Physiological Factors Affecting Biennial Bearing in Tree Fruit: The Role of Seeds in Apple

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SUMMARY. The evidence for several hypotheses regarding the mechanism(s) controlling biennial bearing in apple (*Malus*×*domestica* Borkh.) are reviewed, citing relevant evidence from work with citrus (*Citrus* sp.) species and pear (*Pyrus communis* L.). The view that flowering is inhibited by withdrawal of nutrients, primarily carbohydrates, by apple fruit is questionable, given the effects of seed development in inhibiting flowering in facultatively parthenocarpic (normally seedless) apple cultivars. The hypothesis that seeds inhibit flowering by exporting hormones, chiefly gibberellins (GAs), is an attractive one, given a) the effects of application of GAs in inhibiting flowering and b) the high concentrations of GAs in seeds. However, an alternative hypothesis, namely that seeds compete with apices for hormones that are required for flowering, is equally tenable.

Biennial bearing in apple has been an intriguing subject for study for many years. The role of excessive fruiting in reducing flowering, especially in biennial cultivars, was well established as early as 1900 (Downing, 1900). Many experiments were performed in the early 20th Century to determine when fruit removal was effective in inducing flowering (see Dennis, 1999). Harley et al. (1935, 1942) demonstrated that flower initiation declined as fruit removal was delayed, and that this decline was more rapid in a biennial-bearing ('Yellow Newtown') than in an annual-bearing ('Jonathan') cultivar. In the former, no effect of fruit removal was observed ≥60 d after full bloom (DAFB), whereas in the latter fruit thinning continued to affect flowering at 100 DAFB; however, the comparison of cultivars was biased, as the 'Jonathan' branches were ringed.

Why do fruit inhibit flowering?

NUTRIENT DIVERSION. Several hypotheses have been proposed as to why fruit development inhibits flowering. One hypothesis was that the developing fruit diverted nutrients from the buds. The work of Kraus and Kraybill (1918) with tomato (*Lycopersicon esculentum* Mill.), which many readers interpreted to indicate a relationship between the relative amounts of carbohydrates and nitrogen and flowering (see Cameron and Dennis, 1986), inspired many pomologists (e.g., Harley, 1925) to study this relationship in apple.

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INHIBITION BY SEEDS—RESULTS WITH APPLE AND PEAR. The nutrient diversion theory was questioned following Chan and Cain's (1967) demonstration of the role of seeds in flowering. In the facultatively parthenocarpic cultivars 'Spencer Seedless' and 'Ohio No. 3', seedless fruit had little effect on flowering, whereas seeded fruit were inhibitory unless removed within a few weeks of bloom. Thus, seeds appear to be the crucial factor in controlling flowering, rather than the mass of the fruit produced.

All commercial cultivars of apple are seeded; therefore the importance of seeds in flowering of these cultivars is difficult to evaluate. However, 'Bartlett' pear (*Pyrus communis*) sets seedless fruit in the Sacramento Valley of California, and Griggs et al. (1970) compared the effects of seeded and seedless fruit on return bloom. The results were inconclusive, for neither consistently inhibited flowering. However, Huet (1972, 1973) obtained seedless fruit of 'Williams' (= 'Bartlett') pear by preventing cross-pollination, and showed that such fruit were indeed less inhibitory to flowering than were seeded fruit.

INHIBITION BY SEEDS—RESULTS WITH OTHER SPECIES AND CULTIVARS. Limited evidence is available as to the role of seeds in flowering of other species and cultivars of tree fruit. The effects of seeds on flowering of citrus have not been investigated directly. However, Monselise and Goldschmidt (1982) and Davenport (1990) noted that seedless or nearly seedless cultivars are generally annual bearers, with one exception—'Satsuma' mandarin (*Citrus reticulata* Blanco) (Iwasaki and Owada, 1960)—whereas cultivars containing many seeds can be strongly biennial. Moss and

Muirhead (1971) compared yields of 'Washington Navel' (seedless) vs. 'Late Valencia' (few-seeded) orange [(*Citrus sinensis* (L.) Osbeck)] in Australia over a 16-year period. 'Washington Navel' was considerably less biennial than was 'Late Valencia'. However, the former was harvested in July, the latter in October, and delaying harvest can reduce fruit set and/or cropping of 'Valencia' (Hilgeman et al., 1959; Jones et al., 1964; West and Barnard, 1935) of citrus. Other complicating factors in citrus are the long fruit development period (12 to 16 months), resulting in fruit of both old and new crops of some cultivars being present at the same time, and inhibition of shoot emergence by fruit (Davenport, 1990; Plummer, 1987). For example, Davenport (1990) stated that fruit-bearing branches produce no new shoots as long as the fruit remain attached.

