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EARLY VS. ASYMPTOTIC GROWTH RESPONSES OF HERBACEOUS PLANTS TO ELEVATED CO_2

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Abstract. Although many studies have examined the effects of elevated carbon dioxide on plant ''growth,'' the dynamics of growth involve at least two parameters, namely, an early rate of exponential size increase and an asymptotic size reached late in plant ontogeny. The common practice of quantifying CO_2 responses as a single ''response ratio'' thus obscures two qualitatively distinct kinds of effects. The present experiment examines effects of elevated CO_2 on both early and asymptotic growth parameters in eight C_3 herbaceous plant species (*Abutilon theophrasti*, *Cassia obtusifolia*, *Plantago major*, *Rumex crispus*, *Taraxacum officinale*, *Dactylis glomerata*, *Lolium multiflorum*, and *Panicum dichotomoflorum*). Plants were grown for 118–172 d in a factorial design of CO_2 (350 and 700 μL/L) and plant density (individually grown vs. high-density monocultures) under edaphic conditions approximating those of coastal areas in Massachusetts. For *Abutilon theophrasti*, intraspecific patterns of plant response were also assessed using eight genotypes randomly sampled from a natural population and propagated as inbred lines.

The species and genotypes examined generally showed enhanced early relative growth rates (RGR) under elevated CO_2; however, such early growth responses did not necessarily correspond to increases in asymptotic size. As a result, interspecific and genetic correlations between early RGR enhancements and asymptotic size enhancements were weak. Effects of elevated CO_2 also varied systematically among the size metrics examined. The maximum leaf area attained by individually grown plants was generally reduced under elevated CO_2; however, most species showed positive effects of CO_2 on vegetative mass at final harvest. Final biomass responses were greatest in species showing large enhancements in root growth. In addition, CO_2 responses of plants grown in dense monocultures differed from plants grown individually, showing reduced responses for both early RGR and final biomass. Average reproductive responses to elevated CO_2 were positive for individually grown plants, but negative for dense monocultures.

It has previously been suggested that differences in species' growth rates may be the best single predictor of plant growth responses to CO_2. Here we found that RGR (at ambient CO_2) appeared to limit potential early growth responses among species, but that there was no such relationship between RGR and asymptotic size responses. We suggest that the latter may be determined in part by the degree to which large carbon sinks are formed late in plant ontogeny. The overall pattern of early and asymptotic growth responses to elevated CO_2 varied widely both among and within species, and we found little evidence for the existence of discrete ''functional types.'' We argue that both early and asymptotic responses are of fundamental interest from a modeling and a physiological perspective. Both types of growth response should be incorporated in all efforts to understand and predict responses of terrestrial vegetation to rising CO_2 and other aspects of global change.

Key words: asymptotic plant size; carbon dioxide; density; functional types; genetic variation; global change; growth analysis; leaf area index; relative growth rate.

INTRODUCTION

Atmospheric carbon dioxide levels continue to increase at a rate of ~0.45% per year, with the current global average exceeding 360 μL/L (IPCC 1996). The most immediate and well-characterized physiological effects of elevated CO_2 on plants are increased carbon uptake and reduced leaf-level transpiration (e.g., Bazzaz 1990, Bowes 1991, Curtis 1996). Physiological enhancement of carbon gain generally results in increased biomass accumulation over the short term. Accordingly, plant growth enhancements under elevated CO_2 have been extensively documented (Kimball 1983, Cure and Acock 1986, Poorter 1993, Poorter et al. 1996, Curtis and Wang 1998). The most commonly cited generalization to emerge from this work is that plants grown in a doubled CO_2 atmosphere (i.e., 700 vs. 350 μL/L)

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exhibit, on average, a 33–37% increase in biomass (e.g., Kimball 1983, Wullschleger et al. 1995).

Several reviews have recently argued that this 33–37% figure, and enhancement ratios in general, do not adequately summarize CO_2 effects on plant growth (Loehle 1995, Gifford et al. 1996, Körner 1996, Thomas and Jasienski 1996). The essence of this argument, as we see it, is as follows: It is axiomatic that plant growth curves are generally sigmoidal in form, with an early exponential phase followed by a leveling off later in ontogeny (Causton and Venus 1981). A sigmoid growth function (in contrast to, for example, exponential or linear growth functions) must be described by at least two parameters. It follows that effects of CO_2 on plant ''growth'' must also be described by at least two parameters. Most commonly, sigmoid growth functions, such as the logistic equation, are described by an initial exponential parameter describing early growth, and an asymptotic maximal size parameter describing final plant size. Analyses of CO_2 effects on plant growth should thus also explicitly examine effects on these parameters. Enhancement ratios, as conventionally employed, thus obscure two distinct kinds of effects, both of which are of fundamental importance and interest (Fig. 1).

Numerous studies examining plant growth responses to elevated CO_2 have employed one form or another of growth analysis (e.g., Rogers et al. 1984, Tolley and Strain 1984, Bazzaz et al. 1989, Coleman and Bazzaz 1992, Walters et al. 1993, Tremmel and Patterson 1994). There has also been a long-standing debate as to whether CO_2 effects on tree seedling growth will persist in larger trees and whole forests (e.g., Norby et al. 1992, 1996, Bazzaz et al. 1993, Johnson et al. 1996, Hättenschwiler et al. 1997, Idso and Kimball 1997). However, we are aware of no previous attempt to explicitly quantify CO_2 effects on asymptotic plant size per se. Nor has there been any empirical examination of issues that immediately arise from this approach, such as potential relationships between early and asymptotic growth responses. It seems likely that the physiological mechanisms responsible for differences in asymptotic size responses to CO_2 are fundamentally distinct from those responsible for early growth enhancements. For example, the physiological determinants of maximum plant size likely include ontogenetic shifts in allocation to reproductive structures (e.g., Chiariello and Roughgarden 1984, Thomas 1996*a*), biomechanical limitations (e.g., McMahon 1973, Givnish 1988), ontogenetic changes in photosynthetic physiology and water relations (Friend 1993, Yoder et al. 1994, Thomas and Bazzaz 1999), and, in at least some cases, meristem limitation (e.g., Geber 1990). Potential effects of elevated CO_2 on these and other processes may be due to direct or indirect interactions with hormonal regulation of plant growth (cf. Reekie 1996). Hormonal interactions may, for example, help explain accelerated rates of maturation under elevated CO_2 observed in some species, including effects on heteroblastic leaf development (Thomas and Bazzaz 1996), reproductive onset (Farnsworth et al. 1996), and whole-plant senescence (St. Omer and Horvath 1983).

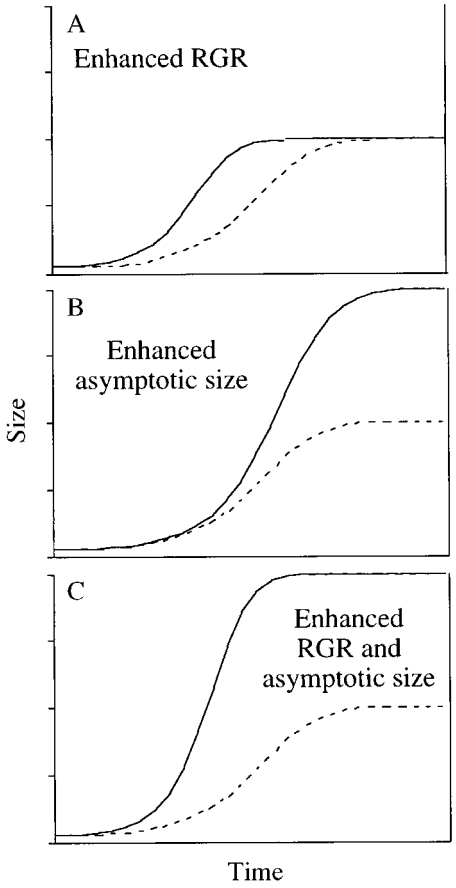

FIG. 1. Hypothetical growth curves illustrating potential patterns of plant growth responses to elevated CO_2: (A) species showing effects on early RGR only; (B) species showing effects on asymptotic size only; and (C) species showing effects on both RGR and asymptotic size. Negative responses might also occur, increasing the range of possibilities. The logistic equation is assumed, with an RGR enhancement of 30%, and an asymptotic size enhancement of 100% for cases showing a growth enhancement.

The present study investigates early vs. asymptotic plant growth responses on the basis of a controlled-environment experiment examining CO_2 responses of eight herbaceous plants characteristic of recently disturbed sites on the Atlantic seaboard of North America. One of these species is replicated at the genotype level, allowing comparisons of intra- vs. interspecific patterns of variation in these variables. Each species was grown individually and in dense monocultures, enabling comparisons of individual plant vs. stand-level responses. The primary questions we address are: (1) Do the plant species in question exhibit increased asymptotic size under elevated CO_2? (2) If so, is there a relationship between early growth responses and asymptotic size

responses? (3) How do asymptotic size responses compare among growth metrics, such as biomass components and leaf area? (4) How do early and asymptotic responses of dense monocultures compare to responses of individually grown plants? and (5) Are early and asymptotic growth response patterns predictable in terms of growth form or other plant characteristics?

Materials and Methods

Plant species and growth conditions.—Species chosen for study include widespread annuals and short-lived perennials characteristic of waste areas in the eastern United States. These include two species of erect annual plants (*Abutilon theophrasti* Medic. and *Cassia obtusifolia* L.), three short-lived perennial rosette species (*Plantago major* L., *Rumex crispus* L., and *Taraxacum officinale* Weber), and three grass species (*Dactylis glomerata* L., *Lolium multiflorum* Lam., and *Panicum dichotomoflorum* Michx.). A third erect annual species, *Ambrosia artemesiifolia* L., was also initially included in the experimental design, but performed very poorly under all treatments, and was therefore excluded from the final analyses. *Plantago* and *Rumex* seeds were collected locally in Cambridge, Massachusetts. Seed of *Cassia, Taraxacum, Dactylis, Lolium,* and *Panicum* was obtained through a commercial source (F and J Weed Seed Suppliers, Woodstock, Illinois), and originally collected from naturally occurring populations in Illinois (with the exception of *Lolium,* which was commercial grass seed originally cultivated in Oregon). *Abutilon* seed was obtained from the selfed offspring of eight cloned genotypes originally sampled in an abandoned agricultural field near Urbana, Illinois. *Abutilon* genotypes were a subset of those used in a previous experiment in which plants were cloned by apical meristem enhancement, and grown under a variety of light, water, and nutrient conditions (for further details see: Bazzaz et al. 1996, Jasienski et al. 1997). For each genotype seed was pooled from several individuals grown under high nutrient, high light conditions. *Abutilon* seed was stored in a dry room at 35°C until use.

