Seed set and the development of fruit shape in apple

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Abstract

Fruit development is affected by seed set. Fruit with few seeds often fail to set and fruit having asymmetrical seed distribution tend to be smaller and more lopsided than symmetrical fruit. Therefore, significant quantities of fruit are rejected because they fail to achieve the required size/shape criteria. Although these relationships are well known, few quantitative studies have been made of them. Here we report how seed set and seed development influence fruit shape of apple via an influence on fruit sector weight. Seeds within a locule had the strongest (first order) effect on the weight of the associated sector. Seeds from the two neighbouring locules had a weaker but still significant (second order) effect, while seeds from the two distant locules had no significant (third order) effect. The weakening influence with distance of the seeds on sector weight is consistent with the idea that seeds regulate fruit growth. This confirms that fruit symmetry is affected by seed development and that misshapen fruit will be a consequence of poor or asymmetrical seed set.

Additional key words: *model, seed weight, carpel, misshapen, lopsidedness*

Introduction

Fruit size and shape are key quality determinants in apples. Significant quantities of fruit are rejected each year because of failure to meet critical size/shape criteria; the magnitude of these losses is unknown. Calculations based upon known losses in the packhouse suggest that over 3 % of the annual crop is rejected because of small size and lopsidedness (Palmer, pers. comm.). This does not include fruit rejected by the picker.

Many studies have indicated that a fruit size/shape to seed set relationship exists in different species including apple (Heinicke, 1917; Alderman, 1918; Murneek and Schowengerdt, 1935; Latimer, 1937; Einset, 1939; Denne, 1963; Dennis, 1986; Tromp, 1990; Brault and De Oliviera, 1995; Brookfield *et al.*, 1996; Broom *et al.*, 1998), pear (Rohitha and Klinac, 1990), strawberry (Nitsch, 1950), orange (Cameron *et al.*, 1960), and kiwifruit (Pyke and Alspach, 1986; Lai *et al.*, 1990; Lewis *et al.*, 1996). However, there are no investigations in which the relationship between seed weight (rather than seed number) and the size/shape of the fruit have been examined in a quantitative manner.

Since the pomaceous ovary is made up of five carpels, it may be possible to view an apple as an assemblage of five replicate sectors instead of as a single organ. This being the case we postulate that the developing seeds may have a localised effect on fruit development. Our objective is to test and quantify the hypothesis that seed distribution at the level of the single carpel affects the subsequent development of that sector so that asymmetrical seed set produces asymmetrical fruit.

Materials and Methods

One row of Granny Smith apples (*Malus domestica* Borkh.) was chosen for this study in 1998. Trees were planted at the Massey University Fruit Crops Unit, Palmerston North, on MM. 106 rootstock and managed according to standard commercial practice. A total of 60 fruit was collected at commercial harvest in mid April 1998. To maximise the effects of uneven seed distribution only obviously lopsided fruits were selected.

Fruit were weighed and cut in half transversely just below the equator to expose the locules without cutting the seeds. Both halves were then sliced longitudinally into five sectors; each sector comprised one locule with its seeds and surrounding flesh. The individual sectors plus seeds, and the seeds alone were then weighed. To evaluate our hypothesis we tested a three-order model, where we related the weight of a particular sector to the weight of the seed within it (as a first-order effect), the weight of the seeds in the two adjoining sectors (as a second-order effect) and the weight of the seeds in the two distant sectors (as a third-order effect). This model is expressed as

$$S = a + b(wi) + c(w_{i-1} + w_{i+1}) + d(w_{i-2} + w_{i+2}) \qquad (1)$$

where S is sector weight; *a*, *b*, *c*, and *d* are the fitted constants and w_i is the weight of the seed(s) in sector *i*. To test the data for the three-order model, analysis was carried out using SAS Proc Mixed procedure with a Toeplitz correlation structure (SAS, 1996), to allow for the expected correlation between data from different sectors in the same fruit. Separate intercepts were fitted for each fruit.

Results and Discussion

The seeds were quite variable in weight, with large seeds sometimes weighing twice as much as other small but fully developed ones. The weight of a particular sector was found to be significantly influenced by the weight of its associated seeds as predicted by the three-order model. The individual terms in this model show a weakening relationship between seed weight and sector weight with:

1. Seeds within a locule having the strongest (first order) effect on the weight of that sector;
2. Seeds from the two adjacent locules having a weaker but significant (second order) effect;
3. Seeds from the two most distant locules having no significant (third order) effect.

Seed weight and distribution, as combined in the model (Eq. 1), was positively correlated with mean sector weight adjusted to the same average intercept (Fig. 1).

Based on this model, lopsidedness is the result of unbalanced fruit development associated with asymmetrical seed weight distribution. A significant physiological effect on the growth of a particular sector may therefore occur not only from the seeds in the sector's own locule but also from those in the two flanking locules. This indicates that seeds from one locule significantly influence development of the neighbouring two sectors as well. Analysis in terms of the seed number distribution (fully developed seeds, ignoring flattened and aborted seeds) showed a much less significant result. The improvement in fit obtained with the seed weight model (as compared with the seed number model) can be interpreted to indicate that big seeds generate a stronger developmental 'signal' than small ones.

These results support a modular view of an apple being an assemblage of five replicate sectors (carpels), where each develops as a unit, influenced to some extent by the adjacent units. Consequently, as seed weight affects sector weight, asymmetrically distributed seed will result in asymmetrical fruit.

