POLLINATION OF ALMOND (*Prunus dulcis* (Mill.) D.A. Webb)

by

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SUMMARY

The yield of almond trees can be increased by increasing nut-set through improving pollination efficiency. At least 50% of flowers can produce nuts, but normally only 10 to 30% of flowers set nuts in Australian orchards. An average nut-set of 50% can be achieved by manipulating the factors of pollination and nut-set. Plants of many species often abort many developing fruit after achieving a high fruit-set, but that has not been reported in almond. Much has been written on the pollination of fruit trees (e.g. Free 1970a), but that information is inadequate for almond because the optimum nut-set for almond is much higher than the optimum fruit-set for most other tree crops.

The variables which are known to influence pollination and nut-set for almond are elucidated in this thesis by experiments and by a critical review of the literature.

All the experiments were done in one almond orchard at Angle Vale, South Australia (34^0 39'S, 138^0 40'E). Several preliminary experiments were performed to relate the experimental orchard and proposed experimental techniques to information obtained from the literature.

Not all flowers are capable of producing nuts. Flowers of the cultivars Chellaston and Davey were examined macroscopically to determine the incidence of flowers that lacked a viable gynaeceum (female-sterile flowers). Five categories and 3 sub-categories of flowers were defined. The flowers of only one sub-category were able to produce nuts. From 10 to 90% of all flowers were female-sterile on any one date, and over the whole 1984 season 22 to 31% of flowers were female-sterile so female-sterility is a significant nut-set factor of almond. Buds and flowers can also be destroyed by frost, birds, hail, wind, passing machinery, and pruning.

The time of day when flowers are open can influence the pollination of many plants, but apparently that is not true for almond because flowers of almond trees in the experimental orchard did not close after they had opened. Some flowers opened during the night, but the rate of flowering was higher during daylight hours. The rate of flowering was related to air temperature and also to solar radiation.

Four experiments elucidated the nature of anther dehiscence and pollen loss in almond flowers with respect to time of day, weather, cultivars, and honeybee behaviour and activity.

Rate of anther dehiscence varied with time but appeared to be independent of flower age. Rate of dehiscence increased with increasing ambient air temperature within the temperature range of 8 to 17°C, and the variation about the regression line was attributed to variation in the intensity of solar radiation; so the rate of anther dehiscence may depend on the temperature of the anther tissue. Anther dehiscence occurred day and night but the rate of dehiscence was higher during the daylight hours, probably as a result of temperature differences. Anthers did not dehisce until 6 to 48 hours after anthesis and all anthers within a flower dehisced after a further 2 to 74 hours. Anther dehiscence occurred during periods of rain, but some anthers that had dehisced were closed by free water on the anthers.

Pollen was available for collection by honeybees for 2 to 6 days after anthesis. Pollen was not lost overnight from caged flowers, even though rain and winds of over 40 k.p.h. occurred. Furthermore, pollen loss from anthers was related to air temperature and sunshine, and pollen loss occurred only when honeybees were foraging; so honeybees were probably the only significant cause of pollen loss from anthers. Pollen loss often did not occur until at least 24 hours after anther dehiscence. Pollen masses left on caged anthers shrank through dehydration.

Honeybee visits to, and pollen loss by, 23 flowers were recorded on video tape during 8 consecutive days. Most flowers were not visited by a bee until the flowers were at least 24 hours old. Pollen-collectors rarely visited flowers that did not contain pollen in dehisced anthers. Every period of pollen loss coincided with at least one visit by a bee that exhibited pollen-collection behaviour. Honeybees collected pollen at the rate of up to 7.5 anthers per second, and so some instances of pollen collection may have gone unnoticed. Honeybees touched the stigma during 58 to 100% of all visits per flower. Many bees hovered momentarily in front of flowers, supposedly to look for pollen or nectar.

The effective pollination period (EPP) is the limit beyond which pollination of a stigma cannot lead to the fertilization of the ovule. EPPs for fruit trees in general vary from a few hours to 12 days, depending on many factors, but little is known about EPPs in almond. If almond EPPs are only 2 or 3 days, then the scarcity of visits by foragers to flowers during that time would be an important factor of nut-set.

Almond flowers must be cross-pollinated, so two cultivars must flower coincidentally and they must be cross-compatible. Date of flowering depends on genetic interaction with winter and spring temperatures, and date of flowering may be altered by many agronomic methods.

Most almond pollen is viable, but fungicides can kill all naked pollen, and so fungicides may inhibit effective pollination for a day or two after spraying, and for several days over a flowering season. Therefore the value of using fungicides during the flowering season is questioned.

Wind-pollination is negligible in almond, and honeybees are necessary for pollination in commercial orchards. Methods of man-aided pollination may be useful but they are expensive compared to the efficient use of honeybees. Strains of honeybees and other insects may be bred specifically for the pollination of particular crops.

Recommendations of putting honeybee colonies into orchards depend on the specifications of the orchards and the hives. Three methods are discussed for the estimation of the optimum honeybee population for orchards. Hive placement, with respect to date of placement, time of day, hive history, landmarks, and hive temperature, are discussed. Artificial colonies may be useful, but they are expensive.

Only foraging honeybees pollinate significant numbers of almond flowers. Whether or not foragers are attracted to particular flowers depends on many factors. Both pollen-collectors and nectar-collectors can effectively pollinate flowers, but the probability of effective pollination occurring during a visit by a forager depends on many factors, including the number of visits by foragers during the EPP, the incidence of stigma touching, and the amount and identity of pollen on the bodies of bees. Mutilated flowers that are devoid of stamens and petals are visited by foragers, but the probability of stigma touching is less than for intact flowers.

The incidence of flower visitation by foragers depends on many factors, and weather is particularly important, especially temperature. Weather influences the times of foraging, the distance foragers fly, and the amount of pollen and nectar available. These factors are important for the determination of the optimum distribution and placement of hives.

Most instances of effective pollination are thought to be due to foragers that visit two or more cultivars during a foraging trip, but secondary pollination pathways, which involve two or more bees, are also

important. The number of foragers that visit flowers of two cultivars during a foraging trip depends on several aspects of the orchard, including the distribution of cultivars, the planting pattern, tree size, distance between trees, and whether or not hedgerows have formed.

Methods of increasing almond yields in existing and future orchards are discussed.

STATEMENT

This thesis has not been previously submitted for a degree at this or any other University, and is the original work of the writer except where due reference is made in the text. This thesis is available for photocopying and loan if accepted for the award of the degree.

Stuart J. Hill

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PREFACE

This thesis is aimed towards increasing the yield of almond trees by getting more flowers to produce nuts. The more specific aims of the thesis are explained in Chapter 1.

The thesis following Chapter 1 is divided into two parts. Part A is a series of reports of experiments that I performed in an almond orchard near Angle Vale, South Australia. The orchard is described in Chapter 2. Part B is a combination of literature review and critique, and it is an attempt to identify and elucidate all the known factors of almond pollination, including the factors examined in Part A. Some sections are discussions of new ideas that I propose, and which are derived from information found in the literature.

Readers who are not familiar with factors that are discussed in this thesis may need to reread some sections because some of the discussion has a cyclic nature. The glossary and index to tables and figures may be useful.

Some sections of this thesis contain long lists of cited references. This is unavoidable if I am to be fair to all relevant authors because many of the areas of research discussed in this thesis either were not reviewed recently, or were poorly reviewed. I have attempted to include only key references, but long lists of references still occur because many authors, especially recent ones, omitted important references.

Most of the cited references contain experimental results, but some references are only extension circulars and notes. The latter references are included because they reflect that which is perceived to be true by many people who are involved in horticulture, but which may not be supported by experimentation, and, indeed, which may actually be opposed by experimental results. Pollen inserts are a good example of this, in that they are used in many orchards, but experiments suggest that they are of little or no economical use (Section 10.5.2). Knowledge of what is perceived to be true is important because the misconceptions of orchardists can themselves be factors of yield, in that the misconceptions may prevent the orchardists from implementing improvements with respect to the known "real" factors of yield. Consideration of this point has led to the inclusion of discussions of factors that may seem, at first, to be of little significance to the reader.

I have included some general comments on almond growing in Australia (e.g. Section 7.2) in order to complete the story told by this thesis. The comments are based on discussions with many orchardists, and visits to their orchards, since 1981.

Some work that is related to, but is apart from, this thesis is presented as Appendices 3 and 4.

GLOSSARY

Colony - the population of honeybees in a hive.

Hive - a box that may or may not contain a colony of honeybees.

Hive strength - page 175.

Cultivar - refers to the genotype of scions that are asexually reproduced (page 21).

Self-pollination and self-fertilization - the pollen and stigma belong to the same cultivar (page 21).

Cross-pollination and cross-fertilization - the pollen and stigma belong to different cultivars (page 21).

Open-pollination - pollination that happens without the aid of man.

Hand-pollination - pollination by using a hand-held brush.

Compatibility and incompatibility - page 163.

Effective pollination - page 143.

EPP (Effective Pollination Period) - page 143.

Nut-set (fruit-set) - percentage of flowers which produce nuts (fruit).

Anthesis - the time when anthers first become visible.

Newly-opened flower - a flower between 0 and 24 hours after anthesis.

One-day-old flower - a flower between 24 and 48 hours after anthesis.

Female-sterile flowers - page 72.

Female-fertile flowers - page 72.

Chapter 1: Increase almond yield by manipulating the factors of nut-set

1.1 The factors of yield

The yield of an almond tree is a function of three variables: the number of flowers (N), the proportion of the N flowers that produce nuts (i.e. nut-set) (S), and the mean weight-per-nut (W). The function is also described in Table 1.1. An increase in any one of those factors theoretically should increase yield, but with most fruit tree crops and for trees of a given size, an increase in the number of fruits per tree is associated with a decrease in the average size of individual fruits (e.g. Langridge and Goodman 1979, 1981). Almond nuts have a similar tendency in that although the gross weight of nuts per tree increases in relation to the number of flowers that set a nut, the average weight-per-nut (W) decreases; so doubling the nut-set (S) will increase the harvest weight (Y_{wt}) by only about 70 to 90% (Hill *et al.* 1987). For most tree crops, a crop of small fruits is often not as valuable compared to a crop of larger, but fewer, fruits; so fruit growers often prefer to limit the number of fruits per tree in order to achieve optimum fruit size and hence optimum financial return. With almond, however, small nuts are often in short supply and are easily sold (Griggs 1953; Kester *et al.* 1963; Griggs 1970; Baker 1980), hence almond growers want the highest number of nuts per tree because financial return is dependent upon total tonnage of nuts.

For almond, the highest number of nuts per tree (Y_{number}) is achieved when both N and S are maximized (Table 1.1). One can aim to increase both N and S to their maximum value because N and S are probably independent of each other within a given year (e.g. Kester and Griggs 1959a). The potential to increase yield by increasing the mean weight-per-nut (W) appears to be small (Hill *et al.* 1987) compared to the potential to increase yield by increasing nut-set (S); therefore W is largely ignored in this thesis.

The number of flowers (N) varies greatly between trees, cultivars and years (Tufts and Philp 1921; Wood 1946), but the maximum possible value of N is unknown. There appear to be several factors of N which may be manipulable (see Bould and Parfitt 1973; Trobisch and Schilling 1970; Looney *et al.* 1985; Hill *et al.* 1987), but they will not be discussed in this thesis.

Theoretically, the maximum possible value of S is 1 (i.e. 100% nut-set).

Table 1.1: The yield of an almond tree can be expressed as

$$Y_{wt} = N \times S \times W$$

and $$Y_{number} = N \times S$$

where Y_{wt} = Gross weight of nuts

Y_{number} = Number of nuts

N = Number of flowers

S = Proportion of the N flowers that produce nuts (i.e. nut-set)

W = Mean weight-per-nut

Realistically, however, S can rarely, if ever, be 1 because not every flower is capable of producing a nut (e.g. Chapter 2). Nevertheless, evidence presented in this chapter shows that S is usually much less than that which is possible; and an increase in nut-set (S), and hence yield, can be achieved by manipulating the factors of nut-set. This thesis identifies and examines the important, known factors of nut-set.

1.2 Three probabilities and the factors of nut-set

Most of the factors of nut-set can be placed into one of three groups, and each group can be related to a probability of particular physiological events occurring. The physiological events for each probability are illustrated in Figure 1.1, and are pollination (P1), pollen tube growth and fertilization (P2), and the development of a mature nut (P3). The latter two probabilities are calculated from the times of pollination and fertilization respectively, so the probability of a nut being harvested from a flower is P1 x P2 x P3.

Each probability may be influenced by factors that are active outside of the periods during which each particular probability is calculated. For example, some factors are dependent on the genotype of the cultivars concerned, and the cultivars for the orchard are chosen before the orchard is planted.

The possible values of P1, P2 and P3 may often be less than the theoretical values, and the relationships between the possible and theoretical values are explained below with the aid of Figure 1.2. Theoretically, the maximum value of P1 should be unity (i.e. all flowers), but not all flowers are capable of producing nuts, so the maximum possible value of P1 (i.e. actual $P1_{max}$) is less than the theoretical value of P1 (i.e. theoretical $P1_{max}$ - Fig. 1.2). The probability (P) that a female-fertile flower will produce a nut is equal to P1 x P2 x P3, where P1 + $P1_{achieved}$ / actual $P1_{max}$, P2 + $P2_{achieved}$ / $P2_{max}$, and P3 + $P3_{achieved}$ / $P3_{max}$. If $P1_{max}$, $P2_{max}$, and $P3_{max}$ are achieved, then $P1_{max} = P2_{max} = P3_{max}$.

However, the maximum possible values of P1, P2, and P3 are rarely attained because usually some factors are suboptimal. This thesis is an attempt to identify the factors and elucidate on their optimisation so that the achieved values of P1, P2, and P3 can be increased, from what they normally are now, to values that are much closer to unity (consider Fig. 1.2).

Figure 1.1: The physiological events for which the three probabilities P1, P2, and P3 are calculated.

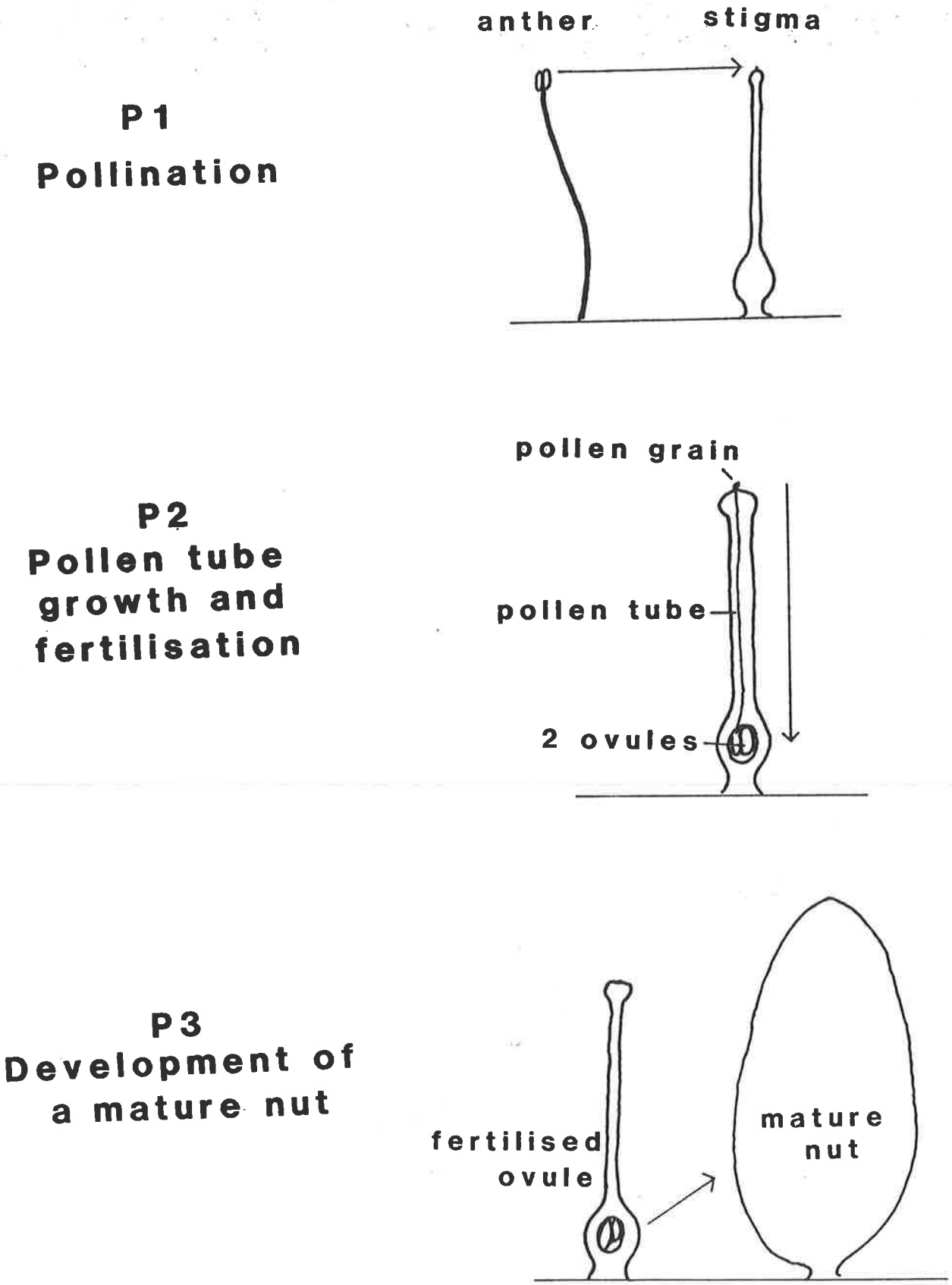
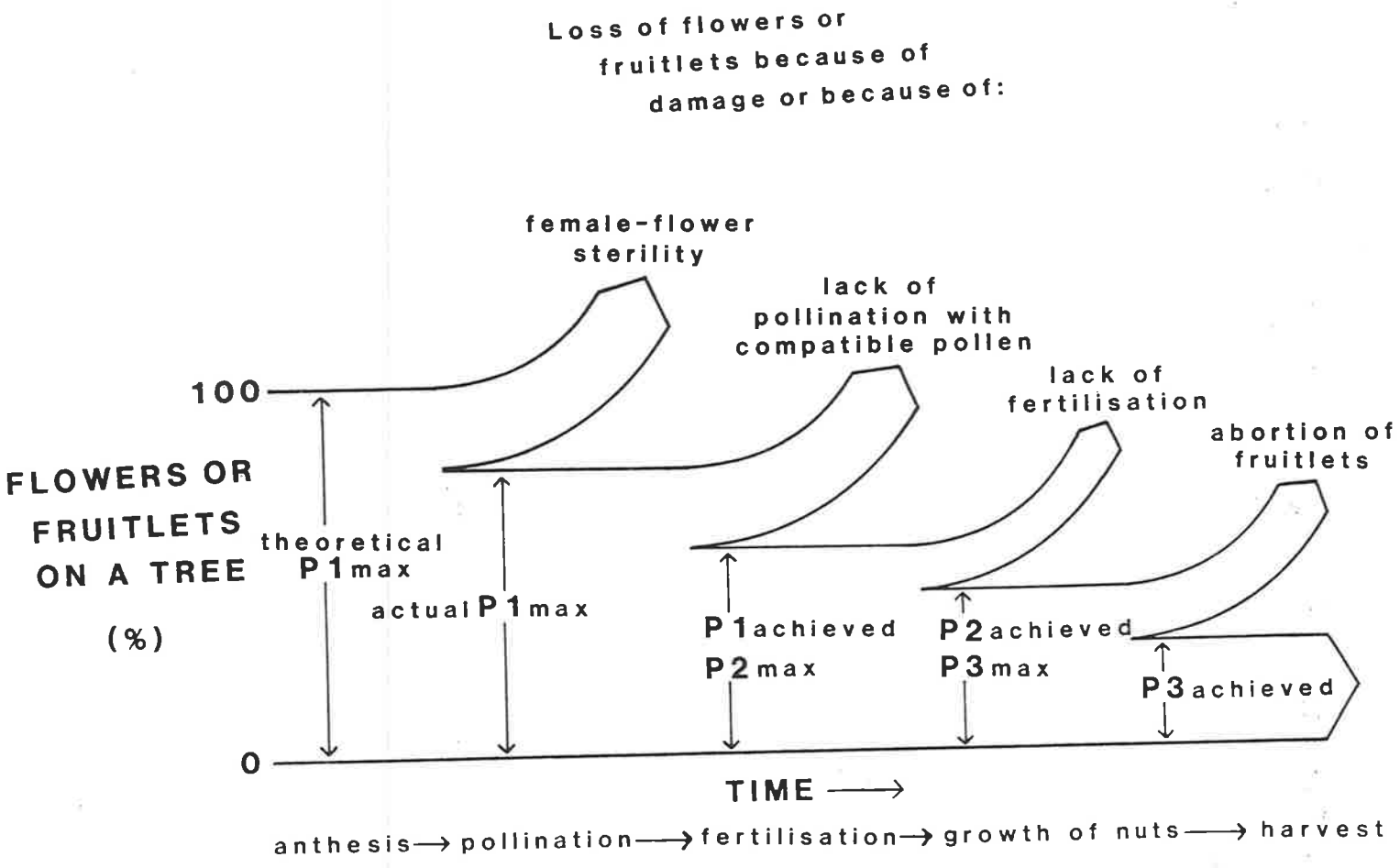


Figure 1.2: A schematic illustration of the relationship "number of flowers or fruitlets on a tree, versus time from anthesis to harvest", with the number being expressed as a percentage of the number of flowers that originally opened. The original number of flowers (theoretical $P1_{max}$) is reduced by several groups of factors which are stated at the top of the figure.



$P1_{max}$ can be achieved, with the aid of man, by placing compatible pollen onto every stigma (i.e. by hand-pollination). Likewise, the probability of fertilization (P2), can be increased by hand-pollination, perhaps to the maximum of one (i.e. $P2_{max}$), through using pollen and flowers from the "most suitable" cultivars and subjecting the flowers to the "most suitable" conditions. The probability of a nut developing to maturity (P3) is apparently not influenced by methods of hand-pollination, and factors contributing to that probability have not been examined, although the important factors may be relatively simple to demarcate (Section 15.2). So, this thesis concentrates on factors contributing to the first two probabilities (i.e. P1 and P2).

Experiments in which the first two probabilities have been increased by hand-pollination, are discussed later in this chapter; but first some background information on almond pollination may be useful to the reader.

1.3 Descriptions of an almond flower and an almond tree

The morphology of a typical almond flower is illustrated in Figure 1.3. It consists of symmetrical whirls of 5 sepals, 5 petals, and 28 stamens around a single carpel. The carpel consists of a single style and stigma which are atop a superior or part-superior ovary which, in turn, contains two ovules. Usually only one ovule is fertilized and develops into a kernel, but sometimes both ovules are fertilized and a nut that contains two kernels, develops. The receptacle is usually lined with orange-coloured nectaries which produce globules of nectar. The petals are usually white, but they may have tinges of blue, yellow and red, and honey-guides (Section 12.4.4) are prominent on the petals of many cultivars.

Common variations from the typical almond flower usually involve either duplication of parts of the gynaeceum, or the number of fertile stamens is not 28 and is usually another multiple of 4 or 14 (e.g. 16, 20, 24, 42, 56 stamens). Partially developed stamens are often found in flowers that have less than 28 fertile stamens.

The stages of the production of an almond tree for commercial use are shown in Figure 1.4. Trees for commercial orchards of Prunus spp., such as almond, are usually reproduced asexually; that is, the scions of all trees of a particular cultivar are of the same genotype. The cultivar to which a tree is said to belong refers solely to the cultivar of the scion. The rootstock is usually of a different cultivar or species and is usually produced sexually.

Figure 1.3: A cross-sectional view of a typical almond flower.

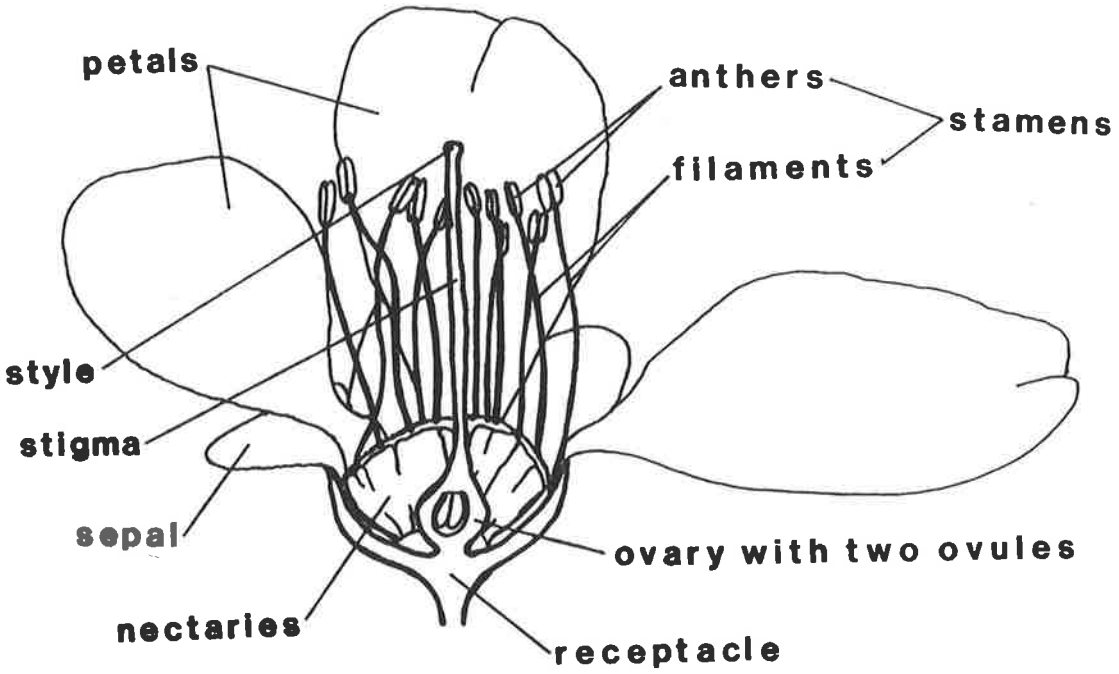
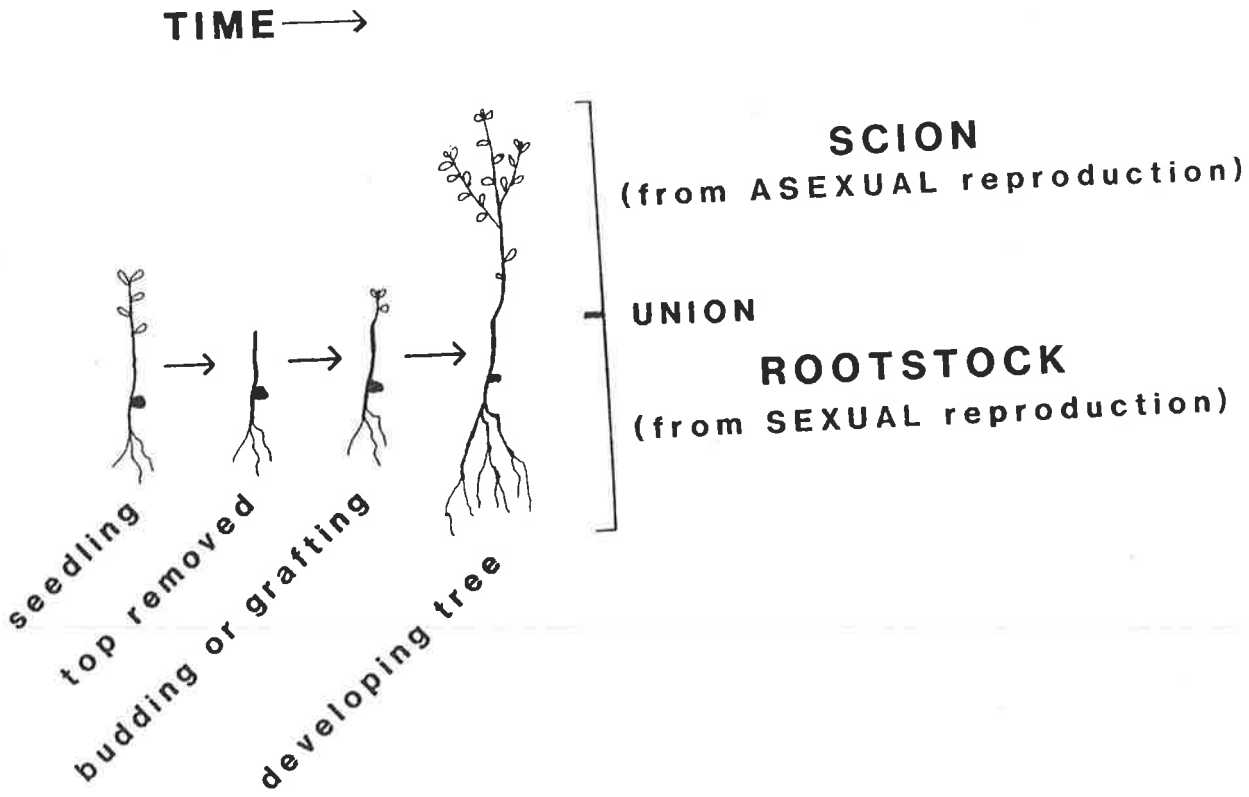


Figure 1.4: The standard nursery procedure for producing an almond tree. A seed is planted (a). The seed may be of the same cultivar, but usually it is not and often it is of a different species or it is a hybrid. The top of the seedling is removed (b), and a bud, or graft stick, of the desired cultivar is added to the remaining rootstock (c). The scion of the tree then develops from the bud or graft stick (d).



1.4 Defining the terms self- and cross- pollination

"Pollination" is the arrival of pollen at the stigma, and "fertilization" is the fusion of the gametes. The prefixes "self-" and "cross-", when used as prefixes for "pollination" and "fertilization", refer to the genotypes of the gametes. Thus "self-pollination" refers to pollination when the pollen and ovules are of the same genotype; which for almond means that the pollen for pollination comes from either the same flower, or from different flowers on the same plant, or from flowers on different trees of the same cultivar (Hartmann and Kester 1983). The alternative is "cross-pollination", which refers only to the situation when the pollen comes from a tree of a different cultivar (see Fig. 1.5). Nevertheless, the above definitions are not rigid because genetic variation within a cultivar can occasionally occur through mutation, and many new cultivars are chance discoveries of mutants (e.g. Lammerts 1941; Kester 1965).

Parthenocarpic (seedless) fruits or nuts can be produced without pollination or fertilization occurring, and this is discussed in Section 15.1. For almond, parthenocarpic nuts are useless because production of kernels (seeds) is the prime aim of orchardists. Therefore, any reference to a nut (or fruit) in this thesis implies that fertilization has occurred.

1.5 The pollination requirements of almond trees

Almond trees require cross-pollination between compatible cultivars to produce an economic crop (Griggs 1953; Gagnard 1954; Baker and Gathercole 1977), so normally trees of 2 or 3 cultivars are grown together, usually with trees within a given row being of one cultivar only, and the rows are usually arranged into one of the planting patterns shown in Figure 1.6. The need for cross-pollination in almond was recognized in California as early as 1885 when Hatch (1886) pointed out that trees of the cultivar Languedoc always produced heavier crops when planted near seedlings, compared to when planted in solid blocks. Later Dargitz (1906) reported that there were many recorded instances of trees of the cultivars Nonpareil, IXL and Ne Plus Ultra being non-bearing when planted in solid blocks on otherwise favourable sites. The explanation given for this non-bearing was lack of adequate cross-pollination. In Australia, however, Quinn (1926) did not appear to be aware of the possibility of poor nut-set being due to poor

Figure 1.5: The difference between self- and cross-pollination in almond. The arrows represent the movement of pollen from an anther to a stigma within and between trees of cultivars A and B.

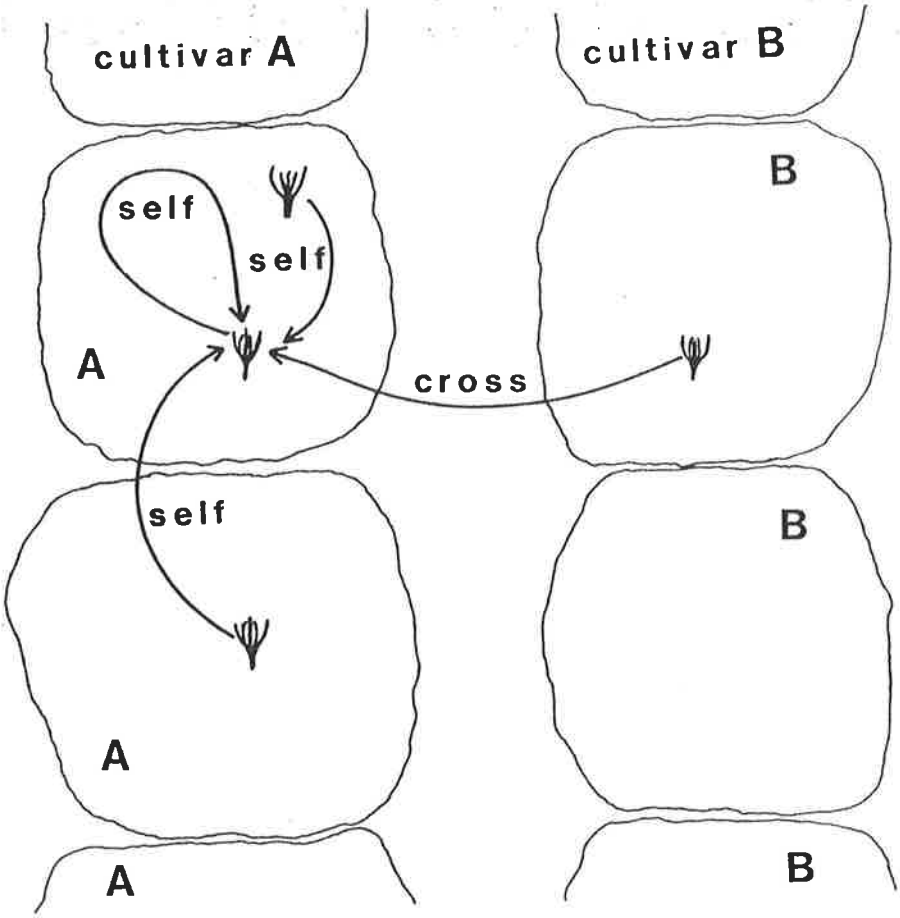


Figure 1.6: Two popular planting designs that are generally regarded by Australian almond growers to be adequate for pollination. Each letter represents a tree of cultivar O, X, or Y, and rows are orientated down the page.

o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o

o x o x o x o x o x o x o x o x
o x o x o x o x o x o x o x o x
o x o x o x o x o x o x o x o x
o x o x o x o x o x o x o x o x
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o x o x o x o x o x o x o x o x
o x o x o x o x o x o x o x o x

pollination, although later he (Quinn 1930a, 1930b) did suggest that poor pollination could limit the yield of almond trees but he thought frost was the major cause of low yields.

