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Differential Effects of Shade on Early-season Fruit and Shoot Growth Rates in 'Empire' Apple

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Abstract. **To determine relative dry-matter partitioning to early-season growth of extension shoots vs. fruits under competitive conditions in the shade, heavily cropping branch sections of 'Empire' apple (*Malus ×domestica* Borkh.) were girdled and shaded to 15%, 40%, and 60% of available light for 9 days, while control branches were girdled and fully exposed. Treatments were applied at both 17 and 27 days after bloom, when fruit diameters averaged 13 and 23 mm, and the number of unfolded leaves on extension shoots averaged 13 and 19, respectively. Fruit diameters, extension shoot lengths, and numbers of unfolded leaves were monitored on the treated branches. Shoot growth was not affected by shading at either growth stage. Fruit growth rate was similar at 100% and 60% available light, but declined 25% at 40% available light and 50% at 15% available light. These results indicate that shoot growth has priority over fruit growth for partitioning in light-limiting conditions early in the season.**

During the first weeks after full bloom (AFB) the growing vegetative and reproductive sinks on an apple tree appear to compete for photoassimilates (Forshey and Elfving, 1989; Hansen, 1977). Growing extension shoots, in particular, appear to compete with early fruit growth for carbohydrates (Quinlan and Preston, 1971). Quinlan (1965) found that the upper eight to nine leaves export assimilates toward the shoot tip, mid-shoot leaves export bi-directionally, and basal leaves export basipetally. He also found that young, rapidly expanding leaves retained much of their labeled assimilates. Further studies with radiolabeled CO_2 by Hansen (1969) and Corelli Grappadelli et al. (1994) and the model of Johnson and Lakso (1986) agree that extension shoots do not start exporting carbohydrates until about a minimum of 10 unfolded (mature and immature) leaves have developed on exposed shoots. These studies did not, however, determine dry-mass growth rates of the shoots and fruits.

The role of light exposure in the patterns of assimilate partitioning has recently been examined. Several studies have shown detrimental effects on fruit growth and fruit set of short periods of shading early during the season, especially around 3–4 weeks AFB, (Byers et al., 1985, 1990, 1991; Kondo and Takahashi, 1987; Lakso and Corelli Grappadelli, 1992; Schneider, 1978). Using $^{14}CO_2$ labeling, Corelli Grappadelli et al. (1994) examined the patterns of carbohydrate partitioning in exposed and shaded branches at different times after bloom. At 1 and 3 weeks after bloom, there was little export to fruit from extension shoots. Artificial shading to 35% of available light completely eliminated export from extension shoots to the fruits at 3 weeks AFB and greatly reduced export at 5 weeks AFB. Shoot and fruit dry-mass growth rates were not measured, however.

Low light levels can reduce fruit growth and set, and increase shoot extension (Byers et al., 1985, 1991; Lakso and Corelli Grappadelli, 1992). However, effects of low light on dry-mass growth and partitioning among shoots and fruits have not been quantified under conditions of heavy competition and limited carbon. Lakso and Robinson (1997) suggested that extension shoot growth is a stronger competitor for carbon than fruit growth early in the season under low light conditions, possibly a response of a perennial plant to improve survival by reducing carbon investment in fruit to allow shoot extension to acquire more light.

The general hypothesis tested in this study was that early in the season the growing shoot tip is the priority sink for carbon so that, under limitations of low light, carbon is disproportionately allocated to shoot growth vs. fruit growth. Accordingly, as light level decreases and total carbon production is reduced on heavily cropping branches, shoot growth would be maintained while fruit growth would be reduced.

Our specific objective was to determine the relative effects of reductions in light levels on early-season fruit and shoot growth on relatively heavily cropping apple branches that were girdled to prevent carbon transport to or from other sites.

Materials and Methods

Healthy, 11-year-old 'Empire'/MM.111 central-leader apple trees of average vigor at the New York State Agricultural Experiment Station orchards in Geneva, N.Y., were used. To provide healthy trees with open canopies, the trees received normal horticultural and pest management programs except for thinning, which was done by hand.

Trees were selected on the basis of uniformly high bloom density, uniformity of shoot lengths, and general appearance. Flower clusters were counted on eight selected, uniform, well-exposed branches on each of four trees (blocks); the few axillary flower clusters on 1-year-old wood were removed. The four light level treatments were randomly allocated to the selected branches on each tree.

