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Leaf senescence and decline of end-of-season gas exchange in five temperate deciduous tree species grown in elevated CO_2 concentrations

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Abstract

We measured rates of leaf senescence and leaf level gas exchange during autumnal senescence for seedlings of five temperate forest tree species under current and elevated atmospheric CO_2 concentrations and low- and high-nutrient regimes. Relative indices of whole canopy carbon gain, water loss and water use efficiency through the senescent period were calculated based on a simple integrative model combining gas exchange per unit leaf area and standing canopy area per unit time. Seedlings grown under elevated [CO_2] generally had smaller canopies than their current [CO_2]-grown counterparts throughout most of the senescent period. This was a result of smaller pre-senescent canopies or accelerated rates of leaf drop. Leaf-level photosynthetic rates were higher under elevated [CO_2] for grey birch canopies and for low-nutrient red maple and high-nutrient ash canopies, but declined rapidly to values below those of their current [CO_2] counterparts by midway through the senescent period. CO_2 enrichment reduced photosynthetic rates for the remaining species throughout some or all of the senescent period. As a result of smaller canopy sizes and reduced photosynthetic rates, elevated [CO_2]-grown seedlings had lower indices of whole canopy end-of-season carbon gain with few exceptions. Leaf level transpiration rates were highly variable during autumnal senescence, and neither [CO_2] nor nutrient regime had consistent effects on water loss per unit leaf area or integrated whole canopy water loss throughout the senescent period. Indices of whole canopy, end-of-season estimates of water use efficiency, however, were consistently lower under CO_2 enrichment, with few exceptions. These results suggest that whole canopy end-of-season gas exchange may be altered significantly in an elvated [CO_2] world, resulting in reduced carbon gain and water use efficiency for many temperate forest tree seedlings. Seedling growth and survivorship, and ultimately temperate forest regeneration, could be reduced in CO_2-enriched forests of the future.

Keywords: CO_2, deciduous, photosynthesis, senescence, trees, water use

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Introduction

Increase in ambient CO_2 concentration [CO_2] leads to increased biomass production largely through increases in photosynthesis and leaf area production (see Strain & Cure 1985). Elevated [CO_2] also decreases stomatal conductance and therefore typically leads to increased water use efficiency (mole CO_2 fixed per mole H_2O transpired; Bazzaz 1990). However, the increases in plant growth under elevated [CO_2] are often accompanied by earlier leaf and whole plant senescence in many herbaceous species (Paez *et al.* 1983; St. Omer & Horvath 1983; Curtis *et al.* 1989). Do similar patterns of accelerated senescence take place during autumnal leaf fall in temperate deciduous trees grown under elevated [CO_2]? Currently there is preliminary evidence that suggests that the timing of bud break and leaf fall for temperate

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deciduous trees can be accelerated by elevated [CO_2] (SL Miao and FA Bazzaz *unpublished manuscript*). In contrast, Gunderson *et al.* (1993) found that elevated [CO_2] did not alter the rate of leaf fall in white oak and tulip poplar, and further, the [CO_2]-enhanced photosynthetic rates were maintained through the senescent period. End-of-season carbon gain is important for seedling regeneration because often at that time the canopy trees have lost a majority of their leaves allowing increased light levels to penetrate the canopy, while the seedlings and saplings have not yet lost their leaves. Accelerated leaf senescence in an elevated [CO_2] environment would lead to a reduction in the end-of-season carbon gain. Thus, for deciduous trees, elevated [CO_2] may result simultaneously in an increase in instantaneous carbon fixation rates while possibly decreasing the annual duration of carbon fixation.

Our current understanding of the growth responses of temperate forest species to elevated atmospheric [CO_2] suggests that some species will show initially high levels of growth enhancement which will decline within 2–3 years while others maintain the earlier growth enhancement (Bazzaz *et al.* 1993; Norby *et al.* 1992). The effect of elevated [CO_2] on tree growth can also be strongly influenced by the nutrient supply (e.g. Conroy *et al.* 1992; Bazzaz & Miao 1993) though a low nutrient supply does not preclude a significant response to CO_2 for all species (e.g. Norby *et al.* 1986). An increased nutrient supply can accelerate leaf and whole plant developmental rates, potentially leading to altered patterns of leaf drop during autumnal senescence and thus altered end-of-season carbon gain (Mooney & Gulmon 1982; Aber & Melillo 1991). It is possible that there are synergisms between nutrient supply and [CO_2] that lead to end-of-season leaf fall and gas exchange that would not be observed independently.

