Leaf area and net photosynthesis during development of *Prunus serotina* seedlings

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Summary

We used the plastochron index to study the relationship between plant age, leaf age and development, and net photosynthesis of black cherry (*Prunus serotina* Ehrh.) seedlings. Leaf area and net photosynthesis were measured on all leaves ≥ 75 mm of plants ranging in age from 7 to 20 plastochrons. Effects of plant developmental stage on leaf area and net photosynthesis were evaluated for leaves of differing age (horizontal series), leaves on plants of constant age (vertical series), and leaves of constant age (oblique series). Regression techniques were used to estimate leaf area from leaf blade dimensions. The best equations for predicting leaf area had R^2 values of 0.991–0.992 and used linear or logarithmic functions of both leaf length and width. Suitable, but less precise, equations with R^2 values of 0.946–0.962 were developed from either leaf length or leaf width. Leaf area development in black cherry seedlings was similar to that in other indeterminate species. Leaves of young plants reached full expansion at a lower leaf plastochron age than leaves of older plants. Maximum net photosynthesis per unit leaf area occurred 2–3 plastochrons before full leaf expansion. There was strong ontogenetic drift in net photosynthesis with leaf age; net photosynthesis decreased as plant age increased in leaves of the same plastochron age. Plots of the oblique series were particularly useful in providing information about interaction effects.

Keywords: developmental stage, leaf age, leaf area, plastochron index, regression models, seedling survival.

Introduction

Leaf age and developmental stage are important determinants of many morphological and physiological processes in plants. The plastochron index is a useful concept for determining the developmental age of leaves and plants non-destructively (Erickson and Michelini 1957, Larson and Isebrands 1971). When plants are grown under uniform conditions, morphological and physiological development are similar in leaves of the same plastochron age. Thus, use of the plastochron index permits adjustment of plant development and metabolism for age effects. For example, in studies of cottonwood (*Populus deltoides* Bartr.) leaves, the plastochron index was used to demonstrate that the rates of net photosynthesis, dark respiration, enzyme production and C^{14} distribution were determined by the stage of leaf development (Dickmann 1971, Dickson 1986). Recently, Hanson et al. (1986) have extended the use of morphological indices to semi-determinate species.

Black cherry (*Prunus serotina* Ehrh.) is an important commercial species in the northeastern United States and reaches its best development in the cherry–maple Allegheny hardwood forests of northwestern Pennsylvania, USA. The species is

considered shade intolerant, although young seedlings persist in the shade of uncut or partially cut stands for up to 3 or 4 years. Most height growth and leaf development of these seedlings occurs during the several weeks between the appearance of leaves on understory seedlings and those of overstory trees. There is little development in height or leaf area after overstory leaf development (Horsley unpublished observations). Because the rate of net photosynthesis is an important determinant of black cherry seedling survival in the understory of Allegheny hardwood stands (Horsley 1991) and leaf development rate and leaf area are important components of net and total photosynthesis, we studied the relationship between plant age, leaf age and development and net photosynthesis in black cherry. We also developed equations for the non-destructive estimation of leaf area.

Materials and methods

Plant growth conditions

Three groups of black cherry seedlings were used in the study. Plants in Groups 1 and 2 were used to develop equations for leaf area estimation. Plants in Group 3 were used for developmental studies of leaf area and net photosynthesis and to validate the equations developed using leaves from Groups 1 and 2 plants. All three groups of plants were grown from half-sib seed in sand culture. Environmental conditions in plant growth chambers were 25/18 °C day/night temperatures; humidity was not regulated. Plants in Group 1 were illuminated with light having 110 μmol $m^{-2} s^{-1}$ PPFD and a red/far-red ratio of 0.5 from daylight fluorescent and special far-red emitting fluorescent tubes (GTE/Sylvania F72/T12/232/VHO). Group 1 seedlings were watered with a complete mineral nutrient solution balanced for total cations and anions. Nitrogen was supplied daily at 140 ppm and an ammonium/nitrate ratio of 20/80 (Horsley unpublished data). Seedlings in Groups 2 and 3 were illuminated with light having 335 μmol $m^{-2} s^{-1}$ PPFD and a red/far-red ratio of 6.5 from cool white fluorescent and incandescent lamps. Seedlings in Groups 2 and 3 were watered daily with a complete balanced mineral nutrient solution containing 210 ppm nitrate as the sole source of nitrogen (Machlis and Torrey 1956).

Leaf area prediction

The length and maximum width of leaf blades of all plants were measured to the nearest mm with a ruler. Leaf area was measured to the nearest 0.01 cm^2 with a Li-Cor LI-3000 area meter. For Group 1 plants, a single area measurement was made on 508 leaves from 64 plants ranging in age from 4 to 12 plastochrons. For Group 2 plants, leaf areas were the mean of three measurements on each of 277 leaves from 14 plants ranging in age from 18 to 40 plastochrons. For Group 3 plants, a single measurement of area was made on 447 leaves from 33 plants ranging in age from 7 to 20 plastochrons. Preliminary analysis of linear regression data from plants in Groups 1 and 2 showed that the coefficients, residuals and R^2 values were similar, so measurements from all 785 leaves were combined for further analyses.

