

Effect of crop load on fruiting and leaf photosynthesis of ‘Braeburn’/M.26 apple trees

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Received August 9, 1996

Summary Four-year-old apple (*Malus × domestica* Borkh.) trees cv. ‘Braeburn’ on M.26 rootstock were thinned at full bloom to establish six crop loads ranging from a heavy crop to a deflowered treatment. At harvest, mean yield per tree varied from 0 to 38 kg and mean fruit weight ranged from 225 g in the heaviest cropping treatment to 385 g in the lightest cropping treatment. Light cropping resulted in a significant advance in fruit maturity as indicated by background color, starch/iodine score and soluble solids. There were small differences in leaf photosynthetic rate among the treatments when shoot growth was active. However, in early January, coincident with cessation of shoot growth and maximum rate of accumulation of fruit weight, leaf assimilation rate was reduced by as much as 65% on the deflowered trees compared to the trees carrying the heaviest crop. Leaf assimilation rate showed a curvilinear response to crop load at this time, with little increase in leaf assimilation when crop load exceeded 12 fruit m⁻² leaf area.

Keywords: assimilation rate, fruit maturity, fruit quality, *Malus × domestica*, yield.

Introduction

Computer models of crop growth require a knowledge of the photosynthetic characteristics of the crop plant in question. In fruit trees such as apple, crop load is known to have a large effect on dry matter production and partitioning (e.g., Avery 1975, Heim et al. 1979, Palmer 1992). Consequently, information is needed on the response of leaf gas exchange to crop load. However, many of the published studies are limited to a comparison between fruiting and non-fruiting trees and so there is little information on the form of the response of leaf assimilation to crop load. Palmer (1986) examined the relationship between crop load and leaf photosynthetic rate of apple over a narrow range of crop loads, 88–284 fruit per tree, but found few significant differences over most of the growing season. In a later study, in which a wider range of crop loads was examined, Palmer (1992) observed that, although crop load had a marked effect on dry matter production and partitioning, significant differences in leaf photosynthetic rate between treatments were restricted to the period of maximum fruit dry weight increase. There was no clear relationship

between photosynthetic rate and crop load over most of the growing season.

Flore and Lakso (1989) noted that studies of fruit effects on leaf photosynthesis of fruit crops have given inconsistent results and postulated that the fruit effect would manifest itself only under conditions where leaf assimilation was at its full potential. Therefore, we designed an experiment to examine the effects of a wide range of crop loads on fruiting characteristics and leaf photosynthesis of apple in the high solar radiation environment of New Zealand, on the premise that under these conditions the effect of crop load on leaf gas exchange would be fully manifested.

Materials and methods

Plant material

This study was conducted during the 1993–94 growing season on 4-year-old (*Malus × domestica* Borkh.) ‘Braeburn’ trees on M.26 rootstock, planted at a spacing of 5 × 2.5 m, growing at the Nelson Research Centre, New Zealand. The 30 experimental trees were arranged in a randomized complete block design, with five blocks of six treatments, and trees blocked by trunk circumference. At full bloom (October 15), the trees were thinned to give six crop load treatments. Spur and terminal flower clusters were reduced to two flowers on (1) every cluster, (2) one in two clusters, (3) one in four clusters, (4) one in eight clusters, and (5) one in 16 clusters, with flowers on all other spur and terminal clusters removed. In addition, all lateral flowers on 1-year-old wood were removed. The trees in the sixth treatment were completely deflowered.

Shoot development and leaf area

At the beginning of November, five bourse shoots on non-fruiting spurs were randomly selected and tagged on each tree. The length of each tagged shoot was measured at 10-day intervals from the beginning of November until the beginning of February, when shoot growth had stopped. Leaf dry weight per unit area was determined from a sample of five bourse shoot leaves per tree that were removed at full canopy at the end of January. Leaf area was measured with a Delta-T Mk 2 area meter

(Delta-T Instruments, Cambridge, U.K.) and the leaves were dried in a forced draught oven at 80 °C.