Regeneration in deciduous forests in central New England occurs primarily within small, single-tree gaps (Sipe & Bazzaz 1995). Thus, the present study examines patterns of leaf senescence and leaf gas exchange throughout autumnal senescence for seedlings of five species of temperate forest trees exposed to elevated [CO_2] at two levels of nutrient supply under light and temperature regimes representative of small gaps. We ask: (1) Does elevated [CO_2] alter rates of leaf drop during autumnal senescence in temperate trees, and are these affects mediated by nutrient supply?; (2) Does elevated [CO_2] alter photosynthetic carbon gain and/or transpirational water loss during autumnal senescence in temperate trees?; (3) Does elevated [CO_2] alter relative patterns of whole canopy end-of-season gas exchange?; and (4) How variable are these end-of-season leaf-level demographic and physiological responses between species?

Materials and methods

Experimental design and protocol

Five early successional temperate deciduous tree species differing in shade tolerance (Bazzaz & Miao 1993) were chosen for the experiment; in order of increasing shade tolerance, grey birch (*Betula populifolia*), ash (*Fraxinus americana*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and striped maple (*Acer pennsylvanicum*). First year seedlings of each species were collected just after germination (ash, striped maple, red maple) or germinated in the greenhouse from seed collected from the Harvard Forest (Petersham, Massachusetts, USA) in late May and early June 1990 (grey birch, yellow birch, red maple). Collected seedlings were transplanted immediately into tree tubes and were transferred within one week to [CO_2] and temperature controlled walk-in growth chambers (Environmental Growth Chambers, Chagrin Falls, Ohio, USA). Germinated seedlings were established *in situ* in the growth chambers. Half of all collected and germinated seedlings were maintained in near current (400 μmol mol^{-1}) and half were maintained in enriched (700 μmol mol^{-1}) atmospheric [CO_2]. CO_2 concentrations were controlled within 20 μmol mol^{-1}, and were maintained via injections of pure, medical grade CO_2 (USP minimum purity 99.6%; factory minimum 99.8% with maximum 2–5 p.p.m. hydrocarbons, MedTech, Inc., Cambridge, Massachusetts, USA). Chambers had day/night temperatures of 22 °C and 15 °C, with a day length of 14 h. On 21–23 June 1990, all seedlings were transplanted into 12.7 cm diameter (1 L) standard plastic pots containing Cornell mix (1:1:1 sterilized sand, sterilized soil and perlite). Half of the seedlings within each CO_2 level, randomly, received high nutrient additions and half received low nutrient additions. The nutrient additions for the first 10 weeks of growth were 1.2 g and 0.12 g of a slow release fertilizer (Osmocote 14–14–14; 8.2% NH_4-N, 5.8% NO_3-N; 14% P_2O_5-P, 14% K_2O-K) for high- and low-nutrient pots, respectively. The low- nutrient treatment is representative of present N mineralization rates and nutrient availability in Harvard Forest (equivalent to an N input of 40 kg ha^{-1} y^{-1}), and the high-nutrient treatment represents a higher mineralization rate with extreme nitrogen deposition (equivalent to 400 kg ha^{-1} y^{-1}) (Aber *et al.* 1989). The high-nutrient plants showed no signs of toxicity. After the first 10 weeks, the slow-release fertilizer was calculated to have been completely released, and nutrients were added weekly in the form of liquid soluble fertilizer (Peter's 20–20–20; 3.9% NH_4-N, 5.8% NO_3-N, 10.0% urea-N, 20% P_2O_5-P, 20% K_2O-K). Low- and high- nutrient pots received 200 mL per pot of 0.042 and 0.42 g fertilizer per litre of water, rates equivalent to 40 and 400 kg N ha^{-1} y^{-1}, respectively. In addition, on 17 August 1990, each pot received an additional supplement of micronutrients in the form of a liquid soluble trace element fertilizer (Peter's Soluble Trace Elements) at the rate of 300 mL of a 0.37 g L^{-1} solution.

On 28 June 1990 the seedlings were randomly assigned to one of three blocks. Within each block was a pair of growth chambers, which were randomly assigned near current (400 µmol mol^{-1}) or elevated CO_2 (700 µmol mol^{-1}) treatments. Initially, day/night temperatures were 24 °C and 17 °C, day length was 14 h, and midday light levels were 378 ± 53 µmol m^{-2} s^{-1}. Throughout the experiment, temperatures and light levels were gradually increased, via two separate 1-h steps, to midday maxima and then gradually decreased, also via two separate 1-h steps, to night-time values. The diurnal light regime was designed to approximate the daily photosynthetic photon flux density in small gaps, ≈ 12.5 µmol m^{-2} d^{-1} at midsummer (Wayne & Bazzaz 1993). Day/night temperatures and day length were increased weekly until midsummer when temperatures were 30 °C and 24 °C and day length was 15 h, corresponding with ambient temperatures observed at Harvard Forest (Harvard Forest Weather Station, Petersham, Massachusetts). Growth chamber set points lagged approximately one month, to compensate for the slower initial growth of the transplanted seedlings. At monthly intervals, the three blocks (and nested [CO_2] assignments per chamber) were randomized. At each randomization, all replicates of each species at each nutrient level were randomized within each chamber. The overall design was a randomized split-plot, with block and [CO_2] as main-plot treatments and species and nutrient level randomized within plots.