1.6 Current nut-set

Nut-sets due to pollination without the aid of man (i.e. open-pollination), are estimates of the mean nut-sets that occur in commercial orchards. Some estimates obtained by various authors are given in Table 1.2. More estimates are given in Reinecke (1930), Pejovics (1963), Nauriyal and Rana (1965), Thorp et al. (1967), and Sections 3.2 and 3.3. Nut-set varies greatly between years and orchards and within orchards. Many authors (e.g. Kester and Griggs 1959a; Griggs and Iwakiri 1964; Griggs 1970; Gary et al. 1976; Baker 1977; Micke and Kester 1978) assumed that usually about 30% of flowers produce mature nuts. Micke and Kester (1978) stated further that the percentage can be "from below 20% to over 40%, depending on season, weather variables, number of flowers on the tree and other factors". However, those percentages appear to have been based on the nut-set that the more productive orchardists obtain, and not on the mean nut-set that is theoretically possible.

1.7 Potential nut-set

Hand-pollination increases the probability of pollination occurring (P1) to 1, and can raise the probability of fertilization occurring (P2), but there are some factors of P2 which may not always be nullified by hand-pollination, so nut-sets obtained by hand-pollination do not necessarily indicate the maximum possible nut-set. Nevertheless, hand-pollination experiments show that there is great potential in increasing nut-set above that which is currently common in commercial almond orchards. The results of hand-pollination experiments performed by some authors are shown in Table 1.3. Several authors obtained nuts from about 50% of hand-pollinated flowers on individual tree limbs, but other authors obtained lower nut-sets because they did not allow for some factors of nut-set, such as the limited life-span of flowers (Section 8.1).

Scepticism on the use of tree limbs instead of whole trees was abated when Erickson et al. (1977) demonstrated that whole trees can achieve nut-sets in excess of 50% and that a nut-set of 50% can be achieved by relying only on honeybees for pollination. Their results, which are given in Table 1.4, ranged from 10 to 56% nut-set, and were similar to nut-sets obtained by other authors who used only single tree-limbs (Table 1.3).

Table 1.2: The percentage nut-set that has been obtained through open-pollination by various authors.

	Author (names given below)										
Cultivar	1	2	3	4	5	6	7	8	9	10	11
Bruce	–	–	–	–	–	–	–	–	–	28	–
Chellaston	–	–	–	–	–	–	–	–	29-46	–	–
Drake	13-22	–	25	–	15-16	–	–	–	–	–	–
Eureka	–	–	14	–	16	–	–	–	–	–	–
Falsa barese	–	–	–	–	–	–	–	–	–	–	22
Filippo Ceo	–	–	–	–	–	–	–	–	–	–	30
Franciscudda	–	–	–	–	–	–	–	–	–	–	13
Genco	–	–	–	–	–	–	–	–	–	–	18
Golden State	–	–	–	–	14-30	–	–	–	–	–	–
Harpareil	–	–	34	–	–	–	–	–	–	–	–
Harriott	9-11	–	1	–	8-16	–	–	–	–	–	–
IXL	–	–	–	–	16-21	–	–	–	–	39	–
Jordanolo	8-11	–	13	–	–	–	–	–	–	–	–
King	–	–	35	–	25-29	–	–	–	–	–	–
Klondike	–	–	11	–	13-30	–	–	–	–	–	–
Languedoc	–	–	21	–	10-22	–	–	–	–	–	–
Lewelling	–	–	29	–	25-37	–	–	–	–	–	–
Milow	–	–	–	–	–	–	–	42-56	–	–	–
Mission (Texas)[A]	20-42	22	37	23-61	21-39	–	24-42	–	–	–	3
Ne Plus Ultra	7	15-25	30	–	16-26	–	–	–	–	–	–
Nonpareil (CPS)[B]	11-35	–	30	16-60	24-28	20-38	–	10-51	17-32	53	8
Peerless	15-31	–	29	–	7-20	–	–	–	–	–	–
Pethic Wonder	–	–	–	–	–	–	–	–	–	46	–
Reams	–	–	29	–	14-23	–	–	–	–	–	–
Scorza verde	–	–	–	–	–	–	–	–	–	–	30
Sloh	–	–	–	–	–	–	–	–	–	94	–
Strout's Papershell	–	–	–	–	–	–	–	–	–	63	–

A: Mission and Texas are synonyms.
B: CPS (Californian Paper Shell) is usually a synonym for Nonpareil, but it can also be used to refer to a group of cultivars that are the progeny of Nonpareil (e.g. Harpareil, Kapareil).

Authors:
1: Brown (1952)
2: Browne et al. (1978)
3: Griggs (1949)
4: Kester and Griggs (1959a)
5: Tufts (1919), and Tufts and Philp (1921).
6: Weinbaum et al. (1980), and Weinbaum (1980)
7: Griggs et al. (1952).
8: Erickson et al. (1977) See Table 1.4 for more details.
9: Hill et al. (1985)
10: Dhaliwal et al. (1979)
11: Gordini (1977)
12: Almeida (1945, 1948)
13: Saparov (1978)
14: Vasilakakis and Porlingis (1984)

Table 1.3: The percentage nut-set which was obtained through hand-pollination by various authors. The wide ranges of nut-set obtained by several authors is due to the use of pollen from several cultivars.

	Authors (names given with Table 1.2)								
Cultivar	4	5	6	9	10	11	12	13	14
Bruce	–	–	–	–	56–74	–	–	–	–
Castelheta	–	–	–	–	–	–	23–50	–	–
Charnequeira	–	–	–	–	–	–	0–38	–	–
Chellaston	–	–	–	12–57	–	–	–	–	–
D. Estrada	–	–	–	–	–	–	13–37	–	–
D. Italiano	–	–	–	–	–	–	22–52	–	–
Desmayo	–	–	–	–	16–38	–	2–30	–	–
Dessertniy	–	–	–	–	–	–	–	12–30	–
Drake	–	11–29	–	–	–	–	–	17–38	–
Falsa Barese	–	–	–	–	–	50	–	–	–
Ferragudo	–	–	–	–	–	–	0–27	–	–
Ferragudeira	–	–	–	–	–	–	6–28	–	–
Filippo Ceo	–	–	–	–	–	33	–	–	–
Fofana	–	–	–	–	–	–	5–50	–	–
Franciscudda	–	–	–	–	–	42	–	–	–
Galtinskiy	–	–	–	–	–	–	–	14–35	–
Genco	–	–	–	–	–	38	–	–	–
Golden State	–	35–38	–	–	–	–	–	–	–
Harriott	–	14–30	–	–	–	–	–	–	–
IXL	–	1–40a	–	–	–	–	–	–	–
J. Dias	–	–	–	–	–	–	11–59	–	–
Jeori Selection One	–	–	–	–	0–50	–	–	–	–
King	–	32–41	–	–	–	–	–	–	–
Languedoc	–	0–17a	–	–	–	–	–	–	–
LeGrand	–	–	38–74	–	–	–	–	–	–
Lobita	–	–	–	–	–	–	0–35	–	–
Lourencinha	–	–	–	–	–	–	0–42	–	–
M. Fuzeta	–	–	–	–	–	–	8–41	–	–
Marcona	–	–	–	–	–	–	23–46	–	–
Mission (Texas)	14–43	0–31a	41–69	–	–	27	–	–	–
Myagkosk	–	–	–	–	–	–	–	18–56	–
Ne Plus Ultra	–	4–36	–	–	–	–	–	–	–
Nikitskiy	–	–	–	–	–	–	–	22–35	–
Nonpareil	20–35	0–37a	42–53	28–60	30–64	17	–	–	–
Pascuala	–	–	–	–	–	–	16–44	–	–
Peerless	–	4–11	–	–	–	–	–	–	–
Pestaneta	–	–	–	–	–	–	18–64	–	–
Pethicks Wonder	–	–	–	–	40–93	–	–	–	–
Reams	–	16–31	–	–	–	–	–	–	–
Ribenton	–	–	–	–	–	–	38–71	–	–
Sloh	–	–	–	–	17–87	–	–	–	–
Strouts Papershell	–	–	–	–	15–62	–	–	–	–
Truoito	–	–	–	–	–	–	–	–	48–56
Tuono	–	–	–	–	–	26–36	–	–	–
Viynosliviy	–	–	–	–	–	–	–	31–50	–

Table 1.4: Nut-set per limb. This data is from Erickson *et al.* (1977). Each replicate consisted of one caged tree, which had branches of the cultivars Milow and Nonpareil, and a normal or artificial (DPU) honeybee colony.

	Replicate				
	1	2	3	4	
Milow flowers	42	54	52	49	in cages with DPUs
	50	44	48	56	in cages with colonies
Nonpareil flowers	42	49	38	45	in cages with DPUs
	10	17	51	28	in cages with colonies

Nut-sets of up to 80% following self-pollination, 94% following cross-pollination, and 94% following open-pollination, have been claimed (Almeida 1948; Nauriyal and Rana 1965; Dhaliwal et al. 1979; Uppal et al. 1984; Weinbaum 1985). These comparatively high nut-sets may have been obtained because nut-set was determined before the final period of nut drop had finished (Kester and Griggs 1959b; Garcia et al. 1980). Alternatively, unusually favourable weather may override factors that elsewhere restrict nut-set. For example, warm weather promotes bee activity and pollen-tube growth (Free 1970a; Griggs and Iwakiri 1975; Socias i Company et al. 1976), and perhaps nut-set (Weinbaum 1985).

High fruit-set is not peculiar to almond. Hand-pollination has produced up to 60% fruit-set in apple (Howlett 1931; Blasse 1984), and up to 80% fruit-set in sweet cherry (Stosser and Anvari 1983; Guerrero-Prieto et al. 1985).

1.8 Potential for increasing almond yield

A comparison of Tables 1.2 and 1.3 shows that orchard nut-set is poor (10-30%) relative to that which is possible (50% or more).

There are several literature reviews on fruit-tree pollination, fruit-set, and honeybees (e.g. Todd and McGregor 1960; H.E.A.F.C. 1960, 1961; Free 1970a; McGregor and Levin 1970; Martin and McGregor 1973; Jay 1986), but their emphasis is on apple trees which only require between 3 and 7% set for an optimal crop (Hutson 1926; Griggs 1953; H.E.A.F.C. 1961; McGregor 1976). Almond, however, apparently has a potential of at least 50% nut-set, and so more factors are likely to influence nut-set in almond than fruit-set in apple. Furthermore, many of the reviews pertaining to topics discussed in this thesis omitted many important references and / or were not adequately critical of the work described in the cited references. Moreover, some aspects of pollination have never been reviewed.

Free (1970a) is perhaps the most valuable review in the field of pollination for temperate tree crops, and it is an excellent source of information, but it is poor in some areas because Free (1970a p66) was conscious of the problem of over-pollination in crops such as apple, and so he ignored or belittled some factors of pollination; but over-pollination is not a problem in almond, so there is a need for a more detailed and critical examination of the factors of nut-set in almond.

1.9 The aims of this thesis

Attempts to increase the yield of agricultural plants generally involve an approach that aims to improve one factor of yield; for example, the selection of better genetic material (e.g. Taylor and Stephenson 1979). Such approaches often achieve increases in yield, but the increases are usually small, possibly because the gains obtained through the manipulation of one factor are lost through the action of other, unknown factors. Also, almond trees and orchards are dynamic ecosystems, and so changing one factor in one ecosystem at one time may improve yield at that time, but the change may have an adverse effect in another ecosystem at another time.

A better approach to increasing the yields of plants is to elucidate all the important factors of yield and the relationships between the factors, and then work towards optimising each and every factor. This thesis is the first stage of such an approach for increasing the yield of almond trees. A similar approach was made for the apple cultivar Delicious by Dennis (1979), but the optimum fruit-set for apple is much less than for almond, and so he considered fewer factors than I do in this thesis.

This chapter has shown that the yields of existing almond trees can be increased greatly on a small scale. The remainder of this thesis identifies and discusses the known factors of nut-set, and the relationships between the factors, with emphasis on the factors pertaining to pollination (i.e. S in the equations in Table 1.1). Factors not discussed in this thesis include factors that are related to tree size and the production of flowers (i.e. N and W in the equations in Table 1.1).

The relationships between pollination factors are many and complex, so, to aid the reader, I have listed many of the factors and their inter-relationships in Appendix 1. I recommend the perusal of Appendix 1 before reading beyond this chapter.

PART A

"In order to understand the pollination ecology of a species, it is necessary to live with its populations and observe the plants at different times of day and night, under different weather conditions, and at different stages of the flowering season..."

from Grant and Grant (1965)

Chapter 2: The experimental orchard

2.1 Location and description.

The experiments described in this thesis were done in one orchard near Angle Vale (34° 39'S, 138° 40'E), 35 km north-northeast of Adelaide, South Australia. The climate, like that of Adelaide (Anon 1975), is a Mediterranean type with a hot, dry summer and a wet winter in which falls most of the annual rainfall of 460 mm. The prevailing wind is from the west. Most of the trees in the orchard were 11 years old in 1983 and had been planted on a deep sandy loam.

Appendix 2 is a map of the orchard as it was in 1984. There were 28 cultivars and seedling groups in the orchard, but the majority of trees were of the cultivars Nonpareil, Chellaston, Johnstons Prolific, Ne Plus Ultra, and Davey. The unusually large number of cultivars was due to the desire of the owners to have a source of bud-wood for their nursery. The mixture of cultivars causes problems with harvesting, handling and marketing, but in some years there has been a significant yield advantage compared to other orchards because Nonpareil, their main cultivar, is always assured of cross-pollination (e.g. Hill *et al.* 1985).

The orchard can be divided into 3 sections by using the roadways as dividers (Appendix 2). Section 1 consisted mainly of trees of Nonpareil, Johnstons Prolific, Chellaston, and Pethic Wonder. Rows 38 to 78 of section 1 are not shown in Appendix 2 because they were owned by another grower. Those trees consisted of alternations of 2 rows of White Brandis and 4 rows of Chellaston, and they were similar in age to the rest of section 1 but they had been managed differently and every row was double-planted with trees of Nonpareil, Fritz, and Ne Plus Ultra.

The original layout of the 42 hectare orchard was a 7.6 x 7.6 metre grid which gave a density of 173 trees per hectare, except that in section 1, rows 2 and 3, and 4 and 5, were only 3.8 metres apart (Appendix 2). Pollination and nut-set were often poor in many parts of the orchard because either those trees flowered when trees of other cultivars were not flowering, or those trees were too far from flowers of other cultivars for enough cross-pollination to occur. The orchardists have attempted to correct these problems by replacing or grafting trees with new cultivars. Consequently, some rows, which originally contained only one cultivar, now contain 2 or more cultivars. Further, parts of some rows were double-planted, that is, new trees were planted between existing trees.

Many such trees were too young to be productive in 1984 and are designated as "x" in Appendix 2. Almond trees generally produce a commercial crop in their fifth year.

Sections 1 and 2 were separated by 2 close-planted rows of Pethic Wonder. Two more close-planted rows existed between section 1 and Fradd Road, and similar rows along Andrews Road were removed in 1983 (Appendix 2).

Sections 2 and 3 were similar to each other with respect to tree size and management, except that the trees northeast of the pine-trees in section 3 were very young and comprised experimental cultivars (Appendix 2). Many trees of sections 2 and 3 were of the cultivar Nonpareil, and many more trees, which were formally Nonpareil trees, were grafted to other cultivars to facilitate pollination. Most of the latter trees attained a size similar to that of the established Nonpareil trees by 1983. The first row of trees, which were grafted with Fritz, was along an old fence line and the trees were smaller than most other trees in 1983 and so they were not included in the numbering of rows in sections 2 and 3.

Andrews Road and Fradd Road were gravel roads, but Andrews Road was bituminized in 1985. Dust from the roads drifted into the orchard when the roads were dry.

2.2 Orchard management.

The trees were drip irrigated with bore water every three days during the growing period to give an annual total of 325 mm water per year. Under-tree sprinklers were installed in section 3 in 1983. Fertilizer was applied at rates determined from leaf analysis tests. Herbicides kept the ground under the trees clear of vegetation throughout the year. Vegetation in the inter-row area was allowed to grow, but it was frequently mowed during winter and spring and it was destroyed with herbicides in summer to facilitate harvesting. Soursobs (*Oxalis spp.*), which grew well on the edges of the de-vegetated areas, were destroyed by spot spraying during the flowering season. Fungicides were sprayed onto flowers every three or four days during the flowering season. Insecticides were rarely used, but miticides were used in some years.

Mature nuts were harvested from January to March by shaking the trees to make the nuts fall onto the ground, following which the nuts were allowed to dry, swept into windrows, and put into bins for transport to the processing plant.

2.3 Honeybees for pollination

Rented hives were placed in the orchard for the flowering seasons of 1983 and 1984. The locations of the hives are shown in Figures 2.1 and 2.2.

In 1983, 368 hives located in 12 groups of from 15 to 66 hives gave a density of 8.7 hives per hectare, and 54 more hives were located in the northern half of section 1 (8.5 hives per hectare) (Fig. 2.1). The strengths of the colonies within the hives were determined by observing the activity at the hive entrances and relating those observations to detailed inspections of several hives. The average hive strength was low (about 2 to 3 frames of bees per hive) but hive strength ranged from 0 to 12 frames of bees per hive, a frame of bees being 100% coverage of both sides of a hive frame and being equivalent to about 3,500 bees. One apiarist had his pollination service fee reduced by 20% because of empty or substandard hives, so the density of "useful" hives was about 7.1 hives per hectare. The experimental orchard had a higher honeybee density than the surrounding region. Neighbouring orchards contained approximately 15,600 almond trees and 346 hives of varying strength, which is a density of about 4.2 hives per hectare. There were approximately 55,000 trees and 1,350 hives within 4 kilometres of the orchard (4.2 hives per hectare), as shown in Figure 2.3. Most trees in the district appeared to be between 10 and 25 years old.

In 1984, 282 hives located in 45 groups, mostly as pallets of 6 hives, gave a density of 6.7 hives per hectare (Fig. 2.2). The average hive strength was only about 2 to 3 frames of bees per hive, and an inspection of the hives proved that 25% of the hives were empty or contained colonies which were too small to be useful for pollination; and so the pollination fee to the apiarist was reduced by 25%. The pollination fee was $8 per "useful" hive and the hives were left in the orchard until early November, two months beyond the almond flowering season, to exploit the nectar and pollen from the weed "Salvation Jane" (*Echium spp.*) and other flowering plants in the surrounding fields. The hive density in the surrounding area was similar to the density of 1983 (Fig. 2.3).

Figure 2.1: Hive locations in 1983. Each dot represents a hive.

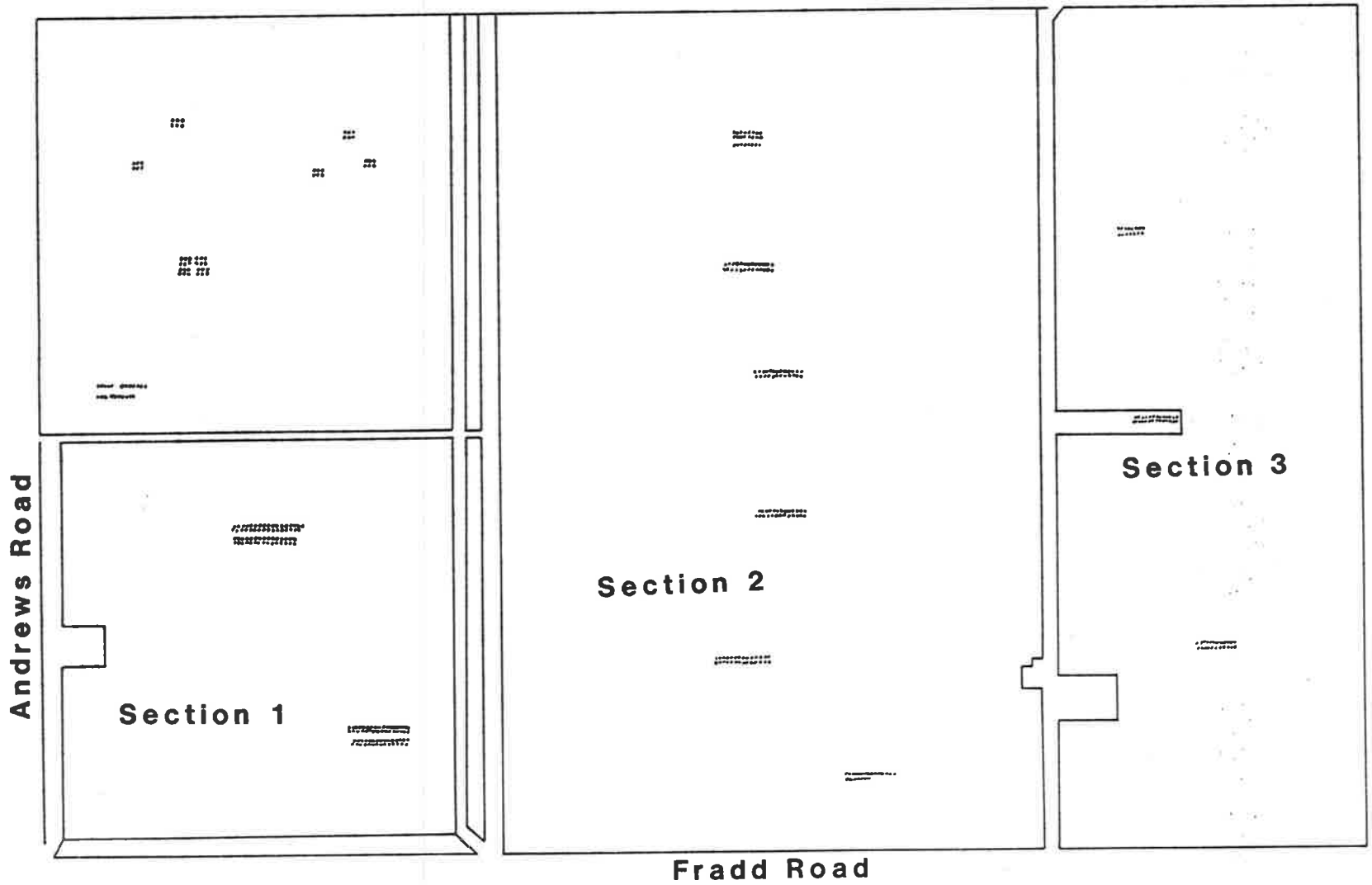


Figure 2.2: Hive locations in 1984. Each dot represents a hive.

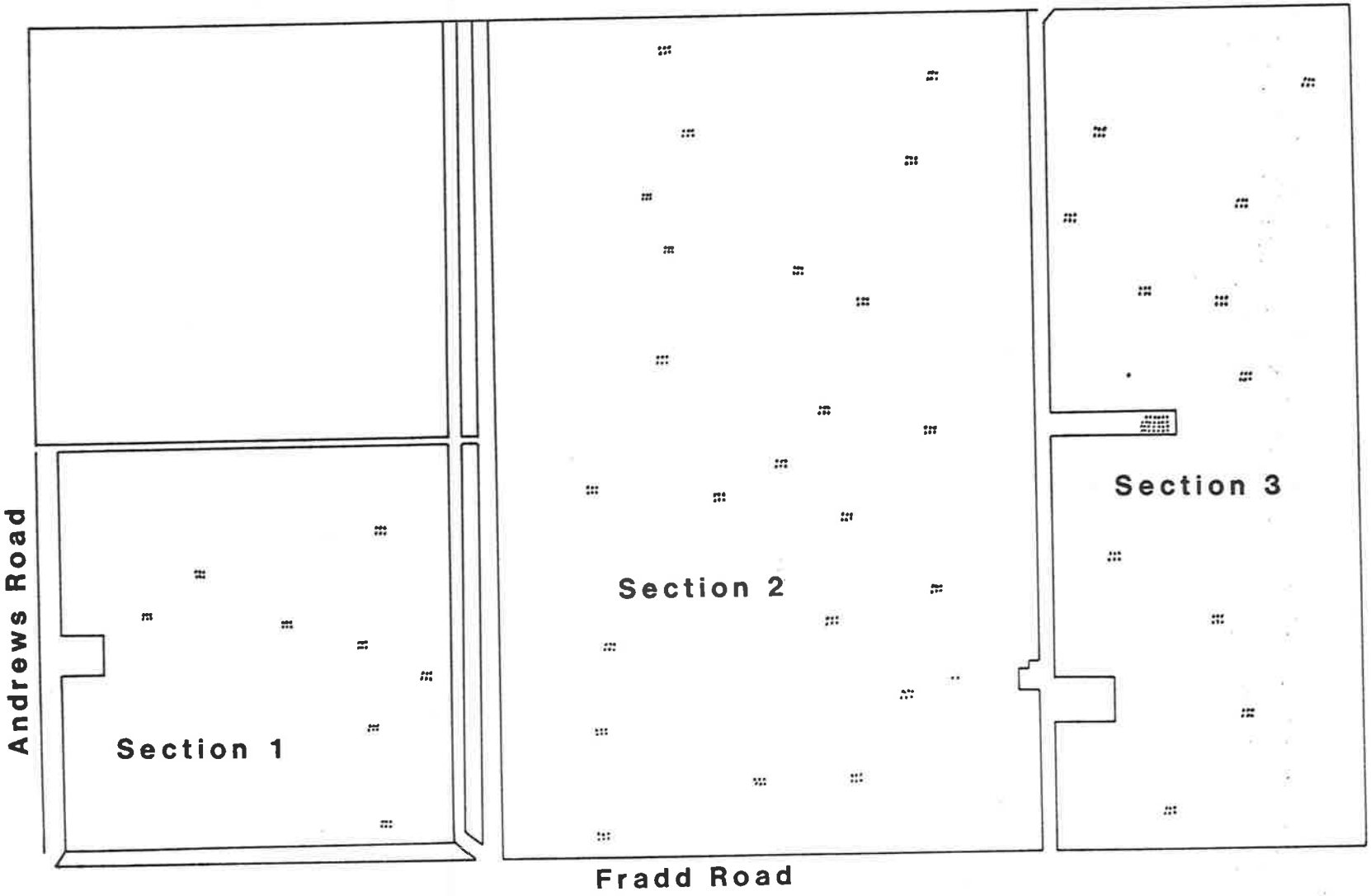
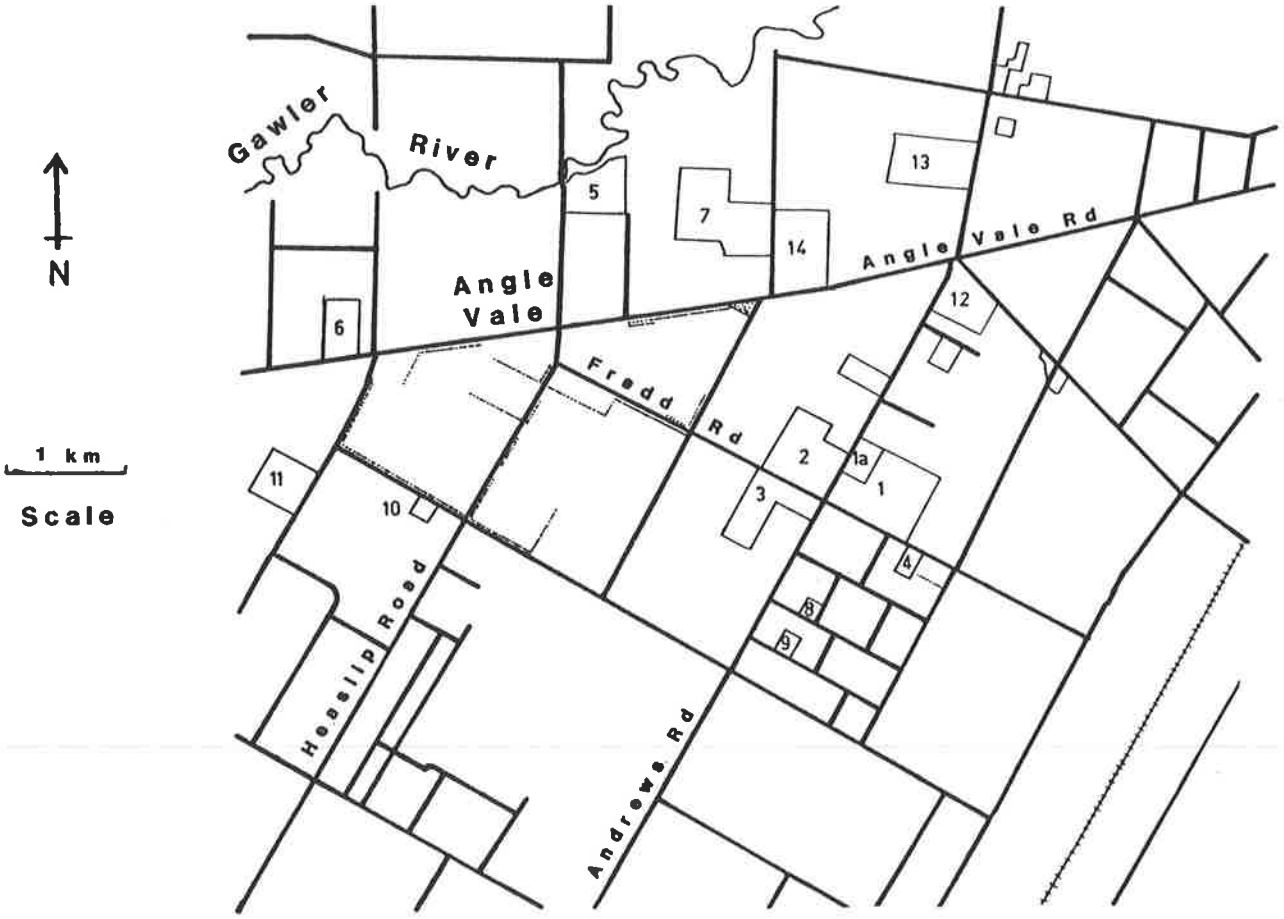


Figure 2.3: Road map showing the locations of orchards in the district surrounding the experimental orchard. The experimental orchard is designated as orchard 1. Dotted lines indicate single rows of almond trees which were planted as wind breaks. The estimations of numbers of mature trees and hives for each orchard are given below. The non-numbered orchards indicated on the map contained small and immature trees. Also, orchards 12 and 14 contained many immature trees.



Orchard	Number of trees	hives
1	8,000	368
1a	1,450	54
2	10,000	200
3	3,000	220
4	180	8
5	6,000	20
6	1,000	60
7	10,000	200

Orchard	Number of trees	hives
8	60	0
9	450	0
10	480	0
11	2,800	80
12	3,000	0
13	3,000	80
14	5,000	10

Table 2.1: Dates of flowering for 1977, 1981, and 1982. The data were collected by the orchardists (Fred and Greg Keane). The type of data collected varied between years. The 1977 data refer approximately to the stages of 1%, 20–80% and 99% flowering, the 1981 data refer approximately to the date of 60–80% flowering, and the 1982 data refer approximately to 10% and 95% flowering. Dashes indicate missing data.

	1977			1981	1982	
Variety	1%	20–80%	99%	60–80%	10%	95–99%
Chellaston	23/7	(1/8–7/8)	10/8	–	29/7	6/8
Grant	26/7	(4/8–15/8)	20/8	–	1/8	10/8
White Brandis		–		1/8	1/8	9/8
Summerton	26/7	(1/8–6/8)	27/8	2/8		–
Johnstons Prolific	26/7	(1/8–9/8)	15/8	3/8	1/8	9/8
Bruce		–		3/8	1/8	9/8
Ne Plus Ultra	26/7	(1/8–6/8)	16/8	3/8	1/8	9/8
IXL		–		–	1/8	7/8
Peerless	1/8	(-------)	16/8	10/8		–
Milow		–		6/8	7/8	13/8
Nonpareil	1/8	(9/8–13/8)	20/8	9/8	7/8	15/8
Baxendale	4/8	(-------)	22/8	9/8	7/8	15/8
Davey	7/8	(11/8–15/8)	22/8	12/8	9/8	15/8
Fritz	7/8	(19/8–22/8)	27/8	6/8	5/8	13/8
Kapareil		–		12/8	7/8	15/8
Drake		–		12/8		–
Mission	16/8	(20/8–26/8)	7/9	–		–

Table 2.2: Dates of flowering for 1983, 1984 and 1985. The dates are means for all trees of the given cultivar. Cultivars which had few representative trees have not been included. "Close" in the table refers to trees which were close-planted and were located in the "boundary rows" which surround section 1 of the orchard (Appendix 2). Dashes indicate missing data. Cultivars are listed in the approximate order of flowering.

Data in 1985 were recorded only on August 27. Data prior to that date were estimated, and the cultivars for which no data are given finished flowering before August 20. Generally, cultivars apparently flowered close together except that a few early flowering cultivars (e.g. Nonpareil - close, Chellaston - close) may have finished flowering several weeks before August 27.

1983	Flowers open (%)						
Cultivar	trace	1%	5%	50%	95%	99%	trace
Ne Plus Ultra	19/7	24/7	28/7	3/8	10/8	12/8	18/8
Fritz	22/7	26/7	29/7	5/8	13/8	16/8	24/8
Nonpareil	3/8	7/8	10/8	13/8	19/8	22/8	26/8

1984	Flowers open (%)						
Cultivar	trace	1%	5%	50%	95%	99%	trace
Chellaston (close)	20/6	29/6	3/7	12/7	24/7	2/8	8/8
Chellaston (normal)	3/7	12/7	24/7	29/7	2/8	7/8	19/8
Strout	3/7	12/7	24/7	29/7	2/8	7/8	19/8
Davey	22/7	30/7	2/8	5/8	9/8	17/8	20/8
White Brandis	24/7	1/8	3/8	5/8	8/8	11/8	22/8
Bruce	-	31/7	2/8	7/8	12/8	16/8	26/8
Johnstons Prolific	28/7	4/8	6/8	7/8	8/8	10/8	21/8
Ne Plus Ultra	24/7	1/8	3/8	8/8	14/8	16/8	20/8
Pethic Wonder (close)	24/7	31/7	7/8	9/8	10/8	13/8	16/8
Pethic Wonder (normal)	1/8	-	-	-	-	-	-
Grant	-	similar to White Brandis				-	-
Summerton Seed	24/7	1/8	7/8	10/8	13/8	16/8	19/8
Fritz	31/7	10/8	-	-	-	16/8	24/8
Golden State	-	-	-	-	-	17/8	22/8
Kapareil	29/7	2/8	4/8	12/8	15/8	17/8	21/8
Peerless	-	-	-	-	-	-	-
Peerless 532-3	1/8	7/8	11/8	12/8	13/8	16/8	22/8
Peerless NFC	3/8	10/8	12/8	14/8	16/8	19/8	24/8
Milow	1/8	6/8	12/8	14/8	16/8	19/8	24/8
IXL	-	-	-	-	-	-	15/8
Baxendale	6/8	11/8	14/8	18/8	22/8	24/8	27/8
Thompson	6/8	12/8	18/8	20/8	25/8	28/8	12/9

(continued)

Table 2.2 (continued)

Nonpareil (normal)	6/8	12/8	14/8	18/8	24/8	26/8	3/9
Nonpareil (close)	–	24/7	8/8	–	–	–	24/8
Nonpareil 15-1	6/8	14/8	18/8	21/8	28/8	3/9	13/9
American Nonpareil (section 3)	5/8	12/8	14/8	18/8	22/8	24/8	1/9
American Nonpareil (section 2, row 22)	22/8	24/8	25/8	27/8	29/8	1/9	8/9
Drake	11/8	19/8	21/8	25/8	27/8	29/8	11/9
Mission	21/8	24/8	25/8	26/8	27/8	29/8	4/9
Mission 126-1	21/8	25/8	27/8	30/8	2/9	4/9	12/9

1985	Flowers open (%)						
Cultivar	trace	1%	5%	50%	95%	99%	trace
Chellaston (close)	–	–	–	–	–	–	–
Chellaston (normal)	–	–	–	–	–	–	27/8
Strout	–	–	–	–	–	–	25/8
Davey	–	–	–	–	–	22/8	26/8
White Brandis	–	–	–	–	–	–	25/8
Bruce	–	–	–	–	22/8	25/8	28/8
Johnstons Prolific	–	–	–	–	–	–	25/8
Ne Plus Ultra	–	–	–	–	–	–	25/8
Pethic Wonder (close)	–	–	–	–	–	–	–
Pethic Wonder (norm)	–	–	–	–	–	–	25/8
Grant	–	–	–	–	–	20/8	26/8
Summerton Seed	–	–	–	–	–	–	–
Fritz	–	–	–	–	–	23/8	27/8
Kapareil	–	–	20/8	22/8	24/8	26/8	30/8
Peerless 532-3	–	–	–	–	–	–	25/8
Peerless NFC	–	–	–	–	–	–	25/8
Milow	–	–	–	–	–	–	–
Baxendale	–	–	–	–	–	23/8	26/8
Thompson	–	–	–	–	22/8	25/8	28/8
Nonpareil (close)	–	–	–	–	–	–	–
Nonpareil (normal)	–	–	–	–	–	21/8	27/8
Nonpareil 15-1	–	–	–	–	–	22/8	27/8
American Nonpareil (section 3)	–	–	21/8	22/8	23/8	25/8	27/8
American Nonpareil (section 2, row 22)	–	–	–	–	–	24/8	26/8
Drake	–	–	–	23/8	25/8	27/8	2/9
Mission	–	–	–	23/8	24/8	25/8	30/8
Mission 126-1	–	–	24/8	25/8	26/8	27/8	30/8
Nonpareil N778	–	–	–	–	–	–	26/8

2.4 Flowering periods of cultivars

Dates of flowering for many cultivars in 1978-80 are given in Hill et al. (1985). Data for 1977, 1981 and 1982 were collected by the orchardists and are given in Table 2.1, and data for 1983-85 are given in Table 2.2. The fore-mentioned data were not applicable to all trees in the orchard because, within cultivars, some trees flowered up to 1 week before or after the majority of trees. Generally and within cultivars, the close-planted trees next to Fradd Road, the trees on the western edge of the orchard, and some trees which were no more than 3 trees from a large space within the orchard, flowered several days earlier than most other trees. Perhaps the early-flowering trees were more exposed to prevailing winds. This would increase the amount of evaporative cooling and hence effect the rates of accumulation of chilling and heating units. This is explained further in Section 8.2.4.

