Plant, Cell and Environment (1999) **22,** 683–714

Tree responses to rising CO_2 in field experiments: implications for the future forest

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ABSTRACT

The need to assess the role of forests in the global cycling of carbon and how that role will change as the atmospheric concentration of CO_2 increases has spawned many experiments over a range of scales. Experiments using open-top chambers have been established at many sites to test whether the short-term responses of tree seedlings described in controlled environments would be sustained over several growing seasons under field conditions. Here we review the results of those experiments, using the framework of the interacting cycles of carbon, water and nutrients, because that is the framework of the ecosystem models that are being used to address the decades-long response of forests.

Our analysis suggests that most of what was learned in seedling studies was qualitatively correct. The evidence from field-grown trees suggests a continued and consistent stimulation of photosynthesis of about 60% for a 300 p.p.m. increase in [CO_2], and there is little evidence of the long-term loss of sensitivity to CO_2 that was suggested by earlier experiments with tree seedlings in pots. Despite the importance of respiration to a tree's carbon budget, no strong scientific consensus has yet emerged concerning the potential direct or acclimation response of woody plant respiration to CO_2 enrichment. The relative effect of CO_2 on above-ground dry mass was highly variable and greater than that indicated by most syntheses of seedling studies. Effects of CO_2 concentration on static measures of response are confounded with the acceleration of ontogeny observed in elevated CO_2. The trees in these open-top chamber experiments were in an exponential growth phase, and the large growth responses to elevated CO_2 resulted from the compound interest associated with an increasing leaf area. This effect cannot be expected to persist in a closed-canopy forest where growth potential is constrained by a steady-state leaf area index. A more robust and informative measure of tree growth in these experiments is the annual increment in wood mass per unit leaf area, which increased 27% in elevated CO_2. There is no support for the conclusion from many studies of seedlings that root-to-shoot ratio is increased by elevated CO_2; the production of fine roots may be enhanced, but it is not clear that this response would persist in a forest. Foliar nitrogen concentrations were lower in CO_2-enriched trees, but to a lesser extent than was indicated in seedling studies and only when expressed on a leaf mass basis. The prediction that leaf litter C/N ratio would increase was not supported in field experiments. Also contrasting with seedling studies, there is little evidence from the field studies that stomatal conductance is consistently affected by CO_2; however, this is a topic that demands more study.

Experiments with trees in open-top chambers under field conditions have provided data on longer-term, larger-scale responses of trees to elevated CO_2 under field conditions, confirmed some of the conclusions from previous seedling studies, and challenged other conclusions. There remain important obstacles to using these experimental results to predict forest responses to rising CO_2, but the studies are valuable nonetheless for guiding ecosystem model development and revealing the critical questions that must be addressed in new, larger-scale CO_2 experiments.

Key-words: atmospheric carbon dioxide; forests; global change; open-top chambers; trees

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TREES, FORESTS, AND CO_2: A PROBLEM OF SCALE

Presenting the experimental evidence on the response of trees to elevated CO_2 is primarily a problem of scale. The rationale for most of the experiments that have been conducted under the global change umbrella is the need to assess the role of forests in the global cycling of carbon and how that role will change as the atmosphere becomes progressively enriched with CO_2. But the scale of most experiments is not that of the forest. Even the longest-duration CO_2 experiments represent only a small fraction of the life of a tree. No matter how well an experiment with a tree seedling is conducted and how well the data are summarized, the effort is of little use if there is no framework for interpreting the results in the context of the decades-long responses of forest trees and the forest ecosystem to rising CO_2. Our challenge is to find an appropriate framework.

Experimental research on tree responses to CO_2 over the past two decades is characterized by a gradual increase in the scale and complexity of investigations. Following a time-honoured paradigm of scientific inquiry, simple experiments gave rise to new insights, new questions and new hypotheses to test. For example, experiments with tree seedlings demonstrated that growth can increase in elevated CO_2 even under nutrient-limited conditions and that photosynthesis usually increases, but that photosynthetic capacity may decline, foliar N values are reduced, and stomatal closure reduces water use. But do foliar N and photosynthetic capacity decline when the roots are not constrained by pots? Does growth continue to be stimulated by elevated CO_2 over several growing seasons under field conditions of multiple, fluctuating environmental variables? These critical questions, and many others, could be answered only in experiments in which the trees were rooted in unconstrained soil and grown in chambers large enough to accommodate several years' worth of growth. Hence, experiments using open-top chambers, an exposure technology proven in air-pollution research and adapted for elevated CO_2 studies (Rogers, Heck & Heagle 1983), were established around the world. These experiments used different species under different conditions to address different questions. Together, they provide a wealth of data and understanding about how forest trees will respond to the inexorably increasing CO_2 concentration in the atmosphere. But we will inevitably find that the data are inadequate, the experimental approaches flawed, and the prospects for understanding forest growth and metabolism in the future still unfulfilled. We should, however, take some lessons from these experiments, and form new questions, new hypotheses, to guide the next wave of larger-scale, longer-term experiments geared toward understanding forest response to global change. Larger-scale experiments, which will inevitably be more expensive and more difficult, will be most profitable if guided by testable hypotheses based on our best and most current understanding. That is the spirit in which we present this review of tree responses to elevated CO_2.

We start with a well established body of published studies, describing many of the mechanisms by which tree species respond to elevated CO_2 and the expression of those mechanisms in the growth of young seedlings. Even the reviews on tree responses are too numerous to list, but much of the progress in the field can be tracked through Oechel & Strain (1985), Eamus & Jarvis (1989), and Ceulemans & Mousseau (1994). Other reviews have focussed on specific processes such as photosynthesis (Gunderson & Wullschleger 1994), below-ground processes (Norby 1994) and nitrogen concentrations (McGuire, Melillo & Joyce 1995; Cotrufo, Ineson & Scott 1998), or have compiled the many data sets in a format useful for modellers (Wullschleger, Post & King 1995a; Curtis 1996; Wullschleger, Norby & Gunderson 1997a; Curtis & Wang 1998). Collectively, these reviews indicate that with an increase in CO_2 concentration to ≈ 650–700 p.p.m., photosynthesis and dry mass increase, and foliar nutrient concentrations decline. Meta-analysis (Curtis & Wang 1998) has indicated that field-grown trees may respond differently from trees in pots, although those conclusions were necessarily tentative because of sparse data sets. Wullschleger *et al*. (1997a) concluded that data derived from short-term experiments may at best set upper bounds on how the larger biosphere might respond to long-term increases in CO_2. As long as our ultimate interest is the long-term response of trees in a forest, then it is critical that we ensure that our projections into the future are based on the most relevant data available. The number of new field studies has increased rapidly, and it is now possible to look at them separately from the large pool of previous CO_2 studies.

Ecosystem models provide a useful organizing tool for summarizing tree responses to global change. The decades-long response of forests can be addressed only through models, and the response of the tree is necessarily a dominant factor in such models. For the models to have a flexible, predictive value, they must contain explicit descriptions of the processes on which the global change factor acts (Jarvis 1995). The mathematical expressions of CO_2 responses in these models are developed on the basis of biological principles, intuition or a qualitative assessment of experimental results. The opportunity to shape and constrain modelling efforts with experimental data is attractive, but in doing so we must be careful that the data we use really are appropriate. Most ecosystem models are organized around the intersecting cycles of carbon, water and nutrients—collectively, biogeochemical cycling. The effects of CO_2 are included primarily in five ways: effects on stomatal conductance and water-use efficiency; photosynthesis and respiration; carbon allocation and growth; plant structure and phenology; and plant nutrient concentrations (Mooney *et al*. 1999). Because of the high priority assigned to the provision of data on tree responses to elevated CO_2 that can guide models, our discussion will be organized around the cycles of carbon, nutrients, and water.

THE DATABASE OF FIELD-GROWN TREES IN ELEVATED CO_2

The primary database we draw on for this review and synthesis is summarized in Table 1. These are the experiments with tree species planted in the ground and exposed with replication to elevated CO_2 for at least one growing season. Additional field experiments have been conducted with mature trees for shorter durations (Wong & Dunin 1987), without replication (Surano *et al*. 1986), with branch bags to enrich only isolated branches (Teskey 1995), with potted seedlings (Murray *et al*. 1994; El Kohen, Venet & Mousseau 1993), or with constructed microcosms (Körner & Arnone 1992; Overdieck 1993; Hättenschwiler & Körner 1998). Such experiments certainly can be valuable and answer specific questions, and our strict criteria are not meant to denigrate other approaches. There have been many reviews and syntheses of tree responses to elevated CO_2 that encompassed the entire data set. Some of the conclusions from these reviews may be challenged because of the many confounding factors related to experimental approach. This synthesis will be based on a much more limited data set, but perhaps a data set that has fewer confounding factors.

The experiments listed in Table 1 were designed with different objectives and different limitations. Simply stated, however, an important objective of all such experiments has been to determine if the responses to elevated CO_2 measured in young seedlings in greenhouses and growth chambers are sustained over several growing seasons under field conditions (Norby, Wullschleger & Gunderson 1996). In all cases compromises were necessarily made in the size and kind of exposure system, the number of replicates, the nature of the initial plant material, and management of the soil environment. Most of the experiments were conducted in open-top chambers, which permitted the plants to be planted directly in the soil and grown under conditions near-ambient except for the introduction of additional CO_2 into the atmosphere. However, open-top chambers attenuate light and elevate temperature, unless they are specifically engineered to control temperature (Norby *et al*. 1997) or are used in an understory (Cipollini, Drake & Whigham 1993). Hence, they cannot be considered to provide true ambient conditions. Furthermore, most of these experiments were not conducted within a true forest setting, and the soil and light conditions (particularly side light) were not typical of the forest (Körner 1995). The duration of most experiments was limited by the size of the chambers. Most of the species that have been investigated are from the North Temperate or Mediterranean forests and encompass a broad range of deciduous, broadleaf evergreen, and coniferous species. Table 1 is not necessarily complete, and experiments under way or recently completed will augment this data base with different species and different interacting variables.

It is especially important to recognize that in none of these experiments was the experimental unit a forest ecosystem. In most cases, the experimental unit was an isolated tree or group of young trees. The objectives of the experiments cannot be to measure the response of forest ecosystems to elevated CO_2, but instead to measure some of the important component processes with the intention that those measurements will provide some insight to the higher-scale processes of interest. This is the perspective we must maintain as we interpret the experimental results.

CARBON CYCLING

The central focus of most of the studies in Table 1, and research on elevated CO_2 effects in general, is the carbon cycle. Will increased tree growth in elevated CO_2 cause a higher fraction of fossil-fuel-derived carbon to be stored in the biosphere, thereby slowing the increase in the atmospheric concentration and forestalling climatic change? Will increased carbon assimilation by trees enhance the flux of carbon to long-lived soil carbon pools? Carbon cycle studies begin with the biochemical processes of photosynthesis and plant respiration and increase in scale to that of whole-plant growth and allocation. At higher scales there are important interactions with nutrient and water cycles, which are critical to whole-ecosystem assessments.

Photosynthesis

The first physiologically meaningful contact between plant and atmosphere takes place at the leaf, and most subsequent effects of increasing CO_2 concentration are linked to changes in CO_2 assimilation. Because of this, a great deal of attention has focused on leaf-level photosynthetic responses to CO_2 enrichment. The undisputed response to increasing [CO_2] is an increase in photosynthesis, but a host of questions have arisen concerning longer-term effects after growth and development at a higher CO_2 concentration. The key question, relative to global change impacts on forests, is how much photosynthesis will increase as atmospheric CO_2 concentrations rise, and what bearing this will have on higher-level processes. The answer may (or may not) be complicated by interactions with other environmental gradients, and may vary within the canopy, seasonally or between species. In addition, because some very early CO_2 enrichment experiments reported complete losses of photosynthetic enhancement after extremely short exposure times (e.g. days to weeks; reviewed for crops by Cure & Acock 1986), there has been a particular focus on detecting and explaining possible decreases in photosynthetic stimulation over time.

The first part of the question, the magnitude of photosynthetic response to CO_2 that can be sustained over a season or several seasons, can be addressed by comparing assimilation at the growth CO_2 concentration, typically measured on single leaves at light saturation. In trees growing outdoors, rooted in the ground, these rates were almost always higher in elevated CO_2, regardless of the duration of the study. Photosynthesis was stimulated 40–80% in most of the studies reviewed here, although in several cases the enhancement was substantially greater (Table 2, Fig. 1a). The mean enhancement of 66% (geometric mean 63%) is greater, and the variability is less, than that reported in a previous review of tree responses (44%, Gunderson & Wullschleger 1994), at which time most available data were from experiments with potted material, and encompassed a wider range of [CO_2].

The field experiments have been useful for describing how other environmental variables could modify the photosynthetic responses to CO_2. The photosynthetic response might be reduced by nutrient deficiency (Eamus & Jarvis 1989; Tissue, Thomas & Strain 1993; Curtis *et al*. 1994; Sage 1994), or conversely, enhanced in combination with other stresses (Long 1991; Idso & Idso 1994), or unaffected by stress (Curtis & Wang 1998). Conflicting interactions between CO_2 and nitrogen concentration have also been related to secondary effects of nutrient supply on growth and sink strength (Pettersson & McDonald 1994), which could complicate the interpretation of experimental results. In three field experiments in which nutrients were deliberately manipulated (Table 2), season-long enhancements were greater in the high-nutrient treatments (Curtis *et al*. 1995; Kubiske *et al*. 1997) or increased after nutrients were added (Curtis *et al*. 1994), but photosynthesis was enhanced by 40–62% even in the lower-nutrient treatments,

Table 1. Protocol of replicated experiments in which whole trees were exposed to elevated CO_2 under field conditions

	CO_2 levels*	Interacting factors	Reps	Plants chamber^{-1}	Area (m^2)	Duration (seasons)	Initial plant material	Cultural treatments	Reference
Angiosperms *Acer rubrum* *Acer saccharum*	2	Temperature	3	20	7.1	4	1-year-old seedlings from nursery	None	Norby *et al*. 1997, Norby *et al*. 1998
Acer rubrum *Betula papyrifera* *Quercus rubra*	2	Shade	6	6	0.5	1	1-year-old seedlings from nursery	Soil boxes	Kubiske & Pregitzer 1996
Acer saccharum *Populus tremuloides*	2	Defoliation	4	18	10.2	2	4-year-old saplings from nursery; seedlings from seed	Irrigated	Roth *et al*. 1998
Alnus glutinosa	2		5	5	0.5	1	3-month-old seedlings	Mixed soil in open-bottom boxes	Vogel & Curtis 1995
Betula pendula	2		6	1	1.8	4	Seedlings grown from seed	Irrigated, fertilized	Rey & Jarvis 1997
Citrus aurantium	2		2	2	13.8–31.6	8†	Seedlings	Irrigated, fertilized	Idso & Kimball 1997
Lindera benzoin	2		3	30	12	2	Naturally occurring ramets in forest understory	None	Cipollini *et al*. 1993
Liriodendron tulipifera	3		2	5	7.1	2.5	Seedlings grown from seed	None	Norby *et al*. 1992
Mangifera indica	2		2	24		3 wet 2 dry	Grafted seedlings	Imported top soil; irrigated, fertilized	Goodfellow *et al*. 1997
Populus clones	2	Clones of different growth rate	2	15	7	2	Unrooted hardwood cuttings	Fertile horticultural soil; irrigated, fertilized	Ceulemans *et al*. 1996
Populus deltoides × *P. nigra*	2	Soil fertility	5	5	0.5	1	Cuttings	Planted in open-bottom root boxes; irrigated	Curtis *et al*. 1995
Populus grandidentata	2		4	9	0.25	1	Rooted cuttings	Homogenized subsoil in open-bottom boxes with added N; irrigated	Zak *et al*. 1993
Populus tremuloides	2	Clones with different O_3 sensitivity	3	12	?	3	3-month-old cuttings	Twice-ambient ozone; irrigated	Karnosky *et al*. 1998
Quercus alba	3		2	5	7.1	4	Seedlings grown from seed	None	Norby *et al*. 1996
Quercus ilex	2		3	2	12.6	3	Natural community	None	Scarascia-Mugnozza *et al*. 1996
Quercus sp. *Serenoa repens*	2		3		4.3	1	Natural community, resprouting after cut	None	Day *et al*. 1996

Table 1. *Continued.*

	CO_2 levels*	Interacting factors	Reps	Plants chamber^{-1}	Area (m^2)	Duration (seasons)	Initial plant material	Cultural treatments	Reference
Gymnosperms									
Picea abies	2		4	1		4	10-year-old trees in situ	None	Dvorak & Oplustilova 1997
Picea sitchensis	2	Nitrogen				2	3.5-year-old seedlings		Lee *et al.* 1998; Murray & Ceulemans 1998
Pinus eldarica	4		2	2	9	2	40-cm tall seedlings from nursery	Irrigated and fertilized	Idso & Kimball 1994
Pinus ponderosa	3	Nitrogen	3	21	11.2	6	Seed	Irrigated	Johnson *et al.* 1996
Pinus radiata	2		4	8	17.3	1	Plantlets from tissue culture	Irrigated and fertilized	Thomas *et al.* 1996
Pinus sylvestris	2	Temperature	4	1	6.2	4	20–25-year-old trees in situ	Irrigated	Wang et al. 1995
Pinus sylvestris	2	Ozone	4	1	3.2	3	30-year-old trees in situ		Kellomäki & Wang 1997
Pinus sylvestris	2		2	11	7		3-year-old seedlings	Imported forest soil; no soil amendments	Janssens *et al.* 1998
Pinus taeda	2		3	24	7.1–19.6	4	Seed	Mixed soil	Tissue *et al.* 1997
Pseudotsuga menzeisii	2	Temperature	3	14	2	3.5	2-year-old seedlings	Imported forest soil in lysimeters; irrigated	Guak *et al.* 1998
Mixtures									
Fagus sylvatica *Picea abies*	2	Wet N deposition; soil type	4	32	6.7	1†	2–3-year old seedlings and clonal cuttings	Imported forest soil	Egli & Körner 1997
Fraxinus excelsior *Quercus petraea* *Pinus sylvestris*	2		2	48	7.1	2	1-year-old seedlings from nursery	Limed	Crookshanks *et al.* 1998
Nothofagus fusca *Pinus radiata*	2		8	31	17.0	1†	Beech seedlings from forest; clonal tissue culture pines	Native beech forest soil added; irrigated and fertilized	Hogan *et al.* 1997

Reps, replications. * Levels of CO_2 included ambient (~350–360 p.p.m.), elevated (~600–700), and in some studies intermediate levels. †Exposure is continuing.