Plants were grown in a glasshouse at Harvard University over a period of 118–172 d from germination to final harvest (over the period August 1993–February 1994). Six glasshouse modules were maintained at a constant temperature regime (26°/18°C) and two CO_2 levels (nominally 350 and 700 μL/L, with daytime levels maintained to within 20 μL/L). A 14-h day length was maintained throughout the experiment, with light levels at bench height maintained at a minimum photosynthetic photon flux density (PPFD) of ~400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ using metal halide lamps. There were three replicate glasshouse modules per CO_2 level, with treatment levels of each module assigned randomly (in a staggered array) prior to the start of the experiment. Seed of all species were initially allocated among CO_2 treatments and blocks, and germinated in plugs of the same soil as used in the experiment. Randomly selected seedlings of healthy appearance were then transplanted into the two density treatments, with timing varying according to the duration necessary for a given species to produce viable transplants. Individually grown plants were maintained in 15 cm internal diameter × 20 cm deep pots (3.5 L soil volume), with 12 replicate individuals per species per module (four in the case of *Abutilon* genotypes). High-density monocultures were planted in a hexagonal array at a density of 540 plants/m^2 in 38 × 48 × 20 cm deep plastic tubs (~35 L total soil volume). The planting design included two rows of ''border plants'' on each side of the tubs not included in the measurements, with a total of 48 ''target'' and 48 ''border'' plants/tub, and two replicate tubs per glasshouse module. *Abutilon* tubs were planted with an equal mixture of the eight genotypes (six replicates/genotype/tub) randomly allocated within the central target area of the hexagonal array. The total sample size initially planted was thus 576 plants/species at high density, and 72 plants/species for individually grown plants (192 in the case of *Abutilon*), giving a grand total of 5304 plants used in the main experiment.

Soil was obtained from a construction site in eastern Massachusetts, and was homogenized, but not sterilized, before use. The soil was texturally a sandy loam, with a pH of 5.2, organic content of 4.4%, and P, K, and Mg levels of 0.027, 0.22, and 0.099%, respectively (i.e., very low P and K, but moderately rich Mg content). (Soil analyses were conducted by the Schweizer Labor für Bodenanalytik und Umwelttechnik, Zürich, Switzerland.) Growth containers were sealed in order to eliminate nutrient loss, and watering was conducted by hand on a daily basis to ensure that soil was moist, but below ''field capacity.'' Measurements of gravimetric soil water content were made at the end of experiment for a subset of growth containers. The average was 14.6 % (dry mass basis), with differences no greater than 4% found among treatments or species (indicating that we were successful in providing similar water levels). Following seedling transplantation, a slow-release fertilizer was added as a top dressing to growth containers (Osmocote R 15:10:10 6-mo release; Sierra Chemical Company, Milpitas, California) at a rate corresponding to 150 kg $N \cdot ha^{-1} \cdot yr^{-1}$, calculated on a soil surface area basis. The N dosage used is at the high end of estimated rates of net mineralization plus N deposition in midlatitude forests (e.g., Nadelhoffer et al. 1983, Aber et al. 1993), so as to approximate soil conditions likely to obtain in abandoned agricultural fields and other ''waste areas'' in the region. Growth containers for both density treatments had the same depth, so that N additions were the same on both an area and a soil volume basis. N addition rates on a per-plant basis naturally differ between the density treatments.

Harvests were conducted after a period of 118–172 d following germination (88–151 d after transplanting);

TABLE 1. Allometric equations used to estimate early plant biomass (M, in grams) as a function of leaf area (A, in square centimeters).

Species	Treatments	Equation
Abutilon theophrasti	350 μL/L, individual	$M = 0.531A^{2.032}$
	700 μL/L, individual	$M = 0.316A^{2.257}$
	350 μL/L, high density	$M = 0.479A^{2.087}$
	700 μL/L, high density	$M = 0.453A^{2.074}$
Cassia obtusifolia	all treatments	$M = 0.011A^{0.905}$
Dactylis glomerata	350 μL/L	$M = 0.013A^{1.234}$
	700 μL/L	$M = 0.028A^{1.094}$
Lolium multiflorum	all treatments	$M = 0.104A^{0.829}$
Panicum dichotomoflorum	350 μL/L	$M = 0.018A^{1.134}$
	700 μL/L	$M = 0.045A^{0.990}$
Plantago major	individual	$M = 0.077A^{0.694}$
	high density	$M = 0.051A^{0.694}$
Rumex crispus	350 μL/L	$M = 0.003A^{1.289}$
	700 μL/L	$M = 0.005A^{1.351}$
Taraxacum officinale	350 μL/L	$M = 0.062A^{0.705}$
	700 μL/L	$M = 0.137A^{0.684}$

Notes: Equations are based on model I regressions of log-transformed data, pooling data from harvested plants that spanned a range of sizes in all treatment combinations. Where separate equations are given by treatment, this indicates that significant differences were found in slope or intercept values by treatment (at $P < 0.05$, ANCOVA F test).

timing varied between species so as to insure that plants had reached a stable or declining leaf area, estimated on the basis of nondestructive measurements (see below). At harvest, plants were divided into above- and belowground parts, and reproductive parts (including fruits, seeds, and flowers), dried to constant dry mass in a forced-air oven, and weighed to the nearest 0.001 g. In the case of the three grass species it was not possible to extract roots separately for each individual plant within dense monocultures. For grasses the central target area of the growth containers was excised and washed, and the total root mass allocated in proportion to measured aboveground biomass for each individual.

Nondestructive allometric estimates of leaf area and plant biomass.—Growth and development of aboveground parts of plants were monitored using periodic nondestructive measurements. At each measurement period the length of every leaf on a given plant was estimated to the nearest centimeter. For most species, this could be accomplished by visual estimates, which greatly reduced physical contact with plants, particularly early in development. These leaf length records were kept for all individually grown plants, and for a subset of 12 plants/tub for plants located in central part of the tub of the high-density treatment. Three to six such sets of measurements were made for each species in each treatment. In addition, frequent notes on canopy height and developmental stage were also maintained to ensure that each species had reached a steady or declining leaf area prior to final harvest.

Several sources of data were used to establish allometric relationships between leaf length and area, and between total plant leaf area and biomass. For each of the study species, an additional set of plants, transplanted into the 3.5-L pots described above, were grown during the course of the experiment, and harvested after 30–50 d of growth. For each species there were six high-density pots (seven plants/pot), and six individually grown plants, giving 48 plants/species at ambient CO_2. Total biomass and leaf area were determined for this set of plants (the latter using a LI-COR 1200 leaf area meter: LI-COR, Lincoln, Nebraska). In addition, relationships between leaf length and leaf area were established for each species using a subset of individuals and at least 50 leaves per species. This data was supplemented by similar measurements made on plants from the final harvest of the main experiment (thus including both CO_2 treatments) for species that did not senesce and drop leaves. For the species that did show marked leaf drop and senescence (*Abutilon theophrasti* and *Cassia obtusifolia*), allometric data for early growth at both CO_2 treatments from other experiments was utilized (S. C. Thomas, *unpublished data*; Farnsworth and Bazzaz, 1995). Species-specific allometric data on leaf size measures, total leaf area and biomass included plants at a wide range of sizes and ontogenetic states in all four density and CO_2 treatment combinations, but excluded senescing plants. The same allometric relationships were applied in all sequential measurements (although such relationships may change with plant growth, particularly in competing populations: e.g., Weiner and Thomas 1992). We acknowledge that the allometric approach used could thus potentially yield biased estimates of early relative growth rate (RGR) enhancements, particularly if there are large transient CO_2 or density effects on root:shoot relationships or leaf mass ratio. However, the early growth enhancements reported here for individually grown plants closely match previously published values on a species-by-species basis (comparing to values summarized by Poorter et al. 1996).

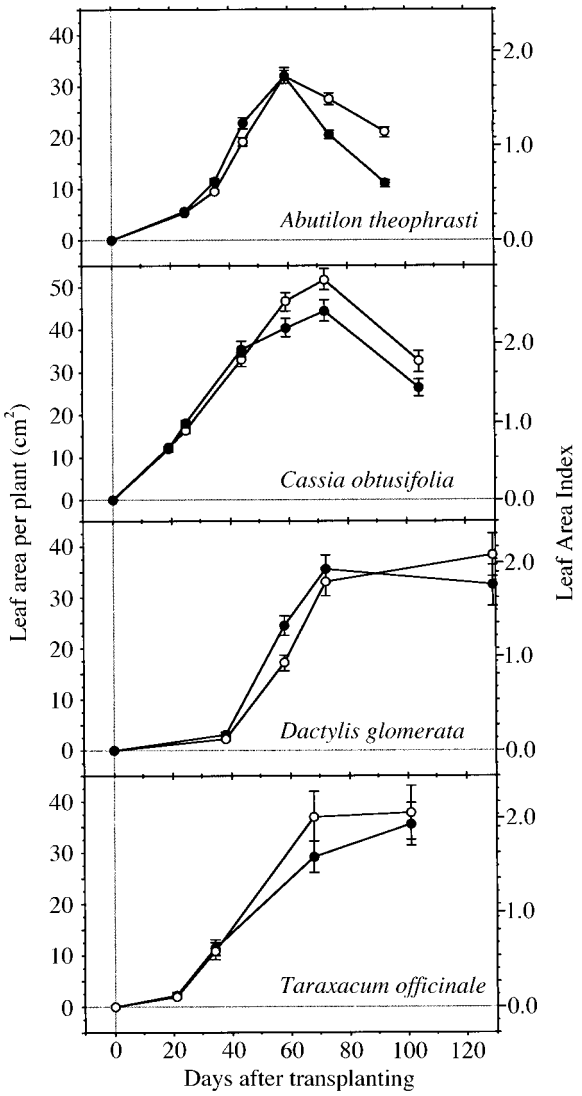

FIG. 2. Observed changes in leaf area through ontogeny in four herbaceous plant species grown in dense monocultures at elevated and ambient CO_2 (350 μL/L [○] and 700 μL/L [●], respectively). Leaf area is quantified both as area per plant (left-hand axis, note different scales), and as leaf area index (LAI, right-hand axis). Means are plotted ±1 SE.