2.5 Location of experiments

Some experiments were difficult to design because of the way cultivars were mixed in the orchard (e.g. Appendix 2). However, this disadvantage was outweighed by the advantage of having a wide range of cultivars, and the consequential long flowering season of late-June to mid-September. Further, data were available from earlier and concurrent experiments performed by me and other persons.

Experiments were done only in the first 40 rows of sections 1 and 2 of the orchard. Rows of trees are identified by the coding "section of orchard - row number" (e.g. 1-22). Reasons for selecting particular locations for particular experiments varied, depending on the requirements and constraints of the experiments and the time and resources available to do them. A major determinant was the disorder in the orchard caused by the replacement and grafting of trees. Other determinants included proximity of the required numbers of trees of particular cultivars, security of experimental equipment, and access to electrical power.

In all experiments, flowers were only sampled from branches which were no more than 2 metres above the ground because the sampling of flowers that were higher would have required too much time. Some factors can vary with height above ground (e.g. date of flowering), but such variation was not apparent in the experimental orchard in 1978-85. Further, only 40% of flowers per tree were beyond my reach, and those flowers are not as important as lower flowers to growers because higher flowers and nuts are

the ones which are usually destroyed by birds (Section 7.2). Also nuts at the tops of trees have a greater risk of being left on the tree by modern harvesting methods.

Most of the experiments described in the following chapters were preceded by preliminary experiments, most of which are not reported in this thesis. The preliminary experiments enabled me to design the main experiments with respect to optimal use of time and facilities, and obtain useful results. Most preliminary experiments were done with Chellaston trees because they flowered early in the season.

Chapter 3: Some preliminary experiments

3.1 The effect of muslin cages on the enclosed microclimate

Introduction

Muslin cages to exclude honeybees were proposed for use in several experiments, but cages and bags around flowers may effect the enclosed flowers by changing the enclosed microclimate, especially temperature and wind speed, relative to the external microclimate (Weinberger 1954; Larsen 1960; Legge 1976; Corbet and Delfosse 1984); so cages that would not significantly alter the enclosed microclimate were sought and tested in 1983.

Methods

White muslin of 1 mm square mesh was used to make cylindrical cages 1.8 metres long and 0.5 metre in diameter. Each end could be closed by a drawstring. In a Nonpareil tree, a shaded thermister was placed under each of 2 caged branches and 2 non-caged branches. Temperature was recorded hourly during the flowering season. A hand-held windmill was placed inside and outside a cage during windy periods to determine the effect of the cage as a windbreak.

Results

Temperature differences were always less than 1°C between replicates within treatments, and were rarely more than 2°C between treatments. Usually caged branches were warmer than non-caged branches, but sometimes the reverse was true, especially when the ambient air temperature was falling. The windmill was slower inside the cage than outside the cage, but the decrease in wind speed was usually only about 30%. Light rain easily penetrated the cage, but large raindrops were shattered by the muslin.

Discussion

The negative temperature differences between caged and non-caged branches probably counterbalanced some of the effect of the positive temperature differences. The remaining unbalanced temperature differences appear to be too small to significantly effect the planned experiments; and the results of other experiments support this statement. For example, rates of flowering and anther dehiscence, which apparently depend on air

temperature (Chapter 5), did not vary noticeably between caged and non-caged flowers (Section 6.4).

The decrease in wind velocity caused by the cages was probably insignificant in comparison to the variation in wind speed due to the windbreak effect of branches and flowers. The cages did not prevent the wetting of the enclosed flowers, but the cages probably reduced the force of impact of raindrops.

3.2 Nut-set throughout the orchard

Introduction

Nut-set can vary greatly between and within orchards (Tables 1.1 and 1.2), but experiments are usually done within a small section of orchard and so there are few published data on the variability of nut-set within orchards which can be used to design experiments.

Nut-set data were collected in 1983 and 1984 to (a) give an indication of the variation in nut-set that occurred throughout the part of the orchard in which later experiments were performed (i.e. in the first 30 rows of orchard-sections 1 and 2 - see Appendix 2), and (b) to estimate the sample size necessary to detect nut-set differences of five percentage points.

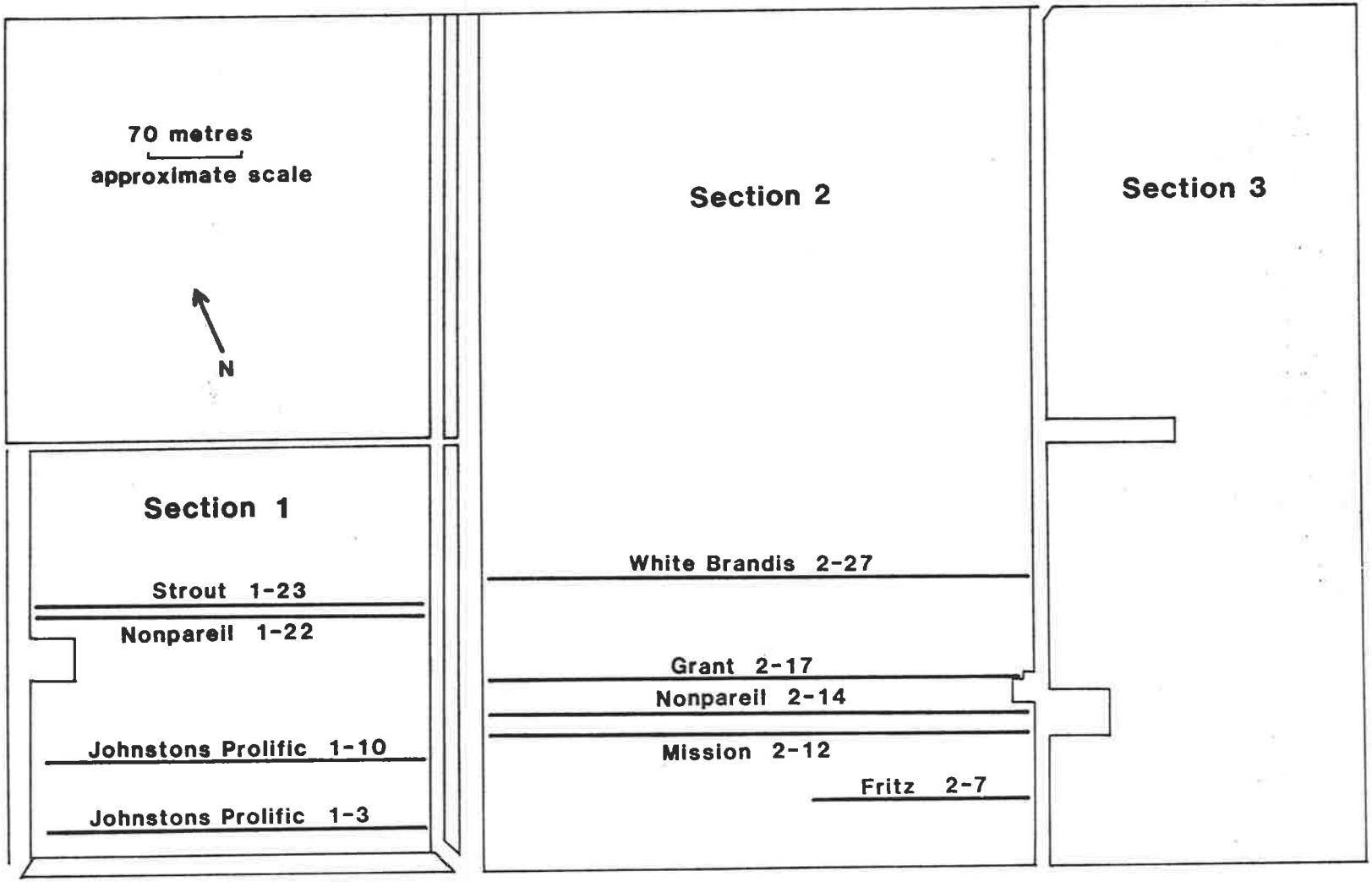
Methods

Trees of the cultivars Mission, Nonpareil, Grant, White Brandis, Fritz, Strout, and Johnstons Prolific were selected and two branches per tree were labelled so that there was a branch on either side of each tree. The selected trees were evenly distributed along certain rows, and their locations are shown in Figure 3.1. Only branches that were between 0.5 and 2 metres above the ground were selected because only those branches were candidates for experiments, in that the buds and nuts on those branches, compared to buds and nuts on the tops of trees, are less likely to be either damaged by birds or left on the tree by modern harvesting methods.

Data were collected in 1983 and 1984. Some branches that were sampled in 1983 were pruned or damaged before they could be sampled in 1984. For each branch, flowers and flower buds were counted when about 20% of the flower buds had opened. Nuts were counted in November.

Data were also collected in 1983 from 2 branches on each of 8 Fritz trees in row 2-7 (see Fig. 3.1). Newly-opened flowers were tagged every day during the flowering season, and nuts were counted in November.

Figure 3.1: The locations of the rows of trees that were sampled for nut-set in 1983 and / or 1984. More details of the orchard are given in Appendix 2.



Results

Some branches that were sampled in 1983, produced few or no flowers in 1984, so nut-set could not be measured on those branches in 1984. The mean nut-set for each row of trees is given in Table 3.1, and the distributions of nut-sets within rows are shown in Figure 3.2. Some distributions were skew and the nut-sets were very low compared to what they can be (Tables 1.1 and 1.2). Mean nut-sets differed greatly within and between rows, and those in 1984 were generally lower than those of 1983 (Table 3.1).

The nut-set data for the Fritz trees are given in Table 3.2. Mean nut-set differed significantly between branches (ANOVA, $P < 0.01$) and between days (ANOVA, $P < 0.001$) (Table 3.2). North-facing (A) branches tended to have higher nut-sets than south-facing (B) branches, and nut-set was lowest at the beginning and end of the flowering season (Table 3.2).

Estimates of minimum sample sizes that would be needed to detect differences of five percentage points between treatments, with 95% confidence, were calculated using the technique described by Snedecor and Cochran (1956 p60). The estimates, which are given in Table 3.1, varied greatly between rows, and the smaller estimates were for rows that had the lower nut-sets.

Discussion

The large range of mean nut-sets (Table 3.1) indicate that the influence of some factors of nut-set varied greatly within the orchard. Most nut-sets were lower than expected, possibly because many flowers were far from the nearest source of compatible pollen, a situation which is discussed further in the next Section. The small number of flowers on some branches in 1984, especially those of Johnstons Prolific, was due to marked biennial bearing, and indicate that biennial bearing must be considered if individual experiments proceed for more than one flowering season.

The differences in nut-set between days and branches for Fritz in 1983 (Table 3.2) may be attributed partly to variation in the proportion of flowers that were female-sterile, because the incidence of female-sterility apparently is highest at the beginnings and ends of flowering seasons (e.g. Chapter 4), which is when nut-set was lowest (Table 3.2). The nut-sets on branches 12A and 16A were significantly higher than the other branches (Table 3.2), possibly because those branches were on the sunny side of trees and 18 bee hives were situated under trees 17 to 21. Honeybees tend to favour the flowers that are both bathed in sunshine and close to their hive (Sections 14.1, 14.2).

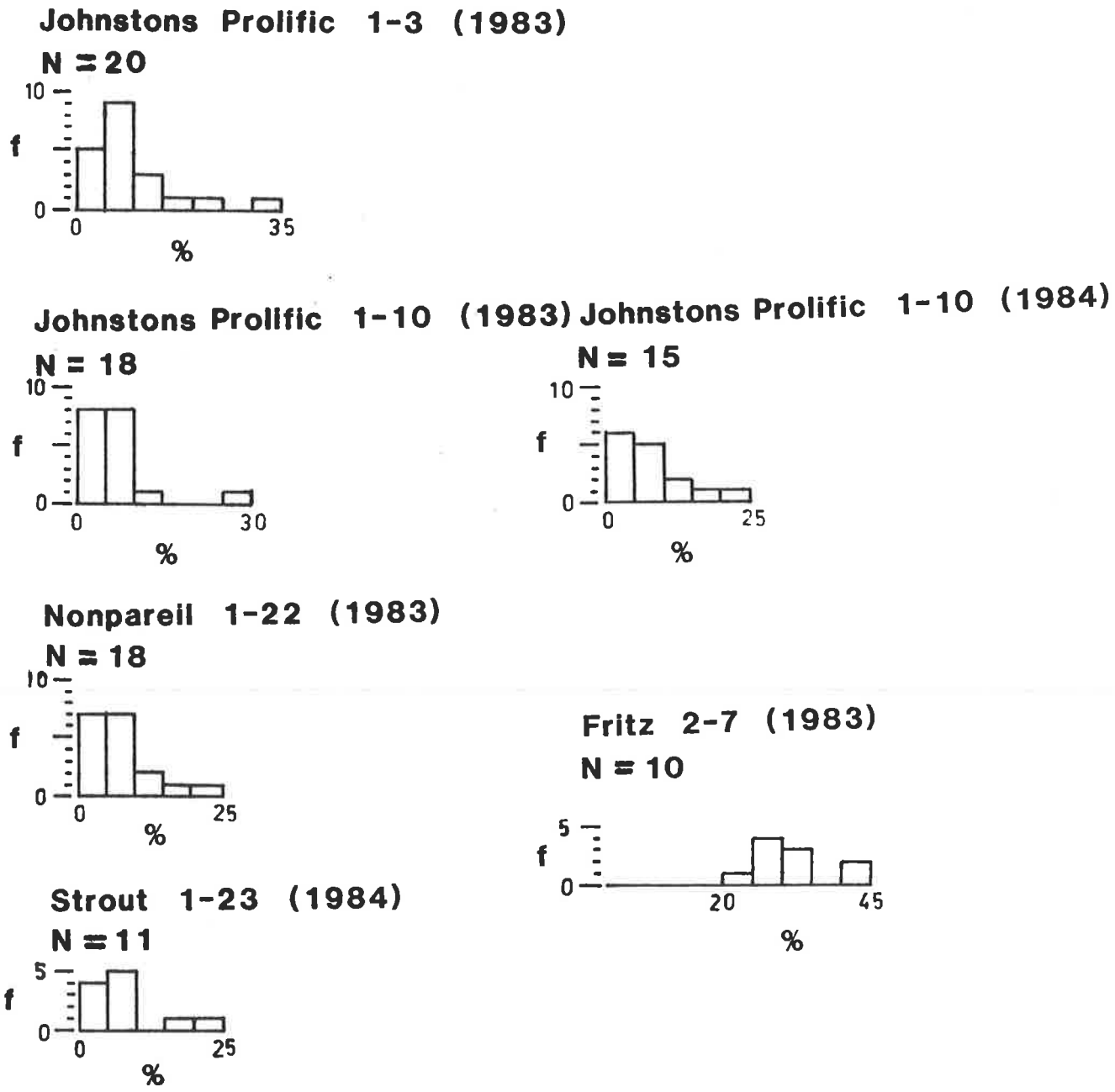
Table 3.1: Mean nut-set per row and per year. Standard deviations are enclosed by brackets. The range of nut-sets per row is also given. The least significant differences (L.S.D.) have a confidence of 95%. "N" is the number of branches sampled. "Estimated N" is the estimate of the minimum sample size that is necessary to detect a difference between treatments of 5 percentage points with 95% confidence. Some calculations were not applicable (n.a.) because there were too few flowers.

Cultivar	Row number	Year	N	Mean per branch		Nut-set (%)		L.S.D. (5%)	Estim. N
				Flowers	Nuts	Mean (S.D.)	Range		
Johnstons Prolific	1- 3	1983	20	94	9	9.8 (7.7)	0-32	3.5	12
Johnstons Prolific	1- 3	1984	12	3	1	n.a.	n.a.	n.a.	n.a.
Johnstons Prolific	1-10	1983	18	81	5	6.4 (5.7)	1-25	2.7	8
Johnstons Prolific	1-10	1984	15	71	6	7.5 (5.8)	0-22	3.2	7
Nonpareil	1-22	1983	18	73	5	7.6 (6.5)	0-21	3.1	9
Strout	1-23	1984	11	129	8	7.8 (6.9)	1-24	4.6	10
Fritz	2- 7	1983	10	298	93	31.3 (6.2)	26-40	3.9	8
Mission	2-12	1983	32	92	30	30.1 (11.3)	12-62	4.0	22
Mission	2-12	1984	7	90	15	21.7 (10.0)	6-35	7.5	18
Nonpareil	2-14	1983	51	61	18	28.5 (12.5)	4-75	3.5	27
Nonpareil	2-14	1984	45	62	11	17.6 (8.6)	0-44	2.6	13
Grant	2-17	1983	50	36	3	9.7 (7.6)	0-33	2.2	12
Grant	2-17	1984	30	91	3	3.9 (4.4)	0-18	1.6	6
White Brandis	2-27	1983	26	40	3	8.1 (5.8)	0-19	2.3	8
White Brandis	2-27	1984	18	92	4	3.7 (2.5)	0-8	1.2	2

Table 3.2: Nut-set versus branch number and date for Fritz trees (row 2-7). Each branch is identified by the tree number and a letter. Means followed by the same letter are not significantly different ($P > 0.05$).

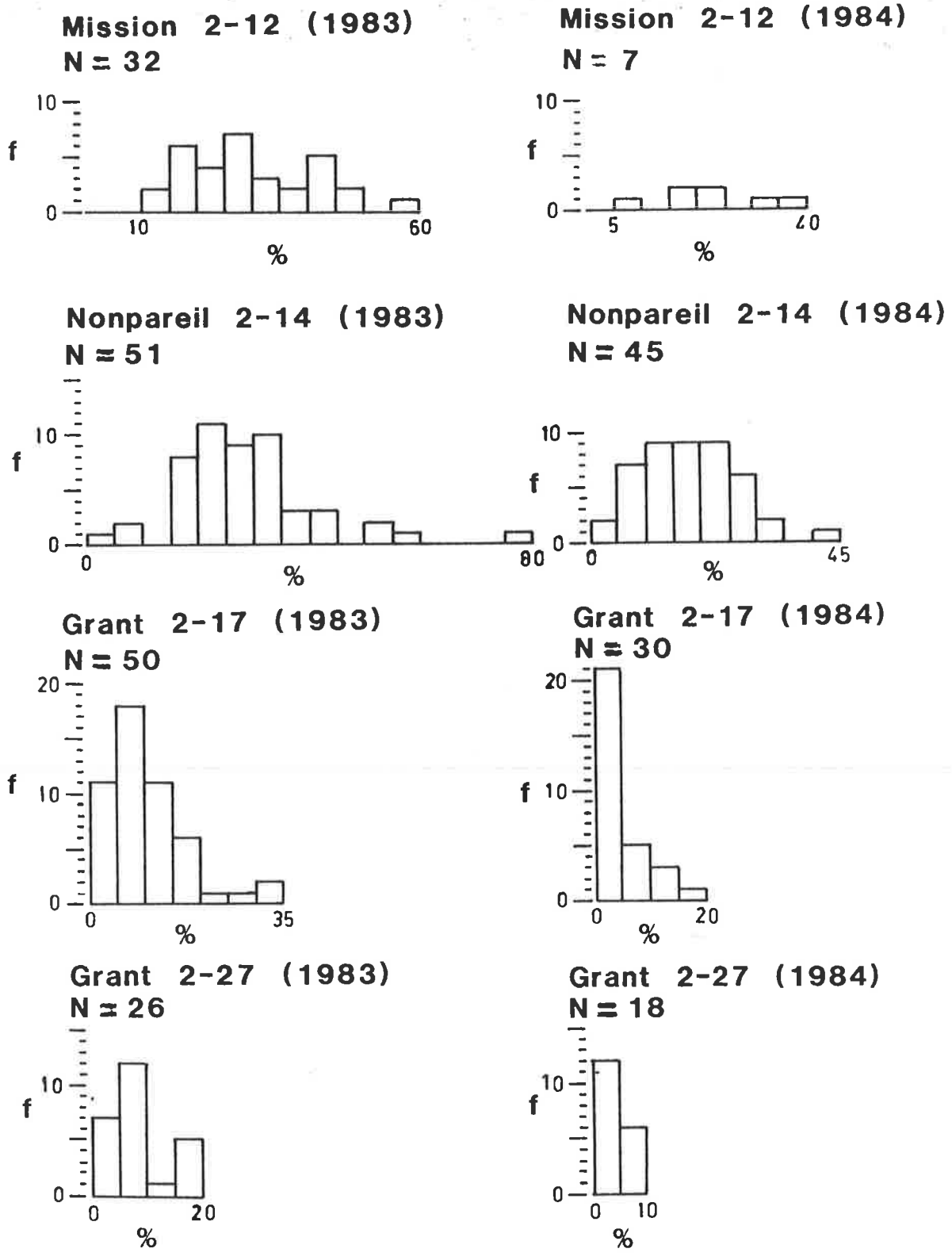
Branch	Date												Mean	
	29/7	30/7	31/7	1/8	2/8	3/8	4/8	5/8	6/8	7/8	8/8	9/8		
4A	25	19	28	43	0	48	50	36	35	30	14	21	29	b
4B	27	19	37	20	48	53	27	6	21	27	15	20	27	b
7A	0	21	7	25	32	57	20	26	24	5	23	25	22	b
7B	0	0	45	60	33	46	6	0	17	23	60	51	28	b
10A	15	33	30	47	32	47	35	37	26	15	14	25	29	b
10B	16	19	41	41	40	60	8	10	20	10	16	0	23	b
12A	0	25	46	45	78	58	45	52	36	44	54	50	44	a
12B	25	4	38	40	22	33	33	11	0	20	33	0	21	b
16A	0	64	41	67	61	64	60	53	52	47	60	37	50	a
16B	0	50	0	14	0	28	47	36	39	35	42	47	26	b
Mean	10	25	31	40	34	49	33	27	27	25	33	27		
	c	bc	b	ab	ab	ab	ab	b	b	bc	b	b		

Figure 3.2: Frequency distributions of nut-sets within rows. The first frequency class is 0 to 4.99%, and subsequent classes are 5% wide. The range of classes is indicated by the numbers in each horizontal axis. The cultivar, row number, year, and number of branches (N) are given at the top of each distribution.



(continued)

Figure 3.2 (continued)



The smaller estimates of sample size should perhaps be ignored because the distributions were skew (Fig. 3.2), and the mean nut-sets per row, which are given in Table 3.1, were much lower than might normally be expected (e.g. Tables 1.1, 1.2). Nut-sets that are commercially acceptable usually range between 15 and 40%, which is when a difference of 5% should be acceptable as a minimum detectable difference between treatments. The data in Table 3.1 suggest that a sample size of about 30 branches is needed to be sure of detecting differences of five percentage points with 95% confidence. Further, the detection of differences of one percentage point would require a sample of about 680 branches.

3.3 Nut-set versus distance from pollen sources

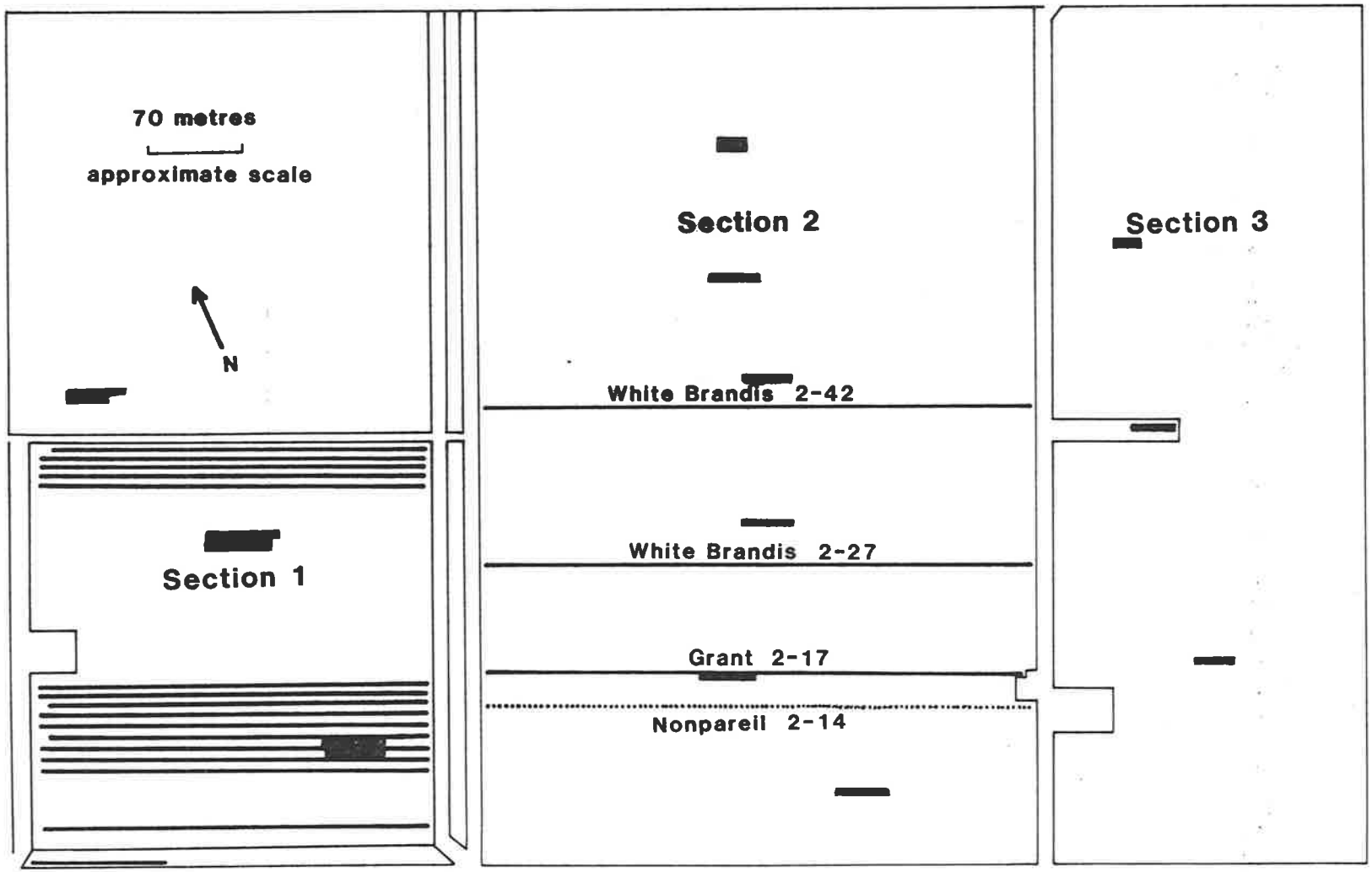
Introduction

Trends of decreasing fruit-set with increasing distance from pollen sources have been recorded on other fruit trees (Free 1970a p406), but such a trend has not been reported in almond, probably because the nature of most modern almond orchards prevents the making of suitable observations; but an opportunity to test such a trend arose in Keane's orchard in 1983 when a row of Grant trees (row 2-17) flowered in 1983 when few other trees were flowering in that section of the orchard.

The locations of all the trees that were flowering at the time, are given in Figure 3.3. During the flowering season of the Grant trees, pollen for cross-pollination could only have come from two areas of orchard, and they were (a) White Brandis trees in rows 2-27 and 2-42, and (b) Chellaston, White Brandis and Johnstons Prolific trees in orchard-section 1. During that time, no other trees flowered in orchard-section 2, and no trees were flowering in orchard-section 3 (Fig. 3.3).

Theoretically, the White Brandis trees in rows 2-27 and 2-42 were unlikely to contribute significantly to the nut-set of the Grant trees in row 2-17 because foraging honeybees tend not to fly large distances between flowers, especially if several hedgerows must be crossed to reach the next flower (Section 14.3.5). So the trees in orchard-section 1 were the only likely source of compatible pollen for cross-pollination of the Grant flowers in row 2-17; and that pollen source was at one end of the row of Grant trees (Fig. 3.3). Foraging honeybees may then be expected to distribute pollen, from orchard-section 1, along the hedgerow of Grant trees, with a resultant trend of decreasing nut-set away from the trees of orchard-section 1 because few bees visit more than 4 trees during a foraging flight (Section 14.3.2).

Figure 3.3: The locations of all trees that were flowering in 1983 when the Grant and White Brandis trees in rows 2-17, 2-27 and 2-42 were flowering. Rows of flowering trees are indicated by thick lines. The row Nonpareil 2-14 is indicated by a dotted line, and its trees flowered after the other indicated trees had finished. The positions of hives are indicated by rectangles. More details of the trees and hives are given in Appendix 2 and Figure 2.1 respectively.



Similarly, the White Brandis trees of row 2-27 were also likely to receive significant quantities of pollen from only the trees in orchard-section 1 (Fig. 3.3), and to show a trend of nut-set along the rows.

Methods

Two branches were selected on each of 25 Grant trees in row 2-17 and 12 White Brandis trees in row 2-27. For each tree, one branch was on the northern half of the tree and one branch was on the southern half of the tree. Most rows in orchard-section 2 contain 51 trees (Appendix 2). For each branch, flowers and flower buds were counted on July 22, and nuts were counted on November 8.

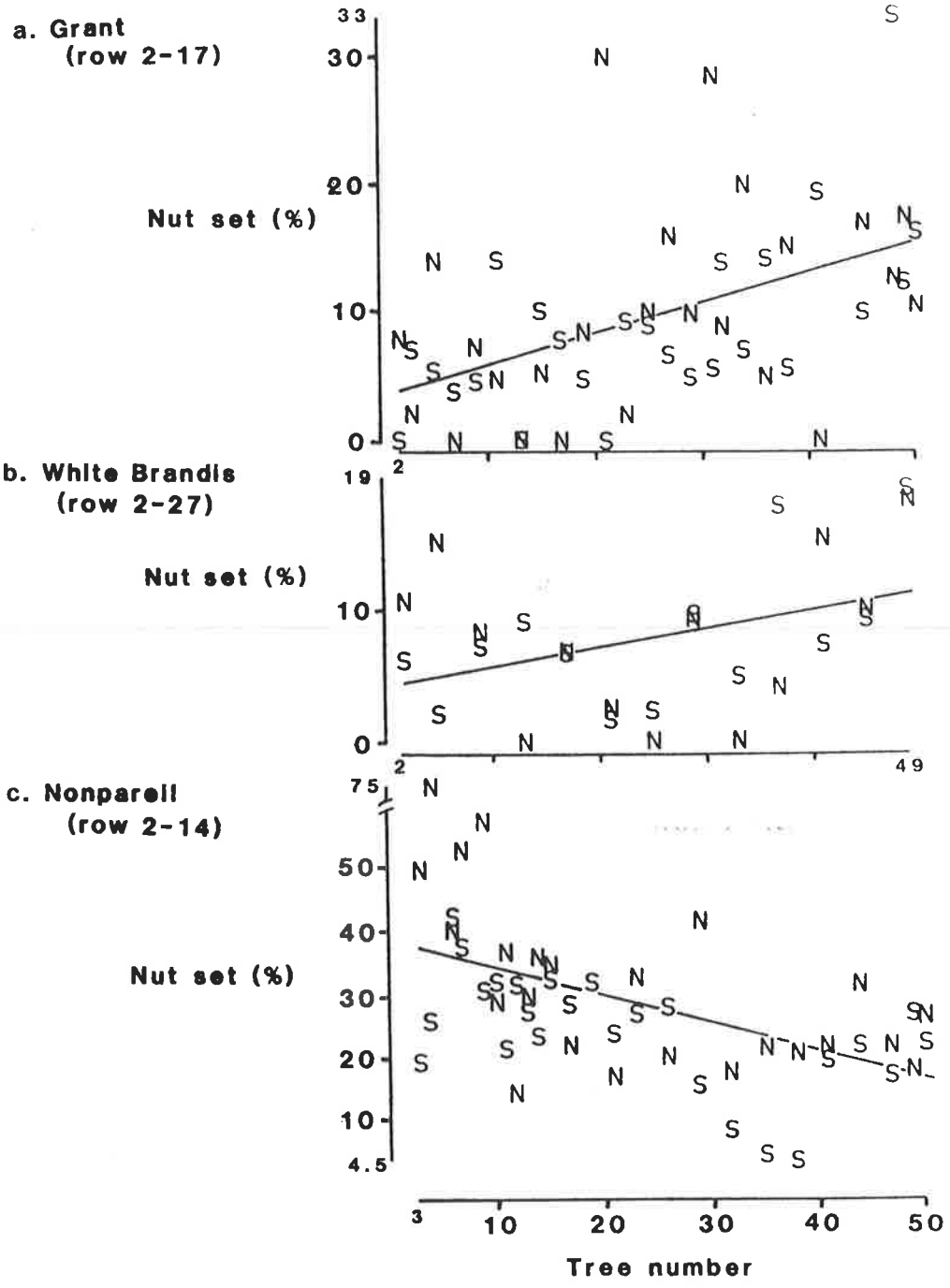
Free (1970a p406) commented that an experiment such as this one does not eliminate the alternative possibility that the variation in fruit-set is due to factors other than the distance from the pollen source. A definitive experiment would be difficult to perform except in an orchard designed specifically for the experiment. Nevertheless, I attempted to partially accommodate Free's comments by testing the further hypothesis that nut-set on the Nonpareil trees in row 2-14 did not change with distance away from the trees of orchard-section 1 (Fig. 3.3). The Nonpareil trees flowered when most of the trees in orchard-section 2 were in flower, including the adjacent Davey trees of row 2-15.

