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LIGHT AND TEMPERATURE EFFECTS ON WHOLE-CANOPY NET CARBON DIOXIDE EXCHANGE RATES OF APPLE TREES

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Abstract

Effects of previous days' light conditions, hours of exposure to sunlight, time of the day, temperature and/or vapor pressure deficit (VPD) on whole-canopy net CO_2 exchange rate (NCER) of cropping field-grown 'Empire' or potted 'Gala' apple (*Malus domestica* Borkh.)/M.9 trees were studied. In most studies, simultaneous single-leaf NCER measurements were also taken. Artificial shading to 24% full sun for two previous days or to 23% full sun until mid-morning did not affect the subsequent whole-canopy and single-leaf NCER diurnal pattern of 'Empire' trees. Light response curves of 'Empire' trees showed higher dark respiration rate (16 vs. 7% of the maximum NCER) and higher light compensation point (84 vs. 32 $\mu mol \cdot m^{-2} \cdot s^{-1}$) for whole-canopy than for single leaves. Whole-canopy NCER of 'Gala' trees was negatively related to increases in air temperature from 15 to 34°C and/or VPD from 7 to 30 $g \cdot m^{-3}$. Whole-canopy and single-leaf NCER of 'Empire' and 'Gala' trees decreased throughout the day in most cases. Possible mechanisms for the observed patterns and suggestions on measuring whole-canopy NCER are discussed.

1. Introduction

In the past, whole-canopy NCER studies in fruit trees were limited to single apple trees (Heinicke and Childers, 1937; Sirois and Cooper, 1964). In recent studies, however, the light-weight clear plastic "balloon" method of Corelli Grappadelli and Magnanini (1993) has allowed inexpensive whole-canopy NCER measurements with portable CO_2 analyzers. We have used eight inexpensive 'Mylar' plastic whole-canopy chambers for diurnal measurements of whole-canopy NCER as affected by foliar pests (Francesconi, *et al.*, 1996; Lakso, *et al.*, 1996). However, a better understanding of the major environmental and/or physiological sources of variation in whole-canopy NCER is fundamental for refining the method for taking such measurements.

Based on natural changes during the day or on different days, Heinicke and Childers (1937) concluded that light was the major factor affecting whole-canopy NCER of apple trees, and temperature was second while Sirois and Cooper (1964) felt CO_2 was the second important factor. Because environmental factors were confounded in those studies, the interpretations of those correlations are difficult. A recent study reported short-term whole-canopy NCER measurements with gradually declining light levels with shade materials (Corelli-Grappadelli and Magnanini, 1993) for one apple tree.

Besides ambient light levels, seasonal observations (unpublished data) on leaf gas exchange over a season have found highest rates occurring on sunny days immediately following cloudy periods, or in sunny afternoons following cloudy mornings. Although other environmental conditions varied, these observations suggested that light conditions in the hours or days prior to measurement may be a source of variation in whole-canopy NCER. The objective of this work was to evaluate sources of variation of whole-canopy NCER related to the time of the day, previous days' light levels, incident light and

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temperature on whole-canopy NCER of healthy apple trees. This work was conducted for two main reasons: 1) to provide the basis for development of efficient and accurate methods of whole-canopy NCER measurements in apple research, and 2) to provide important information for carbon balance modeling.

2. Materials and methods

All experiments were conducted in 1995 on cropped apple trees at the New York State Agricultural Experiment Station, Geneva, N.Y. Normal fertilization and pest control practices, as well as irrigation, were used to assure good health of the trees.

2.1. Effects of hours of exposure to sunshine, previous days' light conditions and short-term light levels on whole-canopy and single-leaf NCER of field apple trees

Field grown 4-year-old 'Empire'/M.9 central leader apple trees, of uniform size (average 1.8 m wide and 2.1 m tall) and bloom density, were hand-thinned to about 4 fruits per cm^2 trunk cross-sectional area on 6 June. Harvest was on 4 October.

