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Photosynthetic Compensation to Partial Leaf Area Reduction in Sour Cherry

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Abstract. The leaf surface area of l-year-old, potted 'Montmorency' sour cherry *(Prunus cerasus* L.) trees was reduced by punching disks from some or all leaves to determine the threshold level of leaf area removal (LAR) necessary to reduce net CO_2 assimilation (A) and whole-plant growth. Removal of 30% of the leaf area of individual leaves reduced A on a whole-leaf basis between 1 and 3 weeks following LAR. Less than 30% LAR was compensated for by higher estimated carboxylation efficiency and ribulose-l,5-bisphosphate (RuBP) regeneration capacity. The threshold level of LAR based on gas exchange of individual leaves was 20%. Although whole-plant dry weight accumulation was reduced at all levels of LAR, a disproportionately large decrease in dry weight occurred as LAR increased from 20% to 30%. This result indicates that *30%* LAR exceeded the threshold LAR level that was noted for A (20% LAR). Wound ethylene production induced by leaf-punching ceased after 24 hours, which indicated that wounds had healed and that ethylene, therefore, did not influence A significantly. The observed threshoId of 20% LAR represents a significant compensation ability for sour cherry, but this threshold may change with crop load, environment, or both.

Sour cherry foliage injury may result from various biotic and abiotic factors. Some of these include: mite or insect feeding; invasion by fungi, bacteria, or viruses; pesticide phytotoxicity; wind or hail damage; and air pollution. As a result of injury, parts of individual leaves may become photosynthetically nonfunctional. The extent and timing of injury may reduce the carbon assimilation potential of the tree.

The response of apple *(Malus domestics* Borkh.) trees to insect and disease infestation has been documented extensively. Infestations by mites reduced apple yield and trunk growth (Lienk et al., 1956), shoot extension and tissue dry weights (Briggs and Avery, 1968), and A and transpiration rates (Mobley and Marini, 1990). Childers et al. (1941) and Proctor et al. (1982) reported reductions in A following infestations with leafhoppers *(Typhlocyba pomaria* McAtree) and tentiform leaf miner *(Phyllonorycter blancardella* Fabricius), respectively. Assimilation rates of apple leaves were also reduced following infection with apple scab *[Venturia inaequalis* (Cke.) Wint.] (Spotts and Ferree, 1979) or powdery mildew *(Podosphaera leucotricha* Salm.) (Ellis et al., 1981).

Several methods of artificial defoliation have been used to simulate pest damage and establish crop damage–yield relationships on various crops. Poston et al. (1976) noted that reducing leaf area with a cork borer adequately simulated painted lady caterpillar *(Cynthiana cardui* L.) and green clover-worm *(Plathypena scabra* F.) defoliation of soybean *(Glycine max* L.). LAR using a cork borer or paper hole-punch (Boucher et al., 1987; Flore and Irwin, 1983), leaf injury by cutting the midrib or pricking the lamina (Li and Proctor, 1984), and leaf removal (Stacey, 1983) have all been used to simulate pest damage.

Many plants are capable of compensating for some level of leaf injury or LAR by increasing their photosynthetic rate. Photosynthetic compensation has been observed in diverse crops (Boucher et al., 1987; Flore and Irwin, 1983; Hodgkinson, 1974; Poston et al., 1976; Proctor et al., 1982; Satoh et al., 1977; Shaw and Samborski, 1956; von Caemmerer and Farquhar, 1984; Wareing et al., 1968). Whole-plant defoliation up to 20% in apple (Flore and Irwin, 1983), 25% in tomato *(Lycopersicon esculentum* Mill.) (Stacey, 1983), and 40% in various hybrid poplar clones *(Populus* sp. L.) (Bassman et al., 1982) were compensated for, as indicated by no decrease in dry weight accumulation, fruit yield, and vegetative growth, respectively.

The objectives of this study were to: 1) determine what the threshold LAR level is for leaf A in sour cherry; 2) characterize the physiological effect of LAR by determining the change in A to a range of physiologically significant CO_2, light, and O_2 levels; 3) determine if the LAR threshold based on gas exchange of individual leaves corresponds to the threshold observed for growth of whole plants; and 4) document the wound response to LAR by leaf-punching.

Materials and Methods

Dormant l-year-old sour cherry trees ('Montmorency' on Mahaleb rootstock) were planted in n-liter plastic pots with 9.5 liters of sterilized greenhouse soil mix [5 sandy loam :3 sphagnum peat :2 torpedo sand (by volume), pH = 7.0]. All trees were cut back to an active bud (0 to 10 cm above the graft union) and placed in an environmentally controlled greenhouse (day and night means 24 and 18C, respectively, 16-h photoperiod provided with high-pressure sodium lamps). Trees were trained to a single shoot from which all laterals were removed as they appeared. Peter's soluble 20N–20P–20K fertilizer (500 ppm) was applied every 3 weeks, and trees were watered every 3 days. Pesticides [5-O-demethylavermectin/(abamectin, Avid), cyano(4-fluoro-3-phenoxyhenyl)methyl-3(2,2-dichloroethenyl)-2,2-dimethylcyclopropanecarboxylate (cyfluthrin, De-