Results

The data are presented as Figure 3.4a-c. The mean number of flowers per branch for rows 2-17 (cv. Grant), 2-27 (cv. White Brandis), and 2-14 (cv. Nonpareil) were 71, 76, and 119 respectively; and few branches produced less than 30 flowers.

The data for individual branches were tested for a linear regression. Nut-set in row 2-17 (Grant) increased significantly from tree 2 through to tree 50 ($t = 3.72$, 48 d.f., $P < 0.001$; Fig. 3.4a). But the linear regression for row 2-27 (White Brandis) was not significant ($t = 1.88$, 24 d.f., $P < 0.11$; Fig. 3.4b). The linear regression for row 2-14 (Nonpareil) was also significant ($t = 4.27$, 48 d.f., $P < 0.001$; Fig. 3.4c), but the regression sloped in the opposite direction to the regression in row 2-17.

Figure 3.4: Nut-set versus tree number in (a) rows 2-17, cv. Grant, (b) 2-27, cv. White Brandis, and (c) 2-14 cv. Nonpareil. These data were used to test the hypothesis that nut-set decreased along the row, and away from the potential pollen source, in rows 2-17 and 2-27. The vertical scale in (c) is different from the scale in (a) and (b). Data points for north-facing and south-facing branches are designated "N" and "S" respectively. The regression equations are (a) Y = 3.57 + 0.24X; (b) Y = 4.61 + 0.14X; (c) Y = 38.8 - 0.44 X.



Testing for a nut-set difference between north-facing and south-facing branches was done by analysis of variance. Mean nut-set in rows 2-27 and 2-17 did not differ significantly between north-facing and south-facing branches ($P > 0.05$). However, mean nut-sets differed significantly between north-facing and south-facing branches on the Nonpareil trees of row 2-14 ($P < 0.05$), being 32.4 and 24.4% respectively.

Discussion

The results from row 2-17 (Grant) support the hypothesis; that is nut-set decreased significantly away from the flowering trees of orchard-section 1 (Fig. 3.4a). A significant trend in row 2-27 (White Brandis) was not detected (Fig. 3.4b), perhaps because fewer trees were sampled in row 2-27 than in row 2-17. Later in the year, nut-set in row 2-14 (Nonpareil) increased away from the trees of orchard-section 1 (Fig. 3.4c), which suggests that the differences in nut-set within row 2-17 were not due to factors related to the locations of individual trees (e.g. soil type, fertility, drainage, orchard management).

Nut-set can decrease with increasing distance from bee hives (Section 14.3.1), but such a relationship cannot explain the results obtained in this experiment because many hives were situated adjacent to midway along each of rows 2-17 and 2-27 during the experiment (Fig. 3.3).

The nut-sets of the trees in the first few trees of rows 2-17 and 2-27 were higher than had been anticipated (Figs. 3.4a, b), possibly for two reasons. Firstly, more bees than expected may have flown across the hedgerows from the other flowering rows in orchard-section 2. This, however, is unlikely because the difference in nut-set between the two sides of the row was negligible. Secondly, two forms of secondary pollination may have been important. Pollen left on flowers by bees may have been unintentionally transferred along the rows to more distant flowers by other bees; and pollen may have been transferred from bee to bee while the bees were in their hive. Secondary pollination is discussed further in Section 13.3.

3.4 Stigma length relative to stamen length

Introduction

Most stamens within a flower end at the same height above the flower receptacle, thus forming a platform onto which pollen-collecting honeybees can land (e.g. Fig. 11.1). The length of the style, relative to the "stamen platform", can vary between flowers within and between trees and cultivars, but by how much is unknown (Forshey 1953; Free 1970a p395). This variation in stigma height may affect the probability of a flower being effectively pollinated by a visiting honeybee; for example, a very high stigma may be touched only rarely, whereas a stigma at about the same level as the stamens may have the best probability of being touched, and lower stigmas may also have a good chance of being touched by either pollen-collectors or nectar-collectors that reach the nectar through standing on the anther platform (see Figs. 11.2, 11.3). This variation is discussed further in Section 13.1.

Preliminary data were sought to elucidate the variation in incidence of flowers of the different categories, between trees and dates of anthesis, in the cultivar Fritz.

Methods

Three categories of flowers were distinguished, depending on where the tip of the stigma was relative to the "anther platform": (1) below the platform, (2) at the same level to within about 1 mm, and (3) above the platform. Differences between the categories are illustrated by Figures 3.5a-c.

Two branches on each of five trees were chosen. The trees were numbers 4, 7, 10, 12, and 16 in row 2-7 (Appendix 2). On each day from July 23 to August 9, but excluding July 25, each newly-opened flower was tagged with date and flower category. Flowers that lacked stigmas were not counted.

Figure 3.5: An almond flower with a stigma that is lower (a), as high (b), or higher (c), than the anther platform.

a.

b.

c.

Results

The observed height separations between stigma tip and stamen platform varied within the range of plus and minus 12 mm, and the stigmas of most flowers in categories 1 and 3 had a height separation of at least 4 mm from the stamen platform. Less than 2% of the sampled flowers were difficult to categorize, and most of those flowers either had a height separation of between 1 and 4 mm, or the stamen platform was indistinct. In other words, flowers were not evenly distributed about a mean height separation, but this cannot be shown because height separations for individual flowers were not recorded. Three flowers that had twin styles, with one style being longer than the other, were put in category 2.

There were a total of 47 (2.0%), 1,191 (52.1%), and 1,050 (45.9%) flowers in categories 1, 2, and 3 respectively. Between 0 and 6% of the flowers were in category 1, depending on date and branch. That range of percentages was too small for the detection of significant differences between branches and dates, so flowers of category 1 were ignored for the following analysis.

The proportions of flowers that were in category 3, for each day and branch, are given in Table 3.3. Data for July 23-29 were combined because few flowers were sampled on those days. The proportions of flowers in category 3 differed significantly between dates (ANOVA, $F = 3.84$, 11/99 d.f., $P < 0.001$) and branches (ANOVA, $F = 2.14$, 9/99 d.f., $P < 0.05$) (Table 3.3).

Some Nonpareil flower buds had long stigmas protruding up to 15 mm out of the flower buds. Such flower buds were seen only on certain Nonpareil trees and not all buds on those trees had that characteristic although the incidence of such buds seemed to differ to extremes between branches within trees. The importance of these buds to nut-set is unknown.

Discussion

The mean data at the bottom of Table 3.3 indicate that the proportion of flowers in category 3 decreased with time. This suggests that long-styled flowers open sooner in the flowering season, rather than later. A weak trend also occurred along the row, in that the proportion of flowers was significantly lower for tree 4 than for the other trees (Table 3.3). If one accepts the suggestion that long-styled flowers open sooner in the flowering season, rather than later, then the differences between trees

Table 3.3: The percentage of flowers with long (category 3) stigmas, in relation to date and branch number. Branches are identified by the tree number and a letter. Also given are the means per day and per branch, for all categories. Means (for category 3 only) followed by the same letter are not significantly different ($P > 0.05$). The percentages are rounded to the nearest integer.

	Date												Mean for category		
Branch	23-29/7	30/7	31/7	1/8	2/8	3/8	4/8	5/8	6/8	7/8	8/8	9/8	1	2	3
4A	74	47	36	75	21	48	20	16	14	5	14	7	2	65	32 a
4B	52	41	25	10	63	23	13	27	28	36	30	20	6	61	32 a
7A	75	52	53	37	52	66	72	43	56	44	7	100	1	44	55 b
7B	66	50	45	0	33	66	50	33	67	47	20	66	1	53	46 ab
10A	66	50	38	17	52	64	32	56	40	61	28	50	2	51	46 ab
10B	75	85	70	33	56	60	48	35	54	26	0	11	4	50	46 ab
12A	50	25	20	50	27	58	59	60	50	63	31	33	1	54	45 ab
12B	83	43	55	55	25	77	66	55	75	40	33	0	0	50	50 b
16A	80	32	47	35	44	56	52	73	45	47	40	37	0	51	49 b
16B	70	100	100	28	42	28	52	36	39	41	34	23	0	51	49 b
Mean for categories															
1	3	1	1	1	1	1	2	3	2	3	3	3	2		
2	29	48	50	64	56	45	50	51	49	55	71	61		52	
3	69	52	49	35	42	54	47	44	48	41	25	35			45
	d	c	bc	ab	bc	cd	bc	bc	bc	bc	a	ab			

may be attributed to the fact that the trees at the beginning of the row (trees 4, 7, 10) flowered a day or two earlier than the trees further along the row (trees 12, 16); that is, the differences between trees can be equated with differences between days.

The few flowers that were of category 1 were probably female-sterile, that is, they were probably incapable of producing a nut (Chapter 4), and, if so, then the length of their stigmas would not be important to nut-set; but this point was not tested because the importance of female-sterility was unknown at the time the experiment was performed.

Stigma length differed greatly within and between trees, but nothing is known about the variation between cultivars and years. Variation in stigma length may effect the probability of a flower being effectively pollinated by a visiting honeybee (Free 1970a p395), and so variation in stigma length between cultivars, parts of trees within cultivars, and between years, should be investigated. Also, the assumption that the probability of effective pollination depends on stigma length has not been tested. Perhaps this could be done by testing the hypothesis that the nut-set for flowers of category 3 is less than the nut-set for flowers of category 2.

This experiment was preliminary to further experimentation, but more experiments on the subject of stigma length were not done.

3.5 Effect of fungicides on pollen viability

Introduction

A large experiment was terminated prematurely in 1983 because some pollen, which was being used for hand-pollination, was not viable, probably because it had been killed by fungicidal sprays. The experiment was an attempt to obtain estimates of effective pollination periods (EPPs - defined in Section 8.1.2) by hand-pollination of flowers in an age sequence, but many flowers were hand-pollinated with non-viable pollen, so the experiment was ruined. I was not sure of the problem at the time, so little information and few data were recorded. Nevertheless, the effect of fungicides appears to be a very important factor of pollination (e.g. Section 8.4.2) so I have made some comments here.

Methods

The orchardist sprayed all flowering trees with a fungicide every 3 or 4 days during the flowering season. The identity and concentration of the fungicide is unknown. Pollen was collected from Fritz trees every one or two days by stripping one-day-old flowers of dehisced anthers and allowing the anthers to dry at room temperature for 24 hours. The pollen was then used to hand-pollinate newly-opened flowers, details of which are not important here. The viability of the pollen was not tested until several days after the pollen had been used for hand-pollination because of the distance to the laboratory and a lack of time to perform the tests earlier.

Pollen viability was tested *in vitro* by dusting pollen onto the surface of hanging drops of 15% sucrose. The hanging drops were stored at 20°C for 48 hours. Pollen was assumed viable if it produced a pollen tube (see Fig. 3.6). Methods of testing pollen for viability are discussed in Section 8.4.

Results

Precise details of the results were not recorded because the details of pollen viability were not important to the original experiment. For many samples, between 70 and 99% of the pollen germinated. These percentages are considered normal for almond (Section 8.4). However, several pollen samples had a viability of less than 1%. Those samples were collected less than 24 hours after fungicide had been applied to the flowers. Also, the latter samples had been used extensively in the hand-pollination experiment, so that experiment was abandoned.

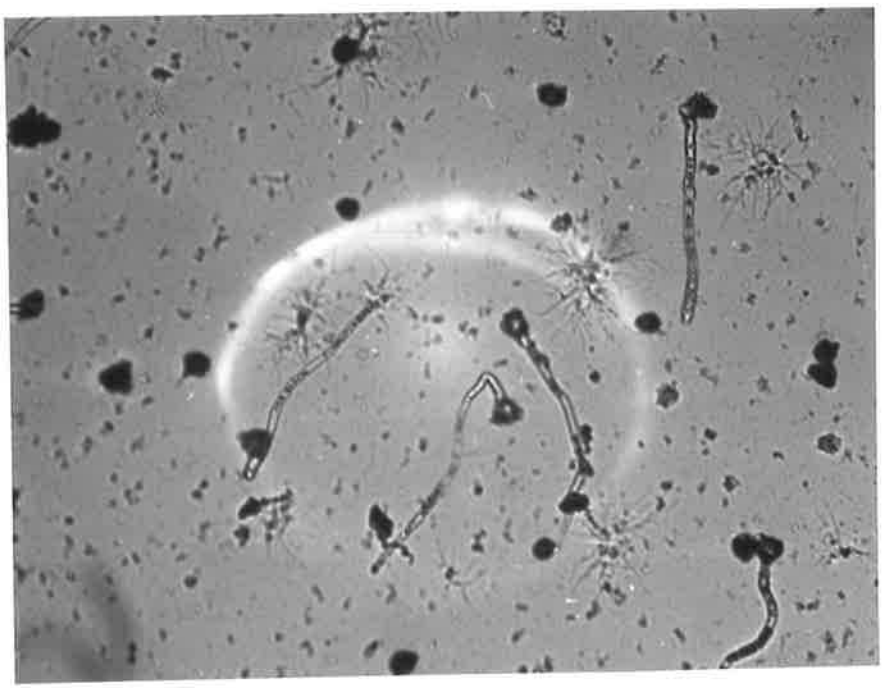
All the pollen samples contained many fungal spores, and they germinated in the hanging drops (Fig. 3.6). The pollen germination shown in Figure 3.6 is high because I did not understand the problem at the time and so I photographed the affected sample with the best pollen germination.

Ironically, a major outbreak of an unknown species of shot-hole fungus became apparent a few weeks after flowering had finished.

Discussion

The ability of fungicides to kill pollen has been investigated in several countries (Section 8.4.2), but the importance of this ability to almond pollination has not been investigated. Fungicides may prevent a significant amount of nut-set in Australian almond orchards (Section 8.4.2), and so the value of fungicides to almond growing needs to be reassessed.

Figure 3.6: Pollen germination on a hanging drop of 15% sucrose. Fungal spores have also germinated.



3.6 Honeybee activity in the orchard

Introduction

Relationships between weather variables and the foraging activity of honeybees have been studied extensively and they are discussed in Chapter 14. The behaviour of honeybees in relation to weather variables varies greatly with time of year and location. So, the preliminary work reported here was done in 1983 to obtain a general understanding of honeybee activity and behaviour in relation to weather variables in the experimental orchard. Subsequent studies of honeybee behaviour were done in 1984 in conjunction with other experiments, and, with one exception, that work is reported elsewhere in this thesis (e.g. Chapter 6).

Methods

Honeybee activity in some trees and near some hives was assessed qualitatively using the categories nil, low, medium and high. Air temperature in a Stevenson Screen was recorded hourly, and the values of other weather variables (e.g. rainfall, wind, sunshine) were noted whenever they changed markedly. Data were recorded from July 24 to August 16, 1983, and casual observations were made throughout the flowering seasons of 1983 and 1984.

The strength and distribution of hives within the orchard is described in Section 2.3. All the hives were placed in the orchard before almond flowers appeared.

Results (1983)

The rate of data collection was somewhat erratic because detailed analysis of the data was not anticipated, so only a summary of the data are presented here. Data for the period July 24 to August 6 is displayed in Figure 6.1.

Bee flight activity was often low or non-existent during some of the days that were overcast, cool, wet and windy. During such days, bees frequently landed on white objects in parts of the orchard where flowers were not present. Such white objects included the white mesh cages, the Stevenson screen, plastic tape, and pieces of paper. Also many dead and distressed bees were noticed on most mornings throughout the orchard on branches and new leaves of flowerless trees. Distressed bees were more apparent during the first few days of the flowering season and, later,

after one or more days of poor foraging weather. The number of distressed bees became negligible after the weed Salvation Jane (Echium spp.) began to flower profusely in adjacent fields in late July. I suspect the distressed bees were starving because they were only noticeable on cold, wet days when there were few flowers available for them to forage on, and most examined hives contained only negligible amounts of stored honey.

The weed Soursob (Oxalis pesaprae) began flowering in the orchard before the almond trees. Open Soursob flowers were visited by many bees, but the flowers were open for no more than a few hours per day, and the flowers did not open at all on days when honeybee foraging activity was low.

The level of foraging activity appeared to depend on weather variables and the time of day. Flight activity during cool weather was generally restricted to the hours between 1000 and 1600 hours, but on warm days bees flew to within 5 minutes of sunrise (approximately 0700 hours) and sunset (1755 hours).

Temperature appeared to be the most important weather variable measured. Flight activity at temperatures over 20°C decreased only during winds of over 20 kph (e.g. July 29 - see Fig. 6.1). Flight activity was moderate to high at temperatures of 15 to 20°C, regardless of whether or not there was cloud, moderate wind, or direct sunshine. Below 15°C, flight activity was low to moderate when the sky was clear and the air still; but cloud, wind and rain tended to stop flight activity. Low temperatures also seemed to restrict the distance foragers flew from their hives to about 50 metres. Flight activity was rare at temperatures below 7 to 10°C.

Direct solar radiation on a hive appeared to increase flight activity, but not necessarily to a high level (Fig. 6.1). Strong solar radiation appeared to counteract the effect of low temperature on foraging activity, but the absence of cloud overhead could also account for increased foraging activity.

On the other hand, foraging activity appeared to be restricted by overhead cloud when the temperature was below 15°C. For example, on several occasions, foraging activity decreased markedly over a 30 second period when the sky overhead became suddenly and temporarily clouded. Many bees appeared to then seek local shelter such as leaves and the lee of branches, and not their hives. The sun was not masked during one such incident, and most times the ambient air temperature did not change. When a cloud passed from being overhead, the foraging activity increased in a few minutes to

what it was before the cloud appeared. Cloud did not affect flight activity when the temperature was above 15°C.

Honeybees foraged during periods of light rain, but only on flowers that were within approximately 20 metres of hives. Most of the periods of rain occurred when the air temperature was between 12 and 14°C. Foraging activity sometimes increased quickly within one minute of the rain stopping when the rain had come from isolated clouds that were passing over the orchard.

Foraging activity appeared generally to be inversely related to wind speed. Foraging activity was affected by winds above about 5 k.p.h., but honeybees continued to forage in winds up to about 20 kph when the day was warm and sunny. Foragers caught by a wind gust were often seen to walk to the lee side of the object they were on.

Discussion (1983)

These results elucidated the local effects of weather on honeybee foraging, and this knowledge enabled me to design experiments that are reported elsewhere. The effects of weather on honeybee foraging are discussed elsewhere in this thesis (e.g. Sections 14.1, 14.2).

Results (1984)

Most of the 1984 data are used and discussed elsewhere in this thesis, but the following comments are not appropriate to other sections of the thesis, so they are given here.

In 1983, the hives were placed in the orchard before the flowering season had begun, and the observed maximum ratio of foragers to flowers was never noticeably more than was expected, which was 1 to 2 foragers per 100 flowers (Section 10.3.2.2).

However, in 1984, the hives were placed into the orchard when some trees were in full bloom (i.e. 50% flowering), and during the 4 days following hive introduction, the density of foragers on flowers was consistently high, and was often 1 forager per 5 flowers. There was also much interference between foragers. The maximum density decreased to 1 or 2 foragers per 100 flowers by the fifth day, and this density was not exceeded noticeably during the remainder of the flowering season.

Discussion (1984)

A high density of foragers on flowers during the first few days following hive introduction has been reported before, but only briefly (e.g. Butler 1943, 1945; Butler *et al.* 1943; Anon 1984), and apiarists I have spoken to said that such behaviour during the first few days after hive placement is normal. I did not have time to perform experiments to confirm the existence of the behaviour.

The number of foragers at a food source is usually proportional to the amount of food available, even when flowers are scarce and there are many honeybees colonies nearby (Section 10.3.2.1). Communication between foragers *within* colonies has been studied extensively (Section 11.5), and such communication can explain why a *single* colony supplies a number of foragers that is adequate, but not excessive, for the exploitation of a food source. However, if every colony in the vicinity of a food source did this, then the number of foragers at the food source should be N times more than is adequate to exploit the food source, with N being the number of colonies present. Such occurrences do not happen except, apparently, during the first few days after hives have been placed into a new area. Therefore, there must be some form of communication *between* colonies, which prevents overexploitation of food sources, and which takes several days to become established. The idea that each colony establishes a territory is too simple because every area of crop usually contains foragers from several colonies (Section 12.6). The nature of the communication between colonies is apparently unknown.

The potential value of this behaviour to almond pollination efficiency is discussed in Section 12.6.

3.7 Does stamen and petal removal prevent pollination in almond ?

Introduction

Many pollination and fruit-tree breeding experiments require that flowers be isolated so that insects cannot pollinate the flowers. Two methods of isolation are (a) the enclosure of the flowers within cages to exclude insects, and (b) the removal of petals and/or stamens from the flowers so that, supposedly, the flowers are no longer attractive to insects, especially honeybees. The former method requires more labour, injures stigmas, and is more difficult to use, compared to the latter method; hence the latter method has been favoured by some authors

(e.g. Tufts et al. 1926; Kester and Griggs 1959a, 1959b; Nauriyal and Rana 1965; Thorp et al. 1967; Guerrero-Prieto et al. 1985).

The latter method was thought reliable by authors because they found that nut-set was less than 1% when some or all petals, sepals and stamens were removed at or before anthesis. Further, they supposed that honeybees are not attracted to the remains of such mutilated flowers (e.g. Tufts et al. 1926; Griggs and Vansell 1949; Griggs et al. 1952; Kester and Hansen 1966; Free 1970a p385). However, although the removal of petals and stamens does eliminate a source of attraction for honeybees (Grant 1950; Percival 1955; Levin and Bohart 1955; Visser and Verhaegh 1980a), nectar in the receptacles of almond flowers is also attractive to honeybees (Thorp 1979; Erickson et al. 1979), and the nectaries in the receptacles cannot be removed completely without difficulty (Vansell 1942; Griggs and Iwakiri 1964; Visser and Verhaegh 1980a). Even if the nectaries are completely removed, odour emitting from the remaining parts of the flowers may attract honeybees (Knoll 1926; Bolwig 1954; Lacher 1964; Thorp 1979; Erickson et al. 1979). In fact, honeybees have been observed visiting mutilated flowers on fruit trees (Howlett 1926; Vansell 1942; Williams and Legge 1969; Williams et al. 1984; Williams and Brain 1985), so mutilated almond flowers may be attractive to honeybees.

Many authors thought that mutilation was a suitable experimental technique because fruit-set of mutilated flowers was negligible (e.g. Kester 1965); but apple flowers that were depetalled and emasculated produced a fruit-set of 14% (Williams and Church 1975). In another experiment, apple flowers that were hand-pollinated, depetalled, but not emasculated, produced seeds, 33% of which were the result of subsequent wind and insect pollination (Visser and Verhaegh 1980a); and again, apple flowers that were hand-pollinated and emasculated, but not depetalled, achieved 64% set (Howlett 1926). Perhaps the morphology of some mutilated flowers prevents honeybees from accidentally touching, and hence pollinating, the stigma.

The following experiment was designed to test both mutilation and cages as means of preventing the pollination of almond flowers by honeybees.

Methods

Four adjacent trees of each of the cultivars Nonpareil and Baxendale were selected in 1983. Six branches of each tree were chosen, one for each treatment, and treatments were allocated so that they were not replicated in the same position relative to the trunk of the respective tree.

All open flowers were removed on August 7, the third day of the flowering period of both cultivars. Then each morning after sunrise, and before the honeybees became active, the following treatments were performed on flowers that had a gynaeceum and had either opened since 1600 hours the previous day or were expected to open during the current day:

1. (Control 1) - no treatment.
2. the stamens were removed with forceps.
3. the petals were removed with forceps.
4. the stamens and petals were removed with forceps.
5. (Control 2) On August 6, each branch was caged to exclude bees. Then, on each day, the stamens and petals were removed with forceps. This treatment provided a comparison with treatments 1-4 to determine the proportion of the nut-set which may be due to man-aided pollination caused by the methods used (i.e. tagging and mutilation).
6. (Control 3) On August 6, each branch was caged to exclude bees. The cages were removed after the flowering period and the dead flowers in each cage were counted. This treatment determined the amount of nut-set attributable to pollination not due to honeybees.

The treatment flowers were then tagged. All non-tagged flowers were removed from each treatment branch each day after the bees had stopped foraging for the day. This removal usually occurred at 1600 hours. Treatments 1 to 5 for one tree were done in less than 10 minutes before proceeding to the next tree. The order of treatment of trees was the same each day, and the Baxendale trees were done before the Nonpareil trees. Honeybee behaviour on mutilated flowers was observed casually. The experiment was discontinued prematurely after eight days because bees were becoming active within 10 minutes of sunrise, so that the treatments could not be applied in the available daylight.

Nuts were counted on October 21 and November 7 for Nonpareil and Baxendale respectively.

The Baxendale trees were 5 to 30 metres from 21 bee hives, while the Nonpareil trees were 25 to 45 metres from the same hives. The behaviour of honeybees on the treatment branches was noted occasionally.

Results

A 3-way ANOVA (treatments x days x replicates) was applied to the data for treatments 1-5 during August 9-14 for Nonpareil, and during August 11-14 for Baxendale. Data for other days were excluded for this particular analysis because the numbers of flowers on those days were too low for comparison. A transformation of arc-sine root x did not change the conclusions reached with the untransformed data. Nut-set differed significantly between treatments (F test, $P < 0.001$ for Nonpareil, $P < 0.01$ for Baxendale). There were no differences between days within treatments (F test, $P > 0.05$), so the data were pooled over days and replicates, and the pooled data are given in Table 3.4. Also given in Table 3.4 are the means of treatments 1-5 and the standard errors from the ANOVA for their comparison. Treatment 6 could not be included in the ANOVA test, but the data in Table 3.4 suggest that treatment 6 was not significantly different from treatment 5.

The data in Table 3.4 were tested further by chi-square tests between each pair of consecutive treatments. The chi-square values and their significance are given in Table 3.4. Treatment 3 and 4 for both cultivars differed significantly. These differences were not detected by the ANOVA test because the chi-square test did not rely on a contribution to the standard error of differences in variances amongst the other treatments (i.e. the ones not being compared).

Comparisons were made within cultivars only. Nut-sets for treatments 5 and 6 were negligible, so nut-sets for treatments 1-4 were probably not increased by the methods of treatment or pollination other than through pollination due to honeybees. Mean nut-sets due to open-pollination (Treatment 1) were similar to nut-sets obtained on trees in other experiments (e.g. Section 13.2).

Table 3.4: The effect of flower mutilation on nut-set. Mean nut-sets and standard errors for Baxendale (a) and Nonpareil (b). Days and replicates were combined to obtain total numbers of flowers and nuts respectively. Treatments with the same letters are not significantly different (ANOVA, $P < 0.05$). Treatment 6 could not be included in the ANOVA test.

The chi-square values and their significance are for consecutive pairs of treatments.

a. Baxendale

Treatment	Total flowers	Total nuts	Nut-set (%) Mean (S.E.)	Chi square prob.
1 (control 1)	88	21	23.7 (4.5) a	
				0.38 n.s.
2 (no stamens)	104	21	17.1 (5.7) a	
				1.10 n.s.
3 (no petals)	90	13	11.3 (5.3) ab	
				5.47 $P < 0.05$
4 (no stamens and petals)	92	4	4.5 (1.7) b	
				3.33 n.s.
5 (control 2)	136	1	0.5 (0.5) b	
				0.02 n.s.
6 (control 3)	110	1	1.0 (1.0)	

b. Nonpareil

Treatment	Total flowers	Total nuts	Nut-set (%) Mean (S.E.)	Chi square prob.
1 (control 1)	149	36	22.4 (4.5) a	
				4.15 $P < 0.01$
2 (no stamens)	108	15	13.6 (3.3) ab	
				3.45 n.s.
3 (no petals)	169	12	7.6 (1.8) bc	
				7.79 $P < 0.01$
4 (no stamens and petals)	240	4	1.5 (0.5) c	
				0.00 n.s.
5 (control 2)	129	2	1.0 (1.0) c	
				not applicable
6 (control 3)	121	0	0.0 (0.0)	

Treatments 2 and 3 of Nonpareil, but not of Baxendale, differed significantly from the nut-sets of treatment 1 (Table 3.4). Treatment 4 of Baxendale and Nonpareil were significantly different from the nut-sets of treatments 1 to 3, but were not significantly different from the nut-sets of treatments 5 and 6 (Table 3.4).

Honeybees apparently gave the mutilated flowers less attention than other flowers, but nevertheless visits by honeybees were frequently observed. Pollen must be brushed onto stigmas by a honeybee if a more than negligible nut-set is to be achieved, but few bees touched the stigmas of flowers that had been either emasculated or depetalled, and no bees were seen touching the stigmas of flowers that had been emasculated and depetalled. Indeed, those bees which appeared to be seeking nectar, had difficulty in standing on the mutilated flowers of treatment 4.

Discussion

Honeybees do visit mutilated almond flowers, but nut-set was negligible when anthers and petals were removed (Treatment 4). The removal of only stamens or petals (Treatments 2 and 3) for Nonpareil also reduced nut-set significantly. Some mutilation probably reduces nut-set by reducing the incidence of stigma touching by honeybees (Section 13.1), so the suitability of flower mutilation as a means of preventing pollination by honeybees may depend on the morphology of the mutilated flower relative to the probability of the stigma being touched and pollinated by a visiting honeybee.

Chapter 4: Flower sterility as a nut-set factor of almond

Introduction

At least 50% of the flowers of an almond tree can set nuts, but in Australian almond orchards usually only 5 to 30% set is achieved and an increase in the net weight of nuts per tree coincides with an increase in nut-set (Hill 1985). This paper is a part of a study to discern the important factors of nut-set in order to eventually increase the yield of almond trees through increasing nut-set. It discusses the importance of almond flowers that lack a viable gynaeceum, which are henceforth referred to as female-sterile flowers.

The occurrence of female-sterile flowers is not unusual amongst the flowers of fruit trees generally. For example, up to 8% of flowers are female-sterile in some peach cultivars (Randhawa et al. 1963); and significant numbers of female-sterile flowers have been found on trees of peach, peach-almond hybrids, apple and olive (Dorsey 1930, Randhawa et al. 1963; Jones 1968; Socias i Company 1976; Rallo and Fernandez-Escobar 1985; Postweiller et al. 1985). Indeed, female-sterility has been claimed to be an important factor of fruit set in apple (Howlett 1936, 1938, Hartman and Howlett 1954), and it is obviously important in some almond cultivars in Europe in which up to 99% of flowers are female-sterile (Pejovics 1963).

However, not enough information is available to determine the importance of female-sterile flowers in almond cultivars in Australia, and so the following survey was conducted in 1984 in the experimental orchard described in Chapter 2.

Methods

Sampling of flowers

Flowers were sampled to: (a) define categories of female-sterility to which flowers could be allocated and to test the validity of the categories, and (b) determine the significance of female-sterile flowers with respect to nut-set.

(a) Categories of female-sterility

The first trees to flower in the orchard were "early-flowering" Chellaston trees on the edge of the orchard. On June 29 every flower within two metres of the ground was removed from four of those trees and examined.

The flowers were allocated to five categories and three sub-categories which were defined on the morphology of the gynaeceum and were based on categories defined by Pejovics (1963). The categories are described in Table 4.1 in association with Figures 4.1 to 4.7. Flowers of only one category, denoted as category 5, were thought to be capable of producing nuts. On July 6 every alternate flower was removed from the 4 trees and allocated to a category. Later, on 6 other days, all flowers deemed to have undergone anthesis on the day of sampling were removed and allocated to categories.

With practice, the internal morphology of the ovary, and hence the category of flower, could be determined by the external shape and size of the ovary; that is, without having to destroy the flower. The method was to hold the petals and sepals and gently split the receptacle to expose, but not damage, the gynaeceum. This method allowed the test of the hypothesis that the supposedly female-sterile flowers were, in fact, not capable of producing nuts - on the assumption that each flower of categories 1-4 had the same probability of producing a nut as did flowers of category 5.

The hypothesis was tested with flowers on two branches on each of eight "later-flowering" Chellaston trees. The branches were at about chest height and on opposite sides of each tree. Every two or three days during the flowering period, all non-tagged flowers were labelled with a tag denoting flower category. Nuts that developed from those flowers were counted in December.

(b) Differences within and between cultivars

The initial sampling of flowers from "early-flowering" Chellaston trees, and the examination of flowers from "later-flowering" Chellaston trees, suggested that there could be significant differences in the incidence of female sterile-flowers between and within the two groups of trees. Consequently, differences between cultivars were also likely to be significant. To test for such differences, further samples of flowers were taken from 34 "later-flowering" Chellaston trees, including the eight trees used in the experiment described above, and 25 Davey trees. The number of trees sampled on any given day depended on the number of flowers present, and only flowers within two metres of the ground were examined.

For "later-flowering" Chellaston, sampling on the first four sampling days consisted of the removal of all flowers from all the trees; and on the

Table 4.1: Descriptions of categories of flowers from trees of the cultivars Chellaston and Davey at Angle Vale. The categories were distinguished solely by the morphology of the gynaeceum. All flowers had sepals, petals and stamens.

Category	Description
1	Female-sterile: gynaeceum completely missing and the receptacle is smooth, that is the gynaeceum has not fallen out (Fig. 4.1).
2	Female-sterile: gynaeceum fallen out or ovary underdeveloped or not developed. The stigma may be brown and is no higher than the internal height of the receptacle (Fig. 4.2).
3	Female-sterile: gynaeceum present but reduced in size with the ovary underdeveloped or not developed. The stigma extends to between the rim of the receptacle and the level of the majority of anthers (Fig. 4.3).
4	Female-sterile: gynaeceum present but reduced in size with the ovary underdeveloped or not developed. The stigma extends to at least the height of the majority of anthers (Fig. 4.4).
5	Female-fertile: Ovary fully developed and apparently contains two fully developed and viable ovules, that is the ovules are tear-drop shaped and are usually loosely attached to the ovary wall near the top of the tear shape. The ovule surfaces are smooth and glistening, and there is little air space inside the ovary. The stigma can be of any length but usually reaches the level of the majority of anthers (Figs. 4.5, 4.6).

The following sub-categories occurred within flower categories 2, 3, and 4.

a	Ovary has partly developed and the ovules are at most two small knobs on the ovary wall. The ovary may have the external appearance of a dehydrated prune, otherwise it is a small blob in the bottom of the receptacle (Fig. 4.2).
b	Ovary has developed but the ovules have not matured in that they are firmly attached to the ovary wall, are rectangular in shape, and the ovule surface is globular (cellular). Usually about 50% of the volume of the ovary is air space (Fig. 4.7).
c	Ovary has not developed. The stigma appears to be normal and may extend above the stamens but the point where the ovary should be is usually the thinnest part of the stigma (Fig. 4.4).

Figure 4.1: Flower of category 1.

Figure 4.2: Flower of category 2a.

