The Pollination of Almonds

by GLORIA DeGRANDI-HOFFMAN*

Of all the crops grown commercially in the U.S. that require honey bee pollination, perhaps the most important, in terms of the number of colonies that are needed, is almonds.

Each year over a million colonies are trucked across the country to pollinate the 570,000 acres of almond orchards in California. Since almond pollination is such a significant part of the beekeeping industry's total contribution to U.S. agriculture, scientists from the Carl Hayden Bee Research Center in Tucson, Arizona conducted research to determine factors that influence successful almond pollination and nut set. In this article I will provide an overview of the research we conducted and our findings on why honey bees are such remarkably efficient pollinators of this crop.

All varieties of almonds require cross-pollination (i.e., the transfer of pollen from blossoms on trees of one variety to those on trees of a different variety) for nut set. Cross-pollination in almonds, and in any other crop, is a dynamic process because the rate that pollen is exchanged between blossoms of different almond varieties changes throughout bloom. The factors that influence how much cross-pollination occurs and how many nuts are set include: 1) weather conditions, 2) the number of open blossoms on trees of each variety, 3) the number of bees in the orchard and 4) the quality of the almond blossoms. All these factors must be taken into account to accurately assess how much cross-pollination and nut set is occurring. During our orchard studies we collected data on each of these factors. I will discuss our findings on each factor individually for its influence on cross-pollination and nut set. Then, I will put together those findings to establish a framework for conceptualizing almond pollination and nut set as a dynamic system.

Weather conditions (i.e., temperature, wind velocity, sunlight, humidity/precipitation) influence how much cross-pollination and nut set is occurring at any point in time because of the effects on almond bloom and bee foraging activity. Temperature affects the rate that blossoms are opening and aging. More blossoms open each day and age at a faster rate when temperatures are warm. Consequently, trees remain in bloom for a shorter period of time when temperatures are high compared with when they are low. We found that bloom on different varieties of almonds progresses through time at different rates even though the varieties are exposed to identical temperature regimes (DeGrandi-Hoffman et al. 1996). This means that the amount of overlap in bloom between two varieties will vary from year to year according to temperature. It is important to consider bloom overlap between varieties in the context of cross-pollination because the number of open blossoms on trees of each variety determines the attractiveness of the tree to bees, and the amount of pollen that is available to be transferred among blossoms.

We counted open blossoms on different varieties of almond trees as part of our study to determine how the progression of bloom varied under different temperature regimes. We found very different bloom progression patterns that were based upon air temperatures during bloom. Bloom patterns of two self-sterile almond varieties (Nonpareil and Neplus) are shown in Figure 1. In Year-1 the first week of bloom was warm. The Nonpareil bloom was progressing faster than the Neplus and reached full bloom by the end of the first week. This provided an abundance of cross-pollen for the Neplus trees, but limited the amount of cross-pollen for the Nonpareil until later in its bloom period. In Year-2, the temperatures during bloom were cooler than in Year-1 and the full bloom period for Neplus and Nonpareil overlapped for several days. In Year-2 there were large amounts of compatible pollen available to set nuts on both varieties. When full bloom among varieties occurs simultaneously, having large populations of honey bees in the orchard will maximize cross-pollination rates and most of the crop may be set during this period.

Weather conditions can change dramatically throughout the day, and honey bees are constantly adjusting their foraging activity to those changes. The number of honey bees foraging a particular almond variety also changes as the number of open flowers on the almond trees change. The more open flowers a tree has, the more honey bee foragers will be attracted to it. The number of bees on trees of each cultivar ultimately determines the rate at which cross-pollination occurs.

The last factor in the almond cross-pollination and nut set system that must be considered is the quality of the blossoms. Quality is determined by the ability of the blossom to set a nut if it is cross-pollinated. Blossom quality changes as blossoms age and as bloom progresses. Usually the first blossoms to open have the greatest chance of setting nuts, particularly on the first day that they open. Afterwards, the chances of a blossom setting a nut declines every day that it remains open and is not pollinated. Temperature also determines whether cross-pollination will lead to nut set. If temperatures are too high (in excess of 90°F) or too low (less than 40°C), cross-pollination might not lead to fertilization of the blossom ovule, so nut set will not occur.

