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Photosynthetic Acclimation of Leaves of Three Apple Cultivars as Affected by Growth Under Different Light Regimes

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Abstract

Photosynthetic acclimation of leaves of young 'Delicious,' 'Golden Delicious,' and apple trees (*Malus domestica* Bork.) as affected by growth under full sun or 15% sun and subsequent transfer to the contrasting light regime was studied. Photosynthetic capacity was reduced in 'Granny Smith,' 'Golden Delicious' and 'Delicious' apple leaves when grown under 15% sun. Leaf nitrogen per area (N) was highly correlated with CO_2 assimilation (A), CO_2 assimilation at saturating CO_2 (A_{max}), and carboxylation efficiency (g'_m). The highest N was in leaves grown under the highest photosynthetic photon flux (PPF). Photosynthetic capacity under 15% sun was reduced to a greater extent in 'Granny Smith' compared to 'Golden Delicious' or 'Delicious.' 'Granny Smith,' however, acclimated photosynthetically to shade-to-sun transitions, whereas 'Delicious' did not acclimate. Since photosynthetic capacity was greatly reduced by shade in 'Granny Smith' and since 'Delicious' and 'Golden Delicious' did not acclimate to shade-to-sun transitions, the greatest photosynthetic productivity in these apple cultivars would be obtained by exposing the greatest portion of the canopy to full sun throughout the season.

Introduction

There has been a world-wide trend favoring high-density orchard systems in the production of fruit crops. High-density orchards come into production earlier and maximize yield per unit area. As canopies develop in fruit trees, interior leaves receive much lower PPF than leaves in exposed positions (10, 38). Observations of early leaf senescence inside the canopies of a variety of fruit species perhaps indicate that reduced light intensity in some high-density trellised systems may have long-term negative effects on productivity as dense canopies develop (16).

Shade has been shown to reduce flower initiation (5, 20), fruit set (7, 35), fruit size (3, 17), spur quality and longevity (3, 14), and fruit quality (11, 14). These negative effects of shade in fruit tree canopies likely are related to the reduction of photosynthetic capacity described in shaded leaves of many plants (4).

Leaves growing in high-light environments are light saturated for A at a higher PPF and have higher light compensation points than those growing in low light environment. Differences in sun-and-shade plants have been related to protein content, leaf anatomy, and physiology (1, 4, 6, 27). Growth PPF has been correlated with leaf dry matter per area (LMH) (9, 21, 22, 23, 37, 38), A_{max} (23), N (8, 9, 38), A (8, 9, 10, 22), g'_m (9, 23), and dry matter production in apple (28). Mooney and Gulmann (25) hypothesized that growth PPF would integrate photosynthetic capacity by re-distributing N to leaves exposed to the highest light to maximize daily carbon gain. A similar hypothesis was proposed by Neumann and Stein (26), which states that the most fully exposed leaves have the highest transpiration and receive the greatest proportion of mineral nutrients and hormones associated with high A. These hypotheses have been supported by the studies of Hunt et al., (18) in a C_4 species, *Amaranthus powellii*, by Field (15) with a drought-deciduous chaparral shrub, and by Dejong and Doyle (9) in peach tree canopies. Since

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nitrogen acquisition, translocation, and assimilation is costly in terms of energy, plants such as deciduous trees would benefit most by allocating more nitrogen to leaves exposed to the greatest PPF. This strategy, however, may not be cost effective in trellised orchard environments where limbs that developed under full sun exposure are trained and tied down to wires in the shaded parts of canopies, or where summer pruning immediately exposes leaves which developed in shade to full sun. Canopy shade has been shown to reduce A and LMA in apple (29), grape (16), and citrus (36). Shade-induced loss of photosynthetic ability, however, is not readily reversible with all plant species. Skene (34) has shown that grana thickness in apple leaves increases, and thereby reduces photosynthetic electron transport capacity, when sun leaves are transferred to shade, whereas shade leaves do not have the capacity to reverse this trend when transferred to bright light. This relationship is not true of all fruit trees, as Syvertsen (36) has shown that for citrus leaves, density and carboxylation efficiency was increased upon transfer from 90% shade to full sun.