Table 2. Photosynthetic enhancement ratios (elevated/ambient, E/A) observed in field grown trees exposed to CO_2 concentrations ≈250–350 p.p.m. above ambient. Ratios in column 6 were calculated from the photosynthetic rates measured at the growth concentration, and those in columns 7 and 8 from rates measured at common C_a. Values in the table represent the mean ratio for an experiment within each species and interacting treatment. Photosynthetic rates were taken from text, tables or estimated from figures in the sources cited. Trends within a treatment (seasonal, with temperature, with decreasing water potential, etc.) are discussed in the text

Species	Additional treatment	Year*	Times†	Reference	Photosynthetic ratio (E/A)‡ Measured at: Growth [CO_2]	Ambient [CO_2]	Elevated [CO_2]
Deciduous broadleaved							
Acer rubrum	Shade	1st	1	Kubiske & Pregitzer 1996	1.63		
Acer rubrum	Sun	1st	1	Kubiske & Pregitzer 1996	1.70		
Acer rubrum	Ambient T.	1st–4th	11	Gunderson, unpublished	1.36		
Acer rubrum	Elevated T.	1st–4th	11	Gunderson, unpublished	1.51		
Acer saccharum	Ambient T.	1st–4th	15	Gunderson, unpublished	1.27		
Acer saccharum	Elevated T.	1st–4th	15	Gunderson, unpublished	1.52		
Alnus glutinosa		1st	4	Vogel & Curtis 1995	1.46		
Betula papyrifera	Sun	1st	1	Kubiske & Pregitzer 1996	1.70		
Betula papyrifera	Shade	1st	1	Kubiske & Pregitzer 1996	1.09		
Betula pendula		4th	3	Rey & Jarvis 1998	1.33	0.74	0.82
Fagus sylvatica		2nd	2	Epron *et al*. 1996		0.93	
Liriodendron tulipifera[1]		2nd–3rd	7	Gunderson *et al.* 1993	1.58		
Liriodendron tulipifera[2]		1st & 4th	2	Wullschleger *et al*. 1992b Gunderson & Wullschleger 1994	1.62		
Liriodendron tulipifera[2]	Coppice	4th	1	Gunderson & Wullschleger 1994	1.61	0.93	
Populus grandidentata		1st	8	Curtis *et al.* 1994	1.62		
Populus tremuloides	Low N	1st	n/a†	Kubiske *et al.* 1997	1.55		
Populus tremuloides	High N	1st	n/a†	Kubiske *et al.* 1997	1.98		
Populus deltoides ×*P. nigra*	High fertility	1st	7	Curtis *et al.* 1995	1.40	0.76	0.87
Populus deltoides ×*P. nigra*	Low fertility	1st	7	Curtis *et al.* 1995	1.40	0.77	0.90
P. trichocarpa ×*P. deltoides*		1st	1	Ceulemans *et al.* 1997	2.64	1.14	1.18
Populus deltoides ×*P. nigra*		1st	1	Ceulemans *et al.* 1997	2.84	1.20	1.13
Populus hybrids (2 clones)	Coppice	3rd	2	Will & Ceulemans 1997	1.60	0.97	0.97
Quercus alba[1]		2nd–3rd	7	Gunderson *et al.* 1993	1.79		
Quercus alba[2]		1st	1	Wullschleger *et al.* 1992b	1.51		
Quercus alba[2]		4th	3	Gunderson, unpublished		0.85	
Quercus rubra	Shade	1st	1	Kubiske & Pregitzer 1996	2.63		
Quercus rubra	Sun	1st	1	Kubiske & Pregitzer 1996	2.57		
Quercus rubra		2nd	5	Dixon *et al.* 1995	1.54		
Evergreen broadleaved							
Citrus aurantium		2nd–3rd	n/a†	Idso &Kimball 1991	2.22		
Eucalyptus tetrodsonta		1st–3rd	3	Eamus *et al.* 1995	1.29		
Mangifera indica		1st–3rd	9	Goodfellow *et al.* 1997	1.20		
Mangifera indica		3rd	1	Goodfellow *et al.* 1997		0.96	0.68
Nothofagus fusca		2nd	1	Hogan *et al.* 1997	1.45	0.87	0.68
Quercus ilex		1st–3rd	7	Scarascia-Mugnozza *et al.* 1996	1.69		
Conifers							
Picea alba		2nd	5	Dixon *et al.* 1995	1.43		
Pinus ponderosa		6th	1	Tissue *et al.* 1998	1.53		
Pinus radiata		2nd	1	Hogan *et al.* 1997	1.47	0.80	0.95
Pinus sylvestris	Ambient T.	4th	3	Kellomäki & Wang 1996	1.41	0.91	0.87
Pinus sylvestris	Elevated T.	4th	3	Kellomäki & Wang 1996	1.62	1.02	0.96
Pinus taeda		1st–2nd 3rd–4th	8	Tissue, Thomas & Strain 1996 Tissue *et al.* 1997	1.73		

*Measurements spanned these years or growing seasons after enrichment began. †Number of times photosynthesis was measured, i.e., number of reported values contributing to the means listed; n/a indicates more than once, exact number not stated. ‡E/A: rate in elevated-CO_2 leaves/ rate in ambient-CO_2 leaves, measured at the concentrations indicated [1,2] indicate two separate experiments with the same species.

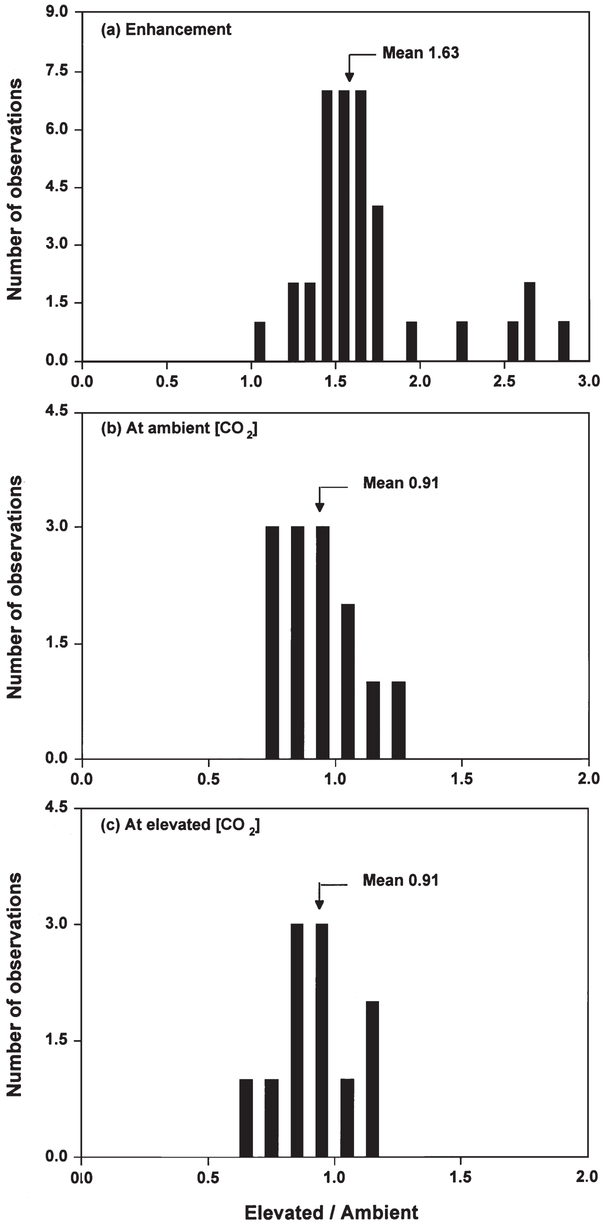

Figure 1. Frequency distribution for the relative photosynthetic responses of field-grown trees under CO_2 enrichment compared to those at ambient [CO_2]. Frequency indicates the number of observations (see Table 2) within each ratio interval for (a) leaves measured at their respective growth [CO_2], (b) leaves measured at ambient [CO_2] concentrations regardless of growth [CO_2], and (c) leaves measured at a common elevated [CO_2].

and there was no evidence of a nitrogen reallocation from ribulose bisphosphate carboxylase/oxygenase (rubisco) to other photosynthetic systems (Curtis *et al*. 1995). In a fourth study (Tissue, Griffin & Ball 1998), annual soil nitrogen fertilization had no significant effect on photosynthetic parameters.

Under some circumstances, responses to CO_2 might be reduced if water deficits are severe enough to limit photosynthetic enzymatic activity, but responses are more likely to be enhanced if elevated [CO_2] reduces the importance of drought-induced stomatal limitation (Chaves & Pereira 1992). Two experiments with mature trees, in which the response to CO_2 enrichment and changes in leaf water potential were tracked during natural droughts, support the latter hypothesis. The relative photosynthetic stimulation increased to 100% enhancement at water potentials of – 4·5 MPa (Scarascia-Mugnozza *et al*. 1996), particularly at elevated temperatures (Kellomäki & Wang 1996). Enhancement was likewise greater during drought for *Picea abies* saplings in an unreplicated open-top chamber experiment, although the four *Quercus rubra* saplings in the same chamber showed the opposite response (Dixon, LeThiec & Garrec 1995). Goodfellow, Eamus & Duff (1997) reported greater impacts of CO_2 enrichment during the tropical dry season when stomatal conductance was low, and leaf water potential was maintained.

Many of the differences in CO_2 effects within studies and perhaps between studies can be explained by temperature differences. As discussed by Long (1991), the relative affinity of rubisco for CO_2 decreases markedly with increasing temperature, but elevated CO_2 concentrations increase the competitive inhibition of oxygenation such that the relative stimulation of assimilation by elevated CO_2 increases with temperature, and the temperature optimum for assimilation increases with increasing [CO_2]. Experiments with temperature manipulation treatments confirm this with higher CO_2 enhancement ratios for trees growing in temperatures raised 2–4 °C above the ambient chambers (Table 2; Kellomäki & Wang 1996; C. Gunderson, unpublished results). Idso *et al*. (1995) compared rates measured at leaf temperatures from 30 to 46 °C over four growing seasons. Relative stimulation by CO_2, already higher at these temperatures than at the more moderate conditions of many studies, increased with temperature, and sharply so, as assimilation rates in the ambient CO_2 trees approached zero at the highest temperatures. Temperature is also a factor in some seasonal patterns reported for CO_2 responses, for example, much of the difference in enhancement of assimilation in *Pinus taeda* in summer months (60–130% increase) versus winter months (14–44%), is explained by seasonal temperature differences (Tissue, Thomas & Strain 1997; Lewis, Tissue & Strain 1996).

Most of the results discussed above are from single healthy leaves at comparable leaf age and position, measured at light saturation and, in some cases, under idealized conditions, minimizing leaf-to-air vapour pressure difference and controlling temperature. This approach minimizes factors that might confound the interpretation of photosynthetic response per se, but does not address the question of canopy-level effects on assimilation, which will change with plant development. Pertinent experimental techniques include single-leaf measurements at multiple positions in the canopy, measurements of the entire canopy (which is difficult for larger trees), and light–response curves to estimate CO_2 effects within a closed canopy. Young saplings of both *Liriodendron tulipifera* and *Quercus alba* sustained comparably higher assimilation rates at multiple canopy positions and leaf ages (Gunderson, Norby & Wullschleger 1993), but photosynthetic enhancement in 1-year-old needles of *Pinus radiata* was lower than in current needles (31% versus 64%; Turnbull *et al*. 1998). One-year-old *Populus tremuloides* demonstrated greater photosynthetic enhancement by CO_2 in the lower half of the crown, without a change in N distribution within the canopy (Kubiske *et al*. 1997), although mid-crown leaves (only) exhibited reductions in photosynthetic capacity. Measurements in these studies, however, were made at light saturation, and in young trees without much self shading. Measurements of *Pinus eldarica* seedlings incorporated self-shading effects by use of a whole-tree cuvette (Garcia *et al*. 1994), but it is essential with such techniques to separate the CO_2 effect on photosynthesis (1·9 times higher in a short-term measurement) from the combined effects of increased canopy leaf area and higher photosynthesis (2·8 times higher). A related approach involved microcosms enclosing small stands of young *Fagus sylvatica* trees, where whole ecosystem measurements were compared to single leaf measurements via modelling procedures (Overdieck 1993).

Light attenuation within a mature forest canopy and the interactions between [CO_2] and leaf acclimation to light environment are important factors in evaluating CO_2 responses at the canopy level, but these issues are not easily addressed in open-top chambers. Single-leaf measurements of light–response curves generally reveal an increase in apparent quantum yield (Kubiske & Pregitzer 1996; Goodfellow *et al*. 1997) and a decrease in light compensation point (Kubiske & Pregitzer 1996) with CO_2 enrichment, because elevated [CO_2] inhibits photorespiration (Long & Drake 1991). A higher initial slope for assimilation versus light has also been noted at the canopy level (Garcia *et al*. 1994) for seedlings at elevated [CO_2]. Variability in leaf response to CO_2 was reported in relation to the light environment and a species' shade tolerance (Kubiske & Pregitzer 1996), and with seasonal and diel variation in irradiance (Goodfellow *et al*. 1997). In general, however, higher CO_2 concentrations should enhance carbon gain at low light levels, for example, in the lower canopy, in understory plants, and on cloudy days.

As indicated by many single and multiyear studies, sustained photosynthetic responses to elevated CO_2 (Table 2, Fig. 1a) have disproved the conjecture that days, weeks or months of exposure to CO_2 would result in a loss of most of the enhancement effect. These data do not by themselves, however, indicate whether there may have been a more subtle biochemical or physiological 'acclimation' to growth at elevated CO_2, a reduction in photosynthetic capacity at equivalent conditions, or a partial loss of enhancement with time. Results of this type have been reported in trees grown in pots, and in other types of plant material (reviewed elsewhere: Gunderson & Wullschleger 1994; Sage 1994; Drake, Gonzàlez-Meler & Long 1997). When reduced stimulation has been found, it has been postulated to arise from either end-product inhibition (i.e. down-regulation by carbohydrate accumulation) or as a result of what may be termed acclimation, a suite of biochemical and physiological adjustments considered to improve plant performance through increased efficiency in use of resources (Sage 1994). These internal changes could be extremely important if they were to have an impact on net assimilation such that photosynthetic stimulation by CO_2 was lost over time, or was much lower than predicted from short-term measurements.

