POLLINATION OF AVOCADOS

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ABSTRACT

Yield is a key driver for profitability when growing avocados. High yields require avocado trees to set large numbers of fruit; this in turn depends on good pollination. Avocado trees have a complex floral biology and to set a fruit the following conditions need to be met: clear, calm, warm days and nights, high quality viable pollen be available, a receptive flower in the female phase, a good number of pollinizers active, trees be in good health with good nutrition and fungi under control so as not to compete with pollen tube growth. Understanding what is required to achieve these conditions is essential in obtaining good fruit set and increasing yield. This review summarizes information published on avocado pollination from around the world and relates this information to orchard practice in New Zealand.
Keywords: floral biology, flowering, fruit set , pollinizers

INTRODUCTION

Large mature avocado trees produce very large numbers of flowers, often in excess of one million, of which very few (< 3 flowers in 1,000) set fruit (Bergh, 1985; Blanke and Lovatt, 1993; Blumenfeld and Gazit, 1974). The complex floral biology of avocado trees has the effect of making the whole process of pollination and fruit set very inefficient. This leads to a high rate of post-pollination fruit drop through unfertilised flowers (Sedgley, 1987). The flowers are very small, 1 cm in width and 6-7mm in length (Davenport, 1986), and are grouped together into structures known as panicles that contain anywhere from several dozen to several hundred flowers. The flowers are pale yellow-green and consist of six perianth members, nine stamens and a pistil (Robbertse, 2001a). At the base of each of the three inner stamen filaments are two bright yellow stalked nectaries. Each anther consists of four pollen sacks, containing 500 to 700 pollen grains, which open with valves to shed the pollen (Davenport, 1986). Abnormalities in avocado flowers are common.

The whole flowering structure, known as an inflorescence, can also be present as determinate or indeterminate flowering shoots (Robbertse, 2001b). A determinate shoot is where the shoot ends or terminates with a flower bud (Figure 1A). The fruit set on these can often be seen on trees where there are bunches of fruit that hang like grapes. Once the fruit are harvested the shoot dies back to the nearest vegetative bud. Very often such shoots are found on the tops of trees where light levels are highest. Indeterminate shoots end in a vegetative bud that will often grow out and continue on to become a branch (Figure 1B). Very often inflorescences on indeterminate shoots die off before setting fruit due to competition with the vegetative shoot. Determinate flowering shoots are thought to be more productive than indeterminate flowering shoots. In New Zealand it is thought that the ratio of determinate to indeterminate shoots is about 50:50 whereas in California this ratio is about 10:90 (Salazar-Garcia and Lovatt, 1996).

Avocado flowers contain both male and female parts but these mature and become functional at different times. This is a flowering behaviour that is known as “synchronous dichogamy”. An individual flower will typically open as female then close and re-open as male over a two day period. Successful fertilisation and fruit set results from pollination of the

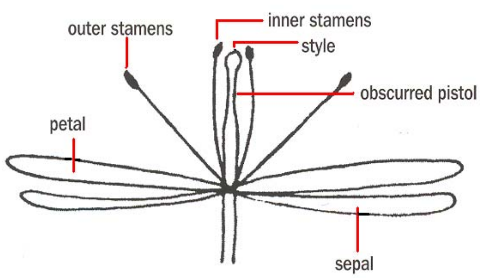
A)

B)

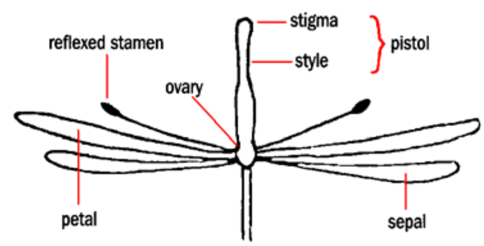
Figure 1. Flowering shoots showing A) determinate and B) indeterminate growth

female flower stage; the male flower stage flower is not receptive to being pollinated (Sedgley, 1987). The male parts of the flower are anthers and stamens, with the anthers containing the pollen. The female parts of the flower are the stigma, style and ovary, the stigma receives the pollen (Arpaia et al, 2001). The timing of the sex phases can be quite precise under certain conditions but the environmental conditions during flowering can affect the duration and timing of the male and female phases (Waser et al, 2001). Groups of avocado flowers open in unison throughout a tree in the order the inflorescences developed on the shoots. The first to flower are those at the ends of shoots with the remainder of flowers opening down the shoot. The flowering period can last for several weeks (Davenport, 1986). In New Zealand flowering typically spreads over 6 to 8 weeks.