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Abbreviations: A, net CO, assimilation; A_{max}, maximum net CO_2 assimilation; C_i, internal CO_2 concentration; K, carboxylation efficiency LA, leaf area; LAR, leaf area removal; PPF, photosynthetic photon flux; R_i, photorespiration; RuBP, ribulose-1,5-bisphosphate; SLD, specific leaf density TCA, trunk cross-sectional area; to, photochemical efficiency or quantum yield.

cathlon), and d-(2-chlorophenyl)-d-(4-chlorophenyl)-5-pyrimidine-methanol (fenarimol, Rubigan)] were applied as necessary.

Statistical design. For all experiments, plants were arranged in a split plot, with position of LAR (between or across lateral veins) as the main plot randomized completely within the plant population; half of the plants had LAR across veins and the other half had LAR between veins. The subplot (LAR levels) were completely randomized on each plant.

Gas exchange experiments. Forty of the most uniform plants were selected based on leaf count, total leaf area, and gas exchange characteristics after 2 months of growth in the greenhouse (20 fully expanded leaves per plant, on average). The four most recently fully expanded leaves on each plant were tagged and leaf area (LA) was determined according to Kappes (1985), where LA = (length × width × 0.671). Each of the tagged leaves was randomly assigned a different LAR treatment corresponding to 0 (control), 10%, 20%, or 30% of the total LA. LA was removed at about the same time using a paper punch (area = 0.33 cm^2). The leaf margin and midrib were not disturbed on any leaf. There were 20 replicate plants for each of the across or between-vein LAR treatments.

Dry weight experiment. A second population of similar plants was grown under identical conditions. The most uniform 64 plants (based on fresh weight at planting) were selected and treatments were randomly assigned. Whole-plant LA was reduced 0 (control), 10%, 20%, or 30% as described above, where half of the plants had LAR across veins and half between veins. LA was reduced weekly on the most recently expanded leaves of each plant until terminal bud set. The experiment was terminated after 20 weeks of growth in the greenhouse, and the following data were collected for each plant (eight replicates per treatment): plant height from the base of the shoot to the terminal bud; total leaf count; actual LA (LA – area removed by punching); trunk cross-sectional area (TCA) at the base of the shoot; and, following 14 days in a forced-air dryer (40C), dry weights of leaves, scion wood, and rootstock. The average specific leaf density (SLD) per plant was determined as the total leaf dry weight per unit of actual area divided by the number of leaves.

Wound ethylene experiment. A third population of plants grown under identical conditions to that described above was selected to evaluate the wounding response (by ethylene production) following LAR. Four replicate plants were used for each treatment and four leaves were measured for each plant. Conditions were identical to those described for the gas exchange experiment, except that tagged leaves were excised at the time of measurement (wound ethylene protocol follows).

Gas exchange measurements. Gas exchange was measured in the laboratory using the open gas exchange system described by Sams and Flore (1982) and modified as follows: a) an ADC 225 MK3 infrared gas analyzer (Analytical Development Co., Hoddesdon, U. K.) was used to measure differential CO_2 concentrations at the inlet and outlet of the leaf chambers; and b) air flow entering the chambers was regulated using the following Matheson equipment (Matheson Instruments, Horsham, Pa.): 8100 series flow meters and 8200 series mass flow controllers connected to a model 8219 multichannel Dyna-Blender. Ambient CO_2 concentrations were measured using a portable ADC LCA2 infrared gas analyzer, and O_2 concentration was determined with a 0-260 Beckman O_2 analyzer (Beckman Instruments, Irvine, Calif.). Trees and assimilation chambers were placed in a Conviron PGV36 walk-in plant growth chamber (Conviron Systems of America, Pembina, N.D.), and temperature, relative humidity, and light intensity around the whole plant were adjusted to coincide with the assimilation chamber conditions.

The effect of LAR on A over time was determined in the following manner. At predetermined intervals (0, 1, 4, 7, 14, 21, and 28 days following LAR), five plants each for both positions of injury were selected from the population of 40 plants and brought to the laboratory. Plants were allowed to acclimate for 90 min in the growth chamber [25C, 50% relative humidity, 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux (PPF)]. Four leaf chambers were used simultaneously in which the following conditions were maintained, unless otherwise indicated: inlet CO_2 and O_2, 350 ± 15 $\mu l \cdot liter^{-1}$ and 21 kPa, respectively; leaf temperature, 25C; vapor pressure deficit (VPD), 1.0 ± 0.2 kPa; inlet flow rate, 3 $liters \cdot min^{-1}$. Measurements were conducted between 9:00 AM and 12:00 noon (to minimize the diurnal effect). On a given day of measurement, A for an individual leaf was expressed as a percentage of the observed A on day 0 for that same leaf; this value was then expressed as a percentage of the A of the control leaf on the same plant for the same day of measurement.