To simulate autumn, from 25 October 1990, day/night temperatures and day lengths were systematically decreased, following smoothed 20 year averages of min/max temperatures from the Harvard Forest weather station. Day/night temperatures were adjusted by –2 °C and + 2 °C, respectively, to account for the measured difference between understorey and weather station measurements (Carlton 1994). Day/night temperatures decreased an average of 2 °C and photoperiod by an average of 30 min per week, with the exception that night-time temperatures did not drop below 2 °C, due to limitations in the growth chambers' cooling systems.

Starting 25 October 1990 and continuing every 4–7 days until 7 January 1991, one replicate of each species × [CO_2] × nutrient level was harvested. Immediately before harvest, photosynthesis and transpiration (P and E, respectively) were measured on the youngest fully developed main stem leaf under ambient light, humidity, temperature and [CO_2] (400 or 700 µmol mol^{-1}) using a portable closed gas exchange system with a 0.25 L leaf chamber (Li-6200, LICOR, Lincoln, Nebraska). Four 0.385 cm^2 disks were taken from the leaf used for gas exchange. Disks were oven-dried and weighed to determine leaf mass per area (g cm^{-1}). The leaves were dried to a constant weight and leaf mass was recorded to the nearest mg.

Curve fitting

Patterns of standing canopy mass and gas exchange rates throughout autumnal senescence were analysed using non-linear regression techniques. Since we had no *a priori* model fit to the data, we used simple polynomial regression techniques (Abacus Concepts 1992). Second-order polynomials gave sufficiently good fits, with no significant improvement in higher order fits. To facilitate comparisons of fitted curves between low- and high-[CO_2] treatments, the difference between the elevated [CO_2] and current [CO_2] (elevated-current) best-fit 2nd-order polynomial equations for each parameter was plotted for each species at each nutrient level. The resulting 2nd-order polynomial curves depict the absolute differences between high and current [CO_2] for each parameter, with no difference between high and current [CO_2] as a zero value.

Whole canopy models

We derived relative indices of whole canopy carbon gain and water loss through a simple summation model based on the instantaneous *in situ* measurements of photosynthesis and transpiration of the youngest fully expanded leaf and whole canopy leaf mass. While we did not measure photosynthetic and transpiration rates throughout the canopy, several lines of evidence suggest that this simple summation technique should provide a reasonably consistent index of maximal whole canopy gas exchange across species and treatments. First, at the time when we began measuring photosynthetic rates (just prior to the onset of autumnal senescence), all canopies had stopped producing new leaves and had experienced leaf loss due to normal canopy ageing. Thus, the photosynthetic gradients throughout each canopy spanned from *in situ* photosynthetic maxima (i.e. the youngest leaf, which was produced prior to the onset of autumnal senescence and aged consistently throughout the senescent period) to net photosynthetic rates at or near zero (i.e. the lowest canopy leaves). Actual rates of decline of photosynthetic rates for progressively lower (older) leaves throughout these first-year canopies are unknown; however, Koike (1988) reports similar rapidly decreasing photosynthetic profiles through a number of early successional seedling (2–4 year) canopies of deciduous trees. Second, whole canopy nitrogen contents, while less than those measured in the laminar tissue

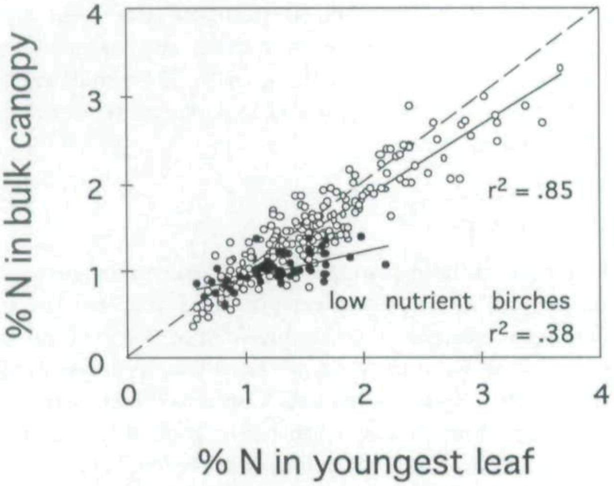

Fig. 1 Nitrogen concentration in bulk canopy leaves vs. the youngest fully expanded leaf (used for gas exchange determinations). The regression includes all species, nutrient regimes, [CO_2] and sample dates (throughout the senescent period) lumped (open circles), with the exception of low nutrient birches (filled circles), which had a significantly lower slope than other groups ($P < 0.05$, homogeneity of slopes test). The dotted line represents a slope of 1.0.

