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FACTORS AFFECTING THE LEAF AND SHOOT MORPHOLOGY AND PHOTOSYNTHETIC RATE OF SOUR CHERRY (PRUNUS CERASUS L. 'MONTMORENCY')

presented by

Carl E. Sams

has been accepted towards fulfillment of the requirements for

Ph.D. degree in Horticulture

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Major professor

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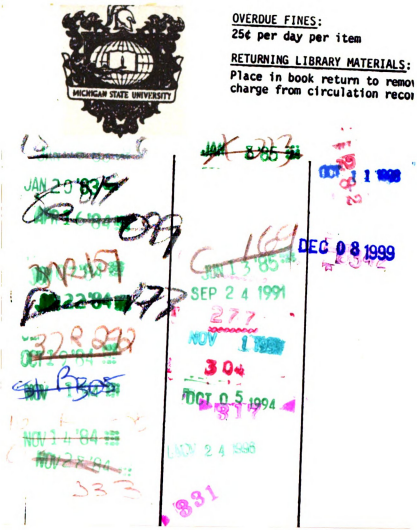
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FACTORS AFFECTING THE LEAF AND SHOOT MORPHOLOGY AND PHOTOSYNTHETIC RATE OF SOUR CHERRY (*PRUNUS CERASUS* L. 'MONTMORENCY')

By

Carl E. Sams

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ABSTRACT

FACTORS AFFECTING THE LEAF AND SHOOT MORPHOLOGY AND PHOTOSYNTHETIC RATE OF SOUR CHERRY (*PRUNUS CERASUS* L. 'MONTMORENCY')

By

Carl E. Sams

The effects of leaf age, leaf position on the shoot, and environmental factors on net photosynthetic rate (Pn) of sour cherry were determined using an infrared, differential open gas analysis system. Diurnal and seasonal patterns of Pn and the effect of fruit on Pn were evaluated. The effects of shading on leaf and shoot morphology and leaf Pn of sour cherry were also determined. Pn was greater for leaves which had recently completed expansion or were at least 50% expanded than for either older, mature leaves or newly expanding leaves on the same shoot. Pn of individual leaves reached a maximum when the leaf was greater than 80% expanded, remained constant for 2 to 4 weeks, then gradually declined.

Maximum Pn occurred at light intensities between 800-1400 $\mu E\ m^{-2}\ s^{-1}$. As temperature decreased from 35 to 10 C higher light intensities were required for maximum Pn. Optimum temperature range for Pn was 15-30 C, and Pn at

optimum temperature was greater at light intensities of 1200 and 2000 $\mu E\ m^{-2}\ s^{-1}$ than at 300 $\mu E\ m^{-2}\ s^{-1}$. In general, Pn was greater at high (85-95%) than at low (30-40%) humidity. Pn increased with increased ambient CO_2 concentration between 0 and 600 ppm, the compensation point being 82 ppm.

There was no significant diurnal change in Pn for individual leaves kept under optimum conditions. However, there was a pronounced diurnal pattern in Pn of whole trees measured under natural sunlight conditions from sunrise to sunset. Maximum Pn was reached before solar noon, remained constant for a short time, then declined.

Seasonal patterns in Pn varied, but, in general, Pn reached a peak early in the season as leaves expanded, remained stable for several weeks, then gradually declined. During the 1978 season leaves on shoots with fruit had a higher average seasonal Pn than leaves on shoots without fruit. However, in the 1979 season there was no significant effect of fruit on average seasonal Pn.

The effect of shading on leaf and shoot morphology and Pn of sour cherry was evaluated by growing one year old potted trees to the 11-15 leaf stage in full sunlight then transferring them to 100, 36, 21, and 9% of full sunlight. Trees grown in full sunlight produced leaves with greater specific leaf weights, less chlorophyll, greater palisade, spongy mesophyll, and total leaf thickness, and smaller average terminal leaf areas than those grown in

shade. Trees grown in full sunlight also produced thicker shoots and a larger number of flowers and flower buds per tree than shade grown trees. Trees grown in less than 36% of full sunlight produced no flowers.

At light intensities of 1200 and 2000 $\mu E\ m^{-2}\ s^{-1}$, the Pn of leaves grown in full sunlight was greater than the Pn of leaves grown in shade. Also, the Pn of leaves which expanded and were then shaded to 9% of full sunlight was greater than that of leaves which completed expansion under 9% of full sunlight. However, at low light intensity (320 $\mu E\ m^{-2}\ s^{-1}$) the Pn was not significantly different among leaves from all shade treatments. Maximum Pn was greater for leaves grown in full sunlight than for leaves grown in shade, and maximum Pn of leaves grown in shade occurred at lower light intensities than that of leaves grown in full sunlight. Pn was greater at 25 C than at 10 or 40 C for leaves grown in both full sunlight and 9% of full sunlight. Pn at 25 C was greater for leaves grown in full sunlight than for leaves grown in 9% of full sunlight.

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Guidance Committee:

The Paper-Format was adopted for this thesis in accordance with departmental and university regulations. The thesis body was separated into four sections. Each section is intended for publication in The Journal of the American Society for Horticultural Science.

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INTRODUCTION

Approximately 60-70% of the national sour cherry crop is produced in Michigan. Almost all of the crop is of one cultivar, 'Montmorency'. There has been a trend toward higher density cropping systems for sour cherry in Michigan which may require more intensive cultural practices due to increased competition for natural resources. An accurate assessment of the effects of environmental factors and current cultural practices on the physiological processes which determine plant productivity is essential for the development of improved cultural practices and for more efficient use of natural resources (energy, water, land).

Photosynthetic efficiency may or may not be the main factor limiting yield, but it certainly has a direct effect on yield. Photosynthetic rate might be influenced by the environment in which photosynthesis measurements are made and by the environment in which a plant develops. The effects of environmental variables on the photosynthetic rate of sour cherry have not been evaluated.

Sour cherry fruit mature approximately 60 days after full bloom, and canopy development is generally completed by fruit harvest. Flower initiation for next year's crop

occurs during this same time period (5-6 weeks after full bloom). Thus, vegetative and reproductive growth are competitive sinks for photosynthate, with both having rapid but short term annual growth. Summer hedging (removing part of the foliage during the growing season) is practiced commercially, yet the effect of this and other cultural practices on photosynthetic potential, flowering, vegetative growth, and translocation pattern (photosynthate, water, nutrients) of sour cherry have not been well documented.

Diurnal and seasonal changes in photosynthetic rate and other physiological processes should be considered when making decisions regarding summer hedging and other cultural practices. Knowledge of how environmental factors and cultural practices affect the growth and development patterns of sour cherry would provide a scientific basis for making decisions concerning orchard management. Therefore, experiments were designed to study the factors affecting the morphology and photosynthetic rate of sour cherry.

The objectives of this research were (a) to characterize the effects of environmental factors on the photosynthetic rate of sour cherry and determine the optimum environmental conditions for photosynthesis, (b) to determine the diurnal and seasonal patterns of photosynthetic rate and to evaluate the effect of fruit on the photosynthetic rate of sour cherry, and (c) to determine the effect

of various levels of shade on leaf and shoot morphology and leaf photosynthetic rate of sour cherry.

SECTION I

THE INFLUENCE OF LEAF AGE, LEAF POSITION ON THE SHOOT, AND ENVIRONMENTAL VARIABLES ON NET PHOTOSYNTHETIC RATE OF SOUR CHERRY (*PRUNUS CERASUS* L. 'MONTMORENCY')

Abstract. An infrared, differential open gas analysis system was utilized in experiments to determine the effects of leaf age, leaf position on the shoot, light intensity, temperature, humidity, and ambient CO_2 concentration on leaf net photosynthetic rate (Pn) of sour cherry. Pn was greater for leaves which had recently completed expansion or were at least 50% expanded than for either older, mature leaves or newly expanding leaves on the same shoot. For individual leaves, Pn reached its maximum when the leaf was greater than 80% expanded, remained constant for 2 to 4 weeks, then gradually declined. Maximum Pn occurred at light intensities between 800-1400 $\mu E\ m^{-2}\ s^{-1}$. As temperature decreased from 35 to 25 to 10 C maximum Pn occurred at higher light intensities. At all light intensities Pn was greater (10-40%) between 15-30 C than at lower or higher temperatures. Pn at optimum temperature was greater (15-60%) at intermediate and high (1200 and 2000 $\mu E\ m^{-2}\ s^{-1}$) than at low (300 $\mu E\ m^{-2}\ s^{-1}$) light intensity. In general, Pn was greater at high (85-95%) than at low (30-40%) humidity, the effect being most pronounced at

high temperature (35 C) and high light intensity (2000 μE m^{-2} s^{-1}). Pn increased with increased ambient CO_2 concentration between 0 and 600 ppm, the CO_2 compensation point being approximately 82 ppm. Optimum conditions for maximum Pn of sour cherry occur when recently expanded leaves are exposed to light intensities between 1000-1200 μE m^{-2} s^{-1}, temperatures of 20-30 C, high (85-95%) humidity, and CO_2 concentrations greater than 300 ppm (normal ambient).

There is a trend toward higher density cropping systems for sour cherry which may require more intensive cultural practices due to increased competition for natural resources (9). Accurate assessment of the effect of environmental factors on the physiological processes that determine plant productivity is essential for the development of improved cultural practices and more efficient use of natural resources (energy, water, land).

The possibility of improving yield by increasing photosynthetic efficiency has often been suggested (15, 19, 29). Though photosynthetic efficiency may or may not be the main factor limiting yield, it certainly has a direct effect on yield. Photosynthetic rate is influenced by the environment in which a plant develops and by the environment in which photosynthetic measurements are made. The influence of environmental variables on the leaf

photosynthetic rate of apple (3, 5, 8, 13, 17, 18), pear (12), citrus (10, 11), and peach (7) has been investigated. Apple trees grown under shade have lower leaf photosynthetic rates at light saturation than trees grown in full sunlight (4, 13). Photosynthetic rates of apple, peach, and citrus increase with increasing light intensity in a hyperbolic pattern typical of most C_3 plants (7, 11, 13). The photosynthetic rate of apple, in general, reaches a maximum between 20 and 30 C then declines at higher temperatures, and the temperature response curve is of a parabolic shape (13). The effects of environmental variables on the photosynthetic rate of sour cherry have not been evaluated.

Therefore, this study was designed to characterize the effects of temperature, light intensity, humidity, and ambient CO_2 concentration on the net photosynthetic rate of sour cherry. Effects of leaf position on the shoot and leaf age were also examined. Information obtained from these experiments will be used to study the influence of cropping systems, nutrition, growth regulators, fruit load, and other factors on the photosynthetic efficiency and carbon utilization of sour cherry.

Materials and Methods

Tree culture. One year old sour cherry trees (Prunus cerasus L. 'Montmorency') on 'Mahaleb' rootstock were

grown in 20 l plastic pots in a mixture of peat, loam, and sand (1:2:1). Fertilizer, pesticides (Cyprex, Guthion, Captan, and Plictran), and water were added as needed. The trees were grown outside under natural conditions and were moved into the laboratory for CO_2 exchange measurements. Unless otherwise indicated, photosynthetic measurements were made using attached leaves on 6-8 week old shoots.

Photosynthetic measurements. A Beckman 865 Infrared Gas Analyzer (Beckman Instruments Inc., Fullerton, CA) was used to measure differential CO_2 concentrations in an open gas analysis system similar to that described by Augustine et al. (1) as modified by Sams and Flore (21). A flow diagram of the system used is shown in Figure 1, and a list of the system components is presented in Table 1.

Individual leaves were placed in controlled environment chambers to measure the steady state exchange of carbon dioxide. Gaseous fluxes were calculated per unit leaf area. Leaf area was measured with a LI-COR Model LI 300 leaf area meter (LI-COR Inc., Lincoln, NB), and photosynthetic rate was expressed as mg CO_2 dm^{-2} hr^{-1}.

Series 500 plexiglass leaf chambers (15.3 x 10 x 10 cm) (Paige Instruments, Davis, CA) were used. The chamber bottom was constructed of finned aluminum heat sink material beneath which water from a refrigerated water bath was circulated for temperature control. A variable speed fan (Pamoter Model 900, Pamoter Co., Burlingame, CA) in the bottom of the chamber provided air circulation. Boundary

Figure 1. Flow diagram of the differential open gas analysis system used for net photosynthetic rate determinations. Solid lines represent gas flow through the system, and dashed lines represent equipment connections.

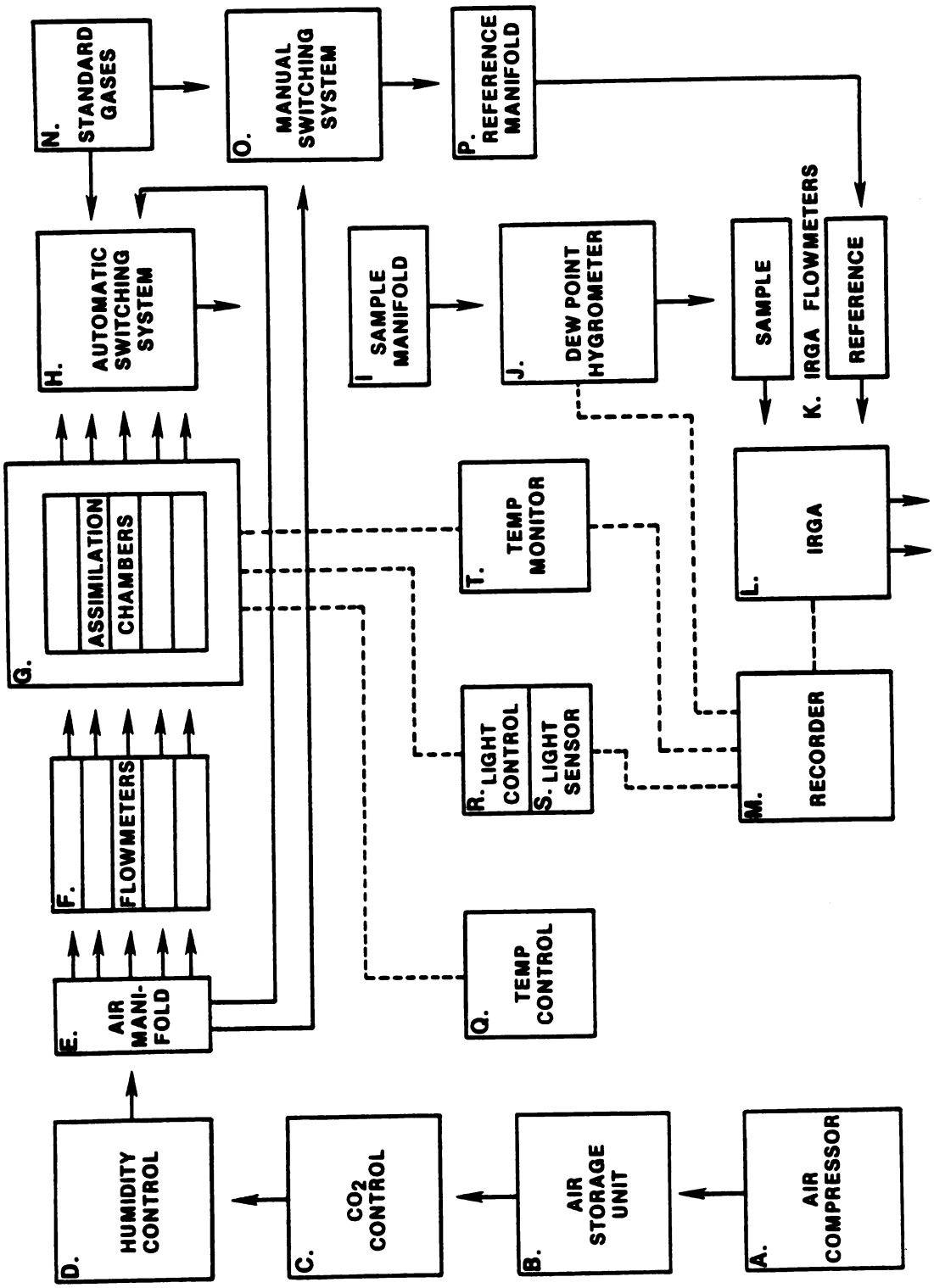
A. AIR COMPRESSOR
B. AIR STORAGE UNIT
C. CO_2 CONTROL
D. HUMIDITY CONTROL
E. AIR MANI-FOLD
F. FLOWMETERS
G. ASSIMILATION CHAMBERS
H. AUTOMATIC SWITCHING SYSTEM
I. SAMPLE MANIFOLD
J. DEW POINT HYGROMETER
K. IRGA FLOWMETERS
SAMPLE
REFERENCE
L. IRGA
M. RECORDER
N. STANDARD GASES
O. MANUAL SWITCHING SYSTEM
P. REFERENCE MANIFOLD
Q. TEMP CONTROL
R. LIGHT CONTROL
S. LIGHT SENSOR
T. TEMP MONITOR

Figure 1

Table 1. A description of the major components of the differential open gas analysis system.

