in the biochemical capacity of photosynthesis, photosynthesis is upregulated. Otherwise, photosynthesis is downregulated (Table 1). Variation of the root/shoot ratio in response to elevated [CO_2] may be explained by increased nitrogen productivity and reduced carbon use efficiency for carbon fixation and nutrient uptake (Luo *et al.* 1994). Variable patterns in tissue construction cost and growth respiration are predictable from CO_2-induced variation in tissue chemistry. A 42% increase in nonstructural carbohydrate and 9% decrease in protein account for most of the 3% decrease in construction cost and 11% decrease in growth respiration (Poorter *et al.* 1997).

Mechanistic studies have been conducted on photosynthetic responses to [CO_2] at molecular and biochemical levels. Increased carbohydrate production at elevated [CO_2] may exceed the demand from sinks (Stitt 1991) leading to depression of gene expression (Nie *et al.* 1995a,b) and reduction in mRNA contents (Krapp *et al.* 1993; Jang & Sheen 1994; Van Oosten & Besford 1994; Van Oosten *et al.* 1994) and photosynthetic enzymes (Besford *et al.* 1990; Krapp *et al.* 1991; Socias *et al.* 1993). The recent molecular studies have suggested that sugar-regulated gene expression is responsible for changes in photosynthetic proteins during acclimation to elevated [CO_2]. In particular, Jang & Sheen (1994) have proposed that the accumulation of leaf hexoses can initiate a signal-response mechanism that involves cytoplasmic hexokinase and ultimately represses transcription of many photosynthetic genes, including rubisco (Table 1). Continued advancement in molecular studies will help reveal the fundamental mechanisms of photosynthetic acclimation to elevated [CO_2].

To date, many results of plant-level studies have been integrated into regional and global models. For example, the photosynthetic model by Farquhar *et al.* (1980) and the growth β factor (Wullschleger *et al.* 1995; Amthor &

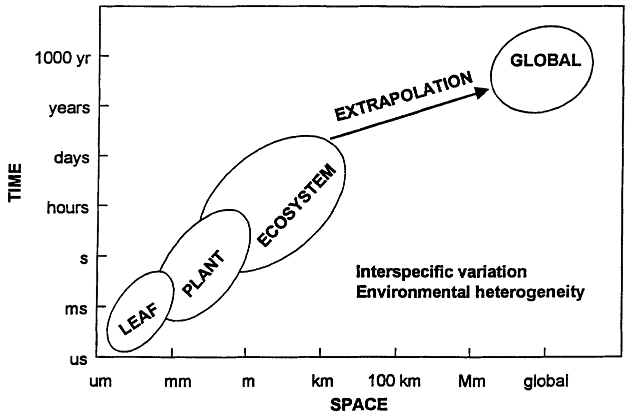

Fig. 3 Illustration of major issues involved in global scaling-up studies of biospheric processes. Global change research is usually designed to address large-scale and long-term issues. However, we can not make any measurements at such large scales but only at leaf-, plant-, or small ecosystem-scales. When we extrapolate the small-scale measurements to predict large-scale changes, we encounter two general problems: interspecific variation and environmental heterogeneity. Any method that can eliminate or diminish their effects on the parameters in question will reduce uncertainties in predicting large-scale changes.

Koch 1996) are used to predict regulation of global carbon cycling by terrestrial ecosystems (Bacastow & Keeling 1973; Polglase & Wang 1992; Ciais *et al.* 1995; Luo & Mooney 1996). The stomatal conductance model by Ball *et al.* (1987) has been used to predict exchange of energy, water, and carbon between the atmosphere and continents (Seller *et al.* 1997). Nutrient and water constraints have also been integrated into global models to predict fluxes of carbon, nutrients, and other trace gases in response to global change (Melillo *et al.* 1993; McGuire *et al.* 1995).

Despite the extensive applications of plant-level knowledge in regional and global studies, scalability has not been examined carefully. When we extrapolate plant-level studies to regional and global scales, we encounter two general problems: interspecific variation and environmental heterogeneity (Fig. 3). Any method which can eliminate or diminish their effects on the parameters in question will reduce uncertainties in predicting large-scale changes (Luo 1998). Recent modelling studies divide geographical maps of world vegetation and soils into grids with relatively uniform environmental conditions and species composition. This approach helps reduce spatial variability. Difficulties in model parameterization and vegetation delineation, however, make such quantification still unsatisfactory (Schimel 1995).

