Competitive status influences tree-growth responses to elevated CO_2 and O_3 in aggrading aspen stands

E. P. McDONALD,*† E. L. KRUGER,‡ D. E. RIEMENSCHNEIDER* and
J. G. ISEBRANDS*

*USDA-Forest Service, Forestry Sciences Laboratory, 5985 Hwy K, Rhinelander, WI 54501, and ‡Department of
Forest Ecology and Management, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA*

Summary

1. Competition effects on growth of individual trees were examined for 4 years in aggrading, mixed-clone stands of trembling aspen (*Populus tremuloides* Michx.) at the Aspen-FACE free-air CO_2 and O_3 enrichment facility in northern Wisconsin, USA. During each growing season stands received one of four combinations of atmospheric $[CO_2]$ (ambient *vs* ~56 Pa) and $[O_3]$ (ambient *vs* ~1·5 × ambient).
2. Non-destructive measurements of annual tree growth were compared within and among clones and treatments in relation to an index of competitive status based on the difference between a tree's height and that of its four nearest neighbours. Competitive status strongly influenced tree growth, and the positive growth response to elevated $[CO_2]$ was greater for competitively advantaged individuals than for disadvantaged individuals of most clones.
3. The magnitude of O_3 effects on growth depended on clone and competitive status: for some clones, negative O_3 effects were stronger with competitive advantage while others showed stronger O_3 effects with competitive disadvantage. The interactive effects of CO_2 and O_3 differed among clones, with negative effects of O_3 amplified or ameliorated by elevated CO_2, depending on clone and competitive status.
4. Treatments modified competitive interactions by affecting the magnitude of growth differences among clones. These modifications did not alter clone rankings of competitive performance, but when CO_2 and O_3 were both elevated, the differences in competitive performance among clones decreased.

Key-words: Competitive interactions, FACE, global change, *Populus tremuloides*

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Introduction

Based on trends in emissions and other human activities, much of the Northern Hemisphere will probably experience substantially increased concentrations of carbon dioxide (CO_2) (Keeling *et al*. 1995) and tropospheric ozone (O_3) (Fowler *et al*. 1999). The impact of these atmospheric changes on terrestrial ecosystems may be considerably modified by an array of biotic interactions (Bazzaz & McConnaughay 1992; Bryant, Taylor & Frehner 1998; Lindroth, Kinney & Platz 1993). Plant–plant interactions could influence responses in natural and managed forests, where competition among individuals is omnipresent and assumed to be an important agent shaping community structure and function (Grace & Tilman 1990; Grime 1979). Free-air CO_2 enrichment (FACE) technology can manipulate atmospheric conditions for whole stands of vegetation

(Hendrey *et al*. 1999) and provides the opportunity to examine competition effects on plant responses. The Aspen-FACE experiment in northern Wisconsin, USA is a long-term field study with temperate hardwood stands exposed to altered concentrations of CO_2 and O_3 (Dickson *et al*. 2000).

One overarching hypothesis of the Aspen-FACE experiment is that O_3 stress will decrease the potential benefit of elevated CO_2 for tree growth. Elevated CO_2 generally increases photosynthesis and growth (Ceulemans & Mousseau 1994, Saxe, Ellsworth, & Heath 1998; Woodward, Thompson, & McKee 1991), while increasing tropospheric O_3 typically has negative effects on these parameters (Bortier, Ceulemans & Temmerman 2000; Clark *et al*. 1996; Hogsett *et al*. 1997). Mounting evidence indicates that tree growth under elevated CO_2 is mediated by the availability of other limiting resources (Comins & McMurtrie 1993; Medlyn *et al*. 2000; Oren *et al*. 2001), and competition may thus compromise growth and survival of individual trees by decreasing availability or acquisition of

†Author to whom correspondence should be addressed.
E-mail: epmcdonald@fs.fed.us

limiting resources. Tree size is an effective integrator and metric of an individual's competitive status (Lorimer 1983). Size relationships among competitors may affect relative resource availability in two ways: (1) larger individuals interfere with the acquisition of available resources by smaller individuals; and (2) larger individuals have more stored resources, decreasing total resource availability for smaller competitors while giving larger individuals greater stress tolerance and capacity for growth response to treatment. For this study, these functional considerations underlie our hypothesis that competitively advantaged trees will be proportionally more responsive to elevated CO_2 and less susceptible to O_3 stress than competitively disadvantaged trees.

Differences in size and inherent growth potential interact to determine competitive outcomes within any given neighbourhood. Size relationships among competitors are probably a spatially autoregressive phenomenon: as growth proceeds, disparate size relationships among adjacent competitors are reinforced through time by net differences in absolute growth, even when competitors have similar relative growth rates. While treatment-induced or genotypic growth differences may dampen or reinforce this trend, disparities in absolute growth among competitors can ultimately lead to differential fitness and survival. Based on previous studies (Coleman *et al.* 1995; Karnosky *et al.* 1998; Kubiske *et al.* 1998; Kull *et al.* 1996), we anticipate treatment-mediated shifts in competitive rankings among aspen clones as a consequence of differing sensitivities to CO_2, O_3, and their interaction. We expect that the treatment effects on genotypic competitive potential will be manifested through relative growth responses.

The primary objective of the present study was to determine how competition influences trembling aspen (*Populus tremuloides* Michx.) responses to elevated CO_2 and O_3 exposures. The second was to examine how these atmospheric constituents influence the competitive potential of aspen clones. We addressed these distinct aspects of competition by examining the role of genotype, atmospheric treatments and their complex of interacting effects on aspen growth. The assessment of competition effects on growth required evaluating the initial size of individuals and their competitive environment as growth determinants (Connolly, Wayne & Bazzaz 2001), as variation in either determinant confers differences in initial advantage to individual competitors (*sensu* Black 1958). Within a stand, an individual's size directly affects its subsequent growth, while the individual's size in relation to competitors indirectly affects growth via competition effects. In this experiment we did not manipulate competitive interactions, but relied on (1) existing variation in size relationships among individuals; and (2) genotypic differences in growth rates, with both resulting in substantial variability in competitive environments among individuals.

Materials and methods

EXPERIMENTAL DESIGN

Dickson *et al.* (2000) described the study background, FACE ring construction, and experimental design. The study site is in Oneida County, WI, USA (45·6° N, 89·5° W), with mixed, frigid, coarse, loamy Alfic Haplorthod topsoil. During this 4-year study, averages for rainfall and temperature during the growing season (May–September) were 536 mm and 16·0 °C, respectively. During 1998, periodic irrigation ensured establishment and survival of the young trees, but no irrigation has occurred since August 1998.

