

Autumnal leaf abscission of sugar maple is not delayed by atmospheric CO₂ enrichment

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Abstract

To investigate the effects of atmospheric CO₂ enrichment on physiology and autumnal leaf phenology, we exposed 3-year-old sugar maple (*Acer saccharum* Marsh.) seedlings to 800 (A8), 600 (A6), and 400 $\mu\text{L}(\text{CO}_2) \text{L}^{-1}$ (AA) in nine continuous stirred tank reactor (CSTR) chambers during the growing season of 2014. Leaf abscission timing, abscised leaf area percentages, leaf number, light-saturated net photosynthetic rate (P_{Nmax}), leaf area, accumulative growth rates, and biomass were determined and assessed. The results suggested the following: (1) no significant differences were found in the timing of leaf abscission in the three CO₂-concentration treatments; (2) P_{Nmax} was continuously stimulated to the greatest extent in A8 at 319% and 160% in A6 until the end of the growing season, respectively; and (3) leaf number, leaf area, and accumulative height growth all significantly increased by elevated CO₂, which led to a 323% increase in A8 biomass and 235% in A6 biomass after 156-d fumigation. In summary, the results suggest, the timing of leaf abscission of sugar maple in fall was not modified by CO₂ enrichment, the increased carbon gain by elevated CO₂ was mainly due to increased leaf area, more leaves, and the continuously enhanced high photosynthesis throughout the growing season instead of the leaf life span.

Additional key words: autumnal leaf phenology; biomass; elevated CO₂; growth; late-season net photosynthesis.

Introduction

As the growing seasons are getting longer due to warmer climate and atmospheric CO₂ rising, the timing of phenological events, such as spring bud break, flowering and autumnal leaf senescence, have been widely reported as changing (Menzel *et al.* 2006, Cleland *et al.* 2007, Rosenzweig *et al.* 2008). This change in the timing of autumnal leaf abscission potentially accounts for the variability in net uptake of CO₂. Goulden *et al.* (1996) found that later canopy senescence of 10 d in 1994 and 1995 resulted in an increase of 500 kg(C) ha⁻¹ gross production in a deciduous forest in New England. However, the responses of autumnal phenology of trees to atmospheric CO₂ rising were very species specific and with large variability due to environmental limitation, which can be characterized as follows: (1) advances (Jach and Ceulemans 1999, Sigurdsson 2001, Warren *et al.*

2011), (2) no changes (Herrick and Thomas 2003, Norby *et al.* 2003a, Norby *et al.* 2003b, Asshoff *et al.* 2006), and (3) delays (Li *et al.* 2000, Asshoff *et al.* 2006, Taylor *et al.* 2008). Therefore, whether the direct effects of future projected elevated CO₂ concentration on leaf autumnal abscission timing of native tree species would affect plant carbon gain is still not clear.

Leaf net photosynthesis is an important aspect for carbon assimilation. Although stimulatory effects of CO₂ on leaf photosynthesis of trees have been widely reported and are fairly well understood (Ellsworth *et al.* 2012, Battipaglia *et al.* 2013, Keenan *et al.* 2013), less is known about the effects on leaf net photosynthesis during the late season since the growing season would be extended. It has been proposed that due to the reduced capacity of “carbon demand” under CO₂ enrichment, determinate species are

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Abbreviations: A4 – 400 $\mu\text{L} \text{L}^{-1} \text{CO}_2$; A6 – 600 $\mu\text{L} \text{L}^{-1} \text{CO}_2$; A8 – 800 $\mu\text{L} \text{L}^{-1} \text{CO}_2$; CSTR – continuous stirred tank reactor; P_{Nmax} – leaf light-saturated net photosynthetic rate.

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more inclined to early senescence which coincides with decreasing leaf net photosynthesis, while for indeterminate species, leaf senescence was delayed because photosynthesis was still active due to the extended growing season (Taylor *et al.* 2008). This suggests that net photosynthesis cannot be determined by only a single instantaneous middle growing season measurement.

