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# Early Season Patterns of Carbohydrate Partitioning in Exposed and Shaded Apple Branches

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***Abstract.*** **The partitioning of photosynthates labeled by $^{14}CO_2$ in exposed and shaded 'Empire' apple (*Malus domestica* Borkh.) branches was examined at 1, 3, 5, and 10 weeks after bloom. Extension shoots, nonfruiting spurs, or fruiting spurs were labeled separately to examine which shoot types exported to the fruit at each time. The general partitioning patterns were observed with autoradiography, while label accumulation in fruit was determined by oxidation and scintillation counting. At each treatment time, half of the branches was preconditioned with artificial shade (to 35% full light) for 48 hours before labeling and returned to the shade for a 2-day translocation period. One and 3 weeks after bloom, extension shoots showed little export to fruit; nonfruiting and vigorous fruiting spurs exported label to weak spurs and extension shoot tips. Shade had no major effect on partitioning patterns at 1 and 10 weeks, but essentially eliminated export from extension shoots at 3 weeks and greatly reduced export to fruit 5 weeks after bloom, as observed on the autoradiograms. At 5 weeks after bloom, the shading effect was equal to a 2-week delay in export. By 10 weeks after bloom, all shoot types were exporting most of the $^{14}C$ fixed to fruit. The photosynthate support of the fruit before fruit set seemed to strongly depend on the spur canopy, especially when the extension shoots were exposed to low light.**

The production, partitioning, and use of carbohydrates in apple follow specific seasonal patterns (Oliveira and Priestley, 1988). Stored reserves decline during early growth, with a minimum near bloom, and increase thereafter during the summer until leaf fall (Hansen, 1967b, 1971; Hansen and Grauslund, 1973; Hennerty and Forshey, 1971; Kandiah, 1979a). At the onset of new growth in the spring, these reserves are primarily used to produce energy for respiration, while subsequent growth seems to depend primarily on current photosynthate production (Hansen and Grauslund, 1973; Kandiah, 1979b).

If fruit development essentially depends on current photosynthesis, two important components need to be evaluated. The first concerns the partitioning patterns of the photosynthates between vegetative development (the extension shoots and the bourse shoots on fruiting and nonfruiting spurs) and reproductive development (fruit set and growth) (Hansen, 1969, 1971; Johnson and Lakso, 1986a; Quinlan and Preston, 1971). The second deals with the effects of light exposure on leaf photosynthetic characteristics and partitioning patterns (Flore and Lakso, 1989; Quinlan and Weaver, 1970; Tustin et al., 1992).

The vegetative development of extension and bourse shoots seems to have priority over reproductive development in the early season, thus negatively affecting fruit set and fruit growth by cell division (Abbott, 1960; Hansen, 1971; Quinlan and Preston, 1971). At a later stage (5 weeks after bloom and beyond), when shoots either terminate or develop more than enough leaves to support shoot tip growth, C partitioning increases to the fruit. Fruit growth can then be supported by the carbohydrates produced by extension and bourse shoots on fruiting and nonfruiting spurs, in addition to continuing support by primary spur leaves (Ferree and Palmer, 1982; Hansen, 1969; Quinlan and Preston, 1971). This general hypothesis on C fixation and partitioning has evolved from the literature, but more detailed information is needed about C fluxes within the branch in the early part of the growing season.

During the first 5 weeks after bloom, the patterns of C fixation and partitioning can influence fruit set and final fruit size by their effect on fruit growth rates and cell division (Lakso et al., 1989). Working with individual spurs, Tustin et al. (1992) showed that 2 weeks after bloom, 30% to 40% of the C fixed by the primary spur leaves is partitioned to the developing fruit, while the bourse shoot contributes ≤1% of its fixed C. Three weeks later, the primary spur leaves contribute from 50% to 80% of their fixed C to the fruit, while bourse shoot contributions range from 20% to 50%. The nonfruiting spur can also efficiently contribute carbohydrates for early fruit development. At June drop (4 to 6 weeks after bloom), only 18% of the $^{14}C$ absorbed was retained in the nonfruiting spur compared to 70% retention in the wood and leaves of the extension shoot (Hansen, 1969). The integration of these single spur observations into a general whole-branch hypothesis is needed to understand the complex early season C fixation and partitioning patterns and their role in determining apple productivity.

A major determinant of the photosynthetic potential of apple leaves and, therefore, of their capacity to contribute carbohydrates toward plant growth, is light in the previous and current season. Primary spur leaves formed from buds that differentiated in shaded positions have lower specific weight than their well-illuminated counterparts, even when developing early in the season before canopy closure (Tustin et al., 1992). Total leaf area on the spur complex (i.e., primary and bourse leaves) is a function of light

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exposure via leaf area and bourse shoot leaf number. Bourse shoots from shaded parts of the canopy had fewer leaves than fully illuminated ones, and temporary shade (1 week at 35% full sun) reduced bourse leaf mean area but did not affect bourse leaf number up to 8 weeks after bloom (Tustin et al., 1992). In addition, primary spur and bourse shoot leaves developed in shade have a lower specific weight and achieve only a fraction of the photosynthetic rates of well-exposed leaves (Barritt et al., 1991; Flore and Lakso, 1989; Tustin et al., 1992).

