# Canopy Development, Photosynthesis, and Vegetative Growth as Affected by Apple Rootstocks\*

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#### Abstract

Fisheye photographs were taken in 1988 from bud break to terminal bud formation under the canopies of 'Starkspur Supreme Delicious' apple trees on nine rootstocks in the 1980 NC-140 cooperative planting in Simcoe, Ontario. Each photograph was computer-analyzed for the percentage of sky cover. Rootstock affected the amount of structural wood, the rate of canopy development and the final leaf area. However, rootstock did not affect the pattern of canopy development. Photosynthesis (Pn) was measured under field conditions using a LI-COR 6200 portable photosynthesis system. Net Pn rates of trees on dwarfing rootstocks tended to be lower than Pn rates of trees on more vigorous rootstocks. Shoot leaves, spur leaves on spurs without fruit (S-F), and spur leaves on spurs with fruit (S+F) from trees on on M.26 EMLA and OAR 1 rootstocks showed no differences in Pn rates due to rootstock. However, for both rootstocks, shoot leaves had the highest, S+F the lowest, and S-F leaves intermediate Pn rates. Growth and yield components were assessed in 1987 and 1988, by harvest and defoliation of sample branches. Leaves were separated into shoot and spur leaves when harvested. Rootstocks strongly affected the number, area, and dry weight of shoot and spur leaves as well as the distribution between leaf types in both years. Rootstocks affected the number of spurs per cm limb circumference. Spur-leaf characteristics were correlated with yield efficiency while shoot-leaf characteristics were correlated with tree vigor.

Among many factors which limit plant productivity, the interception and utilization of light is one of the most important. Jackson (30) and Hunter and Proctor (29) indicated that yield was directly proportional to the light intercepted. Light interception and light distribution can be partially controlled by tree size. Large leaf areas

(28) coupled with relatively high Pn rates (5) and adequate light exposure make large quantities of assimilated carbon available.

The foliar canopy structure in apple trees develops quickly in the spring due to reserves and preexisting tree framework (12), attaining maximum leaf area within a month of first leaf emergence (22, 24, 40). Apple tree foliage can be divided into two leaf types: shoot leaves and spur leaves. Forshey et al. (24) reported that shoot leaves made up 37% of total leaf number, but 46% of total leaf area in 'Mc-Intosh' tree, since they were larger than spur leaves. Increases in the percentage of shoot leaves were associated with decreases in spur leaves and reduced fruitfulness (25).

The apple tree root system interacts with the aboveground portion of the tree, affecting growth, development, fruiting, and tree size. Rootstocks differ in their influence on partitioning of photosynthetically produced dry matter between fruit and wood, even for genetically distinct rootstocks producing trees of similar size (15). Rootstock effects on Pn may represent a mechanism by which the rootstock exerts its effect on scion growth and productivity. However, various studies report the presence or absence of rootstock effects on scion Pn (3, 8, 14, 36, 44, 45).

This study had three objectives: (a) to characterize rootstock effects on seasonal development of the apple canopy in cropping, orchard-grown

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trees. (b) to investigate the effect of various rootstocks on scion Pn, and (c) to determine if rootstocks can affect shoot and spur-leaf characteristics.

### Materials and Methods

The field study reported here was conducted in the 1987 and 1988 growing seasons on apple trees in the 1980 NC-140 regional project rootstock planting at Simcoe, Ontario (38, 39).

Canopy development: In 1988, fisheye photographs were taken from bud break through and after terminal bud formation at permanently marked positions located 50 cm west and east of the trunk (row direction: north-south), using methods similar to those of Lakso (32, 33) and Hunter and Proctor (29). The images of the canopy were digitized and computer analyzed with software similar to Michaels (37).

Photosynthesis: Photosynthesis was measured using a LI-COR 6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). Pn measurements were taken between the hours 09:00-12:00 (EDT) after terminal buds were formed. Environmental conditions during the season ranged from 22-31 C (leaf temperature), 40-60% (relative humidity), 0.31-0.35 mg liter<sup>-1</sup> (CO<sub>2</sub>), and 1200-2000 μmol m<sup>-2</sup> sec<sup>-1</sup> (PAR). Leaves chosen for measurement were fully expanded, healthy, and positioned in the outer canopy (sun leaves).