used for the leaf-level gas exchange, fell on a common regression line for all species and treatments indicating a single nitrogen profile through all canopies, with the exception that low-nutrient birch leaves used for photosynthetic determinations had significantly higher nitrogen contents than leaves in the bulk canopy which could have led to overestimates of canopy photosynthesis (Fig. 1). Finally, light availability gradients throughout these small seedling canopies were probably minimal for at least two reasons: leaf area indices at peak canopy development were modest (≈ 2.18 and 2.42 in 350 and 700 μmol mol^{-1} chambers, respectively) and declined precipitously throughout the senescent period; and the aluminium chamber walls would have reflected any unabsorbed light to lower canopy leaves, effectively reducing the light gradient through the canopies. Nevertheless, species and treatments with large canopies may have experienced significant light attenuation profiles through the canopies, resulting in overestimates of canopy photosynthesis.

Trajectories of the relative indices of whole canopy CO_2 and water exchange, $P_{\Sigma Ci}$ and $E_{\Sigma Ci}$, were second-order polynomials fitted to the product of instantaneous leaf level measurements of gas exchange and whole canopy leaf area. Whole canopy leaf area was estimated from the product of leaf mass per area and whole canopy leaf mass. Relative indices of whole canopy end-of-season CO_2 and H_2O gas exchange ($P_{\Sigma C}$ and $E_{\Sigma C}$, respectively) were made by integrating derived equations of instantaneous whole canopy gas exchange ($P_{\Sigma Ci}$ and $E_{\Sigma Ci}$, respectively). To calculate $P_{\Sigma C}$ and $E_{\Sigma C}$, $P_{\Sigma Ci}$ and $E_{\Sigma Ci}$ were integrated over the period of time from when the first leaf-level gas exchange measures were made (s) to the time when the remaining plants had no leaves remaining (*f*).

$$P_{\Sigma C} = \int_{?}^{f} P_{\Sigma Ci}dt \text{ and } E_{\Sigma C} = \int_{?}^{f} E_{\Sigma Ci}dt.$$

A relative index of integrated end-of-season whole canopy water use efficiency was calculated as the ratio of integrated end-of-season whole canopy carbon gain over water loss ($P_{\Sigma C}/E_{\Sigma C}$).

Results

Leaf area

Plants had lost all their leaves between 60 and 80 days following the onset of the simulated autumn (Fig. 2). Ash and striped maple held their canopies the longest, while yellow birch and red maple lost their canopies the earliest. Second order polynomial regressions of leaf area through the autumnal simulation were significant ($P < 0.05$) for all groups of plants except for high- [CO_2], low-nutrient ash ($P = 0.101$). Plants grown under higher nutrients had much greater leaf mass at the beginning of the simulated autumn and tended to have delayed leaf loss as evidenced by negative curvature (see Fig. 2). Comparing fitted curves (Fig. 3), elevated [CO_2] increased canopy size (pre-senescence) in low nutrient ash and to a lesser extent in low-nutrient yellow birch, but decreased canopy sizes in these species at high nutrients. Conversely, elevated [CO_2] reduced canopy size in high-nutrient grey birch, red and striped maples, but decreased canopy sizes for these species in low nutrients. Elevated [CO_2] had even more variable effects on the dynamics of leaf drop. Leaf drop was accelerated under high [CO_2] for low-nutrient ash and for high-nutrient red and striped maples, decelerated for low-nutrient striped maple (following a very short period of acceleration) and grey birch and for high-nutrient ash and yellow birch. Rates of leaf drop were relatively unaffected by [CO_2] for low-nutrient red maple and yellow birch and for high-nutrient grey birch.

Leaf gas exchange

Photosynthetic and transpiration rates declined steadily throughout the simulated autumn for all species (Fig. 2). Second-order polynomial regressions of photosynthesis through the autumnal simulation were significant ($P < 0.05$) or marginally significant ($0.10 > P > 0.05$; high [CO_2], low-nutrient ash and yellow birch and current [CO_2], high nutrient red maple) for all groups of plants except for high-[CO_2], high-nutrient ash and low-nutrient