The purpose of this study was to characterize N, LMA, and photosynthetic gas exchange in three common apple cultivars grown in full sun or 15% sun (85% shade), and then evaluate changes in these parameters when trees were transferred to the light regime opposite of the growth PPF. This work will allow to test the hypothesis of Mooney and Gulman (25) that N and photosynthetic capacity are greatest in leaves grown under the highest PPF, and it will allow to test a second hypothesis that apple does not have the capability to recover photosynthetic capacity by redistribution of N when transferred from shade to full sun. This work also should provide information relevant to managing densely planted trellised apple orchards.

Materials and Methods

Plant Material. One year old trees of 'Redspur Delicious' ('Delicious'), 'Golden Delicious' (Standard), and 'Granny Smith' (standard) apple on M.7 were planted in to 201 pots (67 pots per cultivar) in a 1 soil:2 sphagnum peat:2 perlite (by volume) medium, pH 6.2. The medium was amended with 744 g of treble superphosphate, 496 g potassium nitrate, 496 g magnesium sulfate,4 kg ground calcitic limestone, and 62 g Peters Frit Industries Trace Elements No. 555 (Peters Fertilizer Products, Fogelsville, PA) per cubic meter. Potted trees were pruned to one shoot and fertilized at each watering with 200 mg·liter-1 each of N and K supplied from 517 mg·liter^{-1} KNO_3 and 367 mg·liter^{-1} NH_4NO_3. Fertilizer solution was maintained at pH 6.0 by injecting 75% (w/w) technical grade phosphoric acid into the irrigation system.

Trees of all three cultivars were randomized and grown for 10 weeks following bud break in full sun or in shade covered houses providing 85% reduction in light intensity (15% sun). Midday irradiance (10 AM - 2 PM PST) during the course of the experiment averaged 2430 and 290 mol m^{-2} s^{-1} for full sun and 85% shade, respectively. Leaf length was measured every other day as they approached full expansion and were tagged when leaf length was the same for consecutive measurements. Three fully exposed leaves per tree were tagged at full expansion and gas exchange response to increasing CO_2 was measured. Three different trees served as replicates with three leaves per tree serving as a composite sample for each tree. These same three leaves per tree were removed and dried in a 80°C air forced oven for 48 hours and measured for dry weight and leaf nitrogen. Three leaves per tree that were fully expanded were then tagged. After-which, trees grown in shade were moved to full sun, and those grown in full sun were moved to shade. Three weeks after this transfer, tagged leaves were again measured for gas exchange, dry weight, and leaf nitrogen. Data were analyzed as a completely randomized factorial design with each tree being a replication and factors being: grown in 100% sun, grown in 15% sun, grown in 100% sun and transferred for 3 weeks to 15% sun, and grown in 15% sun and transferred for 3 weeks into 100% sun.

Gas Exchange. Gas exchange measurements were made using an open system and Plexiglass chamber coated on the inside with clear Teflon tape to reduce water vapor adsorption and absorption. Temperature within the chamber was controlled with a peltier plate (Thermoelectric Corporation of America Model 150HC, Chicago, IL) and air circulation over a nickel-plated aluminum heat exchanger was supplied with a small DC fan. Oxygen, N_2, and CO_2 were mixed manually using multiple valves, and flow rates into the mixing chamber were measured with mass flow meters (Hastings Models ST 2663 and ST 2664, Hampton, VA). Response of A to increasing CO_2 was monitored by measuring CO_2 gas exchange in 8 to 10 step increments from low ($<$ 100 μmol.mol^{-1}) to high CO_2 (1000 μmol.mol^{-1}). The reference, sample, and the CO_2 differential concentrations between the inlet and outlet gas from the chamber were measured with an infrared gas analyzer (ADC Model LCA-2, Analytical Development Co., Hoddesdon, Herts, U.K.). Flow rate into the chamber was controlled at 4-liters min^{-1} and the air temperature inside the chamber was controlled throughout at 25 +/- 0.5C. Air and leaf temperature were monitored using thin-wire thermocouples. Vapor pressure deficit (VPD) was maintained at 0.5 to 1.0 KPa by saturating the gas stream in a temperature-controlled water bath, and then drying part of the air stream with silica gel. Vapor pressure of the inlet gas was measured with a dew point hygrometer (EG & G Model 911, EG&G Co., Burlington, MA). Outlet vapor pressure was measured directly within the chamber using an EG & G Model 200 dewpoint hygrometer. Light supplied by a 1000 W metal halide lamp was filtered through 8 cm of water and neutral density screens. The irradiance level was measured with a quantum sensor (LiCor Model LI-180, Lincoln, NE) at the top of the leaves and was maintained between 1400 and 1600 (PPF μmol. m^{-2}s^{-1}). Gas exchange was calculated using standard equations (24).