Most species showed no pronounced effects of density or CO_2 on leaf shape. A single allometric equation of the form $A = aL^b$ (where A is leaf area, L is leaf length, and a and b are constants, fit using model I regression of log–log transformed data) was therefore used to estimate leaf areas from leaf lengths (data not shown). The three rosette species, *Plantago*, *Rumex*, and *Taraxacum*, did show marked CO_2 effects on leaf shape (see Thomas and Bazzaz 1996), and for these species treatment-specific allometric relationships were used. Allometric equations used to estimate total biomass as a function of leaf area are listed in Table 1.

The earliest stages of postgermination plant growth are often characterized by a stable or even declining temporal pattern of plant biomass when plant growth is dependent mainly on stored seed reserves (cf. Causton and Venus 1981). The period of truly exponential plant growth is also very short, commonly <3 d for agricultural species (e.g., Causton and Venus 1981, Gifford et al. 1996). These facts complicate the interpretation of ''initial'' relative growth rate in plants, and also present methodological difficulties, since plants must reach some appreciable size before nondestructive estimates of biomass are feasible. The estimates of ''early'' growth enhancements presented here are therefore based on a back-calculation procedure (see Poorter et al. 1996). Under the assumption of exponential growth, the difference in RGR between environments may be calculated as:

$$\mathrm{RGR_e} - \mathrm{RGR_a} = \ln(W_e/W_a)/(t_1 - t_2) \qquad (1)$$

where $\mathrm{RGR_e}$ is the relative growth under elevated CO_2, $\mathrm{RGR_a}$ is the relative growth under ambient CO_2 (in $g \cdot g^{-1} \cdot d^{-1}$), W_e and W_a are estimated plant masses at elevated and ambient CO_2, respectively, and $t_1 - t_2$ is the duration of growth, here taken as the time from seedling transplantation to the first measurement. Similar calculations were made for initial relative growth rate on a leaf area basis (leaf area relative growth rate [LARGR], expressed in square centimeters per square centimeter per day).

Statistical analysis.—The overall experiment employed a split-plot design in which CO_2 was the main plot effect, species/genotype and density were subplot effects, and pairs of glasshouse modules were the block (main plot) effect (e.g., Underwood 1997). Block was considered a random effect, and other effects were considered fixed; the denominator mean square for F tests of the CO_2 main effect was thus the CO_2 × block interaction term (i.e., the main plot error term), while the subplot error was used for all other tests. In order to compute a MANOVA for the experiment (and thus present global probability levels that preserve a correct experiment-wide error rate), it was necessary to omit the CO_2 × block interaction, and test all effects using the subplot error term.

Preliminary analyses included examination of residuals for both untransformed and log-transformed data. In both cases there were significant deviations from normality (Levene's test; Levene 1960) for some variables. Also, variances were generally not equal between density treatments (as is generally the case, Weiner and Thomas 1986; analysis based on Lilliefors' test, Lilliefors 1967). This source of heteroscedasticity was not readily eliminated by data transformation. Probability levels should be judged accordingly. For ease of interpretation, we present results based on untransformed data in all cases. Statistical analyses made use of several software packages (Data Desk 4.2 [Velleman 1992]; S-plus [Statistical Sciences 1992]; Systat [Wilkinson et al. 1992]). Hierarchical cluster analysis was

TABLE 2. MANOVA results for pooled analyses examining species, density, and CO_2 effects on the following set of seven growth parameters: measurements at 17–26 d of leaf area and estimated plant biomass (''early'' growth parameters), maximal leaf area, and final biomass of roots and shoots, total vegetative mass, and total plant mass including reproductive parts (''asymptotic'' growth parameters).

Source	Lambda	df	*F*	*P*
A) Variation among species				
Species	0.0068	49	316	<0.0001
Density	0.4168	7	364	<0.0001
Sp × Den	0.0257	42	241	<0.0001
CO_2	0.7098	7	106	<0.0001
Sp × CO_2	0.4936	49	28.2	<0.0001
Den × CO_2	0.7146	7	104	<0.0001
Sp × Den × CO_2	0.6347	42	20.7	<0.0001
Block	0.9289	14	9.77	<0.0001
B) Variation among genotypes				
Genotype	0.6633	49	6.33	<0.0001
Density	0.1297	7	695	<0.0001
Gen × Den	0.7799	49	3.81	<0.0001
CO_2	0.1664	7	519	<0.0001
Gen × CO_2	0.7874	49	3.63	<0.0001
Den × CO_2	0.5870	7	72.9	<0.0001
Gen × Den × CO_2	0.7930	49	3.52	<0.0001
Block	0.7818	14	13.6	<0.0001
C) Combined analysis				
Species/Genotype	0.0063	98	142	<0.0001
Den	0.4152	7	361	<0.0001
S/G × Den	0.0246	91	99.8	<0.0001
CO_2	0.6961	7	112	<0.0001
S/G × CO_2	0.4740	98	14.5	<0.0001
Den × CO_2	0.7134	7	103	<0.0001
S/G × Den × CO_2	0.6207	91	9.77	<0.0001
Block	0.9279	14	9.76	<0.0001

Notes: Analyses are conducted for: (A) the eight plant species examined, (B) the eight genotypes of *Abutilon theophrasti,* and (C) both species and genotype combined as a single class variable. Analyses are based on a subset of 1859 plants (of a total *N* of 5304) for which estimates of all growth parameters were available. Statistical tests utilize Wilks' lambda statistic and approximate multivariate *F* values.

performed using Systat (version 5.2, Wilkinson et al. 1992). The cluster analysis presented used a single-linkage algorithm, and employed Mojena's ''stopping rule'' to estimate group number (as modified by Milligan and Cooper 1985; see Everitt 1993).

RESULTS

Overall patterns of growth and mortality.—Plants of all species established well under the experimental conditions, and closed canopies (leaf area index [LAI] > 1) were formed in the high-density treatments within 30–60 d (Fig. 2). High-density tubs ultimately formed stands with an LAI of 1.8–3.0. Several experimental units were excluded from analyses on an a priori basis: specifically, one block of *Plantago* suffered high mortality and poor establishment at both densities, and several growth containers for other species were severely flooded by a glasshouse roof leak. Excluding these experimental units, mortality was otherwise low for all species, averaging 0.3% for individually grown plants, and 2.2% for the high-density monocultures. Additionally, the seed stock for *Panicum* was contaminated by several other grass species (22% of the total number, mostly of the species *Digitaria sanguinalis* [L.] Scop.), and these plants were also excluded from all analyses.

Pooled statistical analyses.—Multivariate analysis of variance for the entire pooled data set indicates highly significant main effect terms for CO_2, density, and species, as well as significant CO_2 × density, CO_2 × species, and CO_2 × density × species interactions for the matrix of growth metrics examined (Table 2). CO_2, density, and genotype terms, and their interactions, were also significant in analyses using the eight sampled genotypes of *Abutilon* (Table 2; see also Bazzaz et al. 1995, Thomas and Jasienski 1996). In addition, pooled ANOVAs were conducted separately for each of the parameters describing early growth (leaf area and estimated biomass at 17–26 d) and asymptotic growth (maximal leaf area, and final biomass of roots, shoots, total vegetative mass, and vegetative plus reproductive mass). These ANOVA results also indicate significant ($P < 0.05$) main effect and/or interaction terms in most cases (analyses not shown). Both sets of analyses support the general conclusion that growth responses to CO_2 and density treatments were species- (and genotype-) specific, and that CO_2 and density effects were not simply additive.

TABLE 3. Early and asymptotic growth responses for individually grown plants.

Species	CO_2 (μL/L)	Early leaf area (cm^2)	ΔLARGR (d^{-1})	Early biomass (g)	ΔRGR (d^{-1})	Max. leaf area (cm^2)	Change (%)
Abutilon theophrasti	350	8.61	+0.023	0.104	+0.031†	230	−7.3
	700	12.68		0.175		213	
Cassia obtusifolia	350	22.59	+0.018	0.190	+0.016	NA	
	700	31.68		0.258		NA	
Dactylis glomerata	350	8.30	+0.008	0.189	+0.033*	403	−31.6*
	700	9.65		0.346		276	
Lolium multiflorum	350	18.94	+0.013	1.174	+0.011	270	−11.9
	700	24.13		1.433		238	
Panicum dichotomoflorum	350	6.14	+0.041*	0.149	+0.074*	NA	
	700	12.95		0.565		NA	
Plantago major	350	3.61	+0.013	0.187	+0.012	144	+0.7
	700	5.01		0.255		145	
Rumex crispus	350	8.97	+0.010	0.063	+0.044	329	−27.4
	700	11.23		0.171		239	
Taraxacum officinale	350	28.67	+0.001	0.574	+0.038	368	−40.8
	700	29.57		1.282		218	
CO_2 main effect		NS		NS		NS	
CO_2 × species interaction		NS		***		***	
Abutilon theophrasti genotypes							
J	350	9.34	+0.012	0.174	+0.040**	235	+7.4
	700	11.38		0.341		252	
C	350	8.68	+0.014	0.162	+0.042	181	+3.0
	700	11.08		0.332		186	
B	350	7.63	+0.036	0.145	+0.063†	237	−14.8
	700	14.16		0.419		202	
G	350	8.99	+0.039	0.168	+0.065†	233	−8.7
	700	17.51		0.508		213	
H	350	9.04	+0.009	0.169	+0.037	239	−10.3
	700	10.56		0.317		214	
A	350	8.80	+0.017	0.164	+0.044*	217	−12.4
	700	11.68		0.348		190	
D	350	8.95	+0.014	0.168	+0.042†	253	−8.5
	700	11.42		0.341		232	
E	350	7.43	+0.036	0.141	+0.062	240	−10.7
	700	13.65		0.404		214	
CO_2 main effect		NS		†		NS	
CO_2 × genotype interaction		NS		NS		NS	

Notes: ''Early'' size measures were made at 17–26 d following seedling transplant; ''asymptotic'' size measures were made following a leveling-off or decline in leaf area after 88–151 d of growth (118–172 d from germination to harvest). Early leaf areas are based on measurements of every leaf on a subset of plants for each taxon, and early biomass is an allometric estimate based on these measurements (see Table 1). Significance levels indicated are based on a split-plot analysis of variance (NS $P > 0.10$; † $0.05 < P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). CO_2 effects on early growth parameters are expressed in terms of a back-calculated change in initial relative growth rate on a leaf area (ΔLARGR) or biomass basis (ΔRGR); effects on asymptotic growth parameters are expressed as a percentage change relative to the control; NA indicates data not available.