Such major losses of enhancement have not been demonstrated for trees rooted in the ground. Nevertheless, there have been attempts to resolve smaller differences in foliage developed under CO_2 enrichment. A downward trend in photosynthetic enhancement through time might be revealed by repeated measurements during the course of an experiment. There was no such trend in *Acer saccharum*: in ambient temperatures the 25% enhancement on the first day of exposure (C. Gunderson, unpublished results) was almost the same as the 4-year mean (Table 2). Enhancement was higher (53%) in *Eucalyptus tetrodonta* after 2·5 years than in previous years (Eamus *et al*. 1995). Several studies report seasonal differences in sensitivity to CO_2, but these differences cannot be characterized as a general downward trend over time and were often attributed, as indicated above, to other environmental factors, e.g. moisture availability (Dixon *et al*. 1995; Scarascia-Mugnozza *et al*. 1996; Kellomäki & Wang 1996; Goodfellow *et al*. 1997) or temperature (Lewis *et al*. 1996), or to a seasonal change in source–sink balance (Rey & Jarvis 1998). In some cases, enhancement was greater at the end of a growing season, attributed to effects of N availability on late season dynamics (senescence), either from applied N (Curtis *et al*. 1994) or from symbiotic N_2 fixation (Vogel & Curtis 1995).

A second method of assessing photosynthetic capacity in trees from two CO_2 treatments has been 'reciprocal transfer', switching the CO_2 concentrations, either of the whole chamber (Goodfellow *et al*. 1997), or more commonly, of only the leaf cuvette. For the nine species-treatment combinations where these data are available (Table 2), the ratio of enriched-grown foliage to ambient (E/A) ranged from 0·68 to 1·15, for a geometric mean of 0·92 — only an 8% decrease in capacity (Table 2, Fig. 1b,c). This is in marked contrast with the 21% decline calculated from 20 studies of pot-grown tree seedlings (Gunderson & Wullschleger 1994) and more in agreement with the nonsignificant 1% decline noted for trees in pots larger than 0·5 dm^3 (Curtis & Wang 1998) and the 7% decline for a variety of species in rooting volumes > 10 dm^3 (Drake *et al*. 1997). These types of measurements are designed to represent photosynthesis at equivalent conditions, and therefore a ratio less than one purports to indicate a loss of photosynthetic capacity. However, as pointed out by Goodfellow *et al*. (1997), stomatal conductance (g_s) may remain lower in foliage grown under elevated CO_2, even at equivalent cuvette concentrations (C_a), perhaps because of reduced stomatal density (cf. Rey & Jarvis 1998). If a lower g_s reduces intercellular CO_2 concentrations (C_i) in elevated CO_2-grown foliage, as in *Mangifera indica* (Goodfellow *et al*. 1997), then E/A ratios at a common C_a would not represent differences in biochemical capacity at equivalent conditions.

Measurement at equivalent C_i can be assured with the development of A/C_i curves, that is, net assimilation measured at multiple CO_2 concentrations for which C_i are calculated based on stomatal conductance. These curves can also be used to estimate the carboxylation efficiency [V_{cmax}, the capacity of rubisco to carboxylate ribulose bisphosphate (RuBP)] and RuBP regeneration capacity mediated by electron transport (J_{max}) (Sage 1994; Lewis *et al*. 1996). Little or no difference was reported between the A/C_i curves of ambient and elevated CO_2-grown foliage in four species (*Liriodendron tulipifera* and *Quercus alba*: Gunderson *et al*. 1993; *Pinus taeda*: Ellsworth *et al*. 1995; Lewis *et al*. 1996; *Pinus sylvestris* at two temperature treatments: Kellomäki & Wang 1996). The A/C_i curves of N_2-fixing *Alnus glutinosa* were identical early in the season, but V_{cmax} was 16% higher in high-CO_2 foliage later in the season (Vogel & Curtis 1995). Reductions in the A/C_i response were seen in high-CO_2 foliage of *Populus tremuloides*, but only in the middle of three canopy positions (Kubiske *et al*. 1997). V_{cmax} was 12–20% lower in *Populus deltoides* × *P. nigra* in mid-September, but not in early August (Curtis *et al*. 1995). In contrast, elevated CO_2-grown *Betula pendula* had significantly lower A/C_i curves in August and September of the fourth year, and V_{cmax} and J_{max} were numerically lower even in June (Rey & Jarvis 1998). The reduction in V_{cmax} increased from 9% to 23% over the course of the season, which is in agreement with a consistently lower and decreasing E/A ratio at equal C_a (Table 2). An even larger reduction was seen in V_{cmax} and J_{max} (36 and 21%, respectively) of *Pinus ponderosa* in September of the sixth year of CO_2 enrichment (Tissue *et al*. 1998), although photosynthesis at the growth concentration was still stimulated 53%. In *Picea abies*, A/C_i curves were not affected in June, but in September were lower in foliage from the elevated CO_2 treatment (Marek, Kalina & Matouškova 1995). The A/C_i curves from current-year needles of *Pinus radiata* showed no differences even late in the growing season, but were lower in 1-year-old needles at that time (Turnbull *et al*. 1998).

From the range of responses obtained from A/C_i curves, (one increasing, seven no change, one decreasing only at one of three canopy positions, and five decreasing later in the season in at least some foliage), it is apparent that prolonged growth at elevated [CO_2] does not result in a consistent down-regulation of photosynthetic parameters. The pattern does suggest a potential decrease in both V_{cmax} and J_{max}, particularly late in the season, concurrent with decreases in measured rubisco content (and thus activity per unit leaf area) (Tissue *et al*. 1997, 1998; Rey & Jarvis 1998; Turnbull *et al*. 1998), although decreases in rubisco activity, measured biochemically, can occur with little effect on V_{cmax} (Lewis *et al*. 1996; Drake *et al*. 1997).

In most cases, leaf mass per unit area is higher with growth at elevated [CO_2], and, as discussed later, in many cases, leaf nitrogen concentrations decrease while starch, and, less frequently, soluble sugar concentrations increase (cf. Körner & Miglietta 1994). These changes in tissue chemistry form the basis for proposed mechanisms of acclimation based on N reallocation and feedback-driven down-regulation (Drake *et al*. 1997), but they are not necessarily indicative of either phenomenon. In fact, in many of the studies in Table 1, these changes occur without any evidence of altered photosynthetic response, and conversely, some of the changes in A/C_i curves noted above were not associated with changes in N or sugars. With respect to the N reallocation hypothesis, Drake *et al*. (1997) point out that at higher temperatures and increasing [CO_2], a leaf can sustain a substantial loss in rubisco content (which accounts for a significant fraction of foliar N) without an effect on assimilation rate. A model of *Pinus sylvestris* trees in open-top chambers indicated that crown photosynthesis increased 22–27% in elevated CO_2 with only marginal effects of the observed adjustment in leaf biochemistry (Kellomäki & Wang 1997a). Thus, although there are some consistent changes in leaf properties with growth in elevated CO_2, many of the previously reported changes in leaf biochemistry are less pronounced in trees planted in the ground and appear to have minimal impact on photosynthetic enhancement. Seasonal changes in carbohydrate status associated with the cessation of above-ground growth and a reduction in sink strength may explain some of the observations of late-season reductions in photosynthetic response (e.g. Epron, Liozon & Mousseau 1996). Nevertheless, it is important to emphasize that changes in leaf biochemistry, including seasonal declines in V_{cmax} or rubisco, do not eliminate a photosynthetic response to elevated CO_2.

All of the evidence from field-grown trees suggests a continued, and surprisingly consistent, stimulation of photosynthesis, ≈ 60% for a 300 p.p.m. increase in [CO_2]. There is, at present, little reason to expect a long-term loss of sensitivity to CO_2 as suggested by earlier pot studies of trees. Research on the response of photosynthesis to rising CO_2 will continue, of course, to extend our understanding beyond 6-year exposures and to resolve questions about seasonal changes in photosynthetic biochemistry.

Canopy structure

The carbon uptake of a tree or a forest stand cannot be calculated simply from the rates of net photosynthesis of individual leaves. These rates must be integrated over the entire canopy and over the growing season. Tree and forest models accomplish this through calculation of the light extinction within a canopy for a given leaf area index (LAI), coupled with information on the light response of photosynthesis and seasonal trends in temperature, water, and other environmental factors that influence net carbon uptake (Kellomäki & Wang 1997a). Tree growth in elevated CO_2 has the potential to alter many of these relationships. Any effect of CO_2 on maximum LAI, the seasonal development or structure of the canopy, or the single-leaf response to gradients within the canopy will change the relationship between instantaneous net carbon uptake of individual leaves and annual carbon uptake of the whole canopy.

Although canopy structure and processes are clearly critical components of tree response to increasing atmospheric CO_2, there are very few data from CO_2 enrichment studies that are relevant to our scale of interest. Consider first the central question of whether the LAI of a forest stand will be different in a high-CO_2 world. The leaf area of the seedlings and saplings grown in open-top experiments has usually increased with CO_2 enrichment. Leaf area of *Pinus taeda* was 41% greater in elevated versus ambient CO_2 after 4 years (Tissue *et al*. 1997), and it increased 8–18% in *Populus* clones (Ceulemans, Jiang & Shao 1995). An increase in CO_2 concentration resulted in a higher leaf area via an increase in flush length and number of fascicles in *P. sylvestris* (Kellomäki & Wang 1997a). Leaf area *of Citrus aurantium* trees was increased primarily because CO_2-enriched trees had 78% more leaves than trees in ambient CO_2, but average leaf size also increased by 13% (Idso, Kimball & Hendrix 1993a). The increase in leaf area of *Quercus alba* saplings in elevated CO_2 (Fig. 2) also can be attributed to increased leaf number; leaf size and shape changed little (Gregory 1996).

These observations of increased leaf area in elevated CO_2 do not indicate a specific stimulatory effect of CO_2 on leaf production. In the *Q. alba* experiment, for example, leaf area increased with CO_2 enrichment less than whole-plant mass did; hence leaf area ratio (LAR) was lower in elevated CO_2 (Fig. 2). LAR was reduced in *Pinus taeda* as well (Tissue *et al*. 1997). In a compilation of all CO_2 experiments with trees (including growth chamber experiments with seedlings in pots), LAR was on average 15% less in elevated CO_2 (Wullschleger *et al*. 1997a). Hence, we can conclude that the data from open-top chambers mostly show that larger plants had more leaf area.

Unfortunately, these observations tell us little about the potential CO_2 effect on LAI in a closed-canopy forest where LAI is constrained by nutrients, water or light. There have been no manipulative studies in which the experimental trees grew long enough to maintain a closed canopy for several years. Elevated CO_2 might be expected to increase LAI if the light-compensation point for photosynthesis is higher such that leaves are retained deeper in the canopy. Alternatively, if elevated CO_2 exacerbates nutrient constraints, LAI could be reduced. The observation that LAR is reduced in CO_2-enriched trees might also suggest that LAI will be reduced. The only direct measure of a CO_2 effect on LAI comes from unreplicated observations of two coppice forests near CO_2 vents in Italy, where the trees have been exposed to elevated CO_2 concentrations throughout their 35–40 years. There was no difference in LAI between the CO_2-enriched sites and nearby control sites, although LAR was lower in the CO_2-enriched sites (Hättenschwiler *et al*. 1997b).

Changes in canopy architecture could be important even if LAI is not changed, especially if the photosynthetic responses to CO_2 change with light or canopy position. Arnone & Körner (1993) suggested that changes in the vertical leaf display and crown structure might alter the red/far red ratio of light reaching understory tree seedlings,

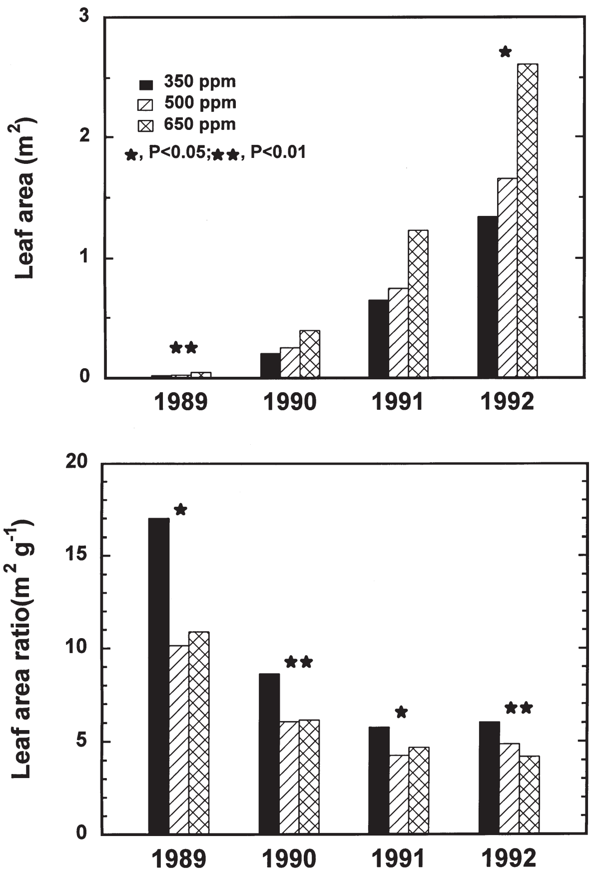

Figure 2. Leaf area and leaf area ratio (leaf area divided by above-ground plant dry mass) of *Quercus alba* trees grown in ambient and elevated CO_2 (Norby *et al*. 1995). The plants were grown in open-top chambers with two replicates for each of the three CO_2 concentrations from April 1989 until September 1992. Leaf area was determined from collections made at the end of each growing season as the leaves abscissed. Above-ground plant dry mass was estimated from height and diameter measurements in 1989–91 and was measured directly when the plants were harvested in September 1992.

thereby affecting their pattern of growth. *Pinus sylvestris* trees not only had more leaf area in elevated CO_2, but there was also a shift in foliage distribution with relatively more leaves toward the base of the crown in CO_2-enriched trees (Kellomäki & Wang 1997a). These adjustments might be important for maximizing light harvesting and minimizing self-shading (Kellomäki & Wang 1997a). Increased secondary branching in elevated CO_2 was indicated by Idso, Kimball & Allen (1991) and Ceulemans *et al*. (1995). Norby *et al*. (1996), however, saw no change in any index of canopy structure in *Quercus alba* or *Liriodendron tulipifera*. Increasing our understanding of branch morphology and crown characteristics will aid in efforts to scale results of physiological studies to the tree or stand level, as large-scale canopy function is an integration of physiological processes and structure at smaller scales.

Recent observations of large-scale carbon fluxes by the eddy covariance approach have demonstrated that canopy phenology, the duration of leaf display, is an important determinant of year-to-year variation in annual net carbon flux (Goulden *et al*. 1996). The possibility of changes in phenology in response to elevated CO_2 was an important reason to conduct experiments in the field over several growing seasons. Most of the observations of phenology in these studies, however, have been somewhat casual, and it is difficult to determine if there are any general patterns. Gunderson *et al*. (1993) quantified the timing of fall senescence in *Liriodendron tulipifera* and *Quercus alba* by measuring the decline in chlorophyll content and the time course of leaf abscission. There were no effects of elevated CO_2 in either species. One clone of *Populus* exhibited delayed bud burst in elevated CO_2, whereas another clone exhibited advanced bud set (Ceulemans *et al*. 1995). *Picea sitchensis* and *Castanea sativa*, growing in pots in field chambers, exhibited both delayed bud burst and advanced bud set (El Kohen *et al*. 1993; Murray *et al*. 1994), but there were no effects of CO_2 on the bud phenology of four other tree species (Murray & Ceulemans 1998). Elevated temperature accelerated bud burst in *Pseudotsuga menziesii*, but elevated CO_2 counteracted this effect; elevated CO_2 also decreased bud hardiness during cold hardening and dehardening (Guak *et al*. 1998). Increased temperature had important effects on the timing of spring bud break and autumn leaf senescence in *Acer saccharum* and *A. rubrum*, but there were no important or consistent effects of elevated CO_2 (Norby *et al*. 1998). There is at yet no basis for ascribing this variation in phenological response to increased CO_2 to inherent differences between species in their ability to optimize the timing of developmental events. Nevertheless, competitiveness and survival of trees can depend on the ability to avoid having periods of growth coincide with periods of subzero temperatures, and a differential response to elevated CO_2 could alter competitive relationships and stand structure.

