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## A meta-analysis of elevated CO<sub>2</sub> effects on woody plant mass, form, and physiology

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**Abstract** Quantitative integration of the literature on the effect of elevated CO<sub>2</sub> on woody plants is important to aid our understanding of forest health in coming decades and to better predict terrestrial feedbacks on the global carbon cycle. We used meta-analytic methods to summarize and interpret more than 500 reports of effects of elevated CO<sub>2</sub> on woody plant biomass accumulation and partitioning, gas exchange, and leaf nitrogen and starch content. The CO<sub>2</sub> effect size metric we used was the log-transformed ratio of elevated compared to ambient response means weighted by the inverse of the variance of the log ratio. Variation in effect size among studies was partitioned according to the presence of interacting stress factors, length of CO<sub>2</sub> exposure, functional group status, pot size, and type of CO<sub>2</sub> exposure facility. Both total biomass ( $W_T$ ) and net CO<sub>2</sub> assimilation ( $A$ ) increased significantly at about twice ambient CO<sub>2</sub>, regardless of growth conditions. Low soil nutrient availability reduced the CO<sub>2</sub> stimulation of  $W_T$  by half, from +31% under optimal conditions to +16%, while low light increased the response to +52%. We found no significant shifts in biomass allocation under high CO<sub>2</sub>. Interacting stress factors had no effect on the magnitude of responses of  $A$  to CO<sub>2</sub>, although plants grown in growth chambers had significantly lower responses (+19%) than those grown in greenhouses or in open-top chambers (+54%). We found no consistent evidence for photosynthetic acclimation to CO<sub>2</sub> enrichment except in trees grown in pots <0.5 l (–36%) and no significant CO<sub>2</sub> effect on stomatal conductance. Both leaf dark respiration and leaf nitrogen were significantly reduced under elevated CO<sub>2</sub> (–18% and –16% respectively, data

expressed on a leaf mass basis), while leaf starch content increased significantly except in low nutrient grown gymnosperms. Our results provide robust, statistically defensible estimates of elevated CO<sub>2</sub> effect sizes against which new results may be compared or for use in forest and climate model parameterization.

**Key words** Elevated CO<sub>2</sub> · Meta-analysis · Woody plants

### Introduction

Forested ecosystems cover approximately 35% of the world's land surface and may accounted for as much as 70% of terrestrial net primary productivity (Meyer and Turner 1992; Mellilo et al. 1993). Their future prospects are of concern to many millions of people who rely on forests directly or indirectly for food, fuel, building material, and the myriad of ecological goods and services they provide. Increasing atmospheric CO<sub>2</sub> has the potential to fundamentally alter forest ecosystem functioning through effects on tree growth, resource use, and species interactions (Eamus and Jarvis 1989). Because of their prominent role in the global carbon cycle, forests may in turn affect the rate of atmospheric CO<sub>2</sub> increase (Walker and Kasting 1992). The extent and manner with which trees respond to changes in CO<sub>2</sub> concentration has thus been of interest to the forest products industry, natural resource managers, ecologists, and atmospheric scientists.

Empirical research on CO<sub>2</sub> effects in forests has proceeded along numerous lines of inquiry, but the great majority of studies share certain common features. In these experiments, the CO<sub>2</sub> treatments to which plants are exposed are typically ambient (*c.* 35 Pa) and twice ambient (*c.* 70 Pa) CO<sub>2</sub> partial pressure with additional levels occasionally included. Atmospheric CO<sub>2</sub> levels are expected to reach 70 Pa in the next 100–150 years (Houghton et al. 1990). Elevated CO<sub>2</sub> treatments are imposed as a single step change from ambient CO<sub>2</sub> levels

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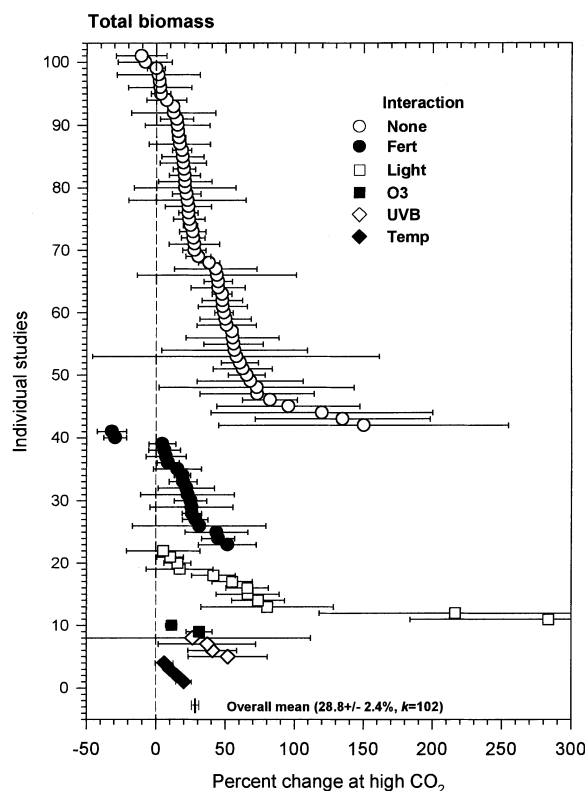
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by adding 100% CO<sub>2</sub> to the input air supply of controlled environment growth chambers (GC), greenhouses (GH) or field-based open-top chambers (OTC) (Schulze and Mooney 1994). First-year seedlings or young plants propagated from cuttings are used most often as experimental material, although occasionally mature trees or branches of trees are studied (e.g., Cipollini et al. 1993; Liu and Teskey 1995). Of considerable interest to workers studying elevated CO<sub>2</sub> has been the effect of interacting environmental variables on the magnitude of CO<sub>2</sub> responses by trees. Consequently, experiments are often set up as two-way factorial designs, with CO<sub>2</sub> crossed with another factor such as nitrogen availability or ozone level. While the specific objectives of individual researchers and the duration of their experiments vary widely, basic measures of plant growth (e.g., biomass, leaf area), physiological performance (e.g., gas exchange), and tissue composition (e.g., leaf N content) are often reported.

These common design and measurement characteristics are an advantage when attempting to integrate results across studies. Nonetheless (and not surprisingly), there is a substantial degree of variation in the magnitude of reported CO<sub>2</sub> effects on trees, ranging from significant inhibition of growth by elevated CO<sub>2</sub>, to enhancements in excess of 500% relative to ambient grown plants (McGuire et al. 1995). An important goal in reviews of this work is to partition this variation into that which can be explained by treatment effects common to groups of studies and that which is due to sampling error or other idiosyncratic effects specific to individual studies. For example, in a set of 102 measurements of total tree biomass, growth at elevated CO<sub>2</sub> resulted in an average weight gain of 29% across a range of from -31% (inhibition) to +284% (stimulation) (Fig. 1). One obvious way to partition this data set is by whether or not another factor that could affect the magnitude of the CO<sub>2</sub> response was included in the experimental design of each study. While this narrows the range of responses within groups, there remains both broad overlap in responses between groups and substantial variation within groups (Fig. 1). Further partitioning of groups might be according to factors not considered explicit treatments by the primary researchers but that could help account for this remaining variation, such as length of study, size of pots in which plants were grown, or "quality" of the science being reported (however that might be defined). One objective of such an exercise is to identify groups of studies whose combined results can lead to meaningful generalizations regarding the response parameter under study, in this case percent change in whole plant biomass.