The design employs three replications of randomized complete blocks containing a 2×2 treatment factorial of ambient and elevated [CO_2] (36 and 56 Pa, respectively) and ambient and elevated [O_3] (ambient and $1·5 \times$ ambient cumulative exposure, respectively). The FACE rings are spaced at least 100 m apart to minimize cross-contamination of treatment gases. Each 30 m diameter FACE ring is divided into sections utilized for separate studies. Atmospheric conditions at the ring centre are monitored and maintained by computerized systems controlling the release of gases on the upwind side of the plot from vertical vent pipes, evenly spaced along the ring perimeter. A buffer zone extends 5 m from the vents, a distance allowing adequate gas mixing to obtain homogeneous atmospheric conditions toward the plot centre. Atmospheric treatments began in 1998 and were applied during the daytime from May to September. One-minute sample averages indicate that elevated CO_2 concentrations were within 20% of the target (56 Pa) more than 90% of the time, and daytime averages of elevated [O_3] during the growing season were 54·5, 51·1, 48·9 and 52·8 p.p.b. compared with ambient [O_3] of 34·6, 36·9, 36·0 and 36·6 p.p.b. for years 1998, 1999, 2000 and 2001, respectively.

PLANT MATERIAL, GROWTH MEASUREMENTS AND COMPETITION INDICES

The eastern half of each ring contains the trembling aspen competition study. The aspen clones (216, 259, 271, 42E and 8L) have been studied extensively in the Great Lakes region, with results indicating that they span a range for O_3 tolerance and phenological characteristics (Karnosky *et al.* 1998; Kubiske *et al.* 1998; Kull *et al.* 1996). In July 1997, rooted cuttings were planted as randomized pairs of each clone with individuals at a 1×1 m spacing. The portion of each ring excluding the buffer contains approximately 130 trees.

In early June 1998, and following leaf abscission at the end of each growing season, stem height was measured to the nearest centimetre, and basal diameter was measured to the nearest millimetre at 3 cm above soil surface for all core trees. Dimensions in June 1998 represent the initial size of individuals for the 1998 growth

analysis, with final dimensions in 1998, 1999 and 2000 serving as initial sizes for the 1999, 2000 and 2001 growth analyses, respectively. To monitor growth non-destructively, an index of tree size was generated based on the product of diameter$^2 \times$ height (D^2H). Analysis of data from a set of aspen trees harvested from all rings in August 2000 showed that total above-ground biomass was linearly related to D^2H ($R^2 = 0.95$, E.P.M., E.L.K. and J.G.I., unpublished results).

Developing a method for quantifying the competitive status of individual trees required: (1) determining the spatial extent of an individual's competitive environment, the 'neighbourhood'; and (2) developing an appropriate metric for the intensity of competition within neighbourhoods. Preliminary information from spatial statistics showed that an individual's growth was negatively correlated with that of its neighbours over a range of approximately 1·3 m, which included the eight nearest neighbours. This finding, that a tree's competitive environment was apparently dominated by its adjacent neighbours, agrees with results of competition studies in deciduous hardwood stands (e.g. Cole & Lorimer 1994; Hix & Lorimer 1990). Alternative neighbourhood types with membership including the four closest neighbours at the cardinal directions or all eight adjacent neighbours were evaluated. Sample size can be maximized by utilizing individuals both as focal plants and as neighbours of other individuals, but this violates the assumption of independence required for many statistics (Mitchell-Olds 1987). In the present study, competition indices developed for four- *vs* eight-member neighbourhoods were highly correlated with one another, and yielded similar results and interpretations. As a conservative strategy, this analysis utilized the competition index based on the four nearest neighbours to yield sufficient sample size (*c.* 70 trees per plot) while meeting independence assumptions, as individuals were tested either as focal plants or as neighbours, but not both.

Several indices of competitive status were compared, including ratios or residuals based on the dimensions (height and D^2H) of each individual relative to its neighbourhood. The characterization of neighbourhood was unrelated to clone, with the mean dimensions of the four members of the neighbourhood used in the calculations, and neighbours missing due to mortality treated as zero values. The competition metric was chosen based on model fit in analysis of covariance (ANCOVA, described below), according to (1) residual variance; (2) model-fitting statistics; and (3) covariance linearity. The mean difference between the height of an individual and the height of its neighbourhood ($\Delta H = \text{height}_{\text{individual}} - \text{height}_{\text{neighbourhood}}$) during the growing season was chosen as the competitive status index, CSI = ($\Delta H_{\text{initial}} + \Delta H_{\text{final}}$)/2. During a given year, an individual taller than its neighbourhood height was competitively advantaged (CSI > 0), while an individual shorter than its

neighbourhood height was competitively disadvantaged (CSI < 0).

GROWTH ANALYSES AND STATISTICAL METHODS

Our study is a split-plot experiment, with the atmospheric treatment (ambient; $+CO_2$; $+O_3$; $+CO_2 + O_3$) representing the whole-plot level. Clones were chosen based on previous performance. Therefore clone and atmospheric treatments were fixed effects in analysis of variance (ANOVA), whereas replication effects and replication × treatment effects were considered random. Data were analysed according to mixed-model ANOVA or ANCOVA (PROC MIXED, SAS Institute Inc., 1989–2001). Appropriate denominator degrees of freedom for *F*-tests and least-squares means (LS means) estimation were determined by Satterthwaite's approximation. The replication × treatment error (a) terms were either pooled or partitioned, based on tests of differences between the −2 restricted maximum likelihood indices associated with pooled and partitioned models (Littell *et al.* 1996). Pooled error (a) terms were appropriate for most analyses.