Sugar maple (*Acer saccharum* Marsh) is a native component of deciduous hardwood forests in eastern North America with a major economic interest in maple syrup. With the exception of Norby *et al.* (2003b), who indicated that *Acer saccharum* Marsh with CO₂ enrichment (+300 $\mu\text{L L}^{-1}$) showed no consistent effects on the timing of budbreak and leaf unfolding, few studies investigated the response of sugar maple autumnal phenology to atmospheric CO₂ enrichment scenarios not

to mention sustained gas-exchange measurements until the end of growing season. Additionally, most field experiments cannot avoid the lack of water, soil nitrogen, and extreme weather conditions. With these facts in mind, in order to determine whether different CO₂ enrichment sceneries would affect the timing of autumnal leaf falling and late-season photosynthesis, we exposed 3-yr old *Acer saccharum* Marsh seedlings to three projected CO₂ concentrations during the growing season of 2014. Water and soil nitrogen were not limiting factors. Our hypotheses were: (1) Elevated CO₂ will not prolong leaf span, so the leaf abscission timing of *Acer saccharum* Marsh will not be delayed; (2) The net photosynthetic rates will continuously increase during the late season and contribute to more growth and biomass.

Materials and methods

Experimental system and design: The experiment was performed in nine continuously stirred tank reactor (CSTR) chambers from 26 June to 28 November (156 d), in 2014, which were located inside a glass greenhouse at the University of Massachusetts, Amherst. The details of the operation of our CSTR chambers and CO₂-control system were previously described (Manning and Krupa 1992, Elagöz *et al.* 2006, Albertine and Manning 2009, Albertine *et al.* 2014). The intensity of illumination inside the CSTR chambers was 75–85% of conditions outside the greenhouse. The time course of irradiance inside the CSTR chambers was adjusted the day before relying on the weather forecast, so the irradiance inside the CSTR chambers was the same as natural environment outside of the greenhouse. The temperature inside the CSTR chambers was 3.7–5.8°C higher, while relative humidity was 12–19% lower than natural environment outside of the greenhouse, respectively (Fig. 1A,B).

Pure CO₂ was administered continuously for 24 h. One LI-7000 CO₂/H₂O analyzer was used to monitor the CO₂ concentration (Li-Cor Inc., Lincoln NE, USA). The CO₂ concentration inside every chamber was checked and adjusted every other day to ensure the target concentrations were reached. Three CO₂ treatments [A8 – 800, A6 – 600, and A4 – 400 $\mu\text{L}(\text{CO}_2) \text{ L}^{-1}$] were set randomly among nine chambers with three replications each. Uniform seedlings ($n = 27$) in height and basal diameter were selected and divided into 9 groups of three pots each.

Plant material and management: Seedlings of *Acer saccharum* Marsh 3-yr old with 3–4 leaves were obtained from the field of north Amherst on 3 June. All seedlings were native but the genotype was unknown. The seedlings were transplanted into pots (bottom diameter of 9 cm, top diameter of 12.5 cm, and height of 12 cm) immediately in the greenhouse with plenty of water. The growing medium was METRO MIX 200 (Sun Gro Horticulture, MA, USA). Before being placed into CSTRs, all seedlings were

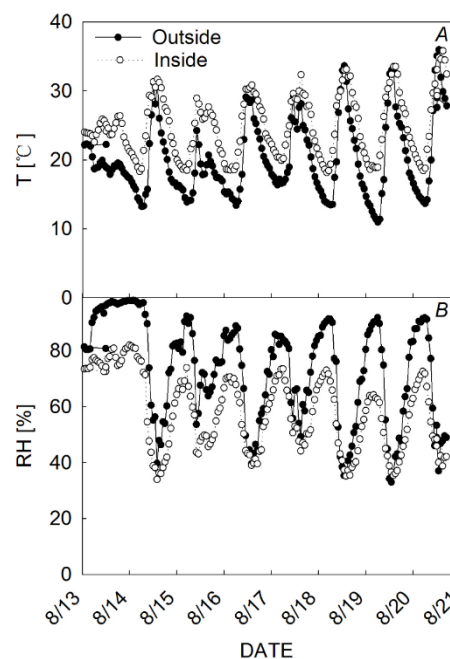


Fig. 1. The temperature (T, A) and relative humidity (RH, B) inside chambers and outside the natural environment during August 2014.