In a traditional narrative literature review, results from those individual studies that are judged by the reviewer to be representative or otherwise noteworthy are summarized qualitatively, serving as the basis for generalization, extrapolation, or other objectives of the reviewer. Although the narrative approach has been, and will no doubt continue to be, of fundamental importance



**Fig. 1** Percent change in total (above + belowground) biomass in woody plants grown under elevated compared to ambient CO<sub>2</sub> as reported in 102 different experiments. Results are grouped according to whether plants were exposed either to no stress (*None*), low nutrient availability (*Fert*), low light levels (*Light*), high ozone (*O3*), high UVB (*UVB*) or low or high temperature (*Temp*) in addition to the CO<sub>2</sub> treatment. Mean  $\pm$  1 SE calculated from the log-transformed response ratio

in synthesizing many types of scientific research, it is inadequate for the quantitative integration of large numbers of research reports (Cooper and Rosenthal 1980). Review of the literature on elevated CO<sub>2</sub> has for some time included both narrative reviews and quantitative summaries, with the latter in some cases involving results from hundreds of published reports (e.g., Cure 1985; Idso and Idso 1994). Quantitative summaries have been important in model parameterization and in establishing benchmarks against which other work can be compared (e.g., Kimball 1983). Unfortunately, their utility has been hampered by *ad hoc* sampling and analysis methods that do not allow statistically robust hypothesis testing or comparison among groups.

Statistical methods have been developed for the quantitative integration of research results from independent experiments (Hedges and Olkin 1985; Cooper and Hedges 1994). Such formal integration, or meta-analysis, of data has been conducted extensively in the social and medical sciences (Mann 1994) and has recently been extended to ecological studies (Arnqvist and Wooster 1995). The advantage of meta-analysis over quantitative methods previously used in reviews of work on elevated CO<sub>2</sub> is the ability to place confidence limits

around effect size estimates, to discriminate statistically among subsets of the data, and to compare critically the variance within and among studies. More generally, it requires of reviewers the same rigor in sampling and analysis as is required of primary researchers.

Here, we used meta-analytic methods to summarize and interpret 508 reports of CO<sub>2</sub> effects on tree physiology and growth taken from 79 separate publications and 59 species (Appendices 1 and 2). This paper extends the work of Curtis (1996) and introduces a new meta-analytic metric, the weighted log ratio. Our review has two primary objectives: (1) to provide estimates of the magnitude and significance of elevated CO<sub>2</sub> effects on tree biomass accumulation and partitioning, gas exchange, and leaf nitrogen and starch content; and (2) to determine how experimental design factors or taxonomic affinity affects the magnitude of these CO<sub>2</sub> responses. We do not address the issue of how, or under what conditions, these results may be scaled up to predict the behavior of entire forests or biomes. As with any effort to integrate and interpret scientific information, considerable caution is advised when extrapolating beyond the range of ones data.

## Methods

### Database development

Bibliographic resources used in developing the meta-database were Strain and Cure (1986, 1994), and the *Current Advances in Plant Science* and *Current Contents* citation indices. Our literature survey was intended to be comprehensive, with all published studies conducted with woody species available through December 1995 included. We extracted information on 36 response variables, ten of which will be reported on here. Those are: total above- + below-ground biomass ( $W_T$ ), below-ground biomass ( $W_B$ ), stem biomass ( $W_S$ ), total leaf biomass ( $W_L$ ), light saturated net CO<sub>2</sub> assimilation ( $A$ ), photosynthetic acclimation or downregulation ( $A_{\text{acc}}$ ), stomatal conductance ( $g_s$ ), leaf dark respiration ( $R_d$ , expressed on a leaf mass basis), leaf starch concentration ( $St_L$ , expressed on a mass basis), and leaf nitrogen concentration ( $N_L$ , expressed on a mass basis).

For results from any given study to be included in the meta-database there was a general requirement that response means

( $\bar{X}_e$ ,  $\bar{X}_a$ ), standard deviations ( $S_e$ ,  $S_a$ ) (or standard errors), and sample sizes ( $n_e$ ,  $n_a$ ) of elevated and ambient CO<sub>2</sub> grown plants respectively be reported as numerical or graphical data in the manuscript, or be available by personal communication. This requirement was necessary for the weighting of response ratios according to precision of the primary results. Given the unevenness with which these basic statistical measures were reported, this requirement resulted in many published observations being excluded from consideration. An additional requirement was that ambient treatments be below 40 Pa CO<sub>2</sub> and elevated treatments be between 60 and 80 Pa CO<sub>2</sub>. Most meta-analytic methods require that individual observations be statistically independent so only one measurement point per treatment per study was used. In most cases these were data obtained following the longest period of CO<sub>2</sub> exposure reported in that study. "Treatment" included species identity as well as crossed experimental factors interacting with CO<sub>2</sub> such as ozone level or soil nutrient availability. Thus, a study examining a number of species in a multi-factorial design could contribute several observations for each response variable measured (e.g., Bazzaz and Miao 1993; Kubiske and Pregitzer 1996).

We were specifically interested in how different categorical variables influenced the magnitude of elevated CO<sub>2</sub> responses. The five categorical variables whose effects we discuss here are, environmental stress factors (Stress), plant functional group (Func Grp), length of CO<sub>2</sub> exposure (Time), pot size (Pot), and type of exposure facility (Method) (Table 1). We required information on each of these variables for a study to be included in the database. For purposes of meta-analysis we established discrete levels for each variable and coded each observation accordingly. In most cases coding decisions were unambiguous but occasionally subjective interpretations were required to place a particular experimental design or treatment within one of these categorical levels. For example, field studies having "native soil" were considered unstressed unless some stress factor had been clearly identified by the author. Low N studies with N<sub>2</sub>-fixing plants and low P studies with mycorrhizal plants were also considered unstressed. The basis for coding decisions was described in more detail by Curtis (1996). The Stress factor associated with each study is also listed in Appendix 2.

### Meta-analysis of response ratios

Meta-analytic studies depend on some estimate of treatment *effect size*, commonly the magnitude of an experimental treatment mean (in this case,  $\bar{X}_e$ ) relative to the control treatment mean (in this case,  $\bar{X}_a$ ) (Cooper and Hedges 1994). In a previous meta-analysis of the elevated CO<sub>2</sub> literature, Curtis (1996) used the standardized difference between experimental and control means, the so-called *d*-index, as the estimate of CO<sub>2</sub> effect size from a particular study. While the *d*-index had certain statistical advantages and was widely used in the social and medical sciences, it was not an effect size

**Table 1** Categorical variables used in describing experimental conditions, and the values (levels) they could assume in the analysis of between-group heterogeneity ( $Q_b$ ). Note that Time and Pot were

entered as continuous variables in the meta-database. There were additional Stress levels encountered in the CO<sub>2</sub> literature but not considered in this analysis

Categorical variable	Level 1	Level 2	Level 3	Level 4	Level 5	Level 6	Level 7	Level 8
Stress	None (optimal growth conditions)	Fert (low N or P treatment)	Light (low light treatment)	O <sub>3</sub> (high ozone treatment)	UVB (high UV-B treatment)	Temp (low or high temperature treatment)	H <sub>2</sub> O (drought treatment)	Comp (competition treatment)
Time	≤59 days	60–99 days	100–365 days	> 365 days				
Func Grp	Angiosperm	Gymnosperm	N <sub>2</sub> fixer					
Pot	≤0.5 l	0.6–2.4 l	2.5–9 l	≥10 l	In ground			
Method	GC (indoor growth chamber)	GH (greenhouse)	OTC (open-top chamber)	FACE (free-air CO <sub>2</sub> enrichment)	Branch (branch chamber)			

metric commonly used to assess responses to elevated CO<sub>2</sub>. A much more common effect size metric in elevated CO<sub>2</sub> studies (as well as in other areas of ecology) is the response ratio,  $r = \bar{X}_e / \bar{X}_a$ . An impediment to the meta-analysis of response ratios, however, has been poor understanding of the sampling distribution of  $r$  and the lack of any formal statistical methods for its integration across independent studies.