To address interannual variation that might affect competitive relationships, growth was assessed year-by-year, accounting for individual size at the start of each growth interval and seasonal CSI. Standard growth analysis requires accounting for initial size differences through covariance analysis or by evaluating growth adjusted for initial size. However, significant clonal differences were always observed in the slope of the relationship between initial size and annual growth (data not shown), which precluded using initial size as a covariate or a basis for adjustment across all clones. Accordingly, to evaluate genotypic, treatment and competition effects simultaneously, a simple method to standardize growth responses was devised to account for differences in initial size and complement the approach used to quantify competitive status. Performance under competitively neutral conditions in the ambient treatment served as the reference for assessing treatment and competition effects. For each year, competitively 'neutral' subpopulations in ambient conditions were identified, and included individuals having CSI values within ±20% of the median tree height for the entire population. Thus competitively neutral trees had heights within ±26, ±50, ±69 and ±82 cm of their neighbourhood for 1998, 1999, 2000 and 2001, respectively. Neutral populations spanned a range of initial sizes, yielding significant regressions of initial D^2H (D^2H_{initial}) *vs* final D^2H (D^2H_{final}) in each year ($P < 0.0001$, R^2 ranges among clones: 0·72–0·92, 0·78–0·93, 0·85–0·94 and 0·88–0·97 for years 1998, 1999, 2000 and 2001, respectively). Each year the regression equations were used to generate predicted final D^2H values ($D^2H_{\text{predicted}}$) for the entire population of trees using D^2H_{initial} values, and standardized net growth (SNG) was calculated as SNG = ($D^2H_{\text{final}} -$

$D^2H_{initial})/(D^2H_{predicted} - D^2H_{initial})$ to facilitate clone comparisons.

The SNG values reflect each clone's net growth in a given treatment and competitive situation relative to performance under competitively neutral, ambient conditions. Annual variation within SNG responses attributable to genotype, atmospheric treatments, CSI, and their interactions can be evaluated using ANCOVA. Once significant covariance was demonstrated ($P < 0.0001$) and unequal slopes among clone and treatment combinations were verified, the full factorial of CSI and fixed effects was tested to explore all patterns of covariance possible within the experimental design. To evaluate average effects during the 4-year period and to condense the presentation of results, the annual SNG and CSI values were averaged for each individual, and those 4-year means were tested with ANCOVA. Significant CSI × treatment effects can lead to misinterpretation of differences among whole-population means for clone × atmospheric treatments due to underlying interactive effects of competition. Different slopes in ANCOVA were accounted for by testing fixed effects and generating LS means at the 10th, 50th and 90th quantiles of the covariate population to capture tree performance at CSI values representative of competitively disadvantaged, neutral and advantaged conditions, respectively. Standard errors (SE) of the LS means calculated by PROC MIXED are valid estimates of true standard errors derived from correct linear combinations of the variance components (Littell *et al.* 1996).

To generate directly comparable relative growth estimates for each clone, the population was restricted to minimize competition effects and avoid initial size × clone effects already described. Sub-sample populations in each treatment included individuals that began and ended a growing season under competitively neutral conditions (i.e. within 20% of mean neighbourhood height yielded adequate representation of all clone × treatment combinations). This approach emphasized the role of genotype, substantially

minimizing other sources of variation. While comparisons among clones for absolute or relative growth cannot be conducted for the entire population, for reasons already stated, these neutral populations were smaller and spanned more limited ranges of initial size than the entire population. Thus relative growth (RG), calculated as $\log(D^2H_{final}) - \log(D^2H_{initial})$, showed consistent behaviour among clones in relation to initial size. In contrast to SNG, which is a measure of relative responsiveness to treatment and competition effects, RG allows direct comparisons of growth potential among clones. Each year, RG results were adjusted to the mean initial size across treatments using the appropriate linear transformation of initial size. The ANOVA results for individual years and the 4-year average for RG were obtained using PROC MIXED.

Finally, treatment effects on competitive performance (CP) were evaluated for each year, based on changes in an individual's D^2H (biomass surrogate) relative to its neighbourhood, where $CP = \Delta D^2H_{individual}/\Delta D^2H_{neighbourhood}$. Initial size ratios (SR) were calculated each year, as $SR = D^2H_{individual}/D^2H_{neighbourhood}$, to serve as covariates for modelling CP results using a PROC MIXED ANCOVA. In this manner, fixed-effects tests and LS means estimated for SR = 1, equivalent to competitively neutral initial conditions, yield CP values for each clone based on growth differences between competitors and neighbours. Average effects were evaluated by testing the mean of annual CP values for each clone from each ring. Annual and 4-year average CP values were ranked by clone, and the significance of crossover effects on clone competitive rankings among treatments were tested using the Van der Laan–de Kroon method (Hühn & Léon 1995; de Kroon & van der Laan 1981).

Results

STANDARDIZED NET GROWTH AND COMPETITIVE STATUS

Competitive status index and its interactions with atmospheric treatments and clone significantly affected SNG in all years; ANCOVA statistics for annual and 4-year average results are reported in Table 1 for reference. The overall positive response of SNG to CSI was consistent among years ($P < 0.0001$, Fig. 1). Although main effects of clone, CO_2 and O_3 were significant ($P < 0.01$), the complex nature of interactive effects can confound the interpretation of main effects. Across all clones and CSI conditions, $+CO_2$ alone had neutral or stimulating effects on SNG. In general, the degree to which $+CO_2$ enhanced growth depended on CSI, the relative enhancement of SNG being 15% greater in competitively advantaged than in disadvantaged conditions (CSI × CO_2, $P = 0.014$). However, the CSI × CO_2 effect was apparently due to responses of clones 216, 259, 271 and 42E, which exhibited stronger growth enhancements in $+CO_2$ under competitively

Table 1. Levels of significance (*P* values) for covariance parameters according to mixed-model analysis of covariance (ANCOVA). Standardized net growth (SNG) responses to CO_2 and O_3 in each growing season were analysed with a factorial of covariance effects utilizing competitive status index (CSI) as the covariate. Average effects of competition were analysed by testing the mean of annual values for SNG and CSI during the 4-year period, with those ANCOVA results identified as the 4-year average