Early growth parameters.—Among individually grown plants, there was a strong CO_2 × species interaction, with enhancements in initial RGR ranging from 0.011 to 0.074 $g \cdot g^{-1} \cdot d^{-1}$ (Table 3). Considering species individually, early growth enhancements were significant only in the case of *Dactylis* and *Panicum*; however, all species showed a qualitative trend toward increased RGR and LARGR under elevated CO_2. Individual genotypes of *Abutilon* also showed consistently positive early growth effects, with enhancements in LARGR ranging from 0.012 to 0.039 $cm^2 \cdot cm^{-2} \cdot d^{-1}$ and in RGR ranging from 0.037 to 0.063 $g \cdot g^{-1} \cdot d^{-1}$ among the eight genotypes. There was a significant CO_2 main effect term, though not a significant CO_2 × genotype interaction term, for individually grown *Abutilon* genotypes.

Positive effects of CO_2 on early growth were also generally found for plants grown in high-density mono-

TABLE 3. Extended.

Final veg. mass (g)	Change (%)	Final root mass (g)	Change (%)	Final reprod. mass (g)	Change (%)
2.31	+14.8	0.52	+4.0	0.89	+13.5
2.66		0.54		1.01	
5.66	+24.9*	1.53	+32.6*	1.85	−23.3
7.08		2.03		1.42	
21.84	+11.9	15.74	+16.4	NA	
24.44		18.32		NA	
18.88	+3.0	9.88	+2.2	0.90	+29.8
19.44		10.09		1.17	
1.64	+115.4†	0.46	+148.4	0.97	−1.9
3.52		1.15		0.95	
3.64	+6.4	2.64	+9.7	NA	
3.87		2.90		NA	
9.79	+26.1*	8.66	+34.2*	NA	
12.34		11.63		NA	
8.68	+61.2	6.43	+77.6†	NA	
14.00		11.42		NA	
NS		NS		NS	
***		***		†	
2.44	+27.8	0.42	+57.2	0.86	+31.0
3.11		0.67		1.12	
1.86	+16.6	0.65	−16.8	0.73	+33.8
2.18		0.54		0.97	
2.40	−11.9	0.54	−28.9	0.93	+30.9
2.11		0.38		1.22	
2.11	+17.8	0.44	+03.7	0.85	+39.9
2.49		0.45		1.19	
2.46	+9.5	0.55	−10.2	1.00	+5.2
2.70		0.49		1.05	
2.29	+0.8	0.45	−2.5	1.06	−19.8
2.31		0.44		0.85	
2.66	+37.5	0.53	+58.1	0.81	−25.3
3.66		0.84		0.61	
2.27	+18.5	0.53	−11.7	0.87	+19.1
2.69		0.47		1.04	
NS		NS		NS	
*		*		*	

cultures, but with some exceptions (Table 4). Four of the eight species examined, and five of eight *Abutilon* genotypes, showed significantly enhanced LARGR, RGR, or both, under elevated CO_2. Surprisingly, *Plantago major* showed significantly reduced LARGR and RGR under elevated CO_2, contributing to a significant $CO_2 \times$ species interaction for early growth responses under high density. There was a significant main effect term for early RGR responses of *Abutilon* genotypes to CO_2 at high density, but no corresponding $CO_2 \times$ genotype interaction.

Pairwise tests indicate that differences in responses of LARGR and RGR to elevated CO_2 were significantly greater in magnitude for individually grown plants than for the high-density monocultures (Fig. 3). This pattern is supported for comparisons among species, among *Abutilon* genotypes, and for the combined data set.

Asymptotic growth parameters.—There were significant $CO_2 \times$ species interactions detected for most asymptotic growth parameters, with both positive and significant negative effects of CO_2 detected (Tables 3 and 4). Negative effects were commonly observed for maximum leaf area, with the majority of species and genotypes showing such a trend under both density conditions. Surprisingly, such declines were larger and more consistent for plants grown individually. In contrast, vegetative mass at final harvest generally increased under elevated CO_2 in both density treatments. In some cases, such as *Rumex crispus* and *Abutilon* genotype E, taxa with negative CO_2 effects on maximal leaf area showed substantial positive effects on final vegetative biomass. All plant species with significant CO_2 effects on final vegetative mass also showed substantial CO_2 effects on final root mass. For some species, such as *Rumex* and *Taraxacum*, biomass enhancements were largely or entirely due to enhanced root growth.

Only four of the species reproduced during the course of the experiment. *Cassia obtusifolia* showed a trend toward declining reproductive mass under elevated CO_2 in both density treatments (Tables 3 and 4; see also Farnsworth and Bazzaz 1995). *Abutilon* genotypes showed both increases and decreases in reproductive mass, with a significant $CO_2 \times$ genotype interaction at high density (Tables 2–4; see also Bazzaz et al. 1995, Thomas and Jasienski 1996). CO_2 effects on reproduction did not reach significance for the two grass species that produced seed during the experiment (*Lolium* and *Panicum*).

Relationships among response variables.—Table 5 lists the correlation matrices among early and asymptotic growth response measures. In all cases significant correlations are positive in sign for both among-species and among-genotype relationships (note that in three cases pairs of variables are not statistically independent: namely, total vegetative mass vs. root or shoot mass, and early LARGR vs. early RGR). However, there were also numerous low negative correlations between response variables, accounting for one-third of the total number (excluding the six autocorrelated variable pairs). For example, species and genotypes exhibiting greater early growth responses tended to show greater reductions in maximal leaf area under elevated CO_2. The overall correspondence between patterns found among species and among genotypes (i.e., the correlation between elements of the species matrix vs. the genotype matrix in Table 5) was low ($r = 0.216$; $P > 0.05$). Among genotypes, early growth responses were correlated with final reproductive responses. Differences between the interspecific and genetic correlation matrices are likely due, at least in part, to the fact that genotypes at high density were grown in competition (see Thomas and Jasienski 1996).

TABLE 4. Early and asymptotic growth responses for plants grown in high-density monocultures.

Species	CO_2 (μL/L)	Early leaf area (cm^2)	ΔLARGR (d^{-1})	Early biomass (g)	ΔRGR (d^{-1})	Max. leaf area (cm^2)	Change (%)
Abutilon theophrasti	350	5.36	+0.003	0.104	+0.031*	35	−6.8
	700	5.61		0.175		32	
Cassia obtusifolia	350	12.35	−0.002	0.111	−0.002	55	+11.0
	700	11.93		0.107		49	
Dactylis glomerata	350	2.26	+0.018†	0.039	+0.054**	44	−19.3
	700	3.14		0.102		35	
Lolium multiflorum	350	11.00	+0.020*	0.745	+0.016	84	+47.8*
	700	15.81		1.000		124	
Panicum dichotomoflorum	350	2.51	+0.002	0.056	+0.041	41	+34.4
	700	2.62		0.116		55	
Plantago major	350	4.63	−0.023	0.137	−0.018*	30	+34.5*
	700	2.53		0.087		40	
Rumex crispus	350	5.38	+0.004	0.029	+0.034*	51	−21.4*
	700	5.87		0.063		40	
Taraxacum officinale	350	1.99	+0.004	0.139	+0.006	52	−17.6
	700	2.17		0.158		43	
CO_2 main effect		NS		NS		NS	
CO_2 × species interaction		***		***		***	
Abutilon theophrasti genotypes							
J	350	5.87	+0.002	0.113	+0.030*	45	−20.3
	700	6.04		0.188		36	
C	350	5.13	−0.003	0.100	+0.025*	25	−10.5
	700	4.87		0.154		22	
B	350	4.97	+0.007	0.097	+0.034	35	−1.9
	700	5.58		0.173		34	
G	350	5.07	+0.002	0.099	+0.030	30	−5.6
	700	5.22		0.164		29	
H	350	5.24	+0.011	0.102	+0.039*	36	+27.5
	700	6.33		0.197		46	
A	350	5.52	+0.004	0.107	+0.032*	35	−24.1
	700	5.94		0.185		27	
D	350	5.63	+0.003	0.109	+0.031	43	−13.3
	700	5.91		0.185		37	
E	350	5.43	−0.004	0.105	+0.024***	34	−5.5
	700	5.07		0.160		32	
CO_2 main effect		NS		*		NS	
CO_2 × genotype interaction		NS		NS		NS	

Notes: "Early" size measures were made at 17–26 d following seedling transplant; the early leaf areas are based on measurements of every leaf on a given plant; early biomass is estimated on the basis of allometric equations estimated separately for each species (see Table 1). Significance levels indicated are based on a split-plot analysis of variance (NS $P > 0.10$; † $0.05 < P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). CO_2 effects on early growth parameters are expressed in terms of a back-calculated change in initial relative growth rate on a leaf area (ΔLARGR) or biomass basis (ΔRGR); effects on asymptotic growth parameters are expressed as a percentage change relative to the control; NA indicates data not available.