Prediction of leaf area from leaf length, width and their product was examined using regression techniques (Wilkinson 1990). We evaluated relationships suggested in the literature for other species and made additional transformations of the data (Table 1). Regressions were evaluated on the basis of proportion of the variation explained (R^2, the coefficient of determination) and visual inspection of residual plots. Because we were interested primarily in the use of the equations for predicting leaf area, we placed more emphasis on plots of the residuals versus

Table 1. Regression models for black cherry used to predict leaf area (y) from leaf length (LL), leaf width (LW) or leaf length times leaf width (LL × LW).

Equation no.	model	x	R^2 for black cherry	Acceptable residual
Linear[1]				
1	$y = b_0 + b_1 x$	LL	0.920	no
2		LW	0.923	no
3		LL × LW	0.992	yes
Hyperbolic[2]				
4	$1/y = b_0 + b_1\, 1/x$	LL	0.718	no
5		LW	0.740	no
6		LL × LW	0.906	yes
Quadratic[3]				
7	$y = b_0 + b_1 x + b_2 x^2$	LL	0.962	yes
8		LW	0.951	yes
9		LL × LW	Singular Matrix	
Logarithmic[2]				
10	$y = b_0 + b_1 \log x$	LL	0.710	no
11		LW	0.731	no
12		LL × LW	0.759	no
Exponential[2]				
13	$\log y = b_0 + b_1 x$	LL	0.881	no
14		LW	0.862	no
15		LL × LW	0.759	no
Power (Allometric)[4]				
16	$\log y = b_0 + b_1 \log x$	LL	0.946	yes
17		LW	0.947	yes
18		LL × LW	0.991	yes
19	$\log y = b_0 + b_1 \log x_1 + b_2 \log x_2$	LL, LW	0.991	yes
Linear plus Logarithmic[5]				
20	$\log y = b_0 + b_1 x + b_2 \log x$	LL	0.961	yes
21		LL × LW	0.992	yes

[1] Ackley et al. 1958, Freese 1967, Kubicek 1971, Isebrands et al. 1977, Wargo 1978, Hughes and Proctor 1981, Elsner and Jubb 1988.

[2] Freese 1967.

[3] Freese 1967, Wargo 1978, Elsner and Jubb 1988.

[4] Freese 1967, Fordham and Holgate 1972, Wargo 1978, Elsner and Jubb 1988.

[5] Larson and Isebrands 1972.

predicted values than on probability plots of the residuals (Draper and Smith 1966). Coefficients of determination for equations using logarithmic transformations were corrected for bias of the transformation by recalculating the R^2 value after taking the anti-logarithm of the predicted value. Thus, R^2 values for all equations presented are directly comparable.

The equations developed from leaves of plants in Groups 1 and 2 were validated by using the equations to predict areas of leaves of Group 3 plants. The predicted values of Group 3 leaves were regressed against the measured values. Values of R^2 were calculated, corrected for transformation bias where appropriate, and plots of the residuals were inspected as described above. High R^2 values indicated a correlation close to 1/1 between the predicted and measured values.

Plastochron index

The plastochron index (PI) was calculated by means of the formula of Erickson and Michelini (1957), except that the index leaf length was set at 75 mm, because juvenile leaves were not consistently unfolded before this length and smaller leaves were difficult to handle in our leaf chambers because of their short petioles:

$$PI = LSN + \frac{\log LL_i - \log 75}{\log LL_i - \log LL_{i+1}},$$

where LSN is the leaf serial number, LL_i is the leaf length in mm (75 mm) of the index leaf and LL_{i+1} is the length in mm of leaf $i + 1$ (> 75mm), the next leaf above leaf i. The value calculated in the second term of the PI equation is between 0 and 1. The PI, or age in plastochrons of a plant with n leaves, is the number of leaves on the plant 75 mm long plus the fraction of a plastochron represented by the current length of the next leaf above the index leaf.

The effects of plant developmental stage on leaf area and photosynthesis were measured in an experiment designed to evaluate true leaf age (horizontal series), constant plant age (vertical series) and constant leaf developmental age (oblique series) (Figure 1). Data were gathered by repeatedly measuring vertical profiles of leaf area and net photosynthesis on plants from Group 3 as they grew in age from 7 to 20 plastochrons. There were three to five replicate plants of each age. Because the cotyledons and the first four true leaves frequently abscised, we routinely removed them when plants reached the 8- to 10-leaf stage. The fifth true leaf produced was given leaf serial number 1 (LSN 1). Means of replicate plants were calculated for the three series and curves were fitted by means of a distance-weighted least squares technique (Wilkinson 1990). This method produces a true, locally weighted curve running through the mean points (McLain 1974). As a result, the curves flex locally to fit the data better and thereby smooth variability among means.