Whole-canopy NCER was monitored by enclosing six trees inside individual whole-tree chambers made of clear 'Mylar' plastic in an open-system described in detail by Francesconi, *et al.* (1996). Four zippers cut from plastic freezer bags were taped around the tree chambers at mid-canopy height to allow reach-in access so that single-leaf NCER could be measured without having to remove the tree chambers. Each tree chamber had about 2,800 L and an air flow of 5,000 $L.min^{-1}$. A ΔCO_2 of 10-15 ppm between inlet and outlet, and a maximum 2°C increase in temperature inside each chamber was maintained in mid-day and inlet and outlet CO_2 was measured with an ADC LCA2 infrared gas analyzer (ADC Inc., Hoddesdon, Herts, UK). Average values between inlet and outlet were used to estimate temperature and VPD for each tree. Air velocity at the inlet pipe was measured with a hot wire anemometer probe. Incident photosynthetic photon flux (*PPF*) was measured with a quantum sensor Model LI-185A (LI-COR, Lincoln, Neb.) positioned normal to the sun at open sky or between the shade cloth and the chamber. A reduction factor of 12% light by 'Mylar' plastic was included in the calculation of *PPF*. Single-leaf NCER was measured with a CIRAS-1 portable open-system gas analyzer (PP-Systems, Hitchin, Herts, UK) with a broad-leaf cuvette that includes 2.5 cm^2 of leaf area placed perpendicular to the sun. At each set of readings, a different combination of four well-exposed mature leaves (half non-fruiting spur leaves and half shoot leaves) was likely to be selected due to changing leaf exposure.

On 9 August (85 days after bloom (DAB)), three whole trees were shaded with black shade cloth to 23% full sunlight (maximum of 400 $\mu mol.m^{-2}.s^{-1}$ *PPF*) from dawn until 9:50 solar time. After shade removal, the three treated and three control trees (not shaded) received full sun. Whole-canopy and leaf NCER were monitored from 8:30 to 15:00 solar time on all trees. In another trial, three trees were shaded to 23% full sunlight for two days (28 and 29 August), while three control trees received natural sunlight. On 30 August (106 DAB), all trees were exposed to natural sunny conditions and NCER were monitored. On 18 July (63 DAB), a clear, sunny day, whole-canopy and single-leaf NCER versus *PPF* responses were measured on two field trees, between 9:30 and 13:10 solar time, starting at full sunlight and decreasing light levels with various layers of shade cloth over the whole-tree chambers at 4 or 5 steps of 30 min each to darkness. Single-leaf NCER was measured immediately after each whole-canopy NCER measurement.

2.2. Effects of temperature on whole-canopy NCER of potted apple trees

On 6 September 4-year-old 'Gala'/M.9 apple trees of uniform size (about 1m wide and 1.7m tall) grown outdoors in 57 L pots were hand-thinned to 20 $fruit.tree^{-1}$. On 11 September, a sunny, cool day, whole-canopy NCER was monitored by enclosing six trees in clear whole-tree chambers. Each chamber had about 1,200 L and an air flow of 1,200 $L.min^{-1}$, providing a ΔCO_2 of 10-20 ppm between inlet and outlet. After an ini whole-canopy NCER reading taken at about 9:30 solar time under similar amb conditions, pairs of whole potted 'Gala' apple trees were then treated until 15:20 solar t as follows: ambient, warmer than ambient, and colder than ambient. For the colder-th ambient treatment, the blower forced the inlet air through a heat exchange unit connecte a barrel of ice water by a circulation pump. For the warmer-than-ambient treatment, electric portable heater was placed at the blower inlet. A concomitant decrease or increas VPD occurred as temperature decreased or increased, respectively, as normally occurs ur natural conditions. Average temperature and VPD were calculated between outlet and i for each chamber.

2.3. Statistical analyses

Genstat (NAG, Downers Grove, IL) was used for fitting negative exponential regressi and for repeated measurement analyses.

3. Results

On 9 August, tree shading to 23% full sunlight until mid-morning did not ca significant changes in the rest of the diurnal pattern of whole-canopy and single-leaf NC (Fig. 1) although both showed a similar significant decline over time ($P < 0.02$). Whole t shading to 23% of full sunlight during two days did not affect significantly the diur pattern of whole-canopy and single-leaf NCER on the following day (30 August) (Fig. Again whole-canopy and single-leaf NCER showed similar diurnal patterns wit significant decline over time ($P < 0.02$ for canopy; $P < 0.004$ for leaf).

