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Influence of Apple Cultivar and Canopy Position on Fruit Spur Leaf Development Within a Season[1]

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Abstract

Flowering and fruiting spur characteristics of 'Granny Smith,' 'Lawspur Rome Beauty' ('Rome') and 'Redchief Delicious' ('Delicious') apples (*Malus domestica*, Borkh.) were examined at two canopy heights throughout a growing season. The first leaves (primary) to develop on the fruiting spur were distinguished from bourse leaves which developed later in the axils of primary leaves and which formed either a rosette of leaves or a short shoot. The primary leaf number/spur (LNO/SP) declined from about eight at full bloom (FB) to five at fruit harvest (FB + 160 days) with all three cultivars. Bourse LNO/SP increased from FB to FB + 104 days and was greatest for 'Granny Smith' and least for 'Delicious.' With each cultivar, bourse leaves had greater area/leaf (LA) and dry weight/leaf (LDW) than primary leaves. Development of primary leaf area/spur (LA/SP) and leaf dry weight/spur (LDW/SP) occurred from 7 days before FB to FB + 21 days. 'Rome' had greater primary LA/SP and LDW/SP than 'Granny Smith' and 'Delicious.' Bourse leaf development started at FB and continued to FB + 104. 'Granny Smith' and 'Rome' had much greater bourse LA/SP and LDW/SP than 'Delicious.' At fruit harvest leaf dry weight/leaf area (LDW/LA, specific leaf weight) was similar for primary and bourse leaves and cultivar differences were small. Cultivar effects were much greater than canopy position effects for all leaf traits except LDW/LA. Fruit dry weight was positively correlated with most bourse leaf traits with 'Granny Smith' but with 'Delicious' the correlations were poor except for LDW/LA.

Introduction

Spurs are the principal sites of apple fruit development (6, 9). The development of spur leaves is essential as early removal of spur leaves and shading of spur leaves reduced fruit set and weight (8, 14, 15, 21). Reduced light level resulted in lower end-of-season spur leaf area and weight with 'Delicious,' and several spur traits were correlated with fruit weight (3). It is not known if all cultivars will show similar reductions in spur leaf area and weight in inside canopy positions with reduced light levels. Spur leaf characteristics differed between cultivars and between strains of 'Delicious' but seasonal development of spur traits was not studied (18, 22, 23). Both pruning and canopy position influenced the seasonal development of spur and shoot leaves (2, 12).

At bloom time apple spurs can be separated into two types, vegetative (non-flowering) and flowering. Flowering spurs may set fruit and become fruiting spurs. By mid-summer when canopy development is complete, vegetative and fruiting spurs differ in leaf number, area and dry weight (3, 12).

The objectives of this study were 1) to compare at two canopy positions the seasonal development of fruiting spurs of 'Rome,' 'Granny Smith' and 'Delicious' and 2) to determine the relationship of spur leaf traits to fruit weight.

Materials and Methods

Flowering spurs and flowering spurs which subsequently set a fruit were collected from 'Granny Smith,' 'Lawspur Rome Beauty,' and 'Redchief Delicious' (Campbell strain) trees, each on MM.106 rootstock, that were 9 to 13 years old and located in a commercial orchard near Wenatchee, Washington. Hand thinning followed

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chemical thinning and provided uniform crop loads. The trees, in north-south rows, were pruned and trained as free-standing, pyramid-shaped central leader trees (11). Trees of all cultivars had filled their allotted space and were being maintained by pruning to a tree height between 2.5 and 3 m and width at the base between 3 and 3.5 m.

Flowering spurs or flowering spurs that had set a fruit (depending on the date) were collected throughout a growing season on eight dates: 13 Apr. (FB - 7), 20 Apr. (full bloom, FB), 27 Apr. (FB + 7), 11 May (FB + 21), 25 May (FB + 35), 15 June (FB + 56), 2 Aug. (FB + 104), and 27 Sept. (FB + 160, fruit harvest). Spurs were collected within a 40-cm-radius sphere centered at the trunk at 1 and 2 m heights in each tree. One spur was collected at each height (canopy position) on 30 trees/cultivar on the eight sampling dates. The 30 replicate trees of each cultivar were randomly selected within the orchard. A high number of replicate trees was used to reduce the effect of early spur removal on subsequent development of spurs to be collected at later dates.