Measurement of net photosynthesis

Net photosynthesis (μmol CO_2 m^{-2} s^{-1}) was measured on individual leaves of
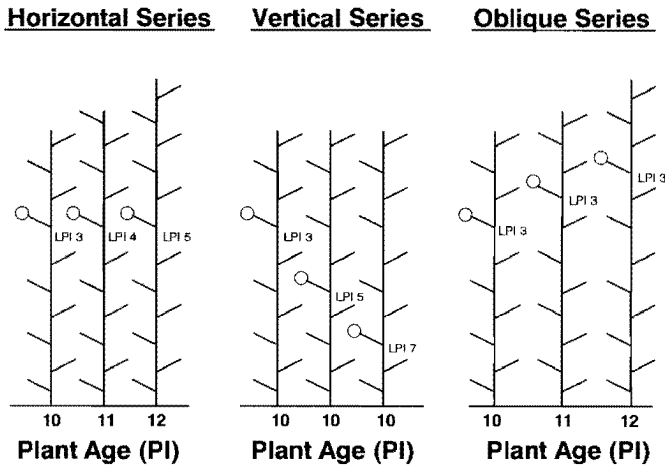
Figure 1. Horizontal (true leaf age), vertical (constant plant age) and oblique (constant leaf developmental age) series for black cherry plants. Leaf age or leaf plastochron index (LPI) is the leaf number up or down from the index leaf (LPI 0). Plant age or plastochron index (PI) is based on the number of leaves from the base of the plant up to and including the index leaf.

Group 3 plants in a 20-cm diameter, water-cooled, Plexiglas leaf chamber with a MSA model 202 infrared gas analyzer operated in an open system similar to that described by Brun and Cooper (1967). On each plant, net photosynthesis was measured on all leaves ≥ 75 mm, beginning with LSN 7 (bottom). For example, only LSN 7 was measured on a plant with a plastochron age of 7, whereas LSN 7 (bottom) through LSN 20 (top) were measured on a plant with a plastochron age of 20. A preliminary experiment showed that light saturation occurred at about 600 μmol m^{-2} s^{-1} for plants grown at 335 μmol m^{-2} s^{-1} PPFD. We used an irradiance of 600 μmol m^{-2} s^{-1} PPFD from a single 400 watt sodium iodide metal arc lamp. Carbon dioxide was provided at 330 ppm, 50% relative humidity and 25 $\pm$ 0.5 °C. Leaf temperature was continuously monitored with a thermocouple taped to the underside of the leaf. Gas flow rate was maintained at 0.015 l s^{-1}. Before insertion into the leaf chamber, leaf area was measured with a Li-Cor area meter. All calculations of net photosynthetic rates were based on actual measurements of leaf area.

Results and discussion

Leaf area prediction

All of the models evaluated gave statistically significant regressions ($P < 0.05$). However, examination of the R^2 values and the residuals suggested that some of the equations were better predictors of leaf area than others. Equations 1, 2, 4–6 and 10–15 had lower R^2 values or plots of residuals having unacceptable patterns, or both, than the other equations (Table 1). Typically, equations with unacceptable plots of residuals versus estimated y values displayed U-shaped or funnel-shaped

patterns, instead of the horizontal band of points expected in acceptable plots. These included models using linear, hyperbolic, logarithmic and exponential forms.

The best predictive equations (Equations 3, 18, 19 and 21) had high R^2 values (0.991–0.992), good residual plots and used combinations of leaf length and width to predict leaf area (Table 2). In Equation 21, the leaf length × width variable was nonsignificant ($P = 0.403$). Therefore, this equation has no advantage over Equation 18. The remaining five equations (Equations 7, 8, 16, 17 and 20), which used only one leaf dimension to predict leaf area, had lower R^2 values (0.946–0.962) and residual patterns were not as good as the best predictive equations, but were still acceptable.

The validations confirmed that Equations 3, 18, 19 and 21 (Table 2) were the best for predicting black cherry leaf area. All had R^2 values of 0.991 and tight horizontal bands of points in residual plots. The remaining five equations (Equations 7, 8, 16, 17 and 20) had R^2 values ranging from 0.893 to 0.930. All had acceptable residual plots, although the points were not as tightly banded as with equations that used two leaf dimensions to predict leaf area. Because Equations 7, 8, 16, 17 and 20 included only one leaf dimension, they may be useful where precision of the estimate has to

Table 2. Prediction equation parameters for leaf area (y) from leaf length (LL), leaf width (LW) or leaf length times leaf width (LL × LW).

Equation no.	Coefficient	Value	P
Best Prediction Equations			
3	b_0	0.3869	0.000
	b_1	0.00593	0.000
18	b_0	−4.837	0.000
	b_1	0.9679	0.000
19	b_0	−4.833	0.000
	b_1	0.9518	0.000
	b_2	0.9877	0.000
21	b_0	−4.807	0.000
	b_1	0.00000211	0.403
	b_2	0.9628	0.000
Good Prediction Equations			
7	b_0	0.823	0.111
	b_1	0.0125	0.329
	b_2	0.00184	0.000
8	b_0	−3.113	0.000
	b_1	0.2458	0.000
	b_2	0.0138	0.000
16	b_0	−4.703	0.000
	b_1	1.682	0.000
17	b_0	−4.161	0.000
	b_1	2.018	0.000
20	b_0	−3.781	0.000
	b_1	0.00457	0.000
	b_2	1.368	0.000

be balanced against measurement time. We saw no reason to favor one of the five equations over another.

