

## Autumnal photosynthesis is extended in nitrogen-fixing European black alder compared with white basswood: possible adaptive significance

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Net photosynthesis was measured at weekly intervals from late September to mid-November in the field on leaves of actinorhizal European black alder (*Alnus glutinosa* (L.) Gaertn.) and nonactinorhizal white basswood (*Tilia heterophylla* Vent.) growing in central Illinois. Black alder retained its leaves and continued to photosynthesize for a month longer than white basswood. Maximum photosynthetic rates occurred in September and declined during the autumn for both species, although weekly values fluctuated widely. Mean maximum CO<sub>2</sub> fixation rates for black alder and white basswood were 11.88 and 4.62 μmol CO<sub>2</sub> · m<sup>-2</sup> · s<sup>-1</sup>, respectively, at the initial measurement in late September. On each subsequent measurement date black alder had a significantly higher rate of CO<sub>2</sub> fixation than basswood. Night temperatures of 0°C and below caused a sharp decline in photosynthesis for black alder on the following day. Stomatal conductance was highly correlated with photosynthesis, but as these two parameters declined over the autumn, intercellular CO<sub>2</sub> concentration increased. Thus, nonstomatal limitations are thought to be involved in the temperature-induced reduction in photosynthesis. Prolonged photosynthesis in autumn may give black alder a competitive growth advantage over other deciduous species, compensate for the high energy cost associated with nitrogen fixation, or be associated with black alder's inefficient conservation of foliar nitrogen via autumnal retranslocation.

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La photosynthèse nette a été mesurée au champ à toutes les semaines de la fin septembre à la mi-novembre sur des feuilles d'Aulne glutineux (*Alnus glutinosa* (L.) Gaertn.) actinorisé et de Tilleul blanc (*Tilia heterophylla* Vent.) non actinorisé croissant dans le centre de l'Illinois. L'Aulne glutineux a conservé ses feuilles et a continué de photosynthétiser pour un mois de plus que le Tilleul blanc. Les taux maximums photosynthétiques sont survenus en septembre et ont diminué durant l'automne pour les deux essences, bien que les valeurs hebdomadaires présentaient de grandes fluctuations. Les taux maximums de fixation du CO<sub>2</sub> pour l'aulne et le tilleul ont été de 11,88 et de 4,62 μmol de CO<sub>2</sub> · m<sup>-2</sup> · s<sup>-1</sup>, respectivement, au moment de la mesure initiale vers la fin de septembre. À chaque mesure subséquente, l'aulne avait un taux de fixation du CO<sub>2</sub> significativement plus élevé que le tilleul. Des températures nocturnes de 0°C ou inférieures à 0°C ont provoqué une diminution marquée de la photosynthèse pour l'aulne durant le jour suivant. La conductivité des stomates était fortement corrélée avec la photosynthèse, mais à mesure que ces deux paramètres déclinaient durant l'automne, la concentration intercellulaire de CO<sub>2</sub> augmentait. Ainsi donc, on pense que des facteurs limitatifs non reliés aux stomates sont en cause dans la diminution de la photosynthèse induite par la température. Une photosynthèse prolongée durant l'automne pourrait procurer à l'Aulne glutineux un avantage compétitif du point de vue de la croissance par rapport à d'autres essences caduques, compenser pour le coût élevé de l'énergie associé à la fixation de l'azote ou encore être associé à la conservation inefficace de l'azote foliaire de l'Aulne glutineux par le moyen de la retranslocation automnale.

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### Introduction

European black alder (*Alnus glutinosa* (L.) Gaertn.) is an actinorhizal plant capable of fixing nitrogen and therefore improving site productivity (Tarrant and Trappe 1971; Debell and Radwan 1979; Friedrich and Dawson 1984). Black alder retains its green foliage longer than other winter-deciduous hardwoods (Côté and Dawson 1986). This characteristic has also been observed in North America for *Alnus rhombifolia* (Arno 1973), *Alnus rugosa* (Hightshoe 1978), *Alnus serrulata* (Dawson *et al.* 1980), and *Alnus rubra* Bong. (R. F. Tarrant, personal communication) growing within their native ranges. In the Sichuan Province of central China, *Alnus cremastogyne* Burk. drops its foliage up to 20 days later than associated deciduous woody angiosperms (Liu Guofan, personal communication), and in northwestern China *Alnus mandchurica* (Call.) H.-Mazz. and *Alnus hirsuta* Turcz. also exhibit prolonged retention of green foliage (Yang Sihe, personal communication).