With each fruiting spur, leaves of two types were distinguished: 1) primary leaves, those which emerged first directly below the terminal flower cluster, and 2) bourse leaves, those which emerged later in the axils of primary leaves as either a rosette of leaves (a leafy shoot with extremely short internodes) or as leaves on a bourse shoot. With both primary and bourse leaves, the following characteristics were determined: leaf number/spur (LNO/SP), leaf area/spur (LA/SP), leaf dry weight/spur (LDW/SP), area/leaf (LA), dry weight/leaf (LDW), and leaf dry weight/leaf area (LDW/LA). LDW/LA mg/cm^2), often referred to as specific leaf weight, was determined by dividing LDW/SP by LA/SP. Leaf area measurements were made with a LI-COR (Lincoln, Neb.) area meter (LI-3000/LI-30500). Fruit dry weight was determined at the last three sampling dates. At each date, data were analyzed as a split plot with cultivar as the whole units and canopy position as subunits.

Results and Discussion

Leaf number/spur

Primary LNO/SP (mean of two canopy positions) declined with each cultivar from about 8 leaves at FB - 7 to 5 leaves at harvest (FB + 160) (Fig. 1A). 'Rome' had the highest primary LNO/SP during the first four sampling dates but had the fewest primary leaves for the last three dates. Bourse LNO/SP increased rapidly from FB + 7 to FB + 35 with each cultivar (Fig. 1B). 'Granny Smith' had the highest and 'Delicious' the lowest bourse LNO/SP at each date. Bourse LNO/SP was greater than primary LNO/SP from FB + 35 onward.

Cultivar influenced the distribution of bourse LNO/SP when sampled on 2 Aug. (Fig. 2A). With 'Delicious' an average of 6.3 bourse leaves formed a rosette while with 'Granny Smith' a bourse shoot was produced with an average of 12.5 leaves. With 'Granny Smith' more than 50% of the fruiting spurs had >10 bourse leaves but with 'Delicious' less than 10% of the fruiting spurs had >10 bourse leaves. The distribution of bourse LNO/SP with 'Granny Smith' was influenced by canopy position (Fig. 2B). At the 2 m position over 65% of the spurs had >10 bourse leaves while at the 1 m position only 36% of the spurs had >10 leaves. Spurs at the 1 m height were more shaded in the center of the tree than spurs at the more open part of the tree at the 2 m height. Both vegetative and fruiting spurs of 'Delicious' located in the shaded lower portion of the canopy had reduced LNO/SP (2, 3, 4).

Bourse LNO/SP observed here with 'Redchief Delicious' was similar to the number for 'Starkrimson Delicious' (21). Bourse LNO/SP for 'Rome' and 'Granny Smith' in the present study

