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Autumnal Photosynthesis in Short-Rotation Intensively Cultured *Populus* Clones*

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Abstract

Many exotic hybrid *Populus* clones grown under short-rotation intensive culture (SRIC) in the Lake States region of the U.S.A. retain green leaves in the autumn for 2—6 weeks after native aspen (*P. tremuloides* and *P. grandidentata*) have lost their leaves. Leaves on the terminal shoots of five such clones tested in southern Michigan and northern Wisconsin had substantial leaf conductances to CO_2 and photosynthetic rates (P_G) during this late-season period of leaf retention. P_G was high enough to suggest that autumn retention of green leaves may be an important factor contributing to the rapid growth of poplars under SRIC in this cold northern temperate area. Leaf conductances and P_G declined gradually before the first hard frosts of the autumn in the northern Wisconsin experiment, indicating normal autumn leaf aging and senescence, but did not change appreciably in the southern Michigan experiment until the first hard frosts. The first hard frosts reduced P_G and leaf conductance in most of the clones, dramatically in the northern Wisconsin experiment. Leaf conductances and P_G in two of the clones in the southern Michigan experiment were reduced only moderately by the first hard frosts. Leaf conductance and P_G exhibited generally parallel seasonal trends in both experiments.

When exotic *Populus* hybrids are grown under short-rotation intensive culture (SRIC) in the Lake States region of the U.S.A., many clones retain green leaves in the autumn for 2—6 weeks after native aspen (*P. tremuloides* and *P. grandidentata*) have lost their leaves. We have suspected that this late season leaf retention may be one factor contributing to the rapid growth of exotic poplars under SRIC. A central question is whether the leaves retained during the autumn period exhibit significant photosynthesis. This study is an investigation of photosynthetic rates in the autumn in several poplar clones grown under SRIC in southern Michigan and northern Wisconsin, U.S.A. In addition to quantifying photosynthetic rates, we also report information on internal and environmental control of photosynthesis during the late-season period.

MATERIALS AND METHODS

East Lansing, Michigan, U.S.A. experiment:

Autumn photosynthesis was measured in four hybrid poplar clones that retain green leaves for much of the autumn in southern Michigan — NC-5326, NE-58, NE-308, and NE-353 (Table 1). Unrooted hardwood cuttings (25 cm) were planted at a 0.3 × 1 m spacing in three 6 × 8 m plots in late April and early May 1977 at the Michigan State University Tree Research Center

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Table 1

Identification of *Populus* clones used to determine autumnal photosynthesis.

Clone designation	Cultivar name	Parentage
NC-5326[a]	Eugenei	*P. deltoides* × *P. nigra*[b]
NE-1 (NC-5272)	Strathglass	*P. nigra* × *P. laurifolia*
NE-58	—	(*P.* × *rasumowskyana*) × *P. nigra* cv. *incrassata*
NE-308	—	*P. nigra* var. *charkowiensis* × *P. nigra* cv. *incrassata*
NE-353	—	*P. deltoides* × *P. nigra* var. *caudina*[b]

[a] NC = North Central Forest Experiment Station number, and NE = Northeastern Forest Experiment Station number, U.S. Forest Service. All clones other than Eugenei were developed by the NE Forest Experiment Station.

[b] Also *P.* × *euramericana.*

(latitude 42°47′ N, longitude 84°35′ W). Two of the plots contained a single *Populus* clone (NC-5326 and NE-58; Table 1); the third plot contained a random mixture of clones NE-308 and NE-353. The soil was a sandy loam and had previously been planted with vegetable crops. Before planting, each plot was sprayed with a tank mix of amitrole-T and simazine at rates of 0.47 cm^3. $.m^{-2}$ *a.i.* and 0.28 g m^{-2} *a.i.*, respectively, to suppress weeds. Plots were fertilized on May 17 with 22.4 g m^{-2} of 10-20-20 (N-P-K) fertilizer and again on August 1 with 7.5 g m^{-2} ammonium nitrate. The plots were not irrigated. A complete description of the mensurational characteristics of this planting is given by Gottschalk and Dickmann (1978).

Field measurements of photosynthesis and leaf conductance were taken on five dates from mid-September to late October 1977. At this time the first-year shoots averaged 1.2 to 1.3 m tall, and, for clones NE-58 and NC-5326, had produced about 75 leaves. Shoots in the NE-308 and NE-353 mixture, however, had produced an average of 300 leaves because of profuse lateral branching. Three trees of each clone randomly selected from the interior of each plot were measured on each date. On each measurement date leaves at three positions on the main stem were sampled: (*1*) the third leaf below the terminal bud, (*2*) a leaf in the middle of the crown, and (*3*) the lowest leaf not showing visible signs of senescence. Leaves at any one position were measured on all clones in a randomized order before measurements at the next position began. Measurements were done between 10.00 and 15.00 (Eastern Daylight Time) on sunny or partly sunny days.