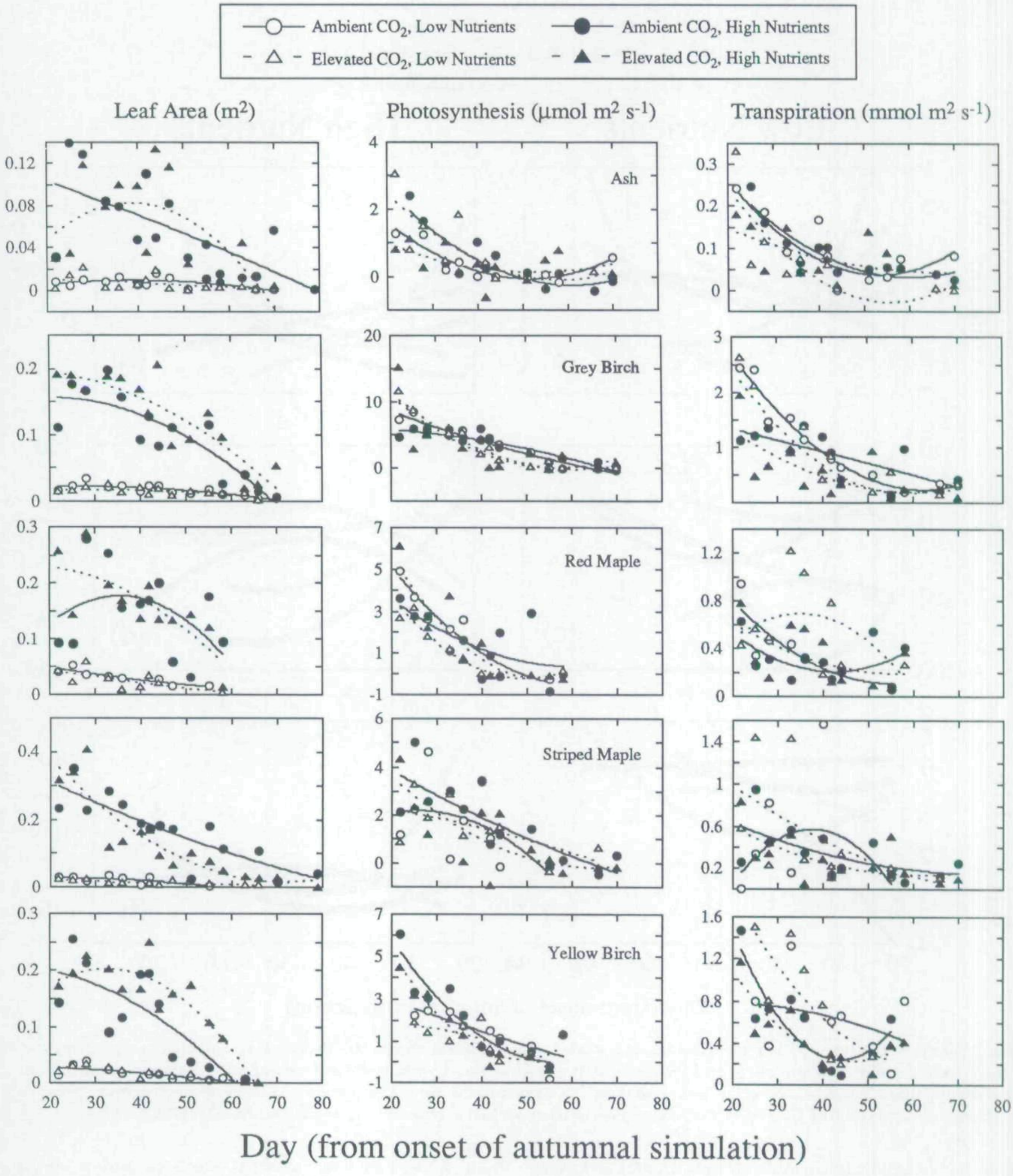

Fig. 2 Leaf area and photosynthetic and transpiration rates of standing leaves throughout autumnal senescence for seedlings of five temperate forest tree species grown under ambient and elevated atmospheric CO_2 concentrations and with two nutrient supply rates. The lines drawn through the data are best-fit second-order polynomials.

striped maple. There was a larger number (8) of non-significant regressions for transpiration, and, in general, these relationships had lower coefficients of determination. Throughout the simulated autumn, grey birch maintained substantially higher and ash substantially lower photosynthetic and transpiration rates than the other