Eight comparable fruiting spurs, each with two to three fruits per spur, were marked on each branch. Each branch section had one actively growing terminal extension shoot and ≈20 fruits. The number of fruitlets on the eight spurs was recorded, as was the number of lateral short shoots per branch. On each branch, eight comparable fruits, one per cluster, were selected and tagged for diameter measurements. Branches were girdled below the lowest selected fruiting spur 17 d AFB (6 June) when average fruit diameter was ≈13 mm and extension shoots averaged 13 unfolded leaves. Girdling removed a 2-mm ring of bark to isolate the branch from any carbohydrate transfer from the rest of the tree (Hansen and Christensen, 1974; Palmer et al., 1991). At 27 d after full bloom (16 June), the same experiment was conducted on the remaining four branches on the same trees. The fruits averaged 23 mm in diameter and the shoots averaged 19 unfolded leaves at that time.

Shading was achieved by covering branches with woven strips of black, neutral density polypropylene shadecloth with 35% transmission mounted on curved, half-cylinder wire frames ≈1 m long and with a base diameter of 0.4 m (design by P. Bowen). The woven design was used to simulate the spatial variability of natural shade conditions, since the light environment in a canopy is not uniform. The different shade levels were obtained by varying the number and spacing of strips per frame. The curved frames were oriented ≈N–S so that the direct sunbeams were always near-normal to the shade structure and the degree of shade was reasonably consistent over the day. Actual percentages of photosynthetic photon flux (*PPF*) transmission for the shade structures were determined by calculating the mean light transmission several times over a day using an 80-cm-long ceptometer quantum sensor (Decagon Instruments, Pullman, Wash.). The line sensor was placed both over and under the shade structures in the branch position to estimate transmission.

Treatments were continued for 9 d, after which fruits and shoots were harvested to

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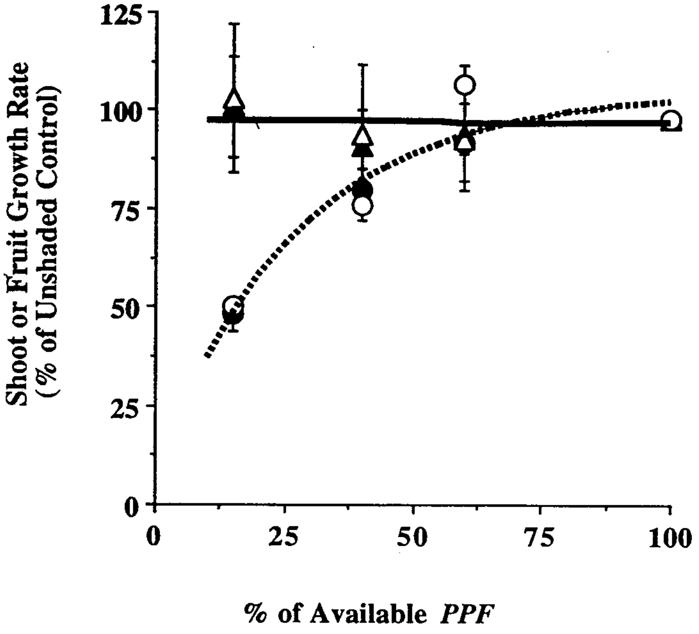

Fig. 1. The relative effects of early-season shading of heavily cropping 'Empire' branches on the growth rate of fruits **(circles)** and extension shoots **(triangles)** during two shading periods. Shade treatments were applied at 17 DAFB (fruit ≈13 mm in diameter, extension shoots with ≈13 unfolded leaves) **(closed symbols)**, or at 27 DAFB (fruit 23 mm, shoots with 19 leaves) **(open symbols)**. Each point is the mean of four shoots or 32 fruits. Dry-mass growth rates of fully exposed controls during the first and second experimental periods, respectively, were 210 and 230 mg·d^{-1} for shoots, and 50 and 80 mg·d^{-1} for fruits. The pooled regressions were: $Y = 97.2 - 0.003X$, $r^2 = 0.01$ for shoots, and $Y = 104.8 - (97.4)(0.9643^X)$, $r^2 = 0.94$ for fruits.

determine final diameter, length, and dry mass. Related studies and observations on effects of girdling branches in the same orchard at the same stage of fruit and shoot development indicated that girdling branches had no significant effects on leaf photosynthesis rates or fruit growth rates for ≈10 d (A. Lakso, unpublished). Shoot and fruit growth rates on the exposed control branches showed no unusual trends over the 9-d period, so it was concluded that the girdling caused no specific effects during the experiment.