This study was divided into three experiments:

Experiment 1. Rootstock effect on shoot-leaf Pn was studied in summer, 1988. Pn measurements were taken on August 30, 31, and September 8. Five mid-shoot leaves from each tree were measured on each day.

Experiment 2. The light response curve of shoot-leaf photosynthesis for trees on M.26 EMLA and OAR 1 rootstocks was studied over an 8-day period (July 18, 20, 25, 1988). The two rootstocks M.26 EMLA and OAR 1 were selected because of their similar tree size but very different growth habits and yield

efficiency. The location of the sun and the presence or absence of cloudy conditions combined to produce a range of light intensities. Exponential curve was fitted, and light compensation point was calculated using the low light data (80–200 µmol m<sup>-2</sup> sec<sup>-1</sup>) linear regression slope.

Experiment 3. Rootstock effect on Pn of different leaf types was examined nine times in 1988, between July 18 and September 26. Leaves were separated into three categories: shoot leaves, spur leaves on spurs without fruit (S-F), and spur leaves on spurs with fruit (S+F). On each measurement date, three leaves were chosen on each tree, one representing each leaf type.

Vegetative growth: In fall 1987 and again in 1988 a representative limb from each tree was chosen (20, 21). All shoot leaves and spur leaves were harvested separately on each sample limb in October, prior to leaf drop. The total foliage area of each leaf type was determined using a LI-3000 Area Meter (LI-COR, Inc., Lincoln, NE.) Following this procedure the leaves from each category were counted, weighed, and then oven-dried at 80°C to a constant weight. Prior to analysis, data were standardized to a per cm limb circumference (PCLC) basis. The number of leaves per cm limb circumference (LFNO), the leaf area per cm limb circumference (LFAR), and the dry weight of leaves per cm limb circumference (LFDW) in each foliage category were determined. In 1988 the number of spurs on each sample limb was counted.

### Results and Discussion

Canopy development: Canopy development as affected by the different rootstocks was examined by plotting the percentage of sky cover against the number of days after bud break (Fig. 1). The exponential curve of foliage development was divided visually into two parts: Stage I consisted

of rapid development until bloom, followed by a phase of slower canopy expansion. In stage II final canopy development was attained and remained stable thereafter. The percentage of sky cover determined by fisheye photography was highly and inversely correlated with photosynthetically active radiation (PAR) levels at the photographic site (r = -0.90, n = 86), as shown previously (29, 32, 33, 34). The initial percentage of sky cover before bud break was accounted for by the structural wood, which differed in amount among rootstocks. Flowering was detected by the fisheye photography and contributed a temporary increase of 5-10% to the percentage of sky cover at bloom. Our study agrees with Lakso (34) in detecting a reduction in leaf area development rate during the bloom period in all rootstocks. This phenomenon resulted from the cessation of growth in spur-leaf canopy as shoot leaves began to develop. In stage I the rate of change in percent sky cover with time corresponded fairly well to tree vigor. The differences in sky cover percentages among trees on all rootstocks, established early in the season as the result of canopy growth-rate differences, were maintained throughout stage II. Between mid-May and mid-June (day 30 to 55 after bud break), canopies developed very rapidly, which agrees with results reported by Lakso (32) and Agha and Buckley (1). Our data suggest that there is no rootstock effect on the dates of scion bud break, full

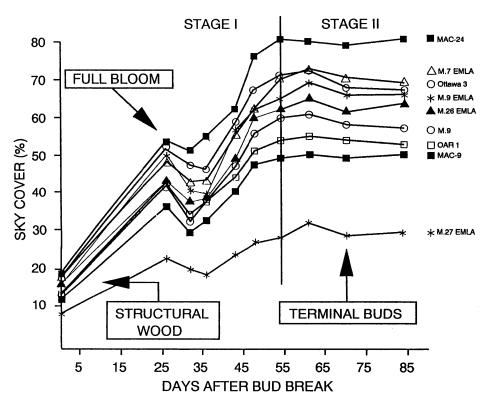


Figure 1. Effect of apple rootstocks on percent sky cover in 1988.

bloom and the establishment of full canopy. This in agreement with Forshey et al. (24) who compared a small tree on M.7 rootstock with a large tree on seedling root. In contrast, Barlow (9, 10) suggested that rootstocks strongly influence the seasonal canopy growth pattern.