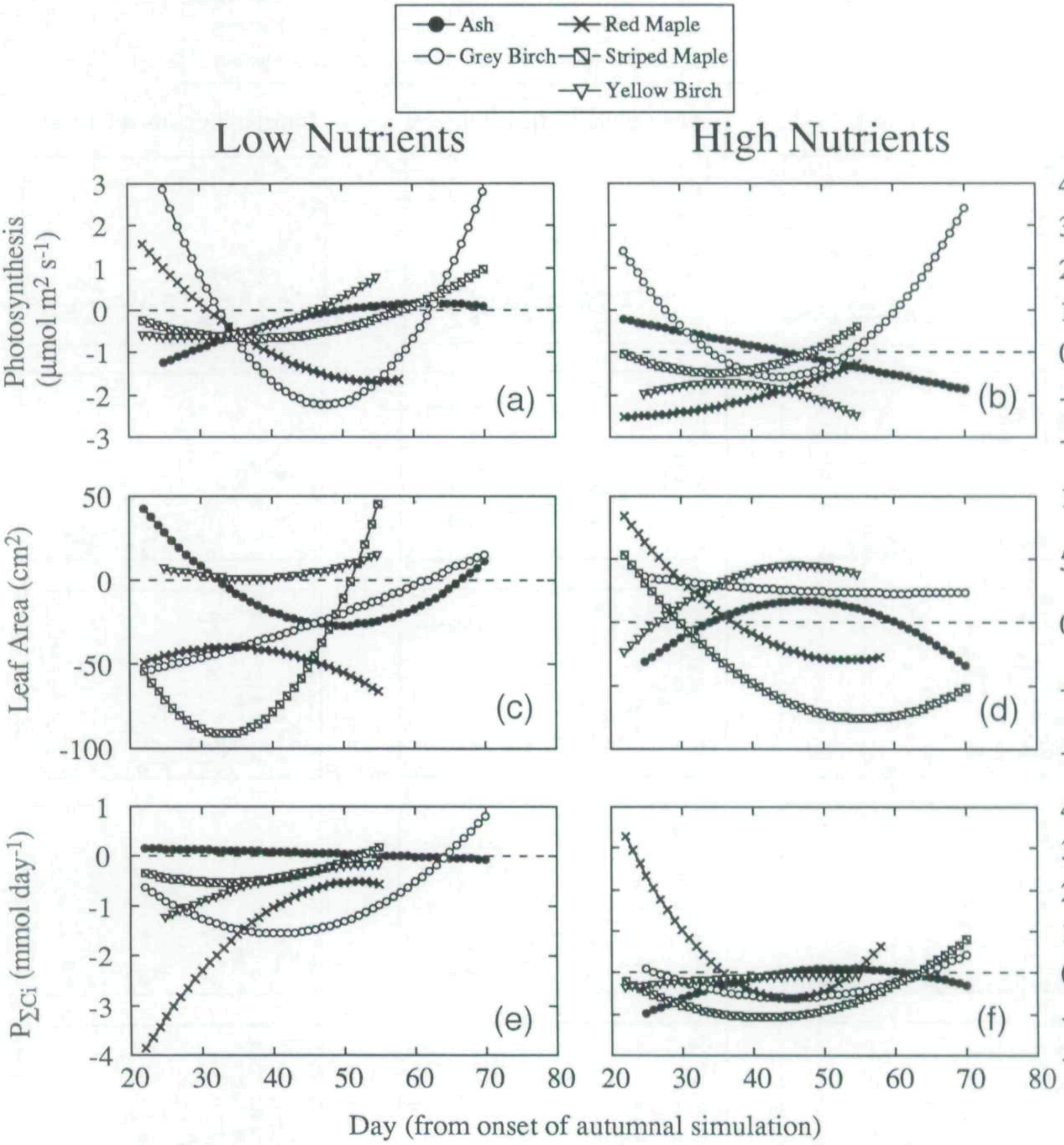

Fig. 3 Effects of elevated [CO_2] on the dynamics of leaf-level photosynthesis, canopy size (leaf area) and whole canopy carbon gain ($P_{\Sigma Ci}$). Each line within a given plot represents the difference between the elevated [CO_2] and current [CO_2] (elevated-current) bestfit 2nd-order polynomial equations. Within each plot there is a dashed line at zero. Any portion of a curve above this level represents an instantaneous POSITIVE CO_2 effect. Portions of a curve below this level represent instantaneous NEGATIVE CO_2 effects.

species. For yellow birch, low nutrients resulted in lower photosynthetic but not lower transpiration rates. Elevated [CO_2] generally reduced photosynthetic rates (Fig. 3). [CO_2]-induced increases in photosynthetic rates were seen for low-nutrient red maple, for high-nutrient ash, and for grey birch at both nutrient levels, though these rates had dropped below those at current [CO_2] by the middle to end of the simulated autumn. Overall, nutrient and [CO_2] had few consistent effects on end-of-season leaf-level transpiration patterns.

Relative whole canopy estimates of P and E

As expected from canopy size and rates of gas exchange, grey birch generally had the highest and ash the lowest index of integrated end-of-season whole canopy gas

Table 1 Estimated end-of-season whole canopy carbon gain, water loss, and water use efficiency (WUE) for seedlings of five species of temperate forest tree seedlings exposed to two CO_2 and nutrient levels. Values represent integrations from 20 days following the onset of autumnal senescence through total canopy loss (a total duration of 35– 60 days). See Materials and Methods for a description of how whole canopy end-of-season gas exchange values were calculated.