Notes on the condition of the trees and time of budset were kept throughout the study period. Environmental parameters were also monitored. Maximum and minimum temperatures, relative humidity, and total solar irradiance were extracted from data published by the U.S. National Weather Service in Lansing, Michigan. Precipitation was recorded from a standard rain gauge at the study site.

Rhinelander, Wisconsin, U.S.A. experiment:

Autumn photosynthesis was monitored in two hybrid poplar clones that retain leaves well into the autumn in northern Wisconsin — NC-5326 and NE-1 (NC-5272) (Table 1). Each clone was growing near Rhinelander, Wisconsin (latitude 45°35′ N, longitude 89°34′ W) in a separate

70.6 m^2 multiple-spaced plot at spacings of 0.3 to 1.2 m. Details of plot design can be found in Nelson *et al.* (1980). The soil was a sandy loam located in what was formerly the Hugo Sauer Nursery. The trees, 2-year-old coppice on 6-year-old roots, were grown under SRIC conditions, including fertilization (11.2—16.8 g m^{-2} per year N as NH_4NO_3, 8.4 g m^{-2} per year P from 1977 through 1979 only, 8.4 g m^{-2} per year K from 1977 through 1979 only), irrigation (2.5 cm of water per week, including rainfall, from June 1 to September 1 only), weed control (establishment year: handweeding and linuron at 0.22 g m^{-2} *a.i.*; second year: handweeding), and insect control (malathion in 1978 for aphid control). There was no irrigation during this experiment. Average trees from the plot interior were selected for monitoring of photosynthetic rates. Only the tallest coppice sprout on a stump was used. The average height at budset was 3.5 m for NC-5326 and 4.7 m for NE-1. At budset the average number of leaves on the current terminal shoot $\geqq$ 30 mm long was 48 for NC-5326 and 60 for NE-1.

One or two trees (usually two) of each clone were selected for the measurements at each sampling time, approximately every two weeks from August 25-October 18, 1979. Because the sampling was destructive, new trees were selected each time. Only leaves on the current terminal shoot were monitored for photosynthetic rate. Leaves were selected to represent the upper, middle, and lower portions of the terminal shoot. Before terminal budset, the upper shoot position was the second fully expanded leaf below the shoot apex. After budset this position was represented by the ninth or tenth leaf below the bud. The lower shoot position was the 12th leaf from the base of the shoot, excluding the 4 small preformed basal leaves. The middle position was the leaf approximately halfway between the upper and lower positions. Photosynthetic measurements were made between 11.00 and 16.00 (Eastern Daylight Time) on either completely sunny or completely overcast days.

Budset times, leaf condition, and the environmental parameters precipitation, irradiance, temperature, and relative humidity, were monitored throughout the experiment. The environmental parameters were measured continuously with instruments at the USFS Harshaw Experiment Farm, located about 16 km northwest of the plots used in this experiment. Precipitation was measured with a standard 20.3 cm diameter rain gauge, total solar radiation was measured in the open with a bimetallic mechanical pyranograph solarimeter (*Weather Measure*, U.S.A.), and temperature and relative humidity were measured with a hygrothermograph (*Bendix*, U.S.A.).

Linear regression was used to investigate relationships between photosynthetic rate (dependent variable) and the independent variables measured or tabulated at the time of photosynthesis determinations: (*1*) the environmental parameters: quantum irradiance (400—700 nm) (I), leaf temperature, vapour pressure deficit (VPD), and the number of days before or after terminal shoot budset, and (*2*) leaf conductance. The budset variable was used in the form of the transformation, number of days after budset +100, to avoid mixed negative and positive values. Simple linear regression statistics were computed for photosynthetic rate *versus* the independent variables. Simple correlation coefficients between the independent variables were also computed to identify independent variables that are highly intercorrelated. Multicollinearity problems were avoided by keeping indepedent variables consistently having a correlation coefficient greater than 0.5 ($p \leq 0.05$) in separate multiple regressions. As a result, the maximum number of independent variables in any multiple regression tested was three. The multiple regression model used was linear and of the form $Y = a + b_1x_1 + b_2x_2 + \dots b_kx_k$.

Independent variables were introduced into the multiple regression in the order of their contribution to the F value. Log transformations of the independent variables were tested in some multiple regressions where non-linearity was suspected. The multiple regressions explaining the greatest amount of variation (R^2) were selected, and the homogeneity of variance assumption was confirmed for each "best" regression with standard residual plots. Separate regressions were calculated for each shoot position, except for the lower terminal position of NC-5326, which was excluded from regression analysis because of an insufficient number of data points.

Photosynthesis and associated measurements:

Similar techniques were used in both experiments to measure photosynthetic rate (P_G) and the associated parameters that were measured at the time of ech P_G determination — leaf conductance, I, leaf and air temperature, and ambient relative humidity.