During February, at full canopy, the leaf area per tree was estimated from a sample of leaves on each of 12 trees. Each fiftieth leaf was removed and placed in one of two bags depending on whether it was a spur or extension shoot leaf. The leaves in each bag were counted and their total leaf area measured. This sampling method enabled both the total leaf area and the proportion of spur and extension shoot leaves to be estimated.

At full canopy, black and white photographs were taken, within 1 h of solar noon, of the shadow area that each experimental tree cast on large white boards placed under the tree. Each photograph was digitized with a hand-held scanner (Scanman Model 256, Logitech Inc., Fremont, CA). The area of the shadow was measured with an in-house image analysis program that corrected for distortion due to perspective. A regression analysis between cast shadow area and leaf area per tree for the 12 trees measured in detail was used to estimate the leaf area per tree of the other 18 trees in the study.

Fruit growth, yield and fruit quality

Fruit numbers per tree were counted at the beginning of November, end of December and at harvest on March 28, 164 days after full bloom. Five fruits on different spur clusters were randomly selected and tagged on each tree at the beginning of November. At 10-day intervals from initial fruit set to harvest, maximum fruit diameter was measured on each tagged fruit. A sample of 20 fruits from similar trees in the same orchard block was collected at each measurement time to determine the relationship between fruit diameter and fresh weight. This relationship between fruit diameter and fruit weight was used to convert fruit diameter measurements on the experimental trees to fruit fresh weight.

At harvest, fruit number and fruit weight were recorded for each tree. From a random sample of 20 fruit, the following variates were measured: individual fruit weight, maximum fruit diameter, starch/iodine score (0 = all tissues stained black to 6 = no staining), soluble solids (Atago N-20 hand-held refractometer, Atago Co. Ltd., Tokyo, Japan), background color (on a scale from 1 to 8, green to yellow), % area colored red, seed number and dry matter content.

Leaf photosynthesis

Leaf photosynthesis was measured with an ADC LCA3 infra-red gas analyzer (ADC, Hoddesdon, U.K.) at approximately 15-day intervals from initial fruit set (mid-November) until after harvest. Light-saturated leaf assimilation rate was measured in the morning and the afternoon on sunny days when irradiance on the leaf chamber was in excess of 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. On occasions, because of cloudiness, the morning records of one day were combined with the afternoon records of the next day. The early season measurements were made with the leaf cup described by Palmer (1986), because many of the leaves were not large enough for the Parkinson leaf chamber of the LCA3. Records were taken on fruiting and non-fruiting primary spur leaves until the end of November, thereafter

measurements were made on mature and well-illuminated bourse shoot leaves: basal leaves in the first part of the season, mid-position leaves in the middle of the season and apical leaves towards the end of the season. Records were taken from three randomly selected leaves per tree. All gas exchange measurements were made sequentially on each block, with treatments randomized within each block.

Statistical analysis

Analysis of variance was used to analyze the effect of thinning on leaf photosynthesis, yield and fruit quality at harvest, leaf area, leaf mass per unit leaf area (MLA), trunk cross-sectional area and end of season records of total shoot length. The main effect of thinning was separated into linear and quadratic components. Covariate analysis was used where it improved the efficiency of analysis. Regression analysis was used to examine relationships between cast shadow area and leaf area; fruit fresh weight and fruit diameter; and leaf assimilation rate and crop load on a per tree basis.

Results

The flower thinning treatments produced a wide range of crop loads, with an approximate doubling of fruit numbers with each thinning from the one in 16 to the one in one cluster thinning treatments (Table 1). Consequently, differences between treatments in yield per tree and mean fruit weight were large (Table 1). For the fruitlet samples collected during the season and the harvest samples, the regression for log fruit weight to log fruit diameter accounted for 99.7% of the variance, and yielded similar coefficients to those derived by Clarke (1990). This regression was used to convert fruit diameter measurements made through the season to fruit fresh weight (Figure 1). Figure 1 shows that differences between treatments in mean fruit weight observed at harvest were established early during fruit development in response to flower thinning.