Respiration

The supposition that trees will maintain higher rates of leaf and canopy photosynthesis when grown at elevated CO_2 appears to be supported by many field experiments. Photosynthesis is, however, only one determinant of a tree's carbon balance, and researchers have in recent years expanded their focus to consider also the respiratory loss of carbon by woody plants exposed to atmospheric CO_2 enrichment. These studies have provided periodic estimates of respiration for both seedlings and saplings grown at ambient and elevated CO_2 (Idso & Kimball 1992a; Wullschleger, Norby & Hendrix 1992b; Vogel & Curtis 1995; Curtis *et al*. 1995; Ceulemans *et al*. 1997) and have attempted to identify the sensitivity of growth and maintenance respiration to elevated CO_2 in leaves (Wullschleger & Norby 1992; Wullschleger, Norby & Gunderson 1992a; Will & Ceulemans 1997) and stems (Wullschleger, Norby & Hanson 1995b; Carey, DeLucia & Ball 1996; Dvorak & Oplustilova 1997). The energetic costs of tissue construction have similarly been examined in leaves, stems, and roots for field-grown trees exposed to elevated CO_2 (Carey *et al*. 1996; Wullschleger *et al*. 1997b), and these effects have, in potted *Pinus ponderosa* and *P. taeda* seedlings, been attributed to CO_2-induced changes in the biochemical composition of leaves (Griffin, Winner & Strain 1996b).

While these studies have advanced to some extent our understanding of the potential response of woody plant respiration to CO_2 enrichment, it is unfortunate that no strong scientific consensus has yet emerged from these observations. Single-leaf rates of respiration are often reported to be lower for field-grown trees exposed to elevated CO_2 (Idso & Kimball 1992a; Wullschleger *et al*. 1992a; Teskey 1995; Ceulemans *et al*. 1997). These effects range from a 14% suppression of respiration for needles of *Pinus taeda* in branch bags (Teskey 1995) to 60% or more for one clone of hybrid poplar (Ceulemans *et al*. 1997). There are, however, equally compelling observations that respiration is unresponsive to CO_2 enrichment (Vogel & Curtis 1995; Curtis *et al*. 1995; Ceulemans *et al*. 1997; Will & Ceulemans 1997). This inconsistency of response has been observed both within individual experiments and between studies conducted by different investigators. Ceulemans *et al*. (1997), for example, studied the respiratory response of two contrasting *Populus* hybrids grown at ambient and elevated CO_2 in open-top field chambers. Elevated CO_2 had no long-term effect on leaf respiration for the slow-growing clone Robusta (*P. deltoides* × *P. nigra*), but rates of respiration for the fast-growing clone Beaupré (*P. trichocarpa* × *P. deltoides*) were more than 60% lower at elevated CO_2 concentrations. Genotypic variation such as this, if substantiated, could be used to explore mechanisms whereby respiration changes in response to CO_2 enrichment. Unfortunately, these clonal differences were not observed in a subsequent study conducted on coppice regrowth of the original plant material (Will & Ceulemans 1997), so there is some question as to whether the clone-specific response observed by Ceulemans *et al*. (1997) represents true genetic variation or instead reflects variability attributable to experimental protocol.

There are, of course, other possibilities that could be invoked to explain the highly variable and inconsistent response of respiration to CO_2 enrichment: complications caused by expressing respiration on a leaf mass or area basis, stages of plant development, leaf age and carbohydrate composition, chamber leaks and artifacts resulting from methodology, and interacting factors such as temperature or nutrient status of the measured tissues. These confounding factors have seldom been considered in measurements of leaf respiration at either ambient or elevated CO_2, and such uncertainties are currently hindering progress in this area. Steps must be taken to resolve these issues by conducting field-based studies that systematically address the short-term direct effects and long-term acclimation effects of elevated CO_2 on leaf respiration. A direct effect is defined here as an immediate response in which rates of respiration are altered by a change in CO_2 surrounding a leaf or whole plant; it is a reversible effect and occurs within minutes of a step change in CO_2 (Drake *et al*. 1999).

An acclimation effect, by comparison, occurs when rates of respiration for trees grown in elevated CO_2 differ from those grown in ambient CO_2, with the stipulation that all measurements are made at a common CO_2 partial pressure. This latter definition implies that the acclimation effect is persistent and thus reflects an intrinsic change in tissue chemistry (e.g. N or protein content) or in some whole-plant process (e.g. growth or biomass allocation) that is subsequently reflected in measurements of respiration.

The utility of separating direct from acclimation effects has been nicely demonstrated in the branch-bag studies of Teskey (1995) and in the whole-shoot investigations of Griffin, Ball & Strain (1996a). Each of these studies observed that short-term increases in CO_2 could elicit an immediate and apparently reversible suppression of respiration. This direct effect ranged from a 6–14% suppression of respiration as [CO_2] surrounding branches of 21-year-old *Pinus taeda* was raised from ambient to ambient + 330 p.p.m. (Teskey 1995) and from a 3–13% inhibition of respiration as [CO_2] was increased from 350 to 700 p.p.m. around whole-shoots of *Pinus ponderosa* seedlings (Griffin *et al*. 1996a). Although this latter study was conducted on potted seedlings, it nonetheless illustrates an experimental approach whereby the direct and acclimation effects of elevated CO_2 can be separately addressed. This is an important consideration, as Griffin *et al*. (1996a) demonstrated that the magnitude of a direct suppression of needle respiration was correlated in *P. ponderosa* with longer-term changes in tissue C/N ratios; the direct effect of elevated CO_2 on respiration was greatest in shoots with a higher C/N ratio. These findings are particularly relevant given the often reported observation that leaf [N] is lower in woody plants exposed to long-term CO_2 enrichment (Curtis & Wang 1998). Thus, barring unforeseen changes in leaf carbon content, a decrease in tissue C/N ratios may strengthen any direct response of leaf respiration to elevated CO_2 concentration.

A mechanistic explanation and a series of testable hypotheses are urgently needed for the direct and, to a lesser extent, the acclimation effects of elevated CO_2 on respiration. It is likely that without such an explanation future measurements of leaf respiration at ambient and elevated CO_2 will be viewed cautiously. Once a cause-and-effect relationship is proposed, however, there will still be a critical need to integrate this information within the context of whole-tree responses to CO_2 enrichment. Wang, Rey & Jarvis (1998) conducted such a prototype analysis for young *Betula pendula* trees and not only considered the effects of elevated CO_2 on biomass growth, but integrated this information with known or suspected effects of atmospheric CO_2 on photosynthesis and tissue-specific rates of respiration. Trees in their fourth year of growth at elevated CO_2 were 48% larger than those grown at ambient CO_2, and during the growing season trees in the ambient and elevated CO_2 treatments increased their biomass by 4–5-fold. The annual loss of carbon (g C tree^{-1} year^{-1}) for all plant tissues combined (leaves, stems, and roots) was about equally divided between growth (45%) and maintenance (55%) respiration, and accounted for 31–38% of the total CO_2 assimilated in gross photosynthesis (Fig. 3). One surprising finding from this analysis was that a 23% reduction in leaf respiration in elevated CO_2 had little impact on the overall carbon budget of these rapidly growing trees (Wang *et al*. 1998). However, if Wang *et al*. (1998) assumed that both growth and maintenance respiration were reduced in elevated CO_2, then CO_2-enriched trees were simulated to produce and maintain ≈ 60% more leaf biomass (and 43% more leaf area) per tree with an additional respiratory cost of less than 10% (332 versus 361 g C tree^{-1} year^{-1}). A similar conclusion was reached by Norby *et al*. (unpublished results) in their carbon budget analysis of *Quercus alba* where CO_2-induced reductions in growth and maintenance respiration enabled trees at elevated CO_2 to produce and maintain throughout the season more than 90% more leaf biomass at an additional respiratory cost of less than 15% (160 versus 181 g C tree^{-1} year^{-1}). These analyses suggest that while the effects of elevated CO_2 on leaf growth and maintenance respiration may play only a limited role in whole-plant carbon budgets, these effects could nonetheless be of some 'local' significance to the carbon balance of tree canopies.

The carbon budget analysis of Wang *et al*. (1998) admittedly lacks explicit treatment of root turnover and the energy costs of carbohydrate translocation and nutrient uptake, although these issues are critical unknowns for the carbon balance of CO_2-enriched trees. Wang *et al*. (1998) emphasized that much uncertainty surrounds the large respiratory losses associated with fine-root production and growth of

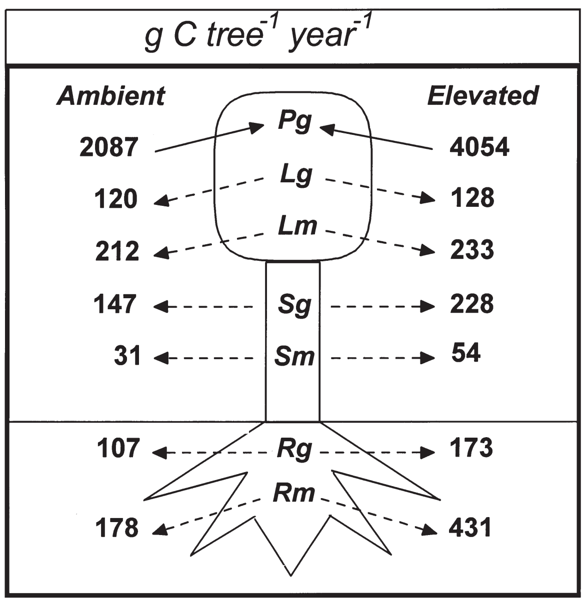

Figure 3. Annual carbon fluxes (g C tree^{-1} year^{-1}) for young birch trees during their fourth year of growth at ambient and elevated CO_2 concentration. P_g, gross photosynthesis; *L*, *S* and *R* designate leaves, woody stems and roots; the subscripts $_g$ and $_m$ designate either growth or maintenance respiration. Data were adapted from Table 6 of Wang *et al*. (1998) with the permission of Y.-P. Wang.

the root-associated mycorrhiza at ambient and elevated CO_2 conditions. These topics have received little attention in field-grown trees. Pregitzer *et al*. (1995) suggested that the respiratory costs associated with fine-root turnover (growth and maintenance costs) may account for at least a portion of the carbon that is otherwise missing from comparisons of rates of photosynthesis and estimates of net assimilation made by destructively harvesting plants. At a more refined scale, there was a small but significant reduction in specific respiration rates of fine roots of *Fraxinus excelsior*, *Quercus petraea*, and *Pinus sylvestris* in elevated CO_2 (Crookshanks, Taylor & Broadmeadow 1998). Further uncertainty surrounds the respiratory costs of nutrient uptake in trees exposed to elevated CO_2 conditions. This point was emphasized by BassiriRad *et al*. (1996), who reported that the differential response of root uptake kinetics for NH_4^+ and NO_3^- in field-grown *Pinus taeda* may have important implications for the energy requirements of nutrient acquisition by future forests. Finally, respiration is more than a process whereby carbon is lost from terrestrial vegetation; it provides carbon skeletons and energy for biosynthesis and maintenance of existing biomass, and contributes fundamentally to plant vigour. Studies that focus on the potential effects of elevated CO_2 on respiration must therefore consider also the significance of respiration for forest health and productivity.

Above-ground growth

Above-ground growth is perhaps the most obvious manifestation of the effect of CO_2 on trees in many experiments. It would also appear to be the most important and relevant measure for projecting the response of forests to global change, for it is through growth and standing biomass that the health and functioning of a forest ecosystem is first evaluated. Above-ground growth is relatively easy to measure in comparison to root growth or the more subtle changes in gas exchange or biochemical constituents. Nevertheless, there has been a wide range of responses of tree growth reported from field experiments (Table 3), and a great deal of uncertainty on how to apply the results to the larger questions at hand.

The variety of results was apparent from the first two reports from field experiments on tree growth response to elevated CO_2. *Citrus aurantium* trees were reported to have more than doubled in size in response to CO_2 enrichment (Idso & Kimball 1992a), and that size advantage has continued for 7 years (Idso & Kimball 1997). But *Liriodendron tulipifera* trees, grown for 2·5 growing seasons in elevated CO_2, had only 27% more dry mass than trees grown in ambient CO_2, an increment that was not statistically significant (Norby *et al*. 1992). Subsequent reports have shown intermediate responses. Additional experiments in which there was no significant growth response to CO_2 are known to exist but have not been published in detail (Karnosky *et al*. 1998; D. Olszyk, personal communication). This wide range in response immediately gives rise to numerous questions: Why do the results vary? What is the 'average' response? Is there any meaning to an 'average' response? And perhaps most important, what are the implications of these results for forest response?

Table 3. CO_2 enrichment ratio (E/A) of above-ground dry mass of trees grown in elevated CO_2 compared to trees grown in ambient CO_2 in field experiments

Species and interacting treatment	Growing seasons (no.)	E/A of above-ground woody dry mass	Reference
Acer saccharum/*A. rubrum*	4		Norby *et al.* 1997,1998
Ambient temperature		1.10	
Elevated temperature		1.73	
Betula pendula	4	1.55	Rey & Jarvis 1997
Citrus aurantium	8	2.17	Idso & Kimball 1997
Fagus sylvatica	2	1.91	Mousseau *et al.* 1996
Fagus sylvatica/*Picea abies*	1		Egli & Körner 1997
Low N deposition		0.99	
High N deposition		1.13	
Liriodendron tulipifera	2.5	1.22	Norby *et al.* 1992
Pinus eldarica	2	3.90	Idso & Kimball 1994
Pinus ponderosa	3		Walker *et al.* 1997
Low N		1.73	
Medium N		1.54	
High N		1.71	
Pinus taeda	4	1.90	Tissue *et al.* 1997
Populus deltoides × *P. nigra*	1		Pregitzer *et al.* 1995
Low N		1.19	
High N		1.45	
Populus hybrids	2		Ceulemans *et al.* 1996
P. deltoides × *P. nigra*		1.44	
P. trichocarpa × *P. deltoides*		1.73	
Populus grandidentata	1	1.06	Zak *et al.* 1993
Quercus alba	4	2.52	Norby *et al.* 1995

The simple arithmetic mean of the enrichment response for above-ground woody dry mass of the experiments in Table 3 is 1·73, the log-adjusted mean is 1·64, and the median value is 1·55. These values are higher than but still within the range of values from previous data compilations, which were dominated by seedling studies: 1·40 (Eamus & Jarvis 1989), 1·38 for conifers and 1·68 for broadleaved trees (Ceulemans & Mousseau 1994), 1·40 (Poorter, Roumet & Campbell 1996), 1·30 (Wullschleger *et al*. 1997a), and 1·29 (Curtis & Wang 1998). Although the summary presented here ignores the important principles of meta-analysis (Curtis & Wang 1998), no degree of sophistication in calculating a mean value will circumvent the dubious value of a mean over such a wide range for understanding the response or predicting future responses. These are our most important challenges. Can the diversity of results be explained by the growth rate or growth potential of the different species, effects of environmental interactions, or differences in experimental protocol? Is there a better expression of growth that would be more informative and useful for longer-term predictions?

One of the most commonly invoked explanations for the differences in response illustrated in Table 3 (as well as for differences in photosynthesis, allocation, or almost any other measured response to elevated CO_2) is that species respond differently. On the surface this statement is almost a truism — several different species have been tested and their responses to CO_2 are different — but the conclusion is not supported by rigorous analysis. Clearly, the potential effect of species is completely confounded by many other factors, including soil conditions, weather, length of growing season, duration of the experiment, plant culture, chamber conditions and biases (which we hope do not exist!) of the experimenter. Although variation between species under identical site conditions (*Liriodendron tulipifera* versus *Quercus alba*) is large, so too is the variation within a species attributable to environmental factors (N or temperature) and the variation within a genus (*Pinus*, *Populus*) in different studies. A coherent description of differential responses to CO_2 enrichment, based on species characteristics or functional groupings of species, could be a useful input for ecosystem models, and several such schemes have been proposed (Poorter *et al*. 1996). However, without a rigorous demonstration that species characteristics were responsible for differences in the observed CO_2 response in a controlled experiment, this common reliance on 'species differences' to account for disparate responses should be avoided.

Increases in atmospheric CO_2 will be accompanied by changes in temperature, precipitation, N deposition, and tropospheric ozone. Any of these factors can be expected to modify the response of trees to CO_2, and likewise, elevated CO_2 could exacerbate or ameliorate the responses to the other factors. Some of the experiments in Table 1 have addressed these critical questions. There was no effect of elevated CO_2 on stem mass of *Populus tremuloides* grown in twice-ambient ozone, which imposed a significant stress (Karnosky *et al*. 1998). Elevated CO_2 compensated for the negative effects of increased temperature in *Acer saccharum* and *A. rubrum* (Norby *et al*. 1998). There were no CO_2–temperature interactions in *Psuedotsuga menziesii* (D. Olszyk, personal communication). Interactions between CO_2 and N additions varied between experiments (Table 3), but it is questionable whether these results are a good model for interactions with deposition of N from the atmosphere (Norby 1998). These data sets from field experiments on interactions between CO_2 and other global change factors are too limited to allow general conclusions to be drawn, but this is clearly a research area that needs to be pursued. Responses to temperature increases in particular have many points of intersection with CO_2 responses and this interaction deserves more attention in future studies (Ceulemans 1997).