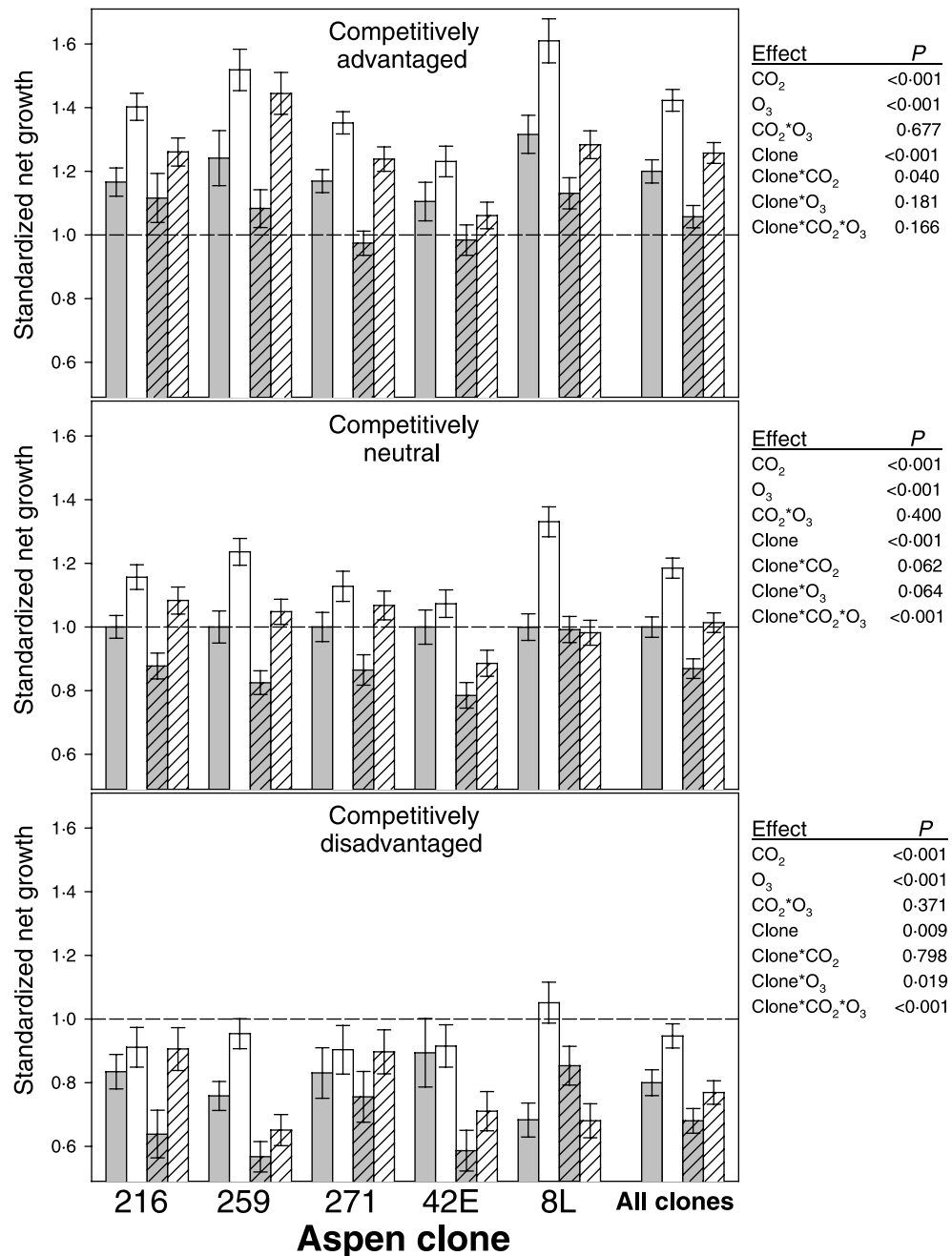| Covariance term	1998	1999	2000	2001	4-year average
CSI	**<0·001**	**<0·001**	**<0·001**	**<0·001**	**<0·001**
CSI × CO_2	0·714	**0·027**	**0·009**	0·261	**0·014**
CSI × O_3	0·186	0·607	0·936	0·656	0·901
CSI × CO_2 × O_3	**0·038**	0·127	0·186	0·524	0·645
CSI × clone	0·443	0·771	**<0·001**	**<0·001**	**<0·001**
CSI × clone × CO_2	0·490	0·902	**0·077**	0·208	0·654
CSI × clone × O_3	**0·034**	0·177	0·958	**0·093**	**0·041**
CSI × clone × CO_2 × O_3	0·286	0·227	0·341	0·402	**0·032**

Fig. 1. Standardized net growth (SNG) responses averaged during the 1998–2001 period for mixed-clone aspen stands exposed to combinations of ambient and elevated CO_2 and O_3. Bars represent least-squares mean estimates (LS means) ± 1 SE for individual clones, with the average response across clones identified as 'All clones'. Shaded bars, ambient CO_2 treatments; unshaded bars, elevated CO_2 treatments; open bars, ambient O_3 treatments; hatched bars, elevated O_3 treatments. The competition status indices (CSI) for this analysis were means of annual CSI values during the 4-year period, with competitively advantaged (+) and disadvantaged (–) LS means calculated at ±90 cm values of the CSI covariate. The dashed horizontal lines denote SNG response in competitively 'neutral' (CSI = 0), ambient conditions, for reference. Analysis of covariance (ANCOVA) results for fixed effects of atmospheric treatments, clone and their interactions under competitively advantaged, neutral and disadvantaged conditions are reported next to each panel. Table 1 reports the significance of covariance parameters for individual years and the 4-year average.

advantaged conditions than under disadvantaged conditions. In contrast, clone 8L showed relatively consistent responses to $+CO_2$ that were minimally influenced by CSI. These clone differences probably contribute to the significant CSI × clone × CO_2 × O_3 effect ($P = 0.032$).

Generally, $+O_3$ alone had neutral or negative effects on SNG (Fig. 1). The magnitude of the O_3 effect on

SNG also depended on clone, with a significant CSI × clone × O_3 interaction ($P = 0.041$) that apparently resulted from some clones (271 and 8L) having larger O_3-induced growth declines in competitively advantaged conditions, whereas other clones (216, 259 and 42E) had larger O_3-induced growth declines in competitively disadvantaged conditions. The $CO_2 × O_3$ effect on SNG was insignificant, while the CSI × clone

$\times CO_2 \times O_3$ effect was significant ($P = 0.032$), together indicating that the interaction of CO_2 and O_3 depended on clone, with CSI modifying these interactive effects. Indeed, the clone $\times CO_2 \times O_3$ effect was more pronounced under competitively neutral or disadvantaged conditions (CSI ≤ 0).