The light conditions experienced by the leaves on a developing shoot should affect their transition from net C import to net export if the shoot tip is the top priority sink for the leaves on the shoot. A partially validated model of the C balance of an extension apple shoot (Johnson and Lakso, 1986a, 1986b) predicted that increased light levels would cause earlier and greater C export. Thus, the shade that naturally develops in the apple canopy in the early season may delay export of C from shoots to external sinks, including fruit. If spur leaves cannot meet the demand for C from the fruit before shoot C export begins, fruit development may be limited by insufficient C availability.

Based on this previous work, the following hypotheses were tested:

1) In addition to the fruiting spur itself, nonfruiting spurs are the other major source of carbohydrates for fruit development within the apple branch for the first 3 to 5 weeks after bloom.

2) The exposed extension shoot is not a significant exporter to fruit until 3 to 5 weeks after bloom (when the growing extension shoots typically has at least 12 to 14 unfolded leaves).

3) Shading of the branch will delay the onset of carbohydrate export from extension shoots to the fruit.

The objective of this study was to test these hypotheses by examining, under field conditions, the interactions of developmental stage and shade on the distribution of labeled assimilates after exposing extension shoots, fruiting spurs, and nonfruiting spurs to $^{14}CO_2$.

## Materials and Methods

Three-year-old fruiting 'Empire' apple trees on MM.106 rootstock with M.9 interstock were grown in the field and managed following normal fertilization and pest-management practices. Ninety branches of uniform size, good but not excessive vigor, and flowering were selected for $^{14}C$ labeling studies. Each branch typically consisted of 3- and 2-year-old wood, bearing 2- or 1-year-old spurs, and 1-year-old extension shoots. While dormant, the 1-year-old terminal shoot on each branch was headed back to lateral vegetative buds to stimulate two to four extension shoots at the end of each branch. Flowers were hand-pollinated at full bloom on 7 May, and on 11 May all flowering spurs were hand-thinned to similar initial crops.

The branches were labeled with $^{14}CO_2$ on four treatment dates in late May through mid-July at 1, 3, 5, and 10 weeks after bloom. One shoot type was treated on each branch : one fruiting spur, one nonfruiting spur, or all the extension shoots growing as result of the terminal heading cut. The nonfruiting spur would either be a nonflowering or a flowering spur from which flowers were removed at bloom (observations indicated that there were no apparent differences in behavior). On the first treatment date, three branches per shoot type–light level combination were treated, but at the three subsequent dates, the number was raised to four replicate branches for each of the six treatment–light combinations. In total, 90 branches were analyzed.

Two days before each treatment date, half of the branches was shaded using 35% transmission black Saran shade cloth to cover all shoot types. The shade cloth was removed just before and replaced soon after labeling was complete. Five μCi $^{14}CO_2$ was released by acid hydrolysis from $NaH^{14}CO_3$ inside a polyethylene bag enclosing the shoot or spur to be labeled under clear or mostly sunny conditions. Typically, the labeling period lasted a minimum of 1 h. Fruit on fruiting spurs were included in the labeling bag. In the extension shoot treatment, all new shoots were enclosed and received $^{14}CO_2$, with a few exceptions at the later dates when the shoots were too large for all to be included in the treatment bag. On the fourth treatment date, due to the large leaf area that had developed on the extension shoots (some of which were 80 cm long), 10 μCi $^{14}CO_2$ was used per branch. In all treatments, a 48-h translocation period was allowed after labeling; then the branches were excised at the base, enclosed in plastic bags, and held at 4C while layouts for autoradiography were prepared.

The layouts for autoradiography were pressed and dried rapidly in a forced-draft oven for at least 2 days at 105C, then mounted with X-ray film (size 35 × 43, O-MAT AR; Kodak, Rochester, N.Y.). The layouts, film, and stiff masonite backings were wrapped in black plastic and placed in a dark room with sufficient pressure to ensure close contact between the film and the plant material. The time of exposure was 3 days for the 1- and 3-week labeling dates. Due to dilution of label in the large number of leaves at 5 and 10 weeks, the film exposure time to define labeling patterns adequately was longer (1 and 4 weeks, respectively). Portions of fruit from all treatment dates were oxidized in a biological oxidizer (model OX 400; Harvey Instrument Corp., Hillsdale, N.J.) and the combustion products were trapped in 15 ml of a 2 Permasorb : 1 Carbosorb (Packard Instrument Co., Downers Grove, Ill.) cocktail. The radioactivity recovered was determined in a scintillation counter (LKB 1209 RACK BETA LKB; Turku, Finland) and counts per fruit were calculated from the fraction of fruit combusted.

Given the degree of variability in the data, which was most likely due to complex systematic phyllotactic influences, and allowing for the potential for alternative analyses, summaries of observations of the autoradiographs are presented to describe the relative patterns of $^{14}C$ label distribution within the branch, according to the type of shoot labeled and the date of labeling (Tables 1–4). Data for each branch are presented as individual differences in shoot counts, locations, and phyllotaxy induced nonrandom variation. The disintegrations per minute (DPM) counts from the fruit were log-transformed, since the standard deviations increased linearly with the means. For the extension shoots at 10 weeks, the counts were divided by two before analysis to adjust for the double amount of label used for those shoots. The counts were then subjected to analysis of variance at each date in a factorial arrangement of light exposure, shoot type, and their interactions.