P_G of individual attached leaves was measured using a labeled carbon dioxide ($^{14}CO_2$) method modified from that described by McWilliam *et al.* (1973). Adaxial and abaxial surfaces of a small section (0.95 cm^2) of the intact leaf lamina midway between the leaf tip and base were exposed to $^{14}CO_2$-labeled air (322 cm^3 m^{-3}) of known specific activity (185 Bq cm^{-3} gas mixture at 21.1 °C and 0.1 MPa) (5.0 µCi l^{-1}) for 20 s at a constant flow rate of 1.33 cm^3 s^{-1}. After ^{14}C treatment, the middle of the exposed section (0.78 cm^2) was removed immediately with a sharp cork borer. After removal the leaf disc was placed in 1.5 cm^3 of 0.6 M *NCS* solubilizer (*Amersham*, U.S.A.) in a 20 cm^3 scintillation vial, 1.5 cm^3 of 0.5% benzoyl peroxide in toluene, a bleaching agent, was added to each vial; and the disc was then digested for 24 h in a 50 °C oven. After the digestion period, three drops of glacial acetic acid and 13 cm^3 of scintillation cocktail [63 cm^3 *Spectrafluor PPO-POPOP* (*Amersham*, U.S.A.) in 1000 cm^3 toluene] were added to the vials. The vials were placed in a darkened scintillation counter for three hours to reduce the effects of chemoluminescence, and the samples were then counted for 5 min on a scintillation counter.

The rate of CO_2 uptake for each sample was calculated as:

$$P_G = \frac{\left(\frac{\text{cpm}}{\text{ce}} \times \text{CCO}_2 \times 1.18\right)}{\text{SA} \times \text{LA} \times t}$$

where P_G [mg CO_2 m^{-2} s^{-1}], cpm is the observed sample count rate (corrected for background), ce is the counting efficiency, CCO_2 is µg CO_2 cm^{-3} gas mixture for the concentration of CO_2 at a standard temperature and pressure (Čatský *et al.* 1971, p. 164), 1.18 is a discrimination factor to account for diffusive and biochemical discrimination within leaves against $^{14}CO_2$ (van Norman and Brown 1952, Austin and Longden 1967, Incoll 1977), SA is the specific activity of the $^{14}CO_2$—$^{12}CO_2$ gas mixture for the same standard temperature and pressure as in CCO_2 [desintegrations per volume gas mixture and time], LA is the area of the excised leaf disc [m^2], and t is the time length of the $^{14}CO_2$ pulse [s]. P_G measured with this technique is greater than net photosynthesis (Incoll 1977, and unpublished data of D. Michael, N. D. Nelson and D. I. Dickmann (1979) and may approximate gross photosynthesis in some cases (unpublished data of D. Michael *et al.* 1979).

In the Rhinelander experiment, the first hard frosts on October 9—10 damaged many of the leaves in the crown. These leaves had 10—100% of surface area browned or blackened after that date. P_G measurements after October 9 were on green areas of leaves only.

In addition to the continuous monitoring of environmental parameters during the course of the experiments, point measurements of environmental factors and leaf diffusion resistance were taken at the time of the photosynthesis measurements. I (µmol m^{-2} s^{-1}) was measured in the adaxial leaf plane at the time of $^{14}CO_2$ application using a quantum flux sensor and meter (*Li-Cor*, U.S.A.). Abaxial leaf diffusion resistance to H_2O [s mm^{-1}] was measured on the half of the lamina not exposed to $^{14}CO_2$ with a diffusive resistance meter and horizontal sensor (*Li-Cor*, U.S.A.) (Kanemasu *et al.* 1969, Morrow and Slatyer 1971). Abaxial leaf conductance to CO_2 [mm s^{-1}] was obtained by taking the reciprocal of leaf diffusion resistance to H_2O and multiplying by 0.623, the ratio of diffusion coefficients for CO_2 and H_2O in air (Jarvis 1971, p. 569). Leaf temperature [°C] was determined by placing a *YSI Model 427* stainless steel thermistor (*Yellow Springs Instrument*, U.S.A.) against the abaxial leaf surface, and air temperature was determined with the same thermistor placed under the leaf. Ambient relative humidity [%]

was measured with a hygrothermograph (*Bendix*, U.S.A.). Vapour pressure deficits [kPa] were calculated for each leaf in the Rhinelander experiment, based on saturation water vapour pressure at abaxial leaf temperature and on ambient air temperature and relative humidity. Leaf diffusion resistance, leaf and air temperature, and relative humidity were measured just before $^{14}CO_2$ application.

The application of ^{14}C and all associated measurements in the field were done with the leaf in its natural orientation. Each treated leaf was removed after the ^{14}C counting disc was excised. Fresh leaf area was measured with a *Lambda* leaf area meter and leaf dry matter was determined after ovendrying at 100 °C. Petioles were included in the areas and masses. SLW was calculated as leaf dry matter per leaf area [mg cm^{-2}].