Data analysis. A logarithmic curve was fitted to the data for A versus intercellular CO_2 (C_i) as reported by Farqzuhar and Sharkey (12). A_{max} (C_i $>$ 500. mol mol^{-1}) was calculated from the plateau phase of the A/C_i curves. Reductions in A_{max} following an environmental stress are indications of non-stomatal limitation of A due to damage to photosynthetic electron transport and thereby regeneration of the substrate RuBP. Carboxylation efficiency was determined from linear regression using the linear portion of the A/C_i curve (0 to 250 μmol.mol^{-1} CO_2). Estimates of g'_m provide a means of assessing the non-stomatal process limiting A following a change in environment, e.g. imposition of water or temperature stress.

Results

Effects of Light: CO_2 assimilation, g'_m, A_{max}, and stomatal conductance to CO_2 (g'_s) were lower in leaves grown in 15% sun or grown in 100% sun and transferred to 15% sun for 3 weeks compared to controls grown and kept in full sun (Table 1). Leaf dry matter per area was also reduced by shade and the response to changes in growth PPF were similar to gas exchange responses (Table 1). Leaf nitrogen per area was lower in shade-grown trees (Table 1).

Effects of Cultivars: When means of cultivars over all light regimes were

Table 1. Gas exchange, leaf nitrogen per area, and leaf dry matter per area (LMA) under different light regimes for pooled values over three apple cultivars.[z]

Light Condition	A (μmol.m^{-2}.s^{-1})	g'_m (mmol.m^{-2}.s^{-1})	A_{max} (μmol^{-2}.s^{-1})	g'_s (mmol.m^{-2}.s^{-1})	LMA (mg.cm^{-2})	Leaf N (mmol.m^{-2})
100%	21.5 a[y]	150.0 a	38.0 a	169.0 a	9.9 a	210 a
15%	14.2 b	85.7 b	26.3 b	101.6 b	7.4 b	150 b
15 to 100%	20.7 a	152.3 a	32.7 a	163.3 a	9.7 a	195 a
100 10 15%	15.3 b	94.3 b	26.0 b	141.6 ab	8.8 ab	170 ab

[z] CO_2 assimilation (A) was measured at 365 μmol.mol^{-1} CO_2, 1500 μmol.m^{-2}s^{-1} PPF, 25 C, and vapor pressure deficits < 1 KPa. A_{max} was measured at saturating internal CO_2 ($C_i > 600$ μmol.mol^{-1}). Carboxylation efficiency (g'_m) was estimated from the linear portion of A/C_i curves (0 to 250 μmol.mol^{-1} CO_2).

[y] Mean separation within columns by Duncan's Multiple Range test at 0.05%.

pooled, 'Golden Delicious' had higher A, g'_m, A_{max}, g'_s, and LMA than other cultivars (Table 2). These differences were, however, only significant for g'_m between 'Golden Delicious' and 'Delicious' and for A_{max} between 'Golden Delicious' and 'Granny Smith' (Table 2).

Shade (15% sun) reduced gas exchange more in 'Granny Smith' (A = 10.0, g'_m = 70, A_{max} = 20.1, g'_s = 73), compared to 'Delicious' (A = 16.0, g'_m = 79.0, A_{max} = 28.5, g'_s = 139), or 'Golden Delicious' (A = 16.3, g'_m = 105, A_{max} = 30.8, g'_s = 86); Units for A, g'_m, A_{max}, and g'_s are: μmol.m^{-2}.s^{-1}, mmol.m^{-2}s^{-1}, μmol.m^{-2}s^{-1}, mmol.m^{-2}s^{-1}, respectively.