## Results

One week after bloom (fruit diameters ≈5 to 7 mm, about four to eight unfolded leaves on extension shoots), little or no apparent export was observed from the extension shoots, whether exposed or shaded (Table 1). The fruiting spurs, however, showed limited export to vegetative shoot tips on extension shoots and to the bourse shoot tips and fruit of other spurs. A similar pattern was observed when the nonfruiting spurs were labeled, although the

Table 1. Apparent patterns of distribution of $^{14}C$ label on autoradiograms after labeling three shoot types with $^{14}CO_2$, branch composition, and total fruit disintegrations per minute (DPM) recovered 1 week after full bloom.

| Exposure | Export pattern from autoradiograms[z] | Branch composition: No. of spurs +Fruit | Branch composition: No. of spurs −Fruit | Branch composition: No. extension shoots | Branch composition: No. of fruit[y] | No. fruit observed with label[x] | Total DPM in fruit per branch (1000s)[w] |
|---|---|---|---|---|---|---|---|
| | | *Fruiting spurs labeled* | | | | | |
| Light | Export to shoot tip | 5 | 1 | 3 | 9 | 8 | 0.26 |
| | Export to bourse tip | 8 | 3 | 3 | 17 | 8 | 0.46 |
| | Export to shoot and bourse tip | 6 | 1 | 3 | 11 | 10 | 0.12 |
| | | | | | | Mean | 0.28 |
| Shade | Traces to shoot tip | 3 | 1 | 5 | 5 | 4 | 1.31 |
| | Traces to shoot tip | 4 | 2 | 4 | 6 | 1 | 0.92 |
| | No apparent export | 13 | 1 | 1 | 26 | --- | --- |
| | | | | | | Mean | 1.12 |
| | | *Nonfruiting spurs labeled* | | | | | |
| Light | Export to shoot, bourse, and fruit | 7 | 1 | 3 | 13 | 3 | --- |
| | Trace to shoot and bourse tip | 2 | 1 | 5 | 3 | 2 | --- |
| | Export to shoot and bourse tip | 2 | 1 | 4 | 4 | 3 | --- |
| Shade | Export to shoot and bourse tip | 4 | 3 | 4 | 6 | 2 | --- |
| | Trace to shoot, bourse, and fruit | 6 | 2 | 2 | 12 | 7 | --- |
| | Trace to bourse tip | 5 | 2 | 3 | 9 | 4 | --- |
| | | *Extension shoots labeled* | | | | | |
| Light | Trace in bourse shoot tip | 4 | 1 | 8 | 8 | 7 | 0.08 |
| | No apparent export | 9 | 1 | 4 | 16 | 8 | 0.06 |
| | No apparent export | 6 | 1 | 3 | 12 | 11 | 0.37 |
| | | | | | | Mean | 0.17 |
| Shade | No apparent export | 3 | 1 | 3 | 6 | 6 | 0.33 |
| | No apparent export | 4 | 1 | 3 | 8 | 8 | 0.20 |
| | No apparent export | 5 | 0 | 1 | 9 | 9 | 0.12 |
| | | | | | | Mean | 0.21 |

[z]Shoot refers to extension shoots, bourse refers to spur lateral bourse shoots.
[y]Total number of fruit per branch.
[x]Number of fruit with apparent label on autoradioagram, excluding those on the treated spur.
[w]Total number of DPM in fruit per branch, excluding counts of fruit on labeled spur.