Compared with the light thinning treatments, the heavy flower thinning treatments resulted in fruits that, at harvest, were more mature as indicated by the background color and starch/iodine score (Table 2), with a statistically significant

Table 1. Effect of flower thinning on yield, fruit number and mean fruit weight per tree at harvest of 'Braeburn'/M.26 apple trees.

Treatment	Yield (kg)	Fruit number	Mean fruit weight (g)
1 in 1	38.0	169	225
1 in 2	34.9	123	290
1 in 4	23.4	73	333
1 in 8	11.7	32	369
1 in 16	6.9	18	385
LSD	7.70	35.0	32.9
Linear trend	*** ¹	***	***
Quadratic trend	ns	ns	*

¹ Abbreviations: ns = not significant; * = $P < 0.05$; *** = $P < 0.001$.

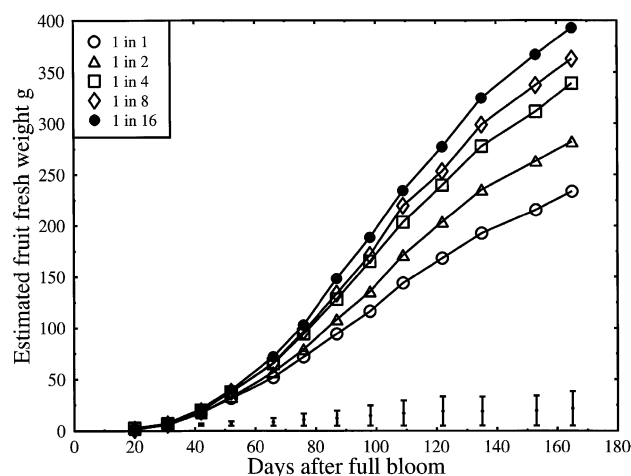


Figure 1. Effect of flower thinning on fruit growth of 'Braeburn'/M.26 apple trees. Fruit fresh weight was calculated from the relationship $w = ad^b$, where w = fresh weight (g), $a = 0.00135$, d = fruit diameter (mm) and $b = 2.741$. Bars show the mean standard error for all treatments.

linear trend. Other fruit quality variates (dry matter content, soluble solids and % red blush) also showed significant linear trends with increasing severity of the flower thinning treatments (Table 2). There were no significant effects of flower thinning on the number of seeds per fruit (data not shown),

indicating that treatment effects on fruit quality were not confounded with seed number.

Tree responses to reduced crop load included increased trunk thickening, longer shoots and an increase in leaf dry weight per unit area (Table 3). Although there were clear treatment differences in the amount of shoot growth on the trees, shoot growth ceased after about 80 days in all treatments (Figure 2). The discrepancies between the treatment effects on shoot length shown in Figure 2 and Table 3 may reflect shoot to shoot variation among the small sample of five shoots per tree. For the 12 trees for which leaf area was recorded, the linear regression between cast shadow area and leaf area per tree accounted for 71% of the variance with the intercept not significantly different from zero ($y = 4.03x$). Application of this regression to estimate leaf area per tree on all the trees in the trial (Table 3) yielded a trend of increasing leaf area with lighter crop loads, but it was not statistically significant.

The measurement of total leaf area of an apple tree based on counting all leaves and measuring leaf areas of subsamples of leaves is time-consuming (Palmer 1987). The relationship between cast shadow area and leaf area per tree shows promise as a quick way of estimating leaf area for trees of similar shape. The method can only be used, however, when the shadow areas from individual trees are distinct. It is also important that the photographs are taken at about the same time of day because the cast shadow area depends on solar altitude.

Table 2. Effect of flower thinning on fruit quality of 'Braeburn'/M.26 apples at harvest. All quadratic effects were nonsignificant.