Component		Description
A.	Air compressor	Speedaire Model 2Z870 oilless air compressor (4.1 cfm) (W. W. Grainger, Inc., Lansing, MI)
B.	Air storage unit	189.3 l reservoir with .69 kg/cm^3 pressure
C.	CO_2 control	Aalborg proportioner with FM102-05 flow meters (Aalborg Instruments and Controls Inc., Monsey, NY)
D.	Humidity control	Air saturation at dew point temperature in a refrigerated water bath
E.	Air manifold	Manifold splits air stream to assimilation chambers and IRGA
F.	Flowmeters	Aalborg Model FM102-05 (Aalborg Instruments Inc., Monsey, NY)
G.	Assimilation chambers	Paige Instruments (Davis, CA) series 500 leaf chambers; custom built tree chamber
H.	Automatic switching system	Versa-valve Type 31 solenoid valves (Herbach and Rademan Inc., Philadelphia, PA) connected to Dataplex 10 automatic signal scanner (Hampshire Control Corp., Exeter, NH)
I.	Sample manifold	Transfers sample gas to IRGA from solenoid
J.	Dew point hygrometer	General Eastern System 1100 AP dew point hygrometer (General Eastern Equipment Corp., Watertown, MA)
K.	IRGA flowmeters	Aalborg Instruments Model FM092-04G (Aalborg Instruments and Controls Inc., Monsey, NY)

Table 1 (cont'd.).

L.	IRGA	Beckman Model 865 Infrared Gas Analyzer with water vapor filter (Beckman Instruments Inc., Fullerton, CA)
M.	Recorder	Linear series 300 three pen (Linear Instruments Corp., Irvine, CA)
N.	Standard gases	Matheson ± 1%; high 345-365 ppm CO_2; low 300-325 ppm CO_2 (Matheson Gas Products, Lyndhurst, NJ)
O.	Manual switching system	Versa-valve Type 31 solenoid valves (Herbach and Rademan Inc., Philadelphia, PA) connected to a push button electrical switch
P.	Reference manifold	Transfers reference gas to IRGA from solenoid
Q.	Temperature control	YSI Model 74 temperature controller (Yellow Springs Inst. Co., Yellow Springs, OH) wired to a Blue M Model MR3210A-1 water bath (Blue M Electric Co., Blue Island, IL) circulating water through assimilation chamber heat sink
R.	Light control	Stands with movable 400 W GE multivapor lamps (General Electric Co., Cleveland, OH) and/or neutral density filters (Herbach and Rademan Inc., Philadelphia)
S.	Light sensor	LI-COR Model LI-190S quantum sensors connected to a LI-COR LI 185 Quantum/Radiometer/Photometer (LI-COR Inc., Lincoln, NB)
T.	Temperature monitor	Omega Model 250 EQ 10 channel digital temperature indicator (Omega Engineering Inc., Stamford, CT) connected to chromel constantan thermocouples (.003") and a YSI Model 47 scanning telethermometer

layer resistance was determined to be less than .2 s cm^{-1}.

GE 400 W multivapor (metal halide) lamps were used as a light source. Control of light intensity was accomplished either by adjusting the distance between the light source and the chamber or by using neutral density plastic filters. The effect of the neutral density plastic filter on the spectral distribution of light was determined with an ISCO Model SR portable spectroradiometer. Spectral measurements of the 400 W lamp through the neutral density plastic filter revealed no apparent change in the spectral distribution within the range of wavelengths tested (Figure 2). Light intensity in all chambers was monitored with LI-COR Model LI 190S quantum sensors connected to a LI-COR Model LI 188 Integrating Quantum/Radiometer/Photometer.

Humidity was controlled by saturating the chamber air stream with water at a temperature lower than or equal to the chamber temperature. The air stream was then warmed to chamber temperature before it entered the chamber. Humidity was monitored by measuring the dew point of the chamber air stream with a flow-through dew point hygrometer (General Eastern System 1100 AP).

CO_2 concentration in the air stream was regulated by mixing ambient air from which the CO_2 had been scrubbed (using soda lime) with air from a compressed air tank which contained 800 ppm CO_2. A mixing pump (FMI Model RRP-D, Fluid Metering Inc., Oyster Bay, NY) was used to

Figure 2. Spectral distribution of GE 400 W multivapor (metal halide) lamp and GE 400 W multivapor lamp through neutral density plastic filter.

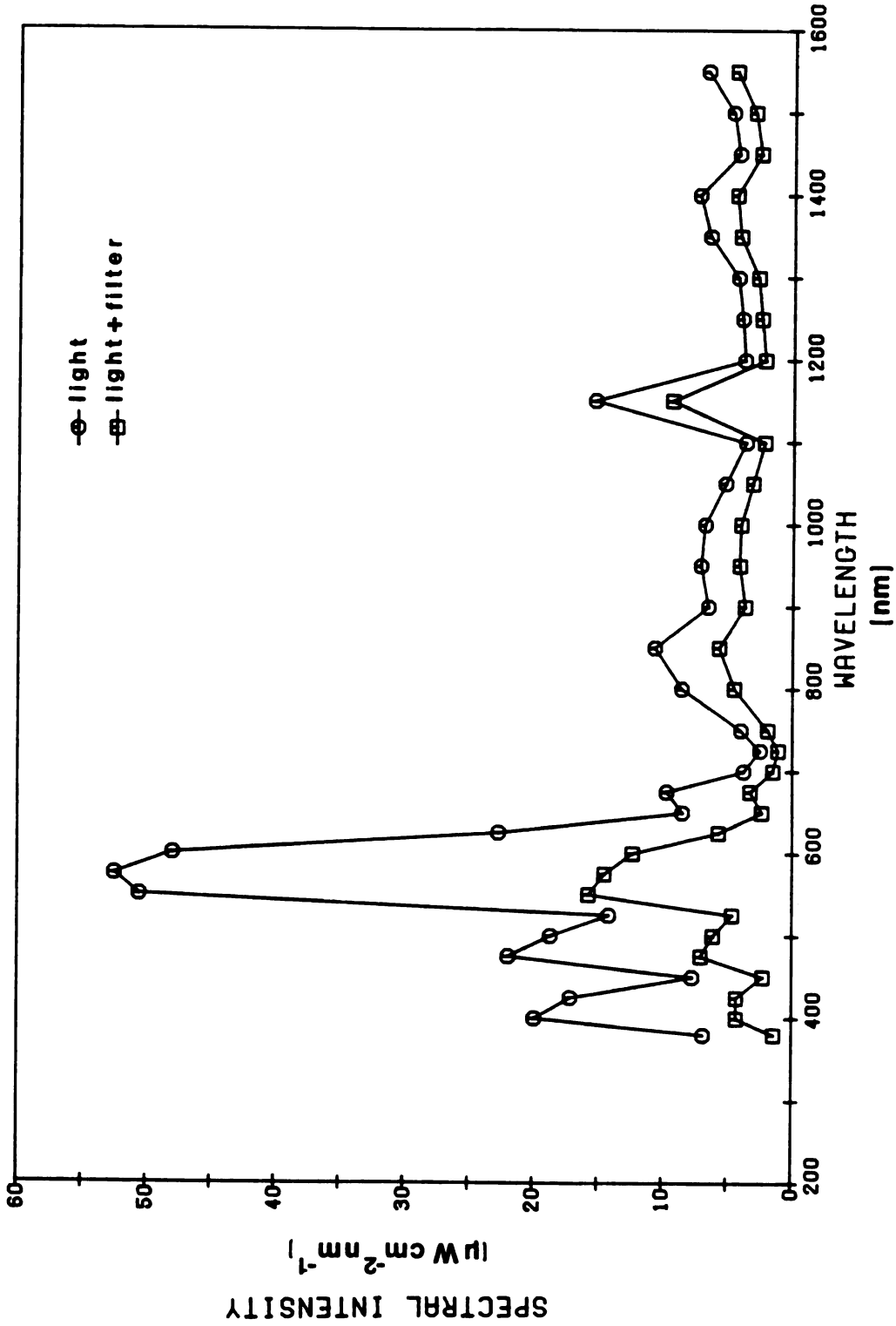
light
light+filter
SPECTRAL INTENSITY
(μW cm-2nm-1)
WAVELENGTH
(nm)
0
10
20
30
40
50
60
200
400
600
800
1000
1200
1400
1600

Figure 2

regulate the proportions of each air supply. The CO_2 concentration of the air stream was continuously monitored using a Beckman 865 analyzer with nitrogen flowing through the reference cell and the chamber air stream flowing through the sample cell.

Experimental procedure and design. Trees with shoots on which the terminal bud had set but on which the terminal leaf had not unfolded were selected for experiments to determine the effects of leaf position on the shoot and leaf age on the Pn of individual leaves. The Pn of alternate leaves, from the terminal leaf to the second leaf from the base of the shoot, was measured. The Pn of the terminal leaf was also monitored periodically from the day it unfolded. A completely randomized design with eight replications (each rep was one tree) was utilized for these experiments.

Light, temperature, and CO_2 response curves were determined using the first new, fully expanded leaf from the apex of each shoot. Pn was measured at light intensities within the range of 0-2400 $\mu E\ m^{-2}\ s^{-1}$ of photosynthetically active radiation (PAR, radiation between 400-700 nm wavelength). General asymptotic curves of the form

$$y = a + bd^x$$

as described by Peat (16) were fitted to the light response curves by computer (SPSS Nonlinear Program) using the Gaussian method of successive approximations as described by Snedecor and Cochran (25). Estimates of maximum Pn

and light compensation point were obtained from the fitted equations. Different symbols on the light response curve represent replications, and each replication is the average Pn of two leaves. Light response curves were determined at both low (30-40%) and high (85-95%) relative humidities for low (10 C), intermediate (25 C), and high (35 C) temperatures.

The effect of temperature on Pn was determined by varying the chamber temperature within the range of 5-40 C while monitoring the steady state CO_2 exchange. Parabolic equations were fitted to the data by computer (SPSS Regression Subprogram). Estimates of optimum temperature and Pn at optimum temperature were obtained from the fitted equations. Different symbols on the temperature response curve represent replications, and each replication is the average Pn of two leaves. Temperature response curves were determined at both low (30-40%) and high (85-95%) relative humidities for low (300 $\mu E\ m^{-2}\ s^{-1}$), intermediate (1200 $\mu E\ m^{-2}\ s^{-1}$), and high (2000 $\mu E\ m^{-2}\ s^{-1}$) levels of PAR.

CO_2 compensation point and the effect of CO_2 concentration on Pn were determined by decreasing the CO_2 concentration in the air stream from 600 to 0 ppm and by increasing the CO_2 concentration from 0 to 600 ppm while monitoring the steady state flux of CO_2. A logarithmic curve was fitted to the data, and CO_2 compensation point was estimated from the equation. Different symbols on the

curve represent replications, and each replication is the average Pn of two leaves. CO_2 response curves were determined at high (85-95%) relative humidity, 25 C, and 1200 $\mu E\ m^{-2}\ s^{-1}$ PAR.

Results

Leaf position on the shoot and leaf age. Leaves on the same shoot which were at least 50% expanded or had recently attained 100% expansion had the greatest Pn per unit area (Table 2). Older, fully expanded leaves at the base of the shoot and younger, less than 50% expanded leaves at the apex had lower Pn. Pn of individual leaves was monitored from the first day the leaf unfolded until several weeks after full leaf expansion (Figure 3). The Pn of individual leaves increased until the leaf reached greater than 80% full expansion, remained constant for 2-4 weeks, then began to decline.

Light response curves. Leaf Pn response to light was determined at both high (85-95%) and low (30-40%) relative humidities for high (35 C), intermediate (25 C), and low (10 C) temperatures (Figure 4). The best fit asymptotic equation was determined for each light response curve. These equations and the predicted values for maximum Pn and light compensation point are shown in Table 3.

The maximum Pn was higher for 25 C than for either 10 or 35 C at both high and low humidities. At low humidity

Table 2. The effect of shoot position on net photosynthetic rate of 'Montmorency' cherry leaves.

Number of nodes from base of shoot	Leaf area (cm^2)	Pn^z (mg CO_2 dm^{-2} hr^{-1})
2	14.1	19.3 b[y]
4	22.3	20.7 b
7	24.7	20.9 b
9	25.5	24.3 ab
11	20.3	30.4 a
12	19.8	30.9 a
13	14.8	27.5 a
14	13.1	20.6 b
15 (terminal)	10.2	8.2 c

[z]Determined by differential infrared gas analysis under constant conditions (1200 μE m^{-2} s^{-1} light intensity, temperature 25 C, and 85-95% relative humidity).

[y]Mean separation by Duncan's multiple range test, 5% level.

Figure 3. The effect of leaf age on net photosynthetic rate of sour cherry. Closed circles represent percent maximum net photosynthetic rate, and open circles represent percent full leaf expansion. Each point is the mean of eight leaves ± SE.

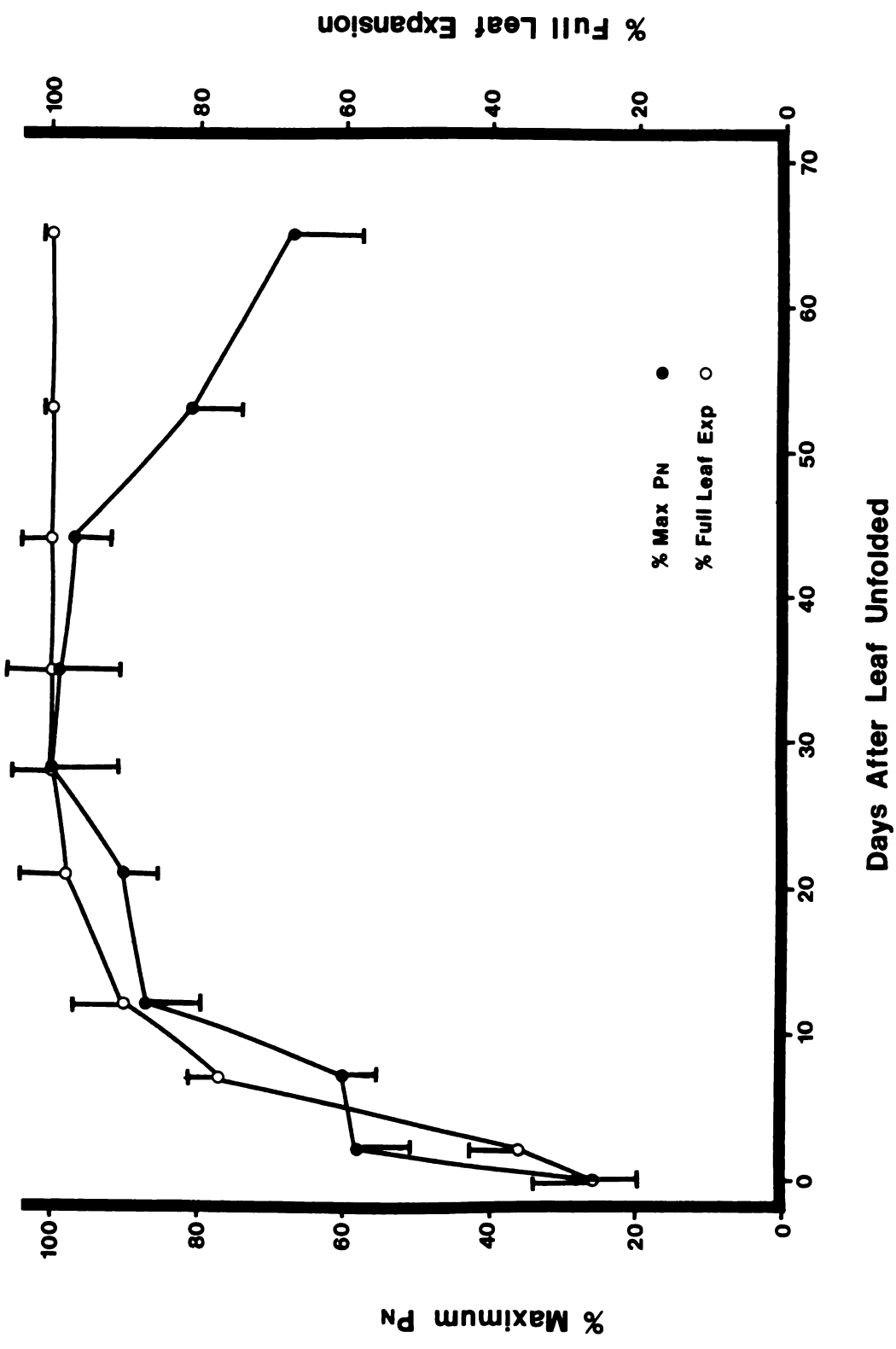
% Maximum P_N
% Full Leaf Expansion
Days After Leaf Unfolded
% Max P_N
% Full Leaf Exp
0
20
40
60
80
100
0
10
20
30
40
50
60
70

Figure 3

Figure 4. Light response curves for 'Montmorency' cherry leaves measured under the following conditions:

A. 30-40% relative humidity and 10 C.

B. 85-95% relative humidity and 10 C.

C. 30-40% relative humidity and 25 C.

D. 85-95% relative humidity and 25 C.

E. 30-40% relative humidity and 35 C.

F. 85-95% relative humidity and 35 C.

Different symbols on the curve represent replications, and each replication is the average Pn of two leaves.