For broad-leaved deciduous species, autumnal leaf senes-

cence is associated with a decline in the rate of photosynthesis (Drew and Bazzaz 1979; Nelson *et al.* 1982; Jurik 1986; Davis 1987), because nitrogenous leaf compounds necessary for CO<sub>2</sub> fixation are hydrolyzed and retranslocated to other plant structures. Black alder fixes nitrogen symbiotically and retranslocates proportionately less nitrogen during leaf senescence than other deciduous species do (Dawson *et al.* 1980; Dawson and Funk 1981; Côté and Dawson 1986), which results in nitrogen-rich leaf litter (Redko 1958; Mikola 1958; Côté and Camiré 1985). Because black alder retains a higher percentage of its nitrogen, and keeps its green foliage longer, we hypothesize that it continues to photosynthesize later in the autumn than other deciduous species.

In autumn, decreasing day length and low temperatures trigger leaf senescence and can also directly reduce photosynthesis of trees. In plants defined as chilling sensitive, net photosynthesis gradually ceases between 5 and 10°C as the activation energy for many chloroplast functions increases abruptly (Larcher and Bauer 1981). In plants defined as frost sensitive, there is often a temporary postfreezing inhibition

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of photosynthesis, which may be due to delayed and incomplete opening of the stomata, or to an impairment of the membrane-bound reactions in the chloroplasts (Larcher and Bauer 1981).

To determine whether black alder is capable of photosynthesizing in late autumn after other winter-deciduous tree species have lost their leaves, we measured changes in net photosynthesis, stomatal conductance, and intercellular CO<sub>2</sub> concentration in black alder trees from late September to mid-November, and compared the changes with those in white basswood (*Tilia heterophylla* Vent.). *Tilia* was selected for this comparison because it drops its foliage in late October, at the same time as most other local deciduous angiospermous trees, and because it was growing adjacent to alder on the same type of soil at the study site. The correlation between levels of photosynthetic activity during the autumn and concurrent daily minimum air temperature was determined.

### Materials and methods

The study site was located in grassy parkland on the campus of the University of Illinois in Urbana (40°6'N, 88°12'W), described previously by Côté and Dawson (1986). Black alder and white basswood trees had been planted on the site in 1969. Trees were vigorous, with average heights of 13 m for basswood and 18 m for black alder. Black alder is a native of Europe, while white basswood occurs as a native species in southern Illinois. Although the source of black alder seed is unknown, most Illinois black alders originate from German provenances, and black alder's natural range is almost entirely at latitudes more northerly than the planting site in Illinois. The soil was a mesic Typic Haplaquoll, which is a poorly drained prairie-derived soil from loessal parent material overlying glacial till.

Photosynthetic and leaf water potential measurements were made at 1–2 m above ground on unshaded, fully expanded leaves retaining the most green color, and therefore probably represent the maximum leaf photosynthetic rate for a tree. Photosynthetic measurements were made on 12 leaves per tree from three black alder and three white basswood trees on each sampling date.

A portable infrared gas analysis system (P.K. Morgan Instruments Inc., Andover, MA.) was used to measure fluxes of CO<sub>2</sub> and water vapor under field conditions. A portion (6.25 cm<sup>2</sup>) of a single attached leaf was enclosed in a Parkinson-type cuvette and gas exchange measurements were made under ambient air temperature, irradiance (photosynthetically active radiation, 400–700 nm wavelength), and CO<sub>2</sub> concentration. Air was drawn from a 4 m high telescopic sampling tube to avoid local variation in CO<sub>2</sub> concentration, and was pumped at a controlled rate through two silica gel columns into the leaf chamber. Individual measurements were completed within 30 s to avoid a stomatal response to dry air entering the cuvette. The calculations of CO<sub>2</sub> and water vapor fluxes were based on a differential measurement of gas concentration in the sample and reference air. Reference air for water vapor was 0% RH. Net photosynthesis, stomatal conductance, and intercellular CO<sub>2</sub> concentration (*C<sub>i</sub>*) were calculated using the equations of von Caemmerer and Farquhar (1981).

The diurnal pattern of net photosynthesis was determined on October 8 to establish the time of day when maximum photosynthesis occurred. Maximum rates for black alder occurred between 10:00 and 12:30 (solar time), while peak rates for white basswood occurred on average less than 1 h later. Consequently, black alder foliage was measured first on each day.