Treatment	Background color score	Red blush (%)	Soluble solids (Brix)	Starch/iodine score	Dry matter (%)
1 in 1	3.6	34.9	10.9	1.4	13.5
1 in 2	3.7	45.2	11.5	1.5	14.7
1 in 4	4.3	43.5	11.6	1.8	15.0
1 in 8	5.0	48.4	12.3	2.0	15.7
1 in 16	5.3	54.6	12.4	2.5	15.6
LSD	0.76	10.07	0.66	0.59	1.05
Linear trend	*** ¹	***	***	***	***

¹ Abbreviations: *** = $P < 0.001$

Table 3. Effects of flower thinning on mean leaf area per tree, leaf mass per unit leaf area (MLA) taken in late January, total number of shoots, total shoot length and mean shoot length per tree, and mean autumn trunk cross-sectional area (TCA) of 'Braeburn'/M.26 apple trees. All variates, except leaf area and MLA, are calculated using spring trunk cross-sectional area (TCA) as a covariate. All quadratic effects were nonsignificant.

Treatment	Leaf area (m ²)	Leaf MLA (mg cm ⁻²)	Number of shoots	Total shoot length (m)	Mean shoot length (cm)	Autumn TCA (cm ²)
1 in 1	8.4	11.5	182	30.3	16.3	20.3
1 in 2	8.7	11.7	199	36.5	17.9	21.4
1 in 4	8.8	13.1	190	36.1	18.5	22.8
1 in 8	9.2	13.4	206	43.2	20.7	25.1
1 in 16	8.7	13.9	190	41.3	21.0	25.7
No fruit	9.3	14.9	224	43.3	19.4	27.0
LSD	1.40	1.38	40.8	12.3	4.12	1.34
Linear trend	ns ¹	***	ns	*	*	*

¹ Abbreviations: ns = not significant; * = $P < 0.05$; *** = $P < 0.001$.

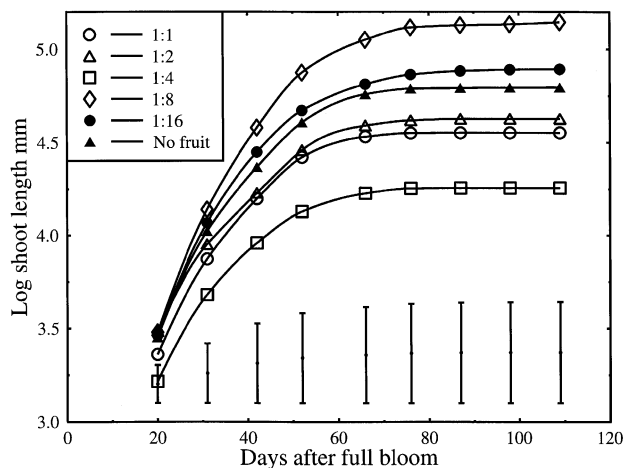


Figure 2. Effect of flower thinning on shoot growth of 'Braeburn'/M.26 apple trees. Bars show the mean standard error for all treatments.

Leaf assimilation rate showed a marked response to crop load (Table 4). Because leaf responses were similar in the morning and afternoon, only the means are presented in Table 4. Decreases in leaf assimilation rates of the non-cropping trees of 50% or more over the rates of heavy cropping trees were recorded from 83 to 109 days after full bloom (DAFB), with highly significant linear trends with flower thinning treatments. Because the thinning treatments applied were in an approximately geometric series, linear trends with treatment are curvilinear with crop load. Figure 3 gives the relationship between crop load and mean leaf assimilation rate for the mean of the 83 and 94 DAFB records, and shows a clear curvilinear response, with little increase in leaf assimilation rate when crop load exceeded 12 fruit m^{-2} leaf area.

