

FLOWERING, FRUIT DEVELOPMENT AND MANIPULATION OF YIELD IN AVOCADO

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FLOWERING AND FRUITSET

Avocado flowers are dichogamous which means that the female stage and the male stage are separated in time. A very unusual phenomenon is the fact that the flower closes after the female phase, re-opens for the male phase and closes again after the male phase. Opening of the flower in the female phase involves the unfolding of the perianth leaves to expose the pistil with its receptive stigma for a few hours and then closing again. The next day, in the morning or in the afternoon, depending on the cultivar, the flower will reopen to expose the dehiscing anthers which will then shed the pollen grains (Davenport, 1986).

There is a major difference between A and B-type cultivars regarding the time of opening and closing of flowers of the two sexual phases. Opening of the flowers is mainly controlled by environmental conditions, of which temperatures seem to be the most important. In unfavourable weather conditions, the rhythm of the flowers can, however, be totally disturbed on certain days so that flowers will not open at all, thus excluding the possibility of pollination and fruit set (Robbertse *et al.*, 1996).

Pollination is the transfer of pollen from the anthers to the receptive stigma. Avocado pollen is sticky and heavy and therefore suitable for insect-pollination. Different insects are found on avocado flowers, but bees play the major pollinating role (Robbertse *et al.*, 1996). Bee activity is related to weather conditions and corresponds to a great extent with the opening and closing of the avocado flowers.

In spite of the overlap of male and female phase flowers in the same cultivar, pollen donors with an alternate flower-opening cycle might be beneficial. In this regard, 'Ettinger' can serve as an effective pollen donor for 'Hass', as Robbertse *et al.* (1996 and 1997) showed with *in vitro* experiments. There are reports from Israel that 'Hass' trees planted close to 'Ettinger'

have shown considerably higher yields (Guil and Gazit, 1992; Degani *et al.*, 1989).

Similar field experiments in South Africa have not lead to proven yield increases in 'Hass' to date (Robbertse *et al.*, 1996). In South Africa, commercial avocado orchards, in which the pollination experiments are carried out, are situated in summer rainfall areas. Here the winter is arid, spring is generally mild and dry, with cool but frost-free nights and usually warm, sunny days. Many insects, particularly honeybees, occur naturally in the orchards, as they are attracted by flowers of irrigated crops in an otherwise dry environment, with little bee attractive vegetation.

While an increase in 'Hass' yield adjacent to pollen donors was only observed during one year in a single orchard, there is clear evidence that the number of bees visiting flowering avocado trees and the number of fruits harvested from such trees are positively correlated (Table 1). A high bee activity in an avocado orchard seems to be more beneficial than the presence of pollen donor cultivars of the opposite flowering type. In South Africa, the minimum number of bees which should be visible per square metre of flowering canopy area (or per 20 inflorescences) is five. In some orchards and years, the required bee population was achieved naturally due to an abundance of feral bees, while in other orchards (or years), placing additional beehives was thought to be advantageous (Johannsmeier *et al.*, 1997).

Table 1. 'Hass' yield as influenced by caging with 'Ettinger' or 'Hass', with or without bees and open pollination (Robbertse <i>et al.</i>, 1998).	
Treatment	Yield (kg/tree)
Ettinger and Hass, caged with beehive	31.6
Ettinger and Hass, caged without beehive	2.6
Hass and Hass, caged with beehive	28.5
Hass and Hass, caged without beehive	1.7
Hass (open pollination 5m*)	30.5
Hass (open pollination 50m*)	28.2
*Distance between this specific 'Hass' tree and the closest 'Ettinger' tree.	

Since 'Ettinger' fruit is not of economic importance in South African markets, it seems preferable to spend money on introducing additional beehives rather than interplanting large

numbers of 'Ettinger' pollen donors under local conditions.

Once the pollen grain lands on the stigma it germinates. Pollen tubes are competing to reach the embryo sac where the egg cell and the central cell must be fertilized before the ovule will start developing into an avocado seed. The developing seed in turn will stimulate the ovary to develop into the fruit.

FRUIT DEVELOPMENT

In avocado, more than 99% of the flowers and fruitlets drop (Addicott, 1983), resulting in low yields. Anatomical investigations of abscised avocado fruitlets have revealed the majority of fruitlets that dropped during the first few weeks after flowering to be unfertilized. All fruits dropped from one month after flowering onwards were fertilized and showed normal embryo and endosperm development (Sedgley, 1980). These observations rule out fertilization defects as the causal factor for the high fruit drop rate. A source and/or sink limitation or competition for assimilates could therefore be possible reasons for low yields in avocado.

Source limitation?

Possingham (1986) describes the foliage (source) of evergreen fruit trees as being exceptionally well developed; this also applies to the avocado (Lahav *et al.*, 1971). The assimilative capacity of avocado leaves has been investigated by Scholefield *et al.* (1980). To determine whether photosynthetic output (source) might limit fruit yield, avocado leaf:fruit ratio was measured by Kohne (1989). A leaf:fruit ratio of 100:1 can be adopted for avocado as a norm for well bearing trees (yield equivalent to 20t/ha). However, observations indicate that the vigorous vegetative growth of the avocado and thereby rapid increase in leaf number, accompanied by considerable fruit drop, often lead to leaf:fruit ratios well in excess of 100:1.

The question is how to interpret an avocado leaf:fruit ratio of approximately 100:1 in the light of possible source limitation. For comparison, in most apple and pear cultivars good fruit development and adequate flower bud formation for the following year is regarded as a

certainty if 15-30 leaves are present per fruit immediately after the June drop (Schumacher, 1975). However, in view of the differences in size, lifetime and photosynthetic capacity of the leaves as well as in energy content and weight of fruit, this rule can not be applied directly to avocado.