In the Rhinelander study, a sub-experiment examined the permanence of the very low leaf conductances in NE-1 found on October 10, the day following the first hard frost of the autumn. On October 16, the second of two consecutive sunny days (max. temp. 13—18 °C) following hard frosts on October 9—10, 12—13, 13—14, diffusion resistances of leaves from near the upper and middle terminal positions of three trees were measured at midday under clear sky conditions. The leaves were then excised, the petioles were immediately inserted in vials of distilled water and were transported in continuous light to a growth room. They were left in the growth room for 90 min at 23—27 °C, 65% relative humidity, and 150 µmol m^{-2} s^{-1} (fluorescent and incandescent lights), and diffusion resistance was measured again. The leaves were then given a high irradiance treatment (325 µmol m^{-2} s^{-1}) for 6½ h, followed by 6 h of darkness, followed by 325 µmol m^{-2} s^{-1} for six more hours, after which diffusion resistance was again measured. Diffusion resistance was measured as in the main experiment on remaining green areas of the leaves (from 10—40% of the surfaces of the leaves used in the sub-experiment were browned by the hard frosts of October 9—10, 12—13, and 13—14).

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RESULTS

East Lansing, Michigan, U.S.A. experiment:

From early September to late October 1977 (Fig. 1, *left*), maximum and minimum temperatures declined steadily, with light frosts recorded on October 7 and 14 and hard frosts (air temp. —2 °C or less) on October 13, 16, and 17. Precipitation during the late spring and summer (18 cm total) was substantially below normal, but above-average rainfall during the study period, beginning with nearly 4 cm on September 13, maintained soil moisture levels at near-optimum levels.

High leaf conductances and high P_G were maintained after budset in all clones at all leaf positions (Fig. 2). Only after the hard frost of the early morning of October 13 were conductance and P_G substantially reduced at all leaf positions, although a slight decline in P_G was evident after mid-September. Even following three hard frosts, however, substantial rates of photosynthesis were observed in all clones, with values as high as 0.22 mg CO_2 m^{-2} s^{-1} measured in the upper canopy of the NE-308 + NE-353 plot on October 20. Leaf abscission in all clones precluded measurements past October 20. The reduction in conductance after the hard frost on October 13 indicates that stomatal functioning, as well as photosynthesis, was adversely affected by freezing temperatures.

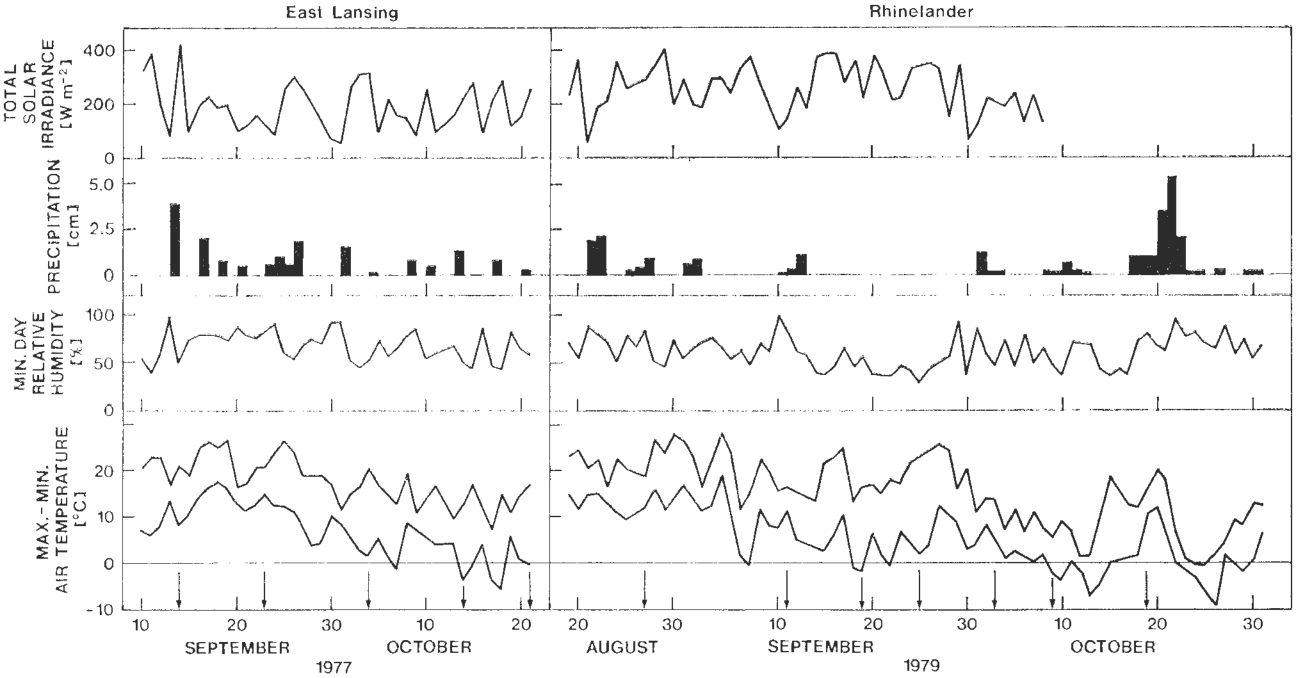

Fig. 1. Climatic data (arrows indicate dates of photosynthesis and conductance measurements) for the East Lansing, Michigan, U.S.A. study site — (autumn 1977), and Rhinelander, Wisconsin, U.S.A. experiment, monitored at the USFS Harshaw Experiment Farm (16 km northwest of the experiment) — (autumn 1979). Total solar irradiance in the Rhinelander experiment was monitored only through early October.