The largest difficulty in interpreting the data in Table 3, and a probable cause of the wide range of values, is the dominant effect of tree developmental patterns (ontogeny) on the attainment of dry matter. Tree and forest stand development must be a primary consideration in the interpretation of field experimental results and their application to longer-term predictions. In all of the experiments represented in Table 3, the trees were undergoing exponential growth for all or most of the exposure period. Larger plants have more leaf area, which increases their capacity to take up CO_2 and make more stem and leaf tissue, which further increases their capacity to take up CO_2 and grow. The effect of any factor that increases leaf area early in an experiment, such as random variation between individuals, differences in how seedlings were raised or planted, or specific effects of CO_2 enrichment, will be magnified over time by the principle of compound interest (Ceulemans & Mousseau 1994; Norby *et al*. 1996). As long as there are no constraints on leaf area production, spectacularly large CO_2 responses can occur. But in a forest stand there are always constraints to leaf area development — depending on the site, the constraint may be low nutrient availability, dry conditions, or ultimately not enough light to support the deepest leaves of a dense canopy. A CO_2 stimulation that depends on an ever-increasing leaf area index cannot be expected to be sustained, and projections that ignore this critical determinant of tree growth (Idso 1991) are certain to be false or misleading.

The large increase in final dry mass of *Quercus alba* (Norby *et al*. 1995) was shown to be a result of an early stimulation by CO_2; subsequent responses to elevated CO_2 included photosynthetic enhancement compensated by a downward adjustment in leaf area development from the expected exponential increase. The net result was a large difference in final dry mass without any increase in relative growth rate (RGR) over the last 3 years of the 4-year study. One interpretation of the growth trends in that experiment was that trees in elevated CO_2 would reach canopy closure 1 year earlier than those in ambient CO_2 (accelerated ontogeny), and at that point the relative CO_2 effect would decline. But as in other experiments, the trees were harvested while they were still in an exponential growth phase, so the projections about future responses are only speculation. Ultimately, we are interested in absolute growth rate, not relative growth, and RGR (a difficult term to apply to trees in which much of the biomass is dead) is useful only to the extent that it guides long-term predictions from experimental data.

Leaf area constraints have probably come into play in some of the longer open-top chamber studies. The group of *Pinus ponderosa* trees in chambers had a closed canopy in the sixth and final year of the experiment, and the final increase in above-ground growth was less than that shown in Table 3 (J.T. Ball, personal communication). *Citrus aurantium* trees were grown individually, so there was not mutual shading by adjacent trees, but leaf area development was nevertheless constrained by the walls of the chamber, and the relative enhancement of above-ground growth (including fruit rinds) began to decline steadily in the third year of exposure (Idso & Kimball 1997). A decline in growth response with time, as has been observed in these experiments as well as in experiments (Bazzaz, Miao & Wayne 1993) with potted tree seedlings (where the constraint is on root development), is frequently cited as evidence that CO_2 fertilization is transitory and not likely to have a long-term influence on forest productivity. Actually, however, a decline in relative enhancement of woody biomass is expected and consistent with the patterns of tree development. Long-term predictions should not be based on the biomass enrichment ratio at the end of an experiment of only several years' duration.

If the biomass enrichment ratio is not an appropriate parameter on which to base long-term predictions, is there another expression of growth that accounts for developmental patterns and could be more robust? Norby (1996) proposed a 'canopy productivity index' (CPI) to normalize growth responses to equal leaf area. It is calculated as the annual increment in stem mass per unit leaf area. A better expression might include woody root increment as well, but such data are rare, and an index is useful only if there are data to support it. The CPI was used by R. H. Waring (Waring & Schlesinger 1985) as 'growth efficiency' (although the term does not properly meet the definition of an efficiency), as an indication of a tree's responses to environmental stresses. The CPI is relevant only on an annual time step. It should not be confused with net assimilation rate (NAR), an instantaneous expression of growth that can be integrated over time under certain conditions. NAR has been a useful analytical tool in short-term CO_2 enrichment experiments (Norby & O'Neill 1989, 1991), but there rarely are sufficient data to support its use in longer-term experiments.

Considering all of the field experiments with broadleaf trees for which growth increment and leaf area data were available, the effect of CO_2 on CPI varied over a much smaller range than the CO_2 effect on final dry mass (Norby 1996). The average of the eight values was a 29 ± 7% enhancement (range 19–37%). We can extend this analysis to include several new studies, which slightly lowers the mean value and expands the range of observed values Table 4). Nevertheless, the increase in CPI is still seen to be a consistent response of trees to elevated CO_2. *Pinus taeda* is the only conifer included in Table 4. Calculating a CPI for a tree with several cohorts of leaves contributing to annual stem growth, and each cohort contributing to 2 or more years of stem growth, is computationally difficult while the leaf area is still increasing. Tissue *et al*. (1997) were able to calculate the CPI in their study because of their extensive data set on leaf area.

Table 4. Response of annual stem production per unit leaf area (canopy productivity index, CPI) of field-grown trees to elevated CO_2. Table modified from table in Norby (1996)

Species	% increase in CPI	Reference
Acer saccharum/A. rubrum		Norby *et al.* 1997,1998
Ambient temperature	11	
Elevated temperature	28	
Betula pendula	9	Rey & Jarvis 1997
		Wang *et al.* 1998
Citrus aurantium	33	Idso & Kimball 1993,
		Idso *et al.* 1993c
Fagus sylvatica	31	Mousseau *et al.* 1996
Liriodendron tulipifera	35	Norby *et al.* 1992, 1996
Populus deltoides x *P. nigra* (Eugenei)		Curtis *et al.* 1995
Low fertility	22	Pregitzer *et al.* 1995
High fertility	18	
Populus deltoides x *P. nigra* (Robusta)	37	Ceulemans *et al.* 1995, 1996
Populus trichocarpa x *P. deltoides* (Beaupré)	22	Ceulemans *et al.* 1995, 1996
Pinus taeda	27	Tissue *et al.* 1997
Quercus alba	37	Norby *et al.* 1995, 1996
Average ± SD	26 ± 10	

In each experiment the trees were planted directly in the ground and exposed in open-top chambers to CO_2 partial pressures ≈350 p.p.m. (ambient) and 650–700 p.p.m. CPIs of *L. tulipifera* and *Q. alba* were calculated by regression analysis of annual stem mass increment versus leaf area. Other calculations were based on published values of mean stem dry mass or dry mass increment (or a surrogate measure) and leaf area or relative increase in leaf area.

The value of this index is that it provides a simple, measurable CO_2 response parameter from experimental studies that might be independent of tree and stand development. Badeck *et al*. (1997) criticized its use because the CPI could be highly sensitive to differences in LAI between ambient and elevated treatments. As LAI increases, the fraction of less productive shade leaves increases, and therefore CPI should decrease even while productivity per unit ground area might still increase (Badeck *et al*. 1997). The CPI declines with age and in response to environmental stress (Waring & Schlesinger 1985); hence, its absolute value at the end of an experiment should not be extrapolated into the future. But there is no obvious reason to assume that its relative response to CO_2 will change as LAI increases, although this is clearly a conjecture that must be tested. The index is also useful because it separates structural responses to elevated CO_2, such as changes in canopy structure discussed in the previous section, from functional responses — the physiological reactions of photosynthesis, respiration, carbon allocation, and so on. Structural and functional responses can be considered separately in ecosystem or global models (Woodward, Smith & Emanuel 1995), and separating them experimentally can help to focus research toward meaningful, testable hypotheses about tree response to elevated CO_2. The observation that the CPI response to CO_2 is remarkably similar across so many very different experiments under different conditions improves the prospects for success in projecting future response to atmospheric CO_2 enrichment and belies the general statement that 'species differ in their response to CO_2'.

This analysis emphasizes the point that short-term tree growth responses cannot be extrapolated outside of the context of stand development. The very large growth responses observed in some experiments are unlikely to be sustained for many years under forest conditions. Much of the variation among experimental results can be explained by differences in leaf area development. On the basis of an analysis of growth per unit leaf area, the predicted long-term response to CO_2 (in the absence of interacting factors and environmental feedbacks) is only slightly less than that indicated by seedlings experiments: an increase of about 27% with a 300 p.p.m. increase in [CO_2]. This analysis gives rise to several questions. Is the short-term stimulation of leaf area development and tree growth an experimental artifact or an indication of an important effect of CO_2 on seedling establishment? Is the enhancement of growth per unit leaf area (or LAI at the stand scale) a robust response; that is, will this response persist after canopy closure? Alternatively, will the response to CO_2 continue to decline such that there ultimately is no difference in annual increment, and the only effect of CO_2 is the gain from the initial stimulation of growth increment? Or, will there be no gain from CO_2 at all in the end, the only effect being to shorten by several years the time over which maximum biomass is attained? These questions cannot be answered from the current database of open-top chamber experiments. Nevertheless, the observations from those experiments have enabled us to ask better questions, and they should be an important guide to interpreting long-term data sets as they become available.

Although decades-long records of response cannot yet come from any manipulative experiments, the vegetation growing in the vicinity of the surface vents of deep geothermal springs, such as those in central Italy (Miglietta *et al*. 1993), can be a useful alternative source of data on long-term responses of trees to an atmosphere enriched in CO_2. Naturally elevated CO_2 concentrations can be assumed to have occurred for hundreds of years in these areas, and the vegetation has been subject to a concentration gradient determined by distance from the vent (Miglietta *et al*. 1993). But the CO_2 springs are not ideal experimental systems (Amthor 1995) — the exposure history and dynamics are uncertain, there are no true controls, and environmental conditions may be atypical — and the data must be interpreted with caution. Hättenschwiler *et al*. (1997a) described the tree ring record of *Quercus ilex* trees at two natural CO_2 springs in Italy. The trees have been exposed continuously to high CO_2 since they were seedlings (31–36 years), and throughout that time they have been larger than equal-aged trees in adjacent sites away from the CO_2 emissions. An analysis of the relative difference in tree ring width, however, indicated that the response to CO_2 was declining with time and had disappeared by the time the trees were 25–30 years old (Hättenschwiler *et al*. 1997a). Stem basal area of trees in elevated and ambient CO_2 was reconstructed from the tree ring records, and we can analyse this record with the assumptions that basal area is a good correlate of above-ground biomass, that the relationship between basal area and biomass is the same for trees in ambient and CO_2-enriched trees, and that the relationship has been constant through time. Figure 4(a) shows the relative CO_2 stimulation of basal area as a function of tree age at the Rapolano site, and there clearly was a steep decline in response from year 3 to year 13, but the record then levelled off at about 1·26, or a 26% increase in basal area in elevated CO_2. Annual basal area increment (Fig. 4a), which is presented as a 3-year running average to smooth out large year-to-year fluctuations, was always higher in the CO_2-enriched site, except for the last several years. Starting at year 9, the slope of BAI versus age was not significantly different from zero and centered on an enrichment ratio of 1·19. The record from Laiatico (not shown) was similar except for a sharp rise in BAI only in the control site in 4 of the last 5 years. The BAI record at Rapolano is consistent with predictions from the open-top chamber experiments. The approximate doubling of growth during the earliest years was not sustained, possibly declining as LAI reached maximum values for the sites. (There is no record of leaf area development for these stands, but it is reasonable to assume that as a coppice stand, they reached their maximum LAI fairly early; S. Hättenschwiler, personal communication). Since LAI was the same at enriched and control sites (4·0 for Rapolano and 3·5 for Laiatico; Hättenschwiler *et al*. 1997a), the data support the premise that enhancement of

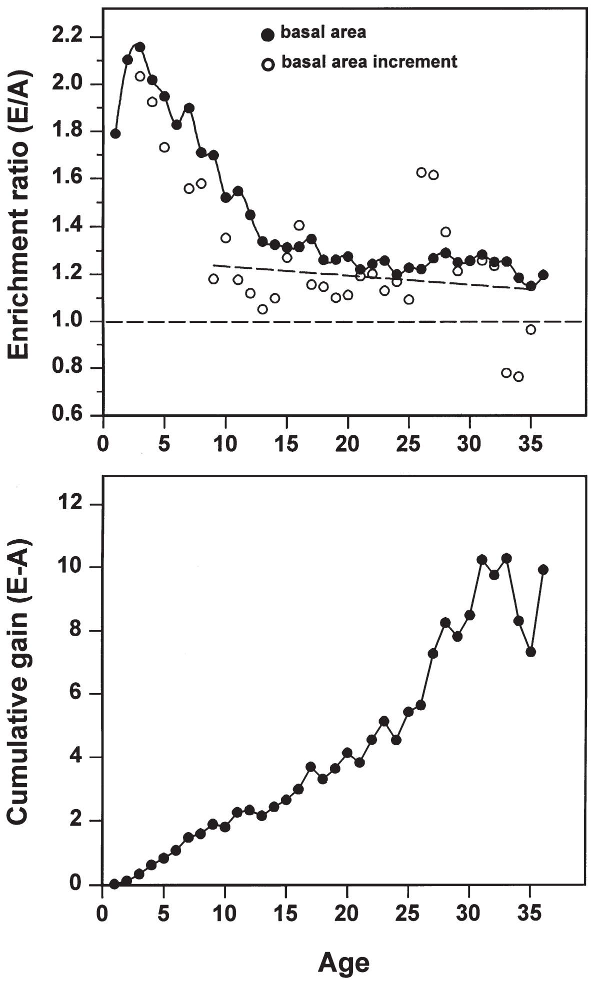

Figure 4. (a) CO_2 enrichment ratios (E/A) for basal area and basal area increment (BAI) of *Quercus ilex* trees in the vicinity of the Rapolano spring, Italy, and an adjacent control site. Basal area increments are presented as the 3-year running average. The regression line for BAI beginning at year 9 is: E/A = – 0·007 × age + 1·36; R^2 = 0·09. (b) Cumulative increase in basal area of CO_2-enriched trees compared to trees in ambient CO_2. Data courtesy of S. Hättenschwiler from experiment described in Hättenschwiler *et al*. (1997a).

annual growth per unit leaf area is a sustained response to CO_2 enrichment, albeit at somewhat less than the average value in Table 4. As a result of this sustained response, the cumulative gain in basal area (biomass) attributable to CO_2 enrichment increased with age and was not simply the result of the early stimulation of growth (Fig. 4b). Whether the unexplained decline in response in the last several years of the record at both Rapolano and Laiatico is the result of some aspect of stand development that will eventually lead to a complete loss of the CO_2 response, or a relatively short-term environmental fluctuation that will average out over time, cannot be determined. Hence, even with this much longer record of CO_2 response than has been available before, it remains difficult to predict the response in future decades. Nevertheless, these important data sets from the CO_2 springs substantially extend the observation that the stimulation of tree growth by elevated CO_2 can be sustained over time under field conditions.

Allocation below ground

The allocation of carbon to below-ground tissues, and the growth, physiological activity and death of roots that results, are key points of intersection between the carbon cycle and the water and nutrient cycles. If experiments on tree responses to elevated CO_2 are to have relevance to forest ecosystem responses, there must be consideration given to the responses of root systems and associated below-ground processes. Unfortunately, of course, root responses are most difficult to study, and the inherent limitations in experimental approaches have meant that most of the observations are single observations at the end of an experiment, which is clearly problematic for such a dynamic system. The increasing use of minirhizotron systems has enabled more frequent observations, but the data can be difficult to quantify.

Earlier studies based on the responses of potted tree seedlings generally concluded that the ratio of root mass to shoot mass increases in elevated CO_2 (Oechel & Strain 1985), although perhaps only in low nutrient conditions (Eamus & Jarvis 1989; Bazzaz 1990). There are many problems with the measurement and interpretation of root-to-shoot ratio (Stulen & den Hertog 1993; Norby 1994), and past generalizations probably have little relevance to the issues of tree responses. It is especially important to separate the response of woody root mass from that of fine roots (Norby 1994). On the one hand, an increase in woody root mass implies storage of carbon just as an increase in bole wood does, but this cannot be surmised from young seedlings in which all of the roots are small. On the other hand, changes in whole-root system mass of older saplings or trees will tell us little about fine-root mass or turnover. Because of their much higher turnover rate, a large amount of carbon may be allocated to the production of fine roots, but the standing crop of fine roots can be a small percentage of the whole root mass. Nevertheless, the production and turnover of fine roots are critical processes linking plant response to soil response. Fine roots are the mechanism for nutrient uptake from the soil, the platform for microbial activity related to nutrient turnover, and the source of much of the carbon influx to soil (Norby 1994). Hence, we shall consider the experimental evidence for woody roots and fine roots separately.