Extension shoot length and leaf plastochron index (LPI = number of unfolded leaves longer than 2 cm) (Erickson and Michelini, 1957) were recorded at the beginning of the treatment, and every 3 to 4 d thereafter. Fruit diameters also were measured every 3 to 4 d. At the end of the treatment period, the branches were harvested and fruit diameters and mass, shoot length, LPI, leaf area, and leaf dry mass were determined. Fruit and shoot samples were collected throughout the experimental period from adjacent but similar branches to develop regression equations to estimate dry mass from the nondestructive measurements on the treated branches; r^2 values were >0.9 in all cases. Fruit diameter, shoot length, and leaf plastochron index were measured on the treated branches during the experiment. Shoot leaf areas were measured in the lab with a Decagon image analysis system (Decagon Instruments). Fruit, leaf, and shoot dry masses were measured on samples dried in a forced-draft oven at 70 °C.

Data were analyzed by comparing growth rates of fruits and shoots estimated from dry-mass data. To facilitate comparison between fruit and shoot growth rates, growth rates were expressed as a percentage of the rate of fully exposed controls (100% of available *PPF*). For each experimental period the shoot growth rates vs. available light were best fitted by linear regression, while the fruit growth rates vs. available light were best fitted with negative exponential regressions. The regressions between the two experimental periods were tested and found to be statistically the same; therefore, a pooled regression for the two periods was used to simplify the presentation of results.

Results and Discussion

Shoot growth rates, as measured by terminal shoot extension, dry mass, LPI, or leaf area gain per day, were not affected by shading during either experimental period (Fig. 1). Dry-mass growth rates of the fully exposed shoots for the first and second periods were 210 and 230 mg·d^{-1}, respectively.

Variability in fruit growth rate increased toward the end of the shade period, especially in the first experiment, as some fruit in the 15% light treatment stopped growth and were about to abscise. Therefore, the rates were compared primarily in the first 7 d of the treatment periods. The reduction in fruit growth rates in response to shade was very similar during both periods (Fig. 1). Unlike the shoot growth rates, which were similar at both times, the maximum mean fruit dry-mass growth rates on the exposed controls were ≈50 mg·d^{-1} at the 13-mm stage to ≈80 mg·d^{-1} at the 23-mm stage. This increase in growth rate would be expected since the fruits were still in the cell division phase and had not yet reached the linear growth phase at these times (Bollard, 1970; Lakso et al., 1995).

It was not possible to compile a full dry-mass partitioning of the branch as not all the fruits were measured and other structural growth likely occurred. However, the increase in dry mass of the fully exposed shoots was equal to that of about four 13-mm fruits or about three 23-mm fruits. At 15% of available *PPF*, shoot growth equaled that of about eight fruits at the 13-mm fruit stage and six fruits at the 23-mm stage.

Since the branches had heavy crops and were isolated from other carbon sources by girdling, the carbon supply was probably limiting for the growth of fruits and shoots. Shading these branches reduced the growth rate of fruits while having no apparent effect on the growth of extension shoots. Quinlan and Preston (1971) demonstrated that in full light the shoot tip was a very strong sink, and that removing the shoot tip provided more photosynthates to the fruit. This improved final fruit set as long as the shoot leaves remained. Similarly, the labeling studies of Corelli Grappadelli et al. (1994) showed that shading to 35% of available light reduced or eliminated carbon export from extension shoots to fruits at this early stage of development.

Our results and those of previous studies suggest that the growing shoot tip has priority over the fruit for assimilates, especially under limiting light conditions early in the season when fruit numbers and fruit cell division are establishing the crop potential. Understanding sink priorities is important to understanding apple tree responses to light, to model dry-matter partitioning, and ultimately to optimize apple tree canopy management. These results should be tested on whole trees, however, to confirm the validity of these findings in the orchard.

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