acclimated to the greenhouse from 3 to 25 June (23 d) until they grew well. All seedlings were moved into the CSTRs on 26 June. The seedlings were watered every other day and fertilized with a soluble fertilizer (3.9 g l⁻¹, 16–17–18; *Peters Professional*; Scotts, Ohio, USA) weekly. A soluble trace element mix (36.9 mg l⁻¹) was applied once on 8 August.

Gas exchange: Leaf light-saturated net photosynthetic rate (P_{Nmax}) was measured using a portable Li-Cor 6400 photosynthesis system with a 6400–02B LED light source chamber (Li-Cor Inc., Lincoln NE, USA). The system

controlled saturating PPFD at 1,000 $\mu\text{mol}(\text{photon})\text{ m}^{-2}\text{ s}^{-1}$, CO₂ concentration inside the leaf chamber was set similar to the CO₂ treatments through a supply from a CO₂ cylinder. Two fully expanded upper sun leaves from each seedling were selected and measured and repeated three times every time. All measurements were conducted during 09:00–11:30 h and 14:00–15:00 h to avoid the “noon-sleep” phenomenon.

Leaf area: New leaves were marked at the beginning of July for leaf area and gas-exchange measurements throughout the growing season. Leaf area was calculated by leaf length and width using the formula (Wargo 1978):

$$Y = 3.676 + 0.490 \times LW \quad (1)$$

where Y was leaf area [cm^2], LW was the product of the longest and widest point length of leaf [cm^2]; 3.676 and 0.490 were absolute constants.

Estimated whole plant leaf area = total leaf number \times leaf area (2)

% abscised leaf area = (abscised leaf number \times leaf area)/total LA (3)

Growth, leaf dynamics and biomass: Height and basal diameter of the seedlings were measured twice a month before October, then once after October. Leaf numbers

were counted twice every month before November, with leaf senescence beginning on 7 October, the frequency was changed to once every other day until total abscission. Because there was no wind or extreme low temperature in the greenhouse, some leaves without photosynthetic activity remained attached to the stem which were tested by very gently shaking. All seedlings were harvested at the end of experiment. Roots, stems, and all leaves collected earlier were separated and the dry mass of each determined after drying at 70°C to constant mass.

Data analysis: Leaf number dynamics and autumnal senescence with time under treatments were considered an ordinal data set and accordingly were analyzed using the *Wilcoxon* rank-sum nonparametric test. The effects of elevated CO₂ on all parameters were analyzed by one-way analysis of variance (*ANOVA*) with a chamber type as experimental replication unit (three chambers at each CO₂ concentration) and the three CO₂ concentrations as the factors. Post-hoc comparisons were completed using the least significant-difference tests (LSD) when CO₂ effect was significant. Prior to analysis, data were checked for normality (*Kolmogorov–Smirnov* test) and homogeneity of variance (*Levene's* test). Results were considered significant at $P < 0.05$. All the analyses were performed with *SPSS* statistics software (version 17.0, *SPSS Inc.*, Chicago, IL, USA).

Results

Leaf properties and autumnal leaf abscission: Leaf number, individual leaf area, and estimated whole plant leaf area were all significantly stimulated by CO₂ enrichment. Total leaf number increased to 21 in A8, 20 in A6, and 17 in AA (Fig. 2A). Individual leaf area increased to the greatest extent by 108% in A8 and 52% in A6 compared with AA (Fig. 2B). Estimated whole plant leaf area increased to the greatest extent by 172% in A8 and 92% in A6 (Fig. 2C).

The initial day of leaf abscission in autumn and abscised leaf area percentages with time were all assessed, however, the results indicated no significant effects of elevated CO₂ on autumnal leaf abscission timing. The starting abscission day of leaves in A8, A6, and AA treatments was the 246, 248, and 253 d of the year, respectively. The percentages of abscission leaf area with time in all treatments were also very close without significant differences (Fig. 2D).

