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Crown carbon gain and elevated [CO_2] responses of understorey saplings with differing allometry and architecture

E. NAUMBURG,*† D. S. ELLSWORTH*‡ and R. W. PEARCY§

**Nicholas School of the Environment, Duke University, Durham, NC 27708-0328, USA, ‡Department of Environmental Sciences, Brookhaven National Laboratory, Upton, NY 11973-5000, USA, and §Division of Biological Sciences, Section of Ecology and Evolution, University of California at Davis, CA 95616, USA*

Summary

1. Attempts at determining the physiological basis of species' differences, such as the ability to grow in deep shade, have been of limited success. However, this basis is fundamental to predicting species' responses to rising atmospheric CO_2 in the forest understorey. We linked a leaf photosynthesis and a tree architecture model to predict the effects of dynamic and steady state photosynthetic characteristics, crown architecture and elevated atmospheric CO_2 concentration ([CO_2]) on crown-level carbon gain (A_{crown}). Twenty-four-h A_{crown} was modelled for shade-tolerant *Acer rubrum* and shade-intolerant *Liriodendron tulipifera* saplings growing for three years in a forest understorey under ambient and elevated [CO_2] in free-air CO_2 enrichment.

2. Two factors best explained A_{crown} in ambient [CO_2]: tree light environment and sapling allometry. Microsite light environment influenced carbon gain via daily photosynthetic photon flux (PFD), average diffuse PFD and sunfleck characteristics. Species differences in specific leaf area (SLA) and size-related biomass allocation to leaves affected the effective leaf area and hence A_{crown}.

3. At a common above-ground biomass, small saplings (100 g above-ground dry mass) of *L. tulipifera* had higher A_{crown} than *A. rubrum* samples due to larger SLA and greater biomass allocation to leaves. Larger saplings of the two species had similar A_{crown} due to greater carbon allocation to leaves with increasing plant size in *A. rubrum vs L. tulipifera*. For saplings > 800 g, A_{crown} was greater in *A. rubrum* than in *L. tulipifera*. Enhancement of A_{crown} by elevated [CO_2] on sunny days was similar for both species.

4. Overall, though the shade-tolerant species had lower A_{crown} than the shade-intolerant species at a common small size, our results indicate that the relative performance of these species can reverse at larger sizes due to allocational differences. These results suggest that elevated [CO_2] may accelerate competition for light between *A. rubrum* and *L. tulipifera* as these species grow larger in the understorey.

Key-words: *Acer rubrum*, daily photosynthesis model, *Liriodendron tulipifera*, shade tolerance, sunflecks

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Introduction

Observations of differential survival rates by tree seedlings and saplings in forest understoreys are well known and are widely applied in forest management. The physiological basis for growth and survival in deep shade ultimately lies in superior whole-plant carbon balance (Walters, Kruger & Reich 1993a; Thompson, Huang & Kriedemann 1992; Givnish 1988). Aside from disease and infrequent catastrophic events, poor growth and survival ultimately results from the inability to assimilate enough carbon to meet long-term respiratory demands and costs of tissue turnover (Givnish 1988; Walters & Reich 1999). Since growth and carbon gain in the forest understorey are light-limited, numerous studies have examined the effect of shade on photosynthetic traits in tree seedlings of different tolerance (reviewed in Walters & Reich 1999). However, steady-state measurements of photosynthesis do not always demonstrate that shade-tolerant species are better adapted to shaded environments by having photosynthetic traits that enhance leaf-level

†Author to whom correspondence should be addressed. Current address: Desert Research Institute, 755 E. Flamingo Rd, Las Vegas, NV 89119, USA. E-mail: elke@dri.edu

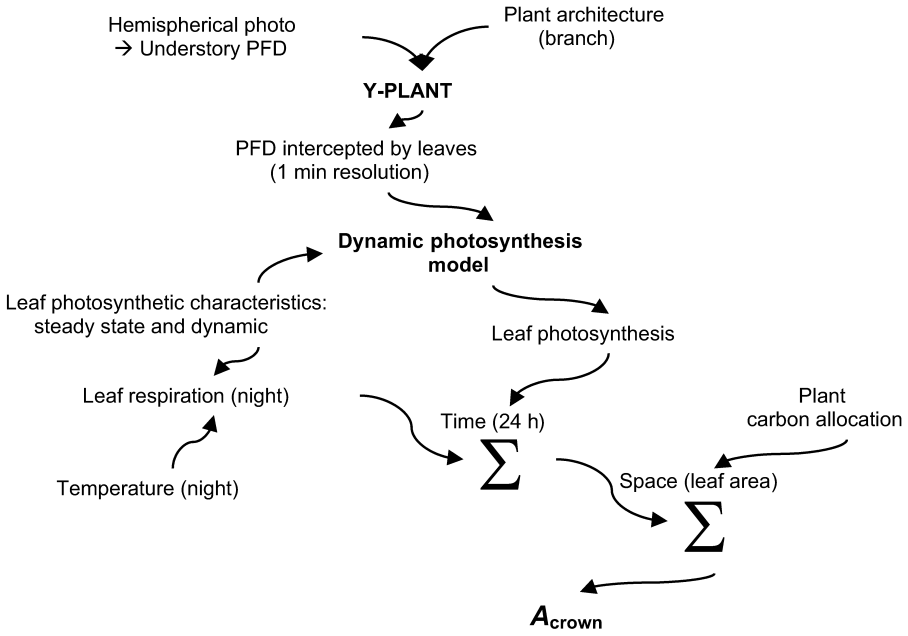

Fig. 1. Schematic of modelling and scaling approach used. Data were fed into two models: Y-PLANT and a dynamic photosynthesis model. For further details see Materials and methods.

photosynthesis in low light (e.g. Naumburg & Ellsworth 2000; Teskey & Shrestha 1985; Kitajima 1994; Barker, Press & Brown 1997; Walters & Reich 1999). Therefore, physiological interpretations of differential biomass accumulation of competing understorey species cannot rely solely on leaf-level photosynthetic mechanisms to explain whole-plant growth dynamics. This is not surprising, since steady-state photosynthetic rates themselves vary greatly in time and space, and are also only one component of whole-plant carbon balance (Givnish 1988; Körner 1991; Walters, Kruger & Reich 1993b).

The current rise in atmospheric [CO_2] has potentially large impacts on plant carbon balance and growth (Norby *et al*. 1999; Saxe, Ellsworth & Heath 1998), so knowledge of whole-plant carbon balance in elevated [CO_2] is critical for understanding future patterns of growth and survival for competing understorey species. Evidence that elevated [CO_2] stimulates photosynthesis more in shade-tolerant species (e.g. Kubiske & Pregitzer 1996; Hättenschwiler & Körner 2000; Kerstiens 1998) raises questions of whether rising [CO_2] will alter patterns in forest succession (Bazzaz *et al*. 1996; Körner 1996). Therefore, the effects of elevated [CO_2] on the leaf physiological and whole-plant components of carbon balance of juvenile trees need to be considered to predict growth and survival in a future higher [CO_2] atmosphere.