To estimate cross-pollination and nut set, all the factors stated above must be considered simultaneously and their impact must be updated over time. Weather conditions set the stage for the amount of foraging activity that will occur,

* Carl Hayden Bee Research Center, USDA-ARS, 2000 East Allen Road, Tucson, AZ 85719.

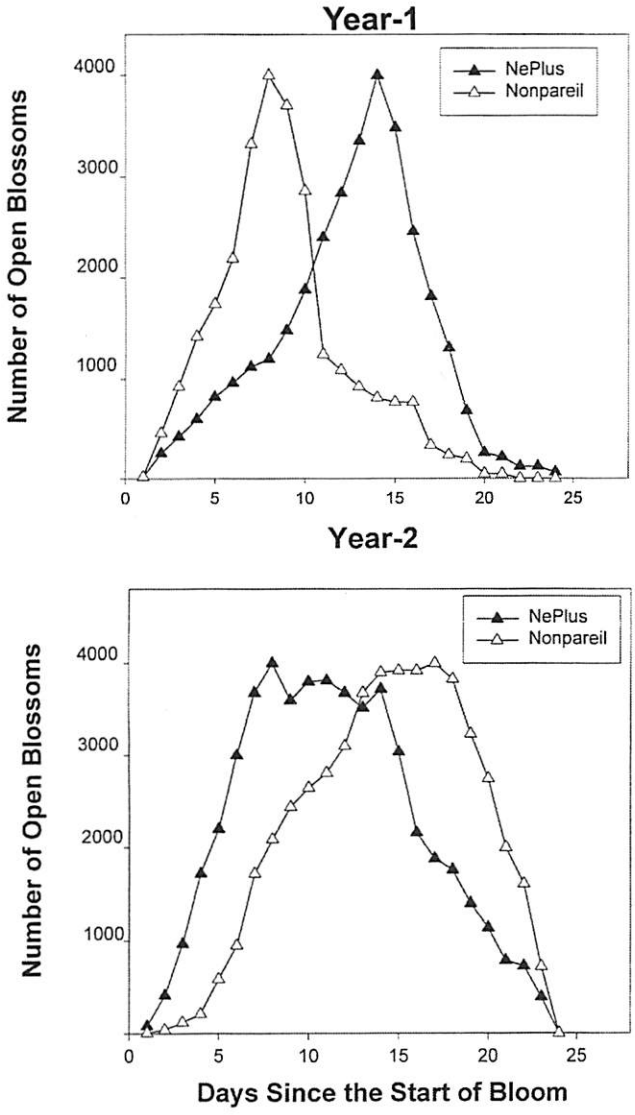

Figure 1. Difference in the number of open flowers during bloom in two almond varieties in two different years.