Relationships were also examined between RGR under ambient CO_2 and observed responses among species and genotypes (Figs. 4 and 5). There was no significant correlation between these measures for individually grown plants ($r = -0.089$; $P > 0.644$: Fig. 4). However, lack of correlation is largely determined by outlying values for a few species that showed quite high RGR values, but very low RGR responses: namely, *Taraxacum* and *Plantago,* as well as the grass *Lolium.* Excluding these species there is a positive correlation between RGR and the observed RGR response, similar to that reported by Poorter et al. (1996) ($r = 0.706$; Model I regression equation: $\Delta RGR = -0.014 + 0.524[RGR]$). In contrast, there is no evidence for any relationship between RGR and the CO_2 response of final plant biomass (Fig. 5).

A hierarchical cluster analysis was conducted to describe patterns of variation in the varying aspects of

TABLE 4. Extended.

Final veg. mass (g)	Change (%)	Final root mass (g)	Change (%)	Final reprod. mass (g)	Change (%)
0.304	+13.8	0.03	+22.3	0.10	−22.7
0.346		0.04		0.08	
0.41	+43.2	0.06	+19.8	0.29	−26.5
0.58		0.07		0.22	
1.44	+9.9	0.87	+0.8	NA	
1.58		0.88		NA	
2.33	+3.5	1.32	−7.6	0.08	+22.2
2.41		1.22		0.09	
0.55	+0.6	0.26	+0.0	0.16	−12.1
0.56		0.26		0.14	
0.77	+11.7	0.53	+10.4	NA	
0.87		0.58		NA	
0.41	+41.9*	0.29	+64.5*	NA	
0.58		0.48		NA	
0.63	+13.2	0.34	+39.9†	NA	
0.71		0.47		NA	
*		NS		NS	
NS		***		***	
0.36	+9.5	0.04	+14.4	0.15	−30.8
0.39		0.05		0.11	
0.21	−15.8	0.02	+2.6	0.60	−16.7
0.18		0.02		0.05	
0.28	+5.2	0.03	+16.5	0.12	+1.6
0.30		0.04		0.12	
0.23	+11.1	0.03	+19.5	0.09	−12.4
0.25		0.03		0.08	
0.31	+66.8*	0.03	+83.7†	0.13	+16.6
0.52		0.06		0.15	
0.34	−13.0	0.03	−7.4	0.09	−50.5
0.30		0.03		0.04	
0.45	+17.5	0.04	+24.0	0.09	−69.7
0.53		0.05		0.03	
0.26	+20.6*	0.03	+20.2	0.11	−35.4
0.31		0.04		0.07	
NS		NS		NS	
NS		NS		NS	

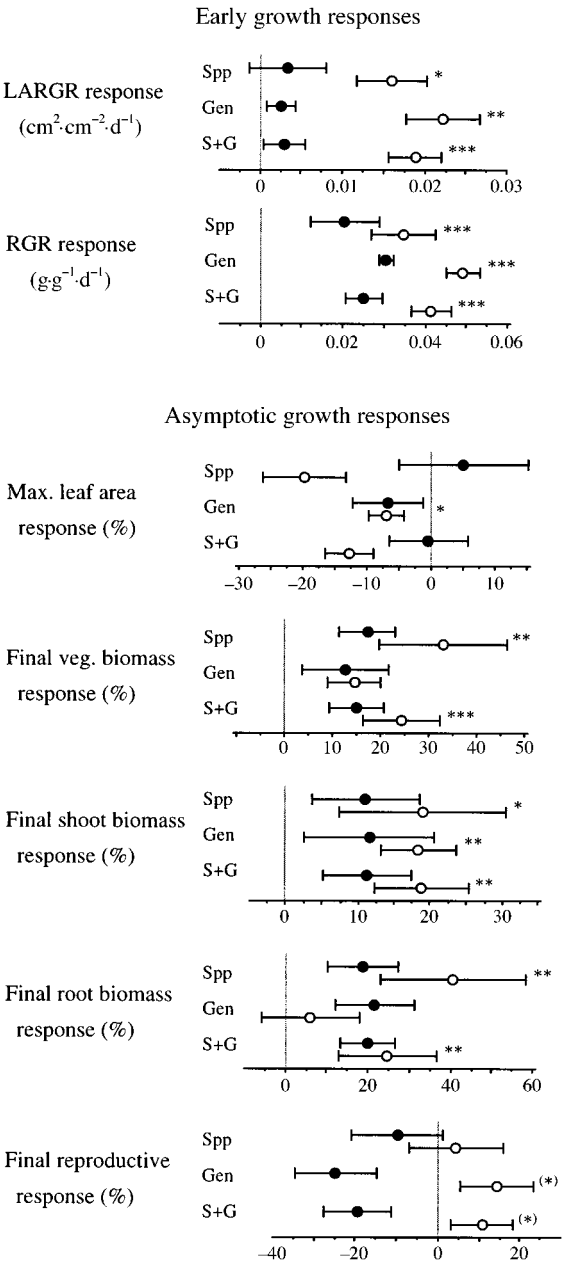

FIG. 3. Responses of individually grown plants (○) and of dense monocultures (●) to elevated CO_2. For each variable, average responses are calculated among species (Spp), among genotypes of *Abutilon* (Gen), and for the combined data set (S + G). Mean responses are plotted ±1 SE. Statistical results are based on paired *t* tests (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

CO_2 response observed among plant species and *Abutilon* genotypes (Fig. 6). Two trends of interest are apparent. First, plant growth forms (namely erect annuals, rosette species, and grasses) were not consistently grouped, but rather interspersed throughout the phenetic tree. Second, although five of the eight *Abutilon* genotypes were closely grouped, response patterns shown by other genotypes are interspersed among the broader sample of species. Genotype H, in particular, was an extreme genetic variant, showing a remarkably high CO_2 response at high density, with a disproportionate root response (Table 3). Genotype H was nearly as divergent in its multivariate response pattern as was the species showing the greatest deviation, *Panicum dichotomofolium*. Application of a standard ''cutoff rule'' segregates three groups: *Panicum*, genotype H, and the residual group of all other species and genotypes (Fig. 6). The cluster analysis thus indicates that the multivariate patterns of response among genotypes are similarly variable to those among species, and also fails to detect discrete groups among the taxa considered.

TABLE 5. Correlation matrices between responses of early and asymptotic growth metrics to elevated CO_2.

	Early		Late				
	ΔLARGR	ΔRGR	ΔMax. LA	ΔVeg. Mass	ΔShoot Mass	ΔRoot Mass	ΔReprod. Mass
Among-species correlations							
ΔLARGR	1.000						
ΔRGR	0.694**	1.000					
ΔMax. LA	−0.162	−0.230	1.000				
ΔVeg. Mass	0.394	0.477	−0.119	1.000			
ΔShoot Mass	0.483	0.316	0.205	0.731**	1.000		
ΔRoot Mass	0.369	0.480	−0.187	0.948***	0.550*	1.000	
ΔReprod. Mass	0.428	0.087	0.193	−0.223	−0.183	−0.196	1.000
Genetic correlations for *Abutilon theophasti* population							
ΔLARGR	1.000						
ΔRGR	†	1.000					
ΔMax. LA	−0.019	−0.016	1.000				
ΔVeg. Mass	0.043	0.045	0.774***	1.000			
ΔShoot Mass	0.168	0.171	0.760***	0.958***	1.000		
ΔRoot Mass	−0.308	−0.309	0.664**	0.805***	0.611*	1.000	
ΔReprod. Mass	0.672**	0.675**	0.480	0.199	0.326	−0.096	1.000

Note: Pearson product-moment correlations are used, pooling both density treatments in all analyses (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

† Not estimated.

DISCUSSION

A primary finding of this study is that enhancements in early plant growth under elevated CO_2 do not necessarily correspond to similar effects on plant size late in ontogeny. In fact, each of the theoretical possibilities illustrated in Fig. 1 was actually found empirically among the species examined (Fig. 7). For example, *Rumex crispus* showed substantial enhancements of both early relative growth and maximum vegetative mass under elevated CO_2. In contrast, *Lolium multiflorum*, while exhibiting significant early growth enhancements, showed almost no CO_2 effect on asymptotic biomass. Finally, *Taraxacum officinale* showed little or no effect of elevated CO_2 on early relative growth, but a positive effect on final biomass. In accordance with this range of patterns, among-species correlations between early vs. asymptotic growth enhancements were quite weak, ranging from −0.23 to +0.48 (Table 5).

The absence of significant correlations between early and asymptotic enhancements does not imply that such effects are unpredictable. Rather, CO_2 effects on asymptotic plant size varied in a consistent manner among plant size metrics, and in response to plant density. Most species exhibited reductions in maximum

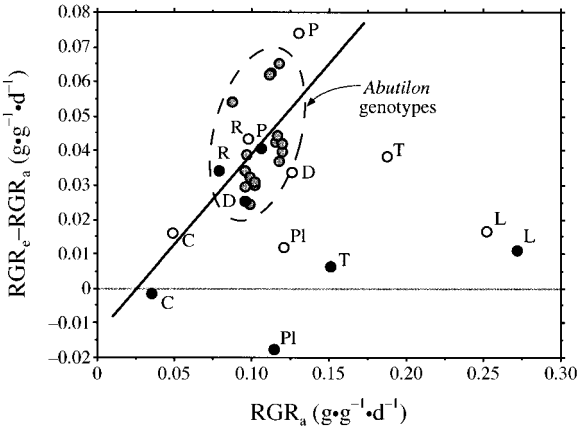

FIG. 4. Early growth responses as a function of RGR relationship between relative growth rate at ambient CO_2 (RGR_a) and the absolute response in RGR to elevated CO_2 ($RGR_e - RGR_a$). Closed symbols indicate plants grown individually, and open symbols indicate plants grown in high-density monocultures. *Abutilon theophrasti* genotypes are denoted by shaded points. Other species are denoted as follows: C, *Cassia obtusifolia*; D, *Dactylis glomerata*; L, *Lolium multiflorum*; P, *Panicum dichotomoflorum*; Pl, *Plantago major*; R, *Rumex crispus*; and T, *Taraxacum officinale*.