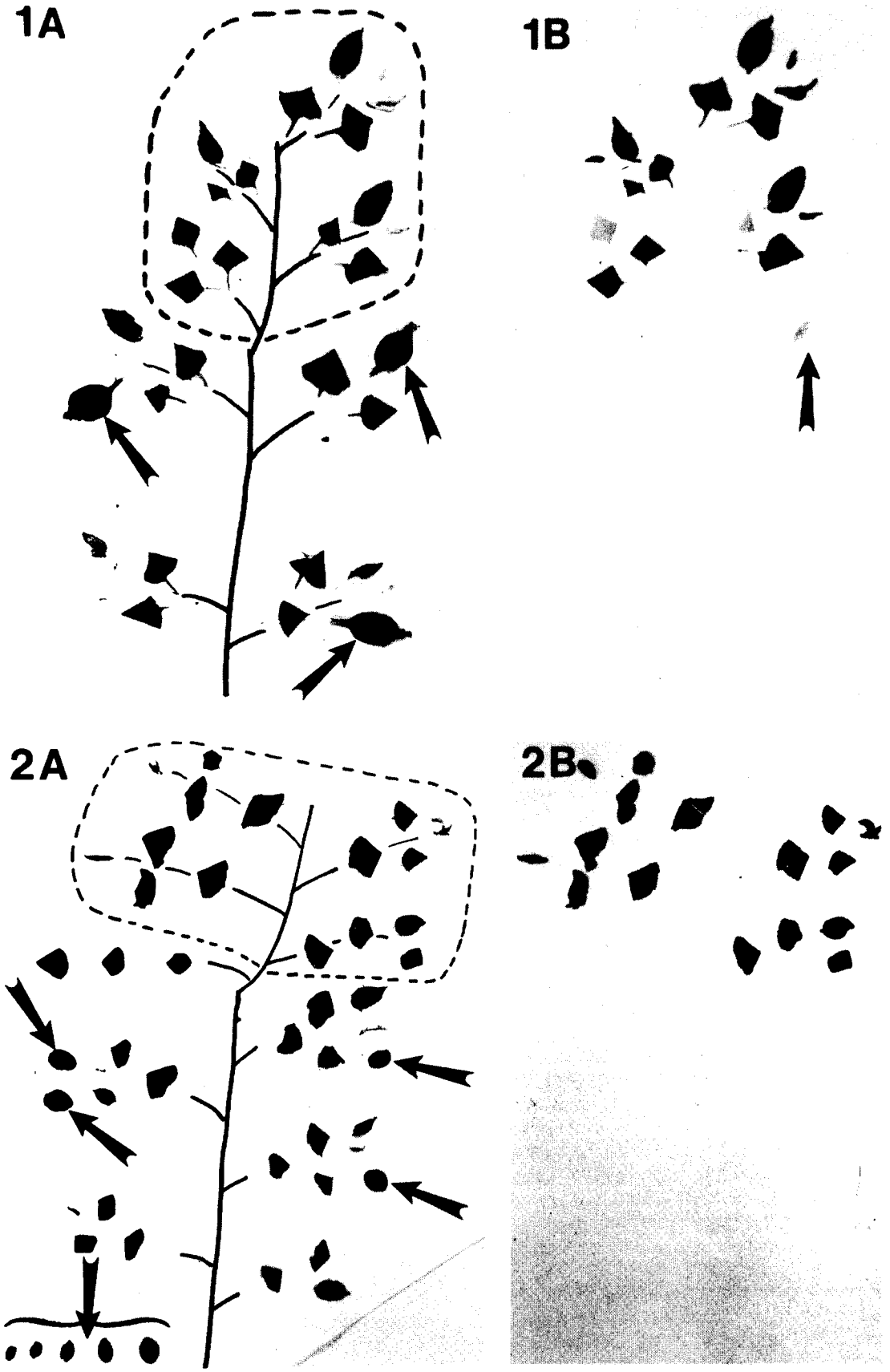
label in the extension and bourse shoot tips was much heavier than with the fruiting spurs. In both spur types, shading seemed to reduce the amount of label translocated, as estimated by the observations of the autoradiograph images (Figs. 1 and 2; Table 1).

Three weeks after bloom (fruit diameters ≈14 to 20 mm, ≈10 to 16 unfolded leaves on extension shoots), a relatively small amount of label fixed by the exposed extension shoots appeared in the fruit and leaves and tips of the bourse shoots (Table 2). Shading extension shoots to 35% of available light eliminated or strongly reduced apparent export of labeled assimilates (Figs. 1 and 2). Fruiting and nonfruiting spurs had similar patterns to those seen at 1 week, with translocation occurring upward to the extension shoot tips and downward to the bourse shoots and fruit on the other spurs. Shading did not prevent translocation, although less label was found in the fruit of the shaded treatments (Table 2). The amounts translocated to fruit on other spurs, however, were 30- to 70-fold larger from the nonfruiting than fruiting spurs, whether exposed or shaded.

Five weeks after bloom (fruit diameters ≈25 to 30 mm, ≈15 to 22 unfolded leaves on growing extension shoots), about one-third of the extension and bourse shoots had set terminal buds and the last fruitlets to drop were abscising. At this time, significant label exported from extension shoots appeared in the fruit; however, shade still caused about a 75% reduction in export of label into fruit based on the mean total DPM in the fruit (Table 3). Generally, no export took place from the fruiting spurs at this stage. In a few cases, some label from a vigorous spur, with only one fruit and 15 to 17 leaves on the bourse shoot, appeared either in extension shoot tips or fruit. The label distribution patterns from nonfruiting spurs were extremely variable and seemed to depend on the phyllotactic location of the relatively few spurs still bearing fruit at this time in relation to the labeled spurs (Table 3). In some cases, export from the nonfruiting spurs was bidirectional, as also shown by Hansen (1969).

Ten weeks after bloom, all extension shoots had set terminal buds and fruit abscission had ceased, leaving an average of two to three fruiting spurs per branch. It seemed that all shoot types could support fruit growth, as label appeared in at least some fruit with all labeling treatments (Table 4). Great variation in amount of label was seen due to the smaller number of fruit at this date and the apparent effect of phyllotaxy on label distribution. At 10 weeks, on average, more label appeared in fruit from the shaded than from the exposed extension shoots, although this seemed to be a function of more fruit on the shaded branches (14 vs. eight); the mean counts per fruit were similar.