A)



C)



B)

D)

Figure 2. Stylized and actual photos of flowers in the male phase (A, B) and female phase (C,D). B = Hass, D = Zutano

In addition there are two types of flowering cultivars known as “A” and “B” types (Table 1) that have different timings of opening male or female (Arpaia, 2001). Type “A” cultivars flowers open female on the first morning then close in the afternoon before reopening as male in the afternoon of the second day. Flowers that are “B” type open female in the afternoon of the first day then close overnight before reopening as male in the morning of the second day. In theory, this should prevent self pollination and facilitate cross pollination between “A” and “B” type cultivars. Observations of flowering behaviour have shown that there is considerable variation in the timing of flower opening and that trees do not open all their flowers at once in the same sex phase (Waser et al, 2001; Schroeder and Hofshi, 2001).

Table 1. Avocado cultivars listed according to flowering type.

“A” type cultivars	“B” type cultivars
Gwen	Bacon
Hass	Ettinger
Lamb Hass	Fuerte
Pinkerton	Sharwil
Reed	Sir Prize
Gem	Walter Hole
Harvest	Zutano
	Marvel
	Nobel

With optimum climactic conditions daily flower openings are uniform and predictable and there is little chance of self pollination (Davenport, 1986). Research in South Africa has suggested that temperatures in excess of 20° C the day before pollination have a positive influence on fruit set (Robbertse et al, 1998). On cold mornings the opening of Hass flowers in the female phase can be delayed until the temperature has risen above 20° C leaving only male phase flowers and thus preventing any fruit set from occurring (Robbertse, 2001b). The cultivar types respond differently to low temperature conditions in terms of the availability of female flowers (Sedgley and Grant, 1983). A reduction in temperature during flowering slows down flower opening so the flowers on a tree lose synchronisation and remains female or male longer than would be expected (Robberste et al, 1995). In type “A” cultivars opening female and male flowers may be retarded so much that they become reversed (Davenport, 1986). Type “A” cultivars like Hass respond better to low temperatures than “B” type cultivars as low temperatures extend the period for which the flowers are female. For “B” type cultivars the female stage can be skipped altogether in low temperature conditions leading to no fruit set. As a result of low temperatures there may be both functional male and female flowers open at the same time on individual trees that allows pollen transfer from flowers in the same inflorescence or trees of the same cultivar. Davenport (1986) refers to this self pollinating process as close pollination. This situation has been observed in New Zealand.

Much of the research on pollination conducted overseas has been in climates that do not reflect conditions in New Zealand. New Zealand can be considered to have a warm temperate climate rather than a cool subtropical climate that results in very variable avocado flowering biology and behaviour. In order to achieve good fruit set, in the often very marginal flowering conditions in New Zealand, orchards need to develop a microclimate that maximizes their potential temperature. Many orchardists do this by selecting a north facing site that is frost free and use shelter belts to reduce wind run that also increases the orchard temperature.

Temperature has a large influence on distortions or variations to the described “synchronous dichogamy” flowering behaviour for Hass (an “A” type cultivar) under New Zealand conditions. The most probable explanation is that there are a number of microclimates that may be operating within a single orchard block which may account for differing floral behaviour between trees. Flowers are often observed to be behaving very differently even on the same flowering structure. Examples include the late opening of female flowers on the first day with closure occurring at dusk, the absence of any desiccation of the stigma under cool temperatures and high humidity levels until the completion of the male phase, and in some cases the appearance of functioning male and female flowers simultaneously on a single tree. Male and female flowers have been observed on 2 lateral flowers on the same peduncle.

The marginal climate for avocado pollination in New Zealand has some important implications. It is most likely that the New Zealand climate increases post-pollination flower abortion, the development of seedless fruit (cukes), higher determinate to indeterminate flower panicle ratios, and a longer flowering period. The variability of synchronous dichogamy under local conditions may also alter the relationships between self-, close-, cross-, and insect pollination. Windy springs in New Zealand may also have the potential to extend the dispersal of pollinizer (Type B) pollen grains to a wider area of receptive Hass stigma without insect transfer.

High temperatures, above 30° C, stimulate vegetative growth at the expense of flowering shoots leading to shedding of flowers and developing fruit (Sedgley, 1987) but such conditions are rare in New Zealand over the flowering period. The length of day and night conditions alter the period of flower opening with decreased daylight reducing the duration of the sex phases (Davenport, 1986).

Avocado pollen remains viable for about 24 hours (Robbertse, 2001b) during which time it is possible the pollen could dry out and become airborne (Davenport, 2001) but there is as yet no empirical evidence for this. The stigmas of the female part of the flower are receptive to pollen for less than 4 hours once opened (van den Berg, 2001) depending on the weather conditions. Most studies have been conducted in low humidity environments that dry out stigmas while stigmas may remain viable for longer in the high humidity conditions prevalent in New Zealand. Stigmas can still receive pollen and allow pollen germination during the flowers' male phase but pollen tube growth ceases quickly and does not reach the ovule preventing fertilisation from occurring (Robbertse, 2001b).