After fruit harvest, leaf assimilation rate on the cropping trees fell to rates comparable with those of non-cropping trees within 11 days. This decrease in leaf assimilation rates was a

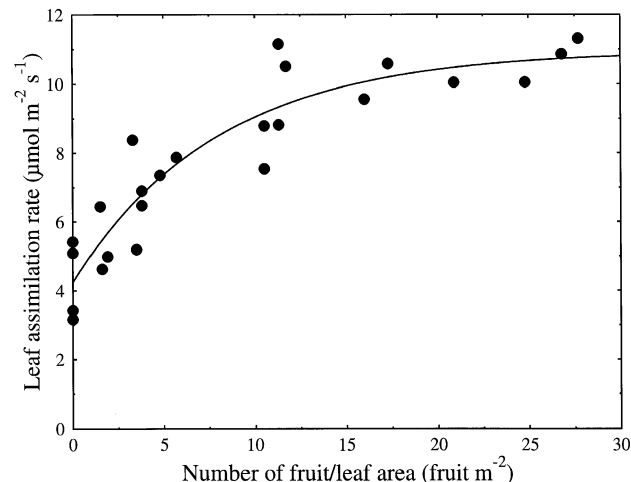


Figure 3. Relationship between mean leaf assimilation rate at 83 and 94 days after full bloom and crop load of individual 'Braeburn'/M.26 apple trees. The fitted curve, $y = 10.96 - 6.72e^{-0.125x}$, accounted for 85% of the variance, where y = mean leaf assimilation rate and x = fruit number per unit leaf area.

direct response to the harvesting of the fruit, because leaf assimilation rates at 175 DAFB of some unharvested trees in the orchard, with comparable crop loads to the heavy cropping trees of the trial, were similar to the rates of the heavy cropping trees at 158 DAFB.

Discussion

Leaf assimilation rate showed a large response to crop load at the time when accumulation of carbohydrates in the fruit was high (Figure 1) and when shoot growth had ceased (Figure 2), indicating that the lightly and non-cropping trees had limited alternative sinks for assimilated carbon. Because the dry weight/fresh weight ratio of 'Braeburn' fruit does not change markedly after about 21 DAFB (J. Wünsche, HortResearch, Nelson, New Zealand, personal communication), the shape of the growth curve for fruit dry weight would be similar to the

Table 4. Effects of flower thinning and date on leaf assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of 'Braeburn'/M.26 apple trees. Data are the means of morning and afternoon readings and harvest was 164 days after full bloom. Mean leaf temperatures for each day's records are given.

Treatment	Days after full bloom									
	25	38	44	59	83	94	109	144	158	175
1 in 1	12.0	15.5	11.0	11.6	10.0	10.8	10.8	12.0	11.5	6.8
1 in 2	11.4	15.1	11.5	11.4	9.8	10.1	9.2	11.9	12.0	6.9
1 in 4	12.4	15.1	10.7	11.0	8.4	9.3	8.8	11.2	10.3	6.1
1 in 8	12.6	14.6	11.4	10.9	6.7	6.7	7.1	9.3	9.2	6.8
1 in 16	11.7	14.1	10.0	10.4	5.7	6.0	6.3	9.1	7.8	7.3
No fruit	11.7	14.4	10.4	9.9	3.6	4.9	5.4	7.7	7.8	7.4
LSD	1.77	1.11	1.63	1.07	2.51	1.85	2.30	1.12	1.36	3.05
Linear trend	ns ¹	**	ns	**	***	***	***	***	***	ns
Leaf temp. (°C)	26.0	22.5	28.0	28.5	30.3	28.5	28.7	26.1	26.0	29.1

¹ Abbreviations: ns = not significant; ** = $P < 0.01$; *** = $P < 0.001$.