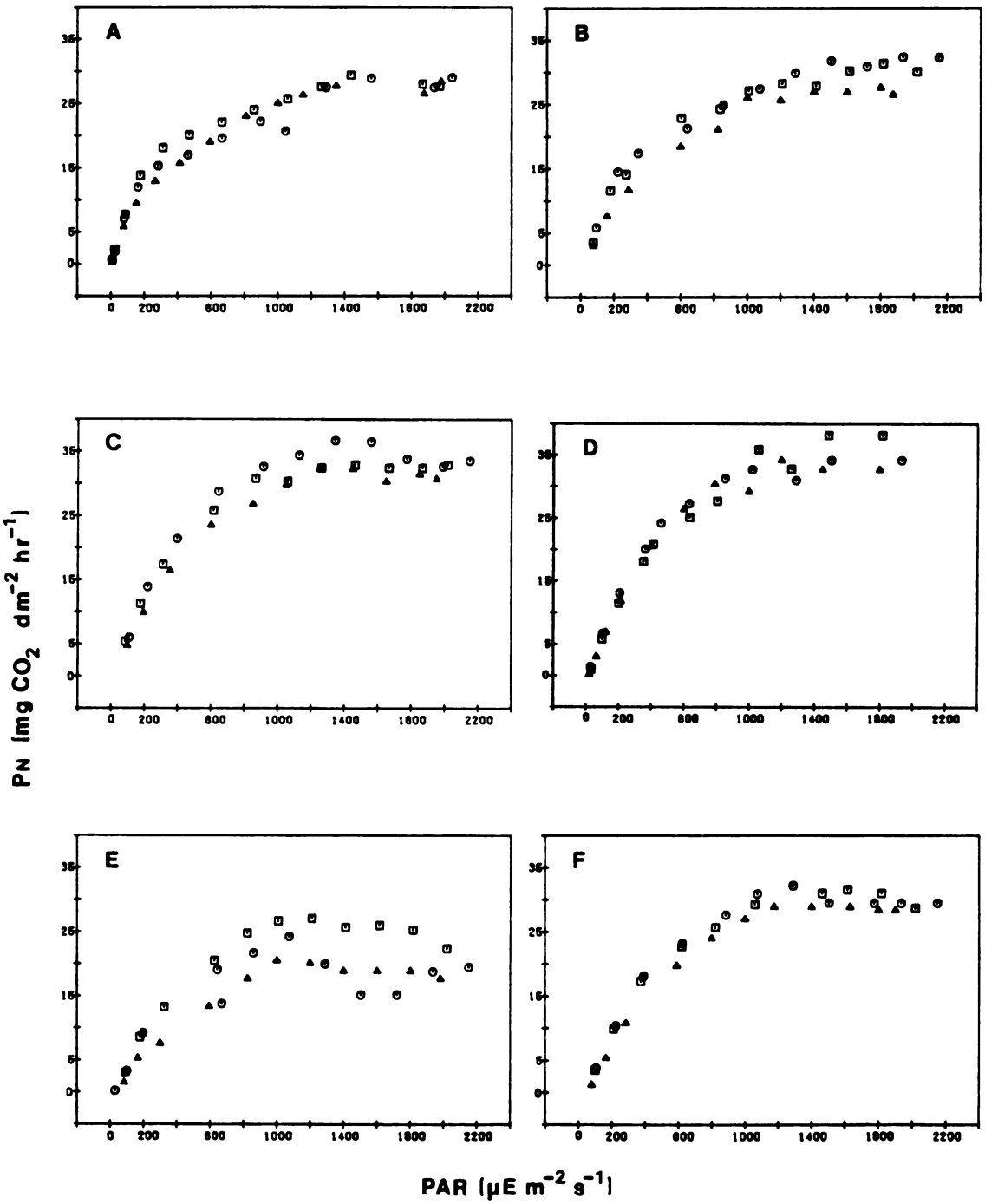
A
B
C
D
E
F
0
5
15
25
35
0
200
600
1000
1400
1800
2200
PN (mg CO2 dm-2 hr-1)
PAR (µE m-2 s-1)

Figure 4

Table 3. The effect of temperature and humidity on maximum net photosynthetic rate and light compensation point as predicted from asymptotic equations of light response curves for 'Montmorency' cherry leaves.

Light response curve	Best fit asymptotic equation	Predicted maximum Pn (mg CO_2 dm^{-2} hr^{-1})	Predicted light compensation point (μE m^{-2} s^{-1})
Temperature 10 C 30-40% relative humidity	$26.8 - 28.1(.998)^x$	26.8	19.6
Temperature 10 C 85-95% relative humidity	$29.9 - 32.2(.998)^x$	29.9	36.5
Temperature 25 C 30-40% relative humidity	$33.5 - 36.3(.997)^x$	33.5	26.6
Temperature 25 C 85-95% relative humidity	$35.8 - 37.4(.998)^x$	35.8	21.7
Temperature 35 C 30-40% relative humidity	$21.5 - 24.9(.997)^x$	21.5	49.5
Temperature 35 C 85-95% relative humidity	$30.5 - 35.2(.998)^x$	30.5	71.5

the maximum Pn for 25 C was approximately 30% higher than for 35 C and 10% higher than for 10 C, while at high humidity the Pn for 25 C was approximately 10% higher than for either 10 or 35 C.

At temperatures of 10 or 25 C the maximum Pn was similar for both high and low humidities. However, at 35 C the maximum Pn was greater for high than for low humidity.

Maximum Pn occurred between 800-1400 $\mu E\ m^{-2}\ s^{-1}$ PAR for both humidities at all three temperatures. However, slightly higher light intensities were required for maximum Pn at 10 C than at 25 C, and at 25 C higher light intensities were required than at 35 C. Light compensation occurred between 20-80 $\mu E\ m^{-2}\ s^{-1}$ PAR for both humidities at all three temperatures. The light compensation point was higher at 35 C than at either 25 or 10 C for both humidities.

Temperature response curves. The effect of temperature on Pn was determined for low (300 $\mu E\ m^{-2}\ s^{-1}$), intermediate (1200 $\mu E\ m^{-2}\ s^{-1}$), and high (2000 $\mu E\ m^{-2}\ s^{-1}$) levels of PAR at both high (85-95%) and low (30-40%) relative humidities (Figure 5). The best fit parabolic equation was determined for each temperature response curve. These equations and the predicted optimum temperature and maximum Pn for each curve are given in Table 4.

Maximum Pn occurred between 15-30 C and was 15-60% greater than at either higher or lower temperatures for

Figure 5. Temperature response curves for 'Montmorency' cherry leaves measured under the following conditions:

A. 30-40% relative humidity and 300 $\mu E\ m^{-2}\ s^{-1}$ light intensity.

B. 85-95% relative humidity and 300 $\mu E\ m^{-2}\ s^{-1}$ light intensity.

C. 30-40% relative humidity and 1200 $\mu E\ m^{-2}\ s^{-1}$ light intensity.

D. 85-95% relative humidity and 1200 $\mu E\ m^{-2}\ s^{-1}$ light intensity.

E. 30-40% relative humidity and 2000 $\mu E\ m^{-2}\ s^{-2}$ light intensity.

F. 85-95% relative humidity and 2000 $\mu E\ m^{-2}\ s^{-1}$ light intensity.

Different symbols on the graph represent replications, and each replication is the average Pn of two leaves.

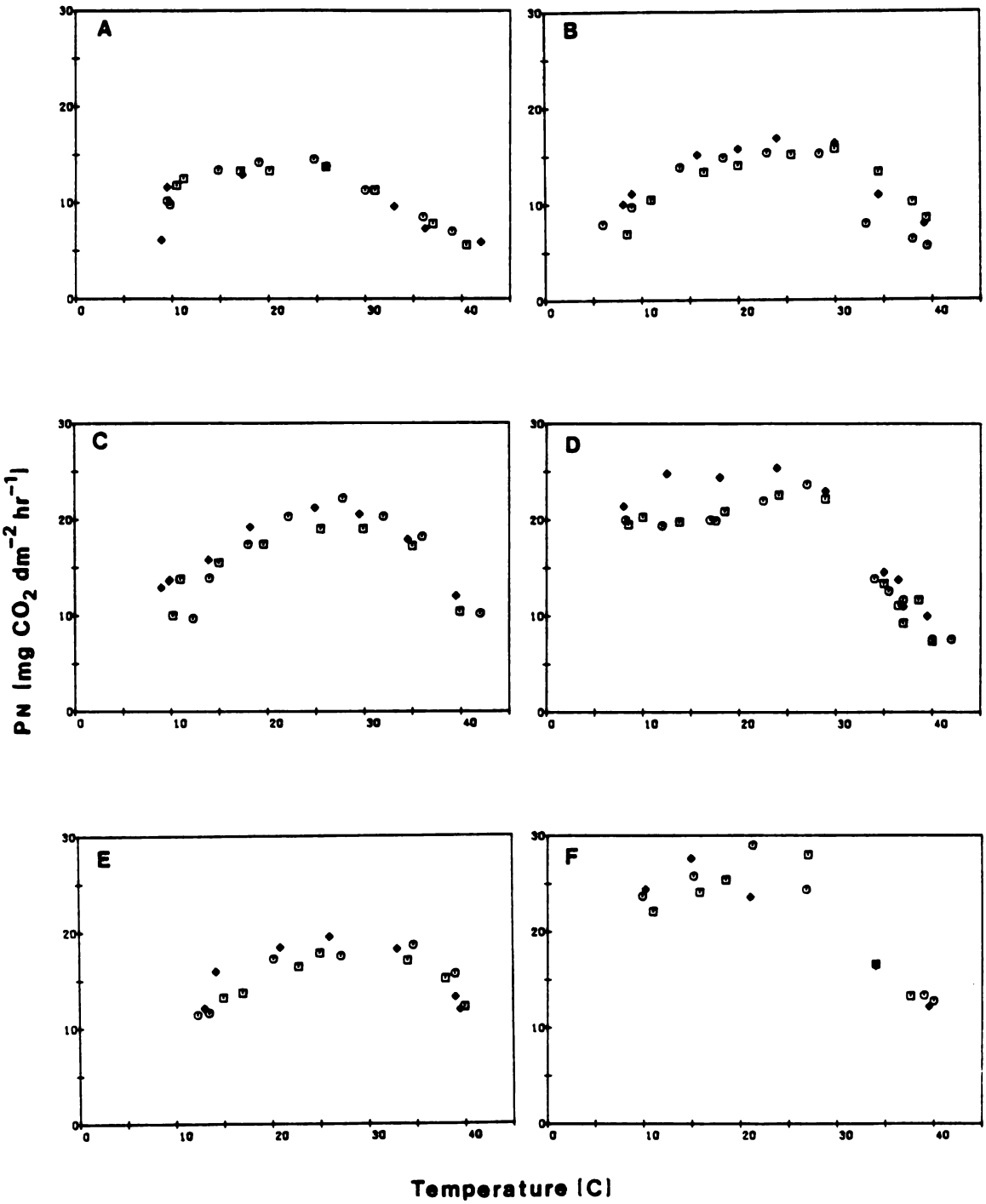

Figure 5

Table 4. The effect of light intensity and humidity on maximum net photosynthetic rate and optimum temperature as predicted from parabolic equations of temperature response curves for 'Montmorency' cherry leaves.

Temperature response curve	Best fit parabolic equation	r^2	Predicted optimum temperature (C)	Predicted Pn at optimum temperature (mg CO_2 dm^{-2} hr^{-1})
300 µE m^{-2} s^{-1} PAR 30-40% relative humidity	$9.3 + 0.5x - .02x^2$	.91	16.8	11.7
300 µE m^{-2} s^{-1} PAR 85-95% relative humidity	$- 0.4 + 1.4x - .03x^2$	.90	22.7	15.7
1200 µE m^{-2} s^{-1} PAR 30-40% relative humidity	$- 3.2 + 1.9x - .04x^2$	.90	25.4	20.1
1200 µE m^{-2} s^{-1} PAR 85-95% relative humidity	$11.3 + 1.3x - .03x^2$	.94	18.9	23.1
2000 µE m^{-2} s^{-1} PAR 30-40% relative humidity	$12.1 + 0.2x - .002x^2$	.36	increasing over range tested	16.7
2000 µE m^{-2} s^{-1} PAR 85-95% relative humidity	$13.3 + 1.4x - .04x^2$	.95	19.3	26.3

all three levels of Par at both relative humidities.

At optimum temperature the Pn was greater at high and intermediate levels of PAR than at low levels of PAR for both high and low humidities. For intermediate and low levels of PAR the Pn at optimum temperature was only slightly higher at high humidity than at low humidity. However, for the high level of PAR, Pn at optimum temperature was much greater at high humidity than at low humidity.

CO_2 effect. The effect of ambient CO_2 concentration on Pn was evaluated at 1200 $\mu E\ m^{-2}\ s^{-1}$ light intensity, 25 C, and 90% relative humidity (Figure 6). Pn increased with increased CO_2 concentration between 0 and 600 ppm. The CO_2 compensation point predicted from the best fit logarithmic equation was 82 ppm.

Discussion

Leaves which had recently attained 100% expansion or were at least 50% expanded had greater Pn than younger or older leaves on the same shoot (Table 2). Similar findings have been reported for mulberry (22). The Pn of individual leaves increased from the time the leaf unfolded until it reached full expansion, remained constant for a time, then declined (Figure 3). This finding is in general agreement with reports for other species that Pn increases as the leaf expands (14). From these results it appears that leaf

Figure 6. The effect of ambient CO_2 concentration on the net photosynthetic rate of sour cherry. Different symbols represent replications, and each replication is the average Pn of two leaves.

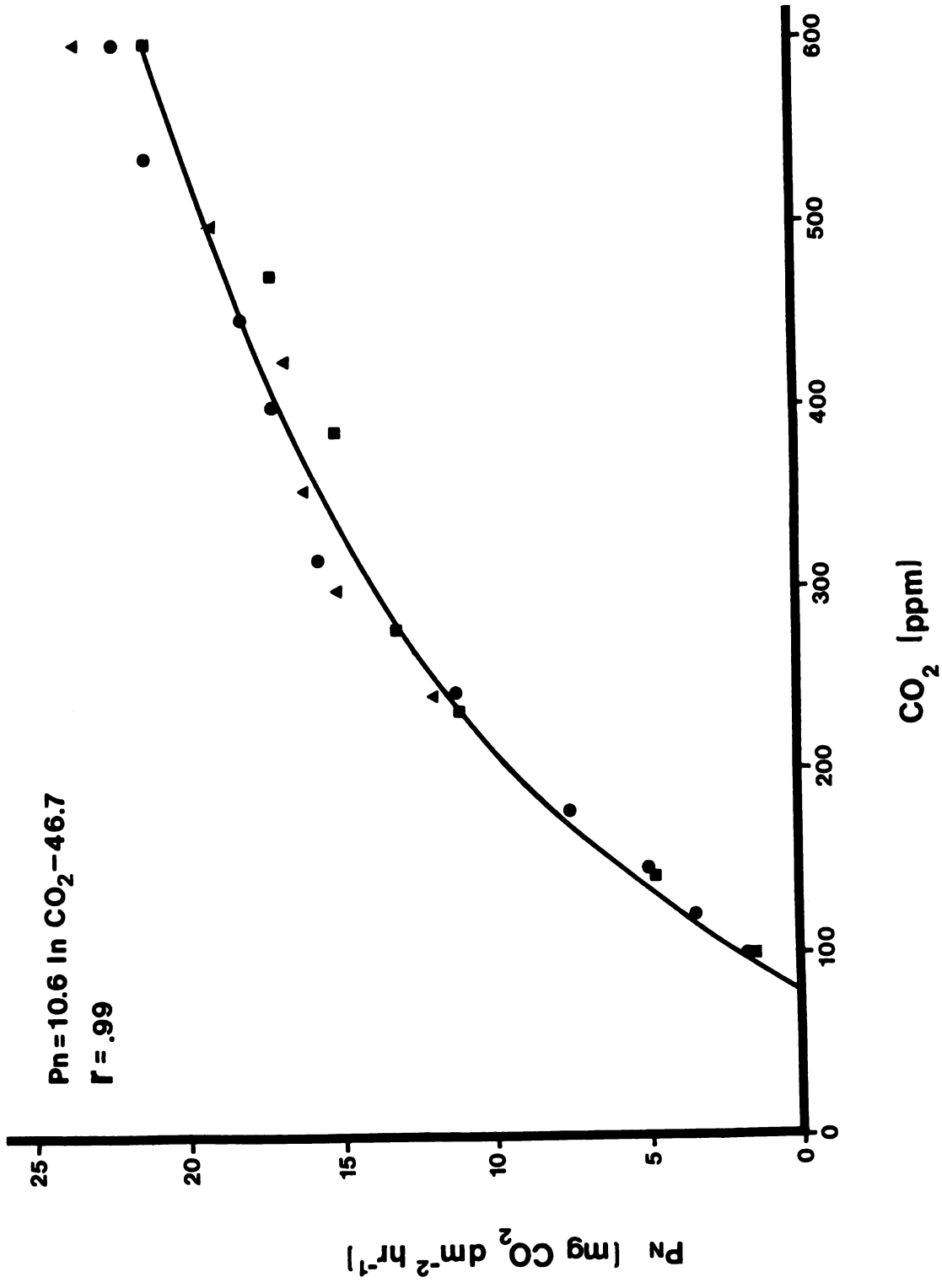
Pn=10.6 ln CO2−46.7
r = .99
PN (mg CO2 dm-2 hr-1)
CO2 (ppm)
0
5
10
15
20
25
100
200
300
400
500
600

Figure 6

age is more important in determining photosynthetic potential than position on the shoot. The lower Pn of young leaves might be due to the presence of immature stomates as has been reported for apple leaves (24), or the photosynthetic apparatus in the leaf may not be completely developed. The lower Pn of older, fully expanded leaves is probably due to normal senescence of the leaves.