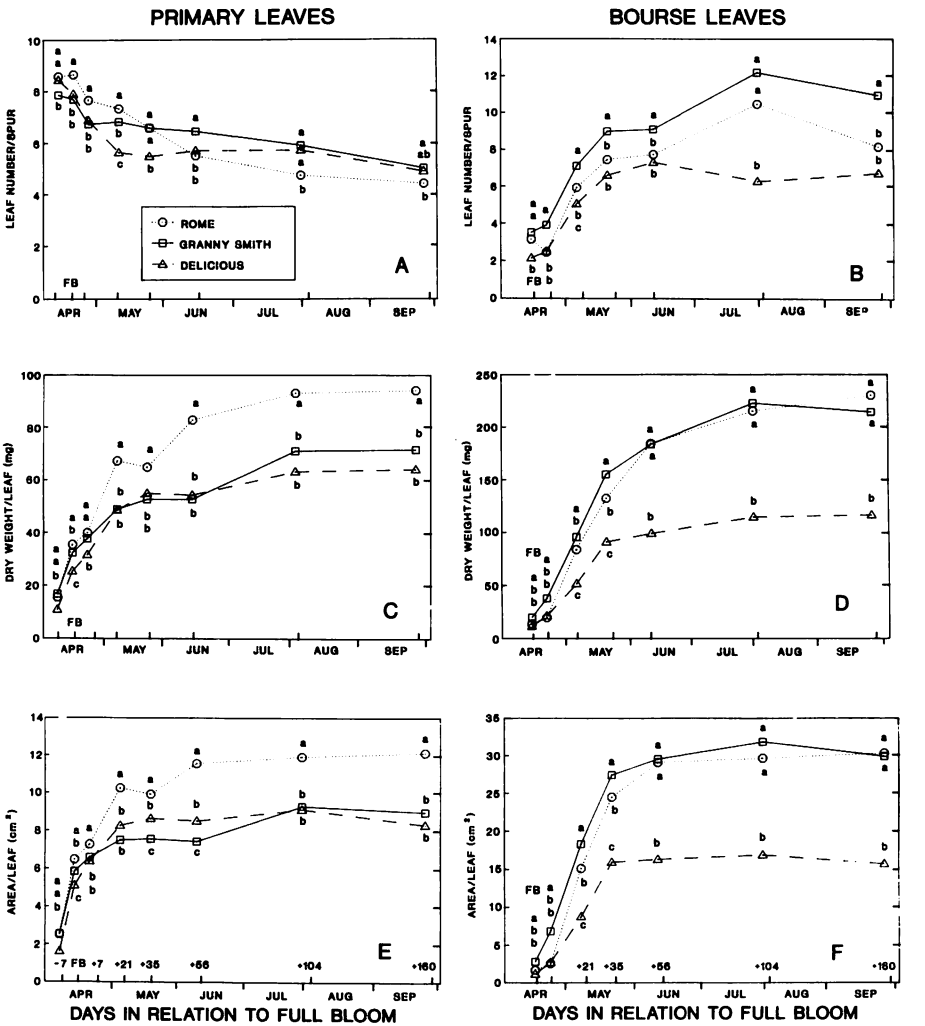

Figure 1. The effect of cultivar on the seasonal development of fruiting spur primary and bourse leaf number/spur (A, B), dry weight/leaf (C, D) and area/leaf (E, F). Note the different Y-axis scale for primary and bourse leaves. Full bloom (FB) was 20 Apr. Mean separation within dates by LSD, 5% level. Data points are means of 60 observations, 30 each at the 1 m and 2 m canopy positions.

were similar to those reported for 'Macspur McIntosh' (10). The total LNO/SP (primary plus bourse leaves) in the present study with 'Redchief Delicious' and in a previous study with 'Oregon Spur Delicious' was similar (3). With all three cultivars total fruiting spurs LNO/SP (primary and bourse) was approximately the same as LNO/SP for vegetative spurs taken from the same trees (2).

Dry weight/leaf and area/leaf

Primary LDW increased rapidly from 7 days before FB to FB + 21 and then increased slightly to FB + 104 (Fig. 1C). 'Rome' had greater primary LDW than 'Delicious' at each date and

greater LDW than 'Granny Smith' on six of eight dates. Bourse LDW for 'Granny Smith' and 'Rome' increased steadily from FB to FB + 104 (Fig. 1D). With 'Delicious' there was little change in LDW after FB + 21. 'Rome' and 'Granny Smith' had similar bourse LDW and each had greater bourse LDW than 'Delicious' on 5 of 7 dates. By FB + 104 bourse LDW was two to three times greater than primary LDW. Cultivar and seasonal trends for LA were similar to those for LDW except that LDW continued to increase later in the season (Fig. 1E, 1F).

Bourse LA was much greater than primary LA with all cultivars in the present study and with 'Oregon Spur Delicious' and 'Starkrimson Delicious' (4, 21). For 'Rome,' 'Granny Smith' and 'Delicious,' fruiting spur bourse LA and LDW were similar to vegetative spur LDW for spurs collected from the same trees (2). With 'Oregon Sour Delicious' LA of vegetative spurs was greater than for fruiting spur bourse leaves which, in turn, had greater LA than primary leaves (4).