At each sampling date from late September to mid-November 1987, measurements were made between 10:00 and 12:30 (solar time). Whenever possible, sampling was done on sunny days to reduce variability between measurement dates. Immediately following the photosynthetic measurements, 3–5 of the 12 leaves were

harvested for determination of water potential, using a pressure chamber (Ritchie and Hinckley 1975). Climatological data were obtained from a weather station within 200 m of the study site.

Petiole tissue taken from black alder leaves on October 30 was examined microscopically to determine whether an abscission zone had formed, and percent leaf drop was estimated visually at each sampling date.

Confidence limits were used to compare means of species at each measurement date. Linear regression was used to model the response of photosynthesis in black alder to the minimum air temperature of the previous night. The relationships between gas exchange parameters and other environmental factors were not examined. The relationships between the measured parameters for the two species were determined by calculating correlation coefficients.

### Results

Black alder continued to photosynthesize for a substantially longer period during the autumn than white basswood did (Fig. 1A). By October 20, white basswood foliage had ceased to photosynthesize, and measurements indicated a net efflux of CO<sub>2</sub>. At this time respiration apparently exceeded any vestigial photosynthetic activity in the few leaves remaining on the trees. On this day black alder had an average net photosynthetic rate of 9.4 μmol CO<sub>2</sub> · m<sup>-2</sup> · s<sup>-1</sup>. Photosynthesis continued in black alder for another month; the rate immediately before abscission was 2.1 μmol CO<sub>2</sub> · m<sup>-2</sup> · s<sup>-1</sup>. At all measurement dates photosynthesis was significantly (*p* < 0.05) higher in black alder than in white basswood (Fig. 1A).

Net photosynthesis declined for both species over the period of measurement (Fig. 1A). For black alder there was considerable fluctuation between weekly measurements. An air temperature below 0°C on the night preceding measurements depressed the photosynthetic rates in black alder (Fig. 1A). A linear regression of photosynthesis against the minimum temperature of the previous night indicated a significant relationship (*p* < 0.0001) that accounted for 50% of the total variation (*r*<sup>2</sup> = 0.50). Photosynthetic activity in white basswood leaves declined earlier than in black alder, and all leaves had fallen by October 21. Even so, leaf photosynthesis declined further in white basswood after initial autumn frost (Fig. 1A). The seasonal decline in maximum and minimum temperatures and the occurrence of air temperatures below 0°C are shown in Fig. 1E. Intercellular CO<sub>2</sub> concentration (*C<sub>i</sub>*) was significantly (*p* < 0.05) higher in white basswood than in black alder and increased steadily over the measurement period for both species (Fig. 1B).

The pattern for stomatal conductance over the autumn period was similar to that for photosynthesis (Fig. 1C). Black alder had consistently higher conductances than white basswood, and a temperature below 0°C the previous night was associated with a decrease in stomatal conductance the next day.

In contrast to photosynthesis and stomatal conductance, leaf water potential tended to increase (i.e., become less negative) over the measurement period, although there was much fluctuation for black alder among measurement dates (Fig. 1D). The leaf water potential was not measured on the second of two subsequent measurement dates that occurred immediately after October 20 (Fig. 1D), although photosynthetic characteristics were measured on both dates. A temperature below 0°C the previous night was associated with an increase in leaf water potential.