While the effects of CO_2 and O_3 on SNG were generally antagonistic, the clone $\times CO_2 \times O_3$ effects at the representative CSI levels indicate that highly variable responses occurred among clones in the $+CO_2 + O_3$ treatment, with non-additive effects $+CO_2$ and $+O_3$ on SNG in combination. The clone $\times CO_2 \times O_3$ interaction resulted from broad differences in the magnitude of antagonistic effects, ranging from stronger negative effects of $+O_3$ in elevated CO_2 to complete amelioration of negative O_3 effects in elevated CO_2 for some clones in some competitive environments. Differences among clones are exemplified by competitively neutral responses, where clones 259 and 42E apparently showed additive effects of CO_2 and O_3; clone 8L showed non-additive effects resulting from stronger O_3 effects in elevated CO_2; and clones 216 and 271 showed non-additive effects resulting from weaker O_3 effects in elevated CO_2. Furthermore, whether CO_2 and O_3 effects on SNG were additive or non-additive is not consistent within a clone but depended on CSI, hence the CSI $\times$ clone $\times CO_2 \times O_3$ effect ($P = 0.032$). For example, clone 8L apparently showed additive effects of CO_2 and O_3 in competitively advantaged conditions but non-additive effects in competitively disadvantaged conditions.

RELATIVE GROWTH AND COMPETITIVE PERFORMANCE

Under competitively neutral conditions, average relative growth (RG) during the 4-year period was increased by $+CO_2$ and decreased by $+O_3$ (Fig. 2; Table 2). The main effect of clone was strong ($P < 0.001$), with clones ranked as 259 < 216 < 271 = 42E < 8L in order of increasing RG when averaged across treatments. Clones responded similarly to either $+CO_2$ or $+O_3$ (i.e. no clone $\times CO_2$ or clone $\times O_3$ effects). However, significant clone $\times CO_2 \times O_3$ effects ($P =$ 0.002) resulted from non-additive effects of CO_2 and O_3 for clones 271 and 42E, which had diminished negative responses to $+O_3$ in elevated CO_2, whereas clone 8L had stronger negative responses to $+O_3$ in elevated CO_2.

The average competitive performance (CP) results during the 4-year period did not reveal significant main effects of $+CO_2$ or $+O_3$ (Table 2), with a marginal interaction ($CO_2 \times O_3$, $P = 0.109$). The main effect of clone was strong ($P < 0.001$), with clones ranked as 259 < 216 < 271 < 42E < 8L in order of increasing CP when averaged across treatments. Significant clone $\times CO_2 \times O_3$ effects ($P = 0.046$) apparently resulted from convergence of CP responses among clones in the $+CO_2 + O_3$ treatment. However, the non-parametric test results indicated that clone rankings were maintained, with no evidence of significant crossover effects on clone rankings among treatments ($P > 0.4$, all years). Moreover, across treatments and years, CP was strongly and positively related to the inherent growth potential of each clone (Fig. 2).

Discussion

Based on SNG results, we found general support for our hypothesis that growth enhancement in elevated CO_2 is increased by competitive advantage. As competitive status index (CSI) and O_3 did not interact significantly, we did not find evidence that competition consistently influenced O_3 responses as hypothesized, but we did find that the interaction of CSI and O_3 depended on clone. Clones 216, 271 and 259 were previously characterized as having low, moderate and high O_3 sensitivity, respectively (Coleman *et al.* 1995; Karnosky *et al.* 1998; Kull *et al.* 1996). Notably, clones 216, 259 and 42E were most sensitive to O_3 under competitively disadvantaged conditions (Fig. 1), in keeping with findings that suppressed individuals, by virtue of the leaf and crown characteristics found in low light environments, may be particularly vulnerable to modest O_3 exposure (Fredericksen *et al.* 1995; Fredericksen *et al.* 1996). In striking contrast, however, clones 271 and 8L showed their greatest O_3 sensitivity under competitively advantaged conditions. As O_3

Table 2. Levels of significance (*P* values) for fixed-effects tests of relative growth (RG) and competitive performance (CP) according to mixed-model analysis of variance by year. Average effects were tested utilizing annual RG and CP results from each ring averaged during the 4-year period, with those results identified as 4-year average

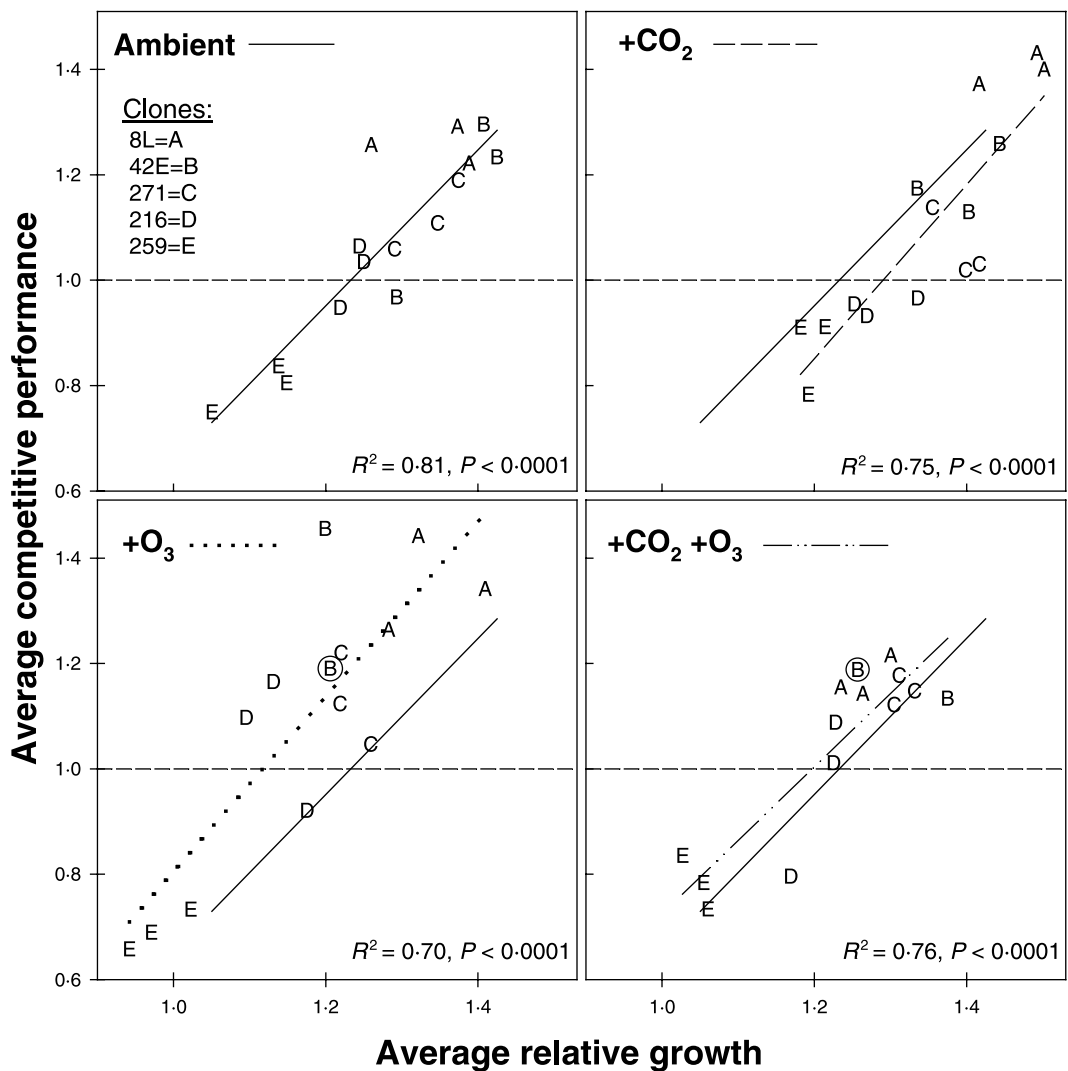| Effect	1998 RG	1998 CP	1999 RG	1999 CP	2000 RG	2000 CP	2001 RG	2001 CP	4-year average RG	4-year average CP
CO_2	0·630	**0·100**	**0·017**	0·962	**0·034**	**0·065**	**0·001**	0·651	**<0·001**	0·476
O_3	**0·058**	0·136	**0·002**	0·254	0·594	0·501	**0·020**	0·755	**<0·001**	0·779
$CO_2 \times O_3$	0·892	0·521	0·103	**0·005**	0·658	0·643	**0·075**	0·138	0·496	0·109
Clone	**<0·001**	**<0·001**	**<0·001**	**<0·001**	**<0·001**	**<0·001**	**<0·001**	**<0·001**	**<0·001**	**<0·001**
Clone $\times CO_2$	0·268	**0·070**	**0·014**	0·716	0·329	**0·050**	**<0·001**	**0·007**	0·658	0·198
Clone $\times O_3$	0·102	0·114	**<0·001**	**0·009**	**<0·001**	0·360	**0·029**	**0·014**	0·422	0·102
Clone $\times CO_2 \times O_3$	**0·007**	0·559	**0·002**	0·123	**0·051**	**0·036**	**0·031**	0·313	**0·002**	**0·046**