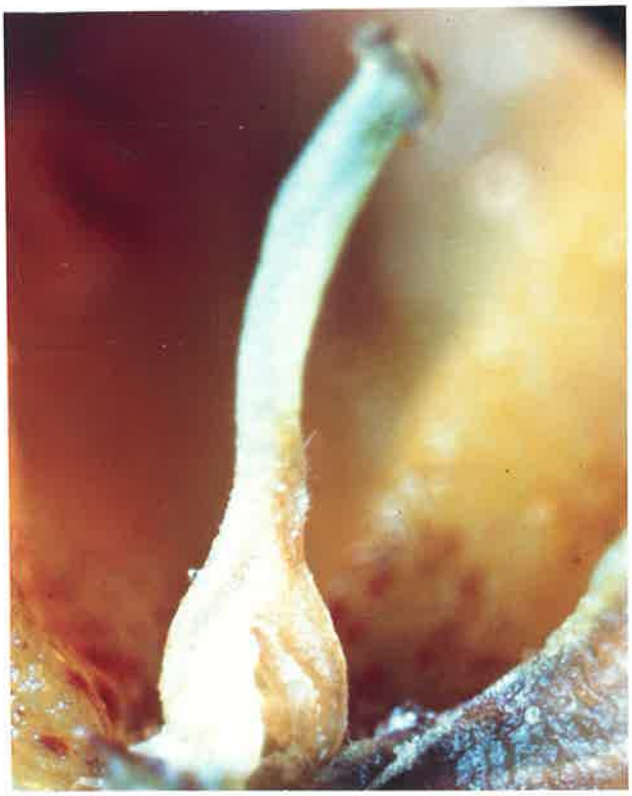


Figure 4.3: Flower of category 3b.

Figure 4.4: Flower of category 4c.

Figure 4.5: Flower of category 5.

Figure 4.6: Flower of category 5 with a cut away view of the ovules.

Figure 4.7: A cut away view of a flower of category b showing the two underdeveloped ovules.

Figure 4.8: A cut away view of a flower of category 5 showing two "normal" ovules, with one larger than the other.

fifth and sixth sampling days all flowers were non-destructively sampled on 17 and 8 trees respectively. For Davey, sampling on the first three sampling days consisted of the non-destructive sampling of all flowers on all the 25 trees; the next three sampling days involved 8 trees, and the last sampling day involved 16 trees.

Flowers of the cultivars Fritz and Nonpareil were also examined, but few flowers were counted because of the reasons given below.

For each group of sampled trees, the dates on which 1, 5, 50, 95, and 99% flowering occurred were estimated by noting the ratio of flowers to flower buds on various parts of each tree, and then averaging within and across trees.

Results

(a) Categories of female-sterility

The data for the tagged flowers, given in Table 4.2, were used to test the hypothesis that the "female-sterile" flowers in categories 1-4 could not produce nuts. The hypothesis would have been rejected if only one nut was produced by a "female-sterile" flower of categories 1-4. The hypothesis was tested by assuming that each "female-sterile" flower had the same probability of producing a nut as did a flower of category 5. Further, each flower was thought to be independent because, overall, each flower was thought to have the same chance of being pollinated even though sometimes flowers within categories were clumped. Of the 755 tagged flowers allocated to category 5, 685 did not produce a nut, so the probability of a flower not producing a nut was estimated to be 0.90728. The probability that N flowers would not produce a nut, was calculated as 0.90728 to the power of N. The number of flowers tagged, and the probability for each flower category, are given in Table 4.2.

The hypothesis was tested only for flower categories 3a and 4b because there were too few flowers in the other categories for a critical level of significance to be reached (Table 4.2). Nevertheless, only the validity of category 4b was in question because the flowers of other categories had ovaries that were obviously under-developed (Table 4.1, Figs. 4.1 to 4.8), and so flowers of categories 1-4 were accepted as being female-sterile.

Most Chellaston and Davey flowers fitted easily into one of the categories. The ovary of each flower of category 5 had two ovules, and usually the ovules were similar in size (Fig. 4.6); however, a few ovaries

Table 4.2: Testing the hypothesis that Chellaston flowers of categories 1-4 could not produce nuts - assuming that each flower was as capable of producing a nut as was a flower of category 5. The hypothesis would have been rejected if one nut was produced by a "female-sterile" flower, and the probability of N flowers not producing a nut is 0.90728 to the power of N. The number of tagged flowers in each flower category and the number of nuts produced by them, are shown. Note that not all flowers on each limb were tagged; therefore the absolute abundance of flowers of the categories is not shown by this table, but the relative abundance of flowers of the categories is suggested. Levels of significance are * $P < 0.05$, *** $P < 0.001$.

Flower category	Number of flowers tagged	Number of nuts	Nut set (%)	Probability	
1	4	0	0	0.678	ns
2a	15	0	0	0.232	ns
2b	2	0	0	0.823	ns
2c	1	0	0	0.907	ns
3a	47	0	0	0.010	*
3b	26	0	0	0.080	ns
3c	0	not applicable		not applicable	
4a	6	0	0	0.558	ns
4b	122	0	0	0.000007	***
4c	6	0	0	0.558	ns
5	755	70	9.3	not applicable	

contained one ovule which was much larger than the other ovule (Fig. 4.8). The significance of this size difference is unknown. Sometimes, too, the allocation of flowers to categories 4b rather than 5, and vice versa, was difficult. For example, of the 140 Chellaston flowers tagged as category 4b, 18 flowers were marked as possibly being in category 5 instead; and six of those 18 flowers produced nuts but none of the "definitely 4b" flowers produced nuts. Conversely, a few flowers tagged as category 5 may actually have been in category 4b, and so the nut-set of flowers of category 5 may have been higher than recorded. The former error was amended by listing the "doubtful 4b" flowers as category 5 flowers, but the latter error was not corrected because the true identity of the flowers could not be verified.

(b) Differences within and between cultivars

The total numbers of non-tagged flowers recorded for each category for early-flowering Chellaston, late-flowering Chellaston, and Davey, are shown in Table 4.3. These data are not a good estimate of the absolute abundance of the different categories because of differences in the numbers of flowers examined on each day, and variation in the number of flowers open at a given sample time, relative to the total number of flowers for the season. Also, the abundance of each flower category, relative to the other flower categories, tended to vary with time. The low number of flowers per category per day, in categories other than category 5, prevented the detection of significant changes, with time, in the relative occurrence of each flower category. Consequently, for further analysis, the data for categories 1-4 were grouped together and compared with the data for category 5; that is, so that the number of female-sterile flowers could be compared with the number of female-fertile flowers.

The proportion of the whole season's flowers which were female-sterile was estimated for early-flowering Chellaston, late-flowering Chellaston, and Davey, by using Figures 4.9, 4.10 and 4.11 respectively. The top sections of Figures 4.9 to 4.11 indicate the proportion of flowers which were female-sterile on each given date of sampling, and between 10 and 90% of Chellaston and Davey flowers were female-sterile, depending on the date (top sections of Figs. 4.9 to 4.11). The frequency distribution of open flowers with time often approximates a normal distribution (e.g. Hill *et al.* 1985), and so approximations of "density of normal distribution" curves, referred to here as flowering curves, were drawn by using the dates

Table 4.3: The number of flowers, from "early-flowering" Chellaston trees, "later-flowering" Chellaston trees, and Davey trees, recorded for each flower category. All replicates and dates have been combined, except that tagged Chellaston flowers have been excluded from this table. Note that this table does not show the absolute abundance of the flowers of the categories, but the relative abundance of flowers of the categories is suggested.

Flower category	Chellaston (Early)	Chellaston (Later)	Davey
1	6	223	75
2a	60	130	85
2b	30	15	6
2c	14	45	22
3a	118	190	85
3b	97	146	35
3c	7	22	14
4a	16	54	371
4b	69	134	432
4c	14	18	10
5	959	2165	2649
TOTAL	1390	3142	3784

Figures 4.9, 4.10 and 4.11: The incidence of female-sterile flowers on "early-flowering" Chellaston trees (Fig. 4.9), "later-flowering" Chellaston trees (Fig. 4.10), and Davey trees (Fig. 4.11). The upper section of each figure shows the mean percentages and standard errors of flowers that were female-~~ster~~fert ile on each day of sampling, while the bottom section of each figure shows the flowering curve for total flowers, and the inferred flowering curve for fertile flowers only. For Figure 4.10, data for tagged and non-tagged flowers were combined.

Fig. 4.9

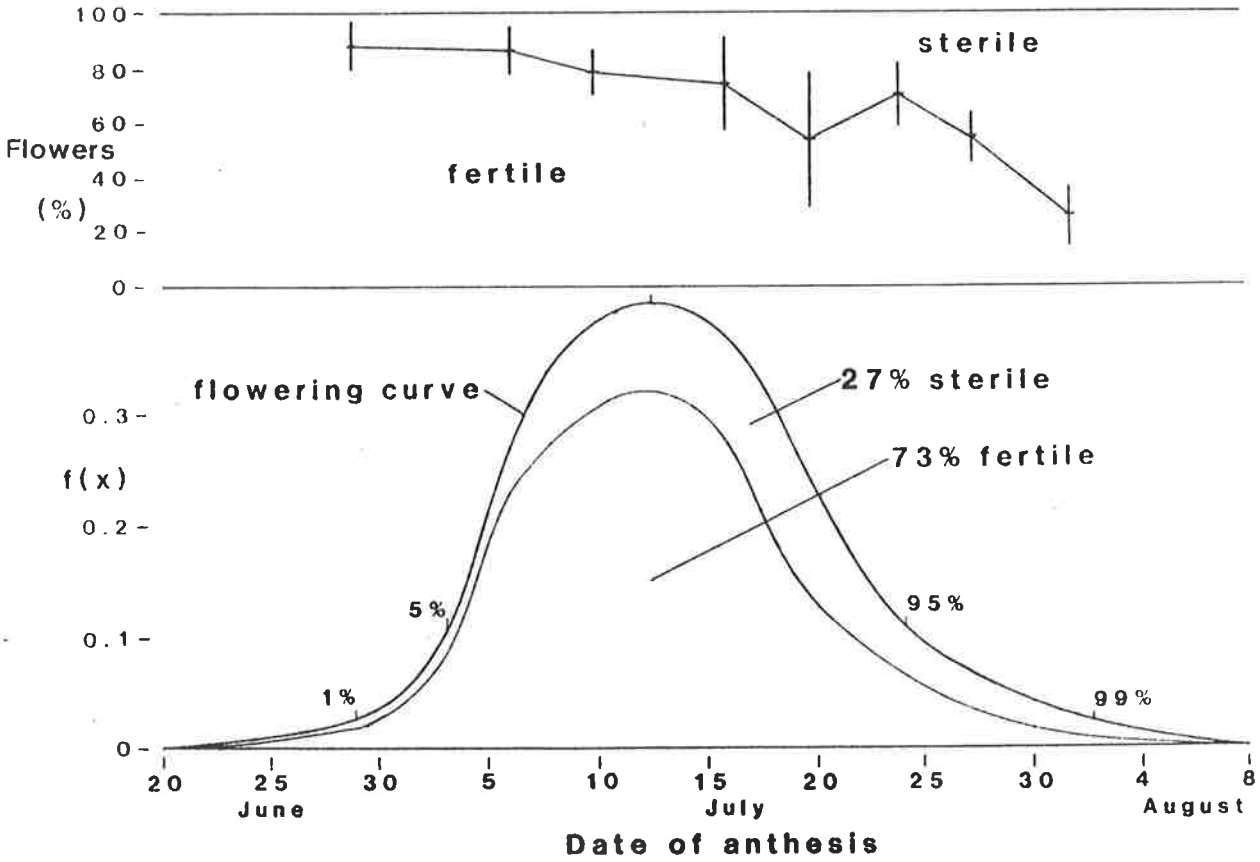


Fig. 4.10

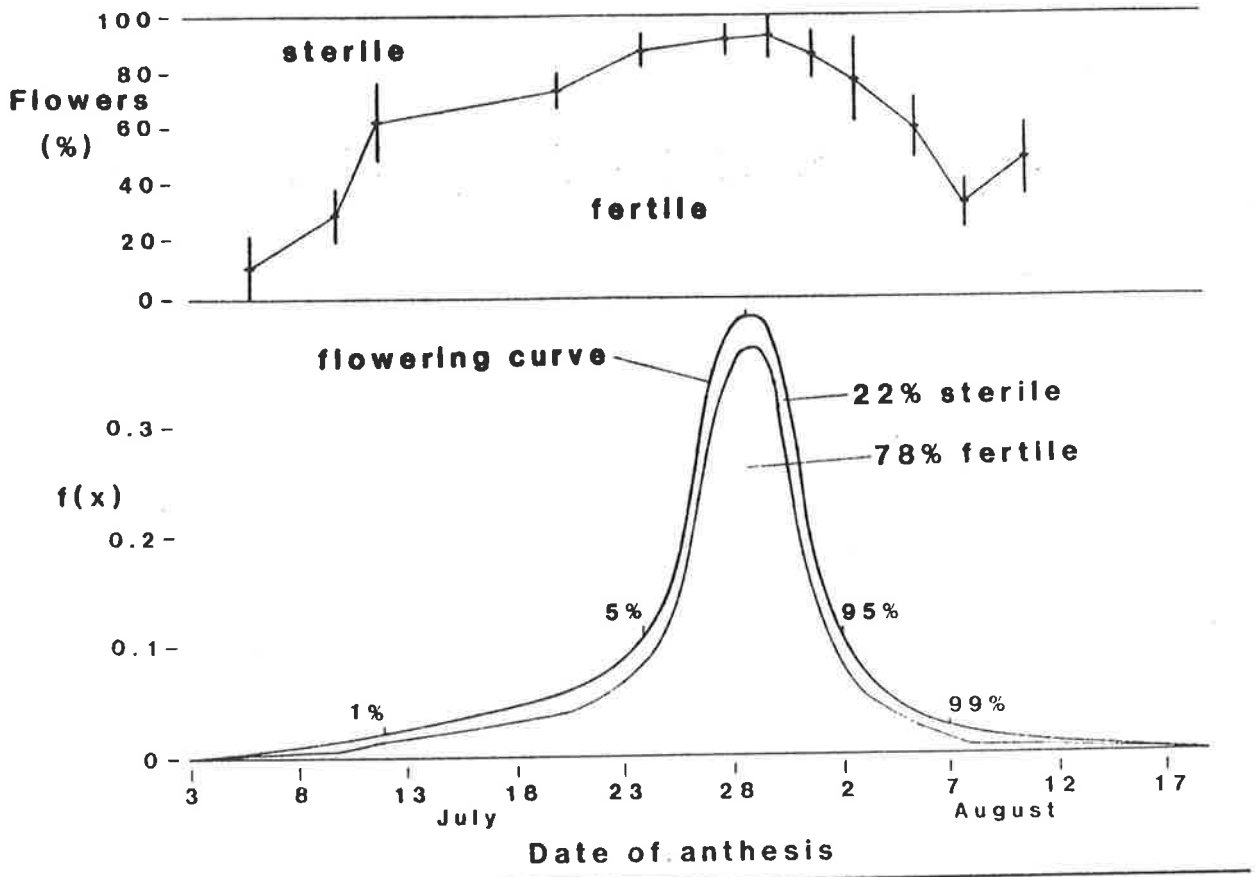
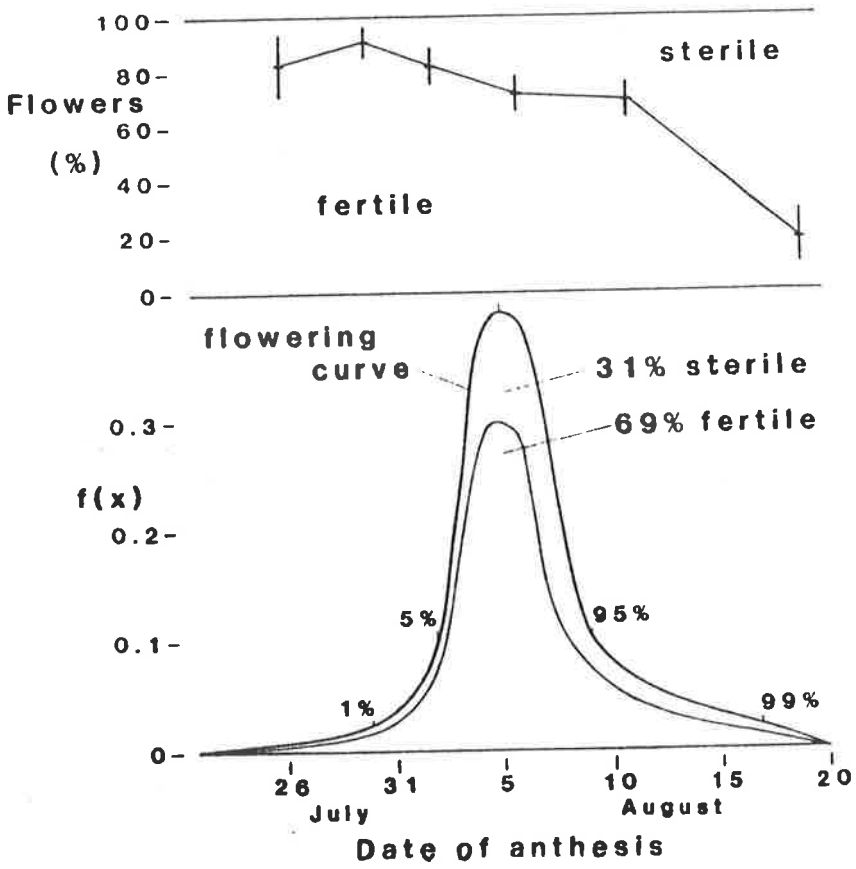


Fig. 4.11



on which 1, 5, 50, 95 and 99% flowering occurred and the "density of normal distribution function" (Bailey 1971 p191). Although the erratic weather at the time would not have allowed the flowers to open with such precise normal distributions (e.g. Hill et al. 1985), each curve allows a reasonable estimate of the proportion of the season's flowers that were female-sterile. Thus, in the bottom sections of Figures 4.9, 4.10 and 4.11, the area under the flowering curve and to the left of a given date, is approximately proportional to the proportion of the whole season's flowers that had open prior to that date. Another frequency distribution curve representing the flower curve for fertile-flowers only may now be drawn under each "total" flowering curve by using the ratios of fertile to sterile flowers in the top sections of Figures 4.9, 4.10 and 4.11. Finally, for each of Figures 4.9, 4.10 and 4.11, the areas under each of the 2 curves can be compared to give an estimate of the percentage of flowers that were female-sterile over the whole season. These estimates were 27% (Fig. 4.9), 23% (Fig. 4.10) and 31% (Fig. 4.11).

In contrast to Chellaston and Davey flowers, Fritz and Nonpareil flowers were difficult to categorize. The lack of correlation between the internal and external morphology of the gynaecea of Nonpareil and Fritz flowers meant that those flowers could only be assessed destructively, and so the validity of the flower categories for those cultivars could not be tested. One problem was that many Fritz and Nonpareil flowers had an ovary that was partly imbedded in the receptacle, and so the flowers could not be classified by using the external appearance of the ovary bulge.

Nevertheless, 55 flowers of category 4b and three flowers of category 1 were among 580 Fritz flowers from four trees at 1% flowering. Out of 215 flowers from ten Nonpareil trees at 1% flowering, 33 flowers were in category 4b and another 40 flowers may have been in category 4b. Otherwise only flowers of category 5 were found. By contrast, on the same Nonpareil trees at 90% flowering, 145 out of 160 flowers were female-sterile. Perhaps some flowers classed as category 5 may actually have been female-sterile. A more elaborate study of Nonpareil and Fritz flowers was abandoned because of the difficulties mentioned above.

Discussion

The precision of the curves shown in Figures 4.9, 4.10 and 4.11 may be questioned, but the evidence nevertheless clearly shows that female-sterility is a significant factor of nut-set. Further, the potential

nut-set of almond trees generally is at least 50% (Hill 1985), so a sample of flowers taken on a day when over 50% of flowers are female-sterile, cannot estimate the average potential nut-set of the sampled trees. Moreover, comparisons of nut-sets between dates and cultivars should not be made without allowing for differential variation in the incidence of female-sterile flowers.

The incidence of female-sterile flowers could be higher than is indicated by this study because microscopic examination of flowers may show that some flowers thought to be female-fertile are actually female-sterile (e.g. Pimienta and Polito 1983). Conversely, nut-sets of over 70%, which were obtained by some authors (e.g. Almeida 1948; Nauriyal and Rana 1965; Dhaliwal et al. 1979; Uppal et al. 1984; Weinbaum 1985), suggest that the incidence of female-sterile flowers may be much lower in some circumstances, perhaps because of the influence of some unknown factors. For example, all the flowers of some avocado cultivars are female-sterile at temperatures below 20°C (Sedgley 1977), and many ovules in nitrogen-deficient apple trees either do not develop to maturity, or they degenerate before fertilization can occur (Dorsey 1930; Howlett 1936, 1938; Copper 1938; Hartman and Howlett 1954). Indeed, almond ovules do not mature until anthesis, so the stage of development of almond ovules at anthesis may depend on several critical factors just prior to anthesis (Pimienta and Polito 1983).

Scions of almond trees are reproduced asexually (Section 1.3). The differences between cultivars, with respect to variation in flower morphology and the incidence of flowers of particular categories, suggest that there is likely to be great variation between plants that are reproduced sexually.

Chapter 5: Rate of flowering in almond versus time of day and air temperature

Introduction

Honeybees can cross-pollinate flowers only during the hours of daylight and during the time when flowers are open and pollen is available. Flower opening varies from one plant species to another; for example, the flowers of some species open for only one day, and the flowers of some other species open on a number of successive days, closing each night and sometimes opening at a different time each day, depending on the age of the flower (Free 1970a). The flowers of Prunus persica and P. laurocerasus may be open during most or all of the hours of daylight (e.g. Percival 1955), but the length of time when flowers are open can vary greatly between species and between cultivars within a species (Percival 1955). Therefore one cannot assume that the flowers of all Prunus spp. are open during most or all hours of daylight.

The rate of flowering is thought to be favoured by low relative humidity and high temperatures, and rain may reduce the rate of flowering (Free 1970a). However, flower opening in three species of Prunus occurs at relative humidities as high as 100%, and in air temperatures as low as 5°C (Percival 1955).

The times of day when almond flowers are open are not recorded in the literature, so the timing of flowering in almond was investigated in 1983.

Methods

Only two trees of each of the cultivars Nonpareil, Ne Plus Ultra and Fritz were selected for this study, because the daily rate of flowering does not differ significantly between branches on different trees within cultivars when the branches are in the same position relative to the trunk of their respective tree (Hill et al. 1985). For each tree, two branches at about chest height were chosen. Unmarked flowers were counted and marked as often as six times per day during the flowering season, and sometimes after sunset and before sunrise. Flowers were deemed to be open when their anthers were visible.

Sunrise and sunset on July 21 occurred locally at 0727 and 1726 hours respectively, and on August 24 at 0655 and 1751 hours respectively. Weather variables (e.g. wind, rain, fog, sunshine) were recorded whenever the weather changed markedly. A device to measure relative humidity became

unreliable and so relative humidity was not measured. Air temperature in a Stevenson Screen was recorded hourly. Mean temperature for each time interval between observations was estimated by averaging the hourly recordings of temperature that occurred during the interval.

Results

Flowers which were open at sunset, were always open before sunrise the next morning; and flowers took from 4 to 6 hours to open from when the anthers became visible to when the petals were at about 90° to the axis of the flower. Once a flower opened, it did not close again. These observations were corroborated by casual observations of flowers on trees of 12 other cultivars in the orchard.

Mean cumulative flowering per day for each cultivar is shown in Figure 5.1. The flowering curves resemble normal distribution curves. Mean cumulative flowering per interval during the flowering season, and for each cultivar, is shown in Figure 5.2a-c. The mean rate of flowering per day during the flowering season can be seen by looking at the right-hand side of Figures 5.2a-c. The rate of flowering per day is indicated by the vertical distance between the lines, that is, a wider distance indicates a higher rate of flowering. The mean rate of flowering during each time interval is indicated by the slope of the line between two consecutive sampling times (Fig. 5.2a-c). A steeper line indicates a faster rate of flowering. The rate of flowering did not differ significantly between branches within cultivars (F test, $P > 0.05$). Many flowers opened overnight but the rate of flowering varied between nights, and was usually greater during the day than during the night (Fig. 5.2). A rate of zero flowers per hour was not recorded for any interval between the cumulative frequencies of 0.1 and 0.9.

Rain, fog and winds of over 30 k.p.h. did not noticeably effect the rate of flowering. For example, there were several periods of continuous light rain during August 8-11, but the process of flower opening was not slowed in that flowers continued to open, and flower buds continued to expand (Fig. 5.2). Consequently rain, and hence humidity, was judged not to be a major factor of flowering during this study.

A test was made of a linear relationship between temperature and the rate of flowering within each cultivar, and between the cumulative frequencies of 0.1 and 0.9 (Fig. 5.3a-c).

Figure 5.1: Mean cumulative flowering per day for the cultivars Ne Plus Ultra, Fritz, and Nonpareil. The data points denote flowering at 1800 hours on each day.

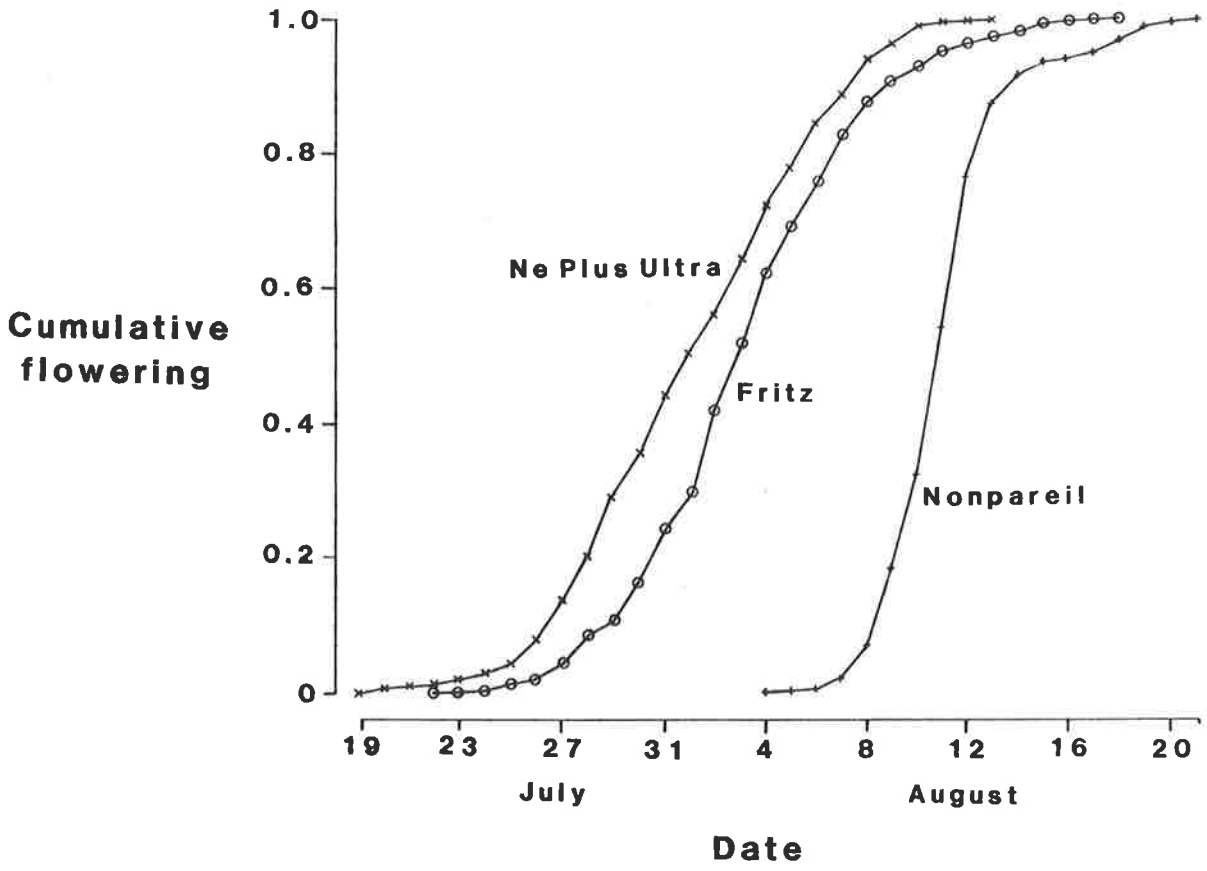
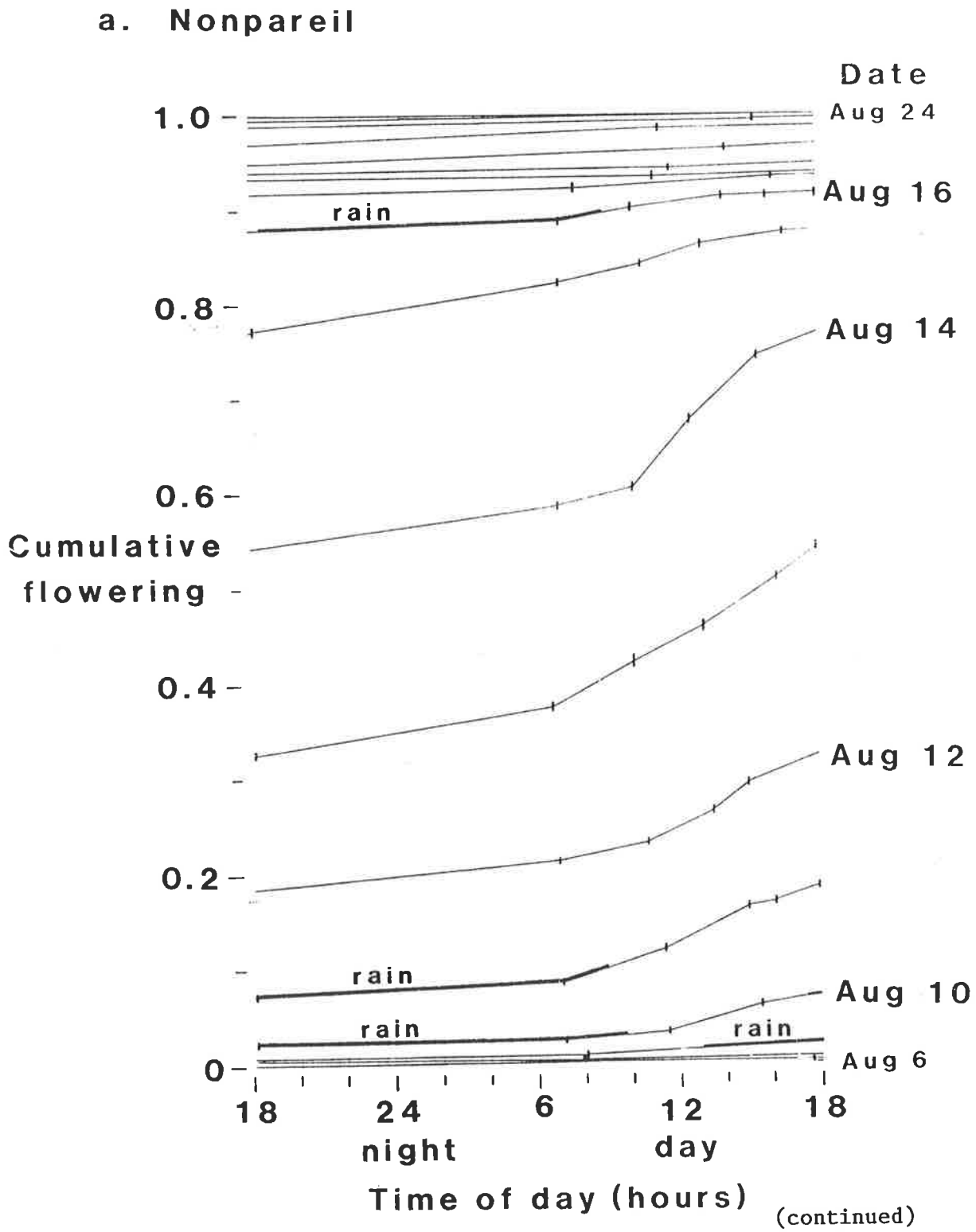


Figure 5.2: Mean cumulative flowering per day for each day over the flowering season of (a) Nonpareil, (b) Ne Plus Ultra, and (c) Fritz. Total flowers counted were 571, 1,126, and 283 flowers respectively. The times of sampling are indicated by vertical dashes, and periods of continuous or intermittent rain and fog are indicated by thickened lines.