On both days that NCER was monitored, temperature and VPD in the whole-canopy single-leaf chambers were positively related to time of the day. In general, temperature the tree chambers increased from low 20s in the morning up to about 30°C in the afterno Incident light levels normal to the sun and light interception per tree did not decrease v time during the measurements (data not shown).

Pooled data from two trees on whole-canopy and single-leaf NCER response to li were fitted well by negative exponential curves, with an R^2 of 0.98 and 0.99, respecti (Fig. 3). Comparison of the estimated parameters of the curves ($y = a + b\ H\ r^{PPF}$) indica that the regressions were parallel, i.e., *a* parameters differed but the slope (*b*) and non-lin parameters (*r*) did not differ significantly. According to the models, dark respiration about 16% and 7% of the maximum NCER in the light for whole-canopy and leaf NC respectively. Light compensation points were 84 and 32 $\mu mol.m^{-2}.s^{-1}$ *PPF* for whole-can and leaf, respectively. No major increases in whole-canopy and single-leaf NCER occur at light levels above 1000 $\mu mol.m^{-2}.s^{-1}$.

On a sunny day, whole-canopy NCER of potted 'Gala' apple trees decreased due increase in air temperature and/or increase in VPD after initially comparable readings (I 4). Trees under warmer conditions (31-34°C and 26-32 VPD ($g.m^{-3}$)) showed significa lower NCER than trees under ambient and colder conditions ($P < 0.006$). Trees under col conditions (13-16°C and 5-8 VPD ($g.m^{-3}$)) showed significantly higher NCER than tr under ambient conditions (20-23°C and 10-14 VPD ($g.m^{-3}$)) ($P < 0.007$). However, NC responses of trees under colder and ambient conditions had similar slopes, both declin over time. Increase in temperature was associated with a decrease in VPD. No obvi reduction in incident light or changes in temperature and VPD within each treatm occurred over the measurement period.

4. Discussion

Under the conditions of our experiment, time of exposure to sunshine and li conditions during two previous days had no noticeable effects on the diurnal pattern whole-canopy and single-leaf NCER of 'Empire' apple trees. These results are not consist with our earlier observations, but cloudy conditions some days before our shading trials may have affected our results. Nevertheless, short-term day-to-day effects appear to be minimal.

The negative exponential models fitted to the light response curves of whole-canopy and single-leaf NCER were similar to previous reports (Corelli-Grappadelli and Magnanini, 1993; Watson, *et al.*, 1978). The higher incident light compensation point for whole canopy than for single exterior leaves is likely due to the inclusion of shaded leaves and to a higher respiration component of whole-canopy NCER due to wood and fruits. Similarly, dark respiration rate was higher for whole canopy than for single leaves. Cropping mature 'Golden Delicious'/M.27 trees showed a 40% higher whole-canopy light compensation point than our trees (Corelli Grappadelli and Magnanini, 1993). Our younger trees probably had a smaller amount of respiratory wood surface and fruits in combination with a better average leaf exposure due to very open canopies.

In the temperature study, a concomitant increase of VPD to about 30 $g.m^{-3}$ as temperature increased may have caused reduction in stomatal conductance at the warmer treatment, but was unlikely to affect stomatal behavior in the ambient or cooler treatments, which is highly coupled to leaf NCER in field grown apple trees, as shown by Lakso (1983). Respiration of all organs of the apple canopy increases exponentially as temperature increases from 10 to 40°C (Butler and Landsberg, 1981; Lakso, 1994), while the optimum range for leaf NCER is between 20 and 30°C (Lakso and Seeley, 1978; Watson, *et al.*, 1978). As whole-canopy NCER is the balance between leaf NCER and the respiration of fruits and wood (Fig. 5), both processes were likely to be involved in the observed decrease in whole-canopy NCER of 'Gala' apple trees as air temperature increased from about 15° to 34°C. This indicates that whole canopy temperature optimum may be lower than previously thought.