L.V. Hedges, J. Gurevitch, and P.S. Curtis (unpublished ms) have developed new statistical methods for the meta-analysis of response ratios. These methods have been incorporated into statistical software for performing meta-analyses (MetaWin, Rosenberg et al. 1996) and this software was used in the present study. In brief,  $r$  first must be log-transformed such that  $lr = \ln(r) = \ln(\bar{X}_e) - \ln(\bar{X}_a)$ . If  $\bar{X}_e$  and  $\bar{X}_a$  are normally distributed and  $\bar{X}_a$  is unlikely to be negative, then  $lr$  is approximately normally distributed with a mean of approximately the true response log ratio and variance,  $v$ , equal to

$$v = \frac{S_e^2}{n_e \bar{X}_e^2} + \frac{S_a^2}{n_a \bar{X}_a^2} \quad (1)$$

The 95% confidence interval for an individual log response ratio is then

$$95\% \text{ CI} = lr - 1.96\sqrt{v} \text{ to } lr + 1.96\sqrt{v} \quad (2)$$

and the corresponding confidence limits for the unlogged response ratio obtained by computing their respective antilogs.

In summarizing results from independent studies, weighted means are normally used since individual experiments often differ in their statistical precision (e.g., Fig. 1). Giving greater weight to experiments whose estimates have greater precision (i.e., smaller standard error) will increase the precision of the combined estimate. The weighted mean log ratio ( $\bar{lr}^*$ ) that produces the greatest precision (minimum variance) is

$$\bar{lr}^* = \frac{\sum_{i=1}^k w_i^* lr_i}{\sum_{i=1}^k w_i^*} \quad (3)$$

where the weighting factor  $w_i^* = 1/(v_i + \hat{\sigma}_k^2)$  is the reciprocal of the total variance of  $lr_i$ . Here, a mixed model analysis is assumed in which the pooled within-class variance,  $\hat{\sigma}_k^2$ , is added to  $v$  (Gurevitch and Hedges 1993).

Because each of the  $k$  individual log ratios is approximately normally distributed, the weighted mean is normally distributed with confidence intervals calculated as in Eq. 2, where the standard error is

$$S(\bar{lr}^*) = \sqrt{1 / \sum_{i=1}^k w_i^*} \quad (4)$$

#### Partitioning variance within and between groups

With meta-analysis, one can test whether categorical groups (e.g., angiosperms or gymnosperms) are homogeneous with respect to effect size (i.e., that observed differences in  $lr$  among studies are due to sampling error), and whether there are significant differences in mean response between those groups (Hedges and Olkin 1985). In a procedure analogous to the partitioning of variance in analysis of variance, the total heterogeneity for a group of comparisons ( $Q_T$ ) is partitioned into within-class heterogeneity ( $Q_w$ ) and between-class heterogeneity ( $Q_b$ ), such that  $Q_T = Q_w + Q_b$ . The  $Q$  statistic follows a chi-square distribution, with  $k-1$  degrees of freedom.

A central goal of our meta-analysis was to understand the source of variation in CO<sub>2</sub> effect size among studies and to determine whether particular growth conditions or groups of species elicited quantitatively different responses. The approach we took was to partition total heterogeneity ( $Q_T$ ) within and between levels of each categorical variable. For example, the categorical variable Time (= length of the CO<sub>2</sub> exposure) was partitioned into short ( $\leq 59$  days), medium (60–99 days), long (100–365 days) and very

long ( $> 365$  days) exposure periods (levels). Grouping the data according to Time classes we could test whether there was significant between-group heterogeneity with respect to CO<sub>2</sub> exposure duration. This is analogous to examining the significance level of a particular source of variation in a conventional analysis of variance.

Partitioning of variance proceeded in two steps. First, between-group heterogeneity ( $Q_b$ ) for each categorical variable was examined across all data for a given response variable. Second, the data set was subdivided according to levels of those categorical variables revealing significant  $Q_b$  and the first step repeated. Mean log ratios were calculated when the number of categorical variables exhibiting significant  $Q_b$  had been reduced to one or zero, suggesting no further partitioning of the dataset was justified. Means were considered to be significantly different from one another if their 95% CIs were non-overlapping and were significantly different from zero if the 95% CI did not overlap zero (Gurevitch and Hedges 1993).

## Results

Biomass responses to elevated CO<sub>2</sub> were strongly affected by environmental stress factors and to a lesser degree by duration of CO<sub>2</sub> exposure and functional group affiliation (Table 2). Total biomass increased significantly at high CO<sub>2</sub> (+28.8%,  $k=102$ , Fig. 1) but there were also significant differences among stress categories (Fig. 2). Plants grown under nutrient stress showed only half the percentage growth stimulation (+15.5%) of plants with no stress treatment (+30.9%) and one-third that of plants grown under low light (+52.3%). Examination of each of these sub-groups for other significant categorical divisions (e.g., Pot or Time) showed no additional significant between-group heterogeneity ( $Q_b$ ) (data not shown). This suggests that *across all studies*, there were significant differences in CO<sub>2</sub> response among plants grown under different stress regimes, but not, for example, among those grown in different pot size classes. The small number of studies incorporating environmental stresses other than Fert and Light (e.g., O<sub>3</sub>, UVB, Temp) resulted in large confidence

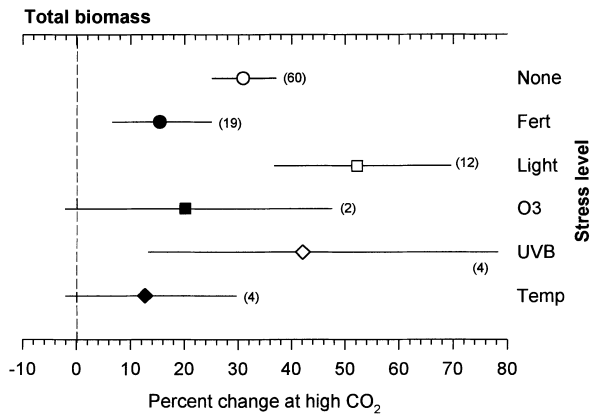
**Table 2** Between-group heterogeneity ( $Q_b$ ) for CO<sub>2</sub> effect size across five categorical variables for total biomass ( $W_T$ ), below-ground biomass ( $W_B$ ), stem biomass ( $W_S$ ), leaf biomass ( $W_L$ ), net CO<sub>2</sub> assimilation ( $A$ ), photosynthetic acclimation ( $A_{\text{accl}}$ ), stomatal conductance ( $g_s$ ), leaf dark respiration ( $R_d$ ), leaf starch concentration ( $St_L$ ), and leaf nitrogen concentration ( $N_L$ ). The categorical variables and their levels are as in Table 1. Each response variable was represented by  $k$  studies

Variable	$k$	Func Grp	Time	Pot	Method	Stress
$W_T$	102	0.23	3.75	1.13	2.03	21.74***
$W_B$	64	2.23	9.40*	3.20	1.40	9.23*
$W_S$	47	1.94	4.88	1.24	1.10	8.47*
$W_L$	50	5.97*	5.60	2.58	2.20	11.80**
$A$	79	0.71	6.19	10.33*	7.91*	1.20
$A_{\text{accl}}$	28	0.24	3.64	9.57*	3.64	2.23
$g_s$	48	0.22	2.32	4.15	2.14	1.34
$R_d$	16	0.26	1.46	3.15	2.46	0.38
$St_L$	17	5.96*	6.58	6.65*	4.84	7.46**
$N_L$	41	0.32	6.39	1.85	1.35	0.03

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

limits and little power to draw statistical inferences regarding the relative magnitude of their mean effects.