Changes in Cultivars When Transferred to the Opposite Light Regime: CO_2 assimilation, g'_m, N, and LMA in all cultivars and A_{max} and $g_{,s}$ in 'Golden Delicious' and 'Granny Smith' increased when trees were transferred from 15% to 100% light and decreased when transferred from 100% to 15% light (Table 3). In 'Delicious,' however, A_{max} did not change and g'_s decreased when trees were transferred from 15% to 100% light (Table 3), and the interaction between cultivars and light for g'_s was significant. When leaves from 'Granny Smith' were grown in 15% sun and transferred to full sun, A increased by 135%, g'_m by 139%, A_{max} by 71%, and g'_s by 138%, whereas increases in 'Golden Delicious' were not as great (Table 3). Gas exchange in 'Delicious' leaves showed very little response to the transfer from shade to full sun (Table 3).

Transfer from full sun to shade (100 to 15%) reduced N by 19 and 27%, respectively, in 'Golden Delicious' and 'Granny Smith,' but by only 7% in 'Delicious' (Table 3). Transfer of shade grown leaves to full sun caused N to increase 18% in 'Golden Delicious', 30% in 'Granny Smith,' and 42% in 'Delicious' (Table 3).

Photosynthetic gas exchange was highly correlated with N (Table 4). Carboxylation efficiency, g'_s, and LMA were also good predictors of A and photosynthetic capacity (Table 4).

Table 2. Gas exchange, leaf N per area, and leaf dry matter per area (LMA) in three cultivars of apple for pooled values over different light regimes.[z]

Cultivar	A (μmol.m^{-2}.s^{-1})	g'_m (mmolCO_2.m^{-2}.s^{-1})	A_{max} (μmolCO_2.m^{-2}s^{-1})	g'_s (mmolCO_2.m^{-2}.s^{-1})	LMA (mg.cm^{-2})	Leaf N (mmol.m^{-2})
'Delicious'	18.0 a[y]	102.0 b	30.0 ab	147.5 a	8.8 a	192.5 a
'Golden Delicious'	18.9 a	143.0 a	34.5 a	155.0 a	9.4 a	177.5 ab
'Granny Smith'	16.9 a	116.8 ab	27.5 b	129.2 a	8.7 a	173.8 b

[z] CO_2 assimilation (A) was measured at 365 μmol.mol^{-1} CO_2, 1500 μmol.m^{-2}s^{-1} PPF, 25 C, and vapor pressure deficits < 1 KPa. A_{max} was measured at saturating internal CO_2 ($C_i > 600$ μmol.mol^{-1}). Carboxylation efficiency (g'_m) was estimated from the linear portion of A/C_i curves (0 to 250 μmol.mol^{-1} CO_2).

[y] Mean separation within columns by Duncan's Multiple Range test at 0.05%.

Table 3. Percentages of changes in CO_2 assimilation (A), carboxylation efficiency (g'_m), CO_2 assimilation at saturating CO_2 (A_{max}), stomatal conductance (g'_s), leaf N per area (N) and leaf dry matter per area (LMA) in three cultivars of apples when trees transferred from 15% sun to 100% and from 100% sun to 15%.[z,y]

Light Condition/Cultivar	A	g'_m	A_{max}	g'_s	N	LMA
15 to 100%						
'Delicious'	+8	+38	0	-7	+42	+32
'Golden Delicious'	+29	+72	+17	+114	+18	+26
'Granny Smith'	+135	+139	+71	+138	+30	+33
100 to 15%						
'Delicious'	-27	-25	-22	-18	-7	-5
'Golden Delicious'	-19	-34	-23	-22	-19	-14
'Granny Smith'	-41	-53	-49	-9	-27	-16

[z] CO_2 assimilation (A) was measured at 365 μmol.mol^{-1} CO_2, 1500 μmol.m^{-2}s^{-1} PPF, 25 C, and vapor pressure deficits < 1 KPa. A_{max} was measured at saturating internal CO_2 ($C_i > 600$ μmol.mol^{-1}). Carboxylation efficiency (g'_m) was estimated from the linear portion of A/C_i curves (0 to 250 μmol.mol^{-1} CO_2).