Fig. 2. Clone comparisons of competitive performance (CP) *vs* relative growth (RG) averaged during the 1998–2001 period for mixed-clone aspen stands exposed to combinations of ambient and elevated CO_2 and O_3. Values represent individual FACE ring results; circled symbols indicate overlapping values of the same clone. The CP term is the resulting departure from competitively neutral initial conditions that occurred each year, as indicated by changes in the ratio of competitor ΔD^2H *vs* ΔD^2H of adjacent neighbours. For example, CP > 1 indicates that the net growth of an individual was larger than the net growth of its neighbours by the factor of the CP value, while CP < 1 indicates that an individual grew less than the net growth of its neighbours by the factor of the CP value. Values of CP = 1 (dashed horizontal lines) indicate that the individual maintained a competitively neutral status relative to its neighbours. Annual RG values, calculated as $\log(D^2H_{final}) - \log(D^2H_{initial})$, were determined for restricted subsample populations that began and ended each year with a competitively neutral status to emphasize genotypic effects on RG responses to atmospheric treatment, and minimize effects of competition. The regression line for the ambient treatment is shown in each panel to display the effect of $+CO_2$, $+O_3$ and their combination for comparison with ambient performance. Table 2 reports ANOVA statistics for CP and RG for each year and the 4-year average.

responses in aspen appear variable and complex, we believe genotypic variation in O_3 sensitivity is probably determined by multiple physiological and morphological attributes not easily reducible to a few quantifiable characteristics. Moreover, the relative importance of different attributes may change as stands mature and deeper, denser canopies potentially influence individual tree responses (Fredericksen *et al.* 1995; Ollinger, Aber & Reich 1997). Because O_3 is highly reactive, it is efficiently scrubbed from the atmosphere by vegetation. In dense canopies, individuals emerging above the average height of the stand may be subject to higher O_3 concentrations than smaller trees (Fuentes

et al. 1992), and our results suggest that the effect of vertical O_3 gradients on growth responses will depend on clone.

Substantial variation occurred among clones for the interactive effects of CSI, CO_2 and O_3 on SNG. In general, whether combined effects of CO_2 and O_3 were additive or synergistic depended on clone (e.g. clone × CO_2 × O_3, $P < 0.001$ for competitively neutral conditions), and CSI effects contribute additional variability to the differences among clones for their response to CO_2 and O_3. To summarize, elevated CO_2 alone had a general stimulatory effect on aspen growth that was enhanced by competitive advantage for most

clones, whereas O_3 and $CO_2 \times O_3$ effects were largely manifested through clonal differences in O_3 sensitivity that were further modulated by CSI. This complex of interactions may have long-term consequences for stand diversity and size structure in response to atmospheric treatments.

Competition entails many interacting factors (Coomes & Grubb 2000), and we have not explicitly addressed individual resources or physiological responses in this study. Our exploration of competition effects examined height and D^2H (biomass surrogate) differences among competitors, with more linear covariance and significantly more variation in annual SNG explained using height-based rather than D^2H-based indices. As the crown position of individual trees in a forest canopy is highly correlated with light capture (Vanninen & Makela 2000), light availability may have been related directly to the differences in tree height quantified as CSI. The $CSI \times CO_2$ effect we observed accords with previous studies where light environment modified tree responses to elevated CO_2 (DeLucia & Thomas 2000; Kubiske & Pregitzer 1996; McDonald *et al.* 1999; Takeuchi *et al.* 2001). Additionally, CSI may have reflected size-mediated differences in access to nutrients and other soil resources that can strongly influence tree growth responses to CO_2 enrichment (Ceulemans & Mousseau 1994). Both relative crown exposure and disparities in tree biomass (and hence resource capital) scale allometrically with height relationships, and the height-based index may be reliable precisely because it captures an individual's light availability and size-dependent competitive potential relative to adjacent competitors.