Plant carbon balance is the outcome of interactions between environmental factors like light and atmospheric [CO_2], and plant traits that affect photosynthetic photon flux density (PFD) interception by leaves, photosynthetic yield, carbon loss to respiration, tissue turnover and other factors. Under shade conditions, components of light capture such as carbon allocation to leaf area and leaf display can be the most important determinants of species differences in seedling carbon gain and growth because of similar and low photosynthetic rates in ambient [CO_2] (Sims, Gebauer & Pearcy 1994; Veneklaas & Poorter 1998; Walters & Reich 1999; Poorter 1999). Moreover, few studies have combined aspects of plant form such as carbon allocation and architecture with leaf photosynthesis to assess carbon balance in shade (Walters *et al*. 1993a; Pearcy & Yang 1998; Walters & Reich 1999).

Most carbon balance modelling approaches employ a highly simplified scheme that incorporates a photosynthetic light response curve in conjunction with PFD data and respiration rates, scaling these rates according to plant allocation to the major plant organs (Walters *et al*. 1993a; Sims *et al*. 1994; Walters & Reich 1999). While appropriate for architecturally simple, very small tree seedlings, this approach ignores the geometric display of leaves in multiple angles and planes, which affects their ability to efficiently intercept light (Ackerly & Bazzaz 1995; Pearcy & Yang 1998). Moreover, photosynthetic responses to natural fluctuating light are often limited by shade-deactivated enzymes and partially closed stomata, thus leading to lower than expected daily photosynthesis (Pearcy *et al*. 1994). These factors are often not considered in assessing the spatial and temporal variability of photosynthesis in the understorey. However, these factors can lead to growth differences among species in the same environment (Wayne & Bazzaz 1993; Watling, Ball & Woodrow 1997).

We modelled crown assimilation and respiration for understorey saplings of two temperate tree species (*Acer rubrum* L. and *Liriodendron tulipifera* L.) at ambient and ambient + 20 Pa [CO_2]. We linked a dynamic photosynthesis model (Pearcy, Gross & He 1997; Naumburg,

Ellsworth & Katul 2001) with a spatially explicit plant architectural model (Pearcy & Yang 1996) that calculated the light environment of individual leaves of plants (Fig. 1). These models allowed us to include architectural effects as well as dynamic photosynthetic responses to PFD to test whether saplings of the two species differ in their A_{crown} over a 24-h period. This study assesses crown carbon balance in ambient and elevated [CO_2] as the major component underlying whole-plant growth. A comprehensive treatment of this subject has rarely been undertaken for understorey trees with contrasting architecture and shade tolerance.

Materials and methods

STUDY SITE AND SPECIES

The study was conducted at the FACTS-1 site in Duke Forest, North Carolina, USA, which is equipped with six free-air CO_2 enrichment (FACE) rings (described in Hendrey *et al*. 1999). The site is located in a loblolly pine (*Pinus taeda* L.) plantation, established in 1983. Understorey vegetation has not been managed since establishment, so hardwood species are abundant in the subcanopy and understorey. Since August 1996, three circular plots 15 m in diameter have been operating at ambient atmospheric [CO_2] + 20 Pa by FACE (Hendrey *et al*. 1999) and three at ambient [CO_2]. At the height of the saplings in the centre of the plot, mean daytime [CO_2] during the 1999 growing season was 56·2 ± 1·8 Pa (mean ± 1 SD) for $n = 3$ elevated CO_2 rings and ~38 Pa in the ambient rings (Hendrey *et al*. unpublished data, see also Hendrey *et al*. 1999).

The two study species differ in shade tolerance, leaf size and crown architecture (Wallace & Dunn 1980). *Acer rubrum* is shade tolerant (Baker 1949; Abrams 1998), while *L. tulipifera* is among the least shade-tolerant species in south-eastern USA (Baker 1949; Busing & White 1997). At the study site, saplings of the two species have shown similar photosynthetic capacity per leaf area under light saturation at ambient [CO_2], while under elevated [CO_2], *A. rubrum* showed a greater photosynthetic enhancement than *L. tulipifera* (Naumburg & Ellsworth 2000). Furthermore, dynamic photosynthetic and stomatal responses to changes in PFD by *L. tulipifera* reduced limitations to sunfleck photosynthesis to a greater extent than the responses of *A. rubrum* (Naumburg *et al*. 2001).

ARCHITECTURAL MEASUREMENTS AND MODEL

Branch architectural data for a spatially explicit tree architectural model (Y-PLANT; Pearcy & Yang 1996) were collected from two saplings per species and [CO_2] treatment ring to yield a three-dimensional computer representation of the branches (Fig. 2). The measurements to parameterize the model are described in Pearcy & Yang (1996) and involve simple dimensional and angular measurements for all foliar and wood elements. For *L. tulipifera*, only one sapling was available in two of the elevated CO_2 rings. For these two plants, data were collected separately on two different branches that were oriented in different directions from the main stem. In addition, the same information was collected for one entire sapling per species and [CO_2] treatment to examine differences between branch-level and whole-plant modelled results.

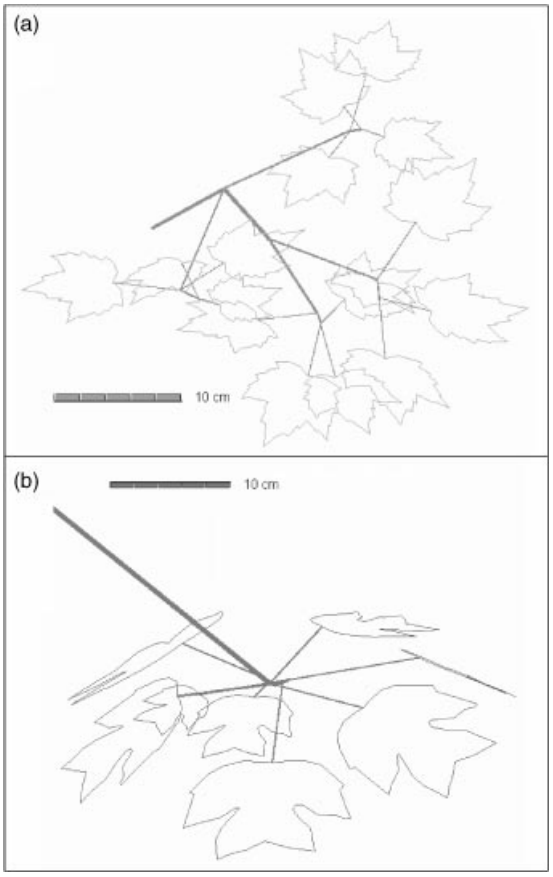

Fig. 2. Examples of branches as they are represented in Y-PLANT. *A. rubrum* (a) and *L. tulipifera* (b) as viewed from a 45° sun angle.