Only a few multiyear studies of trees in elevated CO_2 have ended with a complete destructive harvest, so the data set on woody root response to elevated CO_2 is small. There was no significant effect on root-to-shoot ratio in *Liriodendron tulipifera* (Norby *et al*. 1992), *Quercus alba* (Norby *et al*. 1995), *Betula pendula* (Rey & Jarvis 1997), *Pinus taeda* (Tissue *et al*. 1997), *Pinus ponderosa* (Walker *et al*. 1997), *or Fraxinus excelsior*, *Quercus petraea* and *Pinus sylvestris* (Crookshanks *et al*. 1998). Static measures of root-to-shoot ratio may mask important treatment effects on allocation that are confounded with developmental changes in allocation. Allometric analyses can be a more powerful method for examining allocation shifts. Tissue *et al*. (1997) found no effects of CO_2 on any allometric coefficients, including those describing root-shoot relations. Norby (1994) saw no effect of CO_2 on root–shoot allometry in *L. tulipifera*, but the allometric coefficient for *Q. alba* increased with increasing CO_2. Given the large root mass of many trees, such a shift could lead to underestimates of a CO_2 effect on total carbon storage based only on above-ground mass. For example, if the CPI for *B. pendula* is calculated to include the biomass increment for the stump and coarse root in addition to stem and branch production, the CO_2 effect on CPI increases from 9% (Table 4) to 21%.

In most field studies in which fine-root density (mass of roots per unit ground area) has been measured, fine roots have been shown to be especially responsive to CO_2. In the six studies represented in Fig. 5, fine-root density increased from 60 to 140% in elevated CO_2. Fine-root mass production also increased by 135% in 3-year-old *Pinus sylvestris* (Janssens *et al*. 1998), and fine root length density increased 63% in an oak-palmetto ecosystem (Day *et al*. 1996). Fine-root length production in *Fraxinus excelsior*, *Quercus petraea*, and *Pinus sylvestris* was increased by 95–240% in elevated CO_2 (Crookshanks *et al*. 1998). Although the direct impact of an increase in fine-root mass on whole-plant mass is small, it could nevertheless be important to longer-term ecosystem response. Increased fine-root density could, for example, support increased rates of nutrient uptake or stimulate increased rhizosphere activity. Although these static measures of fine root density tell us nothing about the total carbon flux to fine roots, there is a presumption that increased fine root density indicates increased turnover as well, and root turnover is a mechanism for additional carbon to enter long-lived soil pools.

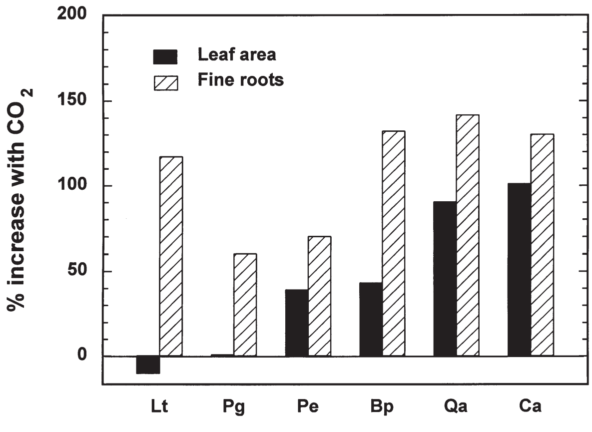

Figure 5. Relative effect of elevated CO_2 (percentage increase) on fine-root density and leaf area of trees exposed to elevated CO_2 in field experiments. Data are arranged in order of increasing effect of CO_2 on leaf area. Lt, *Liriodendron tulipifera* (Norby *et al*. 1992); Pg, *Populus grandidentata* (Zak *et al*. 1993); Pe, *Populus deltoides* × *P. nigra* (Pregitzer *et al*. 1995; Curtis *et al*. 1995); Bp, *Betula pendula* (Rey & Jarvis 1997); Qa, *Quercus alba* (Norby *et al*. 1995); Ca, *Citrus aurantium* (Idso & Kimball 1992b; Idso, Wall & Kimball 1993c).

The large percentage increase in density of small roots (< 7 mm diameter) in *Liriodendron tulipifera* relative to the nonsignificant increase in whole-plant dry mass and decrease in leaf area (Norby *et al*. 1992) apparently confirmed the suggestion from a previous growth-chamber experiment (Norby & O'Neill 1991) that an important CO_2 response in field-grown trees could be a shift from leaf production to fine-root production. Such a mechanism could imply a shift in the tree's functional balance between carbon acquisition versus water and nutrient acquisition. In all of the studies represented in Fig. 5, the stimulation of fine-root density exceeded that of leaf area, and in all but *Citrus aurantium*, the relative response of fine roots also exceeded that of the whole plant. These observations suggest that stimulation of fine-root production may be a specific response to elevated CO_2, not simply a proportionate component of larger plants. Generally, the disparity between fine-root and leaf area response was smaller in those experiments in which leaf area showed the greatest response (the right end of the *x*-axis).

As discussed previously, the increase in LAI observed when open-grown trees are exposed to elevated CO_2 cannot be expected to persist indefinitely as a tree grows into a forest canopy. Likewise, the increase in fine-root density can be assumed to saturate as the soil volume becomes fully occupied. These static measures of fine-root density and leaf area do not predict whether a sustained increase in fine root to leaf area ratio is likely. It should, then, be important to look at the effect of CO_2 on fine roots in relation to the dynamics of the response of the rest of the plants. The use of minirhizotrons has allowed such analyses. Pregitzer *et al*. (1995) found that fine-root growth and mortality were more responsive to CO_2 than was leaf growth throughout their 1-year study, and data from a single destructive harvest would have been very misleading. Tingey *et al*. (1996) related fine-root dynamics of *Pinus ponderosa* to shoot growth dynamics over three growing seasons. Fine-root area density initially increased one to two-fold in elevated CO_2, but did not continue to increase as shoot growth continued. The ratio of fine roots to leaf area declined with time, and there was no effect of CO_2 on this ratio, although N fertilization did initially decrease the ratio.

Although there may well be differences between species or sites in the relative response of fine roots, the more rigorous observations afforded by periodic observations through minirhizotrons do not support the premise that there is a specific stimulation by elevated CO_2 of fine-root density or a shift in the functional balance between roots and foliage that is sustained over time. Nevertheless, it is important that fine-root production is enhanced at least to the same extent as that of the rest of the tree. A greater emphasis on fine-root turnover, instead of static measures of fine-root density, will help to reveal the potential importance of fine-root responses to whole-system function and carbon budget. Observations on the horizontal (Thomas *et al*. 1996) and vertical distribution of fine roots and root carbon in soil through minirhizotron observation and quantification of mycorrhizal colonization (Rygiewicz *et al*. 1997; Runion *et al*. 1997) may make additional links to biogeochemical cycling.

NUTRIENT CYCLING

The importance of nutrient cycling as a control or modifier of CO_2 responses has been long recognized, and the focus has been mostly on nitrogen. Kramer (1981) questioned whether trees whose growth is limited by insufficient N in an unmanaged forest would respond to increased CO_2. Ecosystem models have strongly implicated N interactions as critical to the long-term response of forests to increasing CO_2. Models with strong links between the nutrient cycle and plant production generally predict smaller increases in production because of constraints imposed by N supply. Nitrogen limitation does not completely constrain the NPP response, however, because of internal recycling and seasonality in the limitation (McGuire *et al*. 1997). Various models differ in how N interactions are expressed, and comparison of several models indicated that these differences were the dominant factor in the prediction of the effect of CO_2 on net primary productivity (Ruimy *et al*. 1999). Despite many observations of N concentrations in CO_2-enriched trees and experimental manipulations of CO_2–N interactions, it is uncertain how N cycles will change with CO_2 enrichment and how those changes will influence the carbon cycle. The problem again is one of scale. To what extent can the nutrient budget of a tree seedling growing in a pot provide relevant data for the nutrient budget operating in a mature forest? The responses of trees with roots growing in and influencing unconstrained and unmanipulated soil, and with nutrients mobilized out of senescing leaves, stored in perennial tissue, and remobilized again in the next growing season, may come closer to the nutrient dynamics of a forest.

Foliar nitrogen concentration

The critical points of intersection between the carbon budget (as altered by elevated CO_2) and N cycling include the physiological demand of the tree for N and the annual rate of N uptake from the soil. Physiological demand can be thought of as the amount of N needed to sustain sufficient levels of enzymes for vital growth processes, such as the large requirement for N to maintain rubisco and other photosynthetic enzymes. Nitrogen shortages induced by accelerated growth in elevated CO_2 could cause lower concentrations of N in leaves, which would be expected to reduce the rate of photosynthesis (Field & Mooney 1986) but for the compensating effect of higher internal CO_2 concentration. Compilations of the data from many studies with potted seedlings have shown reductions in foliar [N] to be a common response to CO_2 enrichment (McGuire *et al*. 1995; Curtis 1996; Cotrufo *et al*. 1998). Hence, it is widely thought that enhanced photosynthesis and growth will not be sustained because of N limitations, despite the substantial evidence and analyses to the contrary (Drake *et al*. 1997).

The summary of foliar [N] responses to elevated CO_2 in field-grown trees (Table 5) shows considerable variation, from an 20% increase in [N] to a 35% decrease, with an overall average decline of 11% in gymnosperms and 14% in angiosperms. These averages are less than the average values resulting from analyses of larger data sets that include potted tree seedlings (21%, McGuire *et al*. 1995; 16%, Curtis & Wang 1998; 16%, Cotrufo *et al*. 1998). There appears to be an effect of tree age (or duration of exposure) in that the average percentage reduction is lower in seedlings more than 2 years old, which explains the larger effect reported in previous data syntheses. However, the influence of plant age varies considerably between studies. In one study on *Pinus ponderosa*, there was a decline in the effect of CO_2 effect on foliar [N] with seedling age (e.g. Johnson, Ball & Walker 1997), but in other studies there was no consistent pattern (e.g. Ceulemans *et al*. 1996; Runion *et al*. 1997; Tissue *et al*. 1997). In the truly long-term studies in the natural CO_2 springs in Italy, the effect of elevated CO_2 was negative in one species and slightly positive in another (Körner & Miglietta 1994). Only two studies reported on the effects of soil N status on response to CO_2 (Pregitzer *et al*. 1995; Johnson *et al*. 1997), and again the results were inconsistent. In the *P. ponderosa* study, there were no consistent effects of N fertility on either foliar [N] itself or the response to elevated CO_2 (Johnson *et al*. 1997), whereas in the *Populus* study, both N fertility and CO_2 strongly affected foliar [N], the CO_2 effect being more pronounced at lower N fertility (Pregitzer *et al*. 1995). When all the data are plotted together (Fig. 6), the slope of the line of foliar [N] at elevated versus ambient CO_2 (0·89) is significantly less than 1, and the intercept (4·3 mg g^{-1}) is not significantly different from 0. Thus, this model would predict that the effect of elevated CO_2 is less (in absolute terms) at lower foliar [N]. Reductions in [N] can often be explained by a dilution effect of increased structural or nonstructural carbon in CO_2-enriched leaves (increased leaf mass per unit area) (Epron *et al*. 1996). Although N concentration on a leaf area basis (g N m^{-2}) could not be determined for all of the studies in Table 5, the average decline was clearly much less than the decline in mass-based [N], especially after the first year of exposure (Table 5). In a meta-analysis of all experimental data on trees (Curtis 1996), there was no effect of CO_2 on N per unit leaf area, although mass-based [N] was reduced. This result supports the contention that the apparent decline in foliar N is more a function of the carbon economy of the leaf than a real decline in N.

Nitrogen uptake

Increased uptake of N from soil could allow N-deficient forests to respond to elevated CO_2 or could forestall impending N deficiency. Elevated CO_2 could facilitate increased uptake by stimulating root growth and soil

Table 5. Responses of foliar N concentration to elevated CO_2 in various open-top chamber studies. Entries grouped together are from a common experiment. When multiple measurements were reported, the data shown are averages across growing seasons. Nitrogen concentration on a leaf-area basis was calculated using reported values for leaf mass per unit area if necessary

Species	Group	Exposure duration	N mg g^{-1} Amb. CO_2	N mg g^{-1} Elev. CO_2	% diff.	N mg g^{-1} Amb. CO_2	N mg g^{-1} Elev. CO_2	% diff.	Reference
Gymnosperms									
Picea abies		2 years	24.8	23.9	−4				Le Thiec *et al.* 1995
Picea abies		16 months	15.8	14.0	−11				Marek *et al.* 1995
Pinus palustris		< 1 year	8.9	6.9	−23				Runion *et al.* 1997
		1–2 years	10.7	8.2	−24				
Pinus ponderosa	Low N	1 year	17.2	13.0	−24				Johnson *et al.* 1997
	Low N	2 years	17.6	16.3	−7				
	Low N	3 years	12.1	10.7	−12				
	Medium N	1 year	17.4	11.7	−33				
	Medium N	2 years	17.1	15.2	−11				
	Medium N	3 years	12.0	12.4	3				
	High N	1 year	16.0	11.9	−26				
	High N	2 years	18.9	14.8	−22				
	High N	3 years	12.7	11.9	−6				
Pinus radiata	Current needles	1 year	11.4	17.3	20	1.46	1.96	34	Hogan *et al.* 1996
Pinus radiata	Current needles	4 years	15.3	15.0	−2	1.23	1.32		Turnbull *et al.* 1998
	1-year-old needles	4 years	11.2	9.8	−12	0.90	0.80		
Pinus sylvestris	Current needles	15 months	11.6	11.3	−3	3.20	2.90		Kellomäki & Wang 1997b
	1-year-old needles	15 months	11.0	10.6	−4	3.30	3.40		
Pinus taeda		< 1 year	22.3	19.7	−12	1.08	1.08	0	Tissue *et al.* 1997
Pinus taeda		1–2 years	16.0	13.6	−15	0.81	0.88	9	Lewis *et al.* 1996
		2–4 years	16.9	14.8	−12				
Angiosperms									
Acer rubrum	Ambient temp.	15 months	25.6	19.1	−25	1.41	1.23	−13	Norby, unpublished data
	Ambient temp.	25 months	21.5	20.4	−5	1.20	1.25	4	
	Ambient temp.	36 months	23.6	21.5	−9	0.89	0.77	−13	
	Elevated temp.	15 months	20.7	20.0	−3	1.31	1.35	3	
	Elevated temp.	25 months	20.6	19.7	−4	1.20	1.21	1	
	Elevated temp.	36 months	20.1	19.3	−4	0.80	0.78	−3	
Acer saccharum	Ambient temp.	15 months	22.5	18.2	−19	1.25	1.23	−2	
	Ambient temp.	26 months	20.5	17.8	−13	0.99	0.94	−5	
	Ambient temp.	35 months	19.1	16.9	−12	0.69	0.72	4	
	Elevated temp.	15 months	21.2	20.3	−4	1.35	1.38	2	
	Elevated temp.	26 months	20.1	17.1	−15	1.12	0.98	−13	
	Elevated temp.	35 months	18.8	16.4	−13	0.74	0.70	−5	
Acer rubrum	High light	3 months	11.4	8.1	−29	0.61	0.55	−10	Kubiske & Pregitzer 1996
	Low light	3 months	22.0	18.0	−18	0.57	0.48	−16	
Betula papyrfera	High light	3 months	26.3	24.3	−8	1.99	1.45	−27	
	Low light	3 months	29.3	24.7	−16	0.88	0.75	−15	
Quercus rubra	High light	3 months	19.8	16.6	−16	2.11	1.31	−38	
	Low light	3 months	26.1	21.2	−19	0.96	0.98	2	