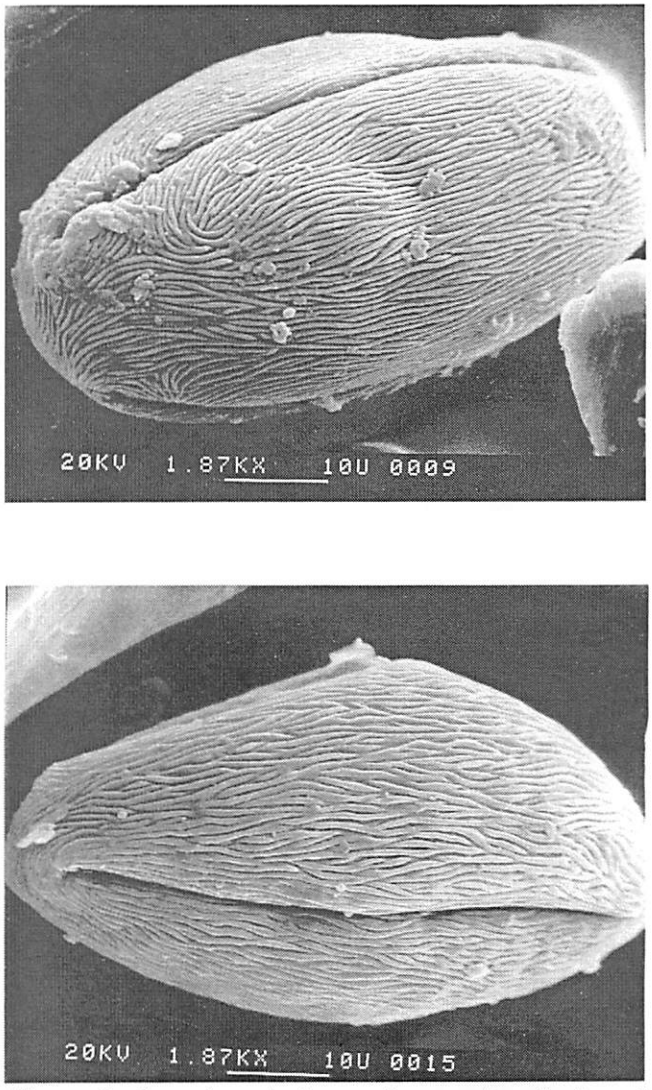

Figure 2. Scanning electron micrographs of almond pollen grains from two different varieties: Neplus (top) and Nonpareil (bottom).

and the rate at which flowers will open and age. The ratio of open flowers on trees of different varieties will determine the amount of cross-pollen that is available. The number of open flowers on each variety also determines how many can be cross-pollinated. Once cross-pollination occurs, the age of the flower that was cross-pollinated, the time during bloom when it opened, and the ambient temperature in the hours after cross-pollination will determine whether cross-pollination will lead to ovule fertilization and nut set.

Now that we have considered weather conditions and the number of blossoms on trees of each variety, the final factor to take into account in the cross-pollination of almonds is honey bee foraging activity on almond trees. Many honey bees may be seen foraging on almond trees, but only those carrying pollen from a different variety (i.e., cross-pollen) on their bodies can cross-pollinate blossoms. Honey bees can obtain cross-pollen by visiting trees of different varieties. However, experiments conducted in apple orchards to determine if honey bees switch between different varieties indicated that individual honey bees show fidelity to a single variety. Honey bees do not switch between trees unless there is insufficient pollen or nectar available (Robinson 1979). We measured nectar and pollen available to honey bees in the morning and afternoon throughout bloom on different varieties of almond trees. We found that the amount of nectar and pollen provided by blossoms was uniform among the varieties we examined. Furthermore, for most of the bloom period honey bees could obtain full nectar or pollen loads from visiting blossoms on just 2-3 blossom clusters on the same tree (DeGrandi-Hoffman et al. 1991). The results from these experiments indicate that the number of honey bees moving between trees of different varieties is probably a small proportion of the total foraging population. The results also suggest that the proportion of the total almond crop that is set by honey bees moving between trees of different cultivars probably is quite small.

The next set of experiments we conducted was to determine the percentage of honey bees that have cross-pollen on their bodies, while they are visiting almond blossoms. We captured honey bees as they foraged blossoms of different almond varieties. We removed the pollen from their bodies and examined it using a scanning electron microscope (SEM). Under an SEM, almond pollen grains from different varieties can be distinguished because each has a characteristic pattern like a fingerprint (Figure 2). We found that more than 90% of the bees we examined had pollen from many almond varieties on their bodies (DeGrandi-Hoffman et al. 1992). Consequently, most of the honey bees visiting almond blossoms probably were cross-pollinating them.

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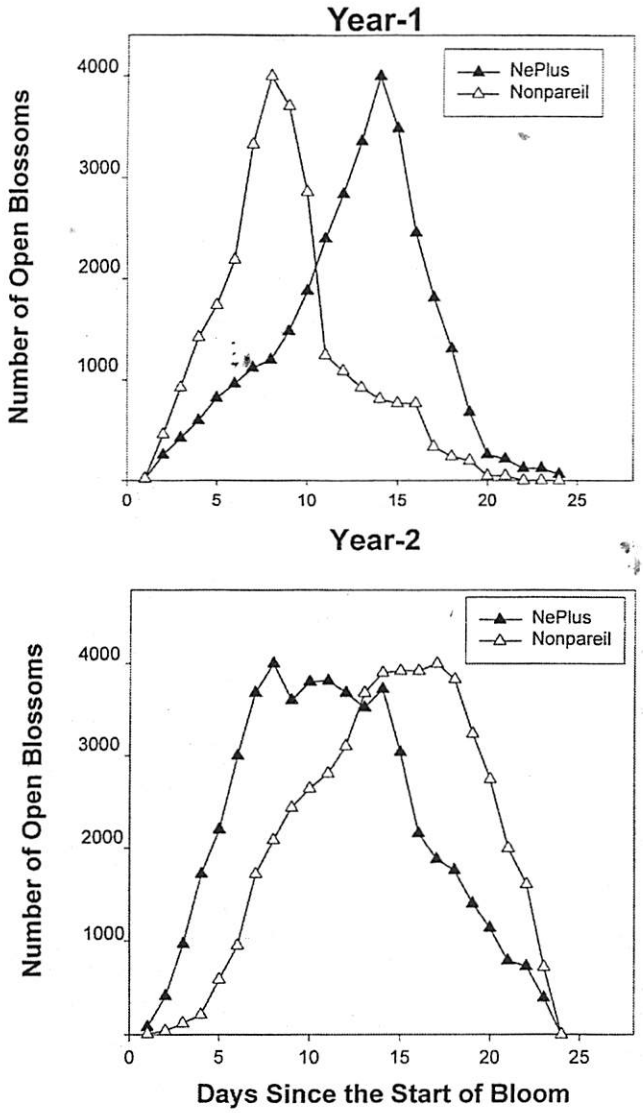