ESTIMATING PLANT-LEVEL PFD

To characterize the local light environments of these branches, a hemispherical photograph (8 mm Nikkor fisheye lens, Nikon Inc., Melville, NY, USA) was taken directly above each branch when the sky was overcast and the overstorey canopy in full leaf. The photographs were analysed with HemiView 2·0 (Delta-T Devices Ltd, Cambridge UK) to yield a gap fraction in each of 160 solar track sectors (8 azimuths × 20 sun angles) and a 1 min time series of direct PFD data. Sky diffusivity was set to 0·15, which yielded a maximum mid-day PFD of around 2000 mmol m^{-2} s^{-1}, similar to measurements at the study site under clear sky.

Daily courses of PFD for each leaf were generated by Y-PLANT using the spatial arrangement of leaves and the modelled light environment above the branches

from hemispherical photographs. While the analysis of hemispherical photographs does not reproduce all features of true understorey PFD, the frequency and duration of sunflecks are generally well predicted (Chazdon & Field 1987; Valladares & Pearcy 1998). Y-PLANT was run at a 1 min time step between sunrise and sunset for a 14·4 h day (day length equivalent to 1 July) to gain high-resolution data for the dynamic photosynthesis model. This PFD output was further integrated over the leaves per branch and the entire day to yield a measure of the daily PFD (per m^2 leaf area) intercepted by the measurement branches.

PHOTOSYNTHESIS MODEL

The dynamic photosynthetic model of Pearcy *et al.* (1997) has been previously described and tested for the study species at the site (Naumburg *et al.* 2001). The model incorporates the Farquhar & von Caemmerer (1982) photosynthesis model, modified to include metabolite pools and time constants reproducing the light-induced activation and deactivation of key photosynthetic enzymes (Pearcy *et al.* 1997). Dynamic stomatal responses to changes in PFD are modelled based on processes in the guard cells such as the influx and efflux of osmotica and water. Thus, the model takes into consideration sunfleck-induced changes in the biochemistry of photosynthesis and stomatal aperture that affect photosynthesis in variable light conditions. For our purposes, we did not consider additional environmental limitations such as temperature or inadequate soil moisture.

Daily photosynthesis (A_{day}, mmol m^{-2} s^{-1}) for the measurement branches was estimated by the photosynthesis model using the 1 min PFD data from Y-PLANT. The model calculated photosynthesis for both the diffuse and direct PFD when sunflecks were present, and then multiplied the diffuse and direct PFD photosynthetic rates by the appropriate leaf areas. Since Y-PLANT averages PFD over the fraction of the leaf that is either in shade or in sunflecks, using the dynamic photosynthesis model with this version of Y-PLANT ignores sunflecks that traverse specific leaves. For example, in reality leaf A is exposed to a sunfleck say 2 min earlier than leaf B, but both leaves go through the same induction response (albeit at differing times). In our modelling approach, this induction response occurs at the same time. Since the temporal spacing of the sunflecks is not affected by this simplification, the introduced error should be negligible.

SCALING TO THE WHOLE-PLANT LEVEL

Whole-crown photosynthesis was estimated using branch A_{day} and site-specific allometric relationships from above-ground harvests of the study species (Fig. 1). We assumed that branch A_{day} was representative of all branches within the crown. Because destructive harvests are not possible in the treatment rings, biomass relationships were determined only for ambient [CO_2] plants growing in the same forest tract. Seven saplings of each species were separated into the main stem and branches. A subset of leaf blades for each branch was measured with a leaf area meter (CI-4200; CID Inc., Vancouver, WA, USA) and then dried and weighed separately to determine their specific leaf area (SLA). For each branch, the stem and remaining leaves were dried separately at 70 °C and weighed. These data were used to calculate sapling allometric relationships (see Fig. 5a–d). To determine allometric relationships of the study branches, we used both data obtained from the treatment rings (SLA) and the biomass harvests. Branch woody dry mass was regressed against a proxy of branch volume: (branch basal diameter [cm])^2 * (branch length [cm]) for harvested saplings to get an estimate of the measurement branch biomass. We considered SLA specific to the species and [CO_2] treatments for the crown-level calculations because decreases in SLA are frequently observed in elevated CO_2 studies (Wolfe *et al.* 1998; Saxe *et al.* 1998; Curtis & Wang 1998). Statistically significant CO_2 effects on whole-plant biomass allocation have not been found in long-term experiments to date (e.g. Rey & Jarvis 1997; Tissue, Thomas & Strain 1997; Centritto, Lee & Jarvis 1999), so we assumed here that allometry for ambient-grown plants could be used for elevated CO_2-grown plants. Thus, A_{crown} was scaled from the modelled branch A_{day} by multiplying by the crown leaf area, which was estimated from biomass relationships gained from harvests and measured SLA (see Fig. 5e,f).

To estimate A_{crown} over 24 h, leaf dark respiration rates for the species were measured in June 1999 using a CIRAS-1 gas exchange system (PP-Systems, Hitchin, UK). Measurements were taken at 37 or 57 Pa CO_2 in ambient and elevated [CO_2] rings, respectively, and at 27·5 °C (the approximate air temperature during the measurement period). Using night-time temperature data collected at the study site at the height of the saplings and a Q_{10} of 2·1 appropriate for tree species (Ryan *et al.* 1995), night-time respiration rates were estimated for the 9·6 h night on 1 July.

STATISTICAL ANALYSES

For statistical analyses that compared treatment means, the data from the two plants/branches per treatment ring and species were averaged, resulting in a sample size of $n = 3$. These variables were analysed by ANOVA. Variables that did not meet the assumptions of normality and homogeneity of variance were log-transformed, while ratio variables were arcsine-transformed. To test whether the species had different biomass and leaf biomass *vs* stem diameter relationships, we used an analysis of covariance that included index variables to test for species effects on regression slopes and intercepts. Because both A_{day} and A_{crown} were related to the intercepted PFD, both were analysed as regressions that included index variables for species and

[CO_2]. For these regressions, we used stepwise forward multiple regression with an entry α of 0·05. Data from the same treatment ring were considered independent in these analyses because understorey PFD was highly variable among locations within each treatment ring (data not shown, but see Fig. 6 for range of PFD data). All analyses were conducted in SAS version 6·12 for Windows (SAS Institute, Cary, NC, USA).