Maximum Pn was higher for 25 C than for either 10 or 35 C at both humidities tested (Figure 4). At temperatures of 10 or 25 C the maximum Pn was similar for both high and low humidities. Thus, the differences in vapor pressure deficit did not affect the Pn. This occurrence is in general agreement with reports for other species that photosynthesis and diffusion resistances of individual leaves are not affected by vapor pressure deficits (20, 27). However, at 35 C maximum Pn was greater at high humidity than at low humidity. Perhaps at this high temperature the plant's ability to supply water to the actively transpiring leaves (at high vapor pressure deficit) has been exceeded, resulting in partial closure of the stomates.

Higher light intensities were required for maximum Pn as the temperature decreased from 35 to 10 C. It is generally accepted that no response to increasing light intensity occurs when CO_2 concentration becomes limiting (14). Thus, the higher light requirement at low temperature could mean that CO_2 is not as limiting at the low temperature as it is at higher temperatures (perhaps due

to a reduced rate of the dark reactions). The general shape of the light response curve is hyperbolic, which is typical of other fruit trees and C_3 plants in general (7, 14, 17, 23). However, we found that an asymptotic curve of the form

$$y = a + bd^x$$

gave a better fit for the data points in most cases. This finding is in agreement with others who have shown that the asymptotic relationship gave a better fit than the hyperbolic relationship (which tends to over-estimate maximum photosynthesis) for light response curves of other species (6, 16).

Optimum Pn occurred between 15 and 30 C for all three PAR levels at both humidities. This finding is similar to that for apple, peach, and citrus, which had optimum temperatures of 20-30 C, 30 C, and 15-30 C respectively (7, 10, 11, 13). At high light intensity the Pn at optimum temperature was greater for high than for low humidity. A similar decrease in Pn at low humidity has been reported for citrus (11). This finding again indicates that under conditions of high temperature and light intensity the plant may not be capable of maintaining the high rate of transpiration which is present under conditions of greater vapor pressure deficit, thus resulting in partial stomatal closure. The general shape of the temperature response curve is parabolic. This finding is in agreement with reports of temperature response curves for

other fruit trees (7, 11, 13).

Pn increased with increased CO_2 concentration between 0 and 600 ppm. This is a typical response of many other plants to increased CO_2 concentrations (2, 11, 14, 26). The CO_2 compensation point was 82 ppm. This value is higher than has been reported for some other fruit trees (11, 26).

Sour cherry leaves exhibit a positive response to increased CO_2 concentration under optimum temperature and light conditions. An increase in CO_2 concentration from 300 to 400 ppm resulted in a 10% increase in Pn. Further increasing the ambient CO_2 concentration to 600 ppm resulted in a 40-50% increase in Pn. It has been stated that the CO_2 concentration of the atmosphere could exceed 600 ppm by the year 2020 if current trends in CO_2 increases continue (28). If this projection is true, an increase in Pn of sour cherry should result, assuming other environmental factors can be optimized.

Leaves which have recently completed expansion have the highest photosynthetic potential under optimum conditions. Optimum conditions for photosynthesis of sour cherry were found to be 1000-1200 $\mu E\ m^{-2}\ s^{-1}$ light intensity, temperature 20-30 C, 85-95% relative humidity, and CO_2 concentrations greater than ambient. Any cultural practice which will improve environmental conditions within the tree canopy might lead to increased productivity if Pn is limiting yield. However, more information

is needed about the effects of environmental factors on photosynthesis and the translocation of photosynthates if better decisions are to be made concerning canopy design and orchard management to optimize Pn. Factors such as the effect of pre-exposure to shading or temperature and humidity stress, the effect of fruit load, and the partitioning and translocation of photosynthates require continued study.

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SECTION II

FACTORS AFFECTING DIURNAL AND SEASONAL NET PHOTOSYNTHETIC RATE OF SOUR CHERRY (*PRUNUS CERASUS* L. 'MONTMORENCY')

Abstract. Diurnal and seasonal net photosynthetic rates (Pn) of sour cherry were determined. Leaf Pn was not affected by shoot excision for 24 hours after the shoot was excised. Under constant light intensity (1200 $\mu E\ m^{-2}\ s^{-1}$), temperature (25 C), and relative humidity (80-90%) there was no significant diurnal change in Pn for individual sour cherry leaves. However, there was a pronounced diurnal pattern in Pn for whole trees measured under constant temperature and natural variation in sunlight from sunrise to sunset. Maximum Pn occurred before solar noon, remained constant for a short time, then declined. Seasonal patterns in leaf Pn varied, but, in general, Pn increased in the spring as leaves expanded, reached a peak, remained stable for several weeks, then gradually declined. The Pn of leaves on terminal shoots was not significantly different from the Pn of leaves on spurs, and the presence of fruit did not have a consistent effect on the Pn of sour cherry leaves.

Diurnal and seasonal changes in photosynthetic rate have been demonstrated for several species (3, 7, 9, 12).

In apple, diurnal fluctuations in photosynthetic rate have been reported, with greater rates occurring in the morning than in the afternoon (16, 25). Other reports have indicated that there is no consistent diurnal pattern of photosynthesis for individual leaves if kept under constant conditions (1, 3, 5). In peach, higher rates of photosynthesis have been observed early in the day, and photosynthetic rates ranged from 3.6 to 12.5 mg CO_2 dm^{-2} hr^{-1} during the growing season (7). Photosynthetic rate of apple increases as the leaf expands, reaches a maximum just after expansion is completed, remains high for several weeks, than gradually declines during the rest of the growing season (4, 9).

Changes in photosynthetic rate have been associated with flowering, fruiting, and vegetative growth (12, 22). The presence of fruit has been reported to increase the photosynthetic rate of leaves of some species (2, 4, 7, 14, 18, 21), while in others lower gaseous diffusive resistances and higher transpiration rates were found when fruit were present (14, 23, 24, 29).

Fruit have been shown to be stronger sinks for photosynthate than vegetative growth in apricot and peach (20). In sour cherry, fruit growth occurs in a double sigmoidal pattern, and fruit mature in about 60 days after full bloom (27). Canopy development is generally completed in sour cherry by fruit harvest, with spur leaf development completed approximately 20-25 days after full bloom

and terminal leaf development completed 60 days after full bloom (8). Flower initiation also occurs during this period (5-6 weeks after full bloom) (11). Thus, vegetative and reproductive growth are competitive sinks for photosynthate, with rapid but short term annual growth.

Current trends toward higher density cultural practices for sour cherry and the increasing use of summer hedging (removing part of the foliage during the growing season) (19) make management decisions regarding when and how to prune more difficult. Diurnal and seasonal changes in Pn and other physiological processes should be considered when making decisions regarding summer hedging and other cultural practices. Knowledge of how environmental factors and cultural practices affect the growth and development patterns of sour cherry would provide a scientific basis for making decisions concerning orchard management. Therefore, experiments were designed to determine the diurnal and seasonal patterns of Pn and to evaluate the effect of fruit on Pn of sour cherry.

Materials and Methods

Tree culture. One year old sour cherry trees (Prunus cerasus L. 'Montmorency') on 'Mahaleb' rootstock were grown in 20 l plastic pots in a mixture of peat, loam, and sand (1:2:1). Fertilizer, pesticides (Cyprex, Captan, Guthion, and Plictran), and water were added as needed.

Potted trees were used in experiments to determine the diurnal patterns of Pn and the effect of shoot excision on leaf Pn. Mature, six year old 'Montmorency' sour cherry trees on 'Mahaleb' rootstock (1.8 m x 4.3 m, Horticulture Research Center, East Lansing, MI) were used in experiments to determine the effect of fruit load on Pn and the seasonal patterns of Pn.

Photosynthetic measurements. Pn was determined utilizing an open gas analysis system as previously described (26). For all measurements except whole tree Pn, CO_2 exchange rates were determined for intact leaves placed in environmentally controlled chambers. The chamber temperature was maintained at 25 ± .5 C, PAR (photosynthetically active radiation, radiation in the 400-700 nm range) at 1200 $\mu E\ m^{-2}\ s^{-2}$, and relative humidity between 85-95% for optimum Pn (26). Pn was expressed as mg CO_2 $dm^{-2}\ hr^{-1}$.

Pn of whole trees was determined for small potted trees in a .9 m x .9 m x 1.2 m clear plexiglass chamber maintained at 25 ± 3 C, and in which relative humidity was monitored and found to be 80-90%. The chamber was placed outside in full sunlight, and Pn was measured from sunrise to sunset. PAR was recorded at the level of the top of the tree canopy within the chamber. Soil respiration was eliminated by enclosing the pot in a plastic bag. The average Pn was calculated as mg CO_2 fixed per dm^2 leaf area per hour.

Shoot excision. Potted trees were selected which had two uniform shoots. An initial determination of Pn was made on the first fully expanded leaf from the terminal on each of the two shoots, then one of the shoots was excised from the tree (15-23 cm below the leaf to be measured) and placed immediately in a beaker of distilled water. The end of the shoot was recut under water, and Pn was determined 1, 2, 4, 5, and 24 hours after excision for leaves on both excised and non-excised shoots. The experimental design was completely randomized with eight replications.

Measurement of diurnal Pn. Pn of leaves from potted trees was monitored from 9:00 a.m. until 7:00 p.m. in individual leaf chambers under constant conditions (temperature 25 $\pm$ .5 C, PAR 1200 $\mu E\ m^{-2}\ s^{-1}$, and 85-95% relative humidity). Diurnal Pn of a whole tree was measured by placing small potted trees inside the whole plant chamber where CO_2 exchange and PAR were monitored under natural sunlight on clear days from sunrise to sunset.

Seasonal trends of and fruit effects on Pn. Two uniform scaffolds were selected on both the east and west sides of individual trees planted in a north-south row orientation. Just prior to bloom and before leaves emerged, the flower buds were removed from one scaffold on each side of the tree. The other scaffold was allowed to flower and set fruit. Fresh weight of 100 fruit, the average number of leaves on terminal shoots and spurs,

and the average leaf area of 50 shoots and spurs were monitored to determine the stage of fruit growth and foliage development.

All Pn measurements were initiated between 9:00 and 10:00 a.m., and standard leaf chamber conditions were used. The Pn of both the first leaf which expanded at the base of each shoot and the first mature leaf from the apex of terminal shoots were monitored by excising shoots periodically throughout the 1978 and 1979 growing seasons. Seasonal trends in Pn were determined for the first mature leaf from the apex of shoots with fruit. The Pn of leaves on terminal shoots was also compared to the Pn of leaves on spurs (both had fruit present).

Results

Shoot excision. The Pn of leaves on excised shoots was not significantly different from the Pn of leaves on non-excised shoots at 1, 2, 4, 5, or 24 hours after shoot excision (Table 1).

Diurnal trends. For individual leaves under constant conditions (1200 $\mu E\ m^{-2}\ s^{-1}$ PAR, 25 C, and 85-95% relative humidity) there was no significant change in diurnal Pn over a ten hour period (Table 2). The experiment was repeated, and similar results were found.

The diurnal trend of a whole tree was determined using small potted trees (without fruit) in a whole plant

Table 1. The effect of shoot excision on net photosynthetic rate of 'Montmorency' cherry leaves.

Treatment	Pn^z (mg CO_2 dm^{-2} hr^{-1})					
	Hours after shoot excision					
	0	1	2	4	5	24
Non-excised	16.6 a^y	16.2 a	16.5 a	16.7 a	16.4 a	17.2 a
Excised	16.3 a	16.6 a	16.8 a	16.8 a	17.0 a	17.9 a

^{z}Determined by differential infrared gas analysis under constant conditions (1200 µE m^{-2} s^{-1} light intensity, temperature 25 C, and relative humidity 85-95%).

^{y}Mean separation by Duncan's multiple range test, 5% level.

Table 2. Diurnal change in net photosynthetic rate of 'Montmorency' cherry leaves under optimum conditions.

Hours after first measurement	Pn^z (mg CO_2 dm^{-2} hr^{-1})
0	16.7 a[y]
1	17.2 a
2	17.5 a
3	18.0 a
4	17.8 a
5	17.1 a
6	17.2 a
7	17.9 a
8	16.9 a
9	17.2 a
10	16.8 a

[z]Determined by differential infrared gas analysis under constant conditions (1200 µE m^{-2} s^{-1} light intensity, temperature 25 C, and 85-95% relative humidity.

[y]Mean separation by Duncan's multiple range test, 5% level.

chamber placed outside from sunrise to sunset (Figure 1). Pn increased to 18 mg CO_2 dm^{-2} hr^{-1} four hours after sunrise, remained constant for two to three hours, then gradually declined toward sunset. Pn reached the maximum level three to four hours before PAR reached its peak intensity, and Pn began to decline before PAR reached maximum intensity.

Fruit effect on Pn. The effect of fruit on Pn was monitored in 1978 and 1979. Measurements of the Pn of leaves on shoots with and without fruit were made at several stages of fruit development and later in the season after harvest. Leaves on shoots with fruit had a higher average seasonal Pn than leaves on shoots without fruit in 1978 (Table 3). The Pn was higher for leaves on shoots with fruit present when measured in stages II and III of fruit growth. However, when measured after harvest no difference was noted.

During the 1979 season there was no significant difference in Pn between leaves on shoots with and without fruit (Table 4). In stages I and III of fruit development the leaves on shoots with fruit tended to have higher Pn. However, in stage II of fruit development and after harvest Pn tended to be higher on shoots without fruit.

Seasonal trends. Pn during the 1978 season was highest at the beginning of the season (41.2 mg CO_2 dm^{-2} hr^{-1}), declined (to about 18-20 mg CO_2 dm^{-2} hr^{-1}) during stage II of fruit development, remained constant for several weeks,

Figure 1. Diurnal pattern of net photosynthetic rate for a sour cherry tree. Closed circles are the photosynthetic rate, and open circles are the PAR levels. Each point represents the average of three replications, and each replication is one tree monitored for one day.

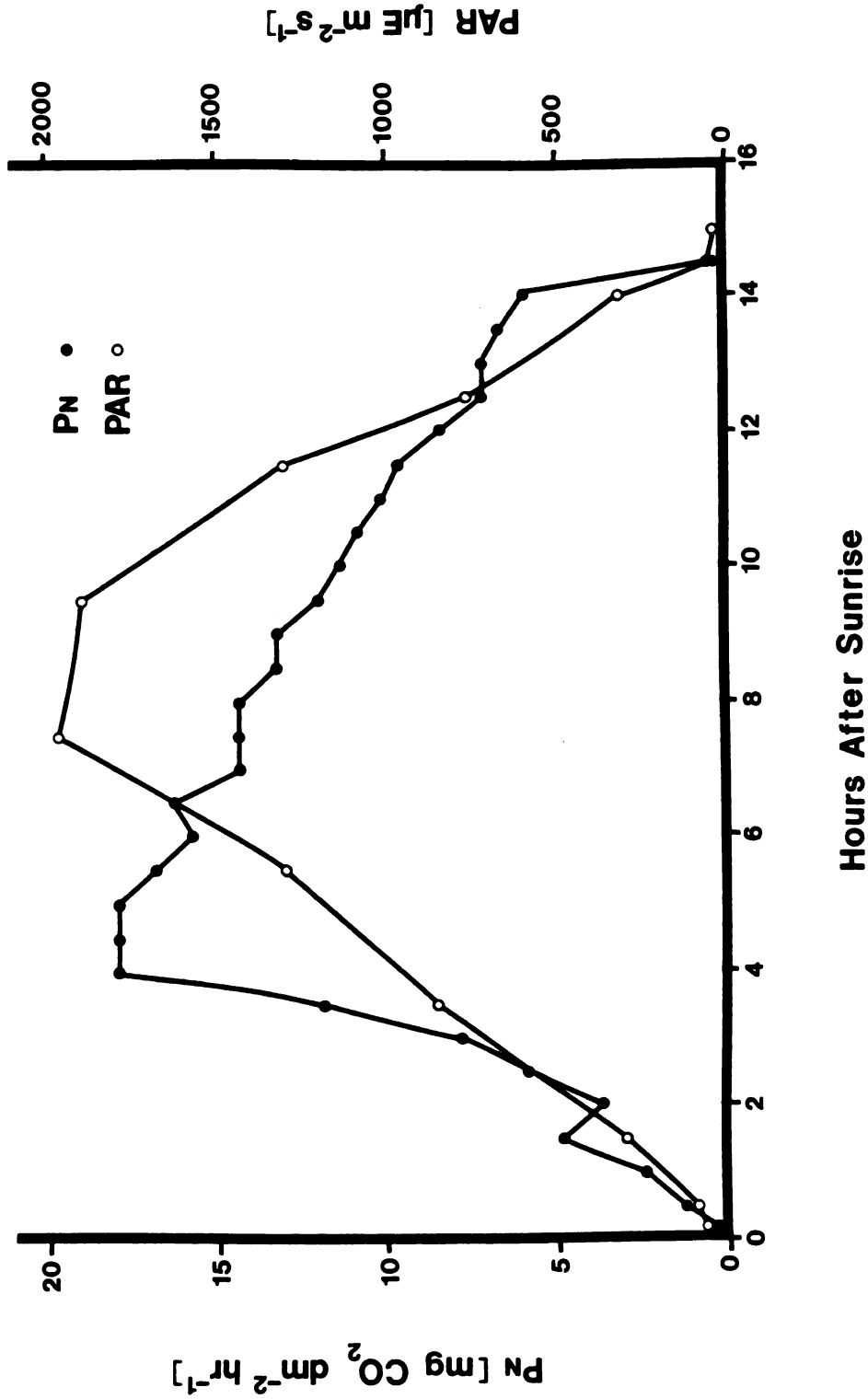
PAR [μE m⁻² s⁻¹]
2000
1500
1000
500
0
16
14
12
10
8
6
4
2
0
Hours After Sunrise
PN •
PAR ○
20
15
10
5
0
PN [mg CO2 dm⁻² hr⁻¹]

Figure 1

Table 3. The effect of fruit on net photosynthetic rate of 'Montmorency' cherry leaves in 1978.