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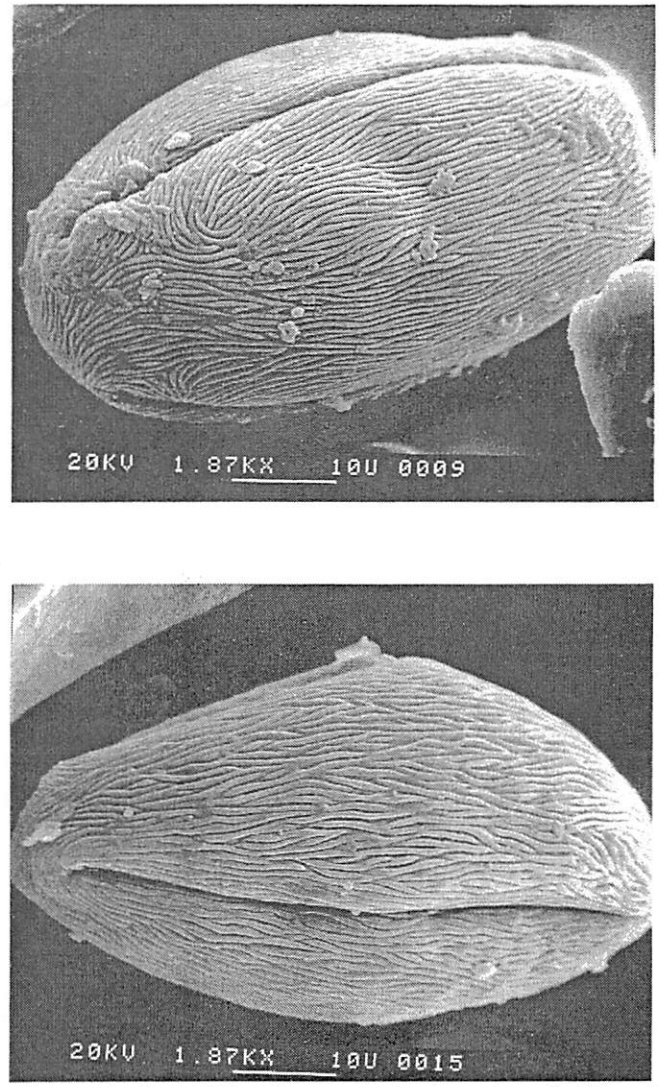

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large population of honey bees with cross-pollen on their bodies, even if the bees restrict their foraging to a single tree or variety, is the transfer of pollen among nestmates inside the hive (Karma and Vickery 1954; DeGrandi-Hoffman et al. 1986). In studies conducted in apple orchards, we found pollen from numerous apple cultivars, as well as other species of plants, on honey bees that we emerged in incubators and released in colonies near apple orchards (DeGrandi-Hoffman et al. 1986). Before releasing the bees in the hives, we marked them and clipped their wings so we were certain they did not forage. The pollen we found on their bodies was acquired solely through contacts with other bees in the hive. We also took some of the bees we released in the colonies and pollinated apple blossoms with them. The blossoms set fruit, thus indicating that the pollen transferred in the hive was viable. As in the apple orchards, we consistently found a large and evenly distributed population of honey bees with different varieties of pollen on their bodies foraging almond blossoms. The large population of bees with cross-pollen on their bodies ,regardless of their location in the orchard, indicates that the foragers most likely were picking up the pollen in the hive from nestmates that were foraging different almond varieties.