Similar diurnal patterns for whole-canopy and single-leaf NCER were found. We believe the reduction in whole-canopy, as also found by Lakso, *et al.* (1996), and single-leaf NCER over time was mostly due to decreased stomatal conductance of leaves after many hours of exposure to full sun, as previously reported for apple leaves (Lakso, 1983), possibly due to feedback inhibition of photosynthesis (Flore and Lakso, 1989; Lakso, 1983). While light levels and light interception of the 'Empire' and 'Gala' trees did not change much, increases in temperature and VPD with time of the day are likely to be at least partially involved on the afternoon NCER decline. However, when 'Gala' trees were exposed to almost constant temperature and VPD during the day, an afternoon decrease in NCER also occurred at the cold and ambient treatments (Fig. 4). The absence of afternoon decline in NCER of the warmer treatment of the 'Gala' trees is not understood, but may be related to a slower accumulation of carbohydrates in the leaf and to a faster consumption of carbohydrates due to increased respiratory activity. Temperature effects on translocation of carbohydrates could be involved, even though that type of data do not seem to be available for apple trees. In the future, whole canopy, single leaf, fruit and wood CO_2 exchange responses to temperature should be done on various trees under successive changes in temperature or under different constant temperatures during the day, under light and dark conditions, and under constant and naturally changing VPD levels, in order to elucidate many of the questions generated by our experiments.

5. Conclusions

Our results suggest that whole-canopy NCER of apple trees is reasonably stable on sunny days between 10:00 and 13:30 h. Time during the day, light, temperature and/or VPD are likely important sources of variation to consider and monitor. There will always be a trade-off between taking many measurements on the same trees throughout the day and taking fewer measurements on each tree in order to measure more than one "block" of trees on the same day in a reasonable period of time. Therefore the final decision on how to set up the experiment and take the whole-canopy NCER measurements will depend on each particular situation. The use of more chambers with an automated system for data collection would allow measurements of more trees at a shorter period of time and more data to be averaged per tree, leading to even more accurate and precise measurements.

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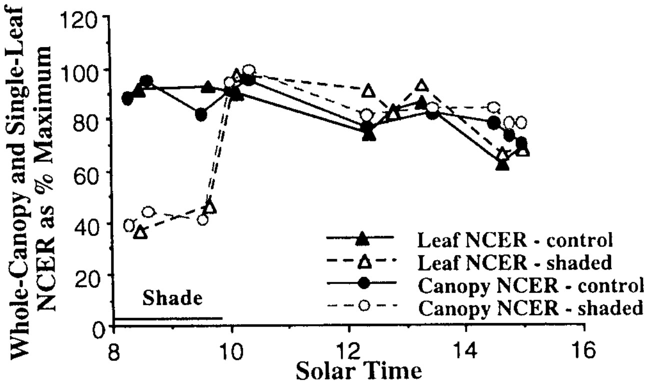

Figure 1. Diurnal pattern of whole-canopy and single-leaf net CO_2 exchange rate (NCER). Treated trees were shaded to 23% of full sunlight until about 9: 50 solar time. Each symbol is the average of three trees. Under full light, average conditions were for tree and leaf chambers: 1500-1660 mmol·m^{-2}·s^{-1} *PPF*, 28.1-31.0°C, and 13.5-23.2 g·m^{-3} VPD. 9 August 1995.

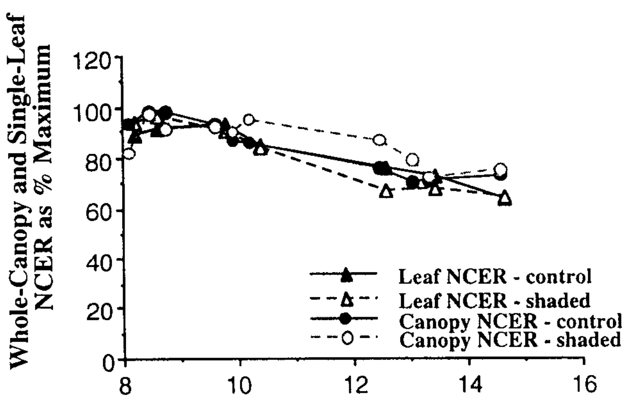

Figure 2. Diurnal pattern of whole-canopy and single-leaf (NCER) in control and in trees shaded to 23% full sunlight for two consecutive previous days. Each symbol is the average of three trees. Under full light, average conditions were for tree and leaf chambers: 1520-164 mmol·m^{-2}·s^{-1} *PPF* , 25.3-28.6°C and 13.5-20.2g·m^{-3} VPD. 30 Aug. 1995.