INTERACTION OF BOURSE SHOOT LENGTH AND SEEDS IN APPLE AND PEAR. Seeds and bourse shoot length interact in affecting flowering in apple and pear. Huet (1972, 1973) demonstrated that pear shoots with limited leaf area failed to flower, whereas those with high leaf area flowered whether they bore seeded or seedless fruit. Nevertheless, seedless fruit were less inhibitory to flowering at any given leaf surface. This differs from the data for 'Bartlett' in California (Griggs et al., 1970), where flowering was consistently greater ($P < 0.001$ when published data were reanalyzed by FGD) in bourse shoots 1 to 25 mm (0 to 1 inch) long than in those > 25 mm in length. In contrast, main effects of the number of fruit per spur (1 versus 2), the time of defruiting, and the presence or absence of seeds were all nonsignificant. Neilsen (1998) and Neilsen and Dennis

Fig. 1. Effects of seed number per spur and bourse shoot length (25.4 mm = 1 inches) in 1996 on percentage of 'Spencer Seedless' bourse shoots flowering in 1997 (from Neilsen, 1998). Numbers on each line indicate mean bourse shoot length (in mm). Shoots < 2 mm long failed to flower regardless of seed number per spur.

Fig. 2. Relationship between spur length (25.4 mm = 1 in) and percentage of spurs flowering in annual- vs. biennial-bearing 'Wealthy' apple. For biennial trees, spur length was measured at the beginning of the "off" or the "on" year (adapted from Roberts, 1920).

(1999) clearly demonstrated the effect of bourse shoot length (longer shoots had more leaves, although leaf area was not measured) on flowering in 'Spencer Seedless' (Fig. 1). Bourse shoots <2 mm (0.1 inch) in length failed to flower regardless of seed number. All shoots >2 mm on spurs that bore seedless fruit flowered, but flowering of those on spurs bearing seeded fruit *decreased* as seed number per spur *increased*. The inhibitory effect of the seeds declined as shoot length increased, and most shoots >9 mm (0.35 inches) flowered.

'Spencer Seedless' and several other seedless cultivars of apple differ markedly from commercial cultivars in being gynococious; the petals are modified to form a second set of sepals, and the stamens are replaced by a second set of 10 carpels, apical to the normal five (Brase, 1937). Thus a single fruit may contain up to 30 seeds. However, the data of Roberts (1920) for 'Wealthy' apple suggest that a similar relationship between spur length and subsequent flowering may exist in seeded cultivars (Fig. 2), except that flowering is greatest when shoot length is intermediate. Although Auchter and Schrader (1923) found support for this in annually bearing trees of 'York Imperial', this was not the case with biennial trees, in which shoots of intermediate length flowered in the "on" year, but not in the "off" year.

We investigated the effect of shoot length on flowering of the commercial, biennial cultivar Paulared/M. 7 planted in 1980 at the Clarksville Experiment Station, Clarksville, Mich. This cultivar is a terminal bearer, and many bourse shoots are as long as 300 to 400 mm (11.8 to 15.7 in). In preliminary experiments in 1991 and 1992, flowering was not affected by removing all fruit from whole trees

between 20 and 60 DAFB; however, it was strongly inhibited if fruit were left until 70 DAFB (Neilsen, 1998). In 1996, six trees with medium or heavy croploads were selected and hand-thinned 24 DAFB. Treatments were randomized among the limbs on each tree, half being thinned to one fruit, half to two fruit per flower cluster; cropload (fruit no./unit limb cross-sectional area) was similar for all limbs. In addition, terminal shoots bearing no fruit were tagged for observation. In 1997, four trees bearing heavy crops were selected; none were thinned. At harvest, bourse shoots were tagged on spurs bearing zero, one, or two fruit.

In 1997 and 1998, flowering was much heavier than had been expected, based upon previous studies. In 1997, none of the limbs on one of the six trees (weak) thinned in 1996 formed flower buds regardless of treatment. In two other trees return bloom was 90% to 100%, regardless of fruit number per spur. Two additional trees were selected in which flowering in 1997 appeared to decline as fruit number per spur in 1996 increased. Although bourse shoots that were intermediate in length on fruiting spurs appeared to form more flowers, the effect of shoot length on flowering was inconsistent (Fig. 3). The results in 1998 were even less encouraging, with no consistent effects on flowering of either shoot length or fruit number (data not shown). Main effect means for flowering percentage were 41, 36, and 32 for bourse shoots on spurs bearing zero, one, or two fruit, respectively, and 27, 61, 36, and 28 for shoots <100, 100 to 200, 210 to 300, and >300 mm (<4, 4 to 7.9, 8.3 to 11.8, and >11.8 inches) long, respectively (mean percentages for 6 to 42 individual bourse shoots $\times$ three or four replications per treatment per tree).