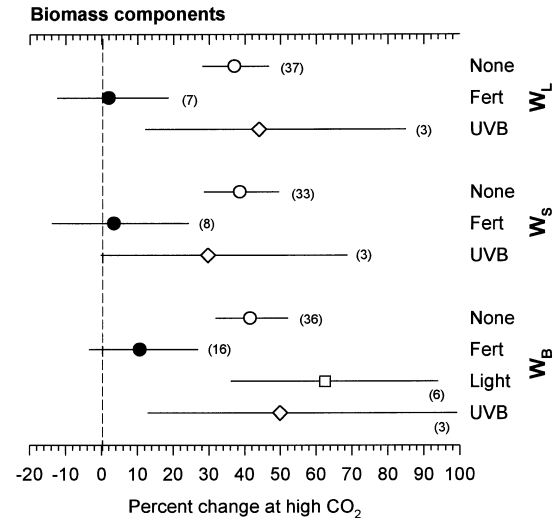
Belowground biomass responses to CO<sub>2</sub> were highly significant overall (+38%,  $k=64$ ) but were affected by environmental stress factors and length of the CO<sub>2</sub> exposure (Table 2). Thus, there were significant time effects (across all stress types), but also significant stress effects (across all time categories). Further partitioning of this dataset showed that for plants exposed to no stress treatment, time categories were no longer significantly different nor was there any other significant  $Q_b$



**Fig. 2** The effect of environmental stress on the biomass response of trees to elevated CO<sub>2</sub>. Plants were exposed either to no stress (*None*), low nutrient availability (*Fert*), low light levels (*Light*), high ozone (*O3*), high UVB (*UVB*) or low or high temperature (*Temp*). Mean  $\pm$  95% confidence interval ( $k$ )

(Table 3). It should be noted that as the data set was divided, not every categorical variable level was represented in each sub-group. For example, there was no pot level 5 (=planting in ground) represented in the 36 studies reporting  $W_B$  measurements in unstressed trees. In this group,  $W_B$  increased 41.5% under elevated CO<sub>2</sub> (Fig. 3).

In contrast to the unstressed group, among all remaining  $W_B$  studies (i.e., those including *Fert*, *UVB*, and



**Fig. 3** The effect of elevated CO<sub>2</sub> on biomass allocation to leaves ( $W_L$ ), stem ( $W_S$ ), or roots ( $W_B$ ) in plants grown with (*Fert*, *UVB*, *Light*) or without (*None*) interacting stress conditions. Mean  $\pm$  95% confidence interval ( $k$ )

**Table 3** Between-group heterogeneity ( $Q_b$ ) for subgroups of response variables presented in Table 2. Data sets were partitioned according to the variable level in **bold type**, and  $Q_b$  for all catego-

rical variables was then calculated. The specific levels represented for each categorical variable in the  $k$  set of studies are also presented

Var	k	Stress level	Stress $Q_b$	Time level	Time $Q_b$	Func Grp level	Func Grp $Q_b$	Pot level	Pot $Q_b$	Method level	Method $Q_b$
$W_B$	36	<b>None</b>	—	All	5.26	Angio, Gymno	0.01	1–4	1.77	All	0.05
$W_B$	25	<b>Fert, UVB, Light</b>	5.58	3,4	7.83**	Angio, Gymno	4.62*	1–3, 5	4.35	All	4.72
$W_B$	22	<b>Fert, UVB, Light</b>	12.44**	<b>3</b>	—	Angio, Gymno	2.33	1–3	0.61	GC, GH	0.66
$W_L$	37	<b>None</b>	—	All	4.78	Angio, Gymno	2.05	All	4.53	All	0.95
$W_L$	10	<b>Fert, UVB</b>	5.38*	3	—	Angio, Gymno	6.69**	1–3	8.06*	GC, GH	3.98*
$A$	59	All	0.90	All	5.78	All	0.12	All	11.31*	<b>GH, OTC</b>	2.78
$A$	50	All	0.80	All	8.94*	All	0.59	<b>3–5</b>	4.49	GH, OTC	0.42
$A$	19	None, Fert	1.03	1–3	0.43	All	4.04	1–4	2.54	<b>GC</b>	—
$A_{\text{accl}}$	24	None	—	All	2.04	All	0.40	<b>2–5</b>	0.53	GC, GH, OTC	1.15
$St_L$	12	None, Fert	0.90	1–3	0.87	<b>Angio</b>	—	3–5	0.92	GC, OTC	0.85
$St_L$	4	None, Fert	7.45**	4	—	<b>Gymno</b>	—	4	—	OTC	—

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

Light stress) there were significant Time and Func Grp effects but no significant differences among Stress categories (Table 3). Examination of these data revealed a small ( $n = 2$ ) group of long-duration studies ( $>365$  days), both involving gymnosperms, whose belowground response was over twice that of the remaining 22 studies. Excluding those two studies (both from Johnson et al. 1994), which restricted Time to level 3 (100–365 days), resulted in a significant Stress  $Q_b$  but no other. That is, there were significant differences among Stress category means, but only after removal of the two outlier studies. While these two studies might well merit further examination (e.g., *why* were they outliers?), they were clearly distinct from the other 22 studies and obscured significant differences among Stress categories in that group. Below-ground biomass response to  $\text{CO}_2$  was not significantly different from zero under fertility stress ( $+10.6\%$ , ns) and was not affected by low light or UVB stress relative to unstressed plants although low sample sizes renders this latter conclusion very tentative (Fig. 3).

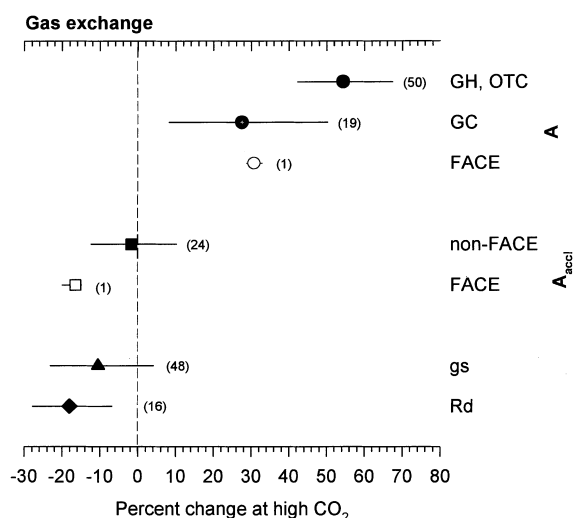
Leaf biomass responses to  $\text{CO}_2$  also showed significant  $Q_b$  for several categorical variables. Across the entire dataset, leaf biomass increased significantly under high  $\text{CO}_2$  ( $+31\%$ ,  $k=50$ ) but the magnitude of this response depended on both interacting stresses and on functional group affiliation (Table 2). Studies with no interacting stress treatment ( $k=37$ ) had no other significant  $Q_b$  (Table 3) and showed a mean stimulation of  $W_L$  under high  $\text{CO}_2$  of  $37.1\%$  (Fig. 3). The remaining ten studies showed significant variation among Stress (Fert, UVB), Func Grp (Angiosperm, Gymnosperm), Pot ( $<0.5$ – $9$  l), and Method (GC, GH) levels. It was not possible to partition this variation completely since several categorical variables were confounded. For example, all four gymnosperm studies were conducted in growth chambers in pots  $<2.5$  l. Stress treatments were not confounded with any other variable, however. Fertility stress reduced the  $W_L$   $\text{CO}_2$  response to zero while the magnitude of the  $\text{CO}_2$  response under UVB stress was not significantly different from that of unstressed plants (Fig. 3). Stem biomass response to  $\text{CO}_2$  showed a very similar pattern to  $W_B$  and  $W_L$  (Table 2, Fig. 3), with unstressed plants having a highly significant response ( $+38.6\%$ ,  $k=33$ ) but with low soil fertility reducing this growth stimulation to zero.