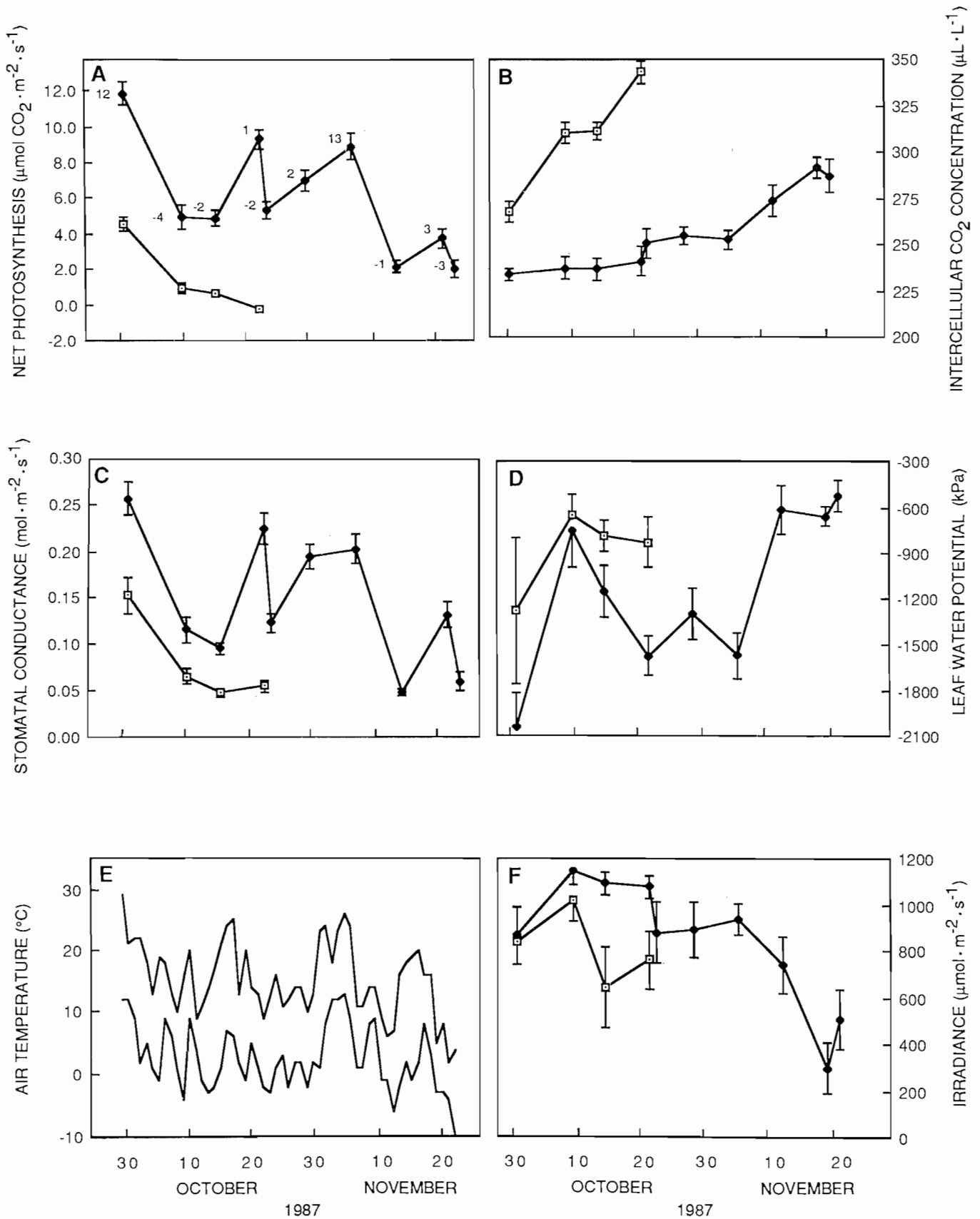


FIG. 1. (A) Seasonal pattern of net photosynthesis (the minimum temperature of the previous night is given for each photosynthetic measurement date). (B) intercellular  $\text{CO}_2$  concentration, (C) stomatal conductance, (D) leaf water potential, (E) maximum and minimum air temperature, and (F) irradiance, for black alder (◆) and white basswood (◻) measured in autumn 1987. Air temperature is first given for September 28; all other parameters were first measured 1 day later. Vertical bars represent confidence limits at  $p < 0.05$ , and lack of overlap indicates significant difference.

The relationships between the various parameters are summarized in correlation matrices for black alder and white basswood (Table 1). The correlation coefficients for the significant relationships between photosynthesis and stomatal conductance were 0.90 for both black alder and white basswood; photosynthesis and  $C_i$  were negatively correlated for both species. In black alder, leaf water potential was negatively correlated with photosynthesis and stomatal conductance, and positively correlated with  $C_i$ . In white basswood, leaf water potential was not as strongly correlated with these parameters (Table 1).

White basswood lost most of its leaves over a short, 2-week period. Black alder, on the other hand, gradually lost its leaves over a period of about 6 weeks, with an accelerated rate of drop during the week preceding November 19. Tissue taken from black alder leaves on October 30 revealed abscission zones extending from the periphery of the petiole to the vascular bundle. Abscission zones often form long before leaf drop in woody perennials, and alder leaves remained metabolically active for at least 3 weeks beyond October 30. Alder leaf separation occurred over a longer period of time than that required for basswood to lose all its leaves.