Table 5. *Continued.*

Species	Group	Exposure duration	N mg g^{-1} Amb. CO_2	N mg g^{-1} Elev. CO_2	% diff.	N mg g^{-1} Amb. CO_2	N mg g^{-1} Elev. CO_2	% diff.	Reference
Acer saccharum		12 months	27.2	24.8	−9				Roth *et al.* 1998
Populus tremuloides		12 months	32.8	28.0	−15				
Alnus glutinosa		3 months	30.8	25.8	−16	1.76	1.94	10	Vogel & Curtis 1995
Betula pendula		3–4 years	25.1	23.4	−6	1.26	1.72	13	Rey & Jarvis 1998
Citrus aurantium		2–4 years	22.1	18.9	−15	2.94	2.77	−6	Peñuelas *et al.* 1997
		4–6 years	21.9	19.8	−10	2.39	2.23	−7	
		6–8 years	21.0	19.9	−5	2.54	2.45	−4	
Lindera benzoin		3 months	27.5	25.9	−6	0.73	0.73	0	Cipollini *et al.* 1993
Liriodendron tulipifera		2–3 years	20.7	13.7	−34	1.37	1.04	−24	Wullschleger *et al.* 1992a
									Norby *et al.* 1992
Nothofagus fusca		1 year	19.7	17.5	−11	2.37	2.24	−5	Hogan *et al.* 1996
Populus deltoides	Low N	< 1 year	23.0	17.0	−26				Curtis *et al.* 1995
× *P. nigra*	High N	< 1 year	33.9	33.2	−2				Pregitzer *et al.* 1995
Populus deltoides		1 year	17.9	12.3	−31	1.30	0.98	−25	Ceulemans *et al.* 1996
× *P. nigra*		2 years	18.6	15.3	−18				
P. trichocarpa		1 year	15.3	11.9	−22	0.97	0.92	−5	
× *P. deltoides*		2 years	18.4	11.9	−35				
Quercus alba		29 months	14.8	12.9	−13	1.08	1.13	5	Norby, unpublished data
		40 months	16.6	14.8	−11	1.21	1.30	7	
Quercus alba		37 months	23.0	19.0	−17				Williams *et al.* 1998
Quercus ilex		> 100 years	12.2	13.2	8				Körner & Miglietti 1994
Quercus pubescens		> 100 years	19.7	16.8	−15				
Quercus rubra		2 years	28.5	27.4	−4				Le Thiec *et al.* 1995
Gymnosperms					−11.4 ± 11.8			−4.6 ± 15.3	
Angiosperms					−13.6 ± 9.3			−6.1 ± 11.6	
All species		< 1 year			−15.8 ± 8.0			−10.4 ± 15.3	
All species		1–2 years			−14.4 ± 12.3			−0.7 ± 14.8	
All species		> 2 years			−9.7 ± 7.9			−2.9 ± 9.3	

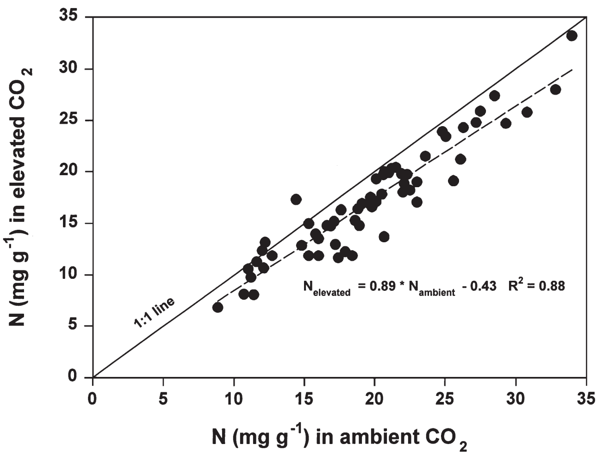

Figure 6. Nitrogen concentration (mg N g^{-1}) of leaves of trees grown in ambient CO_2 compared to leaves of trees grown in elevated CO_2. All of the data are from trees (seedlings, saplings, and mature) rooted in the ground and exposed to CO_2 under field conditions, but the data encompass a wide range of species, interactive treatments, and exposure duration as shown in Table 5.

exploration, as shown in many seedling studies (Norby, O'Neill & Luxmoore 1986; Walker *et al*. 1995), or by increasing N availability through stimulation of N mineralization (e.g. Körner & Arnone 1992; Zak *et al*. 1993) or N_2 fixation. As discussed above, fine-root density has increased in field studies, and the increase generally exceeded that of leaf area, suggesting a potential improvement in the supply of N compared to demand, especially if root uptake capacity and mycorrhization are also stimulated. But the question remains as to whether fine root density, or the ratio of fine roots to leaf area, will continue to be enhanced after the soil is fully occupied by roots.

The data on N mineralization are equivocal. Zak *et al*. (1993) showed that elevated CO_2 caused increases in labile C and N in rhizosphere soil from *Populus grandidentata* seedlings. The authors posed a conceptual model whereby elevated CO_2 creates a positive feedback on soil C and N dynamics and tree growth because of increased carbohydrate allocation and, consequently, increased N availability in the rhizosphere. Curtis *et al*. (1994) report data from later studies of *P. grandidentata* and *P. deltoides* × *P. nigra* supporting this model, at least under conditions with very low soil organic matter and N mineralization potential. On the other hand, the addition of labile organic C with low C/N ratio is known to immobilize available N (Paul & Clark 1989).

Few of the field studies in Table 1 have reported N uptake. The five data sets that we can compare (Fig. 7) are the 3-year study of *Pinus ponderosa* (Johnson *et al*. 1997), the 3-year study of *Liriodendron tulipifera* (Norby *et al*. 1996), the 4-year study of *P. taeda* (Tissue *et al*. 1997), the 1-year study of *Populus grandidentata* (Curtis *et al*. 1994), and the 4-year study of *Betula pendula* (Rey & Jarvis 1997, 1998). Larger trees with larger root systems can be assumed to take up more N. The important question is whether N uptake increases commensurately with growth. This analysis is more difficult because a decline in whole-plant N concentration is an expected consequence of accelerated ontogeny, confounding any direct influence of CO_2 on [N] (Coleman, McConnaughay & Bazzaz 1993). Only in *B. pendula* did N uptake increase with CO_2 enrichment more than plant dry mass; hence, whole-plant [N] increased slightly in *B. pendula* and declined in the other three species. Nevertheless, N uptake increased substantially in all of the species except *Liriodendron tulipifera*. Was this increase attributable to (1) increased soil exploration, (2) increased mineralization, or (3) increased free-living N_2 fixation? In the *P. ponderosa* study, we know that N mineralization was initially reduced and then unaffected by elevated CO_2. Increased soil exploration can be invoked in any of the three studies where N uptake was increased since all experienced an increase in root biomass. An important question arises, however, as to whether mature, closed-

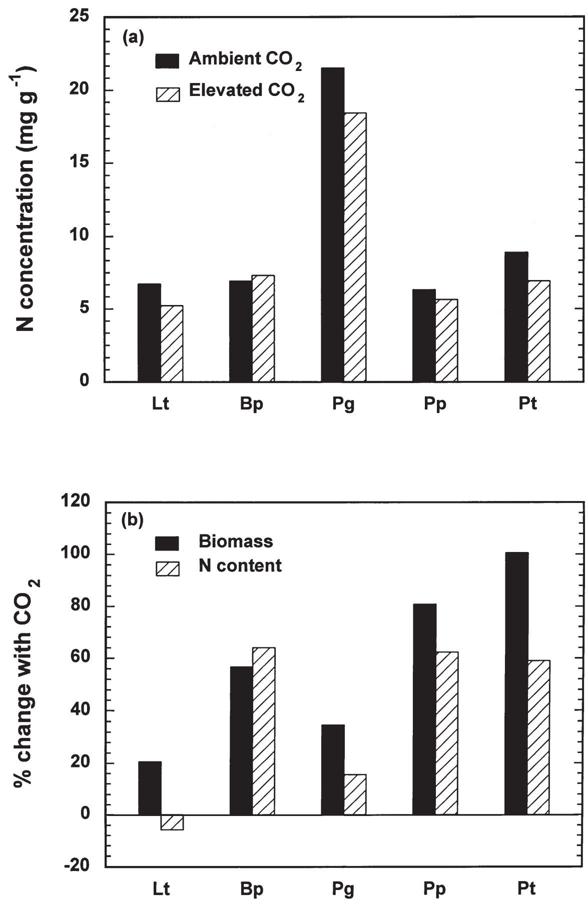

Figure 7. (a) Nitrogen concentration (mg N g^{-1}) of the whole plant (leaves, stems, and roots) of five tree species grown in ambient or elevated CO_2, and (b) the relative effect of CO_2 enrichment (percentage change from ambient) of whole-tree N content and dry mass. Lt, *Liriodendron tulipifera* (Norby *et al*. 1996); Bp, *Betula pendula* (Rey & Jarvis 1997, 1998), Pg, *Populus grandidentata* (Curtis *et al*. 1994 and personal communication); Pp, *Pinus ponderosa* (Johnson *et al*. 1997); Pt (*Pinus taeda*, Tissue *et al*. 1997).

canopy forests, where root systems have been exploring the soil for decades, can increase N uptake by increasing root biomass and soil exploration. The answer to this question is of vital importance in assessing the potential for landscape-scale forest response to elevated CO_2, as most forest ecosystems are at a closed-canopy stage.

None of these CO_2 studies has measured free-living N_2 fixation, but studies by Bormann *et al*. (1993) suggest that this can be a major source of N in *Pinus* species. The effect of elevated CO_2 on this free-living N_2 fixation constitutes a 'free lunch' for those species in which it might occur, especially with the increased below-ground inputs of carbohydrates that are often accompanied by elevated CO_2 (Zak *et al*. 1993). Similarly, enhancement by elevated CO_2 of N_2 fixation by certain lichens could add a small amount of additional N to some forest ecosystems (Norby & Sigal 1989).

Carbon–nitrogen linkages

Modelling studies have suggested that over a time scale of decades there will be significant negative feedback on tree growth because of a decline in decomposition and N cycling rates related to lower-quality litter from CO_2-enriched trees. (Strain 1985; Rastetter *et al*. 1992). A decline in N cycling could be a significant factor in mature forests where > 80% of N taken up by trees every year is recycled (Cole & Rapp 1981). Slow decomposition and forest floor build-up have been connected to progressive N deficiency with stand age in *Pseudotsuga menziesii* ecosystems (Turner 1977). For logistic reasons, there have been no studies of the effects of elevated CO_2 on N cycling in forests. Several researchers have approached the problem, however, by investigating effects on litter quality or decomposition rate, often in the laboratory. The results of these studies have been mixed and generally inconclusive. Cotrufo, Ineson & Rowland (1994) found significant effects of elevated CO_2 on litter quality, decomposition, and N availability in senescent *Fraxinus excelsior*, *Betula pubescens*, and *Acer pseudoplatanus* leaves in a laboratory study. Randlett *et al*. (1996) found no effect of elevated CO_2 on decomposition or N mineralization of leaves of *Populus deltoides* × *P. nigra*. O'Neill & Norby (1996) reported no effect of CO_2 enrichment on litter quality or decomposition (mass loss) of *Liriodendron tulipifera* leaves. Reviewing the studies published at that time, O'Neill & Norby (1996) concluded that most of the reported cases of a CO_2 effect on litter quality (i.e. on the C:N or lignin:N ratio) occurred in potted seedlings in which the litter quality was substantially different from that of trees in the field, suggesting a possible artifact of the nutrient regimen in the pot. Elevated CO_2 has not been shown consistently to reduce leaf-litter quality of field-grown trees. This conclusion has been supported by observations of oak leaf litter in the vicinity of CO_2 springs in Italy. There were no statistically significant differences in N concentration, C:N ratio, or mass loss of senescent *Quercus pubescens* leaves from a high CO_2 area compared to a reference area (Ineson & Cotrufo 1997), although some trends were noted and discussed. More extensive observations of *Q. pubescens* and *Q. cerris* leaf litter at a different CO_2 spring led Gahrooee (1998) to the conclusion that elevated CO_2 has no impact on litter chemistry of Mediterranean *Quercus* species, and consequently litter turnover is not affected. Nevertheless, the importance of this linkage between the carbon cycle and the N cycle as a regulator of long-term forest productivity makes it mandatory to consider possible effects of CO_2 in longer-term experiments.

Herbivorous insects are an important contributor to the fluxes of carbon and nitrogen in forest ecosystems. The observations of lower [N] in leaves of plants grown in elevated CO_2 led to the suggestion that the behaviour of herbivores feeding on those leaves might be affected (Lincoln, Fajer & Johnson 1993). Experiments in open-top chambers made possible more extensive field trials of herbivore interactions under field conditions. Pine sawfly (*Neodiprion lecontei*) larvae consumed more needle tissue from *Pinus taeda* trees in elevated CO_2 to compensate for the lower [N] of the foliage compared to that of ambient-grown trees (Williams, Lincoln & Thomas 1997). Larvae of the gypsy moth (*Lymantria dispar*) had reduced growth, prolonged development, and increased consumption when feeding on leaves of CO_2-enriched *Populus tremuloides* (Lindroth *et al*. 1997), related to marginally reduced [N] and increased content of condensed tannins relative to foliage in ambient CO_2. However, there was no significant effect of foliage quality on final pupal mass or female fecundity. The content of condensed tannins also increased in *Pinus palustris* grown in elevated CO_2 (Pritchard *et al*. 1997). The growth rate of early instar larvae of gypsy moth was significantly reduced when they were presented with young, expanding *Quercus alba* leaves from trees in elevated CO_2 (Williams, Lincoln & Norby 1998). The leaves had lower leaf N content but similar nonstructural carbohydrate and phenolic content compared to leaves from trees grown in ambient CO_2. The growth rate of forest tent caterpillar (*Malacosoma disstria*) larvae was not affected, nor were the consumption rates or growth rates of later instars of either insects that were fed older leaves (Williams *et al*. 1998). In a different study, however, the same species exhibited reduced growth and food processing efficiencies when fed foliage from CO_2-enriched *Acer saccharum* and *Populus tremuloides* trees relative to insects fed ambient-grown foliage (Roth *et al*. 1998). These various observations suggest the possibility that the interactions between trees and herbivorous insects could change as the atmospheric CO_2 concentration increases, but that the responses cannot be predicted simply from the effects of CO_2 on foliar [N]. Although CO_2 effects on herbivory could have important ramifications on forest health, forest productivity and nutrient cycling, there is not yet any framework for integrating these experimental observations with the population dynamics of the insect, as would be necessary for an assessment of the impact on ecosystem productivity.

WATER

Stomatal conductance in response to elevated CO_2

The short-term exposure of plants to elevated CO_2 has long been known to decrease stomatal conductance in a range of herbaceous crops and woody species. The reported magnitude of this response varies from a 40% reduction in stomatal conductance for 16 C_3 and nine C_4 crops (Morison 1985) to a 27% reduction for 20 species of woody plants grown in pots and exposed to atmospheric CO_2 enrichment (Field, Jackson & Mooney 1995). At issue, however, is whether general reductions in stomatal conductance can be expected for both broadleaved hardwoods and conifers exposed to elevated CO_2 in long-term studies conducted under field conditions. Surprisingly, recent studies indicate little or no effect of atmospheric CO_2 on stomatal conductance. There was, for example, no effect of a doubling of CO_2 on stomatal conductance in two hybrid *Populus* clones (Will & Ceulemans 1997), no effect in *Quercus alba* and *Liriodendron tulipifera* seedlings (Wullschleger *et al*. 1992b), only modest reductions (up to 15%) in *Quercus alba* and *Liriodendron tulipifera* saplings (Gunderson *et al*. 1993), a 14% reduction in *Pinus sylvestris* (Wang & Kellomäki 1997), a small to no significant effect in *P. taeda* (Ellsworth *et al*. 1995; Teskey 1995; Tissue *et al*. 1997), and only slight (10%) reductions in *Picea abies* (Dixon *et al*. 1995).

These field studies indicate that the sensitivity of stomatal conductance to elevated CO_2 is far less than that reported for a range of herbaceous species and trees in earlier growth-chamber studies. Saxe, Ellsworth & Heath (1998) suggest that the magnitude of stomatal response to elevated CO_2 is indeed smaller in trees than in crops and herbs, and that differences also exist between woody deciduous and coniferous species. According to their analysis, most conifers show a small or non-significant reduction in stomatal conductance upon exposure to elevated CO_2 in the field, while stomata of deciduous trees show a stronger response. Herbaceous crops and grasses by comparison almost always show a much larger CO_2-induced reduction in stomatal conductance than do trees. While the mechanisms that mediate this differential response of stomata among herbaceous crops, grasses, and deciduous and coniferous trees are not well understood, data collected from recent field studies emphasize that assumptions concerning the perceived sensitivity of stomatal conductance to atmospheric CO_2 enrichment must be re-evaluated. These revised assumptions will not only influence model simulations of whole-plant transpiration and stand water use (Martin 1992), but also help to refine model estimates of evapotranspiration and thereby improve our ability to predict the role of CO_2-induced biotic feedbacks in modifying regional and global climate (Henderson-Sellers, McGuffie & Gross 1995; Pollard & Thompson 1995; Sellers *et al*. 1996).