Species	Nutrients	CO_2	Carbon gain (mmol CO_2)	Water loss (mol)	WUE (mmol/mol)
Ash	Low	Ambient	4.8	1.1	4.3
		Elevated	7.5	0.7	10.4
	High	Ambient	103.6	10.9	9.5
		Elevated	31.5	6.2	5.1
Grey birch	Low	Ambient	132.5	32.5	4.1
		Elevated	87.0	19.4	4.5
	High	Ambient	816.6	181.9	4.5
		Elevated	563.9	137.5	4.1
Red maple	Low	Ambient	84.1	13.8	6.1
		Elevated	33.3	19.9	1.7
	High	Ambient	307.9	55.9	5.5
		Elevated	438.1	79.0	5.5
Striped maple	Low	Ambient	39.7	8.0	5.0
		Elevated	28.0	10.6	2.6
	High	Ambient	628.4	122.9	5.1
		Elevated	347.8	85.2	4.1
Yellow birch	Low	Ambient	41.8	16.9	2.5
		Elevated	24.9	19.8	1.3
	High	Ambient	423.3	87.5	4.8
		Elevated	367.4	109.6	3.4

exchange (Table 1). In all species and at both nutrient levels, elevated [CO_2] resulted in reduced end-of-season carbon gain ($P_{\Sigma C}$), except for low-nutrient ash and high-nutrient red maple (Table 1, Fig. 4). These reductions ranged from 13 to 70% of current [CO_2], but the reductions did not significantly alter relative species ranking. Increased nutrients resulted in massive increases in carbon gain. Indices of whole canopy end-of-season water loss ($E_{\Sigma C}$) were reduced for ash, grey birch and high-nutrient striped maple, and were greater for red maple, yellow birch and high-nutrient striped maple. Integrated end-of-season water use efficiency (WUE, the ratio of end-of-season carbon gain to water loss) was reduced with elevated [CO_2] in most cases, the exceptions being low-nutrient ash and grey birch and high-nutrient red maple.

Discussion

Through the use of a simple integrative model we have demonstrated that, contrary to expectations, elevated atmospheric [CO_2] appears to reduce (8 out of 10 species by nutrient combinations) end-of-season whole canopy photosynthesis for a variety of temperate deciduous forest tree species' seedlings. The consistency of reduced whole canopy end-of-season photosynthesis and, to a lesser extent transpiration, is surprising in light of the high variation in temporal dynamics of standing leaf area and gas exchange in response to atmospheric CO_2 concentration and nutrient supply for the different species. However, for virtually all cases we examined, standing leaf area and per unit leaf area gas exchange rates were reduced by elevated [CO_2] by the beginning or shortly after the onset of the simulated autumnal senescence.

As with all other studies of plant physiological/morphological responses to environmental change, it is important to clearly place this study within the context of the growth conditions which the study was designed to simulate. Specifically, this study focused on the response of one-year-old tree seedlings in light environments representative of small, single-tree gaps (Sipe 1990). We selected this experimental condition because for many of the tree species within temperate deciduous forests regeneration largely occurs in gaps of this size (e.g. Sipe & Bazzaz 1994, 1995). However, we were unable to replicate this light environment fully; while our daily photosynthetically active photon flux was equivalent to those found in small gaps on an average (average of sunny and cloudy days over the season) day, we could not replicate the peaks in light availability (> 400 µmol m^{-2} s^{-1}) that can be found in northern and central sections of these gaps during midday near the middle of the summer (Sipe 1990). While it is possible that our light regime artificially reduced photosynthetic rates at some measurement times (i.e. near midsummer), other