Results

LIGHT ENVIRONMENT

Daily PFD intercepted by the study branches as modelled in Y-PLANT ranged between 2·4 and 13·8 mol m^{-2} for 1 July. These understorey PFD are equivalent to 4–23% of the above-canopy PFD (60 mol m^{-2} d^{-1}) predicted by Y-PLANT. In elevated [CO_2], *L. tulipifera* apparently intercepted less PFD than in ambient [CO_2], although this was because of the shadier microsites in which the plants were growing (Fig. 3).

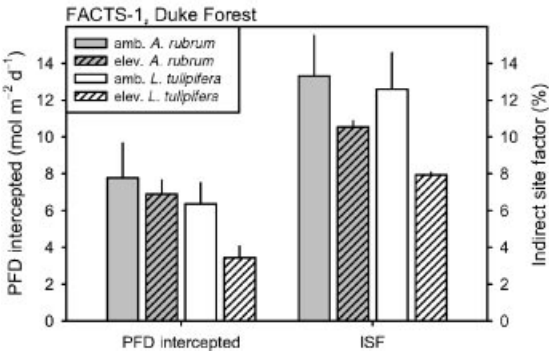

Fig. 3. Mean (± 1 SE) PFD intercepted by leaves on the measurement branches as predicted by Y-PLANT. The indirect site factor (ISF) is derived from the hemispherical photos and indicates relative canopy openness.

BRANCH ALLOMETRY AND ARCHITECTURE

As expected, the two species differed in aspects of crown architecture. In addition to phyllotaxy (opposite *vs* whorled arrangement of leaves), *A. rubrum* leaves were a third as large as *L. tulipifera* leaves (Fig. 2, Table 1). *Liriodendron tulipifera* leaves were also displayed at a steeper angle than *A. rubrum* leaves ($F_{1,8}$ = 20·5, P < 0·01). This led to a comparatively greater projection efficiency, E_p (*sensu* Pearcy & Yang 1996), in *L. tulipifera* than in *A. rubrum* at low sun angles (data not shown), but significantly smaller E_p at high sun angles ($F_{1,8}$ = 19·0, P < 0·01, Table 1). E_p is determined for each sun angle by calculating the branch leaf area that is displayed perpendicular to the direct light incident angle relative to a horizontal surface of the same total area. However, the display efficiency parameter, E_d, which takes leaf overlap into account, showed no significant differences between species or [CO_2] treatments (P > 0·2, Table 1). Also, no significant differences (P > 0·10) between species or [CO_2] treatments existed for E_p–E_d, an indicator of leaf overlap. The leaf overlap indicated by E_p–E_d was generally small for both species in the understorey. The efficiency with which leaves absorbed PFD during sunflecks or shade, E_a, did not differ significantly (P > 0·2) either for the species or [CO_2] treatments, although this parameter was slightly larger for *A. rubrum* at elevated [CO_2]. Patterns similar to those for the branches were observed for the entire plant crowns (Table 1), although as expected, leaf overlap tended to be somewhat greater for whole trees than single branches. Overall, E_a and E_d for the saplings were 10–15% greater than for branches.

Branch-level leaf mass ratio (leaf mass to total mass of branch, BMR) differed significantly between the two species ($F_{1,8}$ = 11·2, P = 0·01, Table 1), with *L. tulipifera* having smaller BMR than *A. rubrum*. There were also marginally significant differences in this

Table 1. Architectural properties of the study species in ambient and elevated CO_2 from direct measurements or computed by the Y-PLANT model (efficiencies). E_a is the PFD absorption efficiency during sunfleck and diffuse PFD periods, E_p the projection efficiency and E_d the display efficiency, which incorporates leaf overlap effects. Values are means (standard error in parentheses). Values within a row with different letters are significantly different at P < 0·05

	Ambient *A. rubrum*	Elevated *A. rubrum*	Ambient *L. tulipifera*	Elevated *L. tulipifera*
Branches (n = 3)				
Leaf mass : branch mass (m^2 kg^{-1})	0·70 (0·02)[a]	0·68 (0·02)[a]	0·67 (0·02)[a]	0·61 (0·02)[b]
Leaf size (cm^2)	41·3 (3·8)[a]	37·8 (2·4)[a]	120·6 (8·4)[b]	104·2 (9·8)[b]
Leaf angle	16·4 (1·1)[a]	15·4 (2·1)[a]	21·3 (1·9)[b]	25·6 (1·5)[b]
E_a sunflecks (%)	74·1 (4·4)[a]	81·2 (4·3)[a]	72·0 (1·9)[a]	75·4 (5·7)[a]
E_a shade (%)	72·6 (4·3)[a]	79·1 (2·0)[a]	73·9 (2·6)[a]	74·8 (2·4)[a]
E_p at 90° solar zenith (%)	94·5 (0·3)[a]	95·7 (0·9)[a]	91·9 (1·9)[b]	87·9 (0·9)[c]
E_d at 90° solar zenith (%)	84·6 (5·1)[a]	91·4 (2·7)[a]	87·1 (3·0)[a]	84·5 (1·4)[a]
E_p–E_d (%)	9·8 (5·4)[a]	4·2 (3·1)[a]	4·9 (1·6)[a]	3·4 (1·5)[a]
Whole trees (n = 1)				
E_a sunflecks (%)	66·5	76·4	64·8	59·2
E_a shade (%)	56·8	75·7	60·8	61·1
E_p at 90° solar zenith (%)	89·7	97·0	91·5	85·7
E_d at 90° solar zenith (%)	65·7	88·2	70·1	70·2
E_p–E_d (%)	24·0	8·8	21·4	15·5

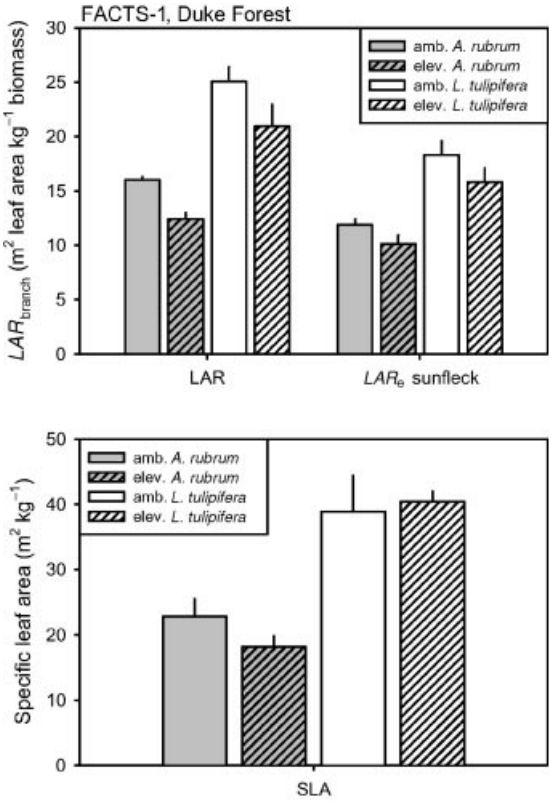

Fig. 4. Mean (± 1 SE) leaf area ratios (LAR) and specific leaf areas (SLA). LAR_e represents the effective LAR during periods when direct radiation was reaching the branches. It is calculated by multiplying the measured LAR by the efficiency with which the branches intercept radiation (E_a, %, see Table 1).