An alternative approach in scaling-up studies is to search for scaleable physiological parameters. Field (1991) has argued for a functional convergence hypothesis indicating that evolution has shaped plants such that some physiological processes reflect the availability of all the resources required for plant growth and thus become scaleable predictors of environmental conditions and resource availability. The validity of this convergence hypothesis has been made evident by the photosynthesis–nitrogen relationship at the leaf level, nitrogen–light at the canopy level, and light-use efficiency at the ecosystem scale. Although it varies in plot-scale measurements, Field (1991) suggested that light-use efficiency (defined as the ratio of dry matter production to the integrated energy absorbed) is a reasonable predictor of net primary productivity at large scales in combination with remote sensing data. In addition, Polglase & Wang (1992) and Luo & Mooney (1996) have recently examined leaf photosynthetic sensitivity to an increase in [CO_2] (normalized photosynthetic response to a small increase in [CO_2]) and found that it is independent of interspecific variation and growth environments for C3 plants and only varies with measurement temperature. This independence has the potential to simplify global extrapolation of leaf-level studies to provide a baseline prediction of a marginal increment in global carbon influx stimulated by a marginal increase in atmospheric [CO_2] (Luo *et al.* 1996). However, the actual increment in global carbon influx as stimulated by rising atmospheric [CO_2] has to account for acclimative changes in leaf, plant, canopy scales, temporal shifting of growing seasons, and biome movement (Luo & Mooney 1995).

Concluding remarks

Current understanding of plant responses to [CO_2]

Extensive research on photosynthetic acclimation to [CO_2] has been conducted. Although variable photosynthetic responses to [CO_2] are generally explainable by interactive changes in leaf biochemistry and morphology, predicting acclimation of different species in natural ecosystems is still challenging. Extrapolation of leaf-level studies to larger scales depends on improved understanding of canopy development and community dynamics in elevated [CO_2]. We are hopeful that molecular studies may improve our fundamental knowledge of photosynthetic acclimation. Even so, it has again been illustrated in the CO_2 research that knowledge regarding individual leaf photosynthetic capacity provides little ability to predict plant growth (Körner 1996; Luo *et al.* 1997). Respiratory responses to elevated [CO_2] have been examined extensively, and a large amount of experimental data is available. Although some of the observed variability in respiratory responses to elevated [CO_2] can be explained conceptually, it seems imperative to evaluate various hypotheses in quantitative frameworks. The study of nutrient uptake kinetics is in its infancy, and much remains to be learned. Generalizations in this subject area should probably not be made until more data become available. To develop a predictive understanding of carbon partitioning is among the most difficult tasks and requires close collaboration between theoreticians and experimentalists. An increased future role for modelers in plant–CO_2 research is highly desirable; they bring the ability to disassemble holistic theories into testable hypotheses. These holistic hypotheses can then be investigated by experimentalists.

Major features in plant–CO_2 research

Scientific activities have been divided in this paper into four major phases that characterize plant–CO_2 research. First, initial assessments derived from the existing knowledge base have perhaps played the most crucial role in the entire process of scientific investigation by directing experimental studies. Most of these initial assessments were biased toward growth analysis and resource balance concepts. Other schools of thought have played a lesser role in directing experimental studies. Second, experimental results have contradicted some of the initial assessments regarding responses of photosynthesis, respiration, and nutrient uptake to elevated [CO_2]. These results suggest that our knowledge base established from studies of plant responses to light and nutrients are not adequate to predict plant responses to other environmental variables. Simple extrapolation of this knowledge to large scales also appears to be unwarranted. Third, the plant–CO_2 research has involved extensive data synthesis because of variable responses of plants to elevated [CO_2]. New methods of synthesizing experimental data from different projects, such as meta-data analysis, have been introduced into plant research. Fourth, research on plant responses to elevated [CO_2] has yielded a great amount of experimental data. The data have been collected largely to confirm whether or not elevated [CO_2] increases photosynthesis, respiration, or growth rates, for example. The new information has contributed less to our predictive understanding, however.

Quest for predictive understanding

The quest for predictive understanding of plant responses to elevated [CO_2] is in nature to identify general principles underlying diverse phenomena. A few historical examples may help illuminate this kind of endeavor. Gregor Mendel crossed flowers of Garden Peas and revealed the general principle of heredity. Brouwer (1962) developed the functional balance theory as a general concept to explain carbon partitioning. This was accomplished by pruning roots and cutting leaves of corn, rye, and bean plants together with manipulation of nutrient supply. Farquhar *et al.* (1980) developed a photosynthesis model by combined theoretical analysis of rubsico kinetics and synthesis of biochemical data. This model now has wide transdisciplinary applications in plant ecophysiology, ecosystem and global biogeochemical cycling. It is a legitimate question for scientists in the plant–CO_2 research area to ask: how can we develop general biological principles underlying variable plant responses to elevated [CO_2]?

Simple experiments, like Mendel's work in genetics, are unlikely to reveal general principles in the plant-CO_2 research because CO_2 affects plants both directly and indirectly in a complex way. As discussed, rising atmospheric [CO_2] has direct effects on photosynthesis and respiration. These effects can then be translated to varying degrees into changes in whole plant growth, allocation, and morphology. The changes in turn have feedbacks on lower hierarchical levels causing, for example, changes in leaf photosynthetic capacity. Feedbacks on higher levels potentially alter community dynamics and ecosystem carbon and nutrient cycling. To develop general principles for such a complex system requires close collaborations between modelers and experimentalists. Towards that end, critical experiments guided by theoretical considerations, as Brouwer (1962) conducted on plant responses to nutrients, will be useful and effective. Combined theoretical and experimental studies of physiological mechanisms, as Farquhar *et al.* (1980) and others accomplished for photosynthesis, will become essential in developing our predictive understanding of plant responses to elevated [CO_2].

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