Transpiration and canopy water use

Much of our interest in the response of stomatal conductance to atmospheric CO_2 enrichment relates to a need for quantitative estimates of leaf transpiration. Few studies report rates of leaf transpiration, although one might conclude from the effects of elevated CO_2 on stomatal conductance that the response is likely to be small. Such was found by Teskey (1995) who, in addition to observing no effect of elevated CO_2 on stomatal conductance in his branch-bag studies of *Pinus taeda*, observed no effect of CO_2 on needle transpiration. Even when reductions in stomatal conductance are observed, there are reasons why these effects may not necessarily contribute to reductions in leaf-level transpiration. For example, CO_2-induced reductions in stomatal conductance and (at least temporally) transpiration should contribute to an increase in leaf temperature. This increase in leaf or needle temperature exerts negative feedback on transpiration, and rates of transpiration may therefore increase after partial stomatal closure. The complex interactions between stomatal conductance, transpiration and leaf temperature have been examined in agricultural studies (Idso *et al*. 1993b), but they have not been addressed experimentally for trees grown at elevated CO_2 concentration. This represents a major shortcoming of previous field experiments and such a deficiency should be remedied in future studies.

Field studies that document effects of elevated CO_2 on stomatal conductance and transpiration will be challenged to apply this knowledge at the scale of whole trees and canopies. This shift in focus from leaf-level determinants of transpiration to those operating at the scale of forest canopies will require that other non-stomatal processes be considered in the control of whole-tree water loss. Boundary layers that surround individual leaves and canopies are of critical importance and, especially for broadleaved species, will probably cause the reductions in the canopy transpiration caused by CO_2-induced stomatal closure to be smaller than would otherwise be inferred from single-leaf measurements. Studies to examine the response of large trees to elevated CO_2 and the implications of CO_2-induced alterations to leaf physiology and canopy biophysics are clearly needed. In this regard, free-air CO_2 enrichment (FACE) facilities and natural CO_2 springs offer unique opportunities to explore trade-offs between stomatal and boundary layer conductances in the control of whole-plant water use. Ellsworth *et al*. (1995) addressed these topics by quantifying canopy water use for *Pinus taeda* exposed briefly (8 d) to atmospheric CO_2 enrichment, as did Tognetti *et al*. (1996) for *Quercus pubescens* and *Q. ilex* at a CO_2 spring in central Italy. This latter study coupled leaf-level measurements of stomatal conductance, transpiration and leaf water potential with whole-tree estimates of sap velocity to compare water relations for trees growing in or near a natural CO_2 spring. Studies that use such a combination of leaf and whole-tree measurements should be expanded, and similar activities at existing FACE facilities and natural CO_2 springs should be encouraged.

Leaf and canopy controls of whole-tree water use will ultimately have to integrate a wide variety of CO_2-induced effects on plant growth, fine-root density and distribution and leaf area production. Enhanced root proliferation for trees grown at elevated CO_2 (Thomas *et al*. 1996; Tingey *et al*. 1997) or a preferential distribution of roots to deeper soil profiles (Day *et al*. 1996) may provide increased access to soil water. While this is an attractive hypothesis, it is doubtful that cause-and-effect relationships can easily be established. Larger plants with greater leaf area, or stands with greater LAI, are expected to offset or compensate for reductions in stomatal conductance and thereby contribute to higher rates of whole-plant water use. As previously discussed, the ability to increase leaf area per plant has been demonstrated in a number of field studies, although the response of LAI in a closed-canopy forest is unknown. The possibility of lower LAI in elevated CO_2 (Hättenschwiler & Körner 1998) can be interpreted as a morphological adjustment or mechanism of down-regulation that operates at the canopy scale, and therefore may have implications for tree water consumption.

WHERE DO WE STAND? WHERE ARE WE HEADING?

Experiments with trees will always be difficult. Trees live for a long time, grow to a large size, and exist in a complex environment of competing species and spatially and temporally variable resources. While it is clearly important to recognize the many problems in interpreting the data from small, young trees in a simplified environment (Lee & Jarvis 1995), and new larger-scale experiments will always be called for, it is also important that we search for innovative and perceptive ways of viewing the available data sets. We maintain that experiments completed with young trees in open-top chambers offer a rich source of information to guide the development of new experimental and modelling approaches.

How good were seedling studies?

A primary rationale for conducting CO_2 enrichment studies in open-top chambers was the need to determine if the responses observed in short-term studies with seedlings in greenhouses and growth chambers are sustained over several growing seasons under field conditions. This was a particularly important question with regard to trees, because so much of what describes tree growth relates to its perenniality — the storage and remobilization of carbon and nutrients from one year to the next, the exposure to many uncontrolled and constantly fluctuating environmental resources and stresses, and the large size resulting from cumulative growth over many years. The database of responses of trees to elevated CO_2 under field conditions is sufficient for us to assess, looking retrospectively, the value and robustness of conclusions from the earlier studies and, looking prospectively, the remaining questions and uncertainties that must be addressed in still larger-scale experiments.

Most of what was learned in seedling studies was qualitatively correct: photosynthesis is enhanced, N concentrations are reduced, plants are bigger at the end of the experiment. Quantitative comparisons are problematic because the range of response can be so large. Nevertheless, it seems safe to conclude that photosynthetic enhancement of tree leaves in the field is similar to (or greater than) that observed in seedling studies. Suggestions that photosynthetic enhancement would not be sustained — an important reason for conducting longer-term studies — turn out not to be valid in most cases. Down-regulation of leaf-level photosynthesis is not consistently observed in the field. Foliar [N] is reduced, at least on a leaf mass basis, but the reduction is less than was indicated in seedling studies, where artifacts of unbalanced nutrition were more likely to occur.

Attempts to compare growth responses are especially problematic, but reveal what are the important considerations for scaling. The average response of final dry mass (which is not the same as growth) of the field-grown trees is a 64% increase (log-adjusted) in elevated CO_2, which exceeds most compilations of the average response of all tree species (dominated by seedling studies). The larger apparent response in the field experiments may be a consequence of exponential growth operating over a longer period, magnifying any effect of CO_2 on growth rate. Our main objective should be to determine the effect of elevated CO_2 not on final dry mass but on growth rate — the parameter closer to annual increase in carbon storage. In the short-term studies that begin with seeds or small seedlings, differences in final dry mass should be indicative of differences in growth rates. In multiyear studies, however, growth rate can change considerably through time and in relation to plant development. An average response to CO_2 enrichment of this dynamic process, as represented by the difference in dry mass at a particular point in time, is not meaningful. Normalization of dry mass increases to a constant leaf area (the CPI) is one way to produce meaningful growth-rate data. The result, a 27% increase in CPI in elevated CO_2, is remarkably close to the most recent values for average growth increases in seedling studies (Wullschleger *et al*. 1997a; Curtis & Wang 1998). Surprisingly, the seedling response may be a better predictor of long-term tree growth response than the simple averages from the field data.

Other predictions from the seedlings studies are less robust. Stomatal conductance was almost universally thought to be reduced by elevated CO_2 (although there were exceptions), but the responses of field-grown trees are less consistent and apparently less important. Leaf-litter quality is not altered by elevated CO_2 in the field as was suggested from controlled environment studies, perhaps because leaf senescence occurs under more natural conditions in the field. Increases in root-to-shoot mass ratio were widely predicted from seedling studies, but there is little indication that allocation is affected by CO_2 in the larger, older trees used in the field experiments. However, there appears to be a specific effect of CO_2 on fine-root mass, as was predicted from a few seedling studies.

The field studies summarized here have provided no reason to challenge accepted views on tree responses to elevated CO_2. Where there are discrepancies with previous understanding, the explanation does not lie in a fundamental difference in biology, but in experimental artifacts created by artificial nutrient regimens (e.g. confined roots, fixed N capital) or in the interactions of response with normal, predictable patterns of plant development. Both of these issues were, or should have been, recognized when the seedling studies were conducted, but the implications were sometimes ignored. It also appears that the research community was too ready to accept as dogma some of the trends observed in response to elevated CO_2 (e.g. litter quality is reduced, stomatal conductance is lower). Many exceptions to these trends have been observed in controlled-environment experiments, and the lack of consistency is now more apparent, but there is no evidence that the basic biology is different.

Can we predict forest responses?

The general concurrence between seedling studies and field studies, as well as the understanding of why there are discrepancies, improves the prospects for success in predicting the responses of larger trees in forests over much longer periods. There are, to be sure, many differences between the young trees in open-top chambers and forest trees (Lee & Jarvis 1995), and it is important to recognize the limitations of the current data set. These limitations are in three major areas: the over-riding influence of tree and stand developmental patterns, the lack of an ecosystem perspective in many of the measured responses, and scaling issues.

Interpreting the responses of trees in open-top chambers or in any other system without regard to developmental patterns will inevitably lead to false conclusions. Do trees use more water in elevated CO_2 even if stomatal conductance is reduced? They do if faster growth has produced a larger canopy, but this conclusion cannot be applied to a forest stand that has reached its maximum LAI. Do trees in elevated CO_2 take up more nutrients? Most of the trees in the open-top experiments had greater nutrient contents (but not concentrations) in elevated CO_2 because their root systems were larger, but this response is not relevant to a tree in a mature stand that has fully occupied the soil. These examples are not meant to suggest that we have learned nothing useful about water use or nutrient uptake but rather to emphasize the importance of separating functional responses from structural differences that are derived from developmental differences. Interpreting a growth response to CO_2 enrichment is a more difficult challenge because growth and development are so closely linked. A common conclusion following assessment of the likelihood of a sustained, long-term stimulation is that growth enhancement will decline with time, and the only lasting benefit of elevated CO_2 is the relatively small effect deriving from faster initial growth (Jarvis 1998). The long-term effect, it is thought, will be much less than that predicted from short-term experiments. This statement is difficult to evaluate without defining what is the expected or baseline response. If the 'expected' outcome is a doubling of plant mass, as occurred in several experiments, then the response will almost certainly decline with time because those large increases are dependent on the compound interest of an increasing leaf area. If, however, the expected outcome takes acount of developmental trends and assumes that the long-term CO_2 effect is the residual (by normalizing to constant leaf area), then there is no clear indication from the experimental data that the annual growth enhancement will decline from a value of about 25–30%.

Modelling exercises have indicated that ecosystem responses to elevated CO_2 will decline with time because of ecosystem-level feedbacks, particularly through the N cycle. An important limitation of the existing database of CO_2 experiments is that the potentially important feedback mechanisms cannot be fully evaluated for forest systems. The simple reason is that forest ecosystems are not the unit of study in open-top chamber experiments. Components of forest systems — individual trees, specific soil processes — are studied, and those studies provide useful input to ecosystem models, but the integration of those components requires a larger-scale experiment. Two examples of this limitation are the lack of a true nutrient cycle in the experimental systems and the absence of competing species in most experiments.

The failure to deal with specific scaling issues is another inevitable limitation of these experimental studies. Most experiments used only two concentrations of CO_2, and those that used additional levels did not have enough statistical power to resolve departures from linearity. It is highly likely, however, that most responses to CO_2 are non-linear (Körner 1995). Hence, our response data are only semi-quantitative, and in this review we usually referred only to 'elevated' CO_2 rather than to a specific concentration. The other important scaling issue is that some important controls on large-scale system response do not pertain to the smaller scale of the field experiments described here. A prominent example is the canopy boundary layer that strongly influences forest stand transpiration but is not so important in controlling plant transpiration in open-top chambers.

Can the current data set guide new experiments?

These limitations are not listed to cast doubt on the value of our existing data set. Instead, this analysis should provide a basis for new experiments that are being conducted at a larger scale. Free-air CO_2 enrichment (FACE) studies can move beyond many of the limitations of open-top chamber experiments: the basic unit of response can be a stand or ecosystem rather than an individual plant, the components of the plant–soil nutrient cycle are fully integrated, there can be a fully developed forest canopy, and different species can compete for resources. The forest stands within FACE arrays, however, will not replicate the forest of 50–100 years in the future — the plant material, soil development and land-use history will all be different, and a few small plots of forest cannot be truly representative of an entire region or forest type. Instead, it is appropriate to think of the FACE experiments as experimental systems for testing specific, well defined hypotheses that will continue to guide the development of ecosystem models of long-term forest response. Those hypotheses should be developed based on the best understanding currently available on tree responses to elevated CO_2. Important hypotheses might include: (1) maximum LAI will increase in elevated CO_2 because shaded leaves deep in the canopy will be retained longer; (2) annual tree growth per unit LAI will continue to be enhanced by CO_2 after canopy closure; (3) fine-root density will not change in elevated CO_2 but fine-root turnover will increase; (4) down-regulation of tree growth responses will occur through long-term changes in the N cycle; (5) tree water use will be decoupled from any persistent CO_2 effects on stomatal conductance; (6) differential effects of CO_2 on competing species during establishment phase will alter long-term stand composition and productivity. There are, of course, many other possible hypotheses that are based on the current data and will increase the scale at which we understand forest response.

Not all important questions about forest response are amenable to FACE experiments, and other approaches need to be pursued simultaneously. The value of investigations in forests surrounding natural CO_2 springs has already been demonstrated (Hättenschwiler *et al*. 1997a), and despite their drawbacks (especially the problem of identifying an appropriate control site), the spring sites offer a unique opportunity to explore the long-term implications of the responses observed in shorter-term studies. Constructed microcosms offer the opportunity to manipulate species interactions and competition (Körner 1995), as long as artifacts through the below-ground environment are avoided. Environmental interactions that cannot currently be manipulated at the scale of a FACE experiment (e.g. air temperature) can still be explored in open-top chambers (Norby *et al*. 1997), although all of the scale-dependent provisos discussed in this review must be recognized. The interaction between temperature and CO_2 is an important parameter of global change, and therefore particularly relevant to explore. Many studies have shown extreme sensitivity of growth processes to rather small changes in growth temperature above or below the current ambient range (Ceulemans 1997). Open-top chamber experiments will continue to be useful in certain low-stature forest systems such as the oak-palmetto system in Florida (Day *et al*. 1996) and the natural Mediterranean macchia (Scarascia-Mugnozza *et al*. 1996), although such systems may not be very representative of more productive forests. This approach might represent a reasonable basis on which to extrapolate results obtained on a canopy of young trees (in a microcosm study, for example) to canopies of larger trees.

The influence of competition on forest stand development is well known, yet barely addressed in CO_2 research except at the scale of small constructed systems in containers. Can the knowledge we have gained at the tree level can be applied to the stand level, given the importance of competition in real forests? In the presence of competing species, the response of the individual may be highly modified and not predict the response of communities (Bazzaz 1990). Every experiment with multiple species has shown differences in response to CO_2 (Körner 1995), and it is quite likely that the response of ecosystem productivity to rising CO_2 will result primarily from changes in species composition brought on by differential species responses to CO_2 (Bazzaz 1990). Nevertheless, there is not yet any basis for summarizing differential responses of tree species to CO_2 or for predicting the effect of elevated CO_2 on the outcome of competition in a regenerating forest. The role of competition is especially important with regard to leaf area and canopy development, which we have emphasized to be a critical uncertainty that hinders our ability to extrapolate from the current data set. Microcosms containing mini-stands of trees that reach a closed canopy status at an early stage might provide a feasible way to address some of these questions (Overdieck 1993).

As the research community moves on to a new generation of experiments, several things seem to be clear. There will be closer integration between experimental studies and ecosystem model development. The new experiments will advance our understanding of forest responses at a larger and more realistic scale than has previously been possible. We will inevitably learn that some of our conclusions from the current data set are wrong, while other conclusions will be supported. We may not be able to provide definitive answers about the global forest in a constantly changing atmosphere, but if the experiments are done correctly and the results are analysed with sensitivity to the inherent regulators and constraints on forest productivity, we shall continue to deepen our understanding while refining the questions.

ACKNOWLEDGMENTS

We thank Ana Rey, Y.-P. Wang, David Olzyck, Jud Isebrands and David Tissue, who shared with us their unpublished manuscripts. Special thanks to Y.-P. Wang who kindly provided unpublished annual estimates of gross photosynthesis and modelled estimates of growth and maintenance respiration for leaves, stems and roots of young birch trees, to Stephan Hättenschwiler for sharing the data used in Fig. 4, and to Peter Curtis for nitrogen data. Research was sponsored by the Global Change Research Program of the Environmental Sciences Division, U.S. Department of Energy, under contract number DE-AC05–96OR22464 with Lockheed Martin Energy Research Corp. This work is part of the Global Change and Terrestrial Ecosystems Core Project of the International Geosphere–Biosphere Programme. Publication no. 4859.

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