parameter between [CO_2] treatments ($F_{1,8} = 4{\cdot}8$, $P = 0{\cdot}06$, Table 1). However, this effect was confounded by *L. tulipifera* saplings growing in shadier microsites in elevated [CO_2] (Fig. 3). Leaf area ratio (leaf area to branch + leaf mass, LAR) differed significantly for both species and [CO_2] treatments ($F_{1,8} = 63{\cdot}8$ and $F_{1,8} = 13{\cdot}8$, respectively, $P < 0{\cdot}01$, Fig. 4). *Liriodendron tulipifera* had larger LAR than *A. rubrum*, and elevated [CO_2] plants had smaller LAR than ambient plants for both species. For *A. rubrum*, this lower allocation to leaf area under elevated [CO_2] was due to a 20% SLA (Fig. 4) that was not statistically significant ($P > 0{\cdot}1$). *Liriodendron tulipifera*, however, had the same SLA under ambient and elevated [CO_2], but its leaf biomass allocation was less under elevated [CO_2], thus causing the smaller leaf area ratio. This difference could be due either to light conditions or to [CO_2] treatment (see above).

Multiplying LAR by the PFD absorption efficiency (E_a) yields LAR_e, the ratio of leaf area to branch mass that is corrected for leaf overlap, leaf angles and leaf absorptances that reduce PFD absorption. During both sunflecks and diffuse shade periods, LAR_e values were significantly larger ($F_{1,8} = 40{\cdot}0$ and $F_{1,8} = 52{\cdot}2$, respectively, $P < 0{\cdot}01$) in *L. tulipifera* than in *A. rubrum*, mostly due to the large differences in LAR itself (Fig. 4). However, differences in LAR_e for both sunfleck and diffuse PFD between elevated and ambient CO_2 plants were marginally significant ($0{\cdot}03 < P < 0{\cdot}06$). This was due to the slightly larger E_a in elevated [CO_2] plants, which compensated for the reduced LAR under elevated [CO_2].

Overall, despite differences in leaf size and leaf display (Fig. 2, Table 1), *A. rubrum* and *L. tulipifera* differed surprisingly little in their light interception in the forest understorey. This was due, in part, to both species minimizing leaf overlap via petiole twisting (Fig. 2). The greatest difference between the two species was due to the larger SLA in *L. tulipifera* than in *A. rubrum*. Furthermore, the only [CO_2] effect on allometry and architecture occurred in *A. rubrum* and was caused by a slight reduction in SLA under elevated [CO_2].

SAPLING ALLOMETRY

Branch-level photosynthesis and respiration were scaled to entire saplings using the allometric relationships derived from the biomass harvests outside the treatment rings. Regressions between log stem diameter and log plant biomass revealed no significant differences in either the slopes or intercepts of the regression lines for the two species ($F_{1,10} = 1{\cdot}1$, $P = 0{\cdot}33$ and $F_{1,10} = 2{\cdot}6$, $P = 0{\cdot}14$ for the intercept and slope, respectively; Fig. 5a). However, the allometric regressions for leaf blade biomass *vs* stem diameter or total above-ground biomass differed significantly (Fig. 5a,b). *Liriodendron tulipifera* had a significantly higher intercept and lower slope than *A. rubrum* for both regressions (biomass intercept, $F_{1,10} = 6{\cdot}6$, $P = 0{\cdot}03$; biomass slope, $F_{1,10} = 8{\cdot}0$, $P = 0{\cdot}02$; diameter intercept, $F_{1,10} = 5{\cdot}8$, $P = 0{\cdot}04$; diameter slope, $F_{1,10} = 7{\cdot}9$, $P = 0{\cdot}02$). Thus, *A. rubrum* showed a steeper increase in leaf blade biomass with sapling size than *L. tulipifera*. Consequently, above-ground leaf: total biomass ratio (LMR) calculated for several size classes based on these regressions increased for *A. rubrum* but decreased for *L. tulipifera* (Fig. 5c,d).

Based on the allometry (Fig. 5a,b) and SLA (Fig. 4), *L. tulipifera* maintained greater leaf area than *A. rubrum* for < 20 mm diameter or 900 g biomass size classes (Fig. 5e,f). Moreover, the small reduction in SLA in elevated [CO_2] relative to ambient-grown *A. rubrum* saplings resulted in less sapling leaf area at all stem sizes (Fig. 5c). This analysis necessarily assumes that LMR does not differ between ambient and elevated [CO_2] plants, since only ambient [CO_2] plants were harvested.

DAILY PHOTOSYNTHESIS AND RESPIRATION OF BRANCHES

Branch photosynthesis was modelled using daily PFD courses output by Y-PLANT for 1 July. Expressing this daily photosynthesis per m^2 leaf area allowed species and CO_2 treatment comparisons that were