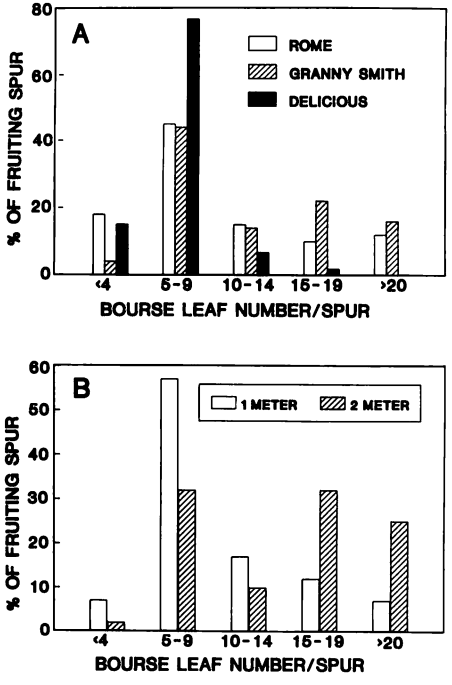

Figure 2. Influence of cultivar (A) and of canopy position with 'Granny Smith' (B) on the distribution of fruiting spurs according to bourse leaf number on 2 Aug. (FB + 104).

Leaf dry weight/spur and leaf area/spur

Primary LDW/SP increased rapidly from 7 days before FB until FB + 21 then changed very little until harvest (Fig. 3A). 'Rome' had greater primary LDW/SP than 'Delicious' at each sampling date and 'Granny Smith' was intermediate.

Bourse LDW/SP increased steadily from FB to FB + 104 with 'Rome' and 'Granny Smith' (Fig. 3B). However, with 'Delicious,' following an initial increase, no additional increase in LDW/SP occurred after FB + 35. Bourse LDW/SP for 'Granny Smith' was greater than for 'Rome' on 5 sample dates and was greater than for 'Delicious' at all sampling dates. Primary and bourse LA/SP had similar cultivar and seasonal trends as LDW/SP (Fig. 3C, 3D).

At harvest, bourse LDW/SP was 7.0, 4.8 and 2.5 times greater than primary LDW/SP for 'Granny Smith,' 'Rome' and 'Delicious,' respectively. Bourse LA/SP with the three cultivars in the present study and with 'Starkrimson Delicious' (21) was greater than primary LA/SP because bourse LA was greater than primary LA and bourse LNO/SP was greater than primary LNO/SP.

Leaf dry weight/leaf area

Primary LDW/LA declined until FB, increased rapidly from FB + 7 to FB + 35 and then increased gradually to harvest at FB + 160 (Fig. 3E). The gradual increase observed with each cultivar from FB + 35 to harvest has also been reported for vegetative spur leaves (2, 4, 19) and for shoot leaves (5, 17, 24). 'Delicious' had lower primary LDW/ LA than 'Granny Smith' on five of eight dates. Bourse LDW/LA declined from FB to FB + 21 and then

increased to the end of the season (Fig. 3F). Cultivar differences in bourse LDW/LA were relatively small and inconsistent throughout the season. With 'Starkrimson Delicious' and the three cultivars in the present study LDW/LA was similar for primary and bourse leaves at the end of the season (21). Differences in vegetative spur LDW/ LA between cultivars and between 'Delicious' strains were small (2, 23).

Source of variation

Cultivar effects were much greater than canopy position effects for all bourse leaf traits except LDW/LA. For LDW on 27 Sept. (FB + 160) 40.1%