Jackson (30) and Agha and Buckley (2) found a linear relationship of yield on light interception for trees on M.9 rootstock in a bed system. In our study, the yield of individual trees on the nine rootstocks in 1988 ranged from 3.2 kg (M.27 EMLA) to 200.3 kg per tree (MAC.24) and was well correlated (r = 0.8, n = 43) with percent sky cover. Our results complement Hunter and Proctor (29) in demonstrating that this relationship also prevails for mature trees on a range of rootstocks.

Photosynthesis: Experiment 1. The largest trees, those on M.7 EMLA and MAC.24, had the highest Pn rate (Table 1). The lowest Pn rate was measured for trees on M.27 EMLA, the smallest trees in this trial. Pn rates for trees on M.26 EMLA, M.9 EMLA, M.9 and OAR 1 did not differ. Ferree and Barden (14) reported that potted trees grown on seedling rootstocks had higher Pn rates that trees on M.7A and MM.106. These results support our observations that trees on the more vigorous rootstocks had higher Pn rates.

Experiment 2. Trees on M.26 EMLA and OAR 1 displayed the normal exponential relationship of Pn to increasing irradiance (Fig. 2) (6, 7, 11, 27, 41, 46). Pn of trees on both rootstocks fit the same relationship. The irradiance at which Pn balanced respiration (compensation point) occurred at about 30 μmol m<sup>-2</sup> sec<sup>-1</sup>. A close value of 24 μmol m<sup>-2</sup> sec<sup>-1</sup> was reported by Proctor et al. (41). Light saturation was reached at about 1000 μmol m<sup>-2</sup> sec<sup>-1</sup> PAR, similar to results of measurements of 'Golden Delicious' Pn carried out in several studies (6, 7, 35, 41, 43). The wide variation of reported apple-tree

Pn rates in the literature was summarized by Avery (5), who concluded that the maximum Pn rate of apple leaves in normal air can be at least 22 µmol CO<sub>2</sub> m<sup>-2</sup> sec<sup>-1</sup>. A large quantity of incident light, high leaf water potential, and a good orchard management program could result in assimilation rates near the maximum value. Proctor et al. (41) found that Pn response to irradiance for the two cultivars 'Golden Delicious' and 'Cox's Orange Pippin' was similar. Differences in yield and yield efficiency of these two rootstocks were probably not due to differential photosynthetic responses to equivalent illumination.

Experiment 3. Leaves in the various foliage type did display significant Pn differences (Fig. 3). Shoot leaves consistently had the highest photosynthetic rates, and S+F leaves the lowest. In our study a mean difference of 16% between Pn of shoot and S+F leaves was found. In the 1987 and 1988 seasons and under various environmental conditions, similar differences in leaftype Pn were confirmed for trees on the rootstocks M.9 EMLA, MAC-9, and M.7 EMLA. In this study shoot leaves were 30-40 days younger than S-F and S+F leaves, and were most exposed to illumination, which may explain why they consistently showed the highest Pn rates. Rom and Ferree

Table 1. Rootstock effect on shootleaf photosynthesis in 1988.

Rootstock	Photosynihesis <sup>2</sup> $\mu$ mol m <sup>-2</sup> sec <sup>-1</sup> )	
M.7 EMLA	20.9a	
MAC.24	20.4a	
M.26 EMLA	19.3b	
M.9 EMLA	18.7bc	
M.9	18.6bc	
OAR 1	18.4bcd	
MAC.9	18.3cd	
O.3	18.3cd	
M.27 EMLA	16.8d	

<sup>Z</sup>Means (combined for August 30, 31, and September 8, n = 15) were separated by LSMEANS (P = 0.05).