The high degree of accuracy of the prediction equations is noteworthy because the data set included a wide range of leaf sizes from small to relatively large seedlings, grown under different lighting and nutritional conditions. This result suggested a strong genetic control of leaf shape as do studies of hybrid poplar (*Populus* spp.) where different equations were used to predict leaf area in different clones (Larson and Isebrands 1972, Isebrands et al. 1977, Ceulemans et al. 1988). Lack of environmental influence on leaf shape and therefore on prediction of leaf area has also been found by others (Boynton and Harris 1950, McKee 1964, Larson and Isebrands 1972, Lim and Narayanan 1972, Isebrands et al. 1977, Pieters and van den Noort 1985). Our prediction equations may, therefore, be useful for leaf area estimation under a range of environmental conditions in the field or in controlled environments.

Leaf development

Plastochron interval, the rate at which new primordia are initiated at the apex or the rate of new leaf emergence from the bud, was estimated from the time a leaf reached the index leaf length of 75 mm until the time the next serial numbered leaf above it reached 75 mm. The plastochron interval varied from 2 to 3 days on different plants in Group 3 (Figure 2). Calculation of the plastochron index assumes a uniform rate and duration of development for each leaf. Under our growing conditions, this prerequisite was met beginning with the appearance of LSN 9. Leaves with leaf serial numbers less than about 9 were shorter, had less leaf area, and often had a longer plastochron interval than later emerging leaves.

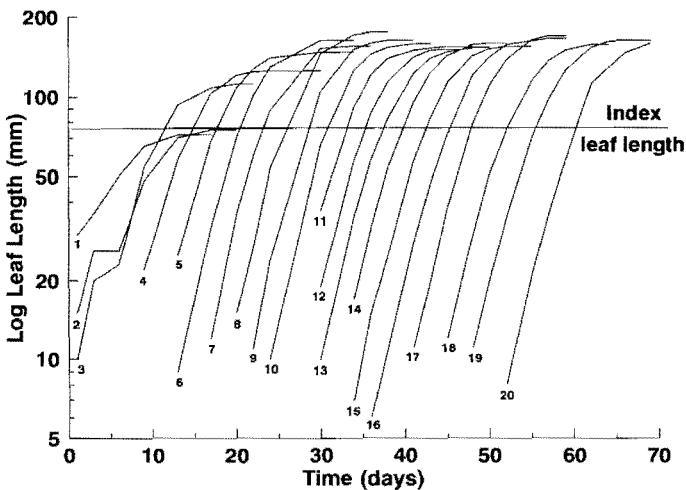Leaf area development varied with leaf plastochron index (LPI) and plant plas-

Figure 2. Leaf development over time for a 24-leaf seedling. Index leaf length line shows a plastochron interval of 2 to 3 days.

Figure 3 — Average leaf area (cm²) by plant plastochron index (PI, vertical series), leaf plastochron index (LPI, oblique series) and leaf serial number (horizontal series). Each cell gives mean ± one standard deviation.

Leaf serial no. (LPI)	PI 7	PI 8	PI 9	PI 10	PI 11	PI 12	PI 13	PI 14	PI 15	PI 16	PI 17	PI 18	PI 19	PI 20
20 (LPI 0)														7.48 ± 1.5
19 (LPI 1)													8.5 ± 1.0	13.9 ± 2.1
18 (LPI 2)												7.6 ± 0.7	17.9 ± 2.2	25.7 ± 1.6
17 (LPI 3)											6.9 ± 1.2	14.4 ± 0.4	26.9 ± 3.0	36.2 ± 3.7
16 (LPI 4)										7.7 ± 1.6	14.6 ± 0.7	24.5 ± 1.8	39.6 ± 5.3	45.9 ± 7.0
15 (LPI 5)									10.1 ± 1.0	18.3 ± 3.2	27.2 ± 2.9	36.1 ± 3.1	48.4 ± 8.1	54.1 ± 8.7
14 (LPI 6)								9.0 ± 1.0	21.0 ± 4.4	28.1 ± 3.3	41.0 ± 5.0	45.3 ± 1.4	55.3 ± 8.3	56.9 ± 4.8
13 (LPI 7)							7.7 ± 1.7	18.5 ± 1.1	35.8 ± 7.9	42.3 ± 7.4	44.6 ± 5.4	57.0 ± 5.4	54.9 ± 7.6	62.1 ± 5.1
12 (LPI 8)						10.0 ± 3.6	16.4 ± 2.4	28.0 ± 4.0	49.6 ± 11.4	49.0 ± 6.9	51.4 ± 4.3	55.9 ± 7.4	54.0 ± 5.0	59.0 ± 6.1
11 (LPI 9)					7.7 ± 1.2	21.4 ± 3.3	33.0 ± 3.1	42.4 ± 9.1	55.0 ± 10.7	50.4 ± 12.1	51.9 ± 7.9	54.0 ± 1.3	57.5 ± 9.6	60.0 ± 6.2
10 (LPI 10)				8.6 ± 0.98	18.7 ± 2.2	40.0 ± 8.8	50.5 ± 6.4	50.1 ± 7.8	56.2 ± 11.8	54.2 ± 13.7	51.1 ± 7.4	60.1 ± 14.0	59.3 ± 8.2	59.5 ± 6.4
9 (LPI 11)			8.5 ± 1.2	20.5 ± 4.0	32.2 ± 9.5	45.7 ± 7.8	56.0 ± 7.9	50.8 ± 6.5	55.9 ± 10.9	54.0 ± 14.6	50.1 ± 7.9	52.1 ± 7.4	54.5 ± 8.8	55.5 ± 6.4
8 (LPI 12)		8.3 ± 1.4	23.6 ± 3.8	37.6 ± 4.8	45.3 ± 8.4	49.5 ± 8.9	54.1 ± 9.5	50.8 ± 9.9	52.9 ± 14.9	52.2 ± 13.5	46.6 ± 12.6	54.1 ± 12.4	54.2 ± 9.1	54.6 ± 8.5
7 (LPI 13)	10.3 ± 2.7	20.8 ± 5.9	32.3 ± 3.7	41.0 ± 7.8	43.4 ± 9.0	45.2 ± 7.5	53.8 ± 11.1	46.9 ± 6.0	51.4 ± 16.0	48.3 ± 16.2	43.7 ± 10.0	47.1 ± 10.0	47.8 ± 5.6	53.0 ± 10.7