Response to changing environmental conditions. Response to PPF was determined on days 11 and 12 following LAR, as described above, by decreasing PPF stepwise (15-min acclimation at each step) to the following levels: 1800, 1300, 1000, 600, 400, 180, and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ Photosynthetically active radiation (PAR) was provided with GE 400-W metal halide lamps. These PPF levels were produced using a combination of neutral density filters. PAR was measured with a LI-COR 190 PAR sensor (LI-COR, Lincoln, Neb.). Dark respiration (R_d) was measured by gas exchange after 20 min in complete darkness.

Photorespiration (R_l) was estimated on day 13 by comparing A at ambient O_2 (21 kPa) with that at reduced O_2 (1.5 kPa). Response to CO_2 was determined on days 15 to 17 following LAR by increasing stepwise to the following levels: 0, 60, 115, 175, 240, 300, 350, 430, 520, and 900 $\mu l \cdot liter^{-1}$. Leaves were allowed to acclimate for 20 min at each CO_2 level.

Gas exchange parameters were calculated using the BASIC computer program of Moon and Flore (1986). Responses of A to PPF and internal CO_2 concentration (C_i) were analyzed for each treatment by nonlinear regression, and curve fitting was performed using the Marquardt compromise method of successive approximations. The best-fit curve, evaluated by analysis of residuals, and r^2 were the monomolecular asymptotic function (Hunt, 1980) of the type: $Y=B(l) \times [1.0 - B(2)\ e^{-B(3)xX}]$, where B(l), B(2), and B(3) are the asymptotic value, minimum value, and rate constant, respectively. This polynomial was selected because it provided direct estimates of specific physiological processes and exhibited curvilinear features that represented the data. Individual leaf A vs. C_i and A vs. PPF response curves were developed using this polynomial.

Carbon dioxide compensation point (Γ) was extrapolated from the AC_i curve as the C_i at which A was zero. Carboxylation efficiency (k) was calculated from the raw data as the slope in the linear portion of the AC_i curve. Stomatal limitation (l_g) was calculated according to the differential method of Jones (1985). Photochemical efficiency or quantum yield (ϕ) was calculated from the raw data as the slope of the A vs. PPF curve in the linear portion between 0 and 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF. The light compensation point (cp) was extrapolated from the light response curve as the PPF level at which A was zero. R_d was calculated from the raw data at 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF.

Wound ethylene measurement. Ethylene evolution was determined according to the method of Lownds (1987) and modified as follows: leaves were excised immediately after LAR, positioned abaxial side outward with minimum overlap in 25 × 200-mm test tubes, and with the petiole immersed in 2 ml of distilled water. Tubes were immediately sealed with rubber serum stoppers, incubated in a constant-temperature water bath (25C), and illuminated with fluorescent lights at 115 µmol·m^{-2}s^{-1} PPF. The ethylene concentration in the tubes was determined from a l-ml headspace sample by gas chromatography (Varian 1440; Varian Associates, Palo Alto, Calif.) using a flame ionization detector. The injection port, column, and detector temperatures were 130, 100, and 150C, respectively. Nitrogen (N_z) flow was maintained at 15 ml·min^{-1}. Ethylene was sampled hourly for the first 12 h following LAR and again at 24, 48, and 72 h. Tubes were flushed with ethylene-free air for 30 sec and then resealed following each determination. The rate of ethylene evolution was expressed in units of nanoliters per gram of leaf fresh weight per hour.

Results

Gas exchange over time. LAR reduced A within 1 day when more than 10% of the LA was removed between lateral veins (Fig. 1A) or when as little as 10% was removed across veins (Fig. lB). Recovery occurred within 4 days when no more than 20% of the LA was removed. Two weeks following treatment, the rates of A were 12% and 66% above the control value in leaves with 20% LAR between and across veins, respectively. The greatest increase in A was observed for leaves 2 weeks following LAR across veins and 3 weeks following LAR between veins. The time to full photosynthetic recovery was slowest when 30% of the LA was removed.

Since enhancement of A was observed between days 7 and 21 following LAR (Fig. 1 A and B), the gas exchange data for these dates were combined for each treatment to describe the effect of increasing levels of LAR on A (Fig. 2). When data were expressed based on the actual LA remaining following LAR (Fig. 2A), the quadratic relationships between A and LAR between and across veins were nonsignificant (r^2 = 0.05) and significant (r^2 = 0.15), respectively. When data were expressed based on the original LA before LAR (Fig. 2B), the quadratic relationship between A and LAR was significant for both methods of LAR (r^2 = 0.18 and 0.36, respectively). Comparison of SE based on actual or original leaf area (Fig. 2) demonstrated that only 30% LAR across veins reduced A relative to the control.