Confirming the indications of the autoradiograms, the analyses of variance of fruit DPM revealed clear main effects for shoot type and a main light level effect at 1 and 5 weeks after bloom (Table 5). An exposure–type interaction was found at 3 weeks, as the shade reduced only export from the extension shoots to the fruit,




Figs. 1 and 2. Examples of autoradiograms of label distribution after $^{14}CO_2$ labeling of exposed (1**A** and 1**B**) or shaded (2**A** and 2**B**) extension shoots 3 weeks after bloom in 'Empire' apple trees in the field. The labeled shoots (all extensions on the branch) are within the area enclosed by dashed lines. Due to large numbers of leaves and shoots, portions of leaves along each shoot plus the shoot tip were used in layouts. 1**A** and 1**B** are layouts and autoradiograms of an exposed branch, while (2**A** and 2**B**) are layouts and autoradiograms of a branch shaded to 35% of available light. Arrows on 1**A** and 1**B** indicate locations of fruit on the layouts. Arrow on 1**B** indicates location of fruit with visible label on the autoradiogram.

Table 2. Apparent patterns of distribution of $^{14}C$ label on autoradiograms after labeling three shoot types with $^{14}CO_2$, branch composition, and total fruit disintegrations per minute (DPM) recovered 3 weeks after full bloom.

| Exposure | Export pattern on autoradiograms[z] | Branch composition: No. of spurs + Fruit | Branch composition: No. of spurs –Fruit | Branch composition: No. extension shoots | Branch composition: No. fruit[y] | No. fruit observed with label[x] | Total DPM in fruit per branch (1000s)[w] | DPM in fruit on labeled spurs (1000s) |
|---|---|---|---|---|---|---|---|---|
| | | | *Fruiting spurs labeled* | | | | | |
| Light | Traces to shoot tip | 4 | 3 | 4 | 8 | 7 | 13.26 | 461.8 |
| | Export to shoot tip | 4 | 2 | 2 | 8 | 7 | 2.81 | 367.6 |
| | Traces to shoot bourse and fruit | 3 | 1 | 4 | 5 | 4 | 14.51 | 785.1 |
| | Trace to bourse tip | 5 | 1 | 3 | 9 | 7 | 1.58 | 447.9 |
| | | | | | | Means | 8.04 | 515.6 |
| Shade | No apparent export | 5(t)[v] | | 3 | 9 | 8 | 0.52 | 341.6 |
| | Export to shoot tip and fruit | 2 | 2 | 2 | 3 | 2 | 10.97 | 1160.4 |
| | No apparent export | 5 | | | 9 | 8 | 3.16 | 713.5 |
| | Export to shoot, bourse, trace to fruit | 6 | 4 | 4 | 12 | 11 | 3.31 | 280.4 |
| | | | | | | Means | 4.49 | 624.0 |
| | | | *Nonfruiting spurs labeled* | | | | | |
| Light | Export to fruit | 3(t) | 2 | 3 | 5 | 5 | 587.4 | |
| | Export to shoot, bourse, and fruit | 4 | 1 | 3 | 9 | 5 | 1.4 | |
| | No apparent export | 5 | 1 | 3 | 9 | 9 | 2.4 | |
| | Export to bourse and fruit trace to shoot | 4 | 2 | 3 | 7 | 7 | 328.4 | |
| | | | | | | Mean | 229.9 | |
| Shade | Export to shoot, bourse, and fruit | 3 | 2(t) | 5 | 9 | 9 | 72.4 | |
| | Export to shoot, bourse, and fruit | 6 | 5 | 4 | 12 | 11 | 93.9 | |
| | Export to shoot, bourse, and fruit | 4 | 1 | 3 | 7 | 7 | 43.0 | |
| | Export to shoot tip and fruit | 3 | 1 | 3 | 4 | 4 | 126.3 | |
| | | | | | | Mean | 83.9 | |
| | | | *Extension Shoots Labeled* | | | | | |
| Light | Export to fruit | 3 | 1 | 4 | 3 | 3 | 82.8 | |
| | Export to fruit and untreated extended shoot leaves | 1 | 2 | 3 | 2 | 2 | 51.8 | |
| | Export to fruit and bourse shoot leaves | 3 | 3 | 2 | 3 | 3 | 49.6 | |
| | Traces to fruit | 4 | 2 | 3 | 6 | 5 | 3.1 | |
| | | | | | | Mean | 46.8 | |
| Shade | No apparent export | 6 | 2 | 4 | 10 | 9 | 0.2 | |
| | No apparent export | 5 | 2 | 3 | 9 | 8 | 0.5 | |
| | No apparent export | 3 | 1 | 3 | 7 | 7 | 0.5 | |
| | Traces to fruit and bourse leaves | 3 | 2 | 4 | 4 | 4 | 5.2 | |
| | | | | | | Mean | 6.4 | |

[z]Shoot refers to extension shoots, bourse refers to spur lateral bourse shoots.
[y]Total number of fruit per branch.
[x]Number of fruit with apparent label on autoradiogram, excluding those on treated spur.
[w]Total number of DPM in fruit per branch, excluding counts of fruit on labeled spur.
[v](t) = terminal but set on shoot.

as described above. Overall, the nonfruiting spurs showed the highest export to fruit until at least 5 weeks after bloom (Tables 1–4).