Light-saturated net photosynthesis ($P_{N\text{max}}$) increased by elevated CO₂ until the end of growing season. The

individual leaf $P_{N\text{max}}$ values ranged from 2.88–9.47 in A8, 1.37–8.96 in A6, and 0.74–6.58 in AA, respectively. The enhancements of individual $P_{N\text{max}}$ in A8 ranged from 44% in September to 319% in early October; those in A6 were from 36% in September to 160% in October (Fig. 3).

Accumulative growth and biomass: Height growth and biomass were all significantly stimulated by CO₂ enrichment. Throughout the experiment, accumulative height was 34.7, 23.6, and 8.0 cm in A8, A6, and AA, respectively. Accumulative stem diameter increased significantly only with the A8 treatment (Fig. 4). Total biomass of seedlings increased to 323% in A8 treatments and 235% in A6 treatments after 156 d of fumigation with elevated CO₂ concentrations (Fig. 5). The biomass of each organ also significantly increased within a range from 205% in root biomass to 267% in stem biomass in A8, and from 89% in stem biomass to 152% in root biomass in A6. No significant differences were found in aboveground to roots biomass ratio between all three treatments.

Discussion

The results indicated leaf $P_{N\text{max}}$ values were around 6.58–9.47 in August (Fig. 3) which is comparable with

similar research on sugar maple (Ellsworth and Liu 1994, Liu *et al.* 1997, Gunderson *et al.* 2000).

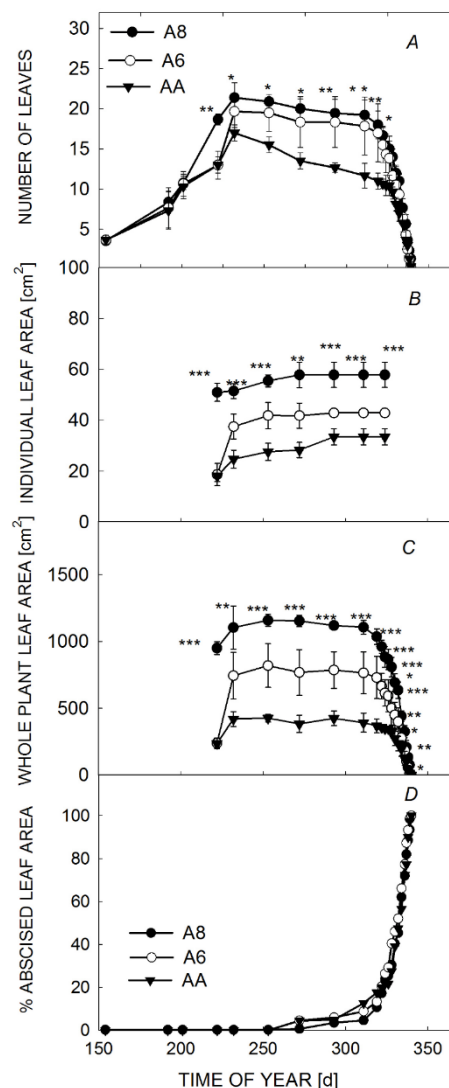


Fig. 2. Dynamics of leaf number (A), individual leaf area (B), estimated whole plant leaf area (C), and abscised leaf area percentage (D) in *Acer saccharum* under 800 (A8), 600 (A6), and 400 $\mu\text{L}(\text{CO}_2) \text{L}^{-1}$ (AA). * – significant differences between three treatments. * – $P < 0.05$; ** – $P < 0.01$; *** – $P < 0.001$.