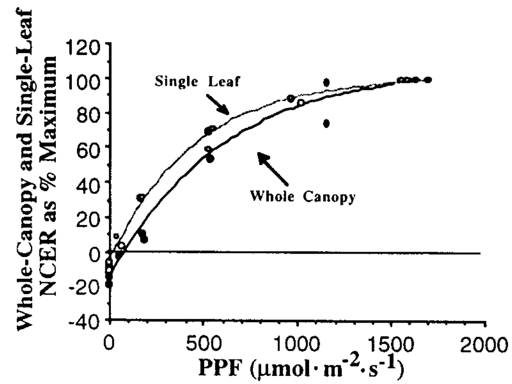

Figure 3. Response of whole-canopy and single-leaf net CO_2 exchange rate (NCER expressed as percentage of maximum rate, to photosynthetic photon flux (*PPI* from 4-year-old 'Empire' apple trees. Pooled data from 2 trees. Negati\ exponential curves were: Whole-Canopy NCER = 106.70 - 122.89] 0.998^{PPF}, R^2 = 0.98; Single-Leaf NCER = 101.23 - 107.82 * 0.998^{PPF}, R^2 0.99. Tree and leaf chambers had an average 30.4-31.7°C and 16.0-20.5 g·m VPD. 18 July 1995.

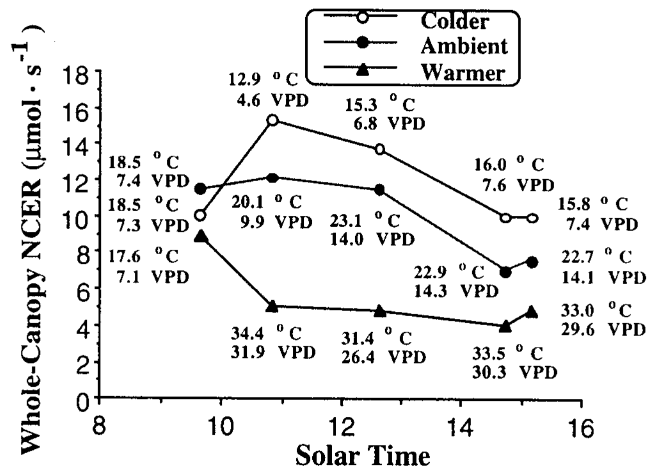

Figure 4. Air temperature effects on whole-canopy net CO_2 exchange rate (NCER) of 4 year-old potted 'Gala' apple trees during the day. Each symbol is the mean of tw(trees. All trees received an average of 1612 ± 51 mmol·m^{-2}·s^{-1} *PPF* during th measurements. 11 Sept. 1995.

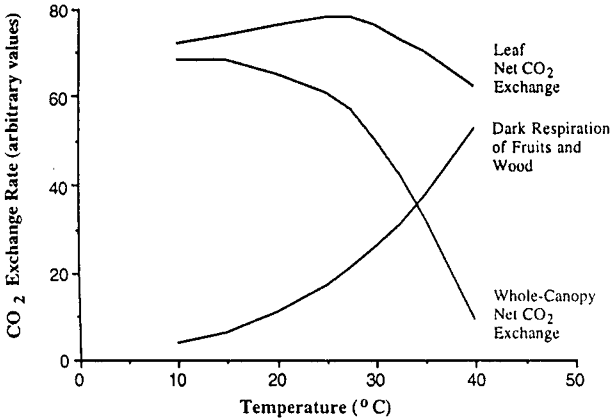

Figure 5. Conceptual diagram of temperature effects on CO_2 exchange rates in the light of single leaf, fruits and wood, and whole canopy of apple trees.