Seed asymmetry (and fruit asymmetry) will therefore be related to seed set. For in a fully seeded fruit (10 seeds) the seed must be symmetrically arranged whereas in a one-seeded fruit the arrangement must be highly asymmetrical. Intermediate number of seeds will be associated with intermediate degrees of seed asymmetry. Given the quantitative link between seed asymmetry and fruit asymmetry it follows, that to minimise the incidence of lopsided fruit the grower should make every effort to maximise seed set.

The New Zealand apple industry loses in excess of $15 million (3 %) annually due to lopsided and undersized fruit. Recognising that these are associated with poor and asymmetrical seed set, the importance of optimising seed set by good orchard design cannot be overestimated. For example, Braeburn (currently 40 % of the NZ crop), which has serious shape problems, flowers very early, and this cultivar should be planted with a suitable

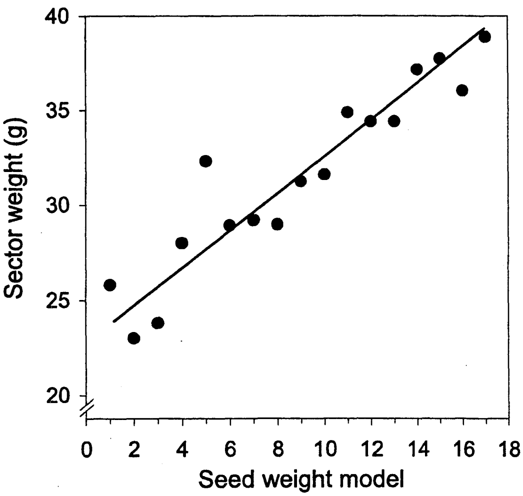

Figure 1. Influence of seed weight on sector weight as predicted by the three-order model. Each point represents the median value of a number of sector weights falling within the same class of seed weight parameter values.

pollinator in close proximity. Ideally, this is Malus Profusion but commonly Royal Gala is used even though this cultivar flowers 1-2 weeks after Braeburn. This is clearly a less-than-satisfactory solution, and many of its shape problems can be attributed to poor orchard design.

References

Alderman, W.H. 1918. Experimental work on self-sterility of the apple. *Proceedings of American Society for Horticultural Science **14***, 94-101.

Brault, A.M. and De Oliviera, D. 1995. Seed number and an asymmetry index of 'McIntosh' apples. *HortScience **30***, 44-46.

Brookfield, P.L., Ferguson, I.B., Watkins, C.B. and Bowen, J.H. 1996. Seed number and calcium concentrations of 'Braeburn' apple fruit. *Journal of Horticultural Science **71***, 265-271.

Broom, F.D., Smith, G.S., Miles, D.B. and Green, T.G.A. 1998. Within and between tree variability in fruit characteristics associated with bitter pit incidence of 'Braeburn' apple. *Journal of Horticultural Science & Biotechnology **73***, 555-561.

Cameron, J.W., Cole, D.Jr. and Nauer, E.M. 1960. Fruit size in relation to seed number in the Valencia orange and some other citrus varieties. *Proceedings of American Society for Horticultural Science **76***, 170-180.

Denne, P.M. 1963. Fruit development and some factors affecting it. *New Zealand Journal of Botany **1***, 265-294.

Dennis, F.G. 1986. Apple. *In* Handbook of fruit set and development (ed. S.P. Monselise), pp 1-44. CRC Press, Florida.

Einset, O. 1939. Correlation of number of seed to weight of fruit in the apple. *Gartenbauwissenschaft **13***, 351-353.

Heinicke, A.J. 1917. Factors influencing the abscission of flowers and partially developed fruits of the apple (*Pyrus malus* L.). *Cornell University Agricultural Experimental Station Bulletin **393***, 43-114.

Latimer, L.P. 1937. Self- and cross-pollination in the McIntosh apple and some of its hybrids. *Proceedings of American Society for Horticultural Science **34***, 19-21.

Lai, R., Wooley, D.J. and Lawes, G.S. 1990. The effect of inter-fruit competition, type of fruiting lateral and time of anthesis on the fruit growth of kiwifruit (*Actinidia deliciosa*). *Journal of Horticultural Science **65***, 87-96.

Lewis, D.H., Burge, G.K., Schmierer, D.M. and Jameson, P.E. 1996. Cytokinins and fruit development in the kiwifruit (*Actinidia deliciosa*). II. Effects of reduced pollination and CPPU application. *Physiologia Plantarum **98***, 179-186.

Murneek, A.E. and Schowengerdt, G.C. 1935. A study of the relation of size of apples to number of seeds and weight of spur leaves. *Proceedings of American Society for Horticultural Science **33***, 4-6.

Nitsch, J.P. 1950. Growth and morphogenesis of the strawberry as related to auxin. *American Journal of Botany **37***, 211-215.

Pyke, N.B. and Alspach, P.A. 1986. Inter-relationship of fruit weight, seed number and seed weight in kiwifruit. *New Zealand Agricultural Science **20***, 153-156.

Rohitha, B.H. and Klinac, D.J. 1990. Relationships between seed set and fruit weight and shape of nashi (*Pyrus serotina* Rehder var *culta* Rehder). *New Zealand Journal of Crop and Horticultural Science **18***, 133-136.

SAS Institute Inc. 1996. SAS/STAT Software: Changes and enhancements through Release 6.11, Cary, North Carolina.

Tromp, J. 1990. Fruit shape in apple under various controlled environment conditions. *Scientia Horticulturae **43***, 109-115.