NOVEMBER 2020

ALL ABOUT ALMONDS

ALMOND BREEDING

POLLINATION BASICS

CONTENTS

Introduction

As almond growers, we all know that bees are needed to pollinate our trees so that we can get a crop. If the pollination is reduced due to adverse weather conditions or the poor synchronisation between varieties is reduced, low yields can result. But why is this? What is the biology involved in an almond tree that requires bees and multiple varieties in order to get a crop? This fact sheet aims to provide the basics between self-incompatibility and self-fertility, why bees are essential for pollination and why more than one variety is needed in the orchard. Honey bee flight and the requirements for successful pollination will also be discussed.

Pollination and germination

In almonds and many other tree crops, fruit (or nuts) will only develop when a flower is correctly pollinated. How does this occur? A flower has male and female parts called the stamen (male) and pistil (female) (Fig. 1). The stamen contains an anther on the end of the filament, which produces pollen grains. The pistil contains the stigma, which receives the pollen grains, and a style which connects the stigma to the ovary. For an outcrossed pollination to occur pollen grains must be transferred from the anther of one flower to the stigma of another either by insects or wind. The pollen grain germinates on the stigma, and then a pollen tube grows down the style to the ovary. Here fertilisation occurs and an embryo is formed which eventually becomes the almond kernel. There are a number of reasons why a flower may not develop into a fruit. It could be that no pollen is received on the stigma (ie lack of pollen transfer) or pollen may be transferred and a pollen tube starts to grow but then aborts. Also the pollen tube may reach the ovary and the embryo starts to grow but aborts before becoming fully developed. The pollen may also be incompatible.

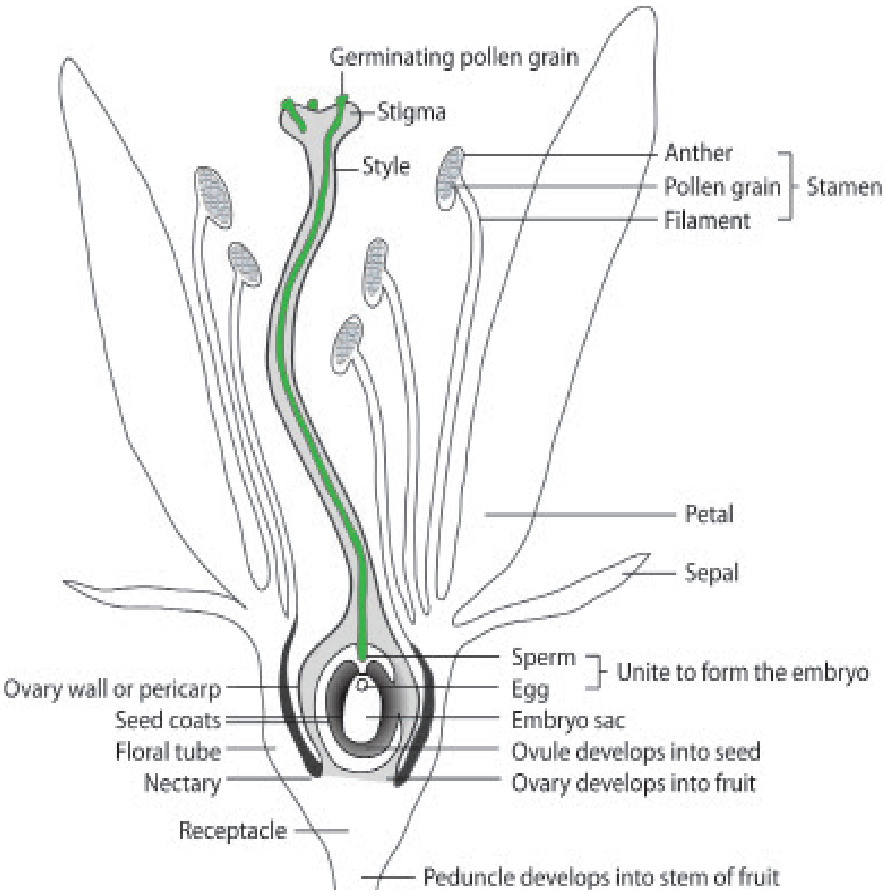

Figure 1: Compatible pollen germinates and the pollen tube grows down to the ovule where fertilization occurs.

Self-incompatibility and self-fertility

Self-incompatibility is a widespread mechanism in flowering plants that prevents inbreeding and promotes outcrossing. The self-incompatibility response in almonds is genetically controlled by S-alleles, and relies on a series of complex cellular interactions between the pollen and pistil. An S-allele refers to a specific variation of the DNA at a given locus, or a specific location on a chromosome. You might have heard of 'Gene Mapping'. Gene mapping is the process of determining which biological trait is associated with each locus, or location on a chromosome. In the case of almonds the S-allele is associated with fertility. The list of known alleles for common almond varieties in Australia is shown in Table 1.