There was no evidence for significant Stress, Time, or Func Grp effects on  $A$  at high  $\text{CO}_2$  (Table 2). Pot and Method did, however, show significant  $Q_b$ . For plants grown in GCs there was no Pot  $Q_b$  (Table 3) and an overall mean stimulation of  $A$  of  $27.5\%$  at high  $\text{CO}_2$  (Fig. 4). For plants grown in GHs or OTCs and in pots  $>2.4$  L,  $A$  was stimulated  $54.3\%$  under  $\text{CO}_2$  enrichment (Table 3, Fig. 4), although there remained a significant Time  $Q_b$  for this group. The time effect was difficult to account for, with the level 3 mean (100–365 days) being greater than means from levels 1, 2, or 4 which were not different from one another (data not shown). Net  $\text{CO}_2$  assimilation in GH or OTC plants grown in pots  $<2.5$  l

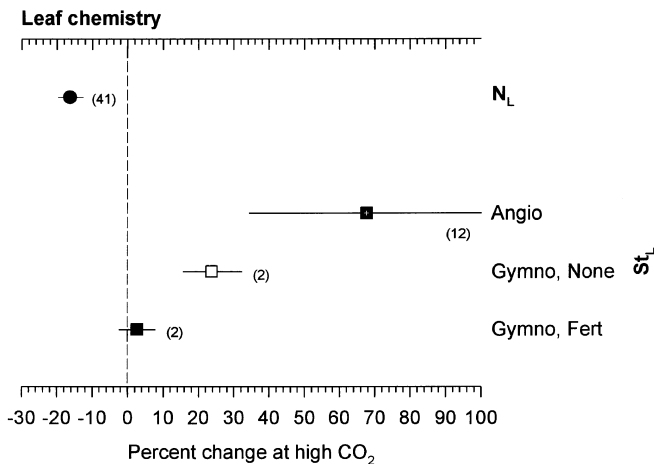
was significantly less ( $19\%$ ,  $k = 9$ ) than in plants grown in larger pots or in the ground.

Elevated  $\text{CO}_2$  stimulation of  $A$  in mature, open-grown *Pinus taeda* exposed to  $c. 55$  Pa  $\text{CO}_2$  for 2 years in a FACE experiment (Ellsworth et al. 1997) was  $31\%$ , outside the  $95\%$  CI of OTC and GH grown plants but very similar to the GC mean (Fig. 4). Part of the explanation for a reduced response relative to other ‘field-grown’ trees may be lower  $\text{CO}_2$  levels used in this free-air  $\text{CO}_2$  enrichment (FACE) study compared to most OTC experiments ( $c. 70$  Pa). Photosynthetic acclimation could also be more severe than in non-FACE systems (see below). With a sample size of one it is impossible to test for a ‘FACE effect’ *per se*, and additional data are of great importance in resolving differences in the  $\text{CO}_2$  response, if any, between FACE-grown trees and those from the bulk of our other experimental systems.

Photosynthetic acclimation, calculated as the ratio of  $A$  in elevated compared to ambient grown plants both measured at elevated  $\text{CO}_2$ , was affected overall only by pot size, with plants in small pots ( $<0.5$  l), showing significant  $A_{\text{accl}}$  ( $-36\%$ ,  $k=5$ ), while plants grown in larger pots showed no evidence for  $A_{\text{accl}}$  under any conditions (Tables 2, 3, Fig. 4). FACE-grown *Pinus taeda* showed  $A_{\text{accl}}$  of  $-16.5\%$ , outside the  $95\%$  CI of other ‘large pot’ studies. The likelihood of low water or nutrient supply contributing to the FACE  $A_{\text{accl}}$  response was low since Stress showed no significant  $Q_b$  in the overall data set. Increased sample size and estimates of among-FACE experiment variation clearly are needed to increase the power of these quantitative comparisons. Stomatal conductance showed a modest ( $-11\%$ ) but not statistically significant reduction in plants grown under high  $\text{CO}_2$  while  $R_d$  (expressed on a leaf mass basis) was significantly reduced ( $-18\%$ ) (Fig. 4). Neither  $g_s$  nor  $R_d$



**Fig. 4** Gas exchange responses of trees to elevated  $\text{CO}_2$ . Net  $\text{CO}_2$  assimilation rate ( $A$ ), acclimation to elevated  $\text{CO}_2$  ( $A_{\text{accl}}$ ), stomatal conductance ( $g_s$ ) and leaf dark respiration ( $R_d$ ) in plants grown under elevated compared to ambient  $\text{CO}_2$ . Mean  $\pm$  95% confidence interval ( $k$ ) (GH greenhouse, OTC field-based open-top chamber, FACE free-air  $\text{CO}_2$  enrichment, GC growth chamber)



**Fig. 5** Leaf nitrogen ( $N_L$ ) and starch ( $St_L$ ) content in elevated compared to ambient  $CO_2$  grown plants. Both nitrogen and starch were reported on a tissue mass basis. Further subdivision of  $St_L$  studies was by angiosperm (*Angio*) vs. gymnosperm (*Gymno*) and no interacting stress (*None*) vs. low-fertility stress (*Fert*). Mean  $\pm$  95% confidence interval ( $k$ )

responses were affected by any categorical variable (Table 2).

Leaf nitrogen (mass basis) showed a highly significant reduction at high  $CO_2$  (−16.4%, Fig. 5) and this response was unaffected by Stress level or other categorical variables (Table 2). Leaf starch response to elevated  $CO_2$  was affected by Stress, Pot, and Func Grp (Table 2). In angiosperms,  $St_L$  increased 67.6% at high  $CO_2$ , significantly more than in unstressed (+23.6%), or stressed (ns) gymnosperms (Fig. 5).

## Discussion

Our meta-analysis of  $CO_2$  responses in trees leads to a number of conclusions that we can state with considerable certainty, being based on many independent studies sharing numerous experimental design features. In particular, it is clear that both  $A$  and  $W_T$  increase significantly at twice ambient  $CO_2$ , regardless of growth conditions. These results agree qualitatively with other reviews of this literature, but our quantitative summary of  $CO_2$  effect sizes often differ significantly from earlier estimates. For example, our  $CO_2$  effect size estimate of +31% for  $W_T$  under non-stressed, control conditions was less than half the  $CO_2$  effect calculated by McGuire et al. (1995). In their review of 77 studies of elevated  $CO_2$  involving N manipulations they found a 71% biomass increase in high  $CO_2$ , higher N treatment trees compared to ambient  $CO_2$ , higher N treatment trees. However, as their results were drawn only from studies involving soil N manipulations, the higher N and lowest N treatments could have provided greater soil N than the typical no-stress and low fertility treatments respectively in our analysis. Interestingly, the 50% relative reduction in the  $CO_2$  growth response calculated by McGuire et al.

(1995) as due to low soil N availability (i.e., only a 35% growth enhancement in the lowest N treatments) was identical to our observation of a 50% reduction in  $CO_2$  stimulation of  $W_T$  in nutrient-stressed plants (+16%). Eamus and Jarvis (1989) also estimated a significantly greater biomass response to elevated  $CO_2$  (+40%) than we found, while Ceulemans and Mousseau (1994) distinguished between the  $CO_2$  growth response of conifers (+38%) and broadleaved species (+68%), a division with no statistical basis in our dataset. Lastly, Wullschleger et al. (1995) calculated virtually the same overall dry weight response to  $CO_2$  in unstressed plants (+32%,  $k=295$ ) as we did, but found no reduction in this response under low nutrient conditions (+30%,  $k=82$ ).

These reviews differ from one another in many respects, including their overall objectives, their scope, and the collection of literature under consideration. It is difficult, therefore, to identify precisely the component(s) responsible for these differences in  $CO_2$  effect size estimates. A contributing factor certainly must be basic differences in the authors' approach to quantitative research integration and the statistical tools (or lack thereof) that were used. To the extent that resolving differences of 2–3 fold in our estimates of  $CO_2$  effects on tree growth is of importance (and we suggest it is) we must abandon ad hoc or ill-defined concepts for summarizing independent research results in favor of statistically robust meta-analytic methods. Only then will we be able to critically evaluate competing estimates of the likely magnitude of  $CO_2$  stimulated tree growth on, for example, low nutrient soils, or the relative importance of taxonomic or functional group affiliation in the  $CO_2$  response.