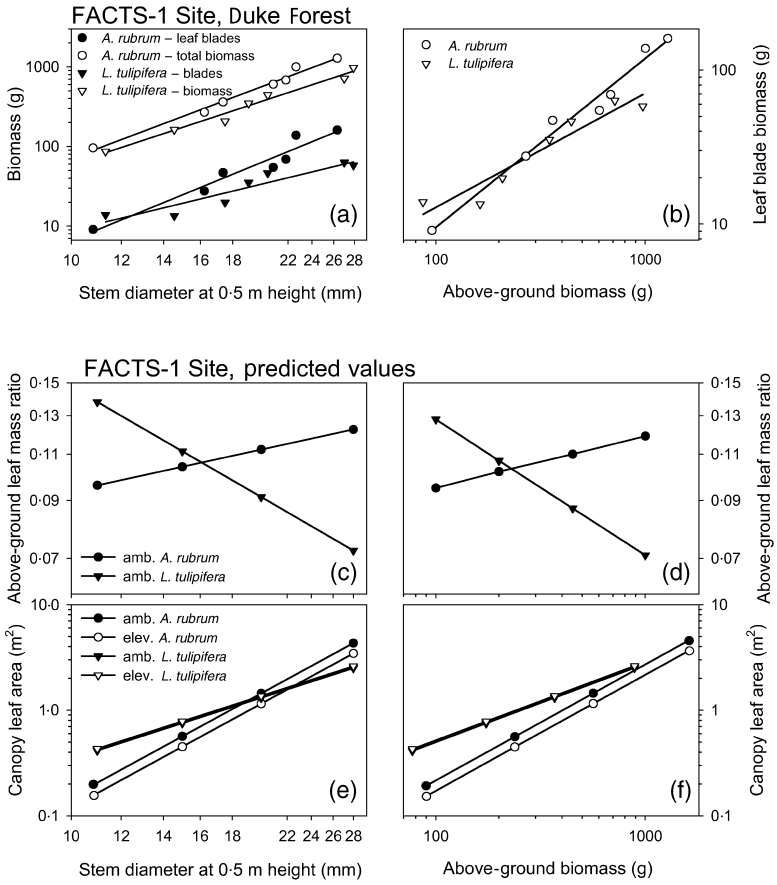

Fig. 5. Allometric relationships for ambient [CO_2]-grown plants of *A. rubrum* and *L. tulipifera* (log-log scale). Relationship between leaf blade and total above-ground biomass *vs* stem diameter measured at 0·5 m above ground (a); leaf blade biomass *vs* total above-ground biomass (b); leaf mass ratio (LMR) for ambient [CO_2] saplings calculated using biomass equations in parts a & b (c,d); and estimated sapling leaf area for ambient and elevated [CO_2] saplings using the leaf blade biomass equations in parts a & b and measured SLA (e,f) (see Fig. 4). Points in (f) correspond to the diameters used for points in (e).

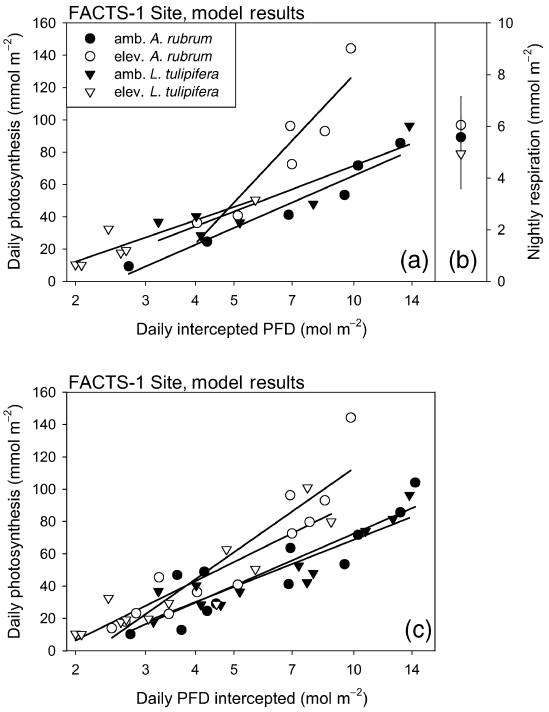

Fig. 6. Modelled photosynthesis (A_{day}) for branches of individual saplings as a function of the PFD intercepted by the leaves. Data are integrated over daylight hours (14·4 h equivalent to 1 July). Photosynthesis modelled using only the original PFD data (a); and using original and PFD data obtained by switching hemispherical photographs between the two species in each treatment ring (c). Photos were switched to enable direct species comparisons under elevated [CO_2] at overlapping PFD ranges. Regressions in (c) were not significantly different between the species while elevated [CO_2] regressions had a significantly greater slope. Respiration rates (b) were estimated using measured dark respiration values corrected for night-time temperatures at the site. Ambient and elevated [CO_2] *L. tulipifera* had identical respiration rates.

independent of branch leaf area. Both *A. rubrum* and *L. tulipifera* showed the same relationship between the daily PFD intercepted and A_{day} at ambient [CO_2] (Fig. 6a). The two regression lines were not significantly different ($P > 0·2$). Comparison of the elevated [CO_2] results of the species, however, was not valid because the PFD range for both species was smaller than for ambient [CO_2] branches and did not show a long overlap (see Fig. 6a). To be able to compare the species at elevated [CO_2], we modelled branch photosynthesis using hemispherical photos switched between *A. rubrum* and *L. tulipifera* plants in the same treatment ring. PFD interception efficiencies, on average, did not differ between those determined with the appropriate photos (Table 1) and the switched photos (data not shown). These additional points extended the range of daily PFD for both elevated [CO_2] *A. rubrum* and *L. tulipifera* (Fig. 6c) without artificially inflating R^2 of the individual regressions (Table 2). Statistical analyses

Table 2. Regression parameters for the species and CO_2 treatment-specific A_{day} *vs* PFD lines in Fig. 6. Parameters are given for both the regressions using the original six data points and for regressions using the original plus an additional six points (obtained by switching hemispherical photos between *A. rubrum* and *L. tulipifera* within the same treatment ring). Regressions are of the form $A_{day} = b_0 + b_1$*ln(PFD)

	b_0	b_1	R^2
Original data set (n = 6; Fig. 6a)			
Ambient *A. rubrum*	– 42·1	107·6	0·94
Elevated *A. rubrum*	– 134·8	262·6	0·86
Ambient *L. tulipifera*	– 22·7	94·4	0·80
Elevated *L. tulipifera*	– 13·4	85·1	0·82
Expanded data set (n = 12; Fig. 6b)			
Ambient *A. rubrum*	– 34·8	107·3	0·80
Elevated *A. rubrum*	– 59·8	172·7	0·85
Ambient *L. tulipifera*	– 28·3	96·9	0·84
Elevated *L. tulipifera*	– 30·4	122·0	0·82