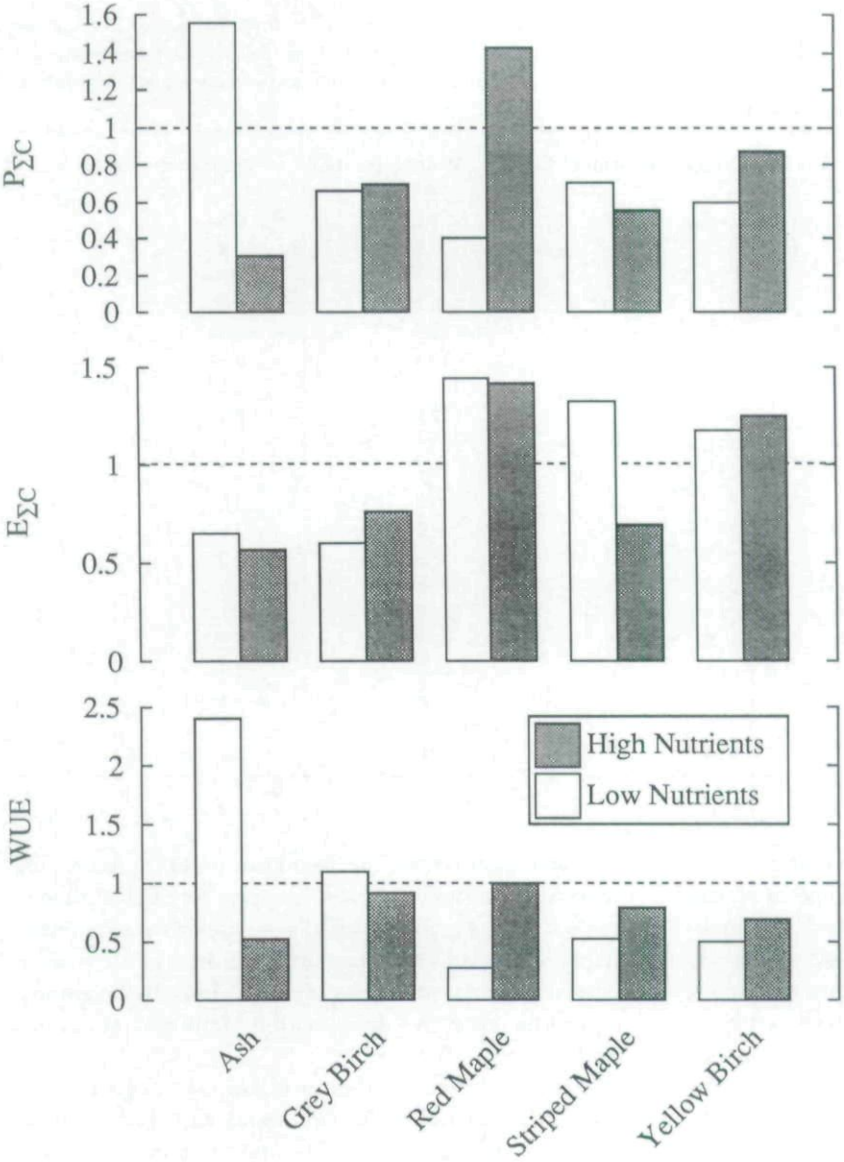

Fig. 4 CO_2 enhancement ratios (elevated divided by current [CO_2] response) in integrated end-of-season whole canopy carbon gain ($P_{\Sigma C}$), water loss ($E_{\Sigma C}$) and water use efficiency ($P_{\Sigma C}/E_{\Sigma C}$) throughout autumnal senescence for seedlings of five temperate forest tree species grown under low and high nutrient supply rates. Actual values used to derive enhancement ratios can be found in Table 1.

researchers have found that temperate tree seedlings grown under small gap conditions experience photosynthetic light saturation at around 350 µmol m^{-2} s^{-1} (Sipe & Bazzaz 1994), making this possibility unlikely.

It has been well established that the effects of elevated [CO_2] on biomass enhancement in trees is dependent on species identity (reviews by Poorter 1993; Ceulemans & Mousseau 1994; Wullschleger *et al.* 1995) and that the interactive effects of elevated [CO_2] and nutrient supply is also dependent on species identity (Bazzaz & Miao 1993). Analogous to the results presented by Bazzaz and Miao (1993), we found that the interactive effects of atmospheric [CO_2] and nutrient supply on the dynamics of autumnal leaf senescence varied between species (see Fig. 2). Interestingly, these species-dependent variations in CO_2 response were not readily apparent in relative indices of integrated end-of-season whole canopy gas exchange as evidenced by the reductions in $P_{\Sigma C}$ observed in 80% of the cases we observed.

These data suggest the following general conclusions for temperate tree seedlings in light environments representative of small gaps. First, during autumnal senescence, whole canopy carbon gain, water loss and water use efficiency are determined largely by the timing and rate of leaf drop and less by rates of leaf-level gas exchange. Second, elevated atmospheric CO_2 concentrations will likely result in smaller canopies during the senescent period, thus reducing whole canopy carbon gain and water use efficiency during this period. Third, there will be species-specific variation in the degree to which carbon gain and WUE will be reduced during the senescent period. We estimated that CO_2 enrichment resulted in a reduction of end-of-season carbon gain of up to 70% in some cases. Even more modest reductions in carbon gain at the end of the season might significantly reduce future seedling growth and survivorship, potentially altering the regenerative capacities of some temperate tree species.

To date, few studies directly incorporate estimates on seedling survivorship and growth in assaying plant community responses to CO_2 enrichment, particularly in long-lived perennial species. The results reported here suggest that we need to consider the growth regulatory effects of $[CO_2]$ in concert with its effects on leaf-level gas exchange throughout the entire growing season in order to estimate yearly carbon gain in temperate forest seedlings. Such measures would provide a framework for predicting regeneration success of temperate forest seedlings and temperate forest community structure and dynamics in a future which will have significantly elevated atmospheric CO_2 concentrations.

Acknowledgements

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