LEAF SERIAL NUMBER (HORIZONTAL SERIES)

LEAF PLASTOCHRON INDEX (LPI) (OBLIQUE SERIES)

PLANT PLASTOCHRON INDEX (PI) (VERTICAL SERIES)

Figure 3. Average leaf area (cm²) of black cherry leaves by plant plastochron index (PI), leaf plastochron index (LPI) and leaf serial number. The first value to the right of each leaf serial number (diagonal of bold numbers) is LPI 0. LPI or leaf developmental stage increases to the right in the horizontal series or down in the vertical series. Leaf area for the horizontal series in leaf serial number 10 and the vertical series for leaf serial number 18 are enclosed with lines. Leaves of constant leaf plastochron index (oblique series) are found along the diagonal, for example leaf areas for LPI 4 leaves on plants of PI 11 to 20 are enclosed within a diagonal set of lines. Each value is the mean of 3–5 leaves ± one standard deviation.

tochron index (PI) (Figure 3). The index leaf (LPI 0) had an area of about 10 cm². As the age of a serial numbered leaf increased, leaf area increased to a maximum and remained constant (Figure 4A, horizontal series). Vertical profiles at a particular plant age showed that leaf area increased to a maximum as leaf plastochron index increased, then decreased with further increase in leaf plastochron index (Figure 4B). The initial increase in leaf area corresponded to the expanding leaf zone at the top of the plant. The subsequent decline in leaf area with older leaves was related to the age and size of the plant at the time the leaves were formed. With constant leaf plastochron index, leaf area changed little with increasing plant age (Figure 3 and Figure 4C, oblique series). As plant age increased, the number of plastochrons to reach full leaf expansion and the maximum leaf area increased (Figures 4A and B). Thus, on older plants there were more leaves in the expanding leaf zone. For example, on plants with 12 leaves, there were three leaves in the expanding leaf zone, whereas on plants with 20 leaves there were five leaves in the expanding leaf zone. Black cherry leaf development was similar to that observed in cottonwood (*Populus deltoides* Bartr.) (Larson and Isebrands 1971, Larson 1980) and in the long
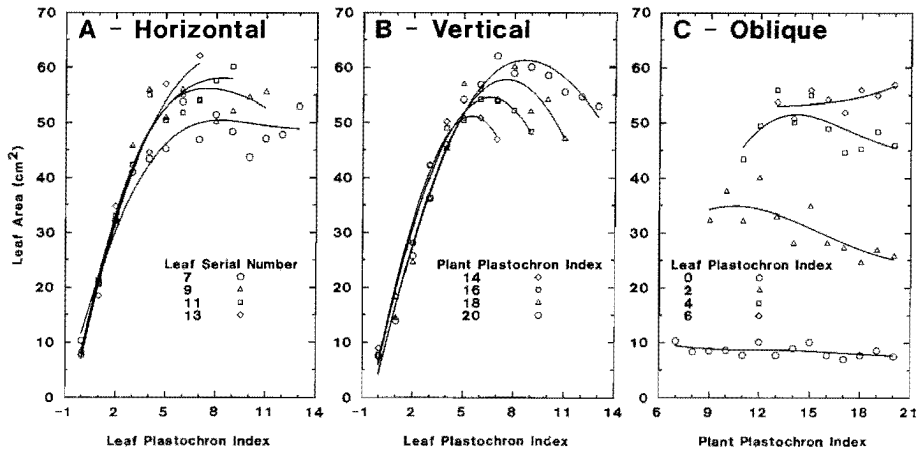
Figure 4. Leaf area development in black cherry seedlings. (A) Horizontal series for leaves at leaf serial numbers 7, 9, 11, and 13. (B) Vertical series for plant plastochron index 14, 16, 18, and 20. (C) Oblique series for leaves at leaf plastochron index 0, 2, 4, and 6. Each value is the mean of 3–5 replicate leaves.

shoots of other indeterminate species (Pollard 1970). Within the expanding leaf zone of black cherry seedlings, the leaf plastochron index was a consistent predictor of leaf area.