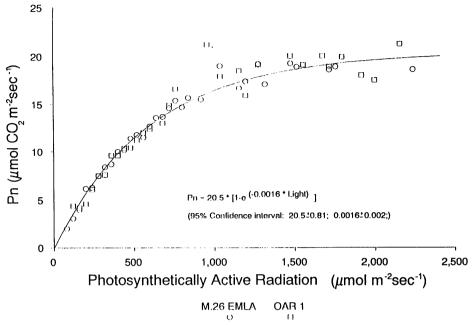


Figure 2. Light response curve for trees on M.26 EMLA and OAR 1 in 1988.

(42) offered an alternative hypothesis, i.e., that the simultaneous development of shoot leaves along with fruit enlargement might have exposed those leaves to particular hormonal and assimilate demand signals. Results reported here suggest that the growth and yield differences of trees on M.26 EMLA and OAR 1 rootstocks were not due to a rootstock effect on the scion-leaf Pn rate per unit leaf area.

Some reports suggest that spur leaves with fruit have the highest Pn rates among apple leaves (26). Proctor et al. (41) reported no effect on Pn after enclosing fruiting spur leaves and followed their Pn before and after fruit removal. Ferree and Palmer (17) found that Pn rates of spur leaves in July did not differ significantly when the spur carried 0, 1, 2, or 3 fruits. Leaves on spurs without fruit in their study had higher Pn rates than on spurs with one or more fruits. Spur ringing reduced apple leaf Pn (16, 17), while Ferree and Palmer (17) detected a reduction in spur-leaf Pn when a bourse shoot was present, indicating a possibility that there were ample carbohydrates available from other sources.

Vegetative growth: Shoot and spur LFNO, LFAR and LFDW differed among rootstocks in both 1987 and 1988. Cropping was very heavy in 1988, much heavier then in 1987. In both years shoot and spur LFAR and LFDW were dependent on LFNO rather than leaf area, with the exception of trees on OAR 1 and M.27 EMLA, which had considerably smaller mean area per spurleaf than on other rootstocks. Shoot leaves were about 50% larger in area and twice as heavy as spur leaves on all rootstocks in both years. However, the mean area per leaf was smaller for shoot and spur leaves in 1988 vs. 1987. Forshey and Marmo (23) reported cropping effects only on spur-leaf size.

In 1987, the canopy leaf area of trees on the most vigorous rootstocks (MAC.24, M.7 EMLA) was composed primarily of shoot leaves (Fig. 4), while canopy leaf area for the other root-

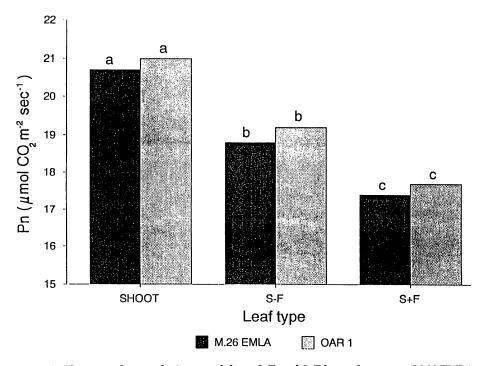


Figure 3. The mean photosynthetic rates of shoot, S-F, and S+F leaves for trees on M.26 EMLA and OAR 1 in 1988.

stocks was divided more or less equally between shoot and spur leaves, as reported by Forshey et al. (24) for 'McIntosh'/M.7. Only trees on OAR 1 had a substantially higher percentage of LFAR (62%) as spur leaves rather than shoot leaves.

In 1988, cropping reduced vegetative growth (4, 18, 23, 31). Trees on all rootstocks except MAC.24 had a higher percentage of canopy area in spur vs. shoot leaves (Fig. 4). The differences in leaf area between the two growing seasons resulted from crop-load related changes in LFNO and actual leaf size. Despite substantial shifts in the proportions of spur and shoot-leaf areas between 1987 and 1988, the total LFAR for each rootstock remained nearly the same for both years except for MAC.9 (Fig. 4). The presence of abnormal tissue development on the rootstock shank of MAC.9 trees, first

noted in 1987 (13), may have contributed to the altered behavior of trees on this rootstock. In other studies, total tree leaf area remained unchanged after treatments such as dormant pruning and deblossoming (23, 34).