(continued)

Figure 5.2 (continued)

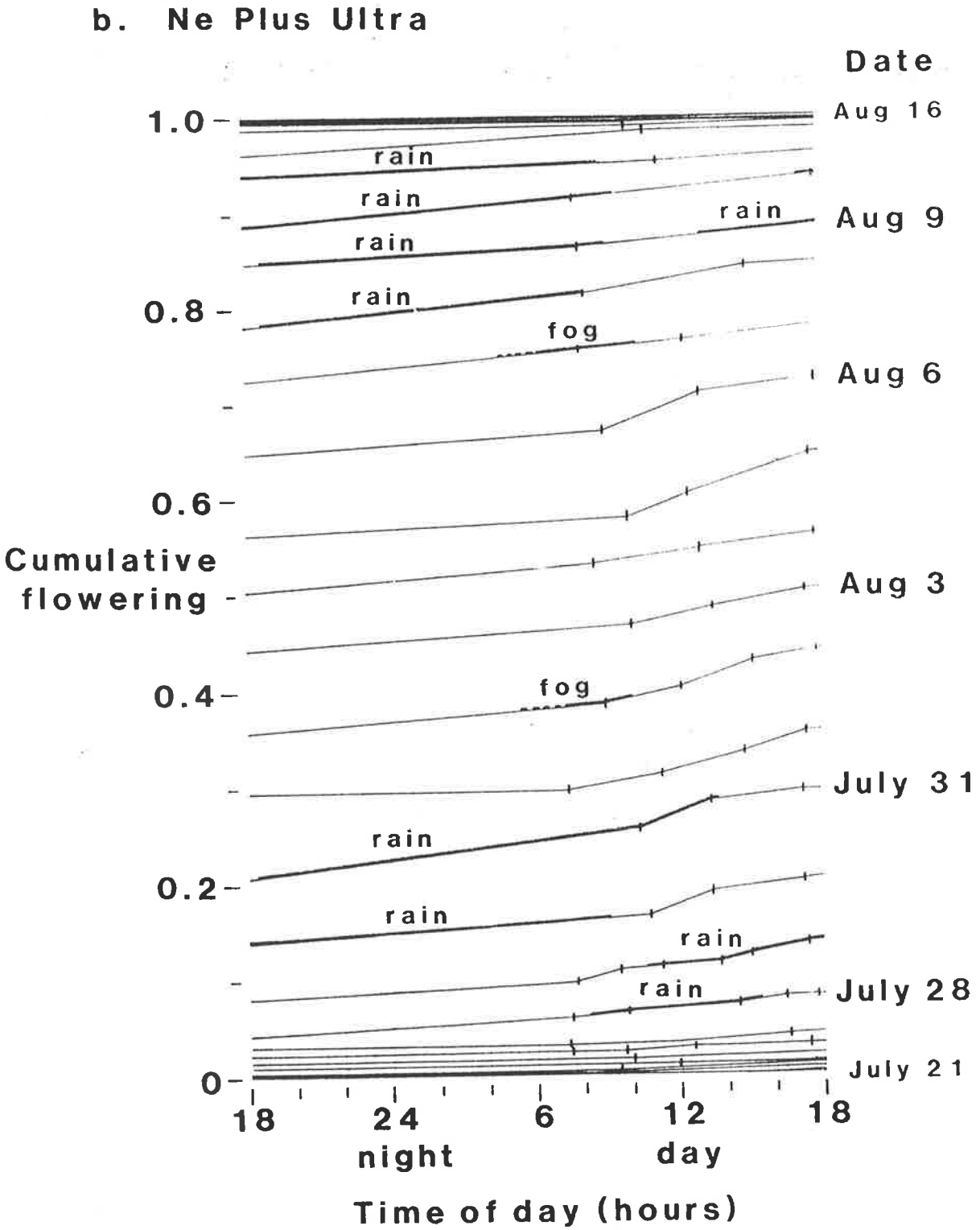


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Figure 5.2 (continued)

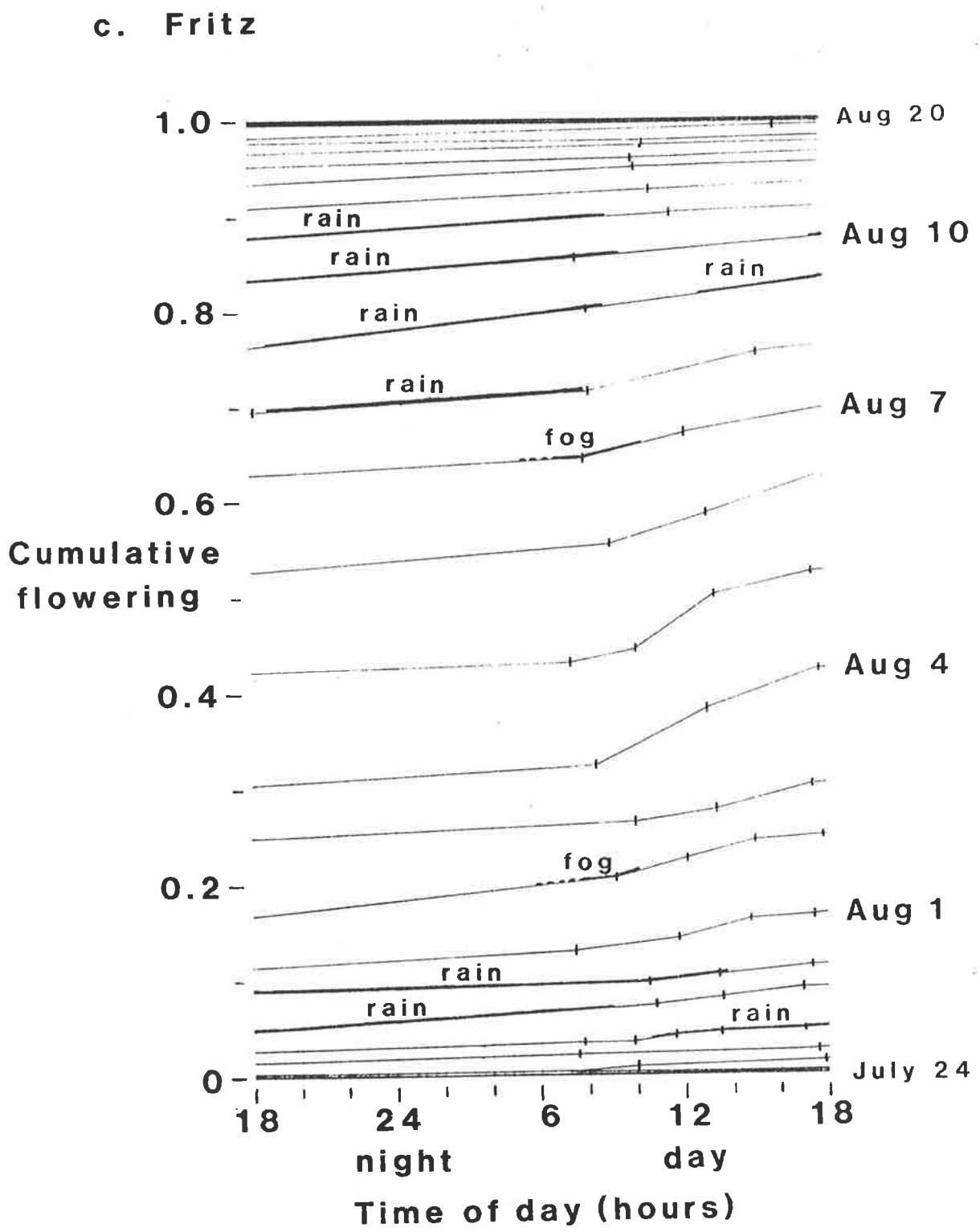
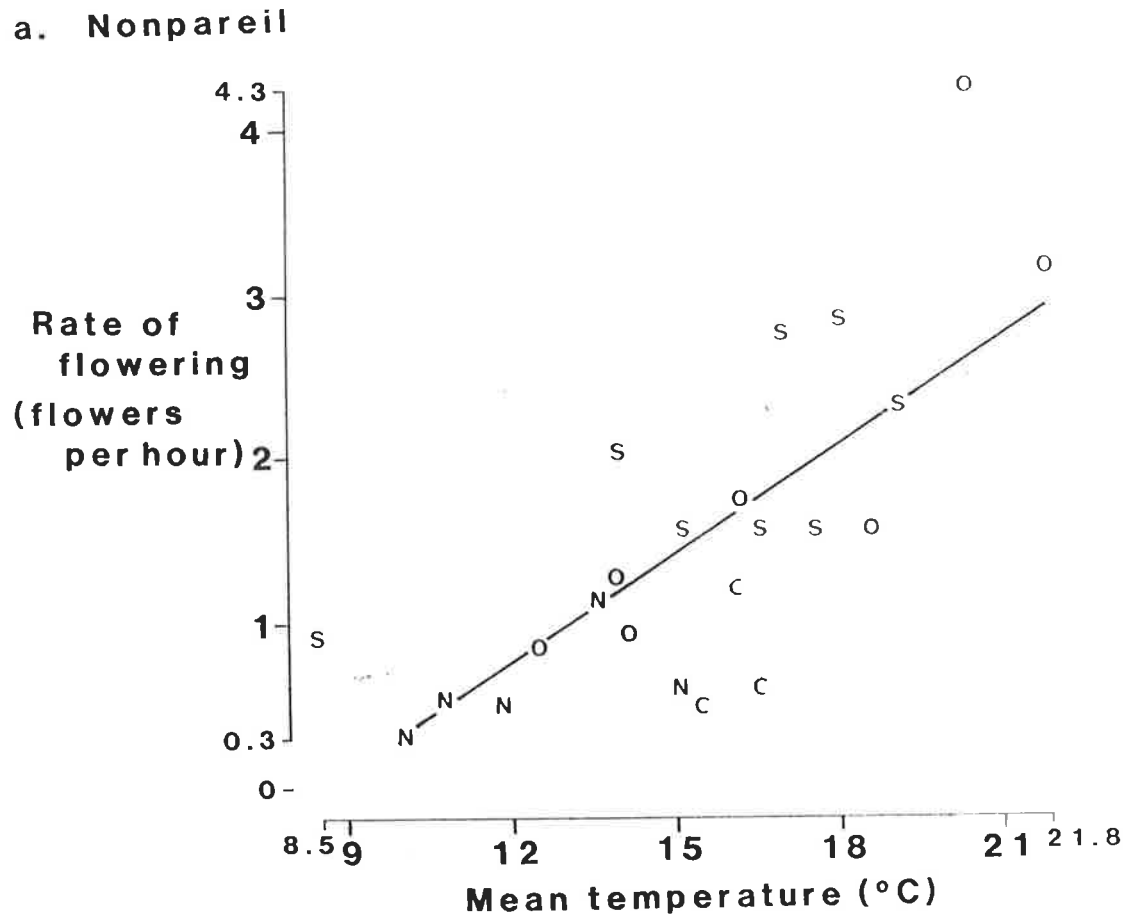


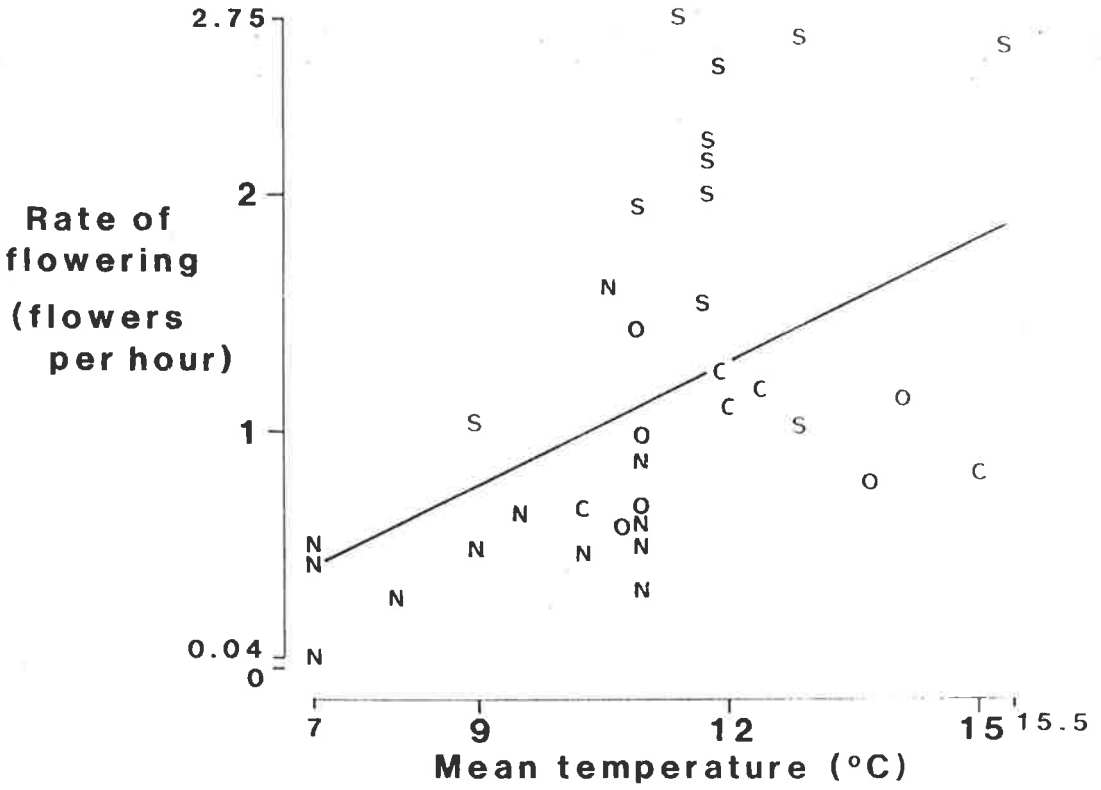
Figure 5.3: Rates of flowering versus mean ambient air temperature for (a) Nonpareil, (b) Ne Plus Ultra, and (c) Fritz. Each point indicates the mean rate of flowering during a time interval. Only rates for intervals between the dates when 0.1 and 0.9 cumulative flowering occurred, have been plotted. The point labels refer to rates that occurred: overnight (N); when the sun shone for at least 75% of the interval (S); when the sun shone for between 10 and 75% of the interval (O); and when the sun shone for less than 10% of the interval (C). The regression equations are (a) Y = 0.23X - 1.99 ***, (b) Y = 0.17X - 0.75 **, (c) Y = 0.05X - 0.24 ***. All regressions were significant (Student's t test, ** P < 0.01, *** P < 0.001).



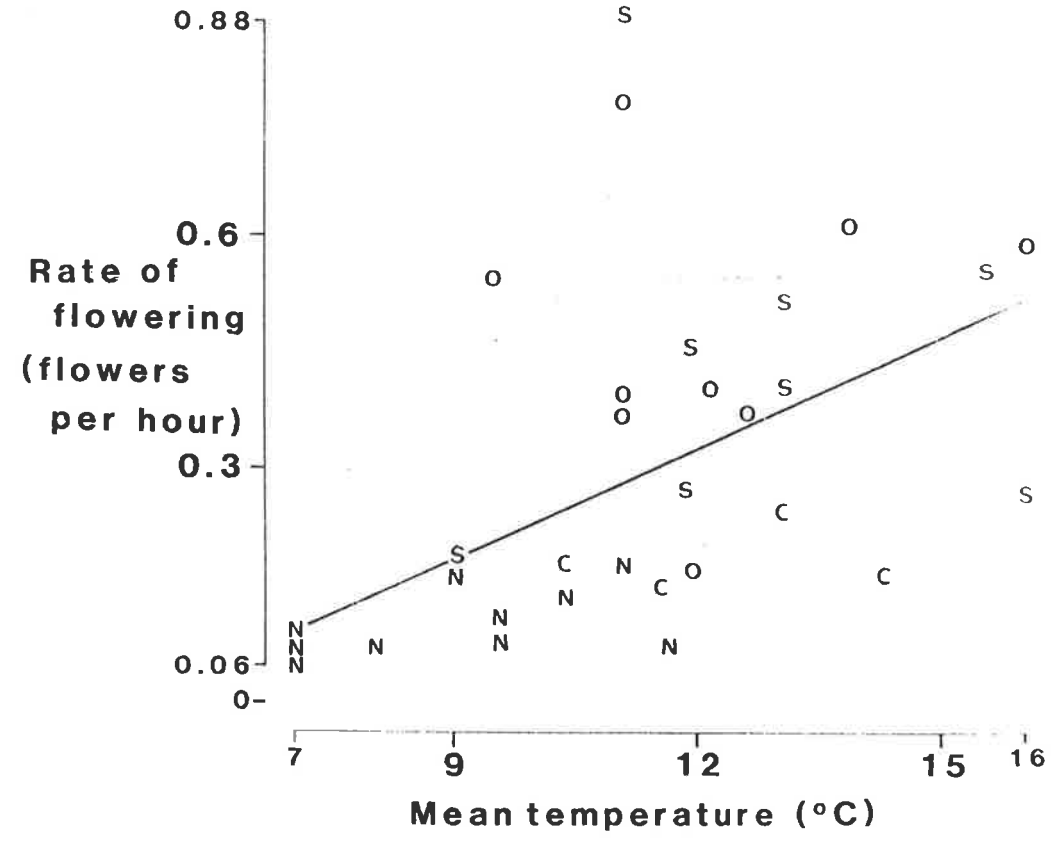
(continued)

Figure 5.3 (continued)

b. Ne Plus Ultra



c. Fritz



The three regressions were significant (Students t test, $P < 0.01$). There was a pattern to the spread of the points about the respective regression lines. Points for intervals that had unobscured sunshine for most or all of the interval (S), were above the regression line unless the interval occurred near dawn or dusk, that is when the heating effect of solar radiation was minimal (Fig. 5.3). In contrast, points for intervals that were cloudy (C) were usually at or below the regression line unless the cloud was so high and thin (O) that the cloud was a relatively minor barrier to solar radiation (Fig. 5.3a). Most of the points for intervals that occurred overnight (N), that is when there was no solar radiation, were below the regression lines (Fig. 5.3a-c). An "N" point in Figure 5.3b was exceptionally high, probably because that interval did not end until 1040 hours on July 31 (see Fig. 5.2b).

Discussion

Almond flowers do not close after they have opened. So almond flowers are open whenever honeybees are active, and the time of day when almond flowers are open is not a factor of pollination. Moreover, flowering in almond is independent of daylight and photoperiodism because almond flowers can open at any time of the day or night (Figs. 5.2, 5.3; also see Vince-Prue *et al*. 1984); but the rate of flowering was greater during daylight hours because it was a function of the ambient air temperature.

However, the rate of flowering may also be a function of solar radiation and may be more closely related to the temperature of the bud tissue. Thus the rate of flowering may be associated more with bud temperature than with ambient air temperature. This can explain why relatively high rates of flowering occurred, at any given temperature, when solar radiation was not blocked by cloud (Fig. 5.3); and it is known that solar radiation can increase the temperature of bud tissue above the ambient air temperature by up to 5°C (e.g. Percival 1955; Corbet and Delfosse 1984). Conversely, at night, heat loss via radiation and evaporative cooling following rain may decrease bud temperature to below the ambient air temperature (Hamer 1975; Rosenberg *et al.* 1983).

Chapter 6: Anther dehiscence and pollen loss from flowers

6.1 Introduction

Honeybees forage during the hours of daylight only, and they can cross-pollinate flowers only when flowers are open and pollen is available for collection by honeybees. Flowers of almond do not close after they have opened (Chapter 5), so the period of the day when flowers are open is not a factor of pollination for almond. Almond pollen is not available for collection by honeybees until the anthers dehisce (Singe 1947) but little is known about anther dehiscence in almond. The optimum temperature range for anther dehiscence in almond is 18 to 27°C, and dehiscence is retarded at temperatures below 15°C (Micke and Kester 1978b); but other information on the subject is limited to comments such as "the anthers start dehiscing their pollination (sic) within a few hours after the flower opens" (Griggs 1958), "the dehiscence of almond pollen (sic) starts within a few hours after flower opening and occurs usually only in the daytime" (Micke and Kester 1978b), and "almond anthers dehisce after the blossoms open in early morning" (Webster *et al.* 1985). Variation in anther dehiscence relative to time of day, weather, cultivars, and honeybee activity, has largely been ignored; so I performed four experiments to elucidate the nature and variability of anther dehiscence and pollen loss in almond flowers.

Anther dehiscence in plants of a given species can be discussed in terms of all anthers: within a single flower, within all flowers of a plant, within all flowers of many plants of a particular cultivar, and within all flowers of all plants within some defined area. Dehiscence of a single anther can be regarded as an instantaneous event, but the period of dehiscence for all anthers within a single flower varies between plant species from at least 26 days down to simultaneous dehiscence of all anthers (e.g. Percival 1950, 1955). Moreover, anther dehiscence within a single flower may only occur at certain times of the day and for a limited number of hours or days after the flower first opens (Dorsey 1919a; Percival 1955; Free 1960a, 1970a). For example, anthers within individual flowers of *Prunus persica* can take from one to five days to all dehisce, with, on average, over half the pollen per flower becoming available on the first day; and anthers dehisced each day between 0900 and 1700 hours, with a peak in the afternoon (Percival 1955). Moreover, the time of dehiscence can vary greatly *between flowers* on a single plant and between flowers on different plants within a cultivar or species.

Generally, low relative humidity and high temperature are thought to favour anther dehiscence, and rain is thought to reduce the rate of dehiscence (see Free 1970a; Langridge et al. 1977; Langridge and Goodman 1979, 1981). Nevertheless, in three species of Prunus, anther dehiscence occurred when the relative humidity was as high as 91 to 100%, and when the air temperature was as low as 5°C (Percival 1955). Furthermore, strong solar radiation may increase the rate of dehiscence when the air temperature is low (Percival 1955), and rain did not prevent anther dehiscence except that free water on anthers sometimes closed dehisced anthers and prevented dehiscence (Dorsey 1919a; Percival 1955; Griggs 1958).

In this thesis, "anthesis" refers to the time when the anthers of a flower first become visible, and a "flower-bud" becomes a "flower" at anthesis. Note that almond flower-buds can open at any time of the day or night (Chapter 5), so a "one-day-old flower" is defined as a flower that underwent anthesis between 24 and 48 hours prior to the time of observation, and a "newly-opened-flower" was less than 24 hours old at the time of observation.

6.2 Experiment 1

Introduction

This preliminary experiment elucidated the general pattern of pollen loss in almond; in particular, the rate of loss of pollen per day, variation between flowers, and the identification of possible relationships between pollen loss, weather variables and honeybee activity. This experiment was combined with several other unrelated experiments and so it may appear unnecessarily large for the purposes of this particular experiment.

Methods

Two branches on each of ten Fritz trees (row 2-7) were selected in 1983 and, on each day during the flowering season, each newly-opened flower was tagged. Pollen loss per flower versus flower age was recorded on 4 days (July 29, August 1, 3, 6) by estimating the amount of pollen remaining in each tagged flower and expressing that amount as a percentage of the pollen that was originally in the flower. All flowers were sampled for pollen loss on July 29, but only the flowers on one branch of each of five trees were

sampled on August 1, 3 and 6. Flowers were sampled during the period 1400-1630 hours on July 29, August 1 and 3, and during the period 1000-1230 hours on August 6.

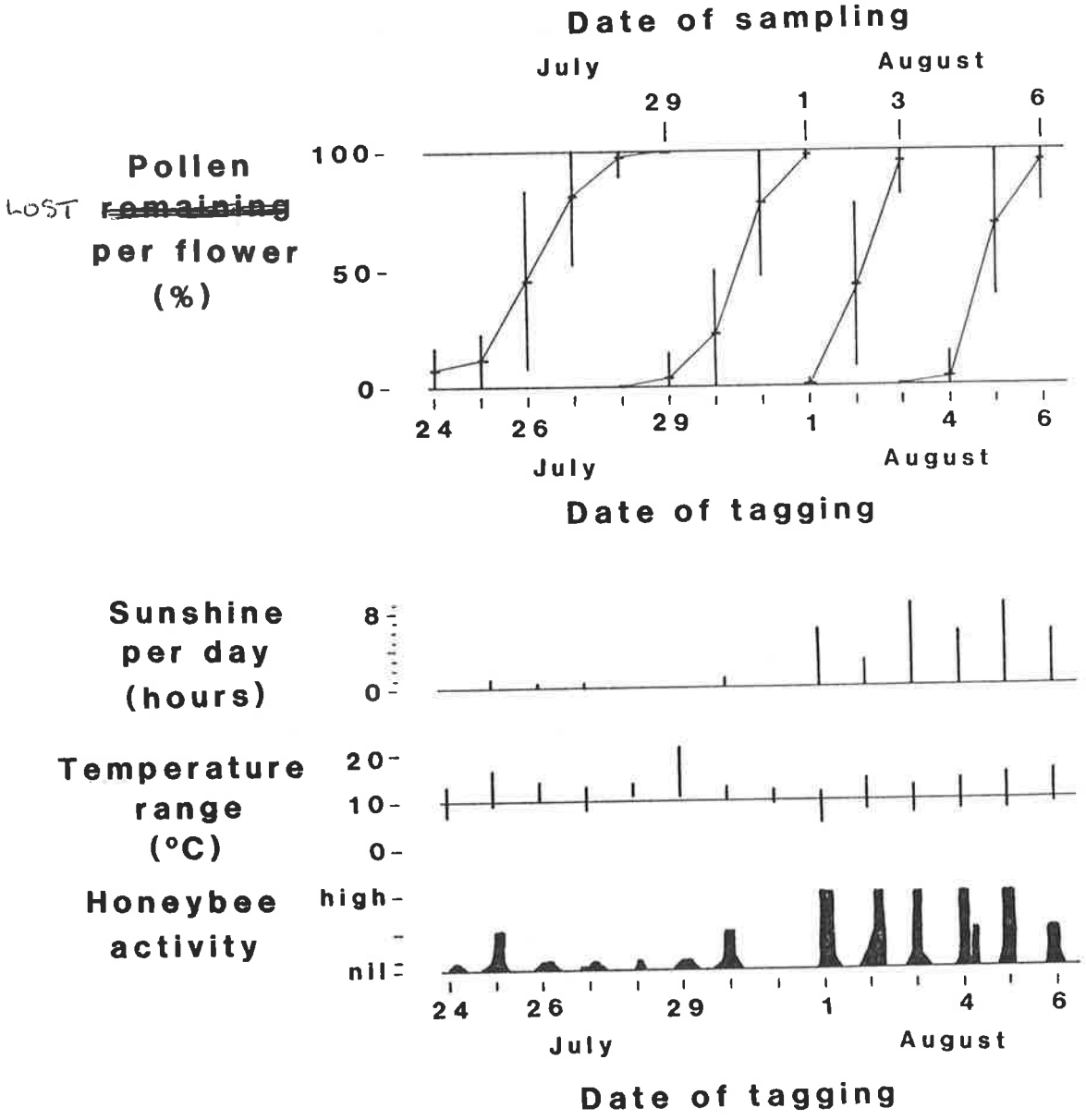
Air temperature in a Stevenson screen was recorded hourly, and the values of other weather variables (e.g. rainfall, wind, sunshine) were noted whenever they changed markedly. Honeybee activity in the trees was assessed qualitatively by using the categories nil, low, medium and high. The trees were within 100 metres of 23 honeybee hives (Appendix 2; Fig. 2.1).

Results and discussion

The data are summarized in Figure 6.1. The number of flowers sampled per day varied from 12 to 105. Rate of pollen loss per flower per day did not vary significantly between trees (F test, $P > 0.05$); but the interval from anthesis to when the average flower had lost all its pollen, varied between the four sampling dates (i.e. July 29, August 1, 3, 6) from 2 to over 5 days. For example, on July 29 pollen remained in five-day-old flowers but on August 3 no pollen remained in three-day-old flowers and only 3 of 66 two-day-old flowers had pollen (Fig. 6.1). This variation between sampling dates appeared to be related to honeybee activity and the occurrence of direct sunshine. For example, the interval of pollen loss, number of hours of direct sunshine per day, and honeybee activity, were all low during the period July 24-29 compared to during the periods August 1-3 and August 3-6 (Fig. 6.1). Ambient air temperature during daylight hours seemed unrelated to pollen loss, but that may have been due to the small temperature range that occurred during this experiment.

Anthers were scored for the presence or absence of pollen, but non-dehisced anthers were not distinguished from dehisced anthers that held pollen. Nevertheless, pronounced variation between days was noticed with respect to the number of dehisced anthers that held pollen. For example, dehisced anthers with pollen were common on July 29, but very few dehisced anthers held pollen on August 1, 3, and 6. Coincidentally, honeybee activity was lower on July 29 than on August 1, 3, and 6 (see Fig. 6.1); so perhaps the lower rate of pollen loss from dehisced anthers on July 29 was due to lower honeybee activity. On the other dates, when honeybee activity was high, the honeybees collected the pollen very soon after the anthers dehisced.

Figure 6.1: Mean amount of pollen remaining per flower, expressed as a percentage of the pollen that was present at anthesis, versus the date of flower tagging. Flowers were sampled for pollen loss on July 29, August 1, 3 and 6. Each mean was calculated from data for between 12 and 105 flowers. The vertical bars denote standard deviations. Also shown, in the lower part of the figure, are the number of hours of sunshine per day, the range of air temperature during the daylight hours of each day, and honeybee activity versus time of day. The dashes on the bottom scale indicate mid-day on each respective day.



On the other hand, pollen loss must also depend on the rate of anther dehiscence because on July 29, some four-day-old flowers contained anthers which had not dehisced, whereas on August 3, all the anthers of all the two-day-old flowers had dehisced (Fig. 6.1).

The highest temperature during this study (Fig. 6.1) was below the lowest temperature reported by Micke and Kester (1978b) to be optimal for anther dehiscence, but the rate of anther dehiscence was high during sunny days; so perhaps strong solar radiation counteracted the effect of low temperature. Days of high bee activity also coincided with periods of strong solar radiation (Fig. 6.1), so perhaps solar radiation is an important factor of pollen loss because solar radiation may affect both anther dehiscence and honeybee activity.

The results suggest that the rate of pollen loss from almond flowers could depend on both the rate of anther dehiscence and the rate of collection of pollen by honeybees. In turn, those rates could depend on air temperature and the incidence of strong solar radiation. These possible relationships were examined further by the next experiment.

6.3 Experiment 2

Introduction

In this experiment, run in 1984, rates of anther dehiscence and pollen loss, honeybee activity, ambient air temperature, solar radiation, and relative humidity, were all examined on an hourly basis and for individual flowers.

Methods

One Nonpareil tree was selected. Four flowers that were within a few minutes of anthesis were tagged, and are referred to collectively as a cohort. Then for every tagged flower, dehisced anthers and anthers without pollen were counted in units of whole anthers. This process was repeated for up to six cohorts on each of six consecutive days, and dehisced anthers and anthers without pollen were counted on 3 more consecutive days. Each process took up to 40 minutes to complete, but all flowers with dehisced anthers were examined within 10 minutes of the recorded time because the oldest flowers were always examined first. All the flowers were on the northern side of the tree, and were in similar positions with respect to shading and accessibility for honeybees. Most flowers faced upwards or sideways and were between 1.5 and 2 metres above the ground.

Honeybee activity from two hives was measured qualitatively by using (a) the categories of nil, low, medium, and high, as in 1983, and by (b) infra-red gates on the hives, which recorded the number of departing honeybees. Problems with the infra-red gates did not allow a reliable continuous record, so the two sorts of measurements were combined, where possible, to produce a measure of honeybee activity on a scale of 0 to 10. On that scale, a one indicates that some bees were outside the hive but no more than one or two bees were flying away from the hive; a 2 indicates that bees were visiting nearby flowers that were not shaded; a 4 indicates that distant flowers were being visited but unshaded flowers were being preferred and the overall density of foragers on trees was low. Six, the highest level attained during this and the following experiments, indicates that shaded and non-shaded flowers were receiving equal attention from bees but the density of foragers on the trees was only moderate compared to what it was on warm, sunny days.

Hourly recordings of air temperature in a Stevenson screen were used to calculate the mean ambient air temperature for each interval between two consecutive times of sampling. Unfortunately, the recordings of relative humidity were unreliable, and equipment to monitor the temperature of anther tissue was not available.

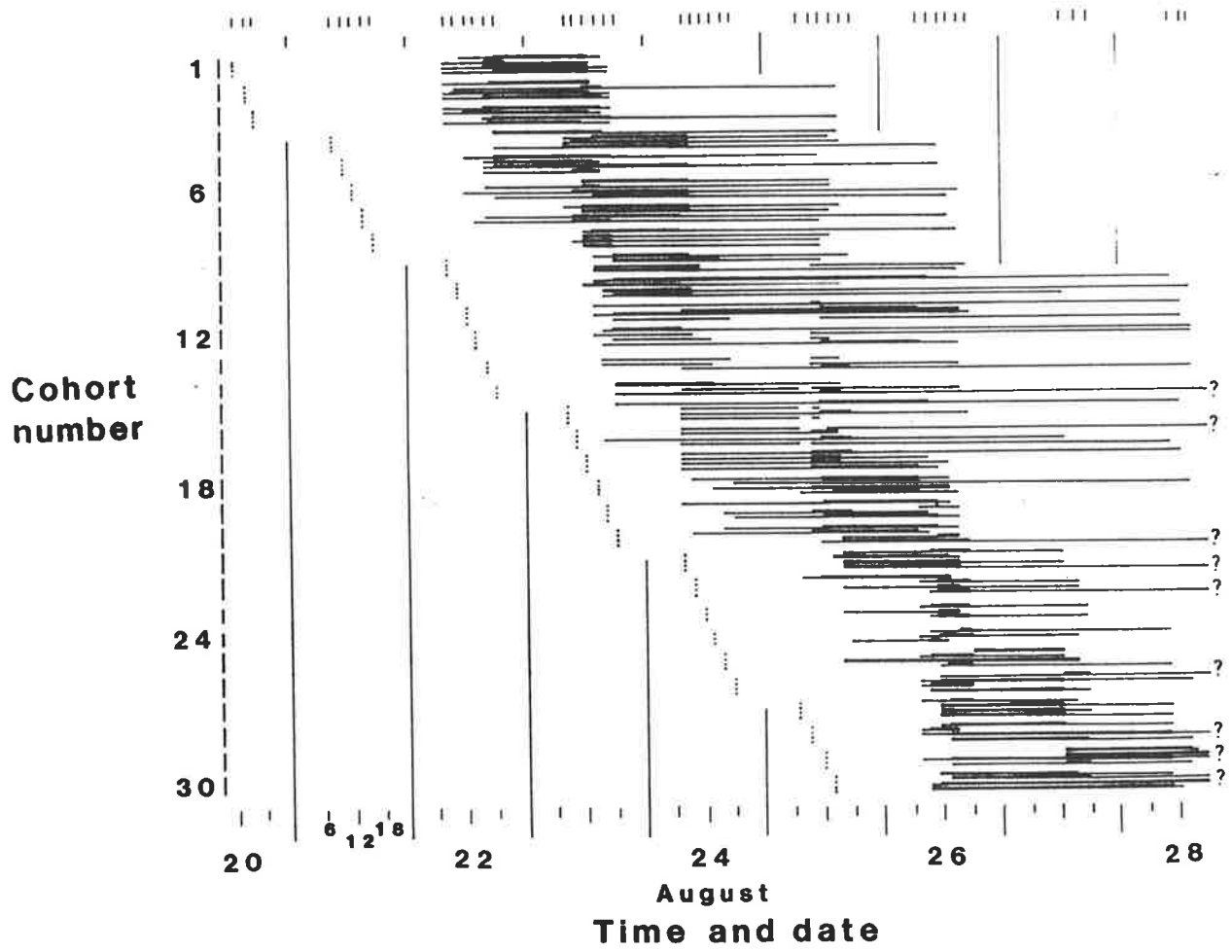
Results and discussion

All flowers had a developed gynaeceum and all except three flowers had 28 anthers each, the exceptions having 20 anthers each. The anther counts for the three exceptions were increased proportionally to total 28 anthers so that they were comparable to the anther counts for the other flowers.

The periods of anther dehiscence and pollen loss for each flower are shown in Figure 6.2. The flowers were grouped into 30 cohorts, each of four flowers except that cohort numbers 13, 14, 23 and 24 consisted of only three flowers each because some excluded flowers were damaged. Data for the cohorts of three flowers were altered, whenever necessary, so that those data were comparable to cohorts of four flowers.

Within flowers, anther dehiscence did not occur until between 6 and 48 hours after anthesis, and the last anther dehisced after another 2 to 74 hours (Fig. 6.2). From August 22, pollen was always available on at least some of the flowers in this study, and pollen remained on anthers within flowers until flowers were between 3 and over 6 days old (Fig. 6.2).

Figure 6.2: The periods of anther dehiscence and pollen loss for each flower. Flowers were in cohorts of four flowers, except that cohort numbers 13, 14, 23 and 24 lost one flower each during the experiment. Flowers within cohorts were of the same age. For each flower: the first dash indicates the time of anthesis, the line starts at the time when the first anther was recorded as being dehisced, the line thickens at the time the first pollen was noted to be missing, the line thins at the time the last anther was noted to have dehisced, and the line ends at the time when the last of the pollen was noted to have disappeared. Some of the points coincided. The data for flowers that did not begin to lose pollen until after all their anthers had dehisced are represented by two lines separated by a gap. The gap represents the time when all anthers had dehisced but no pollen had been lost (i.e. flowers in cohorts 9, 11-16). Question marks indicate the flowers that had not lost all their pollen when the experiment finished at 1450 hours on August 28. The vertical lines are 24 hours apart. Dashes at the top of the figure indicate the times of sampling.



Within flowers, the delay between when the first anther dehisced and when pollen was first lost, varied from zero to 44 hours; and some flowers did not begin to lose pollen until after all their anthers had dehisced, which is indicated in Figure 6.2 by the presence of two separate lines and the absence of a thickened line, for each flower (e.g. flowers in cohorts 9, 11-16). The commencement of pollen loss for many flowers tended to occur at particular times. For example, many flowers first lost pollen between the first and second times of sampling on August 25, even though pollen had been available for at least 24 hours (see Fig. 6.2).

Figure 6.2 suggests that the periods of anther dehiscence and pollen loss did not differ between cohorts, but the analysis of the rates of anther dehiscence and pollen loss was complicated by the variability between flowers within cohorts, which was largely due to the times at which the first and last anthers in a flower dehisced or lost their pollen. For example, within some flowers, there was up to 24 hours between the dehiscence of the first and second anthers, and the period of anther dehiscence was sometimes prolonged by the lengthy delay in waiting for the last one or two anthers to dehisce. If the first ten* and last nine anthers per cohort are ignored, then the variability of anther dehiscence and pollen loss between flowers within cohorts is much reduced and the average behaviour of cohorts can be more usefully studied.