Net photosynthesis

Because our index leaf length was relatively long, most of the leaves measured were net fixers of CO_2. Light-saturated rates of net photosynthesis in individual leaves varied from -0.80 to 7.28 μmol CO_2 m^{-2} s^{-1} depending on leaf age and plant age (data not shown). The lowest net photosynthetic rates were found in leaves at LPI 0. Photosynthesis increased with leaf plastochron index to a maximum, then decreased (Figures 5A and B). The horizontal series in Figure 5A shows the effect of age on net photosynthesis in the same leaf over time. For example, in LSN 7 the maximum net photosynthetic rate was reached at LPI 2–3 and then decreased gradually, whereas in LSN 13 the maximum was reached at LPI 3–4 and then decreased. The vertical series in Figure 5B shows the effect of age on different leaves on the same plant over time. When plants with different ages were compared, younger plants had higher net photosynthetic values at lower leaf plastochron ages than older plants. However, older plants maintained maximum net photosynthetic rates for a longer time. With constant leaf plastochron index, net photosynthesis decreased with increasing plant age (Figure 5C). This was particularly true in the expanding leaf zone.

At light saturation, rates of net photosynthesis in black cherry seedlings were similar to those of other broad-leaved deciduous trees (Jarvis and Jarvis 1964, Loach 1967, Nelson 1984) and to other species of *Prunus* (6–12 μmol m^{-2} s^{-1}) (Crews et al. 1975, Even-Chen et al. 1981, Sams and Flore 1982, 1983). Most studies have considered only the horizontal series (true age effects) when examining the effect of leaf age on net photosynthetic rate (Yamaguchi and Friend 1979, Andersen and
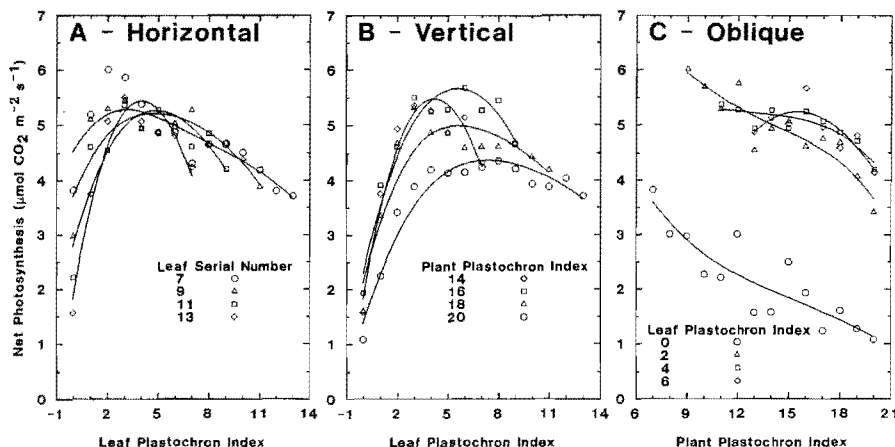
Figure 5. Development of net photosynthesis in black cherry seedlings. (A) Horizontal series for leaves at leaf serial numbers 7, 9, 11, and 13. (B) Vertical series for plant plastochron index 14, 16, 18, and 20. (C) Oblique series for leaves at leaf plastochron index 0, 2, 4, and 6. Each value is the mean of 3–5 replicate leaves.

Brodbeck 1988, Marini and Sowers 1990). We provide evidence that the vertical and oblique series are also useful in visualizing trends. For example, with increasing plant age one would expect plots of net photosynthesis versus plant plastochron index at the same LPI to be horizontal (slope = 0) (Figure 5C). However, plots of the oblique series showed that, in leaves of the same leaf plastochron index, net photosynthesis decreased as plant age increased (Figure 5C). This means that leaves at the same leaf plastochron index were less mature in older plants than in younger plants and corresponds to the observation that the expanding leaf zone increases as plants become older. Past work has stressed the importance of standardizing the leaf plastochron index to remove aging effects from physiological measurements (Lamoreaux et al. 1978). Our work has shown that to make valid comparisons of treatment effects on net photosynthesis in black cherry seedlings, both leaf plastochron index and plant plastochron index must be standardized so that leaves of the same ontogenetic or physiological stage of development are compared.

Interaction of leaf area and net photosynthesis

The maximum rate of net photosynthesis was reached 3–4 plastochrons before full leaf expansion over a range of leaf ages (Figure 6). Most investigations of indeterminate woody plants have found that maximum net photosynthesis is coincidental with or just before full leaf expansion (Dickmann 1971, Furukawa 1973, Dickmann et al. 1975, Sams and Flore 1982). We observed a similar trend over a range of plant ages, but as plant age increased, the interval between maximum net photosynthetic rate and full leaf expansion increased (Figure 7). At a constant leaf developmental stage, leaf area and net photosynthesis showed a strong interaction (Figure 8). Leaf

Figure 6. Comparison of leaf area and net photosynthesis developmental patterns for leaves at leaf serial numbers 7 (A), 10 (B), and 13 (C) in black cherry seedlings (horizontal series). Each value is the mean of 3–5 replicate leaves.

Figure 7. Comparison of leaf area and net photosynthesis developmental patterns for plant plastochron index 20 (A), 17 (B), and 14 (C) in black cherry seedlings (vertical series). Each value is the mean of 3–5 replicate leaves.

area changed little, whereas net photosynthesis decreased. This contrasting pattern represents an ontogenetic drift in net photosynthesis.