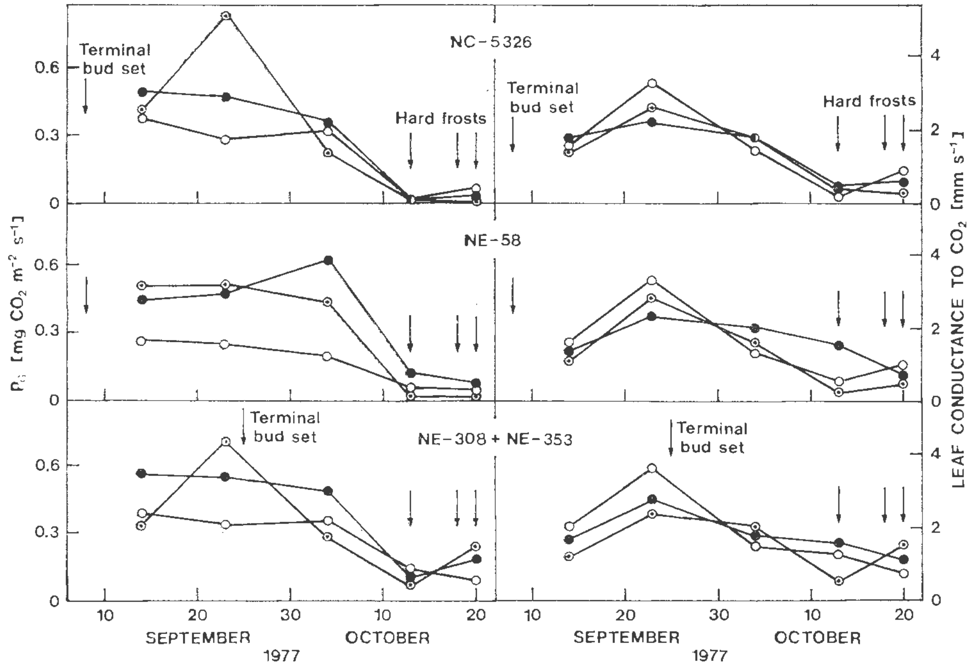

Fig. 2. Photosynthetic rate (P_G) *(left)* and abaxial conductance to CO_2 *(right)* of *Populus* leaves in the upper (⊙), middle (●), and lower (○) portions of the terminal shoot during September and October 1977 near East Lansing, Michigan, U.S.A., for clonal mixture NE-308 + NE-353, clone NE-48, clone NE-58, and clone NC-5326. All trees were one-year-old. Each data point is the average of three trees; standard errors associated with each data point averaged 0.05 mg CO_2 m^{-2} s^{-1} and 0.32 mm s^{-1} for NE-308 + NE-353, 0.03 mg CO_2 m^{-2} s^{-1} and 0.27mm s^{-1} for NE-58, and 0.08 mg CO_2 m^{-2} s^{-1} and 0.21 mm s^{-1} for NC-5326.

Rhinelander, Wisconsin, U.S.A. experiment:

Light frosts occurred on September 8, 19, and 22 (Fig. 1, *right*). The first hard frost (air temp. —2 °C or less) of autumn 1979 occurred during the early morning of October 10, followed by hard frosts on October 13, 14, 25, and 26.

In the Rhinelander area of northern Wisconsin, NC-5326 sets bud on the terminal shoot in early September and retains green leaves for 2—3 weeks after native aspen. In the same area, NE-1 sets bud on the terminal shoot in late September and retains green leaves for 2—5 weeks after native aspen leaves are abscised. Aspen in natural stands in the Rhinelander area normally lose 99—100% of their leaves by September 27.

Although NC-5326 terminal shoot leaves exhibited slight autumnal yellowing by August 27, NE-1 did not exhibit this until October 3. Just preceding the first hard frost, some NE-1 terminal shoot leaves were moderately yellow, but most were green. All NC-5326 leaves were moderately to severely yellow by October 9. Some *Melampsora* rust symptoms became visible on the leaves of both clones in September, and some *Marsonnina* leaf spot was present on NC-5326 leaves after September 12.

The hard frosts resulted in major leaf damage in both clones, particularly to leaves on the terminal shoots. NC-5326 had experienced significant leaf abscission before October 9—10 and had leaves only on the terminal shoots. On October 16 the leaves remaining on the terminal shoots of NC-5326 had 75—100% of surface areas necrotically brown. On October 16 NE-1 terminal leaves showed varying degrees of frost damage, with most having 40—75% of surface areas necrotically brown. Torrential rains and winds up to 48 km h^{-1} on October 21—22, followed by 17 cm of wet snow on October 23, accelerated leaf loss in both clones. By October 24, all NC-5326 leaves had fallen and more than 90% of the leaf area of NE-1 had abscised.