[y] + indicates an increase and – shows a decrease as compared to the condition under the previous light regime.

Discussion

Leaves of all three apple cultivars had higher A, g'_m, A_{max}, and LMA when grown under high PPF. Since these parameters are associated with high photosynthetic capacity, we suggest that growth PPF determines photosynthetic potential and efficiency in apple leaves. Photosynthetic photon flux level has been correlated with both A and g'_m in peach (9), and in tropical timber trees (23). The higher LMA in leaves grown under high PPF observed here (Table 1), and reported for leaves of other tree species (9, 21, 23, 37, 38) could be due to increased soluble protein, but could also be due to structural changes affecting the leaf anatomy.

Stomatal conductance to CO_2 was about 39.8% higher in high-PPF-grown apple leaves (Table 1). Higher transpiration rates expected with high g'_s may contribute to the high photosynthetic potential of the sun leaves by virtue of the fact that more nutrients and phytohormones associate with high A are accumulated via xylem conductance (16). One such nutrient that would be accumulated through the transpiration stream would be leaf nitrogen. Leaf nitrogen per area has been highly correlated with A (9, 18, 30, 33), A_{max} (32, 37), and g'_m (9). The fraction of nitrogen invested in carboxylation enzymes has been shown to increase with increasing N (31, 32). In this study, N was about 28.6% higher in high PPF grown leaves (Table 1), and these higher levels of N were correlated with A, A_{max}, and g'_m (Table 4). The higher N and photosynthetic capacity observed here in apple leaves supports the hypothesis of Mooney and Gulman (25), which states that nitrogen will be distributed to leaves growing in the highest PPF in order to maximize daily carbon gain.

Photosynthetic gas exchange was lower in 'Granny Smith' leaves grown under low PPF (15% sun) compared to 'Delicious' and 'Golden Delicious.' When grown under high PPF and transferred to 15% sun, A, A_{max}, and g'_m were re-

Table 4. Summary of linear regressions of pooled data of all cultivars over all light regimes relating leaf nitrogen (N), carboxylation efficiency (g'_m), and stomatal conductance to CO_2 (g'_s), and leaf dry weight per area (LMA) to gas exchange measurements.[z,y]

Dependent variable	Independent variable	Y-intercept	Slope	Coefficient of determination (r^2)
N	A	-3.33	0.19	0.50**
N	g'_m	-26.81	0.81	0.30**
N	A_{max}	3.06	0.15	0.37**
g'_m	A	6.84	0.09	0.68**
g'_m	A_{max}	13.29	0.15	0.74**
g'_s	A	5.12	0.09	0.69**
LMA	A	-6.06	2.69	0.52**
LMA	A_{max}	3.28	2.97	0.29**
LMA	g'_m	-98.72	24.50	0.55**

[z] n = 36.

[y] units: A(μmol CO_2.m^{-2}s^{-1}), g'_m (mmol CO_2.m^{-2}s^{-1}), A_{max} (μmol CO_2.m^{-2}s^{-1}), N (mmol.m^{-2}) g'_s (mmol CO_2.m^{-2}s^{-1}).

**, NS: Significant at P = 0.01 or nonsignificant, respectively.

reduced from about 40 to 50% in 'Granny Smith,' whereas the reductions in these parameters were about half as great in 'Delicious' and 'Golden Delicious' (Table 3). We suggest that shade during growth or repositioning limbs into shade could have a greater negative effect on the photosynthetic productivity of 'Granny Smith' compared to 'Delicious' or 'Golden Delicious.'