### Discussion

Autumnal photosynthesis in black alder continued until mid-November, 1 month longer than in white basswood and most other local temperate-deciduous tree species. Other studies have examined photosynthesis of broad-leaved deciduous species under field conditions in fall. Nelson *et al.* (1982) found that hybrid *Populus* clones grown under short-rotation intensive culture in Michigan (42°47' N, 84°35' W) and Wisconsin (45°35' N, 89°34' W) retained green leaves and photosynthesized for 2–6 weeks longer than native *Populus* species, although photosynthesis in the clonal populations had ceased by October 20. In a later study, Nelson and Isebrands (1983) confirmed that substantial late-season photosynthesis occurs in the hybrid *Populus* clones and found that moderate to high levels of photosynthate were exported from the leaves to other plant organs. Jurik (1986) examined the seasonal patterns of photosynthetic capacity of several species (*Acer saccharum*, *A. rubrum*, *Populus grandidentata*, *Quercus rubra*, and *Fagus grandifolia*) in a successional forest in northern lower Michigan (45°33' N, 84°42' W); photosynthesis declined rapidly in all species in September and early October.

In our study, at a more southerly latitude, white basswood ceased photosynthetic activity by mid-October, whereas black alder remained active until mid-November. The continuing photosynthesis of black alder is notable, given the more northerly origin of this species in Europe, where the growing period is likely to be shorter than for species native to Illinois. Moving latitudinal tree ecotypes from north to south in temperate regions generally results in a shorter growing season relative to that of local ecotypes (Larcher 1980), and therefore earlier leaf senescence and leaf abscission for trees from more northerly populations. Conversely, moving trees from southerly populations northward, as was the case with white basswood, generally results in a prolongation of the growth period relative to that of local populations.

Although there were weekly fluctuations, both species showed a general decline in photosynthesis and stomatal

TABLE 1. Correlation matrix of gas exchange parameters and leaf water potential measured in black alder and white basswood

	Stomatal conductance	Leaf water potential	$C_i$
Photosynthesis			
Black alder	0.90	-0.82	-0.62
Basswood	0.90	-0.30	-0.87
Stomatal conductance			
Black alder		-0.79	-0.33
Basswood		-0.32	-0.65
Leaf water potential			
Black alder			0.51
Basswood			0.11 ns

NOTE: Correlations are significant at  $p < 0.01$  except where indicated by ns (not significant).  $C_i$ , intercellular  $CO_2$  concentration.

conductance as the autumn progressed. Drew and Bazzaz (1979) reported that leaf senescence in *Populus deltoides* was accompanied by a partial closure of stomata and concomitant reductions in net photosynthesis. They suggested that the functional ability of stomates is unaffected by senescence, at least in the early stages, and that partial closure may be due to processes at the physical or metabolic level within the leaf.

Many reports have shown a relationship between falling air temperatures and falling rates of photosynthesis, although most have dealt with conifers (see Oquist 1983 for review; DeLucia 1987; DeLucia and Smith 1987). Examples of a similar response in deciduous species are rarer. Drew and Bazzaz (1979) found that photosynthesis was depressed in *Populus deltoides* when it was exposed to nighttime air temperatures of 4°C. Hällgren *et al.* (1982) reported that photosynthesis in *Betula pubescens* and *B. tortuosa* declined as leaf temperature was lowered to 5°C, and the autumn decline of photosynthesis in *Betula maximowicziana* and *B. platyphylla* var. *japonica* was associated with a daily minimum temperature of below 10°C (Koike and Sakagami 1985). In our study, minimum nighttime air temperature seemed to have little effect on photosynthesis the following day in black alder unless temperatures fell below 0°C (Fig. 1A), suggesting that 0°C may be a threshold temperature for temporary impairment of photosynthesis in this species.

The high correlation between photosynthesis and stomatal conductance in both species may indicate that there was a stomatal limitation on photosynthesis as air temperatures fell. However, an increase in  $C_i$  indicates that nonstomatal factors may be involved in the reduction in photosynthesis. Even though photosynthesis declined over autumn,  $C_i$  increased, so that for both species there were significant negative correlations between photosynthesis and  $C_i$ . That is, although  $CO_2$  concentration within the leaf increased,  $CO_2$  fixation declined. This phenomenon has been demonstrated for *Betula* (Hällgren *et al.* 1982) and *Xanthium* (Drake and Raschke 1974), and the increase in  $C_i$  may cause the stomata to close. A reduction in photosynthesis of *Coffea arabica* after exposure to chilling temperatures was primarily due to nonstomatal factors, such as impairment of chloroplast function (Bauer *et al.* 1985). In a review of the effects of low temperature on photosynthesis, Oquist

(1983) stated that there are no clear examples of temperature-induced stomatal closure being the primary cause of low-temperature inhibition of photosynthesis. Our results support this idea.