With an average size of 58cm^2 , avocado leaves are three to four times larger than apple leaves, Golden Delicious leaves having an area of $10\text{-}20\text{cm}^2$ for example (Palmer, 1987). Scholefield *et al.* (1980) give the maximum photosynthetic capacity of avocado leaves as $0.30\text{ mg CO}_2\text{ m}^2\text{s}^{-1}$, as compared to $0.97\text{ mg CO}_2\text{ m}^2\text{s}^{-1}$, in apple (Avery, 1977). However, it is reasonable to suppose that the comparatively low photosynthetic capacity of the avocado leaf is compensated for by its larger size and its year-round photosynthetic activity (Monselise, 1986).

According to Wolstenholme (1986), the energy content of avocado fruits with 17% oil content is $807.2\text{ kJ }100\text{ g}^{-1}$, three times that of the apple ($262.8\text{ kJ }100\text{ g}^{-1}$). In view of the high energy content of the avocado fruit and its heavier weight in comparison with the apple, an avocado leaf:fruit ratio of around 100:1 may be regarded as equivalent to an apple leaf:fruit ratio of 15-20:1.

Blaming the high fruit energy content of the avocado and consequent heavy assimilate demand as the cause of the high fruit drop rate is unsatisfactory in view of the fact that 96% of the fruit abscise before the mesocarp has attained an oil content of 1% (Adato and Gazit, 1977). Rapid oil accumulation in the mesocarp does not occur until five months after flowering (Blumenfeld and Gazit, 1972).

Further, one must keep in mind that fruits influence both photosynthetic rate (Avery, 1977) and assimilate partitioning. In experiments with ^{14}C - labelled avocado leaves in the immediate vicinity of fruitlets Finazzo and Davenport (1986) noticed that fruit drop was accompanied by a clear reduction in ^{14}C export from the marked leaves. Normally, leaf assimilate production appears to proceed at a rate below the maximum possible rate, leaving a margin of reserve capacity available in case of necessity (Maggs, 1964; Priestley, 1987). It is therefore highly

unlikely that avocado yields presently achieved (10-15 t/hectare) are limited by the source, i.e. photosynthetic capacity.

Sink limitation?

Assimilate import into a sink organ is a function of sink strength, which is determined by sink activity and sink size, which in turn are influenced by phytohormones (Patrick, 1982). The phytohormones present in the avocado seed play a crucial role in fruit development; seedless avocados, for example, being only one-tenth of the size of seeded avocados (Blumenfeld and Gazit, 1970). The shrivelling of the seed coat (testa) during early fruit development leads to fruitlet abscission (Blumenfeld and Gazit, 1974). The seed and more especially the testa of avocado fruitlets contain auxins (Gazit and Blumenfeld, 1972), gibberellin - like substances (Blumenfeld and Gazit, 1972), cytokinin (Blumenfeld and Gazit, 1970), ethylene, and abscisic acid (Adato and Gazit, 1977). It would appear that in avocado, only very few fruitlets (out of the huge number originally developing) can maintain sufficient sink strength to remain on the tree until they reach maturity.

Competition for assimilates?

A number of authors have proposed assimilate competition between spring flush and developing fruits as a causal factor in fruit drop in the avocado (Scholefield *et al.*, 1985; Sedgley, 1987; Zilkah *et al.*, 1987) Investigations by Buchholz (1986) confirm that in the 'Fuerte' variety the spring flush temporarily acts as a sink, competing with the fruitlets for assimilates.

It is therefore concluded that two problems related to severe fruit drop seem to coincide in most avocado trees: a relatively low sink strength of the reproductive organs compared to the demanding vegetative sinks, and assimilate competition between the young spring flush and developing fruitlets.

MANIPULATION OF YIELD

The relative strengths of reproductive and vegetative sinks and the length of time from bud break to the sink/source transition of shoots (Whiley, 1990), largely determines the success of fruit retention on avocados during the spring. Whiley *et al.* (1988) describe water and nutritional management strategies for avocados, which suppress vegetative sink strength during spring growth thereby improving potential yield. However, management of these criteria is difficult and environmental conditions often nullify attempts at effective growth control.

Paclobutrazol (PBZ), a triazole plant growth regulator which inhibits gibberellin biosynthesis (Davis *et al.*, 1988), gives a predictable effect on vegetative growth of avocado trees. Applied as a foliar spray during anthesis, it has been shown to reduce shoot growth and improve avocado fruit retention during spring (Kohne and Kremer-Köhne, 1987; Wolstenholme *et al.*, 1990). Significant yield increases have been recorded after mid-anthesis foliar application of PBZ on 'Fuerte', especially when sprayed in an "off-year" (Adato, 1990). In 'Hass', mid-anthesis foliar sprays of PBZ increased mean fruit size at harvest by more than 10% (Whiley *et al.*, 1991), indicating that the fruit's sink capacity was increased.

Recently, other plant growth regulators have become available (e.g. uniconazol) which give results similar to PBZ and are useful tools when applied judiciously to manipulate fruit sink capacity in avocado.

Further, skilful orchard management aiming at suppressing excessive vegetative vigour, especially during the time of the spring flush, should lead to better yields. In the longer term it is hoped that superior rootstock-scion combinations become available commercially, which do not necessitate the costly use of plant growth regulators to achieve regular high yields in avocado.

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