Clone NC-5326 had significant leaf conductances and photosynthetic rates over the autumn period, although P_G declined more rapidly preceding the hard frosts of October than in the case of NE-1 (Fig. 3). In NC-5326, leaf conductance generally declined throughout the autumn and had already reached very low conductance values before the hard frosts. Clone NE-1 exhibited substantial, though gradually declining, leaf conductances and P_G in the autumn until the first hard frost occurred on October 10, causing extensive leaf necrosis and a dramatic drop in conductance and P_G (Fig. 3).

In the sub-experiment done to investigate the permanence of the low leaf conductances in NE-1 following the first hard frost of autumn, the first growth room period for the excised leaves in most cases resulted in small increases in the leaf conductances from the values attained in the field (Table 2). The extension of the growth room period past 90 min resulted in no further

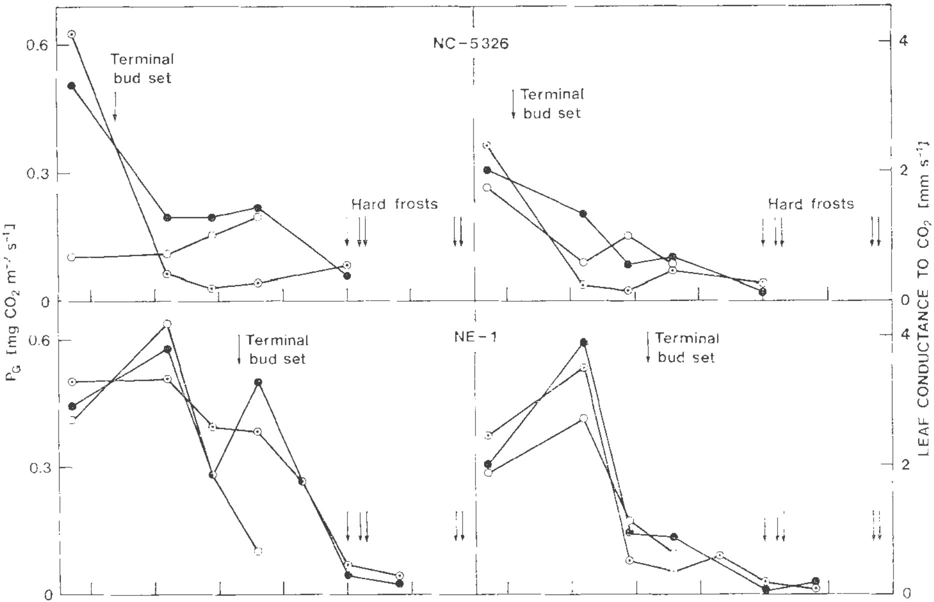

Fig. 3. Photosynthetic rate (P_G) (*left*) and abaxial conductance to CO_2 (*right*) of *Populus* leaves in the upper (⊙), middle (●), and lower (○) portions of the terminal shoot during late August-October 1979 near Rhinelander, Wisconsin, U.S.A., for clones NC-5326 and NE-1. All trees were two-year-old coppice shoots. Each data point is based on values from one or two trees; standard errors associated with each replicated data point averaged 0.04 mg CO_2 m^{-2} s^{-1} and 0.16 mm s^{-1} for NC-5326 and 0.10 mg CO_2 m^{-2} s^{-1} and 0.24 mm s^{-1} for NE-1.

Table 2

Abaxial leaf conductances to CO_2 of the green areas of frost-damaged[a] leaves in clone NE-1 on October 16, 1979, Rhinelander, Wisconsin, U.S.A.

Tree	Position on current terminal shoot	Conductance to CO_2 [mm s^{-1}][b]	
		Field[c]	Growth room[d]
1	Upper	0.11	0.11
	Middle	0.09	0.11
2	Upper	0.10	0.13
	Middle	0.17	0.21
3	Upper	0.09	0.08
	Middle	0.09	0.12

[a] Damaged from the first three hard frosts of the autumn, which occurred on October 9—10, 12—13, and 13—14.

[b] Each value based on 1—2 leaves.

[c] Measured at midday in the field on attached leaves (max. air temperature 18 °C, abaxial leaf temperature 17—20 °C, I at the adaxial leaf surface 300—500 μmol m^{-2} s^{-1}, relative humidity 45%).

[d] Same leaves as measured in field, excised, petioles inserted in distilled water, placed in growth room for 90 min (abaxial leaf temperature 26—30 °C, I at the adaxial leaf surface 150 μmol m^{-2} s^{-1}, relative humidity 65%).

improvement in conductances even through I during this extended period was similar to values during the conductance measurements in the field (325 μmol m^{-2} s^{-1}); thus, those conductances are not shown. The fact that the favorable conditions of the growth room were able to induce further opening of the stomata in the green areas of the frost-damaged leaves indicates that the abaxial stomata in the green areas were still functional. However, the conductance values were still extremely low in the growth room, indicating a severe, although not completely irreversible, impairment of stomatal function due to frost.