Although self-incompatibility functions ultimately to prevent self-fertilization, flowering plants have evolved several unique mechanisms for rejecting the self-incompatible pollen. In almonds the alleles produce proteins which are either compatible or not. In short, if the allele has the same number for both the pollen donor and recipient (and therefore produces the same protein) it is not compatible and will abort the germination process. This means that after the pollen has been transferred from the anther (male) to the stigma (female) the resulting pollen tube growth is aborted, no embryo develops and ultimately no fruit grows. If the allele number is different, then germination is possible (Fig. 2).

By referring to Table 1, you can see that each almond cultivar has a pair of numbered alleles which in turn can be grouped together. Cultivars within the same group (ie the same numbered alleles) are 100% incompatible and therefore cannot fertilise each other to produce fruit. Therefore a cultivar from one group will only be compatible with a cultivar froma different group. However, if two cultivars share a common allele ie Nonpareil and Carmel, then the pollen produced will be partially incompatible.

Pollen produced containing S8 alleles will be incompatible, but pollen containing either the S7 or S5 allele will be 100% compatible. Genetically 50% of pollen produced by Nonpareil and Carmel is compatible. In the orchard this is normally not a problem due to the abundance of pollen. Conversely the pollen from Nonpareil and Peerless is 100% compatible (due to all S-alleles having a different number). Cultivars in group 'O' are mutually compatible with each other and cultivars of all other groups. In the case of some cultivars (Carina, Capella, Mira & Vela) this is due to the presence of the Sf allele which is responsible for self-fertility. The Sf allele is dominant and when present, pollen from the same group or cultivar has the potential to produce fruit.

For more information on the technical side self-incompatibility and self-fertility in almonds, refer to the fact sheet 'Breeding for self-fertility in almonds'.

Table 1: Almond cultivars and S-allele compatibility

Variety	S-alleles	Incompatibility group
Nonpareil	S_7S_8	I
Wood Colony	S_5S_7	III
ABA Breeding selection 6	S_5S_7	III
Aldrich	S_1S_7	IV
Price	S_1S_7	IV
Carmel	S_5S_8	V
Livingston	S_5S_8	V
Avalon	S_1S_8	VI
Butte	S_1S_8	VI
Monterey	S_1S_8	VI
Sonora	S_8S_{13}	VII
Peerless	S_1S_6	XIV
Chellaston	S_7S_{23}	XXVI
ABA Breeding selection 4	S_7S_{23}	XXVI
Marcona	$S_{11}S_{12}$	O
Padre	S_1S_{18}	O
ABA Breeding selection 1	S_7S_f	O
ABA Breeding selection 2	S_7S_f	O
ABA Breeding selection 3	S_3S_8	O
ABA Breeding selection 5	S_7S_f	O
Johnston's Prolific	$S_?S_{23}$	?
Keanes	$S_?S_7$	?
ABA Breeding selection 7	$S_?S_8$	?

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The bugs and the bees

Now the basics of germination and fertility have been covered, how does that apply to the everyday almond orchard? Also, why do we need bees for pollination? No commercially grown almond cultivars in Australia contain the Sf allele and therefore another compatible cultivar is required for successful cross pollination. This is why there are alternating rows of Nonpareil and pollinators. When the weather is suitable for good pollination conditions in August, there will be enough pollen produced by most cultivars to pollinate Nonpareil and vice versa. However if the weather conditions are not optimal and/ or flowering is light, pollen compatibility may be a limiting factor in the potential yield. This may have had some relevance to the flowering and pollination period in spring 2011 and the resulting low yields in 2012. It certainly may not have been the primary factor but may still have played its part. It is interesting to note the recent popular planting pattern of 50% Nonpareil, 25% Carmel and 25% Monterey might deliver profitable yields in a good year but genetically from a pollen compatibility point of view it is less than ideal as each of the cultivars contains the S8 allele. Hence flower numbers (ie pollen production) and synchronisation must be favourable as only 50% of the pollen from each cultivar is compatible to pollinate another cultivar. Another popular planting example is Nonpareil, Carmel and Price. In this case both Carmel and Price are only 50% pollen compatible with Nonpareil but are 100% pollen compatible with each other.

Bees are required for pollination to transfer the pollen from one cultivar to the next ie one row to the next. Since almonds are so dependent on pollen transfer in large numbers, bees and their ability to be managed in colonies is the obvious choice. Wind and other insects are also capable of transferring pollen from the anther to the stigma but because almonds are completely dependent on cross pollination, there is a risk of poor pollination outcomes when there are too few flower visiting insects, or too little wind.

A literature study by Cunningham (2011) confirms the amount of fruit set is related to the amount of cross pollination. Almond trees are generally not resource limited and the potential may exist for every flower to become a fruit if successfully pollinated, although the literature states that as many as 22-31% of flowers can be female sterile. Where almond flowers are hand pollinated the rate of fruit set is higher than when flowers are open pollinated (by bees). The rate of fruit set could be as high as 30-50% but rarely above 60%.