Gas exchange response to CO_2 level. The data fit the model equation used to predict the response of A to C_i very well (r^2 = 0.96). The AC_i curves presented (Fig. 3) are based on the combined data for the four replicate leaves for a-given treatment. As C_i increased, A increased hyperbolically for all treatments. A rates were higher in leaves with 10% or 20% LAR between veins than in the control at most CO_2 levels above 115 µl·liter^{-1} (Fig. 3 A and C, respectively), but not in leaves with 30% LAR between veins (Fig. 3E). LAR across veins reduced A relative to control leaves at CO_2 levels at or exceeding 175 µl·liter^{-1} (Fig. 3 B, D, and F).

Based on the A vs. C_i analysis of individual leaves, the treatment effects on various characteristics were calculated (Table 1). Γ was not significantly affected by LAR position, but it was affected by LAR level. k was significantly affected by position and level of LAR, and there was a significant interaction between position and level of LAR. LAR increased k values 83% and 72% when 10% and 20% of the LA was removed between veins, respectively. LAR resulted in k values that were 33% and 29% lower than for control leaves when 10% or 30% of the LA was removed across veins, respectively. A at ambient CO_2 (A_{350}) was significantly affected by LAR position, level, and the interaction thereof. A_{350} was reduced by LAR across

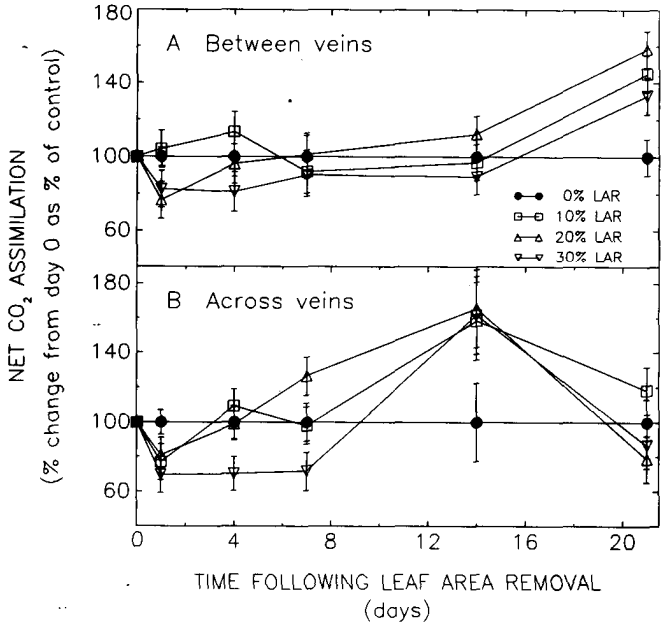

Fig. 1. Changes in A (actual LA basis) over time of sour cherry leaves as affected by removal of 0% (●), 10% (□), 20% (△), or 30% (▽) of the leaf area either between (**A**) or across (**B**) lateral veins by leaf-punching. The A value is expressed as the percent change from the pretreatment value (day-0) for a particular leaf relative to the nondefoliated leaf on the same plant for the date of measurement indicated. Means ±SE (n = 4).

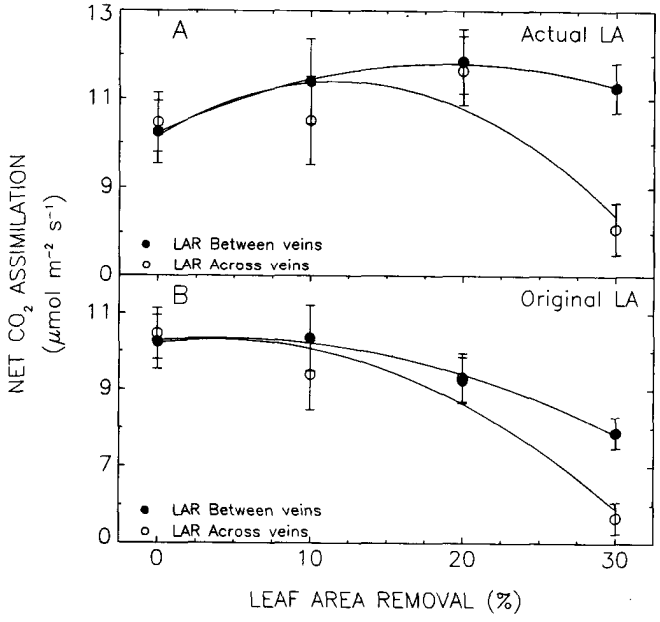

Fig. 2. Effect of LAR of sour cherry leaves by leaf-punching between (●) or across (○) lateral veins on the relationship between percent LAR and A. Data were expressed based on actual LA remaining following LAR (**A**) or on original LA before LAR (**B**). Means ±SE (n = 12).