Based on these results, few conclusions can be drawn with respect to the role of seeds on flowering in 'Paulared', except that a relatively high percentage (50% to 80%) of the bourse shoots on spurs can form flower buds despite the presence of seeded fruit, at least in some years. Given the discrepancies between results for facultatively parthenocarpic vs. seeded cultivars, one can only say with certainty that seeds inhibit flowering in the former.

How do apple seeds inhibit flowering?

HYPOTHESIS 1. EXPORT OF INHIBITORS. Seeds contain relatively high concentrations of GAs (Luckwill et al., 1969), and Luckwill (1970) proposed that GAs from the seeds diffuse to the bourse shoot, where they inhibit flowering (Fig. 4). He presented preliminary evidence that the concentration of GA-like substances was higher in bearing than in defruited spurs of 'Cox's Orange Pippin' (= 'Cox') apple. This theory, although supported by the inhibitory effects of GA application on flowering

Fig. 3. Effects of seed number per spur and bourse shoot length (25.4 mm = 1 inch) in 1996 on the percentage of 'Paulared' apple bourse shoots flowering in 1997. Data for two trees in which flowering appeared to decline as numbers of fruit per spur increased (from Neilsen, 1998).

(Guttridge, 1962; Marcelle and Sironval, 1963), has become dogma among pomologists, but the evidence for it remains tenuous. Hoad (1978) measured GA-like activity both in seeds and in diffusates from pedicels of an annual bearing and a biennial bearing cultivar. Gibberellin-like activity was consistently higher in the diffusates, but not in the seeds, of the latter. Marino and Greene (1981) reported higher levels of GA-like activity in diffusates from fruit-bearing versus vegetative spurs of 'Early McIntosh', however, GA content of seeds did not parallel that of spurs. Stephan et al. (1997) recovered more total GA from pedicel exudates of seedless fruit of 'Spencer Seedless' than of 'Elstar' (seeded and biennial), although much of that in 'Spencer Seedless' was identified as GA₄, which can promote flowering under some conditions.

Several investigators have applied radioactively labelled GAs to apple seeds, or to locules of seedless fruit, and studied the transport of the label to bourse shoots. Again, the results were not conclusive. One to 3 d after application of ¹⁴C-sucrose or ¹⁴C-indole-3-acetic acid (IAA) to exposed seeds of intact fruit, significantly more radioactivity was detected in the bourse, primary leaves, and bourse buds of 'Laxtons Superb' (biennial) than in those of 'Cox' (annual) (Hoad, 1978). Although more radioactivity was also found in the bourse and bourse bud in a parallel experiment with ³H-GA₃, the difference was significant

only in the former. No ³H-GA₉ moved out of the fruit, suggesting that hydroxylation is a prerequisite for transport. Green (1987) injected several GAs and their precursors into seeds of cider apple cultivars, but the maximum amount transported to the bourse bud was <0.1% of that applied. Ban (1997) could detect no radioactivity in the shoot apices following application of ¹⁴C-GA₁₂ to the seeds of 'Spencer Seedless', and only ≈0.5% diffused out of the receptacle of the fruit. Stephan et al. (1997) recovered radioactivity from the bourse shoot equivalent to ≈0.1% to 0.4% of the amounts of tritiated GA₁, GA₃, and GA₄ injected into the core of the fruit or applied to cut pedicels. Prang et al. (1997) measured the levels of GA₃ and GA₄ in exudates from pedicels of excised fruit of 'Elstar' (biennial), 'Golden Delicious' (annual in Germany), and 'Spencer Seedless'. Differences between cultivars in export of GA₃ were not significant in 1995, but 'Spencer Seedless' exported significantly more GA₄ than did the seeded cultivars. These results were not confirmed in 1996, however; more GA₃ diffused from the seeded cultivars than from the seedless one, and GA₄ levels were very low during the flower induction period.

Callejas and Bangerth (1997) suggested that IAA, in conjunction with GAs, might be a critical factor controlling flowering. Spraying with GA₃, GA₄, or GA₇ [250 mg·L⁻¹ (ppm)] 35 d after full bloom increased the amount of IAA

recovered in diffusates from both shoot tips and fruit pedicels sampled 3 to 10 d later. The amount recovered from pedicels also increased with seed number per fruit. The authors suggested that IAA might act as a second messenger in the inhibition of flowering; GAs (from the seeds?) stimulated IAA transport from seeds (and apices?), inhibiting flowering. Nevertheless, they acknowledged that the results obtained with a biennial cultivar (Elstar) did not differ from those obtained with an annual cultivar (Golden Delicious).