The literature study by Cunningham (2011) suggested a 'normal' fruit set may be approximately 25%. No studies have shown whether an almond tree that flowers prolifically can successfully sustain a high crop load to maturity. Another interesting observation that came out of the literature study was that unfavourable weather during flowering doesn't have as much impact on nut set as first thought. A study in 2007 examined yields in California over 23 years against the weather conditions during flowering and found there was no significant link despite the fact bee activity at the hive is clearly less during cold and wet weather.

It is widely known bees can forage for nectar and pollen over large distances but prefer to focus on one resource over shorter distances. What does this mean in the context of an almond orchard? Bees will forage for nectar or pollen closer to the hive and more likely down the row than across the row. Studies have indicated the preference for bees to forage for nectar or pollen will vary according to the amount of storage in the hive. The amount of pollen foraging can therefore be increased by limiting the amount of pollen entering the hive by using pollen traps on the hive entrance. One study in 1985 used pollen traps to strip the bees of pollen and showed a higher rate of fruit set, however the study was not replicated so it is too early to generalise from this. The Almond Board of Australia's R&D project AL11003 – Enhancing Almond Pollination Efficiency will investigate bee flight patterns and the use of artificial methods to increase pollination efficiency. Stage 1 of the project occurred in 2011-12 in a number of orchards in the Riverland. Selected parts of the orchard where chosen to deliberately reduce the hive density to see what effect bee density will have on fruit set. The observations so far conclude that bees preferred moving in the row that contained the hive (N.B. the hive was placed in the middle of the orchard which is not a standard commercial practice) until late in the day when pollen and nectar levels run low. High bee density was sometimes associated with poor fruit set which suggests the link between bee density and fruit set is weak. The main factor associated with poor nut set is poor cross pollination which has been confirmed by hand pollination tests in the field. In other words, even when a tree is exposed to a very high level of bee visits, some flowers still do not receive any cross pollen, probably because self pollen is overwhelming the system. Adding more and more bees to the system will not solve this problem. The second year of the project in 2012-13 will examine pollination with lower bee numbers, and will pilot methods to change foraging behaviour.

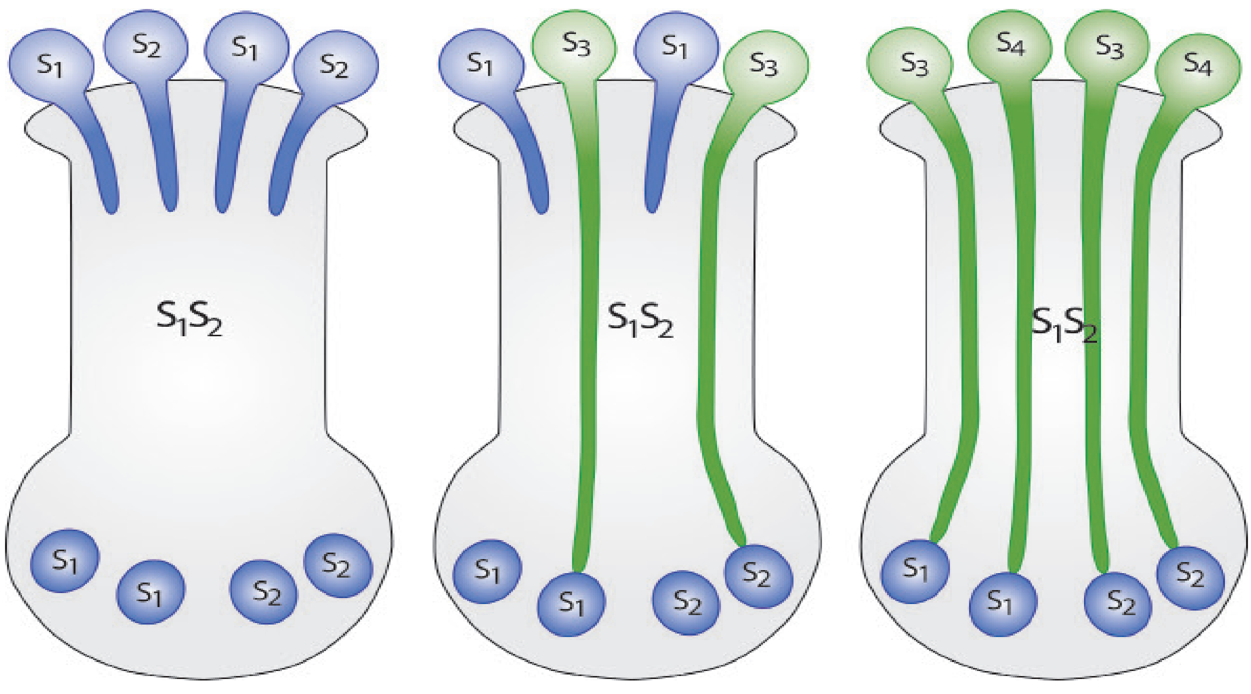

Figure 2: Gametophytic self-incompatibility system. Germination of pollen grains, which carry one of the same S-alleles as the pistil, is inhibited in the upper style.

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OTHER RESOURCES

Australian Almond Breeding Program
https://bit.ly/3pxvwq6

PROJECT CODE

AL12015: Australian Almond Breeding Program

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MORE INFORMATION

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