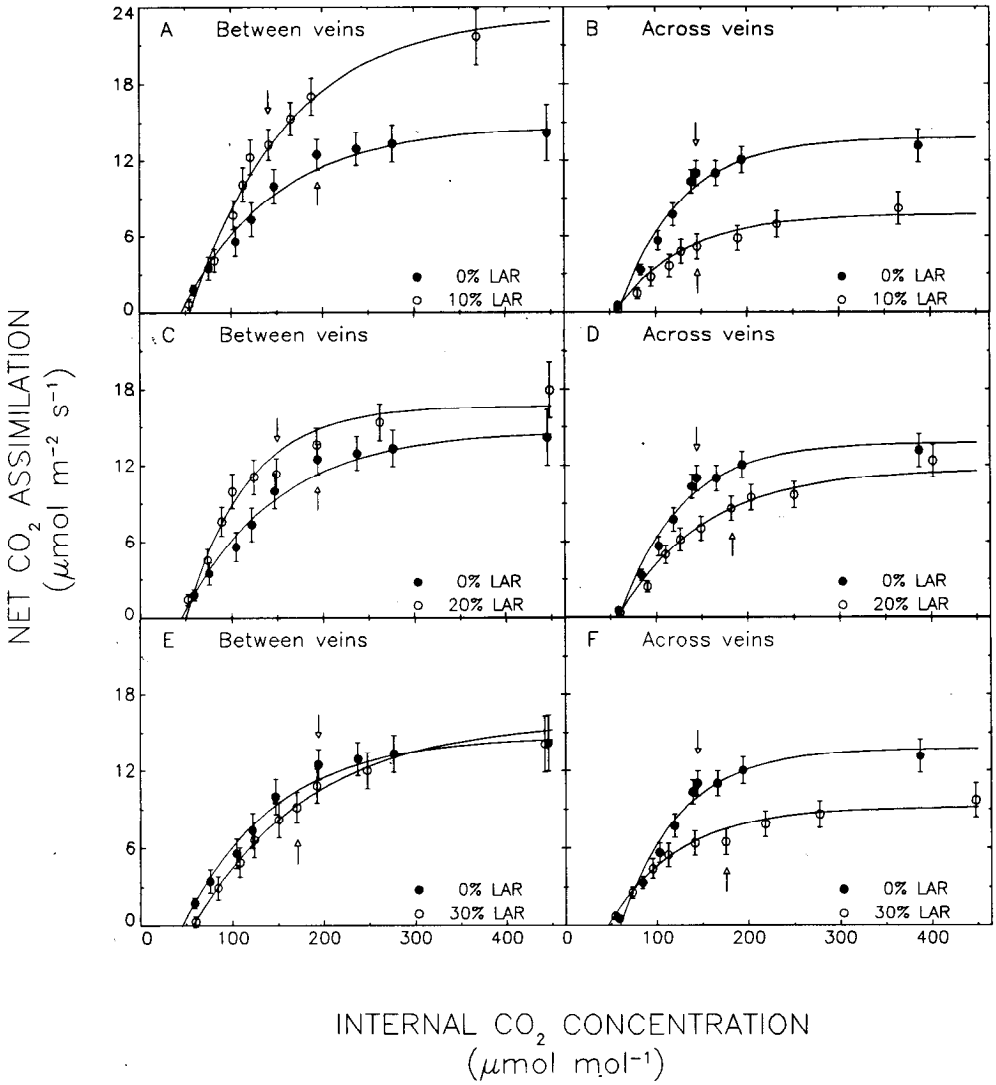

Fig. 3. Effect of LAR of sour cherry leaves by leaf-punching between or across lateral veins on the relationship between A and internal CO_2 concentration. Data for each treatment (○) are presented relative to the noninjured control (●) in each figure. **(A, C, E)** 10%, 20%, and 30% between lateral vein LAR treatments, respectively; **(B, D, F)** 10%, 20%, and 30% across lateral vein LAR treatments, respectively. Arrows correspond to measurements at ambient CO_2 (350 ± 20 µl·liter^{-1}). Means ± SE (n = 4).

veins. A_{350} was significantly lower than the control when 10% or 30% of the LA was removed across lateral veins. Stomatal conductance at ambient CO_2 (g_{s350}) was not affected by position of LAR. Across-vein LAR of 10% or 30% significantly reduced g_{s350} relative to the control. At 900 µl·liter^{-1} CO_2, maximum A (A_{max}) was significantly affected by position and level of LAR. A_{max} was higher than in controls by 53% and 27% at 10% or 20% LAR between veins, respectively. A_{max} was reduced by 39% or 26% at 10% or 30% LAR across veins, respectively. l_g was minimally affected by LAR level.

Gas exchange response to PPF. The data fit the model equation used to predict the response of A to PPF very well (r^2 = 0.94). As PPF increased, A increased hyperbolically for all treatments (response curves not shown). The treatment effects on various calculated values were determined based on the A vs. PPF analysis for individual leaves (Table 2). R_d was not significantly affected by LAR position and minimally affected by LAR level. cp was lower when leaf area was removed between lateral veins. ϕ was significantly affected by LAR position and level. ϕ was reduced from control values by 40%, 32%, or 41% when 10%, 20%, or 30% of the LA was removed across veins, respectively. Maximum A at 1300 µmol·m^{-2}·s^{-1} TPF (A_{max}) was significantly affected by LAR position and level. A_{max} was reduced by 26%, 31%, 27%, or 35% when 30% LAR was removed between veins or 10%, 20%, or 30% of the leaf area was removed across veins, respectively. R_i was significantly affected by LAR position and level. R_i was significantly increased by all LAR treatments.