When grown in low PPF and transferred to full sun for three weeks, leaves of 'Granny Smith' apple dramatically increased A (135%), g'_m (139%), and A_{max} (71%), whereas there was no increase in A or A_{max}, and only a small (38%) increase in g'_m in 'Delicious' apple (Table 3). Thus, it appears that 'Granny Smith' has an acclimation potential to enable high A upon transfer from shade-to-sun, whereas 'Delicious' does not. Leaves of most fruit-tree crops are similar to 'Delicious' in that they cannot acclimate photosynthetically to shade-to-sun transitions (16, 34). However, increases in LMA and photosynthetic capacity have been reported in 'Red Yorking' apple (2) and citrus (36). Ferrar and Osmond (13) observed that a sun clone of *Solanum dulcamara* could increase photosynthetic capacity by increasing Rubisco protein upon shade-to-sun transitions, whereas a shade clone could not acclimate and was damaged by photoinhibition. Since an increase in the amount and activity of the principal leaf protein, Rubisco, almost invariably accompanies acclimation to bright light (4), leaf nitrogen could be an indicator of sun-to-shade acclimation capacity. Leaf nitrogen increased by 30% in 'Granny Smith' and 42% in 'Delicious' when transferred from 15 to 100% sun (Table 3). Thus, the increase in N may not be associated with Rubisco or other enzymes of photosynthetic machinery in 'Delicious' apple leaves. The increased N in 'Delicious' leaves is perhaps associated with structural proteins as indicated by the 32% increase in LMA, and/or in defense compounds. 'Golden Delicious' apple leaves also increased photosynthetic capacity when transferred from shade-to-sun, but the magnitude of the increase was only 29% while the increase in 'Granny Smith' was 135% (Table 3).

The inability to respond photosynthetically to shade-to-sun transitions indicates that 'Delicious' and 'Golden Delicious' may not respond productively to summer pruning. 'Granny Smith' can acclimate to increases in PPF (Table 3), but photosynthetic capacity is reduced to a much greater extent when grown in shade compared to 'Delicious' or 'Golden Delicious.' An orchard management strategy that allows for dense canopy shade to develop for most of the season with summer pruning to increase light just before final sizing of fruit may not result in an increased fruit size in 'Delicious' and 'Golden Delicious' because they cannot respond to the light increase. The same strategy would also be deleterious in 'Granny Smith' because of the dense canopy shade most of the season which drastically reduces CO_2 assimilation. However, it should be kept in mind that summer pruning is not usually done to enhance photosynthesis, but rather to reduce regrowth, and enhance red color development in the fruit. For a solid recommendation for tree training in a high density system and the impact of light penetration on the canopy development, thus fruit quality and bud initiation, several years of data preferably from mature and bearing trees is needed. In this experiment, models for one-year-old trees that are grown with all leaves in the sun or all in the shade are presented. In the orchard situation and in the mature trees, regardless of how dark the canopy interior becomes, many leaves are well exposed that stay that way. Also, in the orchard, form and orientation of hedgerow set an upper limit to potential light interception and also set an upper limit to the extent to which one hedgerow will shade its neighbor (19).

However, based on the conditions and results of this experiment, photosynthetic productivity would be best maximized by training and pruning systems that exposed the greatest amount of foliage to full sun over the entire growing season.