fruit fresh weight growth curve shown in Figure 1. The magnitude of the effect of crop load on leaf assimilation rate was large with non-cropping trees exhibiting a 64% lower rate of leaf assimilation at 83 DAFB than heavy cropping trees. This decline is higher than that observed in 'Crispin'/M.27 for a similar range of crop loads (Palmer 1992), and in 'Golden Delicious'/M.27, where trees were completely defruited at different times from 88 DAFB to harvest (Gucci et al. 1995). The crop load effects reported here are also higher than those reviewed by Avery (1975). In contrast, Schechter et al. (1994a) reported that the presence of fruit had no effect on leaf assimilation rate in 'Sturdespur Delicious'/MM.106, despite large differences in dry matter accumulation per limb. Schechter et al. (1994b) concluded that leaf assimilation rate was not regulated by sinks. The discrepancy between this result and our results may be associated with the use of the semi-vigorous rootstock MM.106 in their first study and the use of branch units rather than whole trees in their second study. The large effects of crop load on leaf assimilation rate observed in our study may be related to the high solar radiation in New Zealand; however, the cultivar/rootstock combination and/or the young trees used in this experiment may also have contributed to the magnitude of the response by reducing the size of alternative sinks.

Although the magnitude of the differences in leaf assimilation between the treatments was higher than that reported in other studies, the timing of the effects was consistent with that reported earlier by Palmer (1986, 1992). Similarly, DeJong (1986) found an increase in carbon dioxide uptake in response to fruiting in peach in the June–July period when fruit dry weight accumulation was high.

Leaf assimilation rate showed a curvilinear response to crop load (Figure 3) during January, with little increase in leaf assimilation beyond a crop load of 12 fruit m⁻² leaf area. Palmer (1992) reported a similar response of total dry matter yield per unit leaf area to crop load, with little increase in yield efficiency beyond 10 fruit m⁻² leaf area in 'Crispin'/M.27. The similarities between the two results are striking considering that the cultivars, rootstocks and growth conditions all differed.

The 'Braeburn' trees were probably limited in their ability to divert photosynthate to sinks other than fruit after flower thinning. Although there were significant increases in shoot growth and trunk thickening on the lightly and non-cropping trees, the leaf assimilation data suggest that these sinks were smaller than the fruit sink on the heavy cropping trees. The increase in leaf dry weight per unit leaf area on the lightly and non-cropping trees suggests a build up of starch within the leaf tissues, as a result of a low demand for assimilate. Root growth was not measured in this study so we do not know the size of the sink created by new root growth. Root growth can be severely limited in heavily cropping trees (Palmer 1992). Moreover, Ebert and Lenz (1991) found that root respiration was highest in August, which would roughly correspond to February in New Zealand. It is therefore possible that increased root activity and respiration in lightly and non-crop-

ping trees was responsible for the "recovery" of leaf assimilation rate in late February and March.

Fruit maturity, as indicated by background color, starch/iodine score and soluble solids, showed a clear response to crop load, with earlier maturity on the light cropping trees than on the heavy cropping trees. Faragher and Brohier (1984) noted that both the rise in ethylene production and anthocyanin synthesis occurred 10 days later on 'Jonathan' apple trees carrying 1800 apples per tree compared to trees carrying 500 apples. Similar effects of thinning on fruit maturity of 'Cox's Orange Pippin' were noted by Sharples (1968), but were not seen on the same cultivar by Volz et al. (1993), possibly because their range of crop loads were not sufficiently large.

We found large effects of crop load on fruit yield, maturity and leaf assimilation and demonstrated a feedback effect of sink activity on the activity of the source leaves. Leaf assimilation on non- and lightly cropping trees was reduced in the absence of sink activity, but we found no indication that leaf assimilation was stimulated by sink activity. Although we observed a significant response of leaf assimilation to crop load, care must be taken in extrapolating from single leaf responses to whole canopy assimilation because only well-illuminated leaves from a small fraction of the periphery of the canopy were used for these measurements.

Acknowledgments

John Palmer and Heather Adams acknowledge the financial support of the New Zealand Foundation for Science and Technology, and Rita Giuliani is indebted to the National Research Council of Italy, Special Project RAISA, Sub Project N.2. We are also grateful to Alistair Hall and Dale Ogilvie of HortResearch, Palmerston North, for deriving the image analysis algorithms to calculate cast shadow areas.

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