There has been considerable debate whether  $CO_2$  enrichment results in shifts in root:shoot ratio (R/S) and, if so, under what conditions this occurs. Biomass allocation models such as functional balance (Davidson 1969) and carbon/nutrient substrate ratio (Reynolds and Thornley 1982) predict that as tissue C:N ratios rise and N becomes more limiting relative to C, biomass allocation to roots will increase. Thus, high  $CO_2$  should elicit similar shifts in R/S as does low soil N. Evidence for such a  $CO_2$  effect in trees has been equivocal, however. Eamus and Jarvis (1989) considered the bulk of the evidence to indicate an increase in R/S, particularly under low nutrient conditions, a conclusion supported by Ceulemans and Mousseau (1994). Norby (1994) observed that  $CO_2$  effects on root allocation could easily be confounded with  $CO_2$  effects on developmental rate and he estimated a modest (+6%) increase in R/S at high  $CO_2$ , with no differential response under nutrient stress. Similarly, neither McGuire et al. (1995) nor Wullschleger et al. (1995) found evidence for a significant  $CO_2$  effect on biomass allocation under any conditions. We analyzed  $CO_2$  effects on individual biomass components rather than R/S, which are rarely reported with error estimates, and found little evidence to support significant shifts in allocation, whether to leaves, stems, or

roots, under most environmental or cultural conditions. The only condition under which allocation might shift in favor of roots was nutrient stress, but this response was not statistically significant. It is interesting to note, however, that the  $\text{CO}_2$  effect on  $W_T$  under nutrient stress although reduced was still significant and the only biomass component with a similar mean  $\text{CO}_2$  effect size under nutrient stress was  $W_B$ . This observation lends qualified support to predictions of increased R/S at high  $\text{CO}_2$  under low soil nutrient availability but additional data clearly will be needed to resolve this important issue.

There is broad agreement among reviewers on the overall magnitude of tree photosynthetic responses to  $\text{CO}_2$  enrichment, although less so on factors affecting that response. Estimates of overall  $\text{CO}_2$  effects on  $A$  range from +44% (Gunderson and Wullschleger 1994) to +54% (this study). Low soil nutrients have often been considered of primary importance in reducing the magnitude of this response (e.g., McGuire et al. 1995; Curtis 1996) but rarely have the relative effects of other environmental factors been compared quantitatively to that of soil nutrients. We found significant Pot and Method  $Q_b$  across all 79 studies in our database but no significant differences among stress categories. However, of 50 GH and OTC studies that were conducted in large pots or in the ground, only 7 involved low nutrient treatments, a small sample conveying relatively little statistical power. While our failure to detect significant nutrient effects may be due to sampling error, this example illustrates a general concern that must be confronted by quantitative reviewers of the literature on the effects of elevated  $\text{CO}_2$ . That is, all identifiable sources of variation in a dataset must be examined before summary statistics are calculated and conclusions drawn. If this is not done, variation due to one factor (e.g., pot size) may be confounded with that of another (e.g., soil nutrients), leading to inaccurate or erroneous conclusions regarding the importance of either factor. This is particularly true for studies with elevated  $\text{CO}_2$  where cultural conditions are known to affect the magnitude of the treatment response (Thomas and Strain 1991; McConnaughay et al. 1993; Kennedy 1995). Our results clearly show that environmental stress is of less importance than certain cultural factors in altering the magnitude of photosynthetic responses to high  $\text{CO}_2$  and that significant, sustained increases in  $A$  can be expected in trees as atmospheric  $\text{CO}_2$  levels rise.

Photosynthetic acclimation, or down-regulation, represents a suite of physiological processes which cause photosynthetic capacity in plants grown under high  $\text{CO}_2$  to decline relative to plants grown under ambient  $\text{CO}_2$  (Stitt 1991). To evaluate the magnitude of  $A_{\text{accl}}$  in trees grown under high  $\text{CO}_2$  we adopted the convention suggested by Gunderson and Wullschleger (1994) of comparing  $A$  in plants grown under elevated and ambient  $\text{CO}_2$  measured at a common  $\text{CO}_2$  level (either internal or external to the leaf). Our results show no consistent evidence for  $A_{\text{accl}}$  (−1%, ns), except in trees grown in pots <0.5 l (−36%,  $P < 0.01$ ). This is in

contrast to both the prevailing view based on narrative reviews (Ceulemans and Mousseau 1994; McGuire et al. 1995) and the overall 21% acclimation response across 20 studies reported by Gunderson and Wullschleger (1994). The 24 “larger pot” studies remaining in our dataset were almost evenly divided among those showing strong  $A_{\text{accl}}$  (e.g., Johnsen 1993; Curtis et al. 1995), no  $A_{\text{accl}}$  (e.g., Downton et al. 1990; Grulke et al. 1993), and significant up-regulation (e.g., Kaushal et al. 1989; Sharkey et al. 1991). Given the heterogeneity of this group, and the small number of studies with common stress treatments, we suggest it is premature to conclude that photosynthetic acclimation is a universal response by trees to growth under high  $\text{CO}_2$  under any particular set of conditions. Additional results from forest FACE experiments could help define those conditions but within and among-study variance estimates will be required for any rigorous statistical tests to be made.

Interpreting the effects of elevated  $\text{CO}_2$  on tree  $g_s$  presents similar problems to those raised regarding  $A_{\text{accl}}$ . Reviewers of data on  $g_s$  responses, including measurements from herbaceous species, generally suggest a significant reduction in  $g_s$  to be the norm, with the well documented sensitivity of stomata to internal  $\text{CO}_2$  level (Farquhar and Sharkey 1982) offered as a plausible response mechanism. Acclimation of  $g_s$  to high  $\text{CO}_2$  is a possibility, however, and while no physiological mechanism for acclimation has been proposed, one result of acclimation could be a change in stomatal sensitivity to  $\text{CO}_2$  (Sage 1994). Eamus and Jarvis (1989) estimated a reduction of from −10% to −60% in  $g_s$  of trees grown under elevated compared to ambient  $\text{CO}_2$  but acknowledged numerous exceptions. We found considerable variation in the magnitude of  $\text{CO}_2$  effects on  $g_s$  as well. Although the overall mean response across 48 studies was a modest −11%, this effect was not statistically different from zero, nor were there significant stress or cultural modifiers to this response. As with the distribution of  $A_{\text{accl}}$  values, our  $g_s$  dataset contained numerous studies reporting strongly negative (e.g., Bassow et al. 1994; Eamus et al. 1995), not statistically significant (e.g., Hollinger 1987; Bunce 1992), and strongly positive (e.g., Norby and O'Neill 1991; Pettersson and McDonald 1992) effects of high  $\text{CO}_2$  on  $g_s$ . Additional data will be required before we can state with certainty either the magnitude or the direction of  $\text{CO}_2$  effects on tree  $g_s$ .

In contrast to the uncertainty regarding  $\text{CO}_2$  effects on  $A_{\text{accl}}$  and  $g_s$ , our analysis provides strong support and robust summary statistics for the widely accepted view (e.g., Amthor 1994; Wullschleger et al. 1994) that growth at elevated  $\text{CO}_2$  results in significant reductions in  $R_d$  and  $N_L$  when both are expressed on a tissue mass basis. Working with a similar, though somewhat smaller dataset, Curtis (1996) found reduced  $N_L$  when reported on a leaf mass but not when reported on a leaf area basis, suggesting that in most circumstances the mass-based N reduction under  $\text{CO}_2$  enrichment was due to increased leaf density rather than N reallocation. In the



present study we documented large increases in  $St_L$  under all conditions except in nutrient stressed gymnosperms. Given the strong positive relationship between tissue N content and both photosynthesis (Field and Mooney 1986) and maintenance respiration (Ryan 1991) it is important to determine when growth at high  $CO_2$  leads to a net decrease in non-storage leaf N content as opposed to reduced leaf N concentration due to changes in specific leaf area. The extent to which  $CO_2$  enrichment leads to functional decreases in  $N_L$  could be an important determinant of long-term growth and allocational responses to elevated  $CO_2$  (Luo et al. 1994). It is also important to determine whether reduced  $N_L$  of green leaves carries over into an increased C:N ratio of naturally senesced leaf litter. Although evidence that elevated  $CO_2$  alters leaf decomposition rates is at present equivocal (O'Neill and Norby 1996), reduced N mineralization from soil organic matter could provide a potent negative feedback on long-term forest productivity with rising  $CO_2$  (Zak et al. 1993).