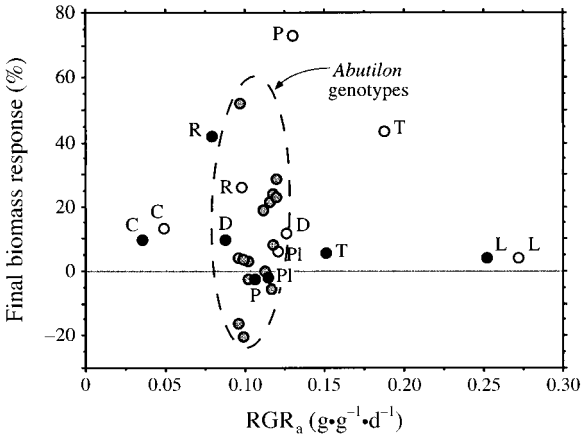

FIG. 5. Asymptotic growth responses as a function of RGR relationship between relative growth rate at ambient CO_2 (RGR_a) and the relative change in total biomass under elevated CO_2 ([mass at 700 μL/L − mass at 350 μL/L]/[mass at 350 μL/L]). Symbols are as in Fig. 4.

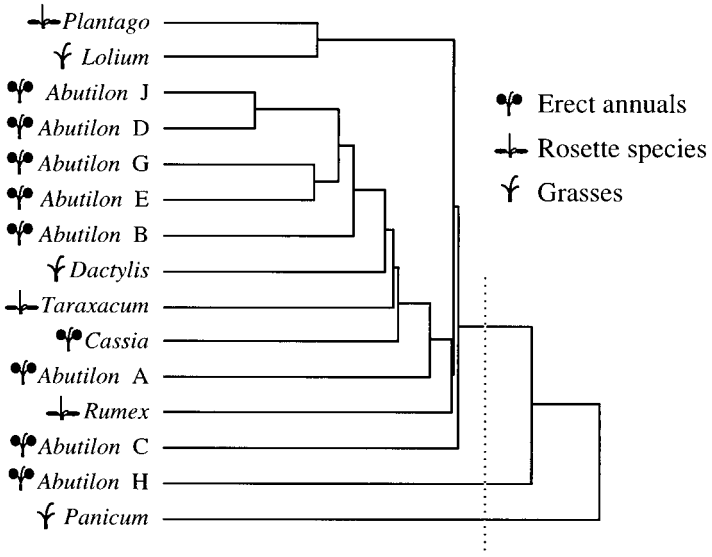

FIG. 6. Cluster diagram generated on the basis of CO_2 growth response parameters for both density treatments, pooling all study species and *Abutilon* genotypes. A single-linkage algorithm was used. The dotted line gives the breakpoint delineating groups given by Mojena's stopping rule at a *k* value of 1.25 (cf. Everitt 1993), which yields a division into two groups of one taxa each (*Panicum* and *Abutilon* genotype H), and a third group comprising all of the remaining taxa. Alternative clustering methods yield similar qualitative results.

leaf area under elevated CO_2, while also showing substantial increases in final biomass (Table 2, Fig. 3). In addition, species exhibiting large increases in final total biomass also tended to show a disproportionate effect of CO_2 on root growth (Tables 3–5). This pattern was especially pronounced in species forming large taproots (i.e., *Rumex* and *Taraxacum*). Early growth responses were lower for high-density monocultures than for individually grown plants, with a threefold difference in average LARGR responses observed between density treatments. Similarly, responses for asymptotic values of biomass components were also much lower at high density than for individually grown plants. The most dramatic interactive effect of density and CO_2 involved reproductive responses, which were positive for individually grown plants, but were, on average, negative for plants at high density (Fig. 3).

Comparisons with previous research.—As noted in the introduction, previous studies examining CO_2 effects on plant growth have not explicitly sought to quantify asymptotic size. However, a closely related issue that has received attention is the response of steady-state leaf area index in single and multispecies stands (Oechel and Riechers 1986, Körner and Arnone 1992, Arnone and Körner 1995, Schäppi and Körner 1995, Hättenschwiler and Körner 1996, Hirose et al. 1996). In general, little or no response in steady-state LAI to elevated CO_2 has been found in nonagricultural systems (cf. Körner 1996). The present study supports this general conclusion, but also indicates substantial variation in potential LAI responses among species. LAI responses averaged only +6%; however, observed values varied from −21% in *Rumex crispus* monocultures, to +48% in *Lolium multiflorum* monocultures (Table 4).

It has often been assumed that changes in LAI under rising CO_2 are driven by decreases in the leaf-level light compensation point (e.g., Valle et al. 1985, Long and Drake 1992, Hirose et al. 1996). However, observations of negative effects of elevated CO_2 on leaf area are not expected under this mechanism. An additional unexpected result in the present study was that individually grown plants showed more consistent effects of CO_2 on leaf area than did high-density monocultures, with a strong trend toward reduced maximum leaf area under elevated CO_2 (Fig. 3). The species with the largest observed reduction in maximal leaf area under elevated CO_2 was *Taraxacum officinale*, which produces an exaggerated ''adult'' leaf morphology under elevated CO_2 (Thomas and Bazzaz 1996). These observations suggest that CO_2 effects on LAI may commonly be determined by species-specific changes in leaf development and morphology, rather than by changes in photosynthetic physiology.

A number of reviews have previously stressed the importance of belowground storage organs and other morphological carbon sinks as a determinant of CO_2 growth responses (e.g., Cure 1985, Körner 1993). Because such structures do not generally develop until late in plant ontogeny, we suggest that this sink strength factor may primarily determine plant responses to CO_2 late in ontogeny, but have little predictive value for early growth responses. This hypothesis is supported by our data: strong responses of final biomass were in every case accompanied by disproportionate effects on root mass at harvest, most notably in species producing taproots. However, such species did not necessarily show strong CO_2 enhancements of growth early in ontogeny (Tables 3–5). A similar result has also recently been reported by Reekie (1996), in a study of agricultural species and varieties within the genus *Brassica.* Taxa that developed large reproductive structures late in ontogeny, such as broccoli and cauliflower, showed the strongest CO_2 responses late in ontogeny, whereas

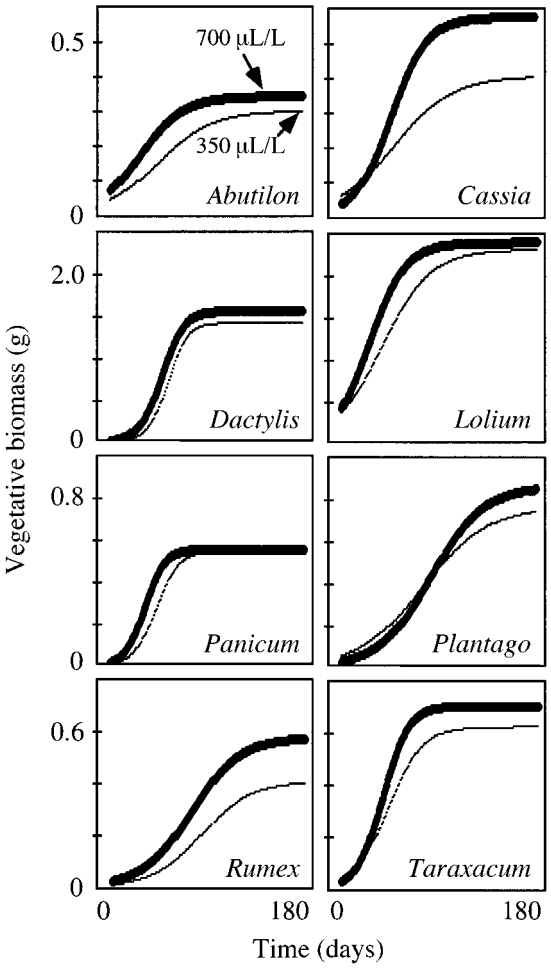

FIG. 7. Estimated growth curves for eight study species under elevated (▬▬) vs. ambient (——) CO_2 atmospheres, for high-density monocultures. Growth curves were fit as a logistic function ($dM/dt = rM((K - M)/K)$, where M is plant mass, t is time, r is initial RGR, and K is asymptotic plant mass), using parameter estimates for early RGR and asymptotic vegetative mass listed in Table 4.

taxa that did not produce such structures, such as mustard and rape, showed little or no size increase at final harvest.

Only a few previous comparisons have been made between growth responses to elevated CO_2 of individually grown plants vs. dense monocultures. Wayne and Bazzaz (1996) have recently reported data for yellow birch (*Betula alleghaniensis*) seedlings, finding that growth enhancements after one season were +49% for individually grown seedlings vs. +16% for dense populations. These figures are not directly comparable to the calculated RGR enhancements presented here; however, both sets of results suggest that CO_2 enhancements of early plant growth are reduced by local crowding. This generalization thus appears to hold for both comparisons between individuals vs. plant monocultures, as studied here, and also for comparisons between individuals vs. mixed-species stands (Ackerly and Bazzaz 1995).