The midmorning water potential of black alder increased as photosynthesis and stomatal conductance declined. As stomates close, transpiration is reduced and plants maintain a more favorable water balance. Furthermore, cooler autumn temperatures can reduce rates of evapotranspiration and evaporation of soil water. Smith *et al.* (1984) found a similar pattern over the autumn for six conifer species when noon xylem pressure potential was measured.

Photosynthesis was consistently higher in black alder than in white basswood. In general, early successional species such as alders have higher rates of photosynthesis than late successional species such as basswood (Bazzaz and Carlson 1982; Côté *et al.* 1988). At the start of measurements in late September, black alder and white basswood had mean photosynthetic rates of 11.88 and 4.62  $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , respectively. The photosynthetic rate for the closely related American basswood (*Tilia americana*) in natural conditions measured at light saturation, optimal temperature, and ambient  $\text{CO}_2$  was about 5.5  $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  (Jurik 1986); for young individuals of this species grown in full sunlight and shade conditions, the photosynthetic rates were 5.6 and 5.3  $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , respectively (Bazzaz and Carlson 1982). Few photosynthetic rates have been reported for alder species and none are available for large field-grown specimens. At high light intensities and 25°C, black alder seedlings had a maximum rate of 17.3  $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  (Côté *et al.* 1988), similar to the value for red alder (*Alnus rubra*) seedlings measured at 20°C (Krueger and Ruth 1968).

Low rates of photosynthesis are often related to low leaf nitrogen concentrations (Mooney *et al.* 1978; Dawson and Gordon 1979; Field *et al.* 1983; Mooney *et al.* 1983; Côté *et al.* 1988). Measurements of autumnal changes in foliar nitrogen and nitrogenous substances have been made on the same trees investigated in this study (Côté and Dawson 1986). During the last 2 weeks before leaf abscission in 1984, the nitrogen concentration in leaves of white basswood declined by 49%, whereas in black alder it declined by only 21%. In addition, black alder had consistently higher leaf nitrogen concentrations than white basswood throughout the autumn. An apparent lack of autumnal foliar nitrogen retranslocation in *Alnus* species has also been reported by Dawson *et al.* (1980), Dawson and Funk (1981), and Rodriguez-Barrueco *et al.* (1984). A large part of the nitrogen in the leaves of trees occurs as enzymes in the chloroplasts and mitochondria (Kramer and Kozlowski 1979). Chlorophyll-protein complexes of reaction centers, which convert light energy into chemical energy in chloroplasts, are also a leaf nitrogen pool (Govindjee 1988). Plant leaf proteins are characterised by a high proportion of one photosynthetic enzyme, RuBP carboxylase-oxygenase, which accounts for up to 50% of total leaf protein (Kawashima and Wildman 1970). Kang and Titus (1980) concluded that more than 90% of the total leaf protein decline in apple leaves during the autumn could be accounted for by the loss of RuBP carboxylase-oxygenase. Thus, the evidence in our study, combined with the complementary findings of Côté and Dawson (1986), indicate that much of the leaf nitrogen retained in black alder in late

fall may be in photosynthetic enzymes and protein complexes.

The ability of black alder to photosynthesize in late autumn may give it a competitive growth advantage over other broad-leaved deciduous species, particularly in situations where rapid early growth is important for successful colonization of a site, as in a successional environment following a disturbance. This, combined with its capacity to fix nitrogen, maintain high leaf nitrogen levels, and utilize high light intensities (Krueger and Ruth 1968), provides black alder with the potential to compete successfully in a wide range of early successional environments. Alternatively, prolonged fixation of carbon may be needed to balance the energy cost of nitrogen fixation. One could also speculate that, given actinorhizal alders' ability to fix nitrogen, there would have been little selection pressure over evolutionary time for mechanisms to conserve foliar nitrogen before leaf fall via efficient translocation of nitrogen-containing substances derived from photosynthetic enzymes, chlorophyll-protein complexes, and other nitrogenous leaf substances. Thus, prolonged photosynthesis in autumn might just as well be a consequence of alders' inefficient foliar nitrogen retranslocation.

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