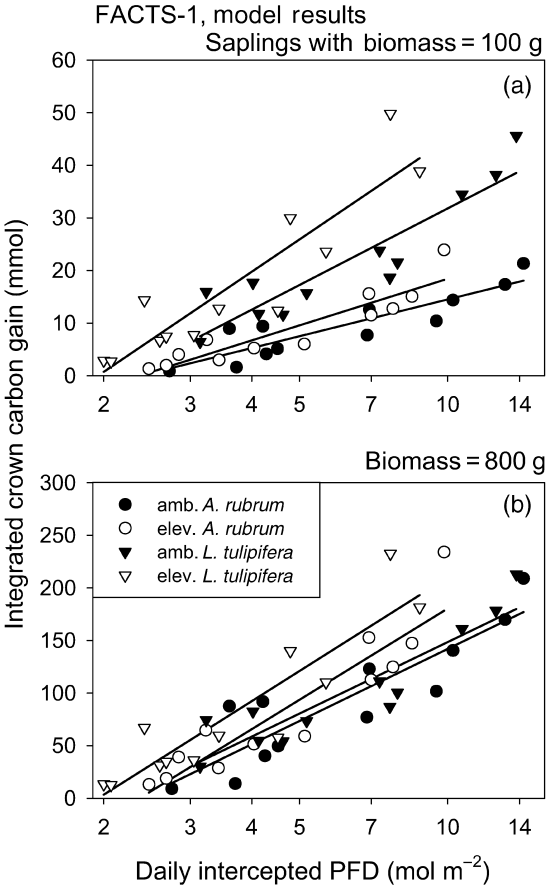

Fig. 7. Crown carbon gain integrated over 24 h for saplings with 100 g (a) or 800 g (b) above-ground biomass as a function of the daily PFD intercepted. Regressions for 100 g saplings differed significantly in their slopes: slopes of elevated [CO_2] *L. tulipifera* > ambient [CO_2] *L. tulipifera* > elevated and ambient [CO_2] *A. rubrum*. Regressions for 800 g saplings differed both in intercept and slope between species: elevated [CO_2] *A. rubrum* intercept < ambient [CO_2] *A. rubrum* and *L. tulipifera*. In addition, elevated [CO_2] regressions had a significantly greater slope than ambient [CO_2] regressions.

including these additional data points showed the same increases in A_{day} with daily PFD for *A. rubrum* and *L. tulipifera*. Elevated CO_2 regressions differed significantly from those at ambient CO_2 by having a lower slope ($F_{1,44} = 28{\cdot}9$, $P < 0{\cdot}001$, Fig. 6a). This difference was largely due to the direct enhancement of photosynthesis by [CO_2]. No significant species differences existed for either CO_2 treatment ($P > 0{\cdot}2$).

Night-time respiration rates estimated from gas-exchange measurements and measured night-time temperatures were similar for both ambient and elevated [CO_2] and the two study species ($P > 0{\cdot}2$, Fig. 6b). Thus, branch-level integrated carbon gain over 24 h closely resembled patterns shown for daily photosynthesis (data not shown).

CROWN CARBON GAIN

We used estimated crown leaf areas (Fig. 5f) to scale the branch-level daily photosynthesis and respiration to entire crowns using the 12 branch-level photosynthesis estimates per species and [CO_2] treatment. For small saplings (100 g biomass), ambient [CO_2] *L. tulipifera* gained more carbon than ambient or elevated *A. rubrum* with increasing PFD (Fig. 7a): the *L. tulipifera* regression had a significantly higher slope ($F_{1,43} = 108$, $P < 0{\cdot}001$). This was mostly due to larger SLA (Fig. 4) and greater allocation to leaves in small *L. tulipifera* relative to *A. rubrum* (Fig. 5) rather than higher photosynthesis (Fig. 6). In addition, elevated [CO_2] *L. tulipifera* had a significantly greater regression slope than ambient [CO_2] *L. tulipifera* ($F_{2,43} = 8{\cdot}5$, $P < 0{\cdot}001$, Fig. 7a). In contrast, the elevated [CO_2] *A. rubrum* regression did not significantly differ from the ambient [CO_2] *A. rubrum* regression. This lack of statistically significant CO_2 enhancement of A_{crown} predicted for *A. rubrum* was due to the smaller crown leaf area in elevated [CO_2] *A. rubrum* caused by smaller SLA (Fig. 4). For *L. tulipifera* in elevated [CO_2], no difference in SLA was observed and the branch-level photosynthetic enhancement was preserved at the crown level.

For larger saplings (800 g biomass), species trends observed for small saplings shifted. For both species, elevated [CO_2] plants had a significantly larger regression slope than ambient plants ($F_{1,44} = 19{\cdot}7$, $P < 0{\cdot}001$, Fig. 7b). In addition, elevated [CO_2] *A. rubrum* had a lower intercept than ambient [CO_2] *A. rubrum* or *L. tulipifera* ($F_{1,44} = 5{\cdot}7$, $P = 0{\cdot}02$). Thus, for this size class, only small differences in A_{crown} existed between the species. When larger saplings were compared at a common diameter, however, *A. rubrum* gained more carbon than *L. tulipifera* under moderate light regimes (data not shown). This can be attributed to the relatively greater leaf area in *A. rubrum* (Fig. 5). While we expressed the relationships of carbon gain with daily PFD intercepted for two different size classes of stems (Fig. 7), these model predictions do not consider below-ground biomass or stem and root respiration rates.

Discussion

The dynamics of understorey sapling growth and survival can determine the future composition of forests. For the size classes of saplings studied here, an inability to maintain competitive status with nearby saplings of other species will result in increased shading, reducing whole-tree carbon balance, which may ultimately trigger mortality. We modelled carbon balance of the entire crown co-occurring saplings of shade-tolerant *A. rubrum* and shade-intolerant *L. tulipifera* in ambient and elevated CO_2 to understand how changes in atmospheric CO_2 may affect whole-tree carbon assimilation as a major mechanism controlling growth dynamics of these understorey trees. Based on the size-dependent differences in allometry observed (Fig. 5), we predict that elevated [CO_2] should accelerate competitive success of *A. rubrum* over *L. tulipifera* as saplings exceed a given size in the understorey.

Surprisingly, differences in 24 h sapling A_{crown} (Fig. 7) between *A. rubrum* and *L. tulipifera* were largely driven by differences in crown biomass allocation to leaf area rather than leaf physiology (see Naumburg *et al.* 2001). Species differences in carbon gain compared at the same above-ground biomass (Fig. 7) or diameter (not shown) were similar because of similar biomass to diameter allometry of the species (Fig. 5a). In contrast, species differences in area-based photosynthesis were relatively minor at the daily time scale (Fig. 6), and steady state photosynthesis measurements were also very similar (Naumburg & Ellsworth 2000). Recently, Walters & Reich (1999) found similar photosynthetic rates between shade-tolerant and shade-intolerant species when expressed on a leaf area basis (comparison of > 100 tree species), in accordance with our earlier results. Thus, understanding species differences in whole-plant carbon balance may depend on knowledge of crown architecture, carbon allocation to leaf area (Walters *et al.* 1993b; Walters & Reich 1999; Lambers & Poorter 1992) and ontogenetic drift in allocation (e.g. with changing plant size or age; Hunt & Lloyd 1987; Poorter & Pothman 1992; Küppers, Koch & Mooney 1988). This information is frequently lacking in contrast to photosynthetic light response data.