Treatment	Pn^z ($mg\ CO_2\ dm^{-2}\ hr^{-1}$)			
	Stage of fruit development			
	II (.71g/fruit)	III (2.66g/fruit)	Post harvest (late)	Season average
Fruit	41.2 a[y]	23.7 a	13.0 a	26.0 a
No fruit	32.6 b	20.6 b	11.2 a	21.5 b

[z]Determined by differential infrared gas analysis under constant conditions (1200 $\mu E\ m^{-2}\ s^{-1}$ light intensity, temperature 25 C, and 85-95% relative humidity).

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

Table 4. The effect of fruit on net photosynthetic rate of 'Montmorency' cherry leaves in 1979.

Treatment	Pn^z ($mg\ CO_2\ dm^{-2}\ hr^{-1}$)				
	Stage of fruit development				
	I (.25g/fruit)	II (.73g/fruit)	III (2.70g/fruit)	Post harvest (late)	Season average
Fruit	25.5 a[y]	24.3 a	24.2 a	19.1 a	23.3 a
No fruit	24.0 a	25.6 a	22.5 a	22.3 a	23.6 a

[z]Determined by differential infrared gas analysis under constant conditions (1200 $\mu E\ m^{-2}\ s^{-1}$ light intensity, temperature 25 C, and 85-95% relative humidity).

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

then declined late in the season (Figure 2). However, the seasonal pattern of Pn was quite different during the 1979 season (Figure 2). The Pn was 27-30 mg CO_2 dm^{-2} hr^{-1} early in the season, remained constant for 8-10 weeks, then declined.

The Pn of the first leaf at the base of each terminal shoot was compared to that of the youngest fully expanded leaf on spurs several times during the 1979 season (Table 5). These leaves completed expansion at about the same time and were the same age. The Pn of leaves at the base of the terminal shoots was not significantly different from that of leaves of a similar age on spurs at any stage of development measured during the season.

Discussion

Twenty-four hours after shoot excision there was no significant difference in the Pn of 'Montmorency' sour cherry between leaves on excised shoots (placed in distilled water) and leaves on shoots remaining on the tree (Table 1). Therefore, we concluded that shoots could be excised from mature trees in the field, placed in water, and taken to the laboratory for measurement of Pn. This procedure allowed measurement of the Pn of mature trees treated in the field without the use of mobile equipment.

Leaves on shoots with fruit had a significantly greater Pn than leaves on shoots without fruit during

Figure 2. Seasonal pattern of net photosynthetic rate of the first mature leaf from the apex of terminal shoots (with fruit present) of sour cherry for two consecutive years. Closed squares represent the 1978 season, and open squares represent the 1979 season. Each point is the average of four replications.

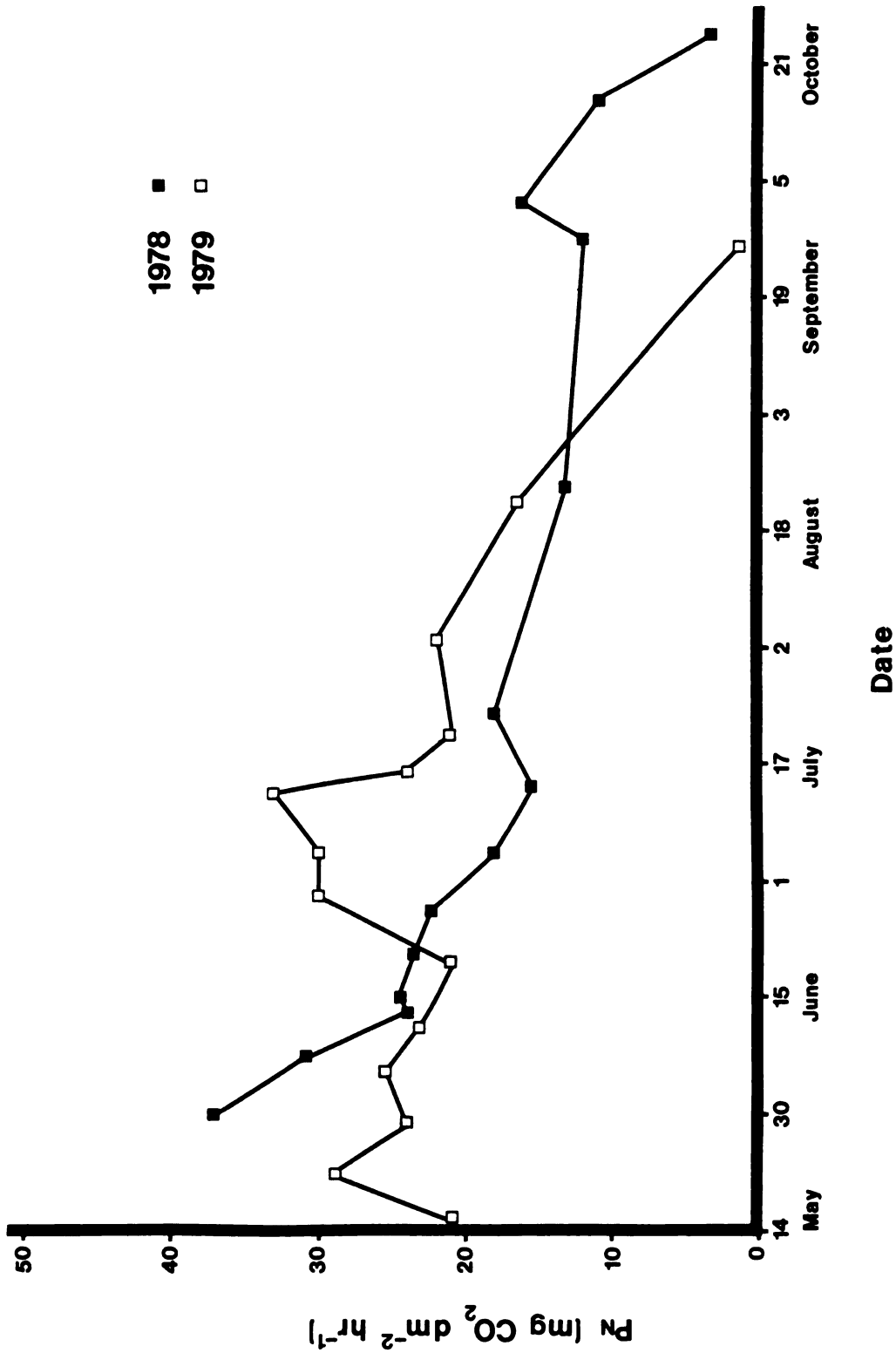
1978
1979
P_N (mg CO_2 dm^{-2} hr^{-1})
0
10
20
30
40
50
14
May
30
15
June
1
17
July
2
18
August
3
19
September
5
21
October
Date

Figure 2

Table 5. Net photosynthetic rate of terminal and spur leaves of 'Montmorency' cherry in 1979.

Leaf type	Pn^z ($mg\ CO_2\ dm^{-2}\ hr^{-1}$)				
	Stage of fruit development				
	I (.25g/fruit)	II (.73g/fruit)	III (2.70g/fruit)	Post harvest (late)	Season average
Terminal	22.0 a[y]	28.6 a	24.3 a	7.6 a	20.6 a
Spur	23.5 a	25.6 a	25.9 a	6.3 a	20.3 a

[z]Determined by differential infrared gas analysis under constant conditions (1200 $\mu E\ m^{-2}\ s^{-1}$ light intensity, temperature 25 C, and 85-95% relative humidity)

[y]Mean separation within columns is by Duncan's multiple range test, 5% level.

the first year of the experiment (Table 3). But in the second year of the experiment, no significant difference in Pn was found between leaves on shoots with or without fruit. Increased Pn of leaves due to the presence of fruit has been reported for peach (6, 7), apple (2, 13, 18), and citrus (21). However, for sour cherry the presence of fruit does not appear to have a consistent effect on the Pn of leaves. Increases in the photosynthetic rate of leaves caused by the presence of fruit has been attributed to many factors, including the hormonal content of the fruit (22) and lower assimilate concentrations in the leaves with fruit present (thus, preventing a decline in the photosynthetic rate due to end product inhibition of enzyme activity) (22). Several hormones have been associated with increased photosynthetic rates of leaves (22). In grape, changes in hormonal levels have been shown to occur when sink strength changes, and the photosynthetic rate changes with these changes in hormonal levels (15).

Cherry is a much smaller fruit than apple, peach, or citrus, and the vegetative growth rate is extremely rapid. Perhaps the apparent inconsistency in the effect of fruit on Pn is due to the rapidly growing shoots and leaves which may be more powerful sinks in some situations. Kriedemann (20) has shown that developing peach and apricot fruits are strong sinks for photosynthetic assimilates, but that in citrus the young vegetative growth is a stronger sink than the fruit.

Differences in fruit load, rate of growth, and environmental conditions between years might cause changes in the sink strength of the fruit and/or vegetation. Temperature has been shown to affect the sink activity of wheat grain, thus influencing assimilate movement (28). Yield data were not taken on the trees used in our study, so differences in fruit load could not be documented.

The Pn of leaves on terminal shoots was not significantly different from the Pn of leaves of similar ages on spurs (Table 5). In apple, spur leaves have been reported to have lower photosynthetic rates than terminal leaves (10). Barden (4) attributed the difference in photosynthetic rate between spur and terminal leaves to differences in light exposure, because spur leaves were inside the canopy growing under heavy shade conditions.

There was no significant change in diurnal Pn for sour cherry leaves when maintained under optimum conditions (Table 2). This finding is in agreement with some reports for other species (1, 3, 17). We therefore concluded that leaves could be used at least for short periods of time in experiments without adjusting for diurnal changes in Pn.

There was a pronounced diurnal pattern of Pn for whole trees when measured under conditions of natural sunlight from sunrise to sunset (Figure 1). Maximum Pn was reached before solar noon, remained relatively constant for a short time, then declined toward sunset. Pn

declined before PAR began to decrease. A similar diurnal pattern of photosynthesis has been reported for apple by Mika (25), who suggested that the plant may experience a progressive water deficit which lowers the photosynthetic rate because of stomatal closure. Since Pn reached a maximum then began to decrease before PAR reached its maximum and decreased, it is possible that PAR levels needed for maximum Pn were reached before solar noon, and that a buildup of photosynthate in the leaves could have resulted in feedback inhibition of photosynthesis. Optimum light intensity for sour cherry has been determined to be approximately 1000-1200 $\mu E\ m^{-2}\ s^{-1}$ (26). This level of PAR coincides with the maximum Pn in Figure 1.

The seasonal trend in Pn was monitored for two consecutive years (Figure 2). In the 1978 season the Pn was very high at the beginning of the year, declined rapidly, leveled off and remained constant for several weeks, then declined in late fall. However, in the 1979 season the Pn was not as high at the beginning of the season. Pn remained constant from the beginning of the season until late in the season when there was a rapid decline. Pn during the season may be affected by many factors including environment (light, temperature, humidity), fruit load, and leaf age. The rapid decline in photosynthetic rate at the end of the season is associated with leaf senescence and may be accelerated by lower temperatures. Figure 3 compares the Pn, number of leaves expanded, and

Figure 3. Seasonal pattern of net photosynthetic rate, number of leaves expanded, and fruit growth for sour cherry in 1979. Open circles are net photosynthetic rates of the first mature leaf from the apex of terminal shoots, open squares are average fresh weight of 100 fruit, and open triangles are number of leaves expanded.

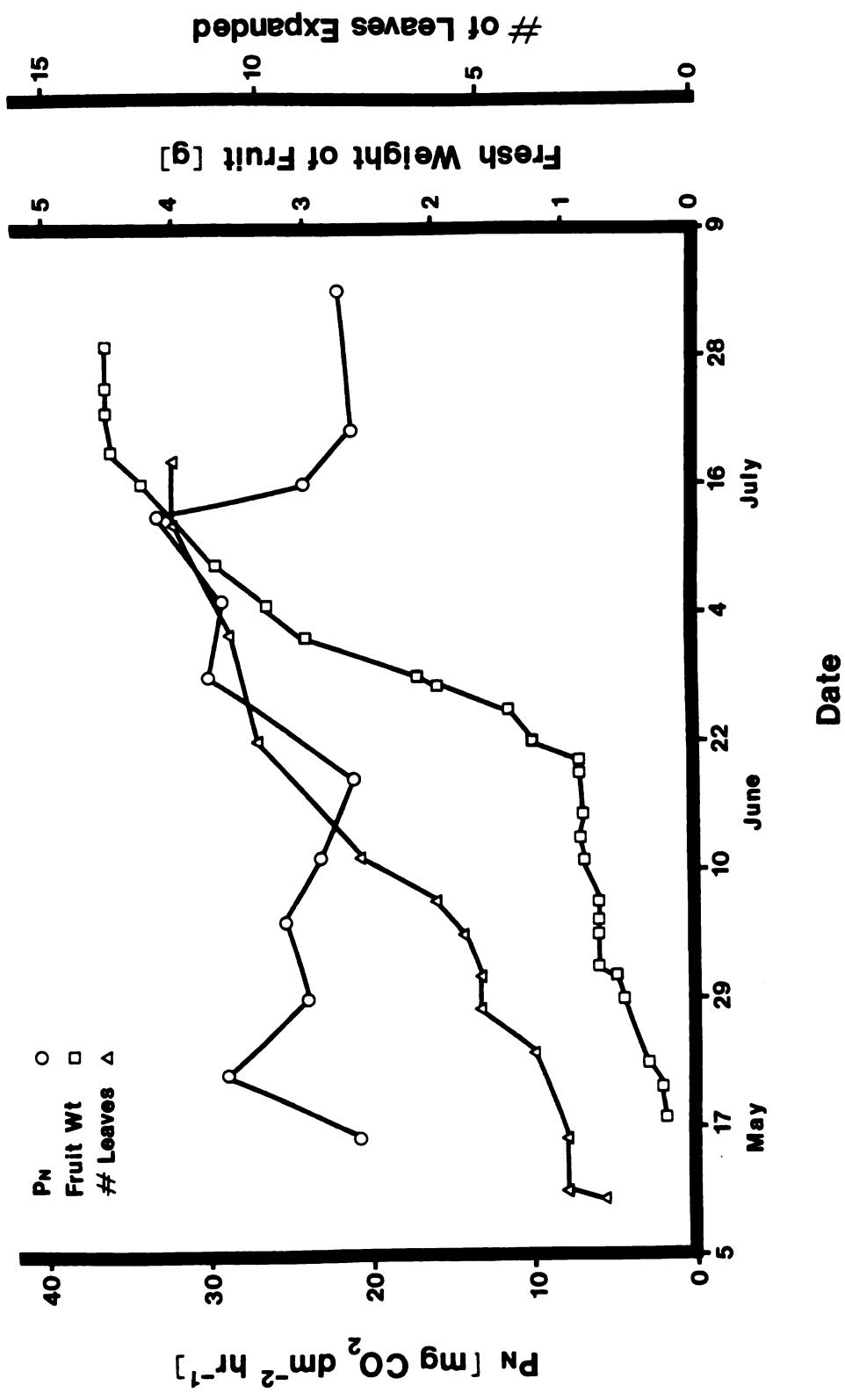
P_N [mg CO_2 dm^{-2} hr^{-1}]
Fresh Weight of Fruit [g]
# of Leaves Expanded
P_N
Fruit Wt
Leaves
May
June
July
Date

Figure 3

fruit growth for part of the 1979 season. It is apparent that leaf and fruit growth are competitive sinks for photosynthates during this part of the growing season. Flower initiation also occurs during this period (5-6 weeks after full bloom) (11), and may also compete for photosynthate during this period. Thus, decisions regarding cultural practices are quite critical during this period because they may affect not only the present, but also next year's crop. For example, summer hedging is becoming a commercially accepted practice and is normally done 6-7 weeks after full bloom (19), which would occur near the time of flower bud initiation, maximum leaf growth, and just prior to early stage III of fruit growth.

The seasonal pattern of Pn for sour cherry is not consistent from year to year (Figure 2). In a given year, environmental factors (light, temperature, water) may be limiting, especially during critical stages of development (such as stage III of fruit development when most of the fruit weight is attained). Optimum conditions for Pn of sour cherry leaves occur at 1000-1200 $\mu E\ m^{-2}\ s^{-1}$ light intensity, 25 C, and high humidity (26). If Pn is limiting yield at certain stages of development, then any cultural practice that would optimize conditions for Pn would be desirable. Further work is needed to determine if Pn is limiting yield (and at which stage of development it is most limiting), and to determine the effects of environmental factors on Pn, vegetative growth, reproductive

growth, and partitioning of photosynthate. The knowledge obtained from such work could be used to develop cultural practices and orchard designs that would optimize yield.