Whole-plant growth. Weekly LAR significantly reduced height, leaf number, actual LA, TCA, and dry weight per plant whether lateral veins were cut or not (Table 3). Average SLD per plant increased significantly as LAR level increased. Only small differences in height, leaf number, TCA, or plant dry weight were noted between the 10% and 20% LAR treatments. However, 30% LAR resulted in disproportionately large reductions of these variables when compared to the 20% LAR treatment.

Wound ethylene evolution. Wound ethylene evolution from LAR treatments increased hourly to a peak rate after 4 h and then decreased to negligible levels 24 h following LAR (data not shown). At each LAR level, ethylene evolution was significantly higher when leaf area was removed across rather than between lateral veins. The highest and lowest rates of ethylene

Table 1. The effect of LAR on CO_2 compensation point (Γ), k, net CO_2 assimilation (A_{350}), and stomatal conductance ($g_{s\ 350}$) at ambient CO_2, A_{max} at 900 ppm CO_2 , and stomatal limitations to A (l_g) of expanded sour cherry leaves.[z]

LAR level (%)	Γ (μmol CO_2/mol)	k (mol CO_2/m² per sec)	A_{350} (μmol CO_2/m² per sec)	$g_{s\ 350}$ (mmol CO_2/m² per sec)	A_{max} (μmol CO_2/m² per sec)	l_g (%)
			LAR between lateral veins			
0	54.0	0.099	12.48	48.3	14.18	41.7
10	50.5	0.181	13.25	64.5	21.68	59.9
20	52.5	0.170	11.33	49.7	17.94	32.4
30	56.0	0.105	9.13	53.0	14.09	51.2
			LAR across lateral veins			
0	63.0	0.103	10.92	83.7	13.14	34.5
10	53.3	0.069	5.14	24.7	8.18	58.7
20	57.5	0.111	8.60	53.7	12.34	41.8
30	48.3	0.073	6.46	38.2	9.68	35.7
Position	NS	***	***	NS	***	NS
Level	*	**	*	*	*	*
Position × level	NS	**	**	NS	NS	NS

[z]Values are the means of four replicates.
NS,*,**,***Nonsignificant or significant at $P = 0.1$, 0.05, or 0.01, respectively. Position and level identify main and split-plot effects, respectively. Comparisons were made 15 to 17 days after LAR.

Table 2. The effect of LAR on dark respiration rate (R_d), light compensation point (cp), ϕ, A_{max} at 1300 μmol·m^{-2}·s^{-1} PPF, and estimated R_l of expanded sour cherry leaves.[z]

LAR level (%)	R_d (μmol CO_2/m² per sec)	cp (μmol CO_2/m² per sec)	ϕ (μmol CO_2 fixed/ mol PPF)	A_{max} (mmol CO_2/m² per sec)	R_l (%)
			LAR between lateral veins		
0	−0.51	13.5	0.0242	16.48	12.2
10	−0.57	16.3	0.0213	15.02	22.6
20	−0.79	18.3	0.0253	17.00	31.2
30	−0.60	13.2	0.0173	12.24	26.7
			LAR across lateral veins		
0	−0.73	13.7	0.0281	16.99	23.3
10	−0.62	19.5	0.0169	11.79	35.8
20	−0.76	22.8	0.0191	12.40	44.4
30	−0.68	27.3	0.0167	10.98	29.9
Position	NS	*	**	***	***
Level	*	*	***	***	***
Position × level	NS	NS	*	NS	NS

[z]Values are the means of four replicates.
NS,*,**,***Nonsignificant or significant at $P = 0.1$, 0.05, or 0.01, respectively. Position and level identify main and split-plot effects, respectively. Comparisons were made 11 to 13 days after LAR.

evolution 4 h following LAR were 99 and 33 nl·g^{-1}·h^{-1}, respectively, for the 20% LAR, including across- and between-vein LAR treatments. After 24 h, ethylene evolution had decreased in these same treatments to 4.7 and 2.5 nl·g^{-1}·h^{-1}, respectively, and were similar to those of the control.