## Discussion and Conclusion

The type and developmental stage of the treated shoots strongly affected the partitioning of the labeled photosynthates during the early part of the season when apple fruit set and size potential are being determined. However, the light levels in the first 5 weeks after bloom seemed to modify these patterns, especially in the extension shoots 3 and 5 weeks after bloom. Export of photosynthates from the extension shoots was not observed until ≈3 weeks after full bloom. The active growth of the shoot tips seemed to consume the available photosynthates until ≈3 weeks after bloom, as was expected. Between 1 and 3 weeks after bloom seems to be the period for the beginning of photosynthate export from exposed extension shoots to the fruit but does not occur until later for shaded shoots. Observations of the many autoradiograms indicated that fully exposed shoots with nine to 17 leaves were able to export label 3 weeks after bloom, but shaded shoots with seven to 18 leaves exported little label. Five weeks after bloom or later, when extension shoots had at least 13 to 22 leaves, export to fruit was substantial. The export of label from shaded shoots at 5 weeks was similar to that of exposed shoots at 3 weeks; therefore, it seems that shading to 35% of full light was equal to the loss of about five to six leaves in terms of shoot C balance.

These results generally agree with those of Hansen (1971), who found that very high levels of fixed label were retained in extension shoots until ≈3 weeks after bloom. Also, the work of Quinlan (1965, 1966) and Johnson and Lakso (1986a) indicates that ≈10 to

Table 3. Apparent patterns of distribution of $^{14}C$ label on autoradiograms after labeling three shoot types with $^{14}CO_2$, branch composition, and total fruit disintegrations per minute (DPM) recovered 5 weeks after full bloom.

| Exposure | Export pattern from autoradiograms[z] | Branch composition: No. of spurs + Fruit | Branch composition: No. of spurs –Fruit | Branch composition: No. extension shoots | Branch composition: No. of fruit[y] | No. fruit observed with label[x] | Total DPM in fruit per branch (1000s)[w] | DPM in fruit on labeled spurs (1000s) |
|---|---|---|---|---|---|---|---|---|
| | | *Fruiting spurs labeled* | | | | | | |
| Light | No apparent export | 1 (t)[v] | 3 | 2 | 1 | --- | --- | 972.9 |
| | Export to fruit | 4 (t) | 1 | 2 | 6 | 5 | 69.0 | 695.9 |
| | No apparent export | 3 (t) | 4 (t) | 3 (t) | 3 | 2 | 0.7 | --- |
| | No apparent export | 2 (t) | 3 (t) | 5 (t) | 2 | 1 | 0.6 | 2373.6 |
| | | | | | | Means | 23.4 | 1347.5 |
| Shade | No apparent export | 4 (t) | 3 (t) | 1 | 7 | 4 | 0.7 | 503.5 |
| | Export to shoot tip and fruit | 2 (t) | 2 (t) | 3 | 2 | 1 | 152.3 | 1058.9 |
| | Export to shoot tip | 1 (t) | 3 | 2 | 1 | --- | --- | 275.6 |
| | No apparent export | 3 (t) | 2 (t) | 3 (t) | 3 | 1 | 0 | 3502.9 |
| | | | | | | Means | 51.0 | 1335.2 |
| | | *Nonfruiting spurs labeled* | | | | | | |
| Light | Export to fruit | 2 (t) | 3 (t) | 1 | 2 | 2 | 1083.8 | |
| | Export to fruit | 5 (t) | 3 (t) | 2 | 7 | 7 | 1514.3 | |
| | No apparent export | 4 (t) | 3 (t) | 2 | 4 | 4 | 3.4 | |
| | No apparent export | 4 (t) | 4 (t) | 3 (t) | 5 | 5 | 24.6 | |
| | | | | | | Mean | 656.5 | |
| Shade | Export to shoot tip | 1 (t) | 3 (t) | 4 (t) | 1 | 1 | 1.3 | |
| | No apparent export | 1 (t) | 3 (t) | 5 (t) | 1 | 1 | 1.5 | |
| | No apparent export | 2 (t) | 2 | 5 (t) | 2 | 2 | 0.7 | |
| | Export to shoot tip | 1 (t) | 4 (t) | 4 | 1 | 1 | 2.3 | |
| | | | | | | Mean | 1.5 | |
| | | *Extension shoots labeled* | | | | | | |
| Light | Export to fruit | 5 (t) | 1 | 3 (t) | 8 | 8 | 314.1 | |
| | Export to fruit | 3 | 1 (t) | 3 (t) | 4 | 4 | 410.7 | |
| | Export to fruit | 2 (t) | 2 (t) | 3 | 2 | 2 | 259.1 | |
| | Export to fruit | 1 (t) | 4 (t) | 3 | 1 | 1 | 102.5 | |
| | | | | | | Mean | 271.6 | |
| Shade | Export to fruit | 2 (t) | 2 (t) | 3 (t) | 3 | 3 | 144.5 | |
| | Traces to fruit | 3 | 3 (t) | 3 | 3 | 3 | 9.2 | |
| | Traces to fruit | 2 (t) | 3 | 2 | 2 | 2 | 89.6 | |
| | No apparent export | 2 (t) | 1 | 2 | 5 | 5 | 8.6 | |
| | | | | | | Mean | 63.0 | |

[z]Shoot refers to extension shoots, bourse refers to spur lateral bourse shoots.
[y]Total number of fruit per branch.
[x]Number of fruit with apparent label on autoradiogram, excluding those on the treated spur.
[w]No other fruit on branch.
[v](t) = Terminal bud set on shoot.