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SECTION III

THE EFFECTS OF ARTIFICIAL SHADE ON THE LEAF AND SHOOT MORPHOLOGY OF SOUR CHERRY (*PRUNUS CERASUS* L. 'MONTMORENCY')

Abstract. One year old potted sour cherry trees were grown in full sunlight to the 11-15 leaf stage then shaded to establish 100, 36, 21, or 9% of full sunlight treatments. At the end of the growing season trees grown in full sunlight had greater terminal (57%) and lateral (46%) shoot diameters than trees grown in 9% of full sunlight. Average internode length of lateral shoots and average leaf area on terminal shoots was greater for trees grown in 21% of full sunlight than for trees grown in full sunlight. Specific leaf weight was greater (38-125%) for leaves on trees grown in full sunlight than for trees grown under shade. There was no difference in leaf chlorophyll content on an area basis. However, leaves on trees grown under 9% of full sunlight had more (48-92%) chlorophyll than those grown in full sunlight when expressed in mg/g leaf dry weight and mg/cm^3 leaf volume. Palisade and spongy mesophyll layers of cells and total leaf thickness were greater for leaves grown in full sunlight than for leaves grown under shade. Trees grown in full sunlight had a greater number of flower buds and flowers per tree the following spring than trees

grown in 36% of full sunlight. Trees grown in 21 and 9% of full sunlight had no flowers present. The number of flowers per bud and the percent fruit set were not significantly different between treatments which had flowers.

There have been many reports concerning effects of shade on the morphology of fruit trees (2, 3, 4, 14, 15, 17). In general, plants grown in shade have greater leaf areas, decreased leaf weights and thickness, and modified leaf structures (5). Many species have a more developed palisade and spongy mesophyll region, resulting in thicker leaves when grown under high light intensity (6, 8, 10, 25). Leaves of Atriplex patula grown under low light intensity have smaller cells, fewer vascular strands, and fewer cell layers across a leaf section than those grown under high light intensity (7). Mesophyll resistance is also higher in plants grown under low light intensities (10, 16, 25). Leaves grown under low light intensities also have more chlorophyll per unit weight or unit volume of leaf, but less chlorophyll per unit area than leaves grown under high light intensities (7, 8). There is often a lower ratio of chlorophyll A to B in leaves grown under low light intensities (7, 8, 12, 22).

Average specific leaf weight of apple has been reported to decrease with increasing shade (3, 17, 27). Shading has also been reported to result in reduced number

and weight of new shoots, reduced increase of shoot girth, and reduced leaf thickness of apple (17). A decrease in flowering of apple due to shading has been reported (9), and Jackson et al. (18, 19) reported that shading also resulted in reduced flower bud formation, reduced fruit set, reduced fruit size, and lower fruit quality of apple. Heinicke (14) suggested that in apple the increased shading with tree size resulted in an increase in leaf area per tree.

Within a canopy, the light spectra resulting from sunflecks (intermittent flashes of light which penetrate the canopy due to wind movement of outer canopy leaves) is similar to that of full sun (23). However, in natural shade (caused by the foliage of the tree) there is a greater ratio of near infrared to photosynthetically active radiation (PAR, light in the 400-700 nm region) (23). Proctor (28) observed more infrared and less visible light within an apple canopy as penetration increased from the top to the bottom of the canopy.

Light studies with different types of sour cherry tree canopies have shown that the degree of shading within the canopy differs significantly among the canopy types tested, the 660/730 nm ratio of light decreased with increased shading, and summer hedging caused a pronounced decrease in inner canopy light intensity (11). There is a current trend in the industry toward higher density plantings of sour cherry, where size control is

accomplished by summer hedging (21).

A better understanding of the effects of shade on tree morphology is essential if a scientific basis for designing more efficient tree canopies is to be developed. Therefore, a study was undertaken to evaluate the effects of shade on sour cherry. The objectives were to determine the effects of various levels of shade on leaf and shoot morphology and on the photosynthetic rate of sour cherry. Herein, we report on the effects of shade on the leaf and shoot morphology of sour cherry and relate these effects to current orchard practices.

Materials and Methods

Tree culture. One year old sour cherry trees (Prunus cerasus L. 'Montmorency') on 'Mahaleb' rootstock were grown in 20 l plastic pots in a mixture of peat, loam, and sand (1:2:1). Fertilizer, pesticides (Captan, Plictran, Guthion, Cyprex, and Benlate), and water were added as needed. Trees were grown to the 11-15 leaf stage in full sunlight then transferred to artificial shade treatments for the remainder of the growing season. The leaf just below the terminal bud was tagged to distinguish pre- and post-shade grown leaves. Six weeks after all shoot and leaf growth had ceased (Sept. 1) the plants were evaluated to determine the effects of shading on leaf and shoot morphology. These experiments were conducted in 1978 and

repeated in 1979. Since results were similar between years, only the 1979 data are reported.

Shade treatments and experimental design. Solar radiation was reduced with pipe frame structures (3.7 m x 2.4 m x 1.8 m) covered with black polypropylene shade fabric (A. H. Hummert Co., St. Louis, MO) which transmitted an average of 36, 21, or 9% of PAR (photosynthetically active radiation measured with a LI-COR Model LI 188 Quantum/Radiometer/Photometer). Full solar radiation was obtained by growing trees outside without shading. Structure ventilation prevented temperature differences of greater than $\pm$ 3 C and relative humidity differences greater than $\pm$ 5%. The effect of the shade cloth on the spectral distribution of light was determined with an ISCO Model SR portable spectroradiometer (ISCO, Lincoln, NB). Spectral measurements of full solar radiation through the lightest (36% of full sunlight) and heaviest (9% of full sunlight) shade cloths revealed no apparent changes in spectral distribution within the range of wavelengths tested (Figure 1).

For chlorophyll, specific leaf weight, and leaf thickness evaluations a completely randomized factorial design with four replications was utilized. There were two leaf ages (a leaf expanded pre-shade vs. a leaf expanded post-shade) and four light intensities (100, 36, 21, and 9% of full solar radiation). For all other evaluations a completely randomized design with four replications of each treatment was used.

Figure 1. Spectral distribution of sunlight and sunlight through two densities of black polypropylene shade fabric.

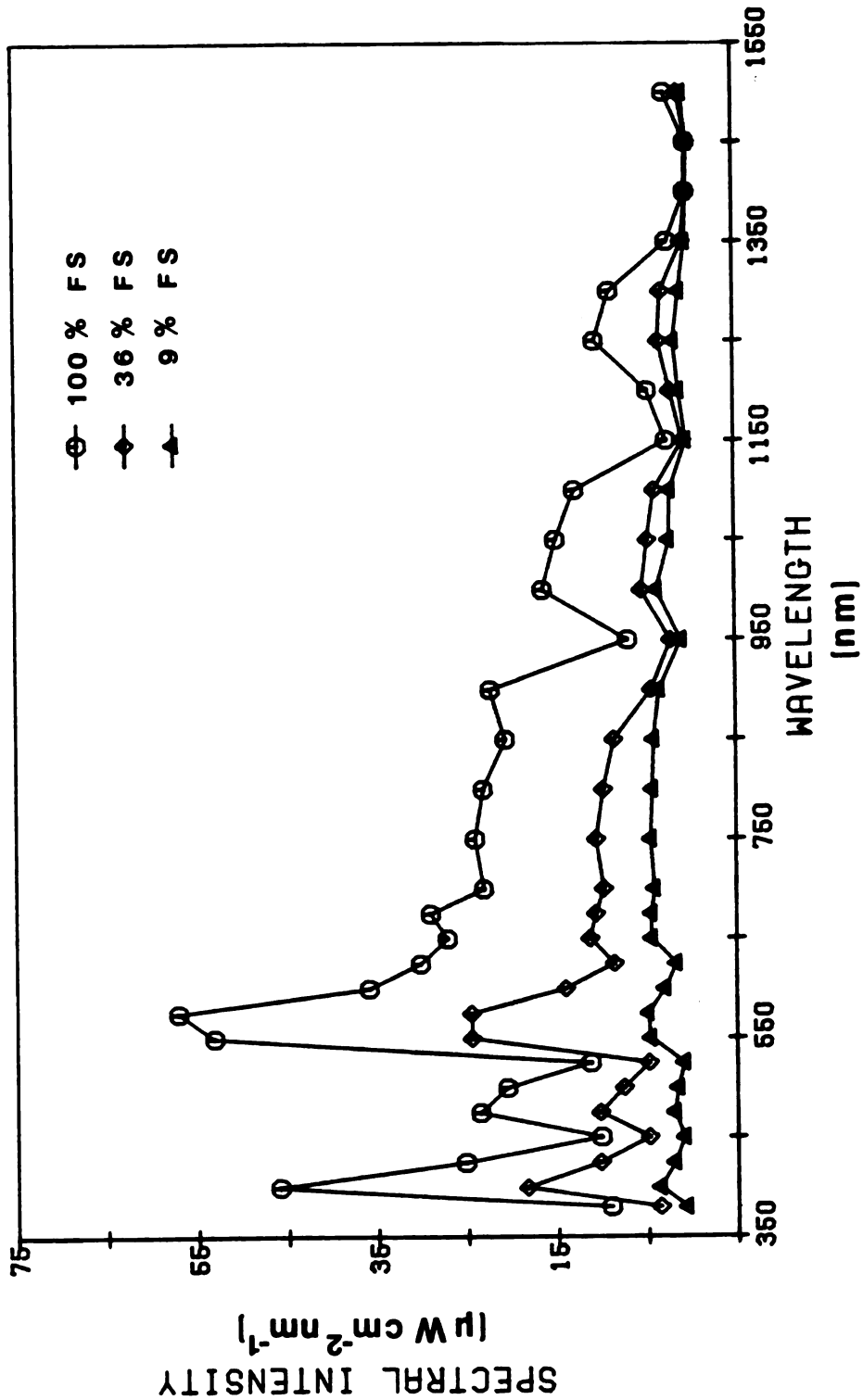
100 % FS
36 % FS
9 % FS
75
55
35
15
350
550
750
950
1150
1350
1550
WAVELENGTH (nm)
SPECTRAL INTENSITY (μW cm⁻² nm⁻¹)

Figure 1

Shoot morphology. Following shade treatment, the length (cm) and diameter (cm) of each shoot were measured. Shoot diameter was measured both at the base and at the point between pre- and post-shade treatments. No lateral shoots were present at the time of shade treatment. The number, length (cm), and base diameter (cm) of lateral shoots were determined for each plant after shade treatment.

Leaf morphology. The number of leaves, average area per leaf, and total leaf area developed both pre- and post-shade were determined for terminal and lateral shoots. Leaf area was determined with a LI-COR Model LI 3000 leaf area meter.

Specific leaf weight, chlorophyll, and leaf anatomy measurements were made for the third leaf on the main shoot above (post-shade) and below (pre-shade) the point where shading was applied. Discs (8.5 mm and 4.0 mm) were cut from the interveinal area of each leaf for chlorophyll measurement and leaf cross sections. After measurement of the remaining leaf area, the leaves were placed in plastic bags, frozen on dry ice, lypholized, and the dry weights were measured. Specific leaf weight (SLW) was calculated as mg leaf dry weight per cm^2 leaf area.

Two leaf discs (8.5 mm diameter) were used for chlorophyll determinations according to the method described by MacKinney (26) as modified by Arnon (1). Smaller leaf discs (4.0 mm diameter) were fixed in FAA (50% ethyl

alcohol, 10% formaldehyde, 5% glacial acetic acid, and 35% water), dehydrated with tertiary butyl alcohol, and infiltrated with paraffin (20). Sections (10 µm) were cut with a rotary microtome, fixed on slides with Weaver's fixer, and stained with safranin-fast green. The number of palisade layers, thickness of the palisade and spongy mesophyll, and total leaf thickness (µm) were estimated by examining five sample sections from each of four replications. Photographs were taken using a Wild M20 research microscope equipped with a 35 mm film carrier and a photoautomat exposure control unit. The average leaf volume (cm^3) was calculated by multiplying the leaf area by the leaf thickness.

Flowering data. At the end of the growing season the plants were removed from the shade structures and placed in a 4 C cooler to fulfill the chilling requirement. The following spring the trees were placed in full sunlight, and the number of flower buds per tree, number of flowers per tree, number of flowers per bud, and the percent fruit set at fruit maturity were recorded.

Results

Shoot growth. Trees grown in full sunlight had greater terminal and lateral shoot diameters than the trees grown in 9% of full sunlight (Table 1). Average lateral internode length was significantly greater for trees grown

Table 1. The effect of different light intensities on the diameter of shoots from 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Terminal shoot[z] diameter at point of shading (cm)	Terminal shoot diameter at base (cm)	Lateral shoot diameter at base (cm)
100	.55 a[y]	1.29 a	.38 a
36	.44 ab	1.00 ab	.34 ab
21	.45 ab	1.18 ab	.34 ab
9	.35 b	.95 b	.26 b

[z]Trees placed under artificial shade when in the 11-15 leaf stage, and measurements determined 6 weeks after terminal set.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

under 21% of full sunlight (Table 2). There were no statistically significant differences among treatments for length of terminal of lateral shoots, number of lateral shoots, internode length of terminal shoots, or total shoot growth per tree. However, there was a general trend for an increase in these growth parameters as percent sunlight decreased to 21%, followed by a slight decrease as light was further reduced to 9% of full sunlight.

Leaf number and area. There were no significant differences among treatments for number of leaves per terminal shoot, number of leaves on lateral shoots, total leaf area on terminal shoots, total leaf area on lateral shoots, or total leaf area per tree. However, average leaf area on terminal shoots for trees grown in 21% of full sunlight was significantly greater than for trees grown under full sunlight (Table 3).

Specific leaf weight. Specific leaf weight was greater for leaves from trees grown in full sunlight than for leaves from trees grown under all shade treatments, regardless of pre- or post-shade expansion (Table 4). Specific leaf weight of leaves expanded pre-shade was not significantly different from the specific leaf weight of leaves which expanded post-shade. There was no significant interaction between shade level and time of leaf expansion.

Chlorophyll determination. Chlorophyll A, chlorophyll B, and total chlorophyll contents were determined

Table 2. The effect of different light intensities on shoot development of 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Terminal		Laterals				Total
	Shoot[z] length (cm)	Average internode length (cm)	Shoots per tree (No.)	Total length all shoots (cm)	Average internode length (cm)	Average shoot length (cm)	Shoot growth per tree (cm)
100	23.0 a[y]	2.4 a	7.3 a	111.7 a	2.2 b	15.3 a	134.9 a
36	22.6 a	2.7 a	9.5 a	208.1 a	2.7 ab	21.9 a	230.6 a
21	25.3 a	3.1 a	9.3 a	201.8 a	2.8 a	21.7 a	227.0 a
9	22.1 a	2.5 a	8.8 a	183.9 a	2.6 ab	20.9 a	205.6 a

[z]Trees placed under artificial shade when in the 11-15 leaf stage, and measurements determined 6 weeks after terminal set.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

Table 3. The effect of different light intensities on leaf development of 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Terminal			Laterals			Total
	Leaves[z] (No./shoot)	Average leaf area (cm^2/leaf)	Total leaf area (cm^2/shoot)	Leaves (total No.)	Average leaf area (cm^2/leaf)	Total leaf area all shoots (cm^2)	Total leaf area per tree (cm^2)
100	9.8 a[y]	29.9 b	293.0 a	49.8 a	16.4 a	816.7 a	1109.7 a
36	8.3 a	27.9 b	231.6 a	77.5 a	17.0 a	1317.5 a	1549.1 a
21	8.3 a	39.0 a	323.7 a	71.3 a	19.2 a	1369.0 a	1692.7 a
9	8.8 a	32.3 ab	284.2 a	69.0 a	17.9 a	1235.1 a	1519.3 a

[z]Trees placed under artificial shade when in the 11-15 leaf stage, and measurements determined 6 weeks after terminal set.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

Table 4. The effect of different light intensities on the specific leaf weight of leaves from 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Specific leaf weight (mg/cm^2)	
	Pre-shade[z]	Post-shade
100	13.7 a[y]	12.6 a
36	9.9 b	8.8 b
21	9.3 b	8.1 b
9	8.0 b	5.6 c

[z]Trees placed under artificial shade when in the 11-15 leaf stage, and measurements determined 6 weeks after terminal set.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

and expressed as mg/dm^2 leaf area, mg/g leaf dry weight, and mg/cm^3 leaf volume (Tables 5-7). There was no significant difference between pre- or post-shade leaves or among shade treatments for chlorophyll A, chlorophyll B, or total chlorophyll when expressed as mg/dm^2 leaf area. However, all chlorophyll measurements were significantly greater for plants grown under 9% of full sunlight when expressed as mg/g leaf dry weight or mg/cm^3 leaf volume. The ratio of chlorophyll A to chlorophyll B in post-shade leaves was similar for all shade levels (Table 8). Pre-shade leaves grown in full sunlight had a higher A to B ratio than leaves grown in 36 or 21% of full sunlight.

Leaf anatomy. The thickness of the palisade and spongy mesophyll cell layers and total leaf thickness was greater for leaves grown in full sunlight than for leaves grown in 36, 21, or 9% of full sunlight regardless of pre- or post-shade expansion (Table 9). The spongy mesophyll of leaves grown under shade was less dense, and there were fewer palisade layers in these leaves (Figure 2). The leaves grown under full sunlight had at least three layers of palisade cells, while leaves grown in 9% of full sunlight had as few as one layer. Leaf volume was not significantly different among shade treatments for either pre- or post-shade leaves (Table 10).