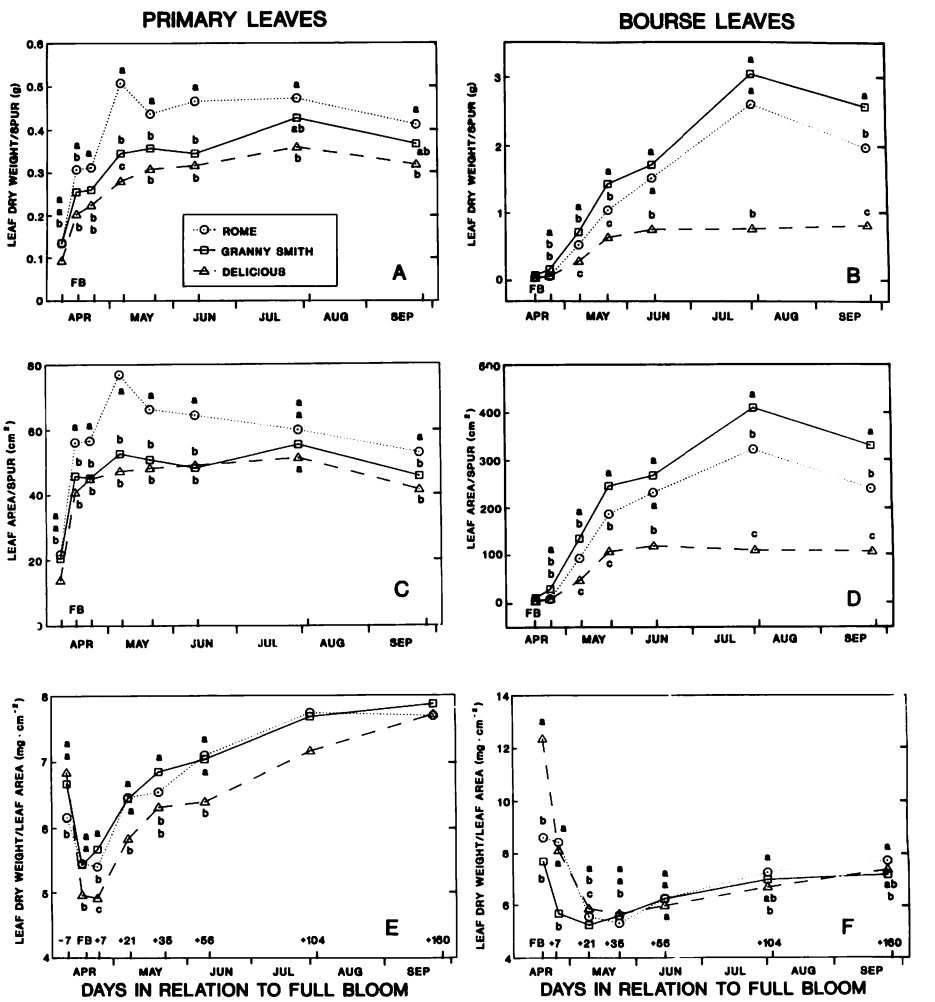

Figure 3. The effect of cultivar on the seasonal development of fruiting spur primary and bourse leaf dry weight/spur (A, B), leaf area/spur (C, D) and leaf dry weight/leaf area (E, F). Note the different Y-axis scale for primary and bourse leaves. Full bloom (FB) was 20 Apr. Mean separation within dates by LSD, 5% level. Data points are means of 60 observations, 30 each at the 1 m and 2 m canopy positions.

and 8.7% of total sums of squares were attributable to cultivar and to canopy position, respectively (both significant F, P = 0.001; CV 27%). For LA 52.7% and 0.4% of total sums of squares were attributable to cultivar and to canopy position, respectively (Cultivar F significant, P = 0.001; CV 23%). On the same date for LDW/LA 2.0% and 33.8% of total sums of squares were attributable to cultivar and to canopy position, respectively (canopy position F significant, P = 0.001; CV 17%). Similar distributions of sums of squares for LDW, LA and LDW/LA occurred on the previous four sampling dates (data not presented) and have also been reported for vegetative spurs (2). The present study confirms that canopy position has a major influence on spur LDW/LA (3, 4, 7, 19). Cultivar had a greater effect on fruit dry weight than did canopy position. On 27 Sept. 59.9% and 9.3% of total sums of squares for fruit weight were attributable to cultivar and to canopy position, respectively (both significant F, P = 0.001; CV 17%).