Spur counts revealed large differences in spur number per cm limb circumference within the same scion when grown on different rootstocks (Table 2). In 1988, spur number PCLC was highly correlated with limb yield efficiency (LYE, gm/cm limb circumference) (r = 0.65, n = 43), suggesting that rootstocks can influence scion yield potential in part by regulating spur formation.

Shoot LFNO, LFDW and LFAR were highly correlated with trunk cross-sectional area (TCSA) in both 1987 (0.67, 0.71, 0.78 respectively) and 1988 (0.83, 0.84, 0.86 respectively). In contrast, spur leaves showed no corela-

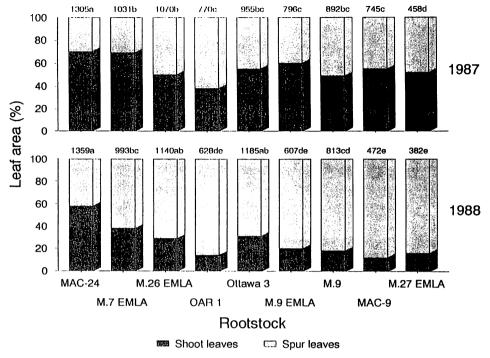


Figure 4. The effect of rootstocks on shoot and spur leaf area distribution in 1987 and 1988 and total leaf area PCLC (indicated above each bar, mean separation by LSMEANS (P = 0.05)). Sequence within bar graph from largest to smallest TCSA.

Table 2. Effect of rootstock on limb yield efficiency and spur number.

	PCLC	
Rootstock <sup>2</sup>	Limb yield efficiency (g)	Spur number
MAC.24	650bcd	15bcd
M.7 EMLA	552bcd	14cd
M.26 EMLA	834ab	20a
OAR 1	442cd	14cd
$O.3^{x}$	1047a	19ab
M.9 EMLA <sup>x</sup>	637bcd	14cd
M.9	724bc	18abc
MAC.9	562bcd	12d
M.27 EMLA	415d	11d

ZArranged in decreasing order of vegetative vigor as measured by trunk cross sectional area. Each mean contains 5 observations except as noted.

tion of any parameter (LFNO, LFEW, and LFAR) with TCSA. Spur-leaf LFNO and LFAR were highly correlated with LYE (r = 0.75 and 0.73 respectively), but the best correlation was established with LYE. The inverse relationship between shoot and spur leaves (19, 22, 23) was evident in this study, as shoot LFNO, LFAR and LFDW were associated with tree vigor while spur-leaf characteristics were linked with LYE.

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<sup>\*</sup>Each mean contains 4 observations.

yMeans within columns separated by LSMEANS (P = 0.05).

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# Pruning Influences on Yield of 'Royalty' Purple Raspberry

A study in New York shows that yield of 'Royalty' was positively related to cane density and length, while fruit size and fruit count per lateral were negatively related to cane and branch length. When branches on tipped canes were shortened in late winter, more buds became fruitful at the proximal end of the branch, but fruiting laterals did not have more flowers or fruit. Fruiting laterals were longer on shortened canes, resulting in a decrease in the fruit:wood ratio. Plants performed similarly whether floricane density was adjusted in late winter or primocane

density was adjusted in late spring. Although potential yield was higher when primocanes were tipped in late spring, harvesting was more difficult because of branch orientation, and the incidence of cane blight infection was higher. Their sutdy suggests that maintaining at least 12 canes per meter of row, avoiding primocane tipping, retaining full cane length, and providing adequate light, moisture, and nutrient levels can result in high yields of large fruit. (From Gundersheim and Pritts. 1991. J. Amer. Soc. Hort. Sci. 116:390-395)