Recent analyses (Walters & Reich 1999; Veneklaas & Poorter 1998) have shown that shade-grown seedlings of shade-intolerant species differ from shade-tolerant species by allocating more biomass to leaves and having larger SLA. This strategy results in large leaf area : biomass ratios in these species, which maximizes whole-plant carbon gain and growth potential under optimal conditions (Lambers & Poorter 1992; Hunt & Cornelissen 1997). Similarly, in our study, small *L. tulipifera* saplings (diameter < 15 mm) allocated relatively more carbon to leaves, resulting in larger leaf areas than for *A. rubrum* saplings (Fig. 5e,f). Since species differences in daily photosynthesis were small, differences in leaf area directly translated into higher A_{crown}. Thus, in the absence of significantly greater stem and root respiration rates in *L. tulipifera* compared to *A. rubrum*, we would expect a more favourable carbon balance in small saplings of *L. tulipifera*.

This conclusion, however, did not hold for larger saplings. Due to species differences in ontogenetic drift in allometry (Fig. 5c,d), *A. rubrum* and *L. tulipifera* saplings had similar A_{crown} (Fig. 7b). One potential consequence of progressively smaller increases in carbon gain with size could be greater mortality for the shade-intolerant species. There is some evidence that seedlings/saplings of shade-intolerant species have fewer carbon reserves due to their apparent preferential allocation of carbohydrates to growth and lower carbon allocation to roots (Walters & Reich 1999; Veneklaas & Poorter 1998; Kobe 1997). Plant carbon balance theory (Mooney 1972; Givnish 1988) suggests that species unable to maintain a favourable carbon balance in competitive environments have an increased probability of mortality (Walters *et al.* 1993a; Kitajima 1994). However, even in the absence of greater mortality due to allocational differences between the species, we expect that a more positive carbon balance would result in greater growth. Therefore, over time, *A. rubrum* would outgrow and overtop *L. tulipifera*, which would be confined to progressively shadier environments than *A. rubrum*.

The predictions of differences in crown carbon balance between *A. rubrum* and *L. tulipifera* discussed above cannot necessarily be extended to whole-plant growth without consideration of differences in other factors such as herbivory, tissue turnover and whole-plant respiration. We have little direct information on these processes in this study, although *L. tulipifera* often drops older leaves in late summer due to ageing in combination with drought (Naumburg, unpublished data). Leaf loss during drought would directly reduce whole-plant carbon assimilation in *L. tulipifera*. Seedling root respiration and whole-plant respiration scale positively with the product of LMR and photosynthetic capacity per unit leaf mass (Walters & Reich 1999). Of the two species, *L. tulipifera* has larger SLA and thus higher mass-based photosynthesis in addition to larger LMR for small saplings. This relationship then implies that *L. tulipifera* should have higher whole-plant respiration rates than *A. rubrum*.

Microsite characteristics such as greater daily PFD obviously result in higher daily carbon gain at the leaf (Naumburg *et al.* 2001) and crown scale (Figs 6 & 7). Scatter around the regression lines in Figs 6 & 7 indicate that variability in the light environment not associated with daily PFD further influenced daily photosynthesis. Variation in the intensity and distribution of sunflecks (e.g. highly episodic *vs* evenly distributed in time) and average shade PFD affect rates of daily photosynthesis independently of daily PFD (Naumburg 2000). Previously, we had shown that in shady microsites, *L. tulipifera* leaves gain more carbon on average than *A. rubrum* (Naumburg *et al.* 2001). This was also the case here when the dynamic photosynthetic model was run on identical diurnal PFD courses (data not shown). However, due to the effects of the light environment, species differences in dynamic photosynthetic behaviour were obscured when photosynthetic estimates from different diurnal PFD courses were compared (Fig. 6). Hence, other light characteristics in addition to total PFD and other factors may contribute to the variability in growth and survival data.

Our modelling indicates that elevated $[CO_2]$-grown plants of both species experienced similar enhancements of daily photosynthesis relative to ambient $[CO_2]$ plants (Figs 6,7). Therefore, we would expect that rising atmospheric $[CO_2]$ will enhance growth in both species similarly and accelerate the rate with which the saplings reach the size class where *L. tulipifera* would be at a carbon gain disadvantage relative to *A. rubrum*. This finding is in contrast to other studies, which suggest that in low PFD, shade-tolerant species tend to have greater biomass enhancements under elevated $[CO_2]$ than less tolerant species, natural light environments

(Kerstiens 1998; Würth, Winter & Körner 1998; Hättenschwiler & Körner 2000) and our own finding of greater photosynthetic enhancement in shade-tolerant species at low daily PFD (Naumburg *et al*. 2001). Here, photosynthetic enhancements at low PFD were marginally greater at the branch level for *A. rubrum* (56%) than for *L. tulipifera* (33%). However, *A. rubrum* did not have greater enhancements in A_{crown} due to the slight reduction in SLA under elevated [CO_2]. Thus, given the large impact of allocational patterns on A_{crown}, the effect of elevated [CO_2] on crown carbon balance will not only depend on the direct effect on photosynthesis at the leaf level but also on whether carbon allocation to leaves decreases or not (Hättenschwiler & Körner 1996).

In this study, it was necessary to assume the same stem diameter to leaf biomass relationship for ambient and elevated [CO_2] plants because allometric data for elevated [CO_2] plants were not available. Thus, we only considered [CO_2] effects in our analysis related to the observed 20% decrease in SLA for *A. rubrum*, and greater enhancement of photosynthesis at light saturation in *A. rubrum vs L. tulipifera* (Naumburg & Ellsworth 2000). Although *L. tulipifera* had lower carbon allocation to leaves under elevated [CO_2], it was unclear whether that difference was due to [CO_2] or its lower growth light environment. Furthermore, other studies have shown no clear [CO_2] effect on biomass allocation patterns (reviewed in Wolfe *et al*. 1998; Curtis & Wang 1998) even after long-term CO_2 exposure (Rey & Jarvis 1997; Tissue, Thomas & Strain 1997; Centritto, Lee & Jarvis 1999), while SLA often (but not always) declines under elevated CO_2 (Wolfe *et al*. 1998; Saxe *et al*. 1998).

In conclusion, differences in carbon balance of contrasting species in a forest understorey with variable light environments are dependent not only on the specific photosynthetic characteristics of leaves (Naumburg *et al*. 2001), but also on allometric relationships that can vary with sapling age and size. Surprisingly, the differences in both dynamic and steady state photosynthesis per unit leaf area and architectural characteristics related to leaf display (e.g. leaf size, angle and leaf overlap) were small. Differences in crown leaf area between *A. rubrum* and *L. tulipifera* indicated a size class beyond which carbon gain in *A. rubrum* surpasses that of *L. tulipifera* saplings in the pine forest understorey, suggesting that competitive dynamics between these species will change for the larger stems – a process that is likely to be accelerated by increased atmospheric CO_2. These findings suggest that physiological approaches utilizing crown architecture for estimating carbon gain can provide useful input to forest growth models, and may aid our understanding of trends for changing species dynamics in forest understoreys with future, higher atmospheric CO_2.

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