Climate/Weather

Temperature conditions during flowering can alter not only the timing of the sex phases but also have a large influence on the successful fertilisation of the flower. Fruit set (Figure 3) is often limited to periods of a few days with the same weather conditions in succession (Robbertse et al, 1995). The rate of pollen tube growth down an avocado flower depends on temperature (Robbertse et al, 1994; 1998) as does successful fertilisation of the ovary. The optimum temperature for pollen tube growth has been observed to be between 25° C and 28° C (Sedgley, 1979). Pollen tube growth to the base of the style occurs within three hours of germination at optimal temperatures but penetration to the ovule occurs only after about 24 hours following pollination (Sedgley, 1987) and a further 24 hours may be required to complete the fertilisation process (Davenport, 1986). Hence the requirement for 48 hours of stable weather conditions to achieve fruit set. The minimum temperature conditions required for successful pollination and fruit set are reported to be two consecutive days where the daytime temperature is greater than 18° C and the night time temperature is greater than 11° C. Such conditions are considered to be a pollination event. Should either of these two temperature conditions be interrupted, for example a cold snap on the second night, fruit set failure can occur (Davenport, 1986). The time at which the set failure occurred can be inferred from the complete lack of fruit set (before fertilisation) or from partial fruit set where seedless fruit are present on the tree. Application of foliar boron and nitrogen at the cauliflower stage of inflorescence has been shown to increase fruit set by increasing both the number of pollen tubes reaching the ovule and ovule viability (Lovatt, 1994; 1998).

Figure 3. Panicle showing various stages of flower development from unopened flower through to fruit set,

Humidity affects pollination by drying out pollen and stigmas (Waser et al, 2001). In humid climates the stigma can remain receptive to pollen throughout the male opening phase but the pollen may fail to fertilise the flower (Davenport, 1986). Pollen from different avocado cultivars has different relative humidity and temperature requirements for germination and growth. For example, Fuerte pollen is sensitive to low humidity while Bacon pollen is less sensitive (Loupassaki et al, 1997).

Cross Pollination

Fruit development is controlled by phytohormones produced by the developing seed and it is possible that genetic material derived from the pollen parent has a significant influence on fruit and seed size. Pollination of one avocado cultivar with another is thought to be beneficial in enhancing yield (Clegg et al, 1996; Francis, 1996; Guil and Gazit, 1992; Robbertse et al, 1994; 1996) but large blocks of Hass trees have been observed to set good crops (Robbertse et al, 1996; Schroeder and Hofshi, 2001). Fruit set from cross pollination has also been observed to result in less subsequent fruit drop (Johannsmeier et al, 1997).

Pollen 'vigour' varies according to cultivar and is generally thought to be better than Hass with respect to pollen tube growth (Robbertse et al, 1996). Cross pollination between cultivars has been observed to result in more fruit set than pollination by the same cultivar (Robbertse et al, 1994). Only about one third of Hass pollen grains deposited on a Hass stigma managed to grow a pollen tube that reached the ovary while about half of Ettinger pollen grains produced pollen tubes that reached Hass flower ovaries (Robbertse et al, 1994). For best pollination large numbers of pollen grains need to be deposited onto avocado stigmas and these should be from another cultivar.

Experiments examining the benefits of cross pollination by different avocado cultivars on Hass yields have shown that certain cultivars are better for raising yield than others (Robbertse et al, 1996). In particular, Ettinger has been used as a pollen donor in both South Africa and Israel to increase yield (Ish-Am and Eisikowitch, 1998; Robbertse et al, 1996). The distance of a pollinator tree from the main cropping trees has an effect on yield. For Hass trees in South Africa yield declined to a minimum at 25m distance with greater yield the closer the trees were to the pollinator (Robbertse et al, 1998). In California the pollinator cultivar and the distance of that cultivar from a Hass tree determined fruit number and yield (Waser et al, 2001). Trees within rows at 2.6m from the pollinator tree had the best yield and trees in the next row at 8.3m distance greater yield than the trees an additional row distant (16.6m).

The next step in setting fruit after pollination is fertilisation. To fertilize a flower the pollen tube enters the embryo sac to release two bundles of genetic material (gametes) that serve to fertilise the egg and the tissue that will form the seed (Robbertse, 2001b).