As a second objective, we examined atmospheric treatment effects on genotypic growth potential, competitive potential, and the relationship between the two. We found limited support for our hypothesis that atmospheric treatments would significantly affect clone competitive rankings due to differing sensitivities to CO_2, O_3, and their interactive effects. The interaction of CO_2 and O_3 altered relative differences in competitive performance (CP) among clones (Table 2), but had little effect on clone CP rankings, which appeared to be strongly dependent on inherent differences in growth potential among clones (Fig. 2). The latter is noteworthy given that CP values represent the net result of differences in absolute growth performance among competitors that incorporates all variation in the study, including that contributed by competitive environment, genotypic growth potential, and individual size. Our findings are for young stands, and further development will probably decrease soil nutrient and water availability as resource demand by larger trees increases. The growth and resulting competitive potential of individual clones may become influenced more strongly by differences in nutrient requirements or susceptibility to water stress, so relative growth potential is likely to be an increasingly complex function, with differences among clones emerging as their growing environment changes.

Competition is a 'zero-sum' game in our analyses: if one individual makes a relative gain, a competitor suffers a relative loss. This reflects the autoregressive nature of growth responses for competing individuals, which results in absolute size disparities among competitors being magnified with time. Regardless of whether the observed rankings of clone CP persist, the possibility of stand exclusion for the slower-growing clones appears likely. Across all years, clone 259 consistently loses (CP < 1) in our assessments, which we believe can be ascribed to comparatively low growth potential that may eventually lead to its exclusion. The consequence of consistently low RG and CP across treatments was that D^2H of clone 259 at the end of 2000 was half that of clone 42E, for example, despite having similar initial sizes at planting (Isebrands *et al.* 2001).

Elevated CO_2 may accelerate rates of stand exclusion because $CSI \times CO_2$ effects and increased RG in elevated CO_2 act synergistically to amplify the autoregressive nature of competition. In terms of relative size differences, this means that the big get bigger and the small get smaller more rapidly in elevated CO_2. As illustrated by the average CP results (Fig. 2), the $+CO_2 + O_3$ treatment resulted in substantial convergence of competitive potential for four of the five clones, suggesting that relative differences among clones diminished in that treatment (Table 2, clone $\times$ $CO_2 \times O_3$, $P = 0.046$). However, the non-parametric tests for crossover effects on CP rankings indicated that treatments did not significantly change clone competitive rankings. The apparent convergence of CP responses in $+CO_2 + O_3$ conditions does suggest that stand diversity may be maintained at a higher level, or that exclusion will be delayed in that treatment compared with the other treatments.

What emerged from our analysis is the tremendous complexity of significant variation: all the factors considered affect growth responses when individual aspen trees compete with one another, and failing to address competition effects can obscure interesting and ecologically important patterns of variation in clone and atmospheric treatment responses. The complexities apparent in this analysis of individual tree responses would not be revealed by leaf- or stand-level responses, demonstrating the important issue of scale. Certainly, disease or other stresses can differentially affect competitors within a neighbourhood, but size relationships among competitors influence subsequent growth of individual competitors. In essence, the size of an individual tree within a stand partly determines its environment and this, in turn, influences its growth. The resulting circularity involving environment and growth, and autoregressive patterns of growth among competitors, emphasize an important ecological consideration: variability matters for treatment effects (Niklaus *et al.* 2001), and variability itself will be

affected by treatment responses (Catovsky & Bazzaz 1999; Weinstein, Gollands & Retzlaff 2001). In more diverse plant communities, we expect that variation in resource requirements, stress tolerance and life history attributes (e.g. phenology, growth strategy) among competitors will substantially affect relative growth and associated competitive outcomes. Our findings have implications for global atmospheric changes, as intra- and interspecific responses may be affected by competition effects that emerge and/or change as the atmosphere changes, with the potential to influence the diversity and structure of plant communities.

References

Bazzaz, F.A. & McConnaughay, K.D.M. (1992) Plant–plant interactions in elevated CO_2 environments. *Australian Journal of Botany* **40**, 547–563.

Black, J.N. (1958) Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum* L.) with particular reference to leaf area and the microclimate. *Australian Journal of Agricultural Research* **9**, 299–318.

Bortier, K., Ceulemans, R. & Temmerman, L. (2000) Effects of tropospheric ozone on woody plants. *Environmental Pollution and Plant Responses* (eds S.B. Agrawal & M. Agrawal), pp. 153–174. CRC Press, Boca Raton, FL.

Bryant, J., Taylor, G. & Frehner, M. (1998) Photosynthetic acclimation to elevated CO_2 is modified by source : sink balance in three component species of chalk grassland swards grown in a free air carbon dioxide enrichment (FACE) experiment. *Plant, Cell and Environment* **21**, 159–168.

Catovsky, S. & Bazzaz, F.A. (1999) Elevated CO_2 influences the responses of two birch species to soil moisture: implications for forest community structure. *Global Change Biology* **5**, 507–518.

Ceulemans, R. & Mousseau, M. (1994) Effects of elevated atmospheric CO_2 on woody plants. *New Phytologist* **127**, 425–446.

Clark, C.S., Weber, J.A., Lee, E.H. & Hogsett, W.E. (1996) Reductions in gas exchange of *Populus tremuloides* caused by leaf aging and ozone exposure. *Canadian Journal of Forest Research* **26**, 1384–1391.

Cole, W.G. & Lorimer, C.G. (1994) Predicting tree growth from crown variables in managed Northern hardwood stands. *Forest Ecology and Management* **67**, 159–175.

Coleman, M.D., Isebrands, J.G., Dickson, R.E. & Karnosky, D.F. (1995) Photosynthetic productivity of aspen clones varying in sensitivity to tropospheric ozone. *Tree Physiology* **15**, 585–592.

Comins, H.N. & McMurtrie, R.E. (1993) Long-term response of nutrient-limited forests to CO_2 enrichment – equilibrium behavior of plant–soil models. *Ecological Applications* **3**, 661–681.

Connolly, J., Wayne, P. & Bazzaz, F.A. (2001) Interspecific competition in plants: how well do current methods answer fundamental questions? *American Naturalist* **157**, 107–125.

Coomes, D.A. & Grubb, P.J. (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs* **70**, 171–207.

DeLucia, E.H. & Thomas, R.B. (2000) Photosynthetic responses to CO_2 enrichment of four hardwood species in a forest understory. *Oecologia* **122**, 11–19.

Dickson, R.E., Lewin, K.F., Isebrands, J.G. *et al.* (2000) *Forest atmosphere carbon transfer storage-II (FACTS II) – the aspen free-air CO_2 and O_3 enrichment (FACE) project: an overview*. General Technical Report NC-214. USDA Forest Service, North Central Research Station, St Paul, MN.