Use of the plastochron index

Duff and Nolan (1953, 1957) in their classical work on xylem production patterns, showed that the effects of tree age, size and environment could be explained by looking at horizontal, vertical and oblique plots of ring width. This provided new insights into wood production that were not evident from the use of traditional
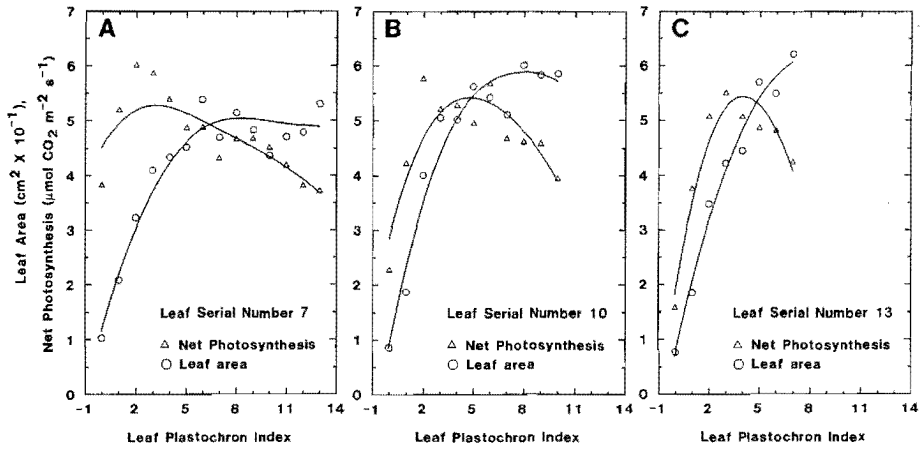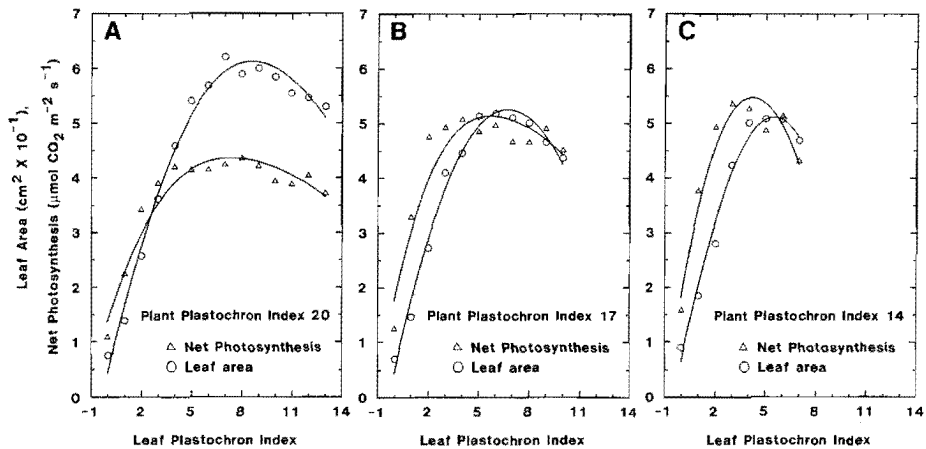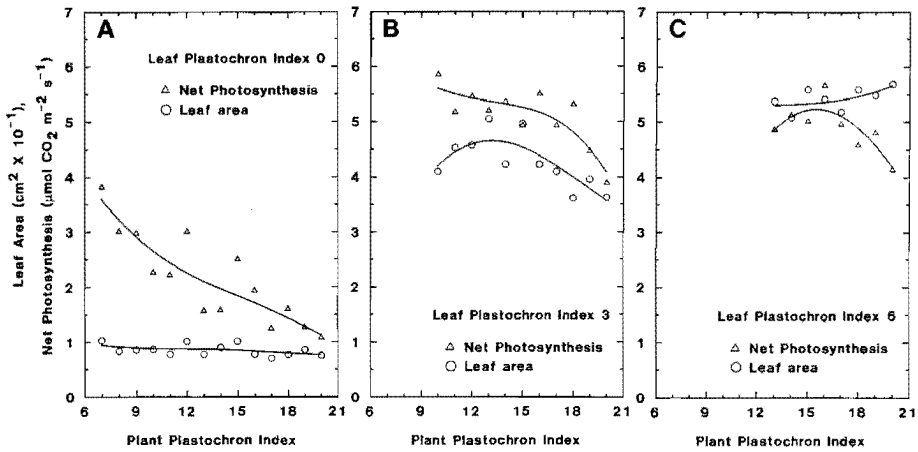
Figure 8. Comparison of leaf area and net photosynthesis developmental patterns for leaves at leaf plastochron index 0 (A), 3 (B), and 6 (C) in black cherry seedlings (oblique series). Each value is the mean of 3–5 replicate leaves.

ring-width analysis. In the same way, the plastochron index provides a tool to standardize measurements of morphological and physiological development in indeterminate plants, greatly reducing variability and permitting insights not obtainable from plots against chronological time (Lamoreaux et al. 1978).