Fruit set failure can occur if the pollination and fertilisation process does not go as described above. The reasons for fruit drop immediately following a pollination period can be any of the following: the stigma was not pollinated, pollen tube growth does not happen, there is no fertilisation, the seed fails to develop, the embryo aborts and the seed coat dies (Robbertse, 2001b).

Pollinators

The difference in the timing of the flower sex phases suggests that avocado flowers require pollinators (usually insects) that take pollen from the male phase flowers to receptive female phase flowers. Ish-Am and Eisikowitch (1998) have done considerable research done on the efficiency of bees used to pollinate avocado flowers and the relationship between the pollinators (bees) and pollinizers (trees used for cross pollination). An 81% reduction in fruit set was noted in Brazil where insects had been excluded from avocado flowers using bags (Malerbo-Souza et al, 2000). In California, excluding bees from avocado trees using cages resulted in only 15 to 20% of the pollination of trees that were exposed to bees (Davenport, 2001). Avocado flowers can be pollinated by a wide range of insects (Eardley and Mansell, 1996) but the most common insect pollinizer is honey bees (Figure 4), sourced from both a managed population and the feral population (van den Berg, 2001). In countries with a Mediterranean climate honey bees are considered to be the main pollinators of avocados and the availability of bees limits avocado fruit set. Bee activity is also affected by weather conditions that may not coincide with flowering further reducing the number of days suitable for fruit set (Robbertse et al, 1995). A certain number of bees are required to visit each avocado tree in order to get good fruit set. In Israel the number of bees required for good pollination needs to exceed 20 bees per tree. Good yield depends on 20 to 30 pollen grains to be present on an individual stigma. Avocado flowers have a limited desirability to bees and the effort bees put into foraging depends on what other flowers are available (Ish-Am and Eisikowitch, 1998). In particular bees prefer citrus flowers to avocado flowers and have been recorded to avoid avocado flowers if flowering citrus trees are within 3 km (Davenport, 1986).

Figure 4. Honey bee working on avocado flower

Only about 20-30% of bees are pollen collectors while the remainder forage for nectar or water (Du Toit and Swart, 1993). Foraging activity by bees in South Africa reaches a peak in mid morning and declines by the afternoon (Du Toit and Swart, 1993). In South Africa research has shown that for maximum pollination potential there should be groups of about 6-10 hives placed 400m apart in avocado orchards (Robbertse et al, 1998) but that 3 hives per hectare would also produce good pollination (van den Berg, 2001). In New Zealand it is generally believed that avocado orchards should have 4 strong hives per hectare for adequate pollination. However, there has been no research to confirm this as best practice for New Zealand conditions. The placement of the hives is also important as bees have been observed to forage along rows of trees (Johannsmeier et al, 1997) and not through rows. Therefore placement of hives in relation to pollen donor trees to facilitate cross pollination will affect fruit set.

CONCLUSIONS

From the information presented above there are three areas of the pollination process where a greater understanding may benefit New Zealand avocado growers with respect to increasing fruit set and subsequently yield. A greater understanding of the effect of climatic conditions on pollination and fruit set would be of value to improve the crop estimate for both the industry as a whole and for individual growers. From the information presented on the influence of temperature on flowering, pollination and fruit set it should be possible to model fruit set based on the climatic factors of temperature and humidity. Temperature conditions in the principal avocado growing districts in New Zealand are cooler than typically found in other countries. The effect of low temperatures is known to considerably alter avocado flowering behaviour such that it will be necessary to establish flowering patterns of avocados for New Zealand conditions before a fruit set model could be determined.

Especially important will be the role cross pollination may play in the enhancement of yield. The marginal temperature conditions experienced during avocado flowering in New Zealand may alter Hass flowering behaviour to make close pollination (self pollination) an important component of fruit set. The behaviour of potential pollen donating cultivars and the evaluation of new avocado cultivars selected for their ability to cross pollinate Hass flowers will need to be established for New Zealand conditions. Of value would also be the evaluation of the placement of pollinator trees within an orchard and the merits of having permanent trees compared to mobile pollinators for their effect on improving fruit set. In addition, the best placement of beehives needs to be determined in order to maximise the potential for bees to pollinate and cross pollinate Hass flowers.

Bees would appear to play a very important role in pollination and fruit set but our current understanding of the most effective way to use bees in avocado orchards is limited. A greater understanding of how bees interact with avocado flowers would improve the effectiveness of bees in avocado orchards. By drawing together an understanding of flowering behaviour, cross pollination and bee behaviour there is considerable potential to improve yields from Hass avocado trees. In order to take advantage of greater fruit set it will be important to ensure avocado tree nutrition and health are well managed as the challenge following a good fruit set is to avoid excessive fruit drop and to grow fruit of the appropriate size.

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