Little evidence exists that auxin has a direct effect on flowering in apple, although naphthaleneacetic acid (NAA) can stimulate flowering when used as a thinning agent. However, Grochowska (1968) observed that replacing seeds with cotton soaked in a solution of NAA promoted flowering. Ramirez and Hoad (1978) obtained some promotion (three significant responses among 24 comparisons), but no inhibition of flowering, after applying IAA to cut petioles of bearing or defruited spurs of 'Egremont Russet'. Therefore, this hypothesis is not well supported.

HYPOTHESIS 2. PRIORITY FOR FLORIGEN. Limited support for the inhibitor hypothesis may reflect technical limitations; future research may indeed show that GAs and/or IAA are indeed key factors in controlling biennial bearing. In the meantime, I propose that we examine another hypothesis, suggested by Ryugo (1988), viz., that the seeds

Fig. 4. Two possible mechanisms by which seeds might affect flowering in apple. (A) Inhibitor (GA?) from seed moves to bourse shoot, where it prevents flowering. (B) Seed has priority for compound produced by leaves that promotes flowering (florigen?), thereby preventing flowering.

have priority for florigen—that hypothetical hormone responsible for inducing flowering—or another compound that is required for the process. This differs from the nutrient diversion hypothesis in that a hormone(s) is involved, rather than carbohydrates or other nutrients. The hypothesis (Fig. 4) appears to fit the data as well as does the inhibitor hypothesis. Instead of exporting an inhibitor, the seed has priority for florigen produced by the leaves. If the bourse shoot is sufficiently long and/or the leaf surface is adequate, flowering can occur despite the presence of a seeded fruit. This might explain the failure of seeded ‘Bartlett’ pear fruit to prevent flowering in California, where water and sunlight are abundant and growth is vigorous. Chan and Cain (1967) reported that when ‘Spencer Seedless’ trees were grown in sand culture in a greenhouse, long bourse shoots developed and seeds had no effect on flowering, suggesting, again, that the supply of florigen was sufficient for both seed development and flower initiation. Both Goff (1899) and Heinicke (1917) may have been correct when they suggested that seeds absorb the “nourishment [read florigen] that might otherwise contribute to the formation of flowers” (Goff), or that “...a tree bearing ... many-seeded fruit is being devitalized to a far greater extent than another tree ... bearing ... fruit ... having relatively few seeds.” (Heinicke).

The major difficulty in pursuing this line of research is that no one knows what to look for. However, a possible

candidate is cytokinin. Luckwill (1970) proposed that flowering in apple shoots was controlled by a balance of GAs produced by the apex and cytokinins produced by the roots. As long as the apex continued to grow, the GAs it produced inhibited flowering. Once growth stopped, cytokinins in the xylem sap could “partially relieve the dormancy of the lateral buds,” leading to flowering. Luckwill also proposed that GAs from the seeds inhibited flowering in the apical buds on the bourse. As noted above, he provided preliminary data indicating that GA-like activity was greater in the bourse shoots of fruiting than of defruited spurs, and suggested that leaves might either produce a flower-promoting substance that antagonized the effects of GAs, or favored transpiration, ensuring a supply of cytokinins from the roots. Although application of benzyladenine (N^6 -benzylaminopurine) (BA) has little effect on flowering of apple, Luckwill’s (1970) proposal is supported by the demonstration (Hoad and Ramirez, 1980; Ramirez and Hoad, 1978) that application of the naturally occurring cytokinin zeatin through cut petioles can stimulate flowering in ‘Egremont Russet’ apple.

Conclusions

Seeded fruit of biennial cultivars of apple and pear inhibit flowering, whereas seedless ones do not. However, few cultivars of apple or pear are seedless, thus the importance of seeds in flowering may be limited to a few genotypes. In ‘Spencer Seedless’ apple and ‘Bartlett’

pear, the effect of the seeds declines as bourse shoot length and/or leaf surface per bourse increases; the effects of these factors in seeded cultivars of apple remain to be demonstrated. The most popular hypothesis to explain the effects of seeds on flowering is that seeds, being rich sources of hormones, export these compounds to the bourse bud, thus inhibiting flowering. Direct evidence for this mechanism has yet to be obtained. A second hypothesis, which appears to be just as feasible, is that seeds compete with apices for a compound (florigen?), produced by the leaves, that promotes flowering. This reduces the quantity available for flower induction. A possible candidate for this promoter is cytokinin.

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