We were also interested in what factors control photosynthesis during the autumn. The influence of leaf conductance, PPFD in the adaxial plane of the leaf, leaf-air VPD, abaxial leaf temperature, and the number of days after terminal budset on photosynthetic rates was tested through simple and multiple regression analysis. Ranges for the environmental variables measured during ^{14}C applications were 50—2100 μmol m^{-2} s^{-1} I, 0.01—3.12 kPa VPD, and 9.9—30.0 °C abaxial leaf temperature.

The regression analyses (Tables 3 and 4) suggest that photosynthetic rates in the autumn in both Rhinelander clones are highly correlated with stomatal or leaf conductance and with time during the season (number of days after budset). P_G was not consistently related to environmental conditions during the photosynthesis measurements; *viz.*, I, VPD, and leaf temperature. The number of days after terminal budset did not occur in any of the "best" multiple regressions (Table 4), because leaf conductance and this variable were highly correlated.

Table 3

Correlation coefficients (r) for photosynthetic rate (P_G)[a] [mg CO_2 m^{-2} s^{-1}] *versus* leaf conductance and environmental variables in the autumn, Rhinelander, Wisconsin, U.S.A.

Clone	Position on current terminal shoot	P_G *versus* abaxial leaf conductance	VPD[b]	I[c]	abaxial leaf temperature	days after bud set + 100
NC-5326	Upper	0.96**[d]	−0.32	−0.30	−0.28	−0.69*
	Middle	0.77*	−0.11	−0.50	0.26	−0.82**
NE-1	Upper	0.78**	−0.06	0.03	0.34	−0.74**
	Middle	0.78**	−0.02	0.18	0.63*	−0.75**
	Lower	0.90**	−0.69*	0.21	−0.33	−0.52

[a] P_G was determined with a $^{14}CO_2$ method and may approximate gross photosynthesis in some cases.

[b] Leaf-air vapor pressure deficit.

[c] Quantum irradiance on the adaxial leaf surface.

[d] ** r significant at $p = 0.01$, * r significant at $p = 0.05$, no * r not significant at $p = 0.05$.

Table 4

Contributions of non-intercorrelated leaf and environmental variables to R^2 in "best"[a] multiple regressions describing photosynthetic rate (P_G)[b] [mg CO_2 m^{-2} s^{-1}] in the autumn, Rhinelander, Wisconsin, U.S.A.

Clone	Position on current terminal shoot	Abaxial leaf conductance	VPD[c]	I[d]	Abaxial leaf temperature	Total R^2
NC-5326	Upper	0.93	0.02	0.01		0.96
	Middle	0.59	0.28	0.01		0.88
NE-1	Upper	0.60		0.14	0.02	0.76
	Middle	0.61		0.06	0.23	0.90
	Lower	0.82		0.12		0.94

[a] The multiple regressions explaining the greatest amount of variation in P_G. See Materials and Methods for detailed discussion of methods of derivation.

[b] P_G was determined with a $^{14}CO_2$ method and may approximate gross photosynthesis in some cases.

[c] Leaf-air vapor pressure deficit.

[d] Quantum irradiance on the adaxial leaf surface.

DISCUSSION

The retention of green leaves well into the autumn is a common feature of many hybrid poplar clones grown under SRIC in the Lake States region of the U.S.A. The results indicated that clones that had prolonged green-leaf retention in this cold north-temperate climate also had appreciable photosynthesis during autumn, at least until the first hard frosts. For example, P_G averaged 0.17 and 0.39 mg CO_2 m^{-2} s^{-1} over the August 27-October 3 period for NC-5326 and NE-1, respectively, in the Rhinelander experiment. Preliminary research at our laboratories has indicated that P_G averages 8% higher than net photosynthetic rate (P_N) for poplar leaves (unpublished data of Michael *et al.* 1979). Thus, P_N for August 27-October 3 approximated 0.16 and 0.36 mg . . CO_2 m^{-2} s^{-1} for NC-5326 and NE-1, respectively. These rates reflected important carbon fixation when compared to data in the literature on P_N for *Populus* under favorable growing conditions. For example, fully expanded leaves of field-grown *Populus deltoides* had average P_N from 0.29 to 0.86 mg CO_2 m^{-2} s^{-1} when measured under laboratory conditions in mid-growing season (Regehr *et al.* 1975, Drew and Bazzaz 1979). Dickmann *et al.* (1975) and Fasehun (1978) reported a maximum P_N of approximately 0.4 mg CO_2 m^{-2} s^{-1} for individual leaves of *Populus* × *euramericana* hybrids grown in a growth chamber and greenhouse, respectively. In a study on trees grown in both a greenhouse and growth chamber, maximum P_N for individual leaves of seven poplar clones, including three interspecific hybrids, ranged from 0.17 to 0.53 mg CO_2 m^{-2} s^{-1} (Ceulemans and Impens 1980, Ceulemans *et al.* 1980). Thus, leaves of the poplar hybrids of our study were able to maintain relatively high levels of carbon assimilation for 2—6 weeks after native aspen had lost their leaves.