Flowering data. Plants grown in full sunlight had a greater number of flowers per tree and a greater number of flower buds per tree than plants grown in 36, 21, or

Table 5. The effect of different light intensities on chlorophyll A content of leaves from 'Montmorency' cherry trees grown under artificial shade expressed as amount per unit leaf area, per unit leaf dry weight, and per unit leaf volume.

Sunlight (%)	Pre-shade[z]			Post-shade		
	Leaf area (mg/dm^2)	Dry weight (mg/g)	Leaf volume (mg/cm^3)	Leaf area (mg/dm^2)	Dry weight (mg/g)	Leaf volume (mg/cm^3)
100	5.6 a[y]	4.1 b	1.6 b	4.5 a	3.7 c	1.5 b
36	3.6 a	3.6 b	1.4 b	4.3 a	4.9 bc	2.0 b
21	3.3 a	3.5 b	1.3 b	4.0 a	4.9 b	1.9 b
9	4.9 a	6.4 a	2.3 a	4.8 a	8.5 a	3.2 a

[z]Trees placed under artificial shade when in the 11-15 leaf stage, and measurements determined 6 weeks after terminal set.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

Table 6. The effect of different light intensities on chlorophyll B content of leaves from 'Montmorency' cherry trees grown under artificial shade expressed as amount per unit leaf area, per unit leaf dry weight, and per unit leaf volume.

Sunlight (%)	Pre-shade[z]			Post-shade		
	Leaf area (mg/dm^2)	Dry weight (mg/g)	Leaf volume (mg/cm^3)	Leaf area (mg/dm^2)	Dry weight (mg/g)	Leaf volume (mg/cm^3)
100	3.0 a[y]	2.2 b	0.9 b	3.6 a	3.0 b	1.3 b
36	3.8 a	3.9 a	1.5 a	3.4 a	4.0 a	1.6 a
21	4.2 a	4.5 a	1.7 a	3.2 a	3.9 a	1.5 a
9	3.3 a	4.2 a	1.5 a	2.5 a	4.4 a	1.6 a

[z]Trees placed under artificial shade when in the 11-15 leaf stage, and measurements determined 6 weeks after terminal set.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

Table 7. The effect of different light intensities on total chlorophyll content of leaves from 'Montmorency' cherry trees grown under artificial shade expressed as amount per unit leaf area, per unit leaf dry weight, and per unit leaf volume.

Sunlight (%)	Pre-shade[z]			Post-shade		
	Leaf area (mg/dm^2)	Dry weight (mg/g)	Leaf volume (mg/cm^3)	Leaf area (mg/dm^2)	Dry weight (mg/g)	Leaf volume (mg/cm^3)
100	8.6 a[y]	6.3 c	2.5 b	8.1 a	6.7 c	2.8 b
36	7.5 a	7.5 bc	2.8 b	7.7 a	8.9 b	3.6 b
21	7.5 a	8.0 b	3.0 b	7.2 a	9.0 b	3.3 b
9	8.2 a	10.6 a	3.7 a	7.3 a	12.9 a	4.9 a

[z]Trees placed under artificial shade when in the 11-15 leaf stage, and measurements determined 6 weeks after terminal set.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

Table 8. The effect of different light intensities on the ratio of chlorophyll A to B for leaves from 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Pre-shade[z]	Post-shade
100	1.99 a[y]	1.38 a
36	1.08 b	1.39 a
21	0.81 b	1.34 a
9	1.58 ab	1.96 a

[z]Trees placed under artificial shade when in the 11-15 leaf stage, and measurements determined 6 weeks after terminal set.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

Table 9. The effect of different light intensities on the cross section thickness of leaves from 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Pre-shade[z]			Post-shade		
	Palisade thickness (µm)	Spongy mesophyll thickness (µm)	Leaf thickness (µm)	Palisade thickness (µm)	Spongy mesophyll thickness (µm)	Leaf thickness (µm)
100	181.0 a[y]	120.0 a	343.8 a	163.0 a	105.0 a	307.8 a
36	126.3 b	58.3 b	261.5 b	102.8 b	69.8 b	216.8 b
21	122.5 b	87.8 b	252.3 b	102.3 b	77.5 b	219.0 b
9	106.0 b	84.5 b	225.5 b	63.3 c	55.3 b	149.5 c

[z]Trees placed under artificial shade when in the 11-15 leaf stage, and measurements determined 6 weeks after terminal set.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

Figure 2. Cross sections of 'Montmorency' cherry leaves which expanded prior to (pre-shade) or after (post-shade) being placed under artificial shade.

A. Leaf expanded pre-shade, 100% full sunlight treatment.

B. Leaf expanded post-shade, 100% full sunlight treatment.

C. Leaf expanded pre-shade, 36% full sunlight treatment.

D. Leaf expanded post-shade, 36% full sunlight treatment.

E. Leaf expanded pre-shade, 21% full sunlight treatment.

F. Leaf expanded post-shade, 21% full sunlight treatment.

G. Leaf expanded pre-shade, 9% full sunlight treatment.

H. Leaf expanded post-shade, 9% full sunlight treatment.

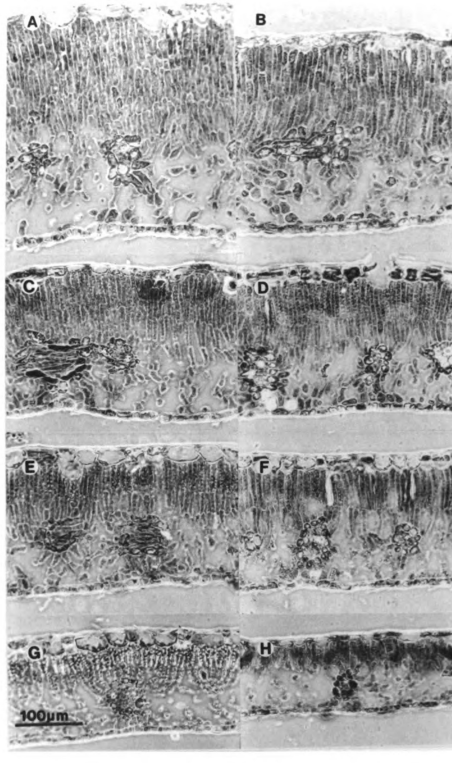

Figure 2

Table 10. The effect of different light intensities on the leaf volume of leaves from 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Leaf volume (cm^3)	
	Pre-shade[z]	Post-shade
100	1.3 a[y]	0.6 a
36	0.8 a	0.6 a
21	0.8 a	0.6 a
9	0.8 a	0.4 a

[z]Trees placed under artificial shade when in the 11-15 leaf stage, and measurements determined 6 weeks after terminal set.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

9% of full sunlight (Table 11). The number of flowers per bud was not significantly different between the 100 and 36% of full sunlight treatments. Plants in the 21 and 9% of full sunlight treatments had no flowers present. The percent fruit set was not significantly different between the 100 and 36% of full sunlight treatments.

Discussion

Levels of shading (36, 21, and 9% of full sunlight) were selected to simulate light intensities found inside cherry tree canopies when grown under commercial conditions. Light intensity within the fruit bearing surface of a cherry tree may be as low as 10-25% of full sunlight, depending on the canopy structure (11). Canopy closure has been shown to be rapid for sour cherry (11). Therefore, trees were grown in full sunlight for part of the growing season and transferred to shade for the remainder of the season to simulate leaves at the base of the shoot (which expand in full sunlight) being shaded by leaves developing later in the season.

Previous reports for cherry and apple trees have indicated that shading either did not affect shoot length or resulted in smaller increases in length (3, 29). Jackson and Palmer (17), however, reported that shading to 37, 25, and 11% of full sunlight resulted in longer shoot length for apple. Our data show an increasing trend

Table 11. The effect of different light intensities on flower development and fruit set of 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Flower buds[z] per tree (No.)	Flowers per tree (No.)	Flowers per bud (No.)	Fruit Set (%)
100	10.2 a[y]	28.8 a	2.8 a	20.5 a
36	1.8 b	3.8 b	2.1 a	18.2 a
21	0.0 c	0.0 c	0.0 b	0.0 b
9	0.0 c	0.0 c	0.0 b	0.0 b

[z]Artificial shade was imposed from the 11-15 leaf stage until 6 weeks after terminal set, and flower development was determined the following spring.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

with decreasing light intensity for all growth parameters. Further, for each parameter the value at 9% of full sunlight was less than the value at either 36 or 21%. These findings indicate a tendency for an increase in shoot length under moderate to heavy shade then a decrease under severe shade. Average internode length of lateral shoots displayed the same tendency, with the length for trees grown under 21% of full sunlight being significantly longer than the length for trees grown in full sunlight (Table 2).

Smaller shoot diameters have been reported for apple trees grown under shade (17). We found that the terminal shoot diameter at the point of shading and average lateral shoot diameter at the base were significantly greater for trees grown in full sunlight than for trees grown in 9% of full sunlight (Table 1). The trend appears to be toward the development of longer and smaller diameter shoots under shade than in full sunlight. Perhaps this occurrence could be attributed to less carbohydrate being produced under shade conditions, resulting in a higher ratio of nitrogen to carbohydrate and increased cell elongation. A reduction in total sugars and dry matter accumulation in cherry trees grown under heavy shade has been reported (13). Maximum terminal growth of cherry has been shown to occur at higher levels of nitrogen than maximum dry weight increases (29). The decreasing trend in shoot growth under severe shade (9%) could result when

the photosynthetic rate is so low that not enough energy is produced to maintain growth (even cell elongation).

Heavy shade has been reported to decrease leaf number and total leaf area (27), to have no effect on leaf number and total leaf area (3), and to increase the total leaf area (14) of apple. We found that the average leaf area on the terminal shoot was significantly greater for trees grown under 21% of full sunlight than for those grown in full sunlight (Table 3). Average leaf area on terminals and laterals, number of leaves on laterals, total leaf area on terminals and laterals, and total leaf area per tree showed an increasing tendency with decreasing light intensity similar to the increase in shoot growth.

Specific leaf weight tended to decrease as the percent shade increased. Similar decreases in specific leaf weight for leaves developed in shade have been reported for apple (3). Leaves developed under full sunlight had thicker palisade and spongy mesophyll layers and greater total leaf thickness than leaves developed in shade. This decrease in leaf thickness and change in leaf structure is characteristic of plants grown in heavy shade (5, 8, 17, 24). Cherry leaves grown in shade had fewer palisade layers, and the spongy mesophyll appeared to be less dense with smaller cells (Figure 2). Shade leaves are typically thinner and have smaller spongy mesophyll cells and less mesophyll surface area, resulting in reduced mesophyll conductance when compared to sun leaves (5).

Although leaf volume was not statistically different among treatments, leaves grown in full sun tended to have greater leaf volumes than those grown in shade. Thus, the leaves from plants grown in shade appear to be larger due to greater surface area, but the actual leaf volume is smaller.

Leaves from trees grown in 9% of full sunlight were found to have a significantly greater content of chlorophyll A, chlorophyll B, and total chlorophyll than those grown in full sunlight when the chlorophyll content is expressed as mg/g leaf dry weight or mg/cm^3 leaf volume (Tables 5-7). When expressed as mg/dm^2 leaf area, there was no significant difference in chlorophyll content of leaves grown at different light intensities. Light intensity has been reported to have similar effects on the chlorophyll content of other species (5, 7, 8). These findings are consistent with the fact that shade leaves were thinner, had lower specific leaf weights, and had smaller leaf volumes than leaves grown in full sunlight.

Leaves grown in shade have been reported to have fewer chloroplasts, but the chloroplasts are usually larger and contain more chlorophyll (5). Boardman (5) has reported that the increase in size of the chloroplast and amount of chlorophyll per chloroplast is are offset by a decrease in number of chloroplasts per unit of leaf surface.

The ratio of chlorophyll A to chlorophyll B in

post-shade leaves tended to be greater for leaves grown under severe shade (9% of full sunlight) than for leaves grown in full sunlight. This finding does not agree with reports for some species in which the ratio of chlorophyll A to B was lower at lower light intensities than at high light intensities (7, 8, 12, 25). The chlorophyll content of pre-shade leaves was greater for leaves grown under heavy shade than for those grown in full sunlight. This occurrence indicates that cherry leaves can adapt to light intensity changes after they have expanded as has been suggested for other species (5).

Trees grown in full sunlight had more flowers per tree and more total flower buds per tree the following spring than trees grown in shade (Table 10). The number of flowers per bud and the percent fruit set was not different between treatments with flowers present. Trees grown in light intensities less than 36% of sull sunlight had no flowering the following year. Decreases in the number of flower buds by shading during the previous year are well documented (18). Although it is obvious that shading has a pronounced effect on flower formation in cherry, additional studies are needed to determine the critical levels of light required for flowering in mature cherry trees grown under commercial conditions and to determine the critical periods during the growing season when light is required.

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SECTION IV

THE EFFECTS OF ARTIFICIAL SHADE ON THE LEAF PHOTOSYNTHETIC RATE OF SOUR CHERRY (PRUNUS CERASUS L. 'MONTMORENCY')

Abstract. Sour cherry trees were grown in full sunlight to the 11-15 leaf stage then shaded to establish 100, 36, 21, and 9% of full sunlight treatments. The effects of shade on leaves which expanded before and after shade application were determined. At 1200 and 2000 $\mu E\ m^{-2}\ s^{-1}$ light intensities the photosynthetic rates of leaves on trees grown in full sunlight were greater (50-150%) than those of leaves grown in 9% of full sunlight. Also, photosynthetic rates of leaves which expanded before shading were higher (70%) than those of leaves which expanded after shading when grown in 9% of full sunlight. However, at low light intensity (320 $\mu E\ m^{-2}\ s^{-1}$) photosynthetic rate was not significantly different among leaves from trees grown in 100, 36, 21, or 9% of full sunlight. Maximum net photosynthetic rate for leaves from trees grown under 9% of full sunlight occurred at lower light intensities than leaves grown in full sunlight. Net photosynthetic rate was greater (25-170%) at 25 C than at 10 or 40 C for leaves grown in full sunlight and in 9% of full sunlight. Net photosynthetic rate at 25 C was greater (47%) for

leaves grown in full sunlight than for leaves grown in 9% of full sunlight.

The effects of shading on the photosynthetic rates of many species have been examined (1, 3, 16, 18, 23). In general, plants grown in shade have higher net photosynthetic rates at low light intensities but lower maximum photosynthetic rates at high light intensities (3). However, Barden (2) has reported that although shade grown leaves of apple had lower photosynthetic rates at high light intensities, the photosynthetic rates at low irradiance were similar for sun and shade grown leaves.

Photosynthetic rates of many types of fruit trees increase with increasing light intensity in a hyperbolic pattern characteristic of most C_3 plants (5, 12, 14). Photosynthetic light response curves for cherry have been reported, with maximum net photosynthetic rates occurring between 800-1400 $\mu E\ m^{-2}\ s^{-1}$ of photosynthetically active radiation (PAR, radiation in the 400-700 nm range) (21). If shading decreased light intensity below this level, a reduction in photosynthesis would result.

Light distribution and penetration patterns of apple have been studied, and it has been reported that interior leaves receive lower light intensities than leaves of the outer canopy (7, 8, 10, 15, 17). Studies have also shown that similar light relations exist in sour cherry canopies (6).

Heinicke (9) hypothesized that daily photosynthetic rate could be calculated if the percent full sunlight received by a leaf and the rate of photosynthesis of a generalized leaf at a given light level were known. Barden (1) has suggested that this hypothesis is an oversimplification, and that to accurately estimate the photosynthetic potential of a leaf requires knowledge of the previous history of the leaf in regard to environmental conditions. We have previously demonstrated that the leaf morphology of sour cherry can be influenced by the light intensity under which the leaf develops and by the light intensity received by the leaf after it has expanded (22).

Predictions of whole canopy photosynthetic potential and the photosynthetic potential of various leaf types within the canopy would be useful in designing more efficient and productive orchards. However, if more efficient orchards are to be designed, increased knowledge of the influence of environmental factors on photosynthesis as well as methods of modifying tree canopy and orchard design to establish desirable environmental conditions is needed. Therefore, experiments were designed to determine the effects of shading on the photosynthetic rate of 'Montmorency' cherry leaves.

Materials and Methods

Tree culture. One year old sour cherry trees (Prunus cerasus L. 'Montmorency') on 'Mahaleb' rootstock were grown in 20 l plastic pots in a mixture of peat, loam, and sand (1:2:1). Fertilizer, pesticides (Captan, Plictran, Cyprex, Benlate, and Guthion), and water were added as needed. Trees were grown to the 11-15 leaf stage in full sunlight then transferred to artificial shade treatments for the remainder of the growing season. Six weeks after all shoot and leaf growth had ceased (Sept. 1), the plants were evaluated to determine the effects of shading on photosynthetic rate. This study was conducted in 1978 and repeated in 1979. Since results were similar, only the 1979 data will be reported.

Shade treatment and experimental design. Solar radiation was reduced with pipe frame strctures (3.7 m x 2.4 m x 1.8 m) covered with black polypropylene shade fabric (A. H. Hummert Co., St. Louis, MO) which transmitted an average of 36, 21, or 9% of PAR (photosynthetically active radiation, measured with a LI-COR Model LI 188 Integrating Quantum/Radiometer/Photometer). Full solar radiation was obtained by growing trees outside without shading. Structure ventilation prevented temperature differences greater than $\pm$ 3 C and relative humidity differences greater than $\pm$ 5%. The shade cloth decreased light intensity without affecting light quality (22). Unless

otherwise indicated, all experiments were completely randomized with four replications.