It is important to note that no single meta-analysis is likely to be definitive, and that multiple approaches and perspectives should be encouraged. For example, while our conclusions regarding  $CO_2$  effects on  $A$ ,  $A_{accl}$ , and  $g_s$  are in broad agreement with those of Curtis (1996), the differences in effect size metric ( $l_r$  vs.  $d$ -index) and in the strategies for partitioning within and between group variance in the two meta-analyses resulted in several qualitatively different outcomes. The most important was for  $A_{accl}$ , where Curtis (1996, Fig. 3a) found a highly significant (although numerically modest) overall  $CO_2$  effect, while in the present study we found no  $CO_2$  effect in non-FACE studies (Fig. 4). However, the overall mean effect size estimate in Curtis (1996) included the responses of plants grown in small pots ( $<0.5$  l) which were shown in both studies to have significantly greater  $A_{accl}$  than plants grown in larger pots. Here, these plants were excluded from the overall analysis, leading to the result of no significant  $A_{accl}$ . In addition, where the number of studies within a category is small, as was the case in numerous instances here, it is particularly important to repeat the meta-analysis as new data becomes available.

In conclusion, quantitative integration of the elevated  $CO_2$  literature has been hampered by inappropriate sampling and statistical methods, leading to uncertainty in the magnitude of  $CO_2$  effects on fundamental processes controlling carbon gain in woody vegetation and of the importance of environmental factors in altering the magnitude of these effects. Statistically defensible methods of integrating diverse research results have been developed over the past 50 years and are now firmly in place in the medical and social sciences (Mann 1990). Meta-analysis is not a substitute for well designed, multi-factorial experiments and it is important to acknowledge the limits to establishing causal relationships from meta-analytic results where categorical groups created by the meta-analyst were not randomly assigned treatments within the primary studies (Miller and Pol-

lock 1994). What meta-analysis does offer is an objective and statistically rigorous methodology for integrating primary research results with the goal of estimating the magnitude of treatment effects within and among categorical groups. We suggest that it is important from a scientific as well as a policy perspective that elevated  $CO_2$  research results continue to be integrated using these tools.

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**Appendix 2** The species, environmental stress factors in addition to CO<sub>2</sub> (Stress), variables measured, and citation for all studies used in the meta-analysis. The variables measured were: total above- + below-ground biomass ( $W_T$ ), below-ground biomass ( $W_B$ ), stem biomass ( $W_S$ ), total leaf biomass ( $W_L$ ), light saturated net CO<sub>2</sub> assimilation ( $A$ ), photosynthetic acclimation or downregulation ( $A_{\text{acc}}$ ), stomatal conductance ( $g_s$ ), leaf dark respiration ( $R_d$ , expressed on a leaf mass basis), leaf nitrogen concentration ( $N_L$ , expressed on a mass basis), and leaf starch concentration ( $St_L$ ,

expressed on a mass basis). The entire database, containing nearly 800 observations (at the time of this writing), is available for public use from the Carbon Dioxide Information and Analysis Center (CDIAC, Oak Ridge National Laboratory). Files may be obtained by anonymous FTP at address: [cdiac.esd.ornl.gov](http://cdiac.esd.ornl.gov), directory pub/db1018. Access codes and other important information are viewable in the readme file. The database can also be accessed via CDIAC's homepage: <http://cdiac.esd.ornl.gov>, under Products and Services, Anonymous FTP Service, FTP area, db1018.

Species	Stress	$W_T$	$W_L$	$W_S$	$W_B$	$A$	$A_{\text{acc}}$	$g_s$	$R_d$	$N_L$	$St_L$	Citation
<i>Acacia mangium</i>	None					*						Ziska et al. (1991)
<i>Acer pensylvanicum</i>	Fert		*	*				*				Bassow et al. (1994)
<i>Acer pensylvanicum</i>	Fert				*							Bassow et al. (1994)
<i>Acer pensylvanicum</i>	Fert/light				*							Bazzaz and Miao (1993)
<i>Acer pensylvanicum</i>	Fert/light	*										Bazzaz and Miao (1993)
<i>Acer pensylvanicum</i>	Fert/light	*										Bazzaz et al. (1993)
<i>Acer rubrum</i>	Fert/light				*							Bazzaz and Miao (1993)
<i>Acer rubrum</i>	Fert/light	*										Bazzaz and Miao (1993)
<i>Acer rubrum</i>	Fert/light	*										Bazzaz et al. (1993)
<i>Acer rubrum</i>	None	*										Bunce (1992)
<i>Acer rubrum</i>	Light					*		*		*		Kubiske and Pregitzer (1996)
<i>Acer saccharinum</i>	None	*				*		*				Bunce (1992)
<i>Acer saccharum</i>	None	*	*							*		Lindroth et al. (1993)
<i>Acer saccharum</i>	Temp					*		*				Norby et al. (1996)
<i>Acer saccharum</i>	None									*		Reid and Strain (1994)
<i>Acer saccharum</i>	None					*						Reid and Strain (1994)