Discussion

Many cultivated plants can compensate for partial defoliation by increasing the photosynthetic capacity of the remaining leaf area (Boucher et al., 1987; Flore and Irwin, 1983; Hodgkinson, 1974; Poston et al., 1976; Proctor et al., 1982; Satoh et al., 1977; Shaw and Samborski, 1956; von Caemmerer and Farquhar, 1984; Wareing et al., 1968). Similar physiological responses occur whether whole leaves or portions of individual leaves are removed. The initial reduction in A following LAR in sour cherry (Fig. 1) has also been observed following leaf area loss in grape *(Vitis vinifera* L.) (Boucher et al., 1987). Depending on the type and extent of defoliation, significant enhancements of A have been observed in as few as 2 to 3 days in bean *(Phaseolus vulgaris* L.) (von Caemmerer and Farquhar, 1984) or 6 days following decapitation of mulberry *(Morus alba* L.) (Satoh et al., 1977). In sour cherry, a significant enhancement of A in the remaining effective LA relative to a control leaf was not observed until 7 days following 20% LAR across lateral veins (Fig. lB). This compensation response of an individual cherry leaf to LAR is slower than that of intact leaves remaining on partially defoliated cherry plants, in which compensation was noted after 1 day (Layne and Flore, 1991). Photosynthetic enhancement of up to 50% to 70% on an actuaI leaf area basis (Fig. 1) was observed 2 to 3 weeks following partial defoliation. In fact, von Caemmerer and Farquhar (1984) observed more than a doubling of A 2 weeks after partially defoliating bean plants. Between 1 and 3 weeks following LAR,

Table 3. The effect of weekly LAR on plant height, leaf number, actual LA, TCA, dry weight, and average SLD of 1-year-old potted sour cherry trees.[z]

LAR level (%)	Plant ht (cm)	Leaf no.	Actual LA (cm^2)	TCA (mm^2)	Plant dry wt (g)	Avg SLD ($mg \cdot cm^{-2}$)
LAR between lateral veins						
0	110	42	2229	152	190	0.262
10	96	39	1910	119	175	0.297
20	93	40	1460	104	161	0.317
30	74	31	1068	78	119	0.387
LAR across lateral veins						
0	112	42	2281	140	203	0.255
10	90	38	1715	103	173	0.304
20	86	36	1457	102	166	0.344
30	85	35	1204	90	128	0.370
Position	NS	NS	NS	NS	NS	NS
Level	***	**	***	***	***	***
Position × level	NS	NS	NS	NS	NS	NS

[z]Values are the means of eight plant replicates.
NS,*,**,***Nonsignificant or significant at $P = 0.1$, 0.05, or 0.01, respectively. Position and level identify main and split-plot effects, respectively.

removal of up to 20% of the LA of individual leaves did not significantly reduce A on a whole-leaf basis, but removal of 30% of the LA did (Fig. 2B). Apparently, 30% LAR exceeds the compensatory capacity of the individual cherry leaf. This apparent threshold, where 20% LAR did not significantly reduce A, has also been observed in other crops (Boucher et al., 1987; Flore and Irwin, 1983; Poston et al., 1976; Proctor et al., 1982).

Photosynthetic compensation following up to 20% LAR between veins (Fig. 3 A and C, Table 1) could possibly be the result of both an enhanced rubisco activity and RuBP regeneration capacity. von Caemmerer and Farquhar (1984) observed similar changes in rubisco activity and capacity of RuBP regeneration following defoliation in bean. Wareing et al. (1968) observed increased rubisco activity in partially defoliated bean leaves and suggested that defoliation increased the demand of the remaining LA for photosynthates. They also noted that noninjured leaves were not operating at their maximum photosynthetic potential; this appears to be the case for noninjured sour cherry leaves as well. Since 1_g was only minimally affected by LAR level (Table 1), the major limitation to A following partial defoliation in sour cherry appears to be the mesophyll.

The increase in R_1 as LAR between and across veins increased (Table 2) should have increased the competition between carboxylation/oxygenation of rubisco for RuBP, thus affecting A most at saturating C_i, when RuBP regeneration capacity should have been limiting (Farquhar and Sharkey, 1982). Hodgkinson (1974) also observed higher R, values in partially defoliated lucerne *(Medicago sativa* L.) plants. A_{max} at saturating C_i was 52% or 27% higher than the control leaves when 10% or 20% of the leaf area was removed between veins, respectively (Table 1), yet R_1 was 85% or 155% higher in these leaves (Table 2). The dramatic increase in R, associated with an increase in A_{max} suggests that the RuBP regeneration capacity of leaves with up to 20% .LAR between veins most likely was enhanced. Since A_{max} was reduced following LAR across veins relative to the control, this reflects a diminished CO_2 assimilatory capacity that cannot be overcome by increasing the CO_2 supply. These data, in addition to k values (Table 1), indicate that photosynthetic compensation for LAR in sour cherry is most likely due to enhancement of both carboxylation efficiency and RuBP regeneration capacity.