Such mean rates of anther dehiscence and pollen loss, per cohort, are shown in Figure 6.3a-b. Standard deviations are also shown. Note that useful data were not recorded until August 22 because the data are for cohorts that had between 11 and 103 dehisced anthers at the beginning and end of a sampling interval. A similar adjustment was made with the pollen loss data so that the data in Figure 6.3b are for cohorts which had between 11 and 103 anthers with pollen (i.e. nondehisced anthers plus dehisced anthers with pollen) at the beginning and end of a sampling interval.

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* Footnote: This would have read "...first nine and last nine..." if there was not an error in a computer program. Data for only one cohort-period was omitted through this error so the data were not reanalysed.

Figure 6.3: Mean rates of anther dehiscence per cohort versus time (a), mean rates of pollen loss per cohort versus time (b), and the level of honeybee activity on a scale of 0 to 10 (c). Usually bees were present at the site of the experiments only when the bee activity was above 3.

For (a) and (b), each horizontal line indicates the rate that occurred during the interval indicated by the length and position of the line, and the vertical line represents the standard deviation. The number of cohorts used to calculate each mean is given at the top of each figure, and the letters in the top line of Figure (a) indicate the incidence of sunshine during the interval: overnight (N), at least 75% sunny (S), between 25 and 90% cloudy (O), and more than 90% cloudy (C). A box around a letter indicates that rain fell during the interval.

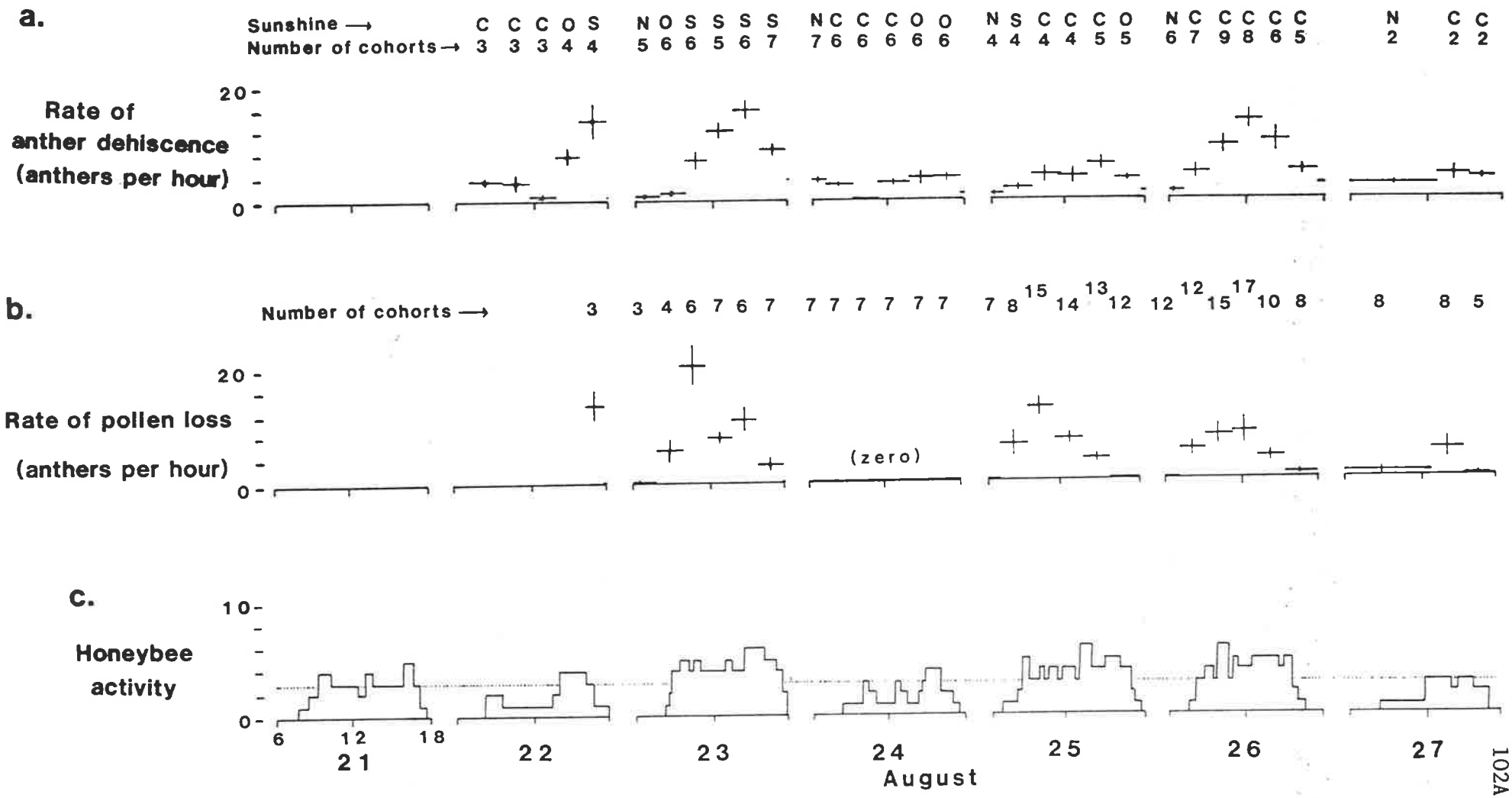
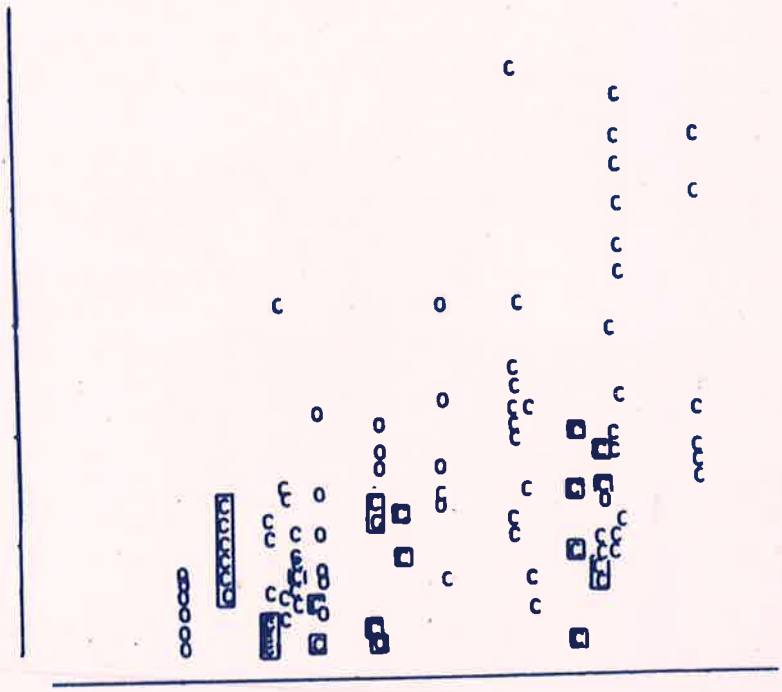
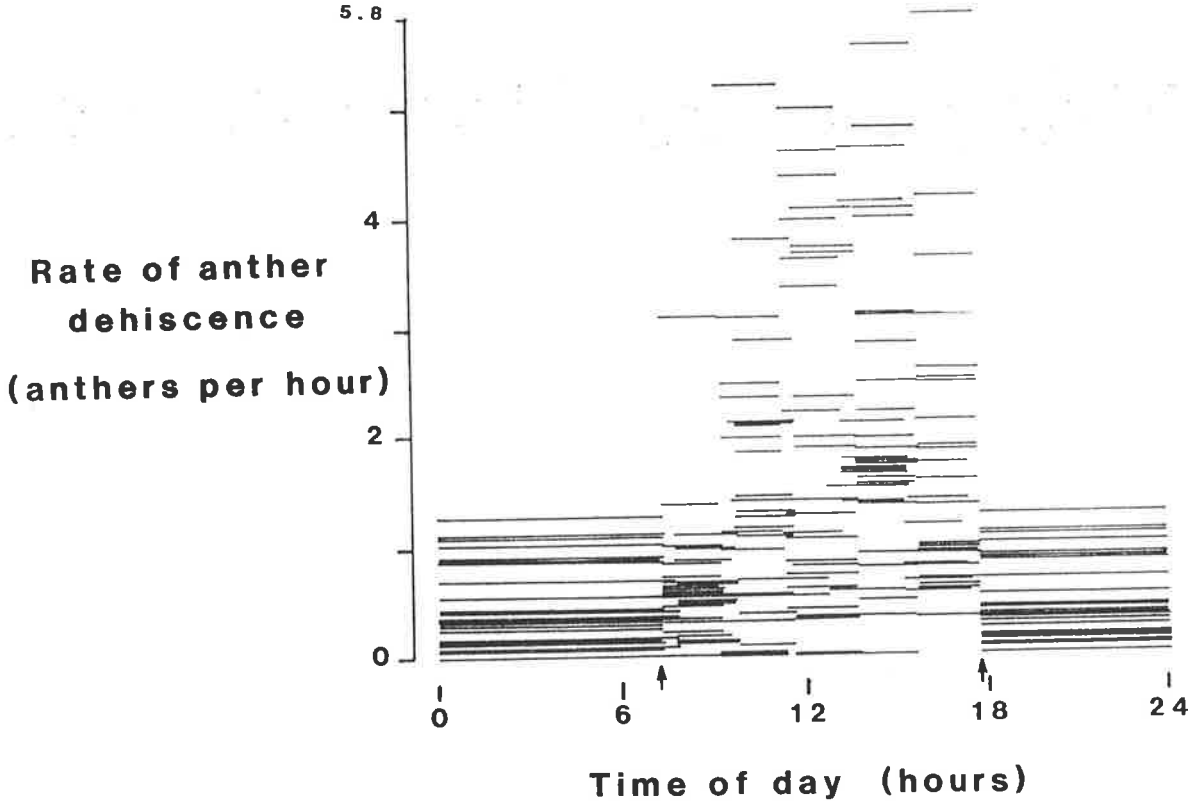
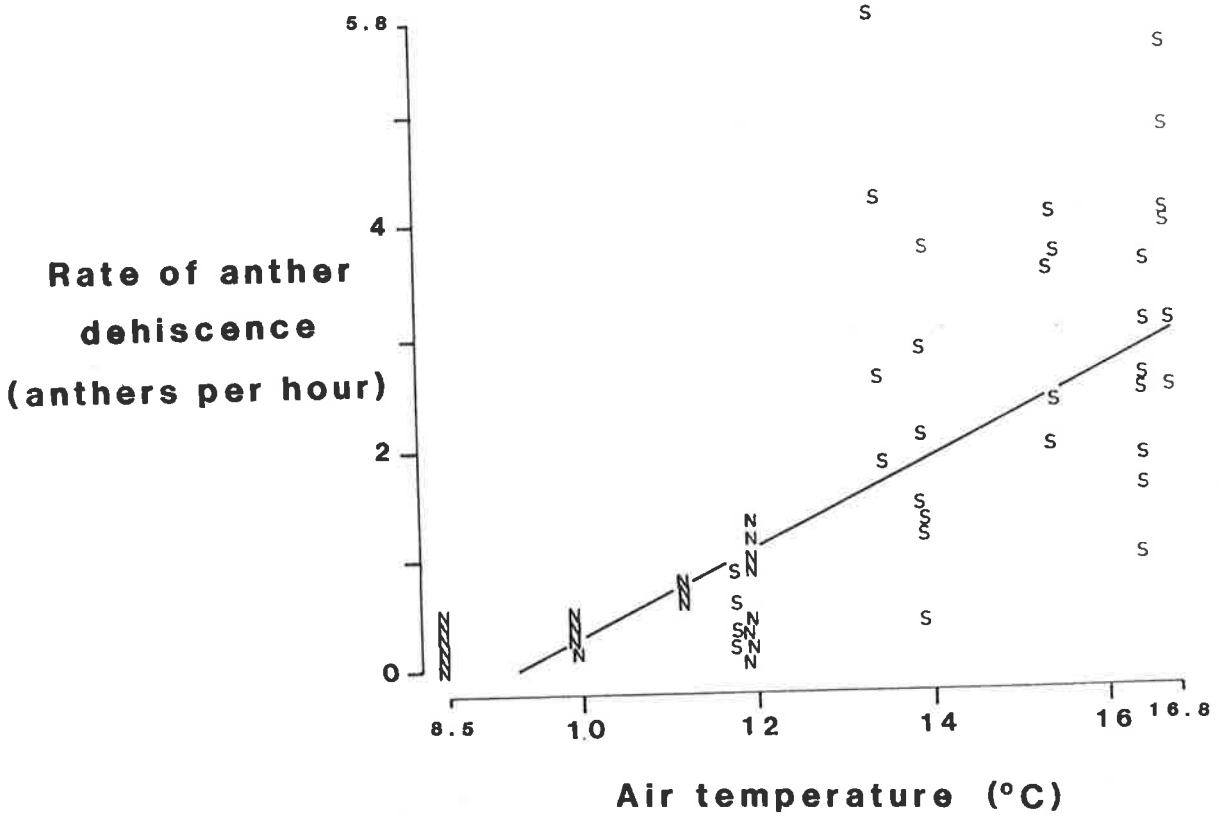

a.
Sunshine →
C C C O S N O S S S S N C C C O O N S C C C O N C C C C C N C C
Number of cohorts → 3 3 3 4 4 5 6 6 5 6 7 7 6 6 6 6 6 4 4 4 4 5 5 6 7 9 8 6 5 2 2 2
Rate of anther dehiscence (anthers per hour)
20
0
b.
Number of cohorts → 3 3 4 6 7 6 7 7 7 7 7 7 7 8 15 14 13 12 12 12 15 17 10 8 8 8 5
Rate of pollen loss (anthers per hour)
20
0
(zero)
c.
Honeybee activity
10
0
6 12 18
21
22
23
24
25
26
27
August
102A

Figure 6.4: Rate of anther dehiscence versus time of day. Each line indicates the mean rate of anther dehiscence per flower within a cohort and during the interval indicated by the position and length of the line. Overlapping rates have been staggered. Arrows indicate the times of sunrise and sunset.

Figure 6.5: The mean rate of anther dehiscence per flower within a cohort, versus the mean ambient air temperature during each sampling interval. The point labels refer to rates that occurred during intervals that were: overnight (N), at least 75% sunny (S), between 25 and 90% cloudy (O), and more than 90% cloudy (C). Boxes surround points if rain fell during much of the interval. Overlapping points have been staggered.




5.8
4
2
0
Rate of anther dehiscence (anthers per hour)
0
6
12
18
24
Time of day (hours)


5.8
4
2
0
Rate of anther dehiscence (anthers per hour)
8.5
10
12
14
16
16.8
Air temperature (°C)

Further analysis of anther dehiscence data

Further analysis of rates of anther dehiscence and pollen loss were similarly confined to the truncated data as described above. The mean rate of anther dehiscence varied significantly between intervals; for example, anther dehiscence was much lower during August 24, than during August 23 and 26 (see Fig. 6.3a). To elucidate the variability of anther dehiscence, the mean rate of anther dehiscence was initially plotted against time of day (Fig. 6.4). The graph shows that some anther dehiscence occurred overnight but generally the rate of dehiscence was higher during daylight hours. This difference between night and day rates, together with the variation in rate of anther dehiscence throughout the daylight hours (Fig. 6.3a), further suggested that anther dehiscence can be usefully related to air temperature. This hypothesis is tested graphically in Figure 6.5. The linear regression was significant ($t = 10.7$, 162 d.f., $P < 0.001$, $Y = 0.41X - 3.82$) but there was considerable variation about the regression line (Fig. 6.5). This variation may perhaps be attributed to the intensity of solar radiation, as follows. The data points in Figure 6.5 are coded with respect to the proportion of time that the sun was obscured by cloud during each interval: "S" for less than 25% cloudy, "O" for between 25 and 90% cloudy, "C" for over 90% cloudy, and "N" for overnight intervals. With each category of data points, approximately equal numbers lie on each side of the regression line in Figure 6.5, but the higher rates of anther dehiscence occurred when the heating effect of solar radiation was high, that is, in the afternoon following and during periods of sunshine (e.g. Fig. 6.3a - August 22 and 23) or thin cloud (August 26). These high rates suggest that the rate of anther dehiscence was increased through solar radiation heating the anther tissue; this relationship has been noticed in flowers of other plant species (e.g. Percival 1955; Langridge and Goodman 1981).

The differences in rate of anther dehiscence between flowers within intervals are indicated by the standard deviations in Fig. 6.3a. Those differences may be attributable to differences in aspect and protection from wind and radiation because the rate of anther dehiscence within intervals did not differ at all beteen flowers that appeared to be in identical circumstances with respect to aspect and shading; and flower age appeared to be unimportant. Perhaps shade from limbs and other flowers affected the rate of anther dehiscence by affecting the temperature of the flower tissue.

Some dehisced anthers closed during intervals of rain on August 24, 25, 26 and 28. In Figure 6.5, points that represent the rates of anther dehiscence for the intervals during which rain fell, are enclosed by rectangles. The anthers that closed were in flowers that were positioned so that water droplets were not shaken off the anthers when wind shook the tree. Free water appeared able to close an anther regardless of whether or not the anther had lost its pollen. Other anthers dehisced during the same wet intervals (Fig. 6.5), so high relative humidities could not be blamed for the phenomenon. Indeed, the effect of high humidity on anther dehiscence may be negligible because many anthers dehisced during wet intervals (Fig. 6.5). Studies of other species of Prunus have shown that relative humidity is a minor factor of anther dehiscence compared to the effect of varying the temperature of anther tissue (e.g. Langridge and Goodman 1973, 1981; Langridge et al. 1977).

Rates of pollen loss

Pollen loss from a given anther usually involved the loss of at least 95% of the anther's pollen, but this was not always apparent because pollen masses left on anthers shrank with age, apparently through dehydration.

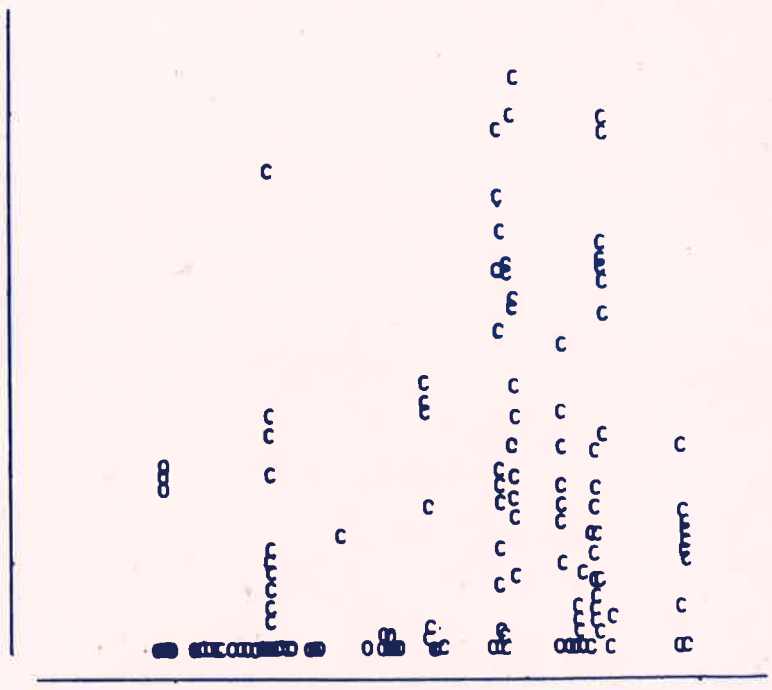
The mean rate of pollen loss per cohort, versus time, was shown in Figure 6.3b. Significant rates of pollen loss did not occur until August 22 because of the way the experiment was designed (see Fig. 6.2). Rate of pollen loss varied significantly between intervals, and no pollen was lost on August 24. The timing of pollen loss from individual flowers varied greatly, in that during a given interval, some flowers did not lose any pollen while other, nearby flowers lost all their available pollen, although both lots of flowers may have had equal amounts of pollen available for a similar time.

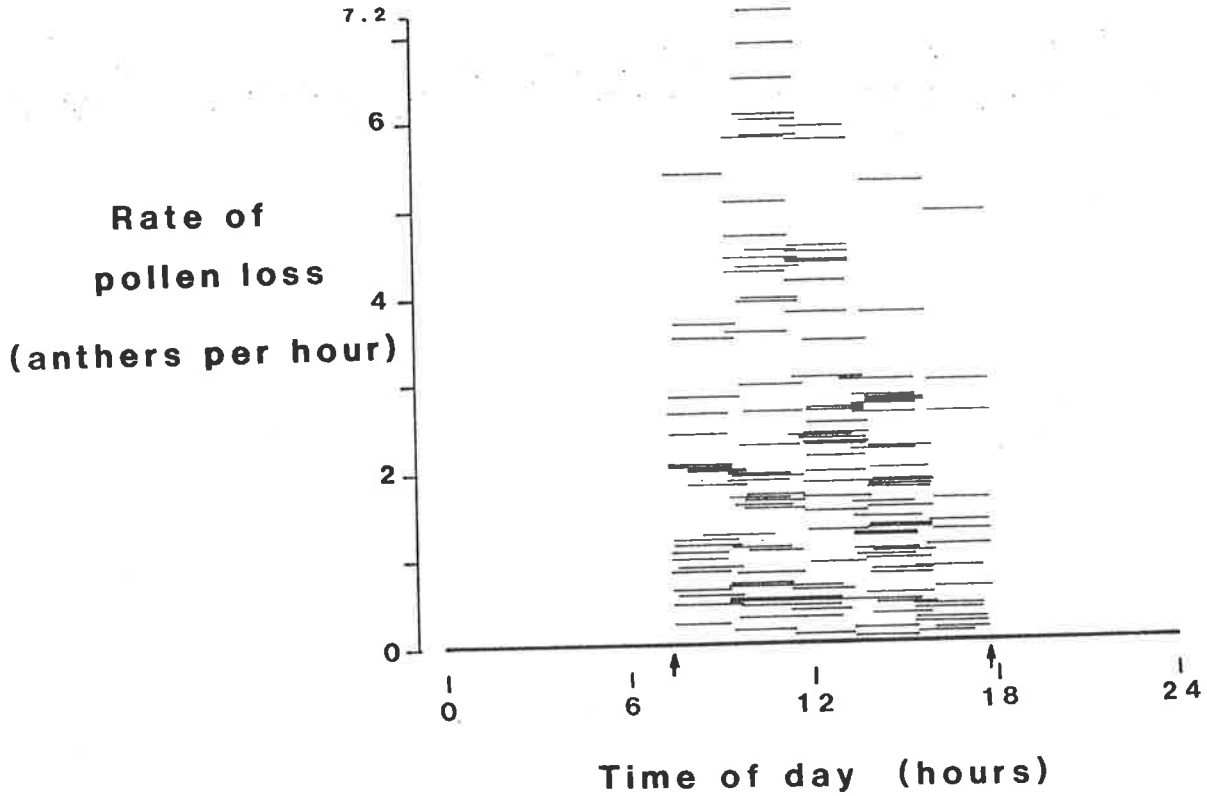
The relationship between rate of pollen loss and time of day is shown in Figure 6.6. Anther dehiscence occurred at all times during this study (Fig. 6.4), but pollen disappeared from anthers during daylight hours only (Fig. 6.6).

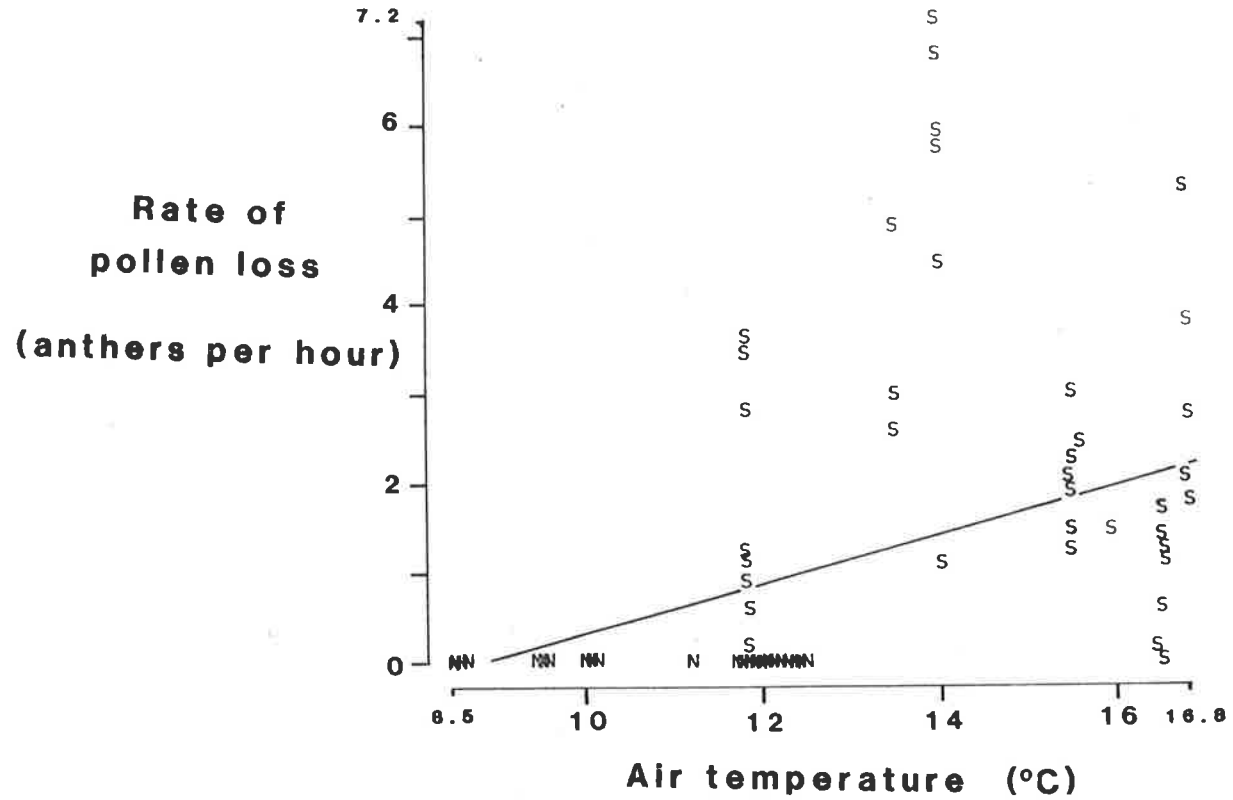
The relationship between air temperature and rate of loss of pollen is shown in Figure 6.7. The simplest relationship envisaged was a linear one which was significant ($t = 5.6$, 246 d.f., $P < 0.001$, $Y = 0.28X - 2.53$). The data points were labelled with the same system of labels used for Figure 6.5.

Figure 6.6: Rate of pollen loss versus time of day. Each line indicates the mean rate of pollen loss per flower within a cohort and during the interval indicated by the position and length of the line. Overlapping rates that were not zero have been staggered. All overnight rates were zero. Arrows indicate the times of sunrise and sunset.

Figure 6.7: The mean rate of pollen loss per flower within a cohort, versus the mean ambient air temperature during each sampling interval.The point labels refer to rates that occurred during intervals that were: overnight (N), at least 75% sunny (S), between 25 and 90% cloudy (O), and more than 90% cloudy (C). Overlapping points have been staggered.




Rate of
pollen loss
(anthers per hour)
7.2
6
4
2
0
0
6
12
18
24
Time of day (hours)


Rate of
pollen loss
(anthers per hour)
7.2
6
4
2
0
8.5
10
12
14
16
16.8
Air temperature (°C)

The overnight rates (N) had a considerable influence on the significance of the regression, but their removal still left a significant linear regression (Student's t test, $P < 0.01$). Nevertheless, there was again a lot of variation about the regression line (Fig. 6.7) which can probably be attributed to combinations of solar radiation and time of day. For example, the higher rates of pollen loss occurred during the middle of the day when, or just after, there were long periods of high solar radiation and little or no cloud. Conversely, the rates were low during the daylight hours near sunset and sunrise or when the interval was largely cloudy (Figs. 6.3, 6.7). Pollen loss occurred during some rainy intervals (Fig. 6.3) and, coincidentally, honeybees flew in light rain during those intervals.

Honeybee activity and the loss of pollen from dehisced anthers.

Pollen loss occurred during daylight hours only (Fig. 6.6) and only when honeybees were at least moderately active (compare Figs. 6.3b and 6.3c). Therefore the primary, and perhaps only, cause of pollen loss during this study was collection by honeybees. Moreover, the relationship of pollen loss with air temperature may also have been measures of the effect of air temperature and solar radiation on the activity of honeybees.

In some flowers on some days, the last pollen was lost within a few hours after the time the last anther dehisced (e.g. Fig. 6.2 - on August 23 for flowers in cohorts 1-3, 5), but on other days, the last pollen per flower was not lost until some days after the last anther dehisced (e.g. Fig. 6.2 - cohorts 6-16). Pollen loss in the former examples (cohorts 1-3,5) appeared to depend primarily on the rate of anther dehiscence, but pollen loss in the latter examples (cohorts 6-16) apparently depended more on the cause of pollen loss; so there appear to be two principal factors of pollen loss. Nevertheless, other causes of pollen loss may exist, so the next two experiments were designed to test for other causes of pollen loss.

6.4 Experiment 3

Introduction

Pollen can be removed from flowers by wind, rain and gravity, as well as by honeybees, but the relative importance of these causes of pollen loss in almond have not been determined, and reports on tree crops generally are contradictory. For example, strong wind has been implicated in the spread

of Prunus pollen although Prunus pollen is considered too sticky to be easily blown off anthers (e.g. Wood 1937; Vansell and Griggs 1952; Free 1960a; Langridge and Goodman 1981). Certainly, strong winds can cause abrasion which injures flowers and rubs pollen off anthers (Micke and Kester 1978b). Rain has also been accused of removing large amounts of pollen from anthers (Hendrick 1915; Micke and Kester 1978b), but such observations can be attributed to the fact that empty anthers can close during periods of rain and open afterwards (Dorsey 1919a; Griggs 1958). However, the initial rain drops of a shower may be capable of washing small amounts of pollen from anthers (e.g. Beach and Fairchild 1893; Dorsey 1919a; Griggs 1958).

The previous experiment (Section 6.3) suggested that honeybees were the primary, and perhaps only, cause of pollen loss from flowers. This hypothesis was tested by the following experiment.

Methods

Two branches of a Chellaston tree were selected and one was caged to exclude honeybees. Between 6 and 15 newly-opened flowers were tagged on each branch at about 1400 hours on each of July 26, 28, 30, and 31. Flowers were chosen carefully so that they would not be abraded by the cage. Dehisced anthers and anthers without pollen for each flower were counted on July 31 between 1400 and 1500 hours.

The experiment was repeated, but in a different fashion. One branch of a Nonpareil tree was caged, and four newly-opened flowers were tagged three times per day and concurrently with the tagging of flowers for experiment 2. Appropriate flowers of experiment 2 were used as the noncaged flowers.

Results

The results for Chellaston and Nonpareil are similar to each other and are shown in Figures 6.8 and 6.9 respectively. The rate of anther dehiscence did not differ significantly between non-caged (N) and caged (C) flowers (Figs. 6.8a, 6.9a); but the loss of pollen from non-caged (N) flowers was substantial while no pollen was lost from caged (C) flowers (F test, $P < 0.001$) (Figs. 6.8b, 6.9b). The pollen masses on the dehisced anthers of caged flowers shrank with age, but microscopic examination showed this to be due to dehydration of the pollen grains, and not due to loss of pollen grains.

Figure 6.8: Number of anthers per Chellaston flower on July 31, that had not dehisced - in (a), or not lost pollen - in (b). In both graphs, the flowers from the noncaged branch are denoted as N, and those on the caged branch are denoted as C. Standard errors that are larger than the point symbols are shown (P = 0.05).

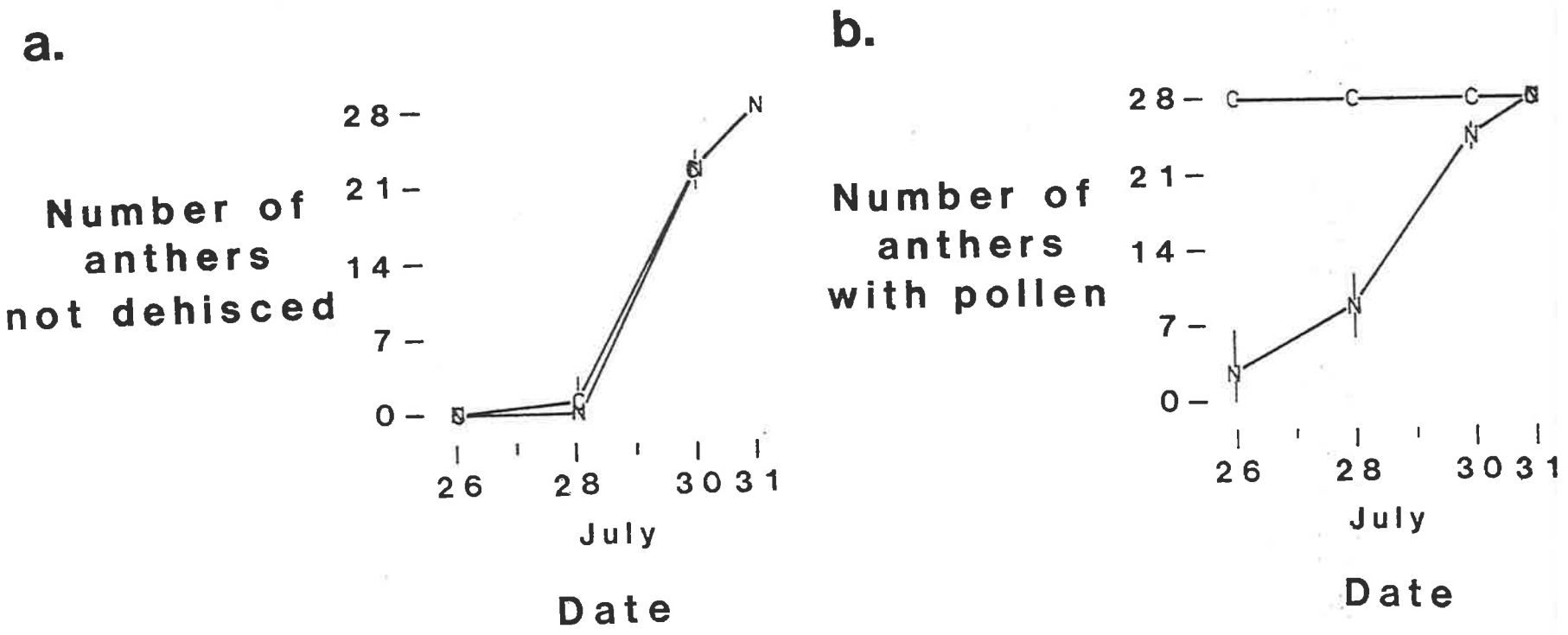
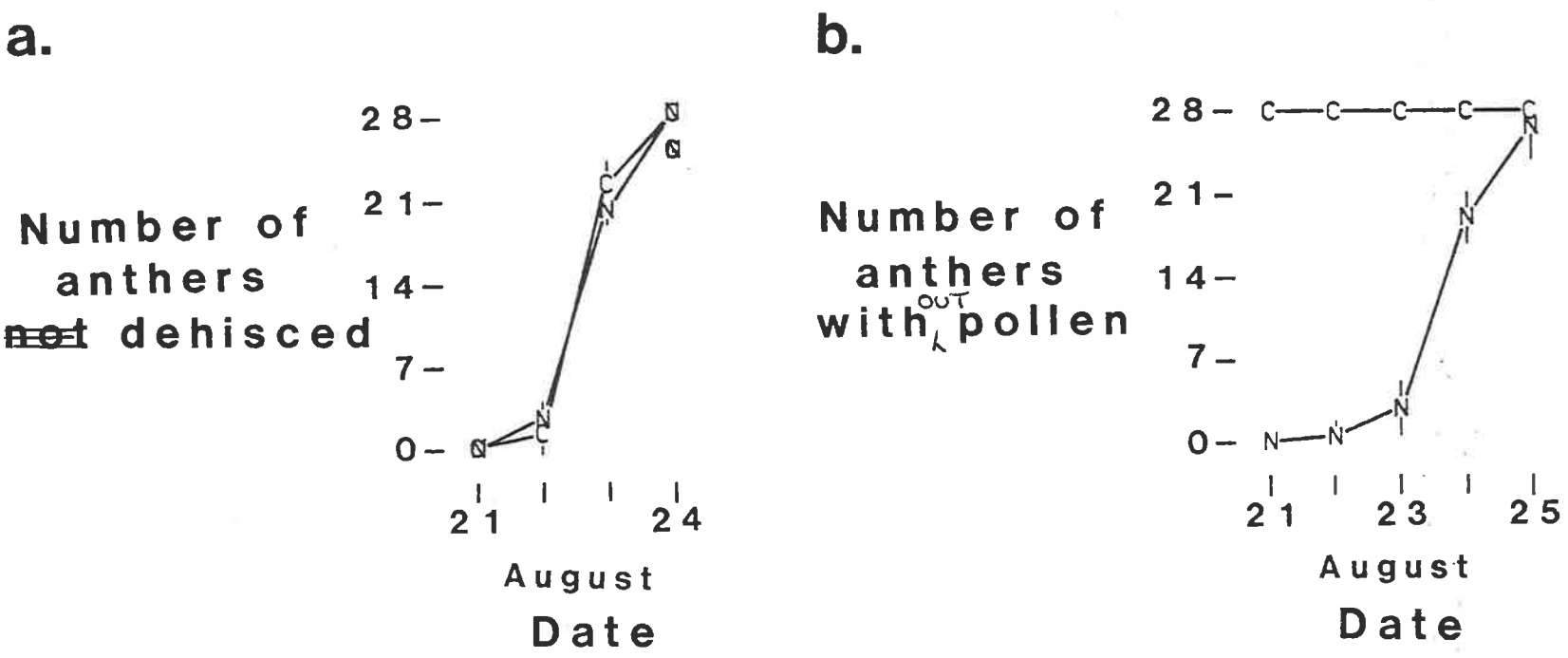


Figure 6.9: Number of anthers per Nonpareil flower, that had not dehisced on August 24 - in (a), or not lost pollen on August 25 - in (b). In both graphs, the flowers from the noncaged branch are denoted as N, and those on the caged branch are denoted as C. Standard errors that are larger than the point symbols are shown (P = 0.05).