Literature Cited

1. Anderson, J. M., 1986. Photoregulation of the composition, function and structure of thylakoid membranes. Ann. Rev. of Plant Physiol. 37:93-136.
2. Barden, J. A. 1974. Net photosynthesis, dark respiration, specific leaf weight, and growth of young apple trees as influenced by light regime. J. Amer. Soc. Hort. Sci. 99:547-551.
3. Barritt, B. H., C. R. Rom, K. R. Guelich, S. R. Drake, and M. A. Dilley. 1987. Canopy position and light levels on spur, leaf, and fruit characteristics of 'Delicious' apple. HortScience 22:402-405.
4. Bjorkmann, O. 1981. Responses to different quantum flux densities. pp. 47-107. In: O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Zeigler (eds.) Encyclopedia of Plant Physiology, New Series, Vol. 12B: Physiological plant Ecology 1. Springer-Verlag, Berlin/Heidelberg/New York, pp. 47-107.
5. Cain, J. C. 1971. Effects of mechanical pruning of apple hedgerows with a slotting saw on light penetration and fruiting. J. Amer. Soc. Hort. Sci. 96:664-667.
6. Chabot, B. F. and J. F. Chabot. 1977. Effects of light and temperature on leaf anatomy and photosynthesis in Fragaria vesca. Oecologia 26:363-377.
7. Doud, D. S. and D. C. Ferree. 1980. Influence of altered light levels on growth and fruiting of mature 'Delicious' apple trees. J. Amer. Soc. Hort. Sci. 105:325-328.
8. DeJong, T. M. 1982. Leaf nitrogen content and CO_2 assimilation capacity in peach. J. Amer. Soc. Hort. Sci. 107:955-959.
9. DeJong, T. M. and J. F. Doyle. 1985. Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach *(Prunus persica)*. Plant Cell and Env. 8:701-706.
10. Fallahi, E. and J. W. Moon, Jr. 1988. Effects of canopy position on quality, photosynthesis, and mineral nutrition of four citrus varieties. Citrus Report, University of Arizona, College of Agriculture, Series P. 76:5-12.
11. Fallahi, E., J. W. Moon, and Z. Mousavi. 1989. Quality and elemental content of citrus fruit from exposed and internal canopy positions. J. Plant Nutrition. 12:523-534.
12. Farquhar, G. D. and T. D. Sharkey. 1982. Stomatal conductance and photosynthesis. Ann. Rev. Plant Physiol 33:317-345.
13. Ferrar, P. J. and C. B. Osmond. 1986. Nitrogen supply as a factor influencing photoinhibition and photosynthetic acclimation after transfer of shadegrown *Solanum dulcamara* to bright light. Planta 168:563-70.
14. Ferree, D. C. 1989. Influence of orchard management systems on spur quality, light and fruit within the canopy of 'Golden Delicious' apple trees. J. Amer. Soc. Hort. Sci. 114:869-875.
15. Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: Leaf age as a control on the allocation program. Oecologia 56:341-347.
16. Flore, J. A. and A. N. Lakso. 1989. Environmental and physiological regulation of photosynthesis in fruit crops. HortReview 10:111-157.
17. Heinicke, D. R. 1966. Characteristics of 'McIntosh' and Red Delicious apples as influenced by exposure to sunlight during the growing season. Proc. Amer. Soc. Hort. Sci. 89:10-13.
18. Hunt, E. R., J. A. Weber and D. M. Gates. 1985. Effects of Nitrate Application on *Amaranthus powellii* Wats. III Optimal allocation of leaf nitrogen for photosynthesis and stomatal conductance. Plant Physiol. 79:619-624.
19. Jackson, J. E. 1980. Light interception and utilization by orchard systems. pp. 208-267. In: J. Janick (ed.) Horticultural Reviews. Vol. 2. AVI Publishing Company, Inc. Westport, Connecticut.
20. Jackson, J. E. and J. W. Palmer. 1977. Effect of shade on the growth and cropping of apple trees: II. Effects on components of yield. J. Hort. Sci. 52:253-266.
21. Jurik, T. W. 1986. Temporal and spacial patterns of specific leaf weight in successional northern hardwood tree species. Amer. J. Bot. 73:1083-1092.
22. Kappel, F. and J. A. Flore. 1983. Effect of shade on photosynthesis, specific leaf weight, leaf chlorophyll content, and morphology of young peach trees. J. Amer. Soc. Hort. Sci. 108:541-544.
23. Kwesiga, F. R., J. Grace, and A. P. Sandford. 1986. Some photosynthetic characteristics of tropical timber trees as affected by the light regime during growth. Ann. of Bot. 58:23-32.
24. Moon, J. W., Jr., and J. A. Flore. 1986. A basic computer program for calculation of photosynthesis, stomatal conductance, and related parameters in an open gas exchange system. Photosyn. Res. 7:269-279.
25. Mooney, H. A., and S. L. Gulman. 1979. Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants. pp. 316-317. In: O. T. Sorbig, S. Jain, G. B. Johnson, and P. H. Raven (eds.) Topics in Plant Population Biology. Columbia University Press, New York, USA.