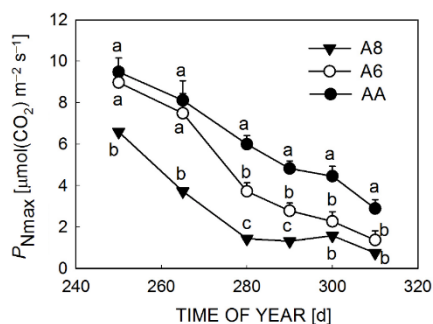


Fig. 3. Light-saturated net photosynthetic rate (P_{Nmax}) of *Acer saccharum* in 800 (A8), 600 (A6), and 400 $\mu\text{L}(\text{CO}_2) \text{L}^{-1}$ (AA). Different letters above the bars indicated multiple comparison results between three treatments. Differences were considered significant when $P < 0.05$.

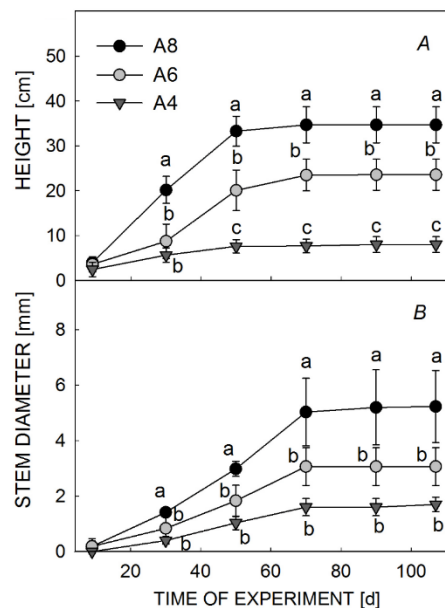


Fig. 4. Accumulative growth of height (A) and stem diameter (B) of *Acer saccharum* in 800 (A8), 600 (A6), and 400 $\mu\text{L}(\text{CO}_2) \text{L}^{-1}$ (AA) during the experiment. Different letters above the bars indicated multiple comparison results between three treatments. Differences were considered significant when $P < 0.05$.

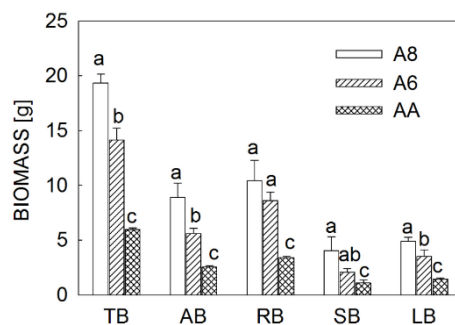


Fig. 5. Total biomass (TB), aboveground biomass (AB), leaf biomass (LB), stem biomass (SB), root biomass (RB) of sugar maple (*A. saccharum*) in 800 (A8), 600 (A6), and 400 $\mu\text{L}(\text{CO}_2) \text{L}^{-1}$ (AA). Values were mean \pm SD. Different letters indicated multiple comparison results between three treatments. Differences were considered significant when $P < 0.05$.

No downregulation of photosynthesis was detected for high P_{Nmax} under elevated CO₂ sustained until early November (Fig. 3), which confirmed the former part of the second hypothesis. There were few studies measuring late-season P_{Nmax} of *Acer saccharum* Marsh but we found similar results of lack of downregulation of P_{Nmax} under elevated CO₂ in other species until the end of growing season, such as *Populusx euramericana* after 158 d under doubled ambient CO₂ concentration (Curtis *et al.* 1995) and *Acer campestre* (L.) after 3 years under 530 $\mu\text{L}(\text{CO}_2) \text{L}^{-1}$ (Zotz *et al.* 2005). It was revealed that the capacity for the acclimation of photosynthesis to elevated CO₂ was determined mostly on some certain genes for determinate or indeterminate growth; downregulation of photo-

synthesis in elevated CO₂ is a result of inability to form sufficient “sinks” for the additional photosynthates (Ainsworth *et al.* 2004, Redding *et al.* 2013). Strictly determinate growth species are more likely to have early senescence and downregulation on photosynthesis due to internal reduced “sink demand”. Therefore, the negative downregulation results should be decided by the determinate growth with partially limited capacity of indeterminate growth style in *Acer saccharum* Marsh (Perttunen *et al.* 2001, Gaucher *et al.* 2005). Environmental factors, such as water, light, soil nitrogen, and micro-elements were not limited in our experiment. The sustained enhanced P_{Nmax} by elevated CO₂ until the end of the season made better growth and carbon-storage gain possible.