Photosynthesis determinations. Shoot terminals were marked at the time the trees were transferred to the shade treatments. Both the third leaf above (post-shade) and below (pre-shade) the marked point were used for photosynthetic rate determinations. Where indicated, gross photosynthetic rate and stomatal resistance of intact leaves were determined with a ventilated diffusion porometer (Model VP-1, Cayuga Development, Ithica, NY) using the method described by Peet et al. (19). The porometer contained a lithium chloride humidity sensor which allowed measurement of stomatal resistance while exposing the abaxial surface of the leaf (1 cm^2) to $^{14}CO_2$ (9.7 µl/l, 330 ppm CO_2, 21% O_2, 14 ml) for 30 s. Immediately after pulsing, the exposed area was excised with a No. 11 cork bore and placed in a scintillation vial containing 0.5 ml of Protosol (New England Nuclear) and was allowed to digest 48 hr. Samples were bleached with 1.0 ml of benzoyl peroxide in toluene (5 g in 30 ml). After 24 hr, 15 ml of scintillation fluid (5 g PPO/l of toluene) was added and radioactivity was determined with a Beckman LS 100 Liquid Scintillation Spectrometer. Corrections were made for background and quenching, and gross photosynthetic rate was calculated as mg CO_2 dm^{-2} hr^{-1} using leaf disc area, exposure time, radioactivity, and specific activity of CO_2. Gross photosynthetic measurements were made outside

in natural sunlight at a temperature between 28-30 C and at low (320 $\mu E\ m^{-2}\ s^{-1}$) and high (2000 $\mu E\ m^{-2}\ s^{-1}$) light intensities.

Net photosynthetic rate determination. Net photosynthetic rate (Pn) was determined in the laboratory using intact leaves placed in environmentally controlled leaf chambers. Unless otherwise indicated, environmental conditions were maintained at 25 $\pm$ .5 C, 85-95% relative humidity, and PAR (photosynthetically active radiation, radiation in the 400-700 nm wavelength region) at 1200 $\mu E\ m^{-2}\ s^{-1}$. A differential open gas analysis system was used as previously described (21). Pn was calculated as the amount of CO_2 fixed (mg) per unit leaf area (dm^2) in one hour.

Temperature study. Terminal leaves which were fully expanded after initiation of the shade treatment were used for the temperature study. Net photosynthetic rates of intact leaves on trees from the 100 and 9% of full sunlight treatments were determined at temperatures of 10, 25, and 40 C, 85-95% relative humidity, and PAR of 1200 $\mu E\ m^{-2}\ s^{-1}$.

Light response curves. Terminal leaves which expanded after initiation of the shade treatment were used for the light response curves. Pn was determined for intact leaves on trees from all shade treatments (100, 36, 21, and 9% of full sunlight) at PAR levels between 0 and 2000 $\mu E\ m^{-2}\ s^{-1}$, a temperature between 25 $\pm$ .5 C, and 85-95%

relative humidity. Asymptotic curves were fit to the data as previously described (21).

Results

$^{14}CO_2$ determination of gross photosynthetic rate.

There was no significant difference in gross photosynthetic rate (Ps) or stomatal resistance among leaves from trees grown under 100, 36, 21, or 9% of full sunlight or between leaves which expanded pre- or post-shade when determined at low light intensities (PAR 320 μE m^{-2} s^{-1}) (Table 1), and there was no interaction between time of leaf expansion and shade treatment. At high levels of PAR (2000 μE m^{-2} s^{-1}) there was no significant difference between leaves which expanded pre- and post-shade, and there was no interaction between time of leaf expansion and shade treatment (Table 2). However, leaves grown in full sunlight had a higher Ps and a higher stomatal resistance than leaves grown in 9% of full sunlight whether the leaf expanded pre- or post-shade (Table 2).

Net photosynthetic rate determination. Both pre- and post-shade leaves which were grown in full sunlight had significantly greater net photosynthetic rates than leaves grown in 9% of full sunlight (Table 3). At a PAR level of 1200 μE m^{-2} s^{-1} there was a decreasing trend in net photosynthetic rate with increasing shade for both pre- and post-shade leaves. Pre-shade leaves did not

Table 1. Gross photosynthetic rate and stomatal resistance of leaves from 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Pre-shade		Post-shade	
	Ps[z] ($mg\ CO_2\ dm^{-2}\ hr^{-1}$)	Stomatal resistance (s/cm)	Ps ($mg\ CO_2\ dm^{-2}\ hr^{-1}$)	Stomatal resistance (s/cm)
100	9.6 a[y]	1.7 a	10.8 a	1.4 a
36	8.5 a	1.4 a	12.1 a	1.5 a
21	9.4 a	1.1 a	9.7 a	1.6 a
9	10.0 a	1.7 a	7.6 a	1.4 a

[z]Determined by $^{14}CO_2$ pulsing technique, 320 $\mu E\ m^{-2}\ s^{-1}$ light intensity and temperature 28-30 C.

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

Table 2. Gross photosynthetic rate and stomatal resistance of leaves from 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Pre-shade		Post-shade	
	Ps[z] (mg CO_2 dm^{-2} hr^{-1})	Stomatal resistance (s/cm)	Ps (mg CO_2 dm^{-2} hr^{-1})	Stomatal resistance (s/cm)
100	15.9 a[y]	1.2 a	15.3 a	1.4 a
9	10.2 b	0.7 b	5.9 c	0.8 b

[z]Determined by $^{14}CO_2$ pulsing technique, 2000 µE m^{-2} s^{-1} light intensity and temperature 28-30 C.

[y]Mean separation calculated independently for Ps and stomatal resistance by Duncan's multiple range test, 5% level.

Table 3. Net photosynthetic rate of leaves from 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Pn^z (mg CO_2 dm^{-2} hr^{-1})	
	Pre-shade	Post-shade
100	22.2 a[y]	22.4 a
36	18.8 ab	16.7 ab
21	15.1 b	13.7 bc
9	13.6 b	8.0 c

[z]Determined by differential infrared gas analysis under constant conditions (1200 µE m^{-2} s^{-1} light intensity, temperature 25 C, and 85-95% relative humidity).

[y]Mean separation within columns by Duncan's multiple range test, 5% level.

differ significantly from post-shade leaves, and there was no interaction between time of leaf expansion and shade treatment.

Temperature study. Leaves from trees grown in full sunlight had greater net photosynthetic rates than leaves from trees grown in 9% of full sunlight at 10, 25, and 40 C (Table 4). Pn was greater at 25 C than at either 10 or 40 C for leaves from trees grown at both 100 and 9% of full sunlight.

Light response curves. Maximum Pn occurred between 400-1000 $\mu E\ m^{-2}\ s^{-1}$ for all treatments. Leaves from trees grown under full sunlight reached maximum Pn at higher levels of PAR than those grown under 9% of full sunlight (Figure 1). Maximum Pn was greater for leaves from trees grown under full sunlight than for those grown under shade. The initial increase in Pn with increasing light intensity was greater for leaves from trees grown in full sunlight than for those grown in shade. The best fit asymptotic equation was determined for each light response curve, and predictions of maximum net photosynthesis were obtained from these equations (Table 5).

Discussion

It is generally believed that sun grown leaves are less efficient under low light intensity than shade grown leaves (3, 4). However, the Ps and stomatal resistance

Table 4. The effect of temperature on net photosynthetic rate of leaves from 'Montmorency' cherry trees grown under artificial shade.

Sunlight (%)	Pn^z (mg CO_2 dm^{-2} hr^{-1})		
	Temperature (C)		
	10	25	40
100	17.72 b[y]	22.15 a	14.37 c
9	10.27 d	15.06 c	5.51 e

[z]Determined by differential infrared gas analysis under constant conditions (1200 µE m^{-2} s^{-1} light intensity, temperature 25 C, and 85-95% relative humidity).

[y]Mean separation by Duncan's multiple range test, 5% level.

Figure 1. Light response curves of leaves from 'Montmorency' cherry trees grown at different light intensities under artificial shade. Each symbol represents the average of three replications.

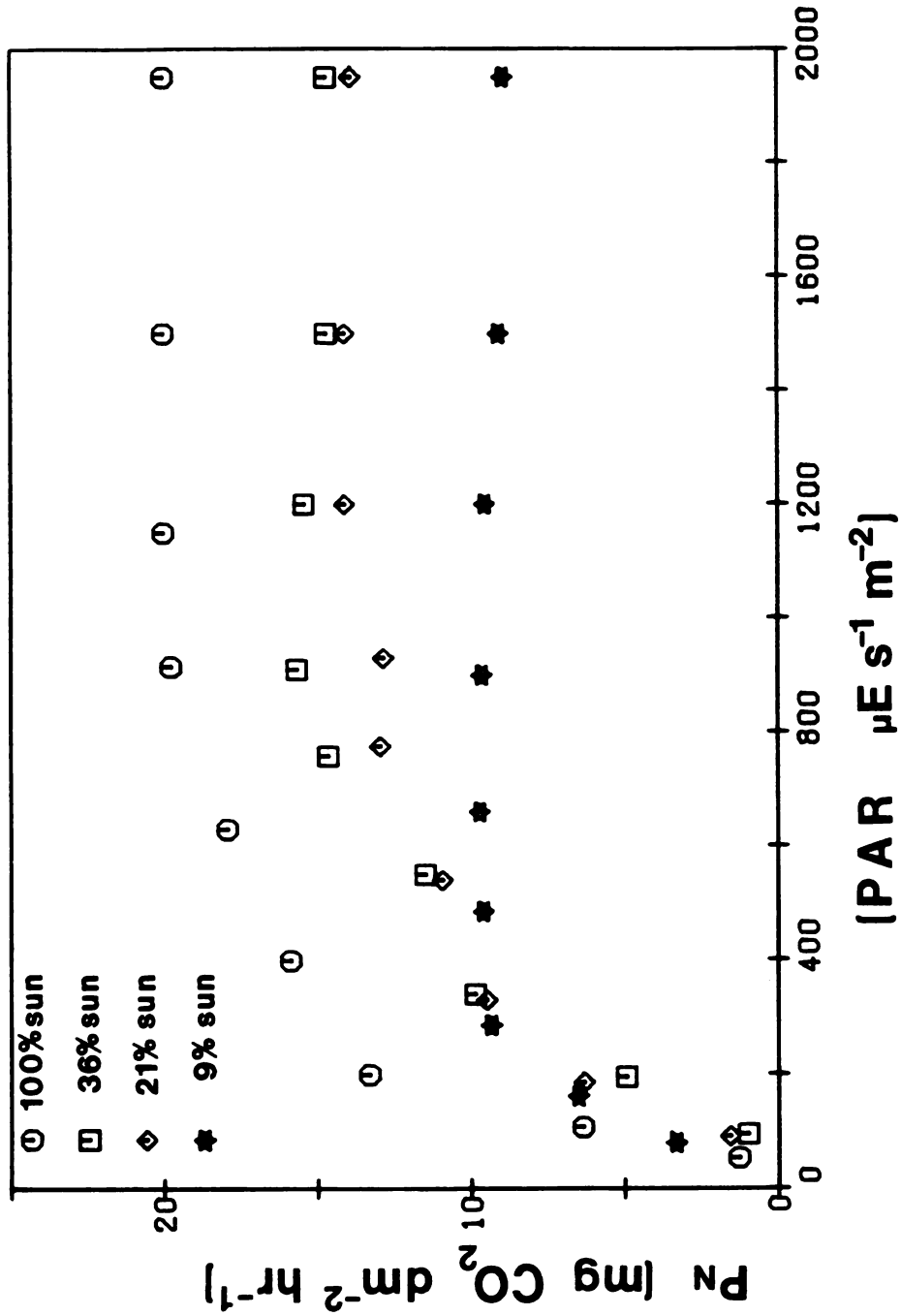
100% sun
36% sun
21% sun
9% sun
0
400
800
1200
1600
2000
[PAR μE s-1 m-2]
0
10
20
PN [mg CO2 dm-2 hr-1]

Figure 1

Table 5. The effect of different light intensities on maximum net photosynthetic rate as predicted from asymptotic equations of light response curves for 'Montmorency' cherry leaves grown under artificial shade.

Sunlight (%)	Best fit asymptotic equation	Predicted maximum Pn (mg CO_2 dm^{-2} hr^{-1})
100	$19.6 - 24.8(.994)^x$	19.6
36	$15.3 - 20.6(.996)^x$	15.3
21	$13.9 - 16.9(.996)^x$	13.9
9	$9.5 - 14.9(.989)^x$	9.5

of sour cherry were not significantly different among leaves grown under 100, 36, 21, and 9% of full sunlight when measured under low (320 μE m^{-2} s^{-1}) light intensity (Table 1). Similar results have been reported for other species (2, 16).

At higher light intensities (1200 and 2000 μE m^{-2} s^{-1}) the photosynthetic rate and stomatal resistance of leaves on trees grown in full sunlight were greater than those of leaves on trees grown in 9% of full sunlight (Tables 2-3). Also, the photosynthetic rates of leaves from the 9% of full sunlight treatment were higher for leaves which expanded pre-shade than for those which expanded post-shade when measured under the higher light intensities. This finding indicates that the shading did not affect the photosynthetic capacity of leaves which developed under full sunlight as much as those which developed under shade. However, the photosynthetic capacity of both pre- and post-shade leaves from the 9% of full sunlight treatment was less than that of leaves from the full sunlight treatment. It has been suggested that anatomical changes are restricted to expanding leaves (3), but that leaves can adapt to light after leaf expansion has ceased due to factors other than basic structural changes (1, 3). The data presented here indicate that heavy shade did decrease the photosynthetic capacity of leaves which expanded in full sun, but that the effect

of the shading was more pronounced on those leaves which expanded under heavy shade.

Sour cherry spur leaves and the lower leaves on terminal shoots complete expansion early in the season and are soon shaded by terminal leaves which develop later in the season (6). The degree of shading depends on the canopy structure. We found the maximum photosynthetic rate to be lower for leaves which expanded in shade than for those which expanded in full sunlight (Figure 1), but Pn increases with increasing light intensity for all the leaves. Similar results have been reported for other species (3, 16). More specifically, our data indicate that the photosynthetic rate of a sour cherry leaf which has been shaded increases as light intensity increases to 500-800 $\mu E\ m^{-2}\ s^{-1}$ then reaches a maximum (Figure 1). Thus, the photosynthetic rates of inner canopy leaves may be limited when light is severely reduced by shading. Summer hedging (removal of part of the terminal shoots which lets more light into the canopy) is becoming a common commercial practice in sour cherry production (11). This practice may lead to increased photosynthetic rates of inner canopy leaves which have been shaded.

Pn was greatest at 25 C for leaves from plants grown in full sunlight and 9% full sunlight (Table 4). Both leaf types had lower Pn at 10 and 40 C. The Pn at optimum temperature was greater for leaves grown in full sunlight than for those grown in 9% of full sunlight.

However, the response of leaves grown in 9% of full sunlight to temperature changes was similar to that of leaves grown in full sunlight. This temperature response may be commercially important if the temperature environment of inner canopy leaves is changed by summer hedging. Summer hedging removes the outer canopy leaves which shade inner canopy leaves from direct sunlight and reduce air movement inside the canopy. It has been suggested that the leaf temperature of some species may exceed the temperature of the surrounding air by as much as 21 C under conditions of high insolation and zero wind speed (20). It also appears that if leaves have been growing in a favorable light environment, they can maintain higher photosynthetic rates at suboptimal temperatures than leaves which have developed in heavy shade.

The data presented indicate that even leaves which have been growing under heavy shade (similar to inner canopy environment) retain the ability to utilize higher light intensities (as could be obtained by summer hedging) for increased photosynthesis. Kriedemann *et al.* (13) has indicated that the photosynthetic rate of inner canopy grape leaves can be increased by intermittent flashes of light (sunflecks) which penetrate the canopy due to wind movement of the outer canopy leaves. The ability of the inner canopy leaves to benefit from sunflecks and respond to the continual fluctuations in light intensity, temperature, CO_2 concentration, and humidity within the canopy

are important factors which affect the photosynthetic rates of sour cherry leaves. Accurate estimates of the photosynthetic potential of sour cherry leaves will require knowledge of these factors as well as the previous history of the leaf as suggested by Barden (1). The maximum Pn of sour cherry leaves grown in shade is lower than the Pn of those grown in full sunlight, but even leaves grown in severe shade do not reach maximum Pn until light intensity is 400-800 $\mu E\ m^{-2}\ s^{-1}$ (Figure 1). Light intensity inside some sour cherry canopies is not this high (6). Sour cherry leaves which expand in full sunlight and are then shaded have lower maximum Pn than leaves which are not shaded after expansion (Tables 2-3). Thus, any cultural practice which leads to better light penetration into cherry canopies might increase the photosynthetic potential of sour cherry leaves.

Many factors remain to be evaluated before final conclusions about the effects of shading can be applied to commercial situations. Is Pn limiting yield, which leaves contribute most to fruit growth, what types of translocation patterns exist in sour cherry, and how many leaves are required for continued fruit and vegetative growth are among the many questions which remain to be answered.

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