Fowler, D., Cape, J.N., Coyle, M. *et al.* (1999) Modelling photochemical oxidant formation, transport, deposition and exposure of terrestrial ecosystems. *Environmental Pollution* **100**, 43–55.

Fredericksen, T.S., Joyce, B.J., Skelly, J.M. *et al.* (1995) Physiology, morphology, and ozone uptake of leaves of black-cherry seedlings, saplings, and canopy trees. *Environmental Pollution* **89**, 273–283.

Fredericksen, T.S., Kolb, T.E., Skelly, J.M., Steiner, K.C., Joyce, B.J. & Savage, J.E. (1996) Light environment alters ozone uptake per net photosynthetic rate in black cherry trees. *Tree Physiology* **16**, 485–490.

Fuentes, J.D., Gillespie, T.J., den Hartog, G. & Neumann, H.H. (1992) Ozone deposition onto a deciduous forest during dry and wet conditions. *Agricultural and Forest Meteorology*. **62**, 1–18.

Grace, J.B. & Tilman, D. (1990) *Perspectives on Plant Competition*. Academic Press, New York.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Chichester, UK.

Hendrey, G.R., Ellsworth, D.S., Lewin, K.F. & Nagy, J. (1999) A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO_2. *Global Change Biology* **5**, 293–309.

Hix, D.M. & Lorimer, C.G. (1990) Growth–competition relationships in young hardwood stands on two contrasting sites in southwestern Wisconsin. *Forest Science* **36**, 1032–1049.

Hogsett, W.E., Weber, J.E., Tingey, D., Herstrom, A., Lee, E.H. & Laurence, J.A. (1997) Environmental auditing: an approach for characterizing tropospheric ozone risk to forests. *Environmental Management* **21**, 105–120.

Hühn, M. & Léon, J. (1995) Nonparametric analysis of cultivar performance trials: experimental results and comparison of different procedures based on rankings. *Agronomy Journal* **87**, 627–632.

Isebrands, J.G., McDonald, E.P., Kruger, E. *et al.* (2001) Growth responses of *Populus tremuloides* clones to interacting carbon dioxide and tropospheric ozone. *Environmental Pollution* **115**, 359–371.

Karnosky, D.F., Podila, G.K., Gagnon, Z. *et al.* (1998) Genetic control of responses to interacting tropospheric ozone and CO_2 in *Populus tremuloides*. *Chemosphere* **36**, 807–812.

Keeling, C.D., Whort, T.P., Wahlen, M. & vander Plicht, J. (1995) Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* **375**, 666–670.

de Kroon, J. & van der Laan, P. (1981) Distribution-free test procedures in two-way layouts: a concept of rank interaction. *Statistica Neerlandica* **35**, 189–213.

Kubiske, M.E. & Pregitzer, K.S. (1996) Effects of elevated CO_2 and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology* **16**, 351–358.

Kubiske, M.E., Pregitzer, K.S., Zak, D.R. & Mikan, C.J. (1998) Growth and C allocation of *Populus tremuloides*

genotypes in response to atmospheric CO$_2$ and soil N availability. *New Phytologist* **140**, 251–260.

Kull, O., Sober, A., Coleman, M.D. *et al.* (1996) Photosynthetic responses of aspen clones to simultaneous exposures of ozone and CO$_2$. *Canadian Journal of Forest Research* **26**, 639–648.

Lindroth, R.L., Kinney, K.K. & Platz, C.L. (1993) Responses of deciduous trees to elevated atmospheric CO$_2$: productivity, phytochemistry, and insect performance. *Ecology* **74**, 763–s 777.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) SAS System for Mixed Models. SAS Institute Inc., Cary, NC.

Lorimer, C.G. (1983) Tests of age-independent competition indexes for individual trees in natural hardwood stands. *Forest Ecology and Management* **6**, 343–360.

McDonald, E.P., Agrell, J. & Lindroth, R.L. (1999) CO$_2$ and light effects on deciduous trees: growth, foliar chemistry, and insect performance. *Oecologia* **119**, 389–399.

Medlyn, B.E., McMurtrie, R.E., Dewar, R.C. & Jeffreys, M.P. (2000) Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO$_2$ concentration. *Canadian Journal of Forest Research* **30**, 873–888.

Mitchell-Olds, T. (1987) Analysis of local variation in plant size. *Ecology* **68**, 82–87.

Niklaus, P.A., Leadley, P.W., Schmid, B. & Korner, C. (2001) A long-term field study on biodiversity × elevated CO$_2$ interactions in grassland. *Ecological Monographs* **71**, 341–356.

Ollinger, S.V., Aber, J.D. & Reich, P.B. (1997) Simulating ozone effects on forest productivity: interactions among leaf-, canopy-, and stand-level processes. *Ecological Applications* **7**, 1237–1251.

Oren, R., Ellsworth, D.S., Johnsen, K.H. *et al.* (2001) Soil – fertility limits carbon sequestration by forest ecosystems in a CO$_2$-enriched atmosphere. *Nature* **411**, 469–472.

SAS Institute Inc. (1989–2001) SAS System for Windows, Release 8.2. SAS Institute, Cary, NC.

Saxe, H., Ellsworth, D.S. & Heath, J. (1998) Tree and forest functioning in an enriched CO$_2$ atmosphere. *New Phytologist* **139**, 395–436.

Takeuchi, Y., Kubiske, M.E., Isebrands, J.G., Pregitzer, K.S., Hendrey, G. & Karnosky, D.F. (2001) Photosynthesis, light and nitrogen relationships in a young deciduous forest canopy under open-air CO$_2$ enrichment. *Plant Cell Environment* **24**, 1257–1268.

Vanninen, P. & Makela, A. (2000) Needle and stem wood production in Scots pine (*Pinus sylvestris*) trees of different age, size and competitive status. *Tree Physiology* **20**, 527–533.

Weinstein, D.A., Gollands, B. & Retzlaff, W.A. (2001) The effects of ozone on a lower slope forest of the Great Smoky Mountain National Park: simulations linking an individual tree model to a stand model. *Forest Science* **47**, 29–42.

Woodward, F.I., Thompson, G.B. & McKee, I.F. (1991) The effects of elevated concentrations of carbon dioxide on individual plants, populations, communities and ecosystems. *Annals of Botany* **67**, 23–38.