Functional types and correlates of CO_2 responses among and within species.—Much recent attention has been given to the issue of elucidating functional types among plants that show similar responses to rising CO_2 and other aspects of global change (e.g., Smith et al. 1997). We agree that it is absolutely necessary to aggregate responses in some manner in order to formulate tractable models. However, this goal may be accomplished in many ways. The idea that discrete functional types exist at all should be treated as a hypothesis, and not as an a priori assumption. The comparative analyses presented here (cf. Figs. 4–6), suggest that readily recognizable growth forms among herbaceous plant species do not correspond closely to patterns of growth response to elevated CO_2. Moreover, genetic variation within a single species was found to be remarkably large, with, for example, the most variant genotype examined being nearly as divergent in response pattern as the most variant species (Fig. 6). This result agrees with other recent analyses suggesting that intraspecific variation in responses to CO_2 rivals the variation observed among species (cf. Curtis et al. 1996, Thomas and Jasienski 1996). Particularly in light of this result, we suggest that the ''problem of aggregation'' would be better approached by using methods analogous to those employed in quantitative genetics (e.g., Lynch and Lande 1993). Ecologists interested in vegetation responses to global change should be quantifying parameters that describe distributions of response and patterns of covariation among response components within and among species, rather than assuming uniform types on an a priori basis.

Comparative studies and reviews have previously noted that species with higher intrinsic growth rates tend to show greater responsiveness to elevated CO_2 (e.g., Cure 1985, Poorter 1993). This pattern has recently been expressed as a relationship between the absolute enhancement in RGR, and RGR under controlled conditions (Poorter et al. 1996). It has also been suggested that differences in intrinsic RGR may be the primary determinant of interspecific variation in CO_2 responses (Poorter 1993, Poorter et al. 1996). Our results do not consistently support this latter hypothesis. Rather, we found a substantial proportion of species with high RGR that do not show large early growth responses to elevated CO_2. Notable examples of this pattern include *Lolium multiflorum* and *Taraxacum officinale* (Fig. 3). As illustrated in Fig. 3, variation in RGR (due to either genetic or environmental effects) appears to impose an upper bound to possible RGR enhancement under elevated CO_2, with some species consistently falling well below this upper bound. This pattern suggests that aspects of physiology and morphological development other than RGR can substantially constrain early growth responses to CO_2 in some taxa. We also examined possible relationships between

RGR and CO_2 responses of asymptotic plant size (Fig. 4). In contrast to the pattern found for early growth, there was no evidence for any relationship. This result, as well as the lack of a close correspondence between early and asymptotic growth responses, supports the general conclusion that physiological determinants differ greatly for early vs. asymptotic growth responses.

In light of the great interest in long-term CO_2 responses of trees (e.g., Norby et al. 1992, 1996, Bazzaz et al. 1993, Curtis and Wang 1998), it is worth considering the potential implications of our results for forest responses to rising CO_2. Woody plants tend to have a lower initial RGR than do herbaceous species, and comparative analyses also indicate that trees display relatively low stimulations of RGR under elevated CO_2 (Poorter et al. 1996). However, our results suggest that asymptotic growth responses are not related to RGR at all, but rather are determined, at least in part, by the degree to which large carbon sinks are formed late in plant ontogeny. Some aspects of tree growth, such as height extension, may be asymptotic (Thomas 1996*b*); however, the limited functional life span of xylem tissue predisposes woody plants to a nonasymptotic pattern of diameter growth and wood production (Zimmerman 1983, Thomas 1996*b*). This growth pattern could also predispose trees to show increasing sink potential, and thus relatively large effects of elevated CO_2 on biomass, late in ontogeny. The longest term data available examining CO_2 effects on tree growth extend to only slightly beyond the inflection point of estimated growth curves (cf. Hättenschwiler et al. 1997, Idso and Kimball 1997). Forest modelers are thus presently compelled either to assume that asymptotic growth responses to rising CO_2 are zero (e.g., Bolker et al. 1995), or to apply the same physiological or growth responses observed for seedlings and saplings to large trees and/or whole forests (e.g., Luxmoore et al. 1990, Kirschbaum et al. 1994). In the absence of direct data, values for asymptotic responses of herbaceous species may provide some indication of possible asymptotic forest growth responses; however, there is a clear and pressing need for experiments examining asymptotic size responses for short-lived woody plants.

Given the lack of correlation between early vs. asymptotic growth responses, the question also arises as to which parameter is of greater ecological significance. This will depend to a large extent on the specific ecological system and time frame in mind; however, we suggest that both kinds of effect are generally of importance and interest. For example, consider the case of forest plantations managed as a carbon sink (e.g., Row 1996). Assuming that harvests occur near the growth curve inflection point, species or genotypes that show higher initial RGR should generally be preferred. A positive correlation between RGR and early growth response simply reinforces this conclusion. On the other hand, initial RGR responses may be of little value in predicting CO_2 effects on carbon storage by older forests. From an evolutionary perspective, we expect that asymptotic growth responses may be more closely related to reproductive output, and would thus be favored by natural selection under rising CO_2. However, in order to predict the consequences of selection to future growth patterns, analyses should examine genetic correlation structure through the entire course of ontogeny (cf. Thomas and Jasienski 1996; M. Jasienski, S. C. Thomas, and F. A. Bazzaz, *unpublished manuscript*). Finally, it should also be emphasized that more than two growth parameters may be necessary to understand many important ecological impacts of rising CO_2. Of particular interest are potential CO_2 effects on reproductive timing, seed germination, and plant senescence (e.g., Farnsworth and Bazzaz 1995, Farnsworth et al. 1996).

In conclusion, fundamental principles and empirical data both point to the importance of distinguishing between what we have termed early vs. asymptotic components of plant growth responses to elevated CO_2. Distinguishing between these two types of response is a necessary step in understanding physiological mechanisms that account for variation in responses among and within plant species. This distinction is also essential in formulating models aimed at predicting vegetation responses to global change. A complete understanding of the multidimensional effects of CO_2 through plant ontogeny, including effects on leaf area, biomass components, leaf and root loss, and allometric relationships among these components, is ultimately desirable. However, we suggest that even for the modest goal of characterizing effects of a stepchange in CO_2 on plant growth for a given species in a given environment, one parameter is not enough.

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LITERATURE CITED

Aber, J. D., A. Magill, R. Boone, J. M. Melillo, P. Steudler, and R. Bowden. 1993. Plant and soil responses to chronic nitrogen additions at the Harvard forest, Massachusetts. Ecological Applications **3**:156–166.

Ackerly, D. D., and F. A. Bazzaz. 1995. Plant growth and reproduction along CO_2 gradients: non-linear responses and implications for community change. Global Change Biology **1**:199–207.

Arnone, J. A., and C. Körner. 1995. Soil and biomass carbon pools in model communities of tropical plants under elevated CO_2. Oecologia **104**:61–71.

Bazzaz, F. A. 1990. The response of natural ecosystems to the rising global CO_2 levels. Annual Review of Ecology and Systematics **21**:167–196.

Bazzaz, F. A., S. L. Bassow, G. M. Berntson, and S. C. Thomas. 1996. Elevated CO_2 and terrestrial vegetation: im-

plications for and beyond the global carbon budget. Pages 43–76 *in* B. Walker and W. Steffen, editors. Global change and terrestrial ecosystems. Cambridge University Press, Cambridge, UK.

Bazzaz, F. A., K. Garbutt, E. G. Reekie, and W. E. Williams. 1989. Using growth analysis to interpret competition between a C_3 and a C_4 annual under ambient and elevated CO_2. Oecologia **79**:223–235.

Bazzaz, F. A., M. Jasienski, S. C. Thomas, and P. Wayne. 1995. Microevolutionary responses in experimental populations of plants to CO_2-enriched environments: parallel results from two model systems. Proceedings of the National Academy of Sciences, USA **92**:8161–8165.

Bazzaz, F. A., S. L. Miao, and P. Wayne. 1993. CO_2-induced growth enhancements of co-occurring tree species decline at different rates. Oecologia **96**:478–482.

Bolker, B. M., S. W. Pacala, F. A. Bazzaz, C. Canham, and S. A. Levin. 1995. Species diversity and carbon dioxide fertilization of temperate forests. Global Change Biology **1**:373–381.

Bowes, G. 1991. Growth at elevated CO_2: photosynthetic responses mediated through Rubisco. Plant, Cell and Environment **14**:795–806.

Causton, D. R., and J. C. Venus. 1981. The biometry of plant growth. Arnold Press, London, UK.

Chiariello, N., and J. Roughgarden. 1984. Storage allocation in seasonal races of an annual plant: Optimal versus actual allocation. Ecology **65**:1290–1301.

Coleman, J. S., and F. A. Bazzaz. 1992. Effects of CO_2 and temperature on growth and resource use of co-occurring C_3 and C_4 annuals. Ecology **73**:1244–1259.

Cure, J. D. 1985. Carbon dioxide doubling responses: A crop survey. Pages 99–116 *in* B. R. Strain and J. D. Cure, editors. Direct effects of increasing carbon dioxide on vegetation. United States Department of Energy Report DOE/ER-0238. National Technical Information Service, Springfield, Virginia, USA.

Cure, J. D., and B. Acock. 1986. Crop response to carbon dioxide doubling: A literature survey. Agricultural and Forest Meteorology **38**:127–145.

Curtis, P. S. 1996. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. Plant, Cell and Environment **19**:127–137.

Curtis, P. S., D. J. Klus, S. Kalisz, and S. J. Tonsor. 1996. Intraspecific variation in CO_2 responses in *Raphanus raphanistrum* and *Plantago lanceolata*: assessing the potential for evolutionary change with rising atmospheric CO_2. Pages 13–29 *in* C. Körner and F. A. Bazzaz, editors. Carbon dioxide, populations and communities. Academic Press, San Diego, California, USA.

Curtis, P. S., and X. Wang. 1998. A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. Oecologia **113**:299–313.

Everitt, B. S. 1993. Cluster analysis. Third edition. Arnold Press, London, UK.

Farnsworth, E. J., and F. A. Bazzaz. 1995. Inter- and intrageneric differences in growth, reproduction, and fitness of nine herbaceous annual species grown in elevated CO_2 environments. Oecologia **104**:454–466.

Farnsworth, E. J., A. M. Ellison, and W. K. Gong. 1996. Elevated CO_2 alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L.). Oecologia **108**:599–609.

Friend, A. D. 1993. The prediction and physiological significance of tree height. Pages 101–115 *in* A. M. Solomon and H. H. Shugart, editors. Vegetation dynamics and global change. Chapman and Hall, New York, USA.