Heavy rain and winds of over 40 k.p.h. occurred, but pollen was not lost overnight from uncaged stamens (Fig. 6.6) or from caged stamens (Figs. 6.8b, 6.9b) during wet and windy intervals, although many flowers were stripped of petals. So rain and wind are probably not significant causes of pollen loss in almond.

Discussion

The absence of a difference in anther dehiscence between caged and non-caged flowers reflects the observation that the cages did not significantly affect the enclosed microclimate with respect to temperature and perhaps shading from solar radiation. The effects of cages on the enclosed microclimate was tested earlier in an experiment which is reported in Section 3.1.

The cages prevented pollen loss from anthers except when flowers were abraded by the cage or parts of the tree; so pollen loss was probably caused only by insects. Insects other than honeybees can be causes of significant pollen loss, but other insects were rarely seen on almond flowers in the orchard in the flowering seasons of 1983 and 1984; so little almond pollen was likely to be lost to insects other than honeybees. Pollen was not lost overnight (Fig. 6.6) so there was no evidence for significant numbers of unknown nocturnal pollen collectors.

After examination on July 31, the caged Chellaston branch was left uncaged and within a few minutes the flowers were found by six pollen-collecting honeybees. Unless disturbed by wind or the observer, each honeybee collected all the available pollen on a flower, which usually meant pollen from 28 stamens. This observation was repeated for the caged Nonpareil branch. Perhaps each pollen collecting honeybee normally collects all available pollen from a flower unless it is disturbed. Experiment 4 tested this hypothesis.

6.5 Experiment 4

Introduction

In experiment 3, honeybees were found to be the only significant cause of pollen loss from anthers. If true, then periods of pollen loss should coincide with visits by honeybees. Further, pollen-collecting honeybees may collect all available pollen when they visit a flower. Also, the

probability of a flower being effectively pollinated so that a nut eventuates, depends on the number of times the stigma is touched by a honeybee before the Effective Pollination Period (EPP) expires. EPPs are explained in Section 8.1.2. No information is available on the incidence of stigma touching in almond.

This experiment aimed to further elucidate the relationships between flower age, anther dehiscence, pollen loss from flowers, and honeybee visitation and behaviour.

Methods

Honeybee activity on the flowers of a north-facing branch of a Nonpareil tree was recorded on video tape during eight consecutive days and in conjunction with experiment 2. The branch was about 0.5 metres above the ground and could receive direct solar radiation during most of each day. Dehisced anthers and anthers without pollen, for each flower, were counted in units of whole anthers once every daylight hour. Traces of pollen were usually ignored because the quantity of such pollen was difficult to measure, and usually all or no pollen was taken from an anther. Notwithstanding the above comments, the loss of the last trace of pollen from each flower was recorded. Nectar production or presence was not measured because such measurements could have damaged the flowers or affected the behaviour of the honeybees.

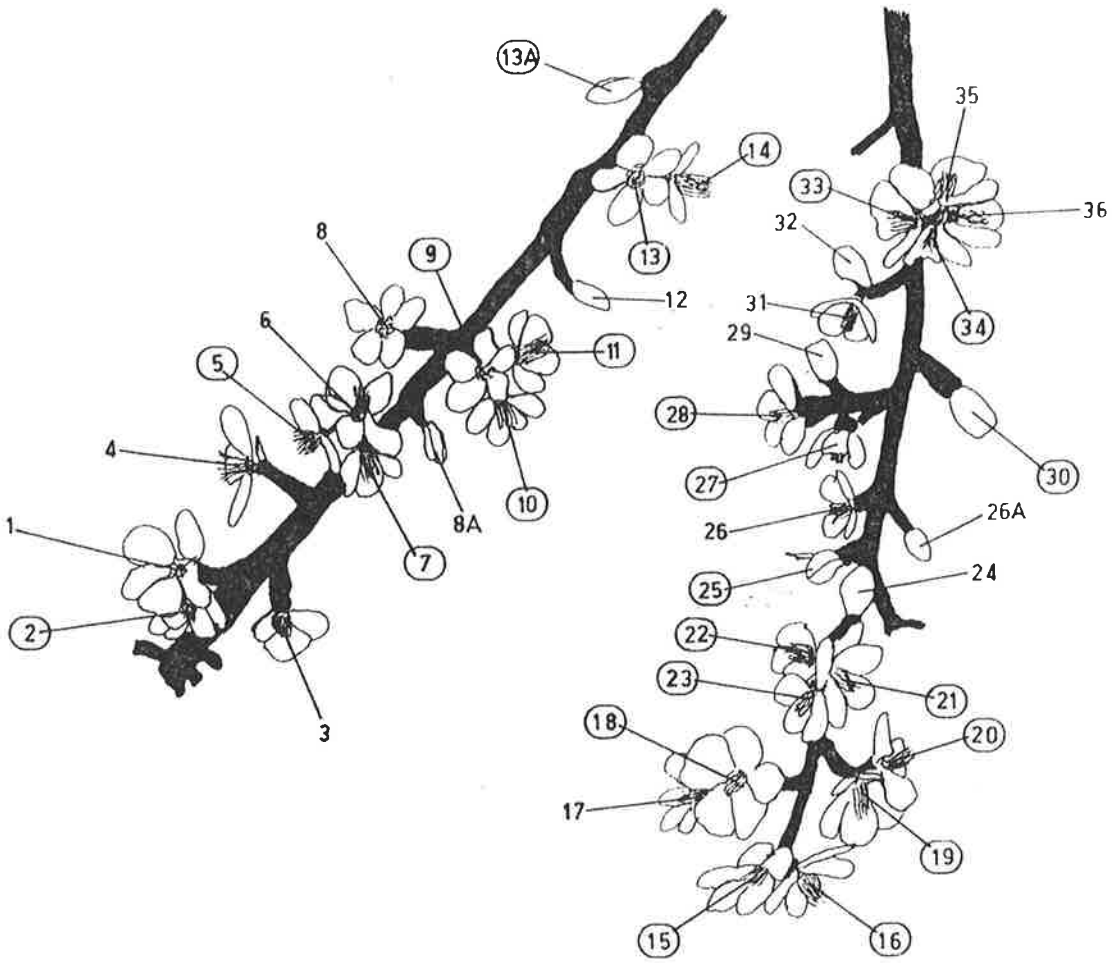
The video tapes were reviewed and the following data were recorded for each honeybee visit to a flower: date, time, flower identity-number, honeybee behaviour on the flower, duration of each type of behaviour, whether or not the honeybee probably touched the stigma during the visit, the origin and destination of the honeybee (i.e. another flower in the field-of-view), and the presence and behaviour of other honeybees in the field-of-view.

The measurements of honeybee activity and weather variables were described in Section 6.3.

Results and discussion

The field-of-view of the video camera is illustrated by Figure 6.10. Thirtynine flowers were in the field-of-view but only data for 23 flowers were used because three flowers abcised during the experiment, some flowers were too old when the experiment began, and bee behaviour on the other

Figure 6.10: The field-of-view of the video camera, showing the positions of the flowers on the branch on day 3 (August 23). Numbers that are enclosed in a circle indicate the flowers whose data were analysed.



omitted flowers was too difficult to observe via the video camera because of the problem of discerning 3-dimensional behaviour on a 2-dimensional video screen. The flowers that were used are indicated by circles around their numbers in Figure 6.10. Each of the flowers appeared to be female-fertile (Chapter 4) and contained 28 anthers, except for flower numbers 2 and 25 which contained 20 and 56 anthers respectively. Most of the data for the 23 flowers are shown in Figures 6.11a-w (see the figures).

Honeybees were the only insects seen to land on flowers during this experiment, but several flies landed on other parts of the branch. Data for honeybee activity are given in Figure 6.11x. Most visits to the flowers in the field-of-view occurred when honeybee activity was at a level above 3 (see Fig. 6.11x). The level of honeybee activity did not exceed 6 during this experiment, probably because the air temperature never exceeded 17°C (see Section 14.1).

Most flowers were not visited until 24 hours after anthesis, and most flowers were visited when several days old, but there did appear to be some preference for some flowers compared to other flowers. For example, flower 10 had 33 visits while flower 11 received only 13 visits although it was adjacent and of a similar age. Similarly, flowers 20 and 19 received 11 and 25 visits respectively although they were adjacent and of a similar age (Fig. 6.10). The data hinted at a preference for flowers facing downwards in opposition to flowers facing upwards, but the data were insufficient to test this hypothesis.

Anther dehiscence and pollen loss

The anther dehiscence and pollen loss data for this experiment were similar to the data of experiment 2, which was conducted concurrently with this experiment. Cumulative anther dehiscence for each flower is indicated by the upper line in the bottom part of each of Figures 6.11a-w. Anther dehiscence generally did not occur until flowers were over 24 hours old, and anther dehiscence occurred overnight in many flowers, but the rates were usually higher during daylight hours. Negative rates of anther dehiscence, which occurred when free water on anthers closed some dehisced anthers during rainy intervals, were recorded as zero.

Cumulative pollen loss for each flower is indicated by the lower line in the bottom part of each of Figures 6.11a-w, and intervals of pollen

Figure 6.11a-x: The data for individual flowers (a-w) and honeybee activity (x). The flowers have been listed in approximate order of time of anthesis. The data for each flower is divided into three parts - (1) cumulative anther dehiscence and cumulative pollen loss, (2) visits by pollen-collectors, and (3) visits by nectar-collectors. So, for each flower:

(1) The bottom axis represents the time between 0600 and 1800 hours on each of a number of given dates. The axis on the left indicates the number of anthers that were in the flower. The lines show cumulative anther dehiscence (upper line) and cumulative pollen loss (lower line) versus time, and in units of whole anthers. The lines end at the time when all pollen had disappeared from the flower. Time of anthesis, if known, is indicated by an arrow.

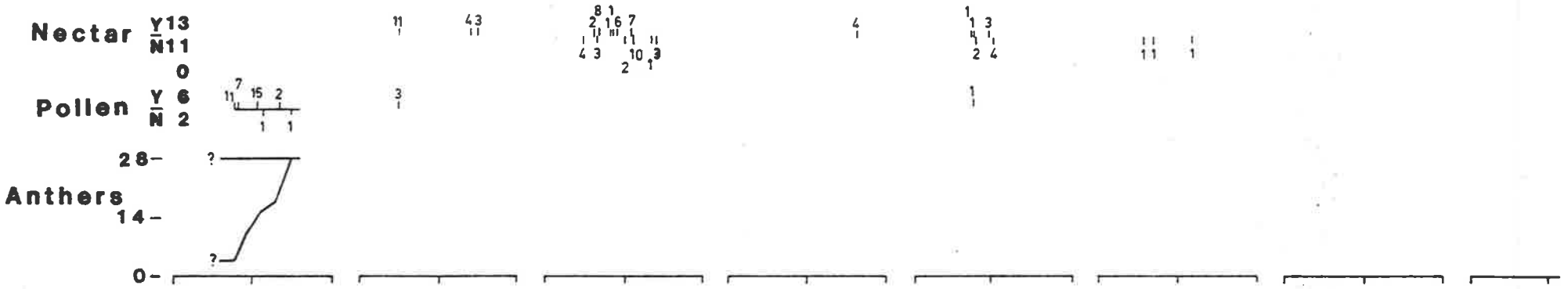
(2) The pollen axis concerns visits by pollen-collectors. The sampling intervals during which pollen was lost from the flower, are indicated by horizontal lines along the medium level of the pollen axis. The time of a visit is indicated by a vertical dash. Whether or not the bee was thought to have touched the stigma is indicated by the position of the dash above or below the medium level respectively (i.e. Y for yes, and N for no), and this distinction is made clearer by the position of a number above or below the dash respectively. The number is the time, in seconds, spent on the flower by the bee. The number of visits for each category is given on the left hand end of the axis.

(3) The nectar axis concerns visits by nectar-collectors, and the data is arranged similarly to the data for pollen-collectors.

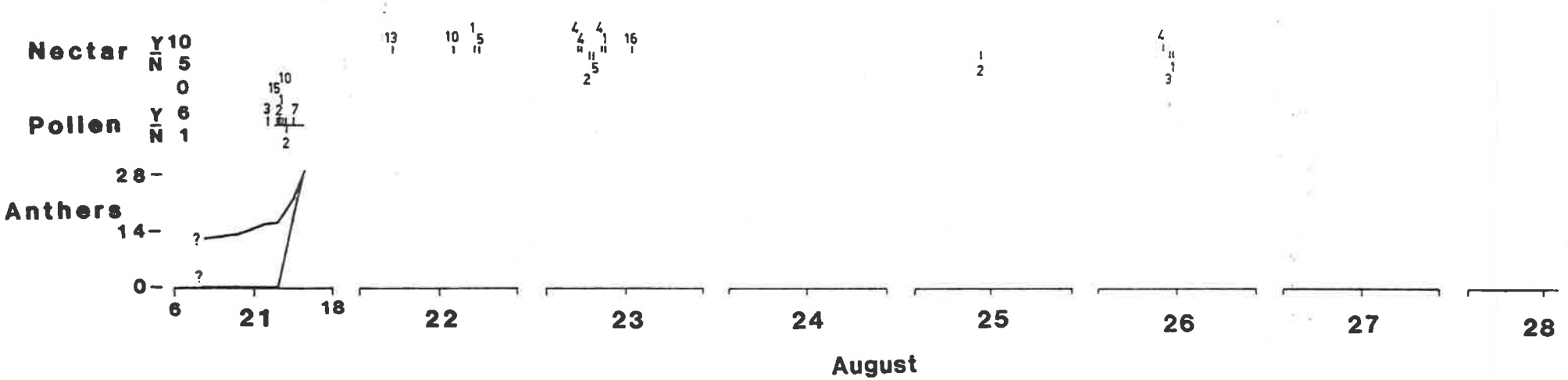
In addition, each visit during which both pollen-collection and nectar-collection behaviour occurred, is indicated by a vertical dotted line between the dashes in the pollen and nectar axes (e.g. Fig. d). For such visits, the numbers next to the dashes in the pollen and nectar axes indicate the time spend doing each type of behaviour. The total number of such visits is given on the left hand side of the figure between the pollen and nectar axes.

The total number of visits is stated in the sub-heading. Honeybee activity, on a scale of 0 to 10, versus time, is given in Figure x.

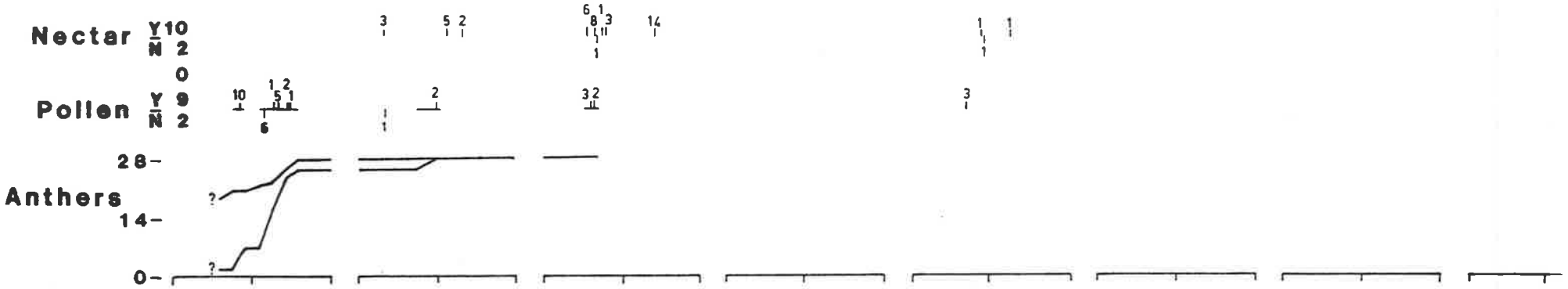
a. Flower 15. Total visits = 32.



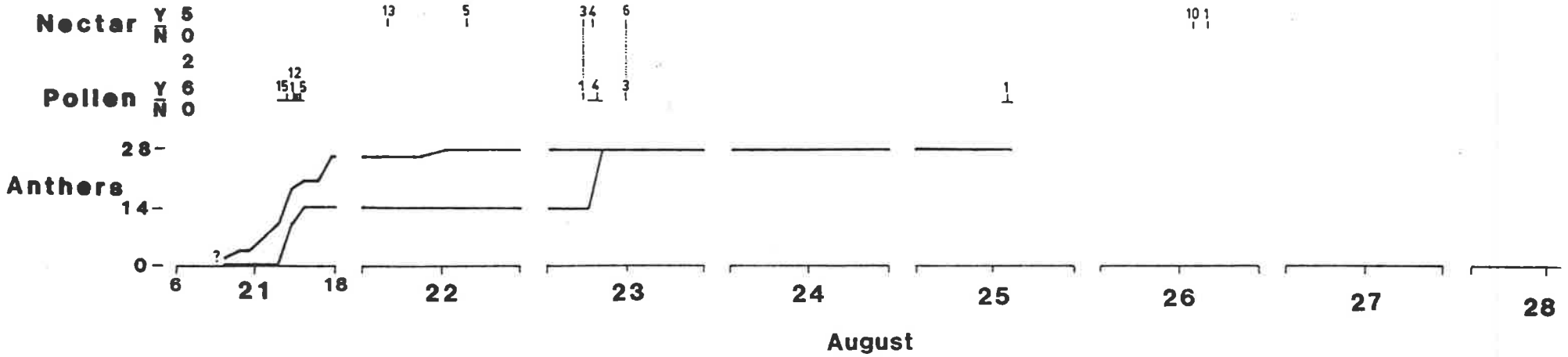
b. Flower 7. Total visits = 22.



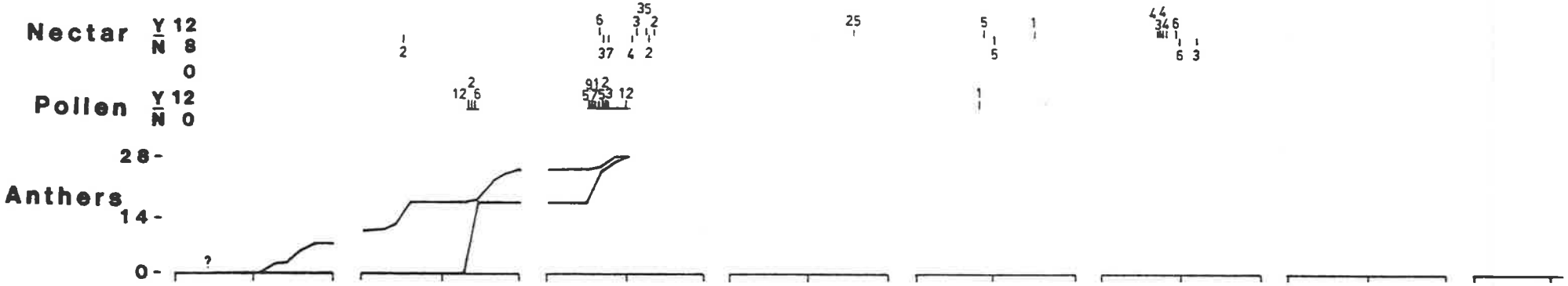
c. Flower 16. Total visits = 23.



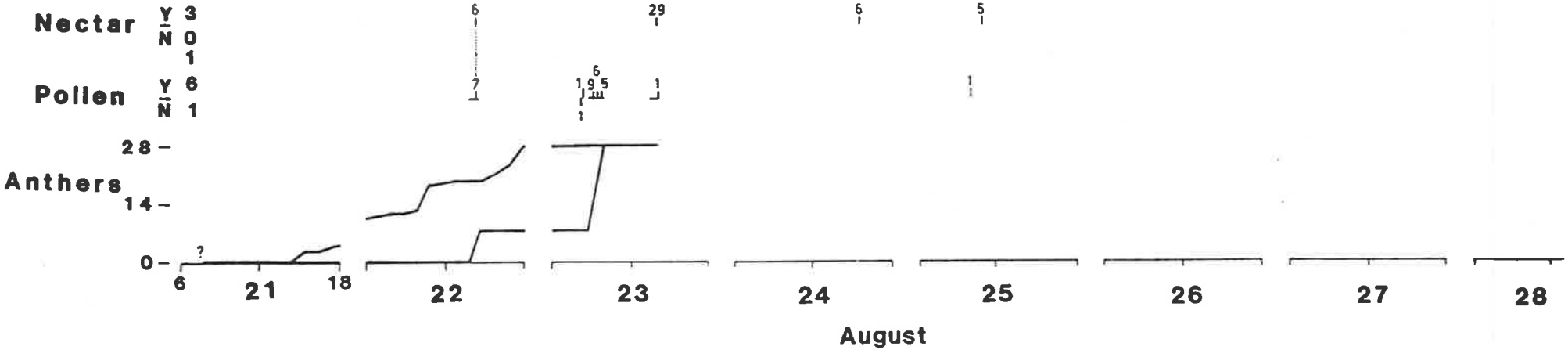
d. Flower 21. Total visits = 13.



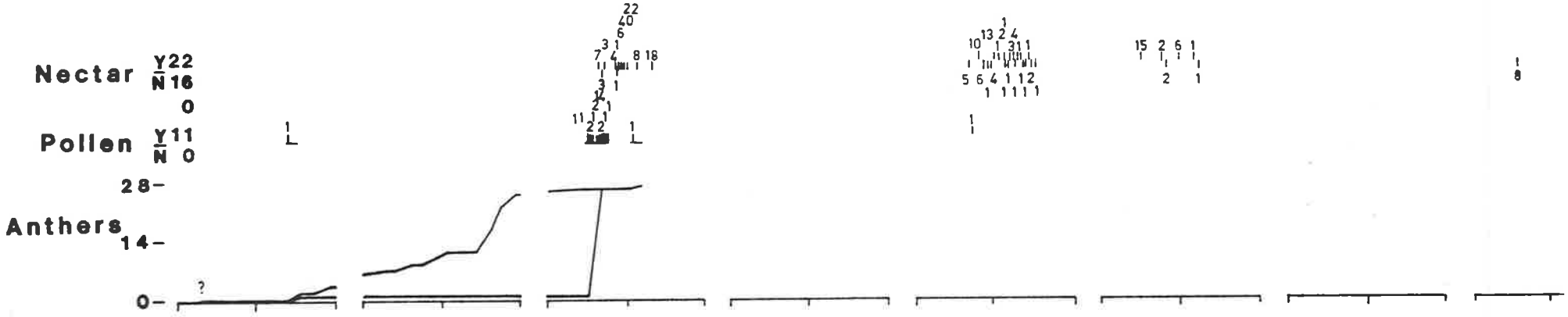
e. Flower 5. Total visits = 32.



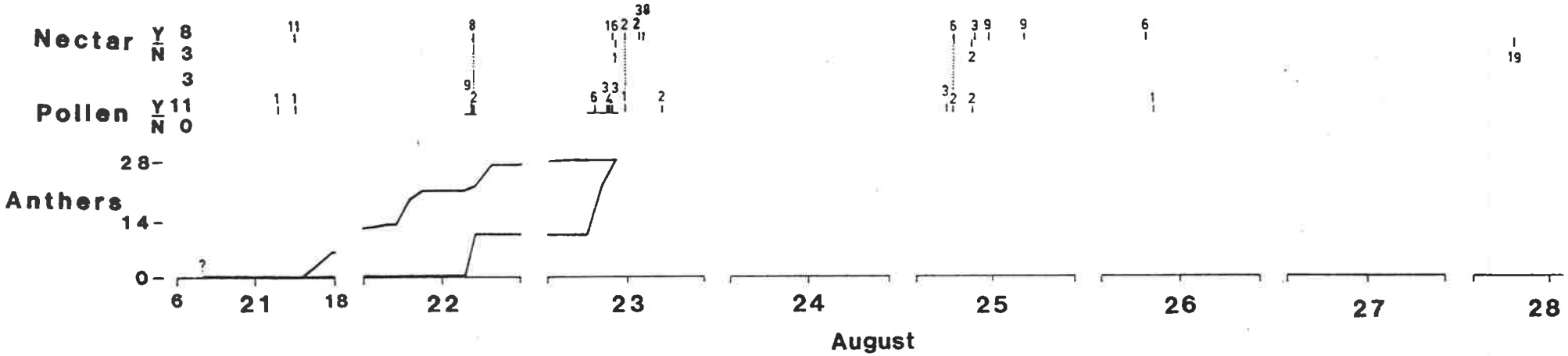
f. Flower 34. Total visits = 11.



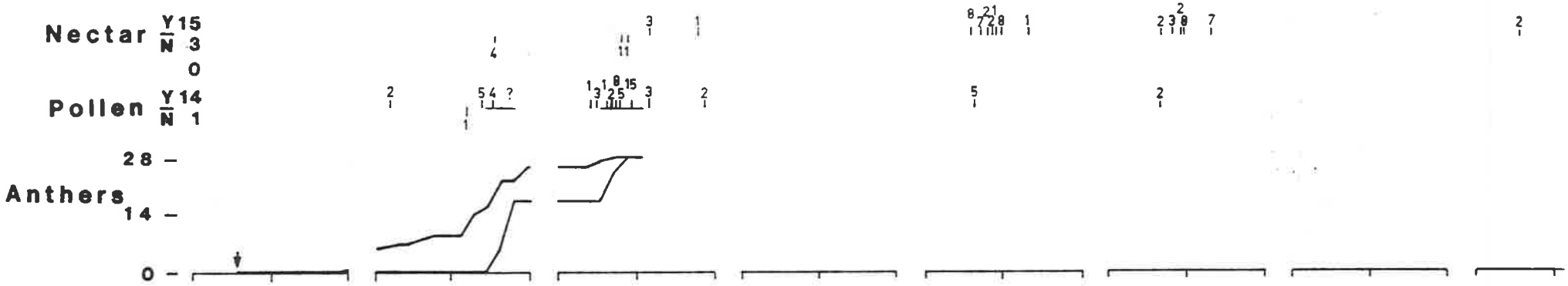
g. Flower 18. Total visits = 49.



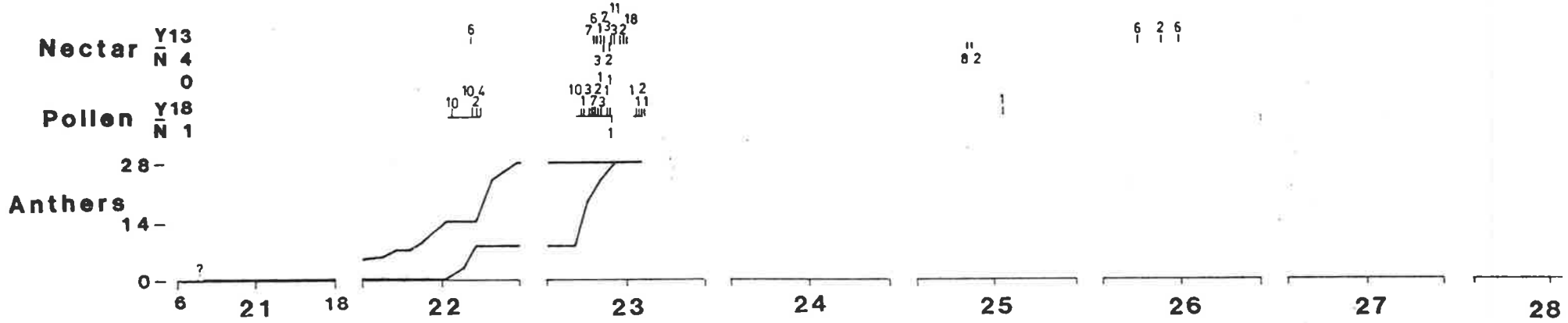
h. Flower 19. Total visits = 25.



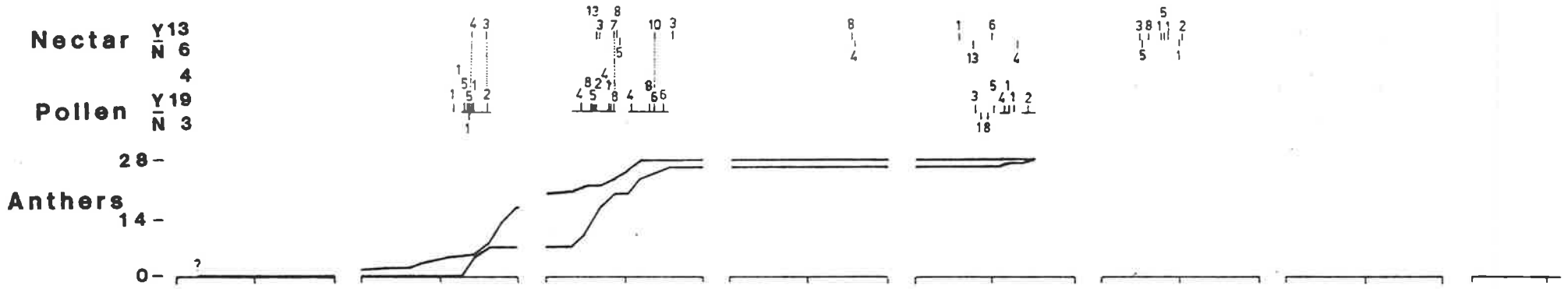
i. Flower 10. Total visits = 33.



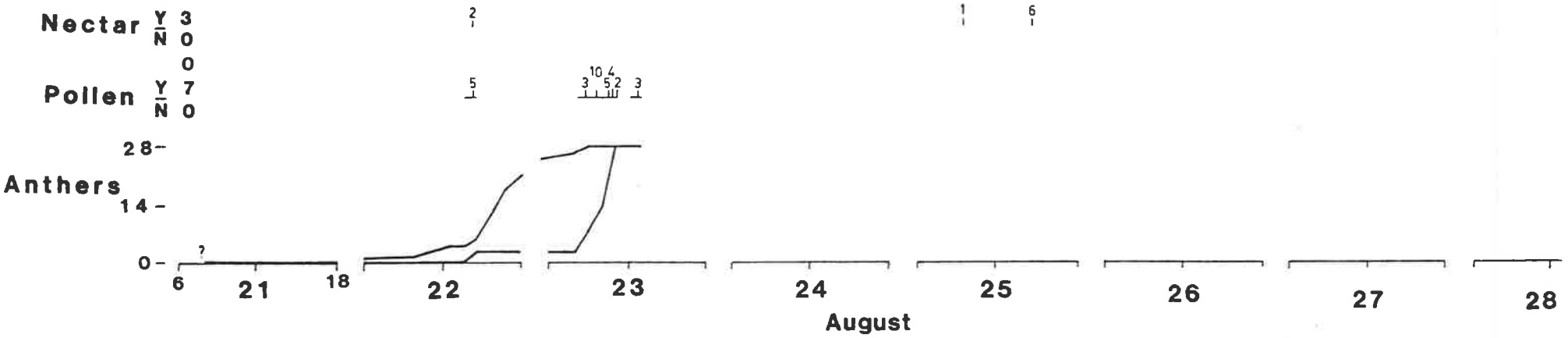
j. Flower 33. Total visits = 36.



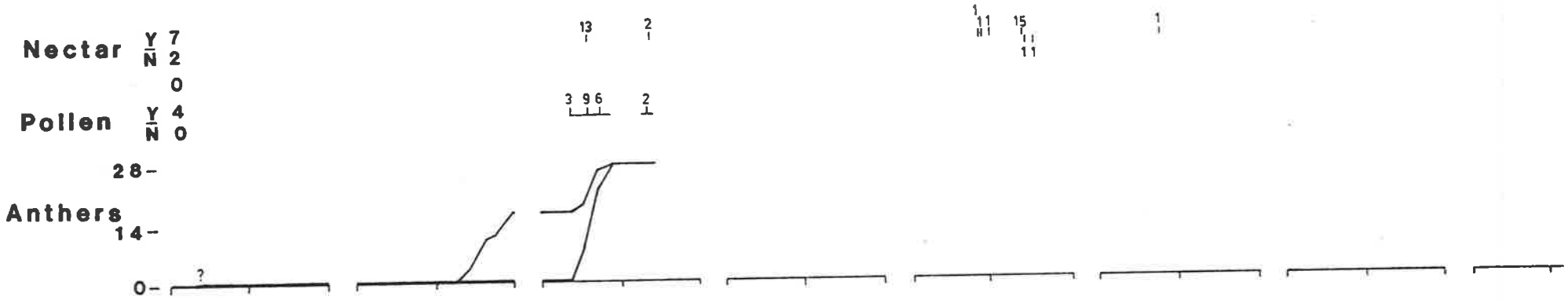
k. Flower 13. Total visits = 45.