Although the results showed that except for maintaining a relatively higher P_{Nmax} throughout the late season, elevated CO₂ did not affect the timing of leaf autumnal senescence shown either in leaf area abscission percentages or in leaf number with time (Fig. 2). The explanation was that the main factors, which generally determine autumnal phenology of *A. saccharum* Marsh, were temperature (Norby *et al.* 2003b) and shortening “photoperiod” (day length relative to night length) (Kozlowski *et al.* 1997, Schaberg *et al.* 2003, Körner and Basler 2010) rather than CO₂ concentration. Dominant long-lived, late-successional species in mature forests are commonly more sensitive to photoperiod compared to early successional species or grasses (Körner and Basler 2010). This characteristic is controlled genetically and cannot be easily changed by transplantation or variable environmental factors (Borchert *et al.* 2005). Similar results were also described by Norby *et al.* (2003a), who found CO₂ enrichment (+300 $\mu\text{L L}^{-1}$) had no contribution to the timing of autumnal leaf abscission after four years in open-top chambers with seedlings planted into the soil. Redding *et al.* (2013) reported that the fall phenology of *A. saccharum* Marsh did not respond to ecosystem acidification, nitrogen enrichment, but it only responds to photoperiod and temperature. Above all, the sensitivity to a photoperiod and determinate growth style all lead to the result of fall phenology had no responses to elevated CO₂.

Leaf number, leaf area, and sustained high net CO₂ assimilation rate under elevated CO₂ concentrations contributed to the elevated biomass. The biomass of seedlings increased by 323% in A8 and 235% in A6 (Fig. 5) which can be comparable with similar studies, such as Bazzaz *et al.* (1990), who reported that 1-yr old *A. saccharum* Marsh increased 267% under 700 $\mu\text{L L}^{-1}$ during 100 d of CO₂ exposure. No significant differences

were found in the aboveground to root biomass ratio; it suggested that CO₂ enrichment had no effects on carbon allocation of *A. saccharum* Marsh seedlings in our experiment. However, the impact of our results was limited in time and space due to the seedling size and short fumigation period. First, the seedling size was small with few leaves which may be more sensitive to elevated CO₂ (Telewski and Strain 1987). Second, the *A. saccharum* Marsh seedlings of this experiment may have not suffered from acclimation of photosynthesis and by a sort of priming effect due to the short CO₂ fumigation period. Other studies indicated that many plants suffered from acclimation of photosynthesis in the long term due to declining N availability (Norby *et al.* 2010) or downregulation of Rubisco (Rogers and Ellsworth 2002). Leaf abscission is caused by changes in autumnal temperature and day length, and also light quality changes associated with day length change in the autumn. Although the above conditions in our experiment were maintained in parallel with conditions outside of the greenhouse, the temperature was higher, while the relative humidity and light quality were lower than those outside, which may lead to early senescence when compared with natural environment. Leaf properties are directly affected by elevated CO₂, but are also affected by factors, such as nitrogen availability, soil water, and species identity. It should be noted that our results only occur when soil nutrition and soil water were not limited which is unlikely to occur in the natural environment.

Conclusions: Plant biomass production is determined by net photosynthetic rates, length of growing season, and the whole plant leaf area with photosynthetic activity during the growing season. Our results illustrated that elevated CO₂ enhanced carbon uptake in *Acer saccharum* Marsh due to an increase in leaf number, leaf area, and sustained higher net assimilation, while leaf span duration had no contribution as insignificant changes were found. This study provided evidence that suggests that future elevated CO₂ is not going to affect autumnal phenology of *A. saccharum* Marsh through altering the length of the growing season directly, although the productivity increase should be considered carefully in a prediction of forest sink capacity. Thus, the response of tree phenology to atmospheric CO₂ enrichment should be species-specific and potentially compounding results with photoperiod, CO₂ enrichment, temperature, and other multiply environmental factors.

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