Pollen transfer among bees inside the hive can generate a large population of foragers capable of cross-pollinating almond blossoms, but only if pollen from two or more varieties is available at the same time. Almond trees differ in their time when bloom begins, depending upon the variety. The difference in the start of bloom between some varieties can be a week or more. The varieties chosen during the establishment of the orchard will determine how much overlap there will be in the bloom periods between different varieties and ultimately how much cross-pollination can occur. An example of a combination of varieties with poor bloom overlap is shown in Figure 3. When Neplus reaches full bloom, there is a relatively small number of blossoms open on the Mission trees. Most of the honey bees will be on the Neplus trees, so most of the almond pollen entering the hive will be Neplus. Those bees visiting the Mission blossoms will probably cross-pollinate them using the Neplus pollen they obtained in the hive. However, since very few Mission blossoms are open, very little Mission pollen will be brought into the hive. Consequently, most of the pollen on bees foraging on Neplus will have Neplus pollen on their bodies, so they will not be cross-pollinating blossoms.

Another factor that can limit the availability of compatible pollen, even if the bloom on trees of different varieties overlap, is the number of trees of each variety in the orchard. If one variety outnumbers another by 4-5 fold, cross-pollination and nut set will be limited because the amount of cross-pollen for the variety that comprises the majority of trees will be limited.

A question that always arises in discussions of pollination is, "How many colonies do I need per acre to maximize nut set?" My answer is always the same, "It depends upon the conditions in the orchard and the strength of the colonies." In years where morning and evening temperatures are low, but afternoons are warm enough for good bee flight, fewer colonies will be needed than in years where warm and windy or rainy conditions prevail. When temperatures are low, the bloom period lasts longer and bees have more days to forage and cross-pollinate blossoms. Conversely, if temperatures are high (thus causing a short bloom period), but wind or rain prevent bees from flying, more colonies are needed to maximize cross-pollination during the periods when bees can forage.

Colony strength also influences the number of colonies needed per acre. Colonies with large populations (i.e., strong colonies) have more foragers than those with smaller populations. Furthermore, colonies with large expanding brood areas require a greater influx of pollen to feed larvae compared with those having less brood. A large amount of pollen coming into a colony increases the rate that pollen is transferred in the hive. If several varieties of almond are blooming simultaneously, strong colonies will have large populations of foragers that can cross-pollinate blossoms.

I hope this article has shed some light on the complexities of the almond pollination system. Almond pollination involves many factors that must come together during the 2-3 week bloom period for a full crop to set. The varieties in the orchard create the infrastructure of the cross-pollination process and the potential rate that blossoms can be cross-pollinated each day. Weather conditions drive the process through time. The number of bees foraging when two or more varieties are in bloom establish the rate that cross-pollination is occurring. Optimum almond yields occur when more than 50% of the blossoms set nuts. Since honey bees can transfer pollen in the hive if the foraging population is divided among several almond varieties, the honey bee is probably the most efficient and economically feasible pollinator of almonds.

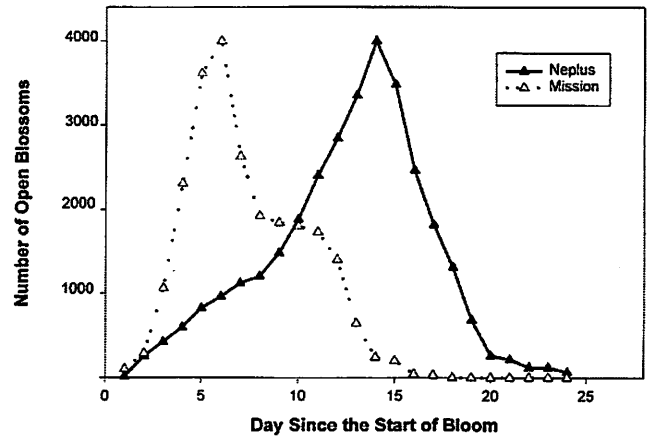

Figure 3. The period of bloom overlap for different varieties of almonds.

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