The use of this autumn leaf photosynthate for current stem and root growth, as well as for the formation of reserves, requires adequate translocation from the leaves during this late-season period. Dickson and Nelson (1982) have demonstrated greatly decreased translocation from the leaves of *Populus deltoides* plants during dormancy induction with short photoperiods and cool nights in a growth room. If such decreases in translocation are prevalent in the field, autumn photosynthesis may be a "wasteful" process that contributes little to the tree. We are currently studying translocation rates in SRIC NE-1 throughout the autumn. If translocation rates are maintained at adequate levels, the autumn photosynthesis in SRIC hybrid poplars may be an important factor contributing to the rapid growth of these exotic poplars in northern temperate areas.

The seasonal trends at the two locations differed in that leaf conductance and P_G declined fairly sharply in the Rhinelander leaves before the first hard frosts of the autumn, while leaf conductance and P_G in the East Lansing experiment diminished only slightly before the hard frosts (Figs. 2 and 3). The decrease in P_G over the autumn is quantitatively illustrated for the Rhinelander experiment by the large negative correlation coefficients between P_G and the number of days after budset (Table 3). Dickson and Nelson (1982) have reported decreases in photosynthetic $^{14}CO_2$ fixation in *P. deltoides* leaves during dormancy induction in a controlled environment that are similar in magnitude to the decreases in P_G in NC-5326 and NE-1 in the Rhinelander experiment before the first hard frost. The more gradual decline in P_G at the East Lansing site may be due to its lower latitude and correspondingly warmer average temperatures in comparison with the Rhinelander site, in addition to the absence of September frosts at the warmer location (Fig. 1).

The earlier drop in P_G in NC-5326 than in NE-1 corresponds with the progression of normal autumn leaf-yellowing in the two clones: *viz.*, substantial yellowing in NC-5326 by early October, but little yellowing in NE-1 before the first hard frost.

Only abaxial stomata were monitored in this study. However, most hybrid poplars have a preponderance of stomata on the abaxial surface, including NC-5326, which has 66% of its stomata on abaxial surfaces, and NE-1, which has 83% on abaxial surfaces (Pallardy and Kozlowski 1979). Furthermore, Drew and Bazzaz (1979) have shown that the conductance of the abaxial stomata of *P. deltoides* decreases more than adaxial conductance during the early stages of autumnal senescence. Therefore, it is expected that abaxial conductance will reflect the most important stomatal changes affecting photosynthesis in hybrid poplars during the autumn.

The similarity in the seasonal trends for P_G and abaxial leaf conductance is confirmed for the Rhinelander data by the high correlation between these variables (Tables 3 and 4). The increase in stomatal resistance during the period preceding hard frosts was probably a normal consequence of leaf aging and senescence. This phenomenon has been documented for the aging leaves of a *P. deltoides* × *P. nigra* hybrid clone (Unal 2) grown in a greenhouse and controlled environment by Ceulemans and Impens (1979) and for the senescing leaves of field-grown *P. deltoides* in the autumn in the north central U.S.A. (Drew and Bazzaz 1979).

Internal resistance (mesophyll + carboxylation) probably also increased during the period of normal autumn senescence (Ceulemans and Impens 1979). For example, in *Populus* the photosynthetic enzyme ribulose 1,5-bisphosphate carboxylase is only synthesized in expanding leaves (Dickmann and Gordon 1975); the higher carboxylation resistances of older leaves are associated with the gradual degeneration of this enzyme. Leaf senescence in plants in general usually entails increases in both stomatal and internal resistances (*e.g.* Constable and Rawson 1980).

The sub-experiment testing stomatal function in the green areas of leaves damaged by hard frost (Table 2) suggests that "surviving" portions of the abaxial leaf surface contain stomata that are nearly or completely closed. Stomatal resistance in such green areas could not be appreciably reduced under conditions favorable for stomatal opening. Thus, it is unlikely that more than negligible photosynthesis occurs in the damaged leaves. These frost-damage results were for clone NE-1 in Rhinelander only. The hard frosts at East Lansing did not have such a permanent and debilitating effect on the clonal mixture NE-308 + NE-353, as indicated by the still substantial though much reduced P_G and leaf conductances in that plot following the hard frosts. Thus, the frosts at East Lansing were not as severe as those at Rhinelander or genetic differences and/or genotype × environment interactions exist in the tolerance of the leaves of these hybrid poplars for autumn frosts.

This study provides evidence that the retention of green leaves in SRIC hybrid poplars in the Lake States region of the U.S.A. for several weeks after leaf fall in native aspen can result in the synthesis of substantial additional photosynthate. The importance of this phenomenon to growth in the current and subsequent growing seasons depends on how much of this assimilate is translocated from the leaves before abscission, and this is the subject of ongoing experiments at our laboratory. If ample translocation during the autumn can also be demonstrated, further research on autumnal photosynthesis in hybrid poplars may be in order, including an investigation of photosynthate partitioning and ultimate use and an investigation of the effect of the origin of parents on the duration of green leaf retention and autumnal photosynthesis of hybrid progeny.

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