26. Neumann, P. M. and Z. Stein. 1983. Xylem transport and the regulation of leaf metabolism. What's New in Plant Physiol. 14:33-36.
27. Nobel, P. S., L. J. Zaragoza, and W. K. Smith. 1975. Relation between mesophyll surface area, photosynthetic rate and illumination level during development for leaves of *Plectranthus parviflorus* Henckel. Plant Physiol. 55:1067-1070.
28. Palmer, J. W. 1988. Annual dry matter production and partitioning over the first 5 years of a bed system of Crispin/M.27 apple trees at four spacings. J. Applied Ecol. 25:569-578.
29. Porpiglia, P. J. and J. A. Barden. 1980. Seasonal trends in net photosynthetic potential, dark respiration, and specific leaf weight of apple leaves as affected by canopy position. J. Amer. Soc. Hort. Sci. 105:920-923.
30. Sage, R. F. and R. W. Pearcy. 1987. The nitrogen use efficiency of C3 and C4 plants. II. Leaf Nitrogen effects on the gas exchange characteristics of *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.). Plant Physiol. 84:959-963.
31. Sage, R. F., R. W. Pearcy, and J. R. Seemann. 1987. The nitrogen use efficiency of C3 and C4 plants III Leaf nitrogen effects on the activity of carboxylating enzymes in *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.). Plant Physiol. 85:355-359.
32. Seemann, J. R., T. D. Sharkey, J. Wang, and C. B. Osmond. 1987. Environmental effects on photosynthesis, nitrogen-use efficiency, and metabolite pools in leaves of sun and shade plants. Plant Physiol. 84:796-802.
33. Sinclair, T. R. and T. Horie. 1989. Leaf nitrogen, photosynthesis and crop radiation use efficiency: A review. Crop Sci. 29:90-98.
34. Skene, D. S. 1974. Chloroplast structure in mature apple leaves grown under different levels of illumination and their response to changed illumination. Proc. R. Soc. Lond. B. 186:75-78.
35. Stephenson, A. G. 1981. Flower and fruit abortion: Proximate causes and ultimate functions. Annu. Rev. Ecol. Syst. 12:253-279.
36. Syvertsen, J. P. 1984. Light acclimation in citrus leaves. II CO_2 assimilation and light, water, and nitrogen use efficiency. J. Amer. Soc. Hort. Sci. 109:812-817.
37. Walters, M. B. and C. B. Field. 1987. Photosynthetic light acclimation in two rainforest Piper species with different ecological amplitudes. Oecologia 72:449-456.
38. Weinbaum, S. A., S. M. Southwick, K. A. Shackel, T. T. Muraoka, W. Krueger, and J. T. Yeager. 1989. Photosynthetic photon flux influences macroelement weight and leaf dry weight per unit of leaf area in prune tree canopies. J. Amer. Soc. Hort. Sci. 114:720-723.

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Improved Rooting of Ottawa 3 Apple Rootstock by Soft Wood Cuttings Using Micropropagated Plants as a Cutting Source

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Abstract

The rooting of Ottawa 3 apple rootstock by softwood cuttings under intermittent mist was improved by using a source of micropropagated plants (63%) in comparison to two conventionally propagated sources (47 and 42%). Softwood cuttings from the micropropagated plants also developed larger root masses than softwood cuttings from the conventional sources. Basal cuttings rooted better than tip cuttings (71 *vs.* 23%).

Ottawa 3 (O.3) is a precocious apple rootstock between M.9 EMLA and M.26 in size-controlling potential (6, 9, 13). The main advantage of O.3 is its resistance to winter injury (2, 12, 15). However, it has the disadvantage of being difficult to propagate by stool-bed-layering (2, 13), the preferred commercial method of apple rootstock propagation. It has been successfully propagated by root cuttings (4), but results with softwood cuttings have been variable. Spangelo et al. (13) reported that rooting of softwood cuttings taken from conventional beds ranged from 34 to 62%, whereas Nelson (8) reported that rooting ranged from 89 to 100%. A 94% success rate was

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