12 unfolded leaves are required on exposed shoots before net export from the shoot occurs. These results are also consistent with the concept that the shoot tip is the top priority sink for the leaves on the shoot.

Treatment time and the presence or absence of fruit influenced the import–export patterns in the spurs. One week after bloom, the leaf area present on the spur was apparently more than sufficient to support the growth of the young fruit, as indicated by the export to other parts of the branch in the case of vigorous spurs. Exported label from fruiting or nonfruiting spurs was distributed distally and proximally in the branches toward the upper extension shoot tips or other spurs. The bidirectional transport was also reported by Hansen (1969) for nonfruiting spurs. The mechanism of this bidirectional transport is not clear.

Three weeks after bloom, during the development of the bourse shoot, vigorous fruiting spurs could still export C outside the spur complex (i.e., spur primary leaves plus bourse shoot and fruit), but they generally required at least nine to 10 leaves and no more than one fruit to exhibit export. Nonfruiting spurs, however, exported to the fruit within the branch ≈30-fold more than fruiting spurs (Table 2). These observations suggest that for exposed spurs with fewer than eight bourse shoot leaves, the demand of one fruit for photosynthates approximates or exceeds spur carbohydrate production by ≈3 weeks after bloom. Normal vigor spurs showed no export and the fruit imported label at this time. Spurs with less leaf area, spurs with multiple fruit, or shaded spurs seem to require significant import of photosynthates to maintain fruit development before 3 weeks after bloom, as observed with import of label from nonfruiting spurs at that time. Photosynthate partitioning at that time seems to be very important for final fruit set and size potential.

Table 4. Apparent patterns of distribution of $^{14}C$ label on autoradiograms after labeling three shoot types with $^{14}CO_2$, branch composition, and total fruit disintegrations per minute (DPM) recovered 10 weeks after full bloom.

| Exposure | Export pattern from autoradiograms[z] | Branch composition: No. of spurs + Fruit | Branch composition: No. of spurs –Fruit | Branch composition: No. extension shoots | No. of fruit[y] | No. fruit observed with label[x] | Total DPM in fruit per branch (1000s)[w] | DPM in fruit on labeled spurs (1000s) |
|---|---|---|---|---|---|---|---|---|
| | | *Fruiting spurs labeled* | | | | | | |
| Light | Traces to fruit | 2(t)[v] | 2(t) | 2 | 2 | 1 | 7.2 | 679.4 |
| | Traces to fruit and spur leaves | 2(t) | 3(t) | 3 | 2 | --- | --- | 1409.3 |
| | Traces to fruit and spur leaves | 2(t) | 2(t) | 3 | 2 | 1 | 4.6 | 744.1 |
| | Traces to fruit and leaves | 2 | 2(t) | 3 | 2 | 1 | 0.6 | 1347.7 |
| | | | | | | Means | 4.1 | 1045.1 |
| Shade | Traces to fruit and spur leaves | 2(t) | 4(t) | 3 | 2 | 1 | 0.3 | 2304.2 |
| | Export to fruit | 4(t) | 1 | 3 | 4 | 3 | 85.7 | 1573.0 |
| | Export to fruit, trace to leaves | 3 | 1 | 2 | 3 | 2 | 6.1 | --- |
| | Export to fruit, trace to leaves | 2(t) | 2(t) | 2(t) | 2 | --- | --- | 6359.6 |
| | | | | | | Means | 30.7 | 3412.3 |
| | | *Nonfruiting spurs labeled* | | | | | | |
| Light | Export to fruit, trace to leaves | 3(t) | 2(t) | 2 | 4 | 4 | 38.4 | |
| | Export to fruit, trace to leaves | 2(t) | 3(t) | 2(t) | 3 | 3 | 15.8 | |
| | Export to fruit | 3(t) | 1(t) | 3(t) | 3 | 3 | 1479.1 | |
| | Export to fruit, trace to leaves | 2(t) | 4(t) | 2 | 2 | 2 | 251.0 | |
| | | | | | | Mean | 446.1 | |
| Shade | Export to fruit and leaves | 2(t) | 4(t) | 4(t) | 4 | 3 | 332.7 | |
| | Export to fruit | 3(t) | 1(t) | 3(t) | 3 | 3 | 154.3 | |
| | Export to fruit, trace to bourse leaves | 2(t) | 2(t) | 2(t) | 3 | 3 | 718.2 | |
| | Export to fruit, trace to leaves | 1(t) | 5(t) | 2(t) | 1 | 1 | 10.6 | |
| | | | | | | Mean | 304.0 | |
| | | *Extension shoots labeled*[u] | | | | | | |
| Light | Export to fruit | 2(t) | 2(t) | 1 | 2 | 2 | 262.0 | |
| | Export to fruit, trace to spur leaves | 2(t) | 3(t) | 2(t) | 2 | 2 | 59.9 | |
| | Export to fruit, trace to spur leaves | 2(t) | 2(t) | 3(t) | 2 | 2 | 144.5 | |
| | Export to fruit, trace to spur leaves | 2 | 2(t) | 2 | 2 | 2 | 144.8 | |
| | | | | | | Mean | 152.8 | |
| Shade | Export to fruit | 2(t) | 3(t) | 3(t) | 5 | 5 | 441.2 | |
| | Export to fruit | 1 | 3(t) | 1 | 3 | 3 | 18.6 | |
| | Export to fruit | 3(t) | 2(t) | 2(t) | 3 | 3 | 539.5 | |
| | Export to fruit | 3(t) | 1(t) | 3(t) | 3 | 2 | 43.7 | |
| | | | | | | Mean | 260.7 | |