Geber, M. A. 1990. The cost of meristem limitation in *Polygonum arenastrum*: Negative genetic correlations between fecundity and growth. Evolution **44**:799–819.

Gifford, R. M., D. J. Barrett, F. L. Lutze, and A. B. Samarakoon. 1996. Agriculture and global change: scaling direct carbon dioxide impacts and feedbacks through time. Pages 229–259 *in* B. Walker and W. Steffen, editors. Global change and terrestrial ecosystems. Cambridge University Press, Cambridge, UK.

Givnish, T. J. 1988. Adaptation to sun and shade: A whole plant perspective. Australian Journal of Plant Physiology **15**:63–92.

Hättenschwiler, S., and C. Körner. 1996. System-level adjustments to elevated CO_2 in model spruce ecosystems. Global Change Biology **2**:377–387.

Hättenschwiler, S., F. Miglietta, A. Raschi, and C. Körner. 1997. Thirty years of *in situ* tree growth under elevated CO_2: a model for future forest responses? Global Change Biology **3**:463–471.

Hirose, T., D. D. Ackerly, and F. A. Bazzaz. 1996. CO_2 elevation and canopy development in stands of herbaceous plants. Pages 413–430 *in* C. Körner and F. A. Bazzaz, editors. Carbon dioxide, populations and communities. Academic Press, San Diego, California, USA.

Idso, S. B., and B. A. Kimball. 1997. Effects of long-term atmospheric CO_2 enrichment on the growth and fruit production of sour orange trees. Global Change Biology **3**:89–96.

IPCC. 1996. Climate change 1995. International Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Jasienski, M., F. J. Ayala, and F. A. Bazzaz. 1997. Phenotype plasticity and similarity of DNA among genotypes of an annual plant. Heredity **78**:176–181.

Johnson, D. W., P. H. Henderson, J. T. Ball, and R. F. Walker. 1996. Effects of CO_2 and N on growth and N dynamics in ponderosa pine: results from the first two growing seasons. Pages 23–40 *in* G. W. Koch and H. A. Mooney, editors. Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, California, USA.

Kimball, B. A. 1983. Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. Agronomy Journal **75**:779–788.

Kirschbaum, M. U. F., D. A. King, H. N. Comins, R. E. McMurtrie, B. E. Medlyn, S. Pongracic, D. Murty, H. Keith, R. J. Rason, P. K. Khanna, and D. W. Sheriff. 1994. Modelling forest response to increasing CO_2 concentration under nutrient-limited conditions. Plant, Cell and Environment **17**:1081–1099.

Körner, C. 1993. CO_2 fertilization: the great uncertainty in future vegetation development. Pages 53–70 *in* A. M. Solomon and H. H. Shugart, editors. Vegetation dynamics and global change. Chapman and Hall, New York, New York, USA.

———. 1996. The response of complex multispecies systems to elevated CO_2. Pages 20–42 *in* B. Walker and W. Steffen, editors. Global change and terrestrial ecosystems. Cambridge University Press, Cambridge, UK.

Körner, C., and J. A. Arnone III. 1992. Responses to elevated carbon dioxide in artificial tropical ecosystems. Science **257**:1672–1675.

Levene, H. 1960. Robust tests for equality of variance. Pages 278–292 *in* I. Olkin, editor. Contributions to probability and statistics. Princeton University Press, Palo Alto, California, USA.

Lilliefors, H. W. 1967. On the Kolmorogrov-Smirnov test for normality with mean and variance unknown. Journal of the American Statistical Association **64**:399–402.

Loehle, C. 1995. Anomalous responses of plants to CO_2 enrichment. Oikos **73**:181–187.

Long, S. P., and B. G. Drake. 1992. Photosynthetic CO_2 assimilation and rising atmospheric CO_2 concentrations. Pages 69–101 in N. R. Baker, and H. Thomas, editors. Crop

photosynthesis: spatial and temporal dynamics. Elsevier, Amsterdam, The Netherlands.

Luxmoore, R. J., M. L. Tharp, and D. C. West. 1990. Simulating the physiological basis of tree-ring responses to environmental changes. Pages 393–401 in R. K. Dixon, R. S. Meldahl, G. A. Ruark, and W. G. Warren, editors. Process modeling of forest growth responses to environmental stress. Timber Press, Portland, Oregon, USA.

Lynch, M., and R. Lande. 1993. Evolution and extinction in response to environmental change. Pages 234–250 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts, USA.

McMahon, T. 1973. Size and shape in biology. Science **179**: 1201–1204.

Milligan, G. W., and M. C. Cooper. 1985. An examination of procedures for determining the number of clusters in a data set. Psychometrica **50**:159–179.

Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen mineralization gradient in Southern Wisconsin (USA). Canadian Journal of Forest Research **13**:12–21.

Norby, R. J., S. D. Wullschleger, and C. A. Gunderson. 1996. Tree responses to elevated CO_2 and implications for forests. Pages 1–22 *in* G. W. Koch and H. A. Mooney, editors. Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, California, USA.

Norby, R. J., S. D. Wullschleger, C. A. Gunderson, E. G. O'Neill, and M. K. McCracken. 1992. Productivity and compensatory responses of yellow-poplar trees in elevated CO_2. Nature **357**:322–324.

Oechel, W. C., and G. H. Riechers. 1986. Impacts of increasing CO_2 on natural vegetation, particularly the tundra. Pages 36–42 *in* C. Rosenzweig and R. Dickinson, editors. Climate-vegetation interactions. Goddard Space Flight Center, Greenbelt, Maryland, USA.

Poorter, H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. Vegetatio **104/105**:77–97.

Poorter, H., C. Roumet, and B. D. Campbell. 1996. Interspecific variation in the growth response of plants to elevated CO_2: a search for functional types. Pages 375–412 *in* C. Körner and F. A. Bazzaz, editors. Carbon dioxide, populations, and communities. Academic Press, San Diego, California, USA.

Reekie, E. G. 1996. The effect of elevated CO_2 on developmental processes and its implications for plant–plant interactions. Pages 333–346 *in* C. Körner and F. A. Bazzaz, editors. Carbon dioxide, populations, and communities. Academic Press, San Diego, California, USA.

Rogers, H. H., J. D. Cure, J. F. Thomas, and J. M. Smith. 1984. Influence of elevated CO_2 on growth of soybean plants. Crop Science **24**:361–366.

Row, C. 1996. Effects of selected forest management options on carbon storage. Pages 59–90 *in* R. N. Sampson and D. Hair, editors. Forests and global change. Volume 2. American Forests, Washington, D.C. USA.

Schäppi, B., and C. Körner. 1995. Growth responses of an alpine grassland to elevated CO_2. Oecologia **105**:43–52.

Smith, T. M., H. H. Shugart, and F. I. Woodward, editors. 1997. Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge, UK.

Statistical Sciences. 1992. S-plus for DOS reference manual. Statistical Sciences, Seattle, Washington, USA.

St. Omer, L., and S. M. Horvath. 1983. Elevated carbon dioxide concentrations and whole plant senescence. Ecology **64**:1311–1314.

Thomas, S. C. 1996*a*. Reproductive allometry in Malaysian rain forest trees: biomechanics vs. optimal allocation. Evolutionary Ecology **10**:517–530.

———. 1996*b*. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. American Journal of Botany **83**:556–566.

Thomas, S. C., and F. A. Bazzaz. 1996. Elevated CO_2 and leaf shape: are dandelions getting toothier? American Journal of Botany **83**:106–111.

Thomas, S. C., and F. A. Bazzaz. 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology **80**:278–294.

Thomas, S. C., and M. Jasienski. 1996. Genetic variability and the nature of microevolutionary responses to elevated CO_2. Pages 51–81 *in* C. Körner and F. A. Bazzaz, editors. Carbon dioxide, populations, and communities. Academic Press, San Diego, California, USA.

Tolley, L. C., and B. R. Strain. 1984. Effects of CO_2 enrichment on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings under different irradiance levels. Canadian Journal of Forest Research **14**:343–350.

Tremmel, D. C., and D. T. Patterson. 1994. Effects of elevated CO_2 and temperature on development in soybean and five weeds. Canadian Journal of Plant Science **74**:43–50.

Underwood, A. J. 1997. Experiments in ecology : their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, UK.

Valle, R., J. W. Mishoe, W. J. Campbell, J. W. Jones, and L. H. Allen. 1985. Photosynthetic response of 'Bragg' soybean leaves adapted to different CO_2 environments. Crop Science **25**:333–339.

Velleman, P. F. 1992. Data desk 4.2 handbook. Data Descriptions, Ithaca, New York, USA.

Walters, M. B., E. L. Kruger, and P. B. Reich. 1993. Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. Oecologia **94**:7–16.

Wayne, P. M., and F. A. Bazzaz. 1996. Seedling density modifies the growth responses of yellow birch maternal families to elevated carbon dioxide. Global Change Biology **1**:315–324.

Weiner, J., and S. C. Thomas. 1986. Size variability and competition in plant monocultures. Oikos **47**:211–222.

Weiner, J., and S. C. Thomas. 1992. Competition and allometry in three species of annual plants. Ecology **73**:648–656.

Wilkinson, L., A. Hill, J. P. Welna, and G. K. Birkenbeuel. 1992. SYSTAT for Windows: statistics, version 5. Systat, Evanston, Illinois, USA.

Wullschleger, S. D., W. M. Post, and A. W. King. 1995. On the potential for a CO_2 fertilization effect in forests: estimates of the biotic growth factor based on 58 controlled-exposure studies. Pages 85–107 *in* G. M. Woodwell and F. T. MacKenzie, editors. Biotic feedbacks in the global climatic system: will the warming feed the warming? Oxford University Press, New York, New York, USA.

Yoder, B. J., M. G. Ryan, R. H. Waring, A. W. Schoettle, and M. R. Kaufman. 1994. Evidence of reduced photosynthetic rates in old trees. Forest Science **40**:513–527.

Zimmerman, M. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, Germany.