Relationship between spur leaf traits and fruit weight

Fruit weight with each cultivar was more closely correlated with bourse LDW/LA than with any other spur leaf trait (Table 1). With 'Oregon Spur Delicious' at harvest fruiting spur LDW/LA was also correlated with fruit weight (3). Between 15 and 60% (coefficient of determination) of the variation in fruit weight was associated with spur bourse LDW/LA which indicates that other factors including shoot leaf traits and crop load also contribute to fruit weight. LDW and LDW/SP were correlated with fruit weight with the tip-bearing cultivars 'Rome' and 'Granny Smith' but to a lesser extent with 'Delicious.' Leaf area and leaf number traits (LA, LA/SP and LNO/SP) were not associated with fruit weight in the present study with 'Redchief Delicious' nor in a previous study with 'Oregon Spur Delicious' (3). Vegetative spur LA/SP and LDW/SP of 'Starkrimson Delicious' were correlated with fruit size (7) but when a large number of 'Delicious' strains was

Table 1. Pearson correlation coefficients (r) for the relationship of fruit dry weight with fruiting spur leaf characteristics for 'Delicious,' 'Rome,' and 'Granny Smith' at three dates.

Date[z]	LDW/LA[y]	LDW	LDW/SP	LNO/SP	LA/SP	LA
			'Redchief Delicious'			
27 Sept.	.46***[x]	.43***	.27*	.02	.12	.23
2 Aug.	.53***	.22	.23	.11	.10	.01
15 June	.47***	.34**	.25	.17	.17	.13
			'Lawspur Rome'			
27 Sept.	.39*	.28*	.31	.29*	.28*	.06
2 Aug.	.45***	.40**	.41**	.32*	.35**	.16
15 June	.55***	.54***	.33*	.16	.24	.39**
			'Granny Smith'			
27 Sept.	.62***	.39***	.42***	.51***	.39***	.18
2 Aug.	.78***	.40***	.56***	.43***	.47***	.26**
15 June	.62***	.43***	.43***	.31***	.29**	.16

[z]15 June was FB + 56, 2 Aug. was FB + 104 and 27 Sept. was FB + 160.
[y]LDW/LA, leaf dry weight/leaf area; LDW, dry weight/leaf; LDW/SP, leaf dry weight/spur; LNO/SP, leaf number/spur; LA/SP, leaf area/spur; LA, area/leaf.
[x]n = 60, ***P = .001, **P = .01, *P = .05.

examined there was no association of vegetative spur leaf traits with fruit weight (23).

The differences between cultivars in the relationships of fruit weight with fruiting spur leaf traits are primarily the result of differences in LNO/SP, particularly bourse LNO/SP. With 'Delicious' there was a narrower range in the number of bourse leaves and a lower mean bourse LNO/SP (about 6 leaves on 2 Aug.) than with 'Rome' or 'Granny Smith' (Fig. 1B, 2A). As a result of the low LNO/SP for 'Delicious,' LA/SP and LDW/SP were also low and in a narrow range and these traits were not associated with fruit weight. However, with 'Granny Smith,' with a much greater range in bourse LNO/SP (Fig. 2A) and with a mean of about 12 leaves, there were significant relationships of LDW/SP, LA/SP and LNO/SP with fruit weight. 'Rome' was generally intermediate between 'Granny Smith' and 'Delicious' in its relationship of fruit weight with spur leaf traits and was also intermediate in terms of bourse LNO/SP.

Spur leaf dry weight traits were more closely correlated with fruit weight than were leaf number or leaf area traits. It appears that leaf dry weight traits are better estimates of the production capacity of the spur than are leaf area and number traits. The rate of photosynthesis has been associated with LDW/LA (16, 19).

'Delicious' and 'Granny Smith' showed major differences in bourse leaf development but had similar fruit weight. Fruit dry weight (g) at harvest was 46.3, 25.4 and 25.4 for 'Rome,' 'Granny Smith' and 'Delicious,' respectively. Fruit weights for 'Granny Smith' and 'Delicious' were less than for 'Rome' ($P = .05$). The lower correlations of fruit weight with most spur leaf traits for 'Delicious' than for 'Granny Smith' suggest that shoot leaves must make a greater contribution to fruit weight with 'Delicious' than with cultivars that have greater spur bourse leaf development such as 'Granny Smith.' Abbot (1) concluded that bourse shoot leaves contribute carbohydrates for apple growth during the cell enlargement stage. It is interesting to note that pruning practices which stimulate production of shoot growth, such as heading cuts, are recommended for spur-type 'Delicious' (11) but are not widely used for nonspur cultivars such as 'Granny Smith' which produce large bourse shoots.

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