[z]Shoot refers to extension shoots, bourse refers to spur lateral bourse shoots.
[y]Total number of fruit per branch.
[x]Number of fruit with apparent label on autoradiogram, excluding those on treated spur.
[w]Total number of DPM in fruit per branch, excluding counts of fruit on labeled spur.
[v](t) = Terminal buds set on shoots.
[u]DPM in fruit are divided by 2 to adjust for the double $^{14}CO_2$ label used at this date on extension shoots; (t) = terminal buds set on shoots.

since a high correlation of final fruit size to fruit relative growth rate in the 1 to 5 week stage has been found (Lakso et al., 1989); also, C balance models indicate a potential limitation of C availability at that time (Lakso and Corelli Grappadelli, 1992). Later in the season, at 10 weeks after bloom, extension shoots and nonfruiting spurs provide carbohydrates for fruit growth in addition to the support of the subtending spur.

The autoradiographs and the actual radioactivity in the fruit indicated that there was great variability in partitioning patterns, especially at 5 and 10 weeks after bloom, when fewer spurs carried fruit due to earlier fruit drop. Effects of phyllotaxy on label distribution were clearly observed in several cases during the season. For example, in one branch, five fruiting spurs imported label; however, two spurs received 99% of the label. This finding agrees with the observations of several workers (Barlow, 1979; Hansen, 1969; Jones and Lamboll, 1980).

Examination of the individual autoradiographs suggested that the partitioning patterns were consistent with 1) phyllotaxy, 2) number of leaves on the subtending spur (i.e., fruit on weak spurs imported more label than fruit on spurs with many leaves), and 3) the relative balance of other exporting sources and competing sinks. These partitioning patterns are consistent with the general understanding in the literature (Hansen, 1967a, 1967b, 1970, 1971; Quinlan and Weaver 1970), but extend the understanding more specifically to the timing and shade effects.

Simulations from the C balance model of Johnson and Lakso (1986b) suggest that shade periods, as used in this experiment, would markedly delay the onset of export from extension shoots. Our results are consistent with these simulations. Although previous studies of shading on partitioning have examined whole-

Table 5. Analysis of variance tables at each time period for log-transformed disintegrations per minute (DPM) counts of $^{14}C$ recovered in the fruit of 'Empire' apple branches with three shoot types labeled at 1, 3, 5, and 10 weeks after bloom.

| | Weeks after full bloom | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | | 3 | | | 5 | | | 10 | | |
| Source | df | MS | $P > F$ | df | MS | $P > F$ | df | MS | $P > F$ | df | MS | $P > F$ |
| Exposure | 1 | 2.76 | 0.052 | 1 | 7.24 | 0.129 | 1 | 41.02 | 0.033 | 1 | 0.37 | 0.749 |
| Shoot type | 1 | 4.02 | 0.026 | 2 | 15.55 | 0.014 | 2 | 31.38 | 0.035 | 2 | 33.12 | 0.001 |
| Exposure × type | 1 | 0.66 | 0.293 | 2 | 11.07 | 0.040 | 2 | 3.76 | 0.617 | 2 | 0.33 | 0.901 |
| Error | 7 | 0.51 | | 18 | 2.86 | | 16 | 7.54 | | 16 | 3.17 | |

season shade on whole-plant (top : root ratios, etc.) partitioning (Oliveira and Priestley, 1988; Palmer, 1986), the results reported here provide more detail of shade effects on localized partitioning to the fruit early in the season.

Also, our trees were relatively vigorous and young; thus, results may be modified in lower vigor trees. The basic patterns should be similar, but if the extension shoots stop growing shortly after bloom, the onset of export would be much sooner than with vigorous shoots. In contrast, low-vigor trees tend to have spurs with a small leaf area and potentially low photosynthetic rates, thus limiting their potential to intercept light and support the fruit. Clearly it is difficult to predict the outcome of these compensating factors.

The results from this study and earlier partitioning studies suggest possible management strategies to improve C availability to the desired fruit during the important cell division period before June drop:

1) Early thinning improves the within-spur source–sink ratio and extends the time in which the spur can support its own fruit.

2) Good nutrition, light exposure, and pruning ensure vigorous spurs with large leaf areas for the reason given above.

3) Good canopy form and management provide high exposure to the spur foliage in the early season.

4) Bending extension shoots to lower angles of growth reduces the demand of the growing shoot tips for C and allows earlier export to the fruit.

All of these techniques have been found to improve apple productivity in practice, yet they seem to have a possible common physiological basis: C production and partitioning.

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