Responses of A to PPF (Table 2) were measured to predict effects of defoliation on other gas exchange characteristics. Dark respiration was only minimally affected by LAR level in sour cherry and was not affected by virus infection of peach [Prunus *persica* (L.) Batsch] leaves (Smith and Neales, 1977) or leaf miner infestation of apple leaves (Proctor et al., 1982). The light compensation point was minimally affected by LAR level in sour cherry and not by virus infection in peach (Smith and Neales, 1977). Photochemical efficiency was significantly reduced in sour cherry leaves, especially when LA was removed across veins or when 30% of the LA was removed between veins. The lower ϕ values for LAR across veins or 30% LAR between veins indicate that light capture and electron transport processes underlying RuBP regeneration may be less efficient in these leaves. Proctor et al. (1982) and Smith and Neales (1977) did not observe significant "effects of leaf miner infestation or virus infection on ϕ of mature leaves, but the latter authors did observe a significant reduction in ϕ upon virus infection of young peach leaves. At saturating PPF, A_{max} was significantly reduced as LAR level across veins increased. Proctor et al. (1982) observed a similar relationship for leaf miner-infested apple leaves. This pronounced decline in A at saturating PPF indicates that RuBP regeneration capacity maybe limiting A since nonlimiting light energy is available.

LAR that exceeded the estimated threshold of 20% in sour cherry affected ϕ more than k (Tables 1 and 2). Leaf volume increased (as indicated by SLD), but LA did not change (Table 3). The actual reduction of leaf surface area for light trapping may have affected A more than the reduction in leaf volume affected carboxylation, especially since leaf volume increased over time. Satoh et al. (1977) and Hodgkinson (1974) have observed leaf thickening following partial defoliation. Mesophyll cell enlargement may have been due to the production of more photosynthetic "machinery" (e.g., proteins such as rubisco), since Satoh et al. (1977) observed a greater depth and more columnar stacking in the palisade and spongy mesophyll. Starch accumulation was less and A was higher in leaves of partially defoliated than nondefoliated mulberry plants (Satoh et al., 1977), presumably due to the increased sink demand of the remaining LA. However, Ramirez et al. (1988) suggested that, as defoliation increased in cucumber *(Cucumis sativus* L.), dry

Weight (and possibly starch) accumulation acted as a feedback mechanism to inhibit A. Since leaf starch content was not determined in these experiments, one cannot rule out a feedback effect on A in noncompensating leaves.

Removal of 25% of the leaf area of tomato (Stacey, 1983) and cucumber plants (Ramirez et al., 1988) did not significantly affect yield or whole-plant dry matter accumulation. Removing 50% of the leaf area of potted apple trees reduced dry weight accumulation only 40% (Maggs, 1964), suggesting that some kind of compensation must have occurred. Flore and Irwin (1983) did not observe a significant reduction in fresh weight or TCA of apple trees until 20% or more of the, leaf area of the whole plant was removed. In our experiments, the reduction of whole-plant dry weight from 10% to 20% LAR between or across veins was only 8% or 5%, respectively, whereas the reduction of whole-plant dry weight from 20% to 30% LAR between or across veins was 32% or 26%, respectively (Table 3). Although whole-plant dry weight accumulation was reduced following LAR in sour cherry, this disproportionately large decrease between 20% to 30% LAR would suggest that 30% LAR exceeded the threshold LAR level, as was noted for the gas exchange study, and that compensation was occurring at the 20% LAR level. It is peculiar that 30% LAR between veins resulted in a slightly lower plant dry weight than the same level of LAR across veins. Based on the gas exchange data, we would not have predicted this outcome. In any event, this threshold for LAR was established for potted l-year-old trees grown in the greenhouse. It represents a significant compensation ability for sour cherry, but the threshold may change with crop load and environment.

Ethylene evolution is usually stimulated by wounding. Ethylene production by tobacco *(Nicotiana tabacum* L.) leaves inoculated with tobacco mosaic virus increased over 8 days as local lesions developed (Nakagaki et al., 1970). Wound ethylene production of sour cherry leaves damaged by leaf-punching dropped off after 12 h and was essentially unchanged after 24 h. Because the wounding event was instantaneous rather than prolonged, as might be expected during an infection, wounds probably healed rapidly and the wounding response was hastened. The wounding response was greater for IAR across than between veins, and wound ethylene evolution increased as LAR increased. LAR across lateral veins is probably more injurious to the leaf than leaf-punching through the lamina. Some plants suffer photosynthetic depression in response to ethylene (Taylor and Gunderson, 1986), while others, including apple (Dozier and Barden, 1971) and tomato (Bradford, 1983), do not. Although the effects of ethylene on gas exchange of sour cherry were not evaluated in this study, we do not believe that it significantly influenced A. Because wound ethylene evolution had essentially ceased after 24 h, the wounds to the leaves were probably healed by then. If ethylene had still been produced at inhibitory levels 7 days following LAR, then the compensation observed (Fig. lB) upon 20% LAR across veins should not have occurred.

Defoliation can dramatically affect productivity of cultivated plants and should, therefore, be kept to a minimum. Studies such as ours aid in determining damage thresholds for a crop. Clearly, many plants can compensate for certain levels of damage or injury. By knowing what these levels are and how to measure them in the field, and by being able to predict responses (e.g., reduced productivity or winter hardiness), the grower may choose to treat or not treat the situation. In circumstances where prophylactic pest control is always used, knowledge of damage thresholds may reduce the frequency of pesticide applications and preserve populations of beneficial insects in the environment.

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