## Appendix 2 (continued)

Species	Stress	$W_T$	$W_L$	$W_S$	$W_B$	$A$	$A_{\text{acc}}$	$g_s$	$R_d$	$N_L$	$St_L$	Citation
<i>Alnus glutinosa</i>	None					*		*	*	*		Vogel and Curtis (1995)
<i>Alnus rubra</i>	Fert	*	*	*	*	*				*		Amone and Gordon (1990)
<i>Betula alleghaniensis</i>	Fert		*	*	*			*				Bassow et al. (1994)
<i>Betula alleghaniensis</i>	Fert/light	*			*							Bazzaz and Miao (1993)
<i>Betula alleghaniensis</i>	Fert/light	*										Bazzaz et al. (1993)
<i>Betula alleghaniensis</i>	None	*	*	*	*					*		Rocheftort and Bazzaz (1992)
<i>Betula lenta</i>	None	*	*	*	*					*		Rocheftort and Bazzaz (1992)
<i>Betula papyrifera</i>	Light					*		*		*		Kubiske and Pregitzer (1994)
<i>Betula papyrifera</i>	None	*	*	*	*					*		Rocheftort and Bazzaz (1992)
<i>Betula papyrifera</i>	None									*	*	Roth and Lindroth (1994)
<i>Betula pendula</i>	Temp	*				*	*		*			Mortensen (1994)
<i>Betula pendula</i>	None	*				*		*		*	*	Pettersson and McDonald (1992)
<i>Betula pendula</i>	Fert									*	*	Pettersson et al. (1993)
<i>Betula populifolia</i>	Fert		*	*	*			*				Bassow et al. (1994)
<i>Betula populifolia</i>	Fert/light	*			*							Bazzaz and Miao (1993)
<i>Betula populifolia</i>	Fert/light	*										Bazzaz et al. (1993)
<i>Betula populifolia</i>	None	*	*	*	*					*		Rocheftort and Bazzaz (1992)
<i>Betula pubescens</i>	O <sub>3</sub> /temp	*	*	*	*							Mortensen (1995)
<i>Brachychiton populneum</i>	None					*						Idso and Kimball (1993)
<i>Castanea sativa</i>	None	*		*								Couteaux et al. (1992)
<i>Castanea sativa</i>	None								*			El Kohen et al. (1991)
<i>Castanea sativa</i>	Fert	*	*	*	*					*		El Kohen et al. (1992)
<i>Castanea sativa</i>	None	*	*	*	*	*						El Kohen et al. (1993)
<i>Castanea sativa</i>	None	*	*	*	*	*			*			Mousseau (1993)
<i>Castanea sativa</i>	None	*		*	*							Mousseau and Enoch (1989)
<i>Cecropia obtusifolia</i>	None/comp	*				*		*				Reekie and Bazzaz (1989)
<i>Cedrus atlantica</i>	None					*	*	*			*	Kaushal et al. (1989)
<i>Citrus aurantium</i>	None		*	*	*							Ferguson et al. (1986)
<i>Citrus aurantium</i>	None					*						Idso et al. (1991)
<i>Citrus sinensis</i>	None	*	*	*	*	*	*					Downton et al. (1987)
<i>Eucalyptus microtheca</i>	None					*						Idso and Kimball (1993)
<i>Eucalyptus</i>	None					*						Idso and Kimball (1993)
<i>polyanthemus</i>												
<i>Eucalyptus tetrodonta</i>	None					*						Eamus et al. (1995a)
<i>Fagus grandifolia</i>	None					*				*		Reid and Strain (1994)
<i>Fagus sylvatica</i>	None					*						El Kohen et al. (1993)
<i>Fagus sylvatica</i>	None					*	*					Jarvis et al. (1994)
<i>Ficus obtusifolia</i>	None					*						Ziska et al. (1991)
<i>Fraxinus americana</i>	Fert/light	*			*							Bazzaz and Miao (1993)
<i>Fraxinus americana</i>	Fert/light	*										Bazzaz et al. (1993)
<i>Garcinia mangostana</i>	None		*	*	*	*	*					Downton et al. (1990)
<i>Gliricidia sepium</i>	Fert									*		Thomas et al. (1991)
<i>Lindera benzoin</i>	None									*		Cipollini et al. (1993)
<i>Liquidambar styraciflua</i>	None					*	*	*				Fetcher et al. (1988)
<i>Liriodendron tulipifera</i>	None								*	*		Wulschleger et al. (1992a)
<i>Liriodendron tulipifera</i>	None					*		*				Gunderson et al. (1993)
<i>Liriodendron tulipifera</i>	Fert	*	*	*	*	*		*		*		Norby and O'Neill (1991)
<i>Liriodendron tulipifera</i>	None		*	*	*	*		*	*			Norby et al. (1992)
<i>Liriodendron tulipifera</i>	None					*		*	*		*	Wulschleger et al. (1992b)
<i>Malus domestica</i>	None	*				*		*				Bunce (1992)
<i>Maranthus corymbosa</i>	None	*	*	*	*			*				Berryman et al. (1993)
<i>Maranthus corymbosa</i>	None					*	*	*				Eamus et al. (1993)
<i>Maranthus corymbosa</i>	None							*				Eamus et al. (1995b)
<i>Myriocarpa longipes</i>	None/comp	*				*		*				Reekie and Bazzaz (1989)
<i>Nothofagus fusca</i>	None	*				*	*	*				Hollinger (1987)
<i>Picea abies</i>	None						*					Marek et al. (1995)
<i>Picea abies</i>	Temp	*				*	*		*			Mortensen (1994)
<i>Picea abies</i>	O <sub>3</sub>	*										Polle et al. (1993)
<i>Picea glauca</i>	UVB	*	*	*	*							Yakimchuk and Hoddinott (1994)
<i>Picea mariana</i>	Fert/H <sub>2</sub> O	*				*	*	*				Johnsen (1993)
<i>Picea mariana</i>	UVB	*	*	*	*							Yakimchuk and Hoddinott (1994)
<i>Pinus banksiana</i>	UVB	*										Stewart and Hoddinott (1993)
<i>Pinus banksiana</i>	UVB	*	*	*	*							Yakimchuk and Hoddinott (1994)

## Appendix 2 (continued)

Species	Stress	$W_T$	$W_L$	$W_S$	$W_B$	$A$	$A_{\text{acc}}$	$g_s$	$R_d$	$N_L$	$St_L$	Citation
<i>Pinus echinata</i>	None	*		*								Norby et al. (1987)
<i>Pinus echinata</i>	None	*	*	*	*							O'Neill et al. (1987)
<i>Pinus eldarica</i>	None		*									Garcia et al. (1994)
<i>Pinus nigra</i>	None					*	*	*			*	Kaushal et al. (1989)
<i>Pinus ponderosa</i>	Temp	*							*			Callaway et al. (1994)
<i>Pinus ponderosa</i>	None		*			*	*	*		*		Grulke et al. (1993)
<i>Pinus ponderosa</i>	Fert				*							Johnson et al. (1994)
<i>Pinus ponderosa</i>	None							*				Surano et al. (1986)
<i>Pinus radiata</i>	Fert							*				Conroy et al. (1988)
<i>Pinus radiata</i>	None	*				*	*	*				Hollinger (1987)
<i>Pinus strobus</i>	None									*	*	Roth and Lindroth (1994)
<i>Pinus sylvestris</i>	Temp					*	*		*			Wang et al. (1995)
<i>Pinus taeda</i>	None					*	*	*				Fetcher et al. (1988)
<i>Pinus taeda</i>	Fert									*		Lewis et al. (1994)
<i>Pinus taeda</i>	None					*	*	*				Liu and Teskey (1995)
<i>Pinus taeda</i>	None		*	*	*							Sullivan and Teramura (1994)
<i>Pinus taeda</i>	None					*						Teskey (1995)
<i>Pinus taeda</i>	Fert					*					*	Tissue et al. (1993)
<i>Pinus taeda</i>	H <sub>2</sub> O		*	*	*							Tschaplinski et al. (1993)
<i>Pinus taeda</i>	None		*							*	*	Williams et al. (1994)
<i>Pinus taeda</i>	None					*	*					Ellsworth et al. (1997)
<i>Piper auritum</i>	None/comp	*				*		*				Reekie and Bazzaz (1989)
<i>Populus euramericana</i>	None					*		*				Gaudillere and Mousseau (1989)
<i>Populus euramericana</i>	Fert	*	*	*	*					*		Pregitzer et al. (1995)
<i>Populus grandidentata</i>	None			*	*	*	*	*		*		Curtis and Teeri (1992)
<i>Populus grandidentata</i>	None					*	*	*				Curtis et al. (1994)
<i>Populus interamericana</i>	None					*						Lemur et al. (1992)
<i>Populus tremuloides</i>	Fert									*		Brown (1991)
<i>Populus tremuloides</i>	None	*	*							*	*	Lindroth et al. (1993)
<i>Populus tremuloides</i>	None					*	*					Sharkey et al. (1991)
<i>Populus euramericana</i>	Fert	*				*	*		*	*	*	Curtis et al. (1995)
<i>Pseudotsuga menziesii</i>	None		*		*							Gorissen et al. (1995)
<i>Pseudotsuga menziesii</i>	None	*				*	*	*				Hollinger (1987)
<i>Quercus alba</i>	None					*		*				Gunderson et al. (1993)
<i>Quercus alba</i>	Fert		*	*	*	*						Norby and O'Neill (1989)
<i>Quercus alba</i>	None		*	*						*		Norby et al. (1986)
<i>Quercus alba</i>	None	*	*	*								O'Neill et al. (1987)
<i>Quercus alba</i>	None					*	*					Sharkey et al. (1991)
<i>Quercus alba</i>	None								*			Wullschleger and Norby (1992)
<i>Quercus alba</i>	None					*		*	*		*	Wullschleger et al. (1992a)
<i>Quercus alba</i>	None								*			Wullschleger et al. (1995)
<i>Quercus prinus</i>	None	*				*		*				Bunce (1992)
<i>Quercus robur</i>	None					*		*				Bunce (1992)
<i>Quercus rubra</i>	Fert/light	*			*							Bazzaz and Miao (1993)
<i>Quercus rubra</i>	Fert/light	*										Bazzaz et al. (1993)
<i>Quercus rubra</i>	Light					*				*		Kubiske and Pregitzer (1996)
<i>Quercus rubra</i>	None	*	*							*	*	Lindroth et al. (1993)
<i>Senna multijuga</i>	None/comp	*				*		*				Reekie and Bazzaz (1989)
<i>Tabebuia rosea</i>	None					*						Ziska et al. (1991)
<i>Trichospermum mexicanum</i>	None/comp	*				*		*				Reekie and Bazzaz (1989)

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