Significance for regeneration

Leaf area development and photosynthetic characteristics may have adaptive significance for black cherry during stand regeneration. Black cherry is one of the fastest growing species in the Allegheny hardwood forest, it is surpassed only by pin cherry (*Prunus pensylvanica* L.). Rapid initial height growth is a species trait that is often associated with dominance over competitors in regenerating stands (Gottschalk and Dickmann 1978). Young black cherry seedlings initially allocate a large proportion of carbon to leaves. Analysis of carbon allocation patterns in Group 3 seedlings revealed a mean leaf dry weight to total dry weight ratio of 0.67 compared with 0.19 and 0.14 for stem dry weight/total dry weight and root dry weight/total dry weight ratios, respectively (Horsley 1991). Carbon allocation to leaves decreases during the first two growing seasons. Gottschalk (1987) found a leaf dry weight/total dry weight ratio of 0.31 after one growing season and 0.21 after two growing seasons. During the short early growth period between the time seedling leaves appear and the time overstory leaves are fully expanded, the seedlings must achieve maximum net photosynthesis quickly and maintain it for a long time. We observed that black cherry seedlings developed maximum net photosynthesis before leaves were fully expanded and maintained rates close to maximum for a long time (Figure 9). We did not measure the rate of respiration in this study; however, other work using Group 3 plants has demonstrated that black cherry exercises considerable control over the rate of respiration. In low light, respiration was much lower than might be expected

LEAF SERIAL NUMBER (HORIZONTAL SERIES)

LEAF PLASTOCHRON INDEX (LPI) (OBLIQUE SERIES)

PLANT PLASTOCHRON INDEX (PI) (VERTICAL SERIES)

Leaf serial no. (LPI)	PI 7	PI 8	PI 9	PI 10	PI 11	PI 12	PI 13	PI 14	PI 15	PI 16	PI 17	PI 18	PI 19	PI 20	LPI
20														1.08 ±1.29	0
19													1.27 ±0.51	2.24 ±1.12	1
18												1.60 ±0.25	3.11 ±0.53	3.42 ±1.00	2
17											1.24 ±0.59	3.35 ±0.79	4.07 ±0.63	3.89 ±1.18	3
16										1.93 ±0.49	3.29 ±0.73	4.67 ±0.80	4.46 ±0.80	4.19 ±1.20	4
15									2.50 ±0.70	3.91 ±1.50	4.75 ±1.65	5.32 ±0.61	4.70 ±0.82	4.14 ±1.12	5
14								1.58 ±1.34	4.18 ±1.34	4.62 ±1.89	4.93 ±1.28	4.86 ±0.15	4.61 ±0.87	4.14 ±0.93	6
13							1.56 ±1.51	3.76 ±1.48	5.06 ±0.76	5.50 ±0.88	5.07 ±1.56	4.86 ±0.33	4.80 ±0.79	4.24 ±1.04	7
12						3.00 ±0.78	3.98 ±1.71	4.93 ±1.21	4.93 ±0.84	5.25 ±1.03	4.85 ±1.03	4.58 ±0.36	4.57 ±0.77	4.35 ±0.58	8
11					2.22 ±0.81	4.61 ±0.74	4.55 ±1.65	5.35 ±0.93	4.94 ±0.88	5.28 ±1.53	4.96 ±0.80	4.61 ±0.22	4.85 ±0.65	4.21 ±0.52	9
10				2.27 ±0.58	4.23 ±0.91	5.75 ±1.58	5.20 ±1.58	5.27 ±0.82	4.95 ±0.56	5.67 ±0.45	4.67 ±0.80	4.61 ±0.08	4.58 ±0.08	3.93 ±0.53	10
9			2.97 ±0.54	5.10 ±0.70	5.30 ±0.77	5.45 ±0.94	4.93 ±1.42	4.86 ±0.92	5.02 ±0.65	5.26 ±0.82	4.65 ±0.32	4.67 ±0.26	4.40 ±0.86	3.88 ±0.54	11
8		3.01 ±1.32	5.43 ±0.54	5.70 ±0.64	5.17 ±0.57	5.27 ±0.77	5.30 ±1.30	5.13 ±0.74	4.71 ±0.41	5.44 ±0.73	4.90 ±0.22	4.43 ±0.32	4.63 ±0.92	4.03 ±0.40	12
7	3.82 ±1.04	5.19 ±0.38	6.01 ±0.38	5.86 ±0.47	5.39 ±0.60	4.87 ±0.97	4.87 ±1.36	4.31 ±1.54	4.66 ±1.06	4.66 ±1.01	4.51 ±0.28	4.19 ±0.06	3.81 ±0.23	3.71 ±0.17	13

Figure 9. Average net photosynthesis (μmol CO_2 m^{-2} s^{-1}) of black cherry leaves by plant plastochron index (PI), leaf plastochron index (LPI) and leaf serial number. The first value to the right of each leaf serial number (diagonal of bold numbers) is LPI 0. LPI or leaf developmental stage increases to the right in the horizontal series or down in the vertical series. Net photosynthesis for the horizontal series in leaf serial number 10 and the vertical series for leaf serial number 18 are enclosed with lines. Leaves of constant leaf plastochron index (oblique series) are found along the diagonal, for example net photosynthesis for LPI 4 leaves on plants of PI 11 to 20 are enclosed within a diagonal set of lines. Each value is the mean of 3–5 leaves ± one standard deviation.

for an intolerant woody plant (Horsley 1991). Proportionally large carbon allocations to leaf development, early maturation of photosynthesis, and low respiration rates all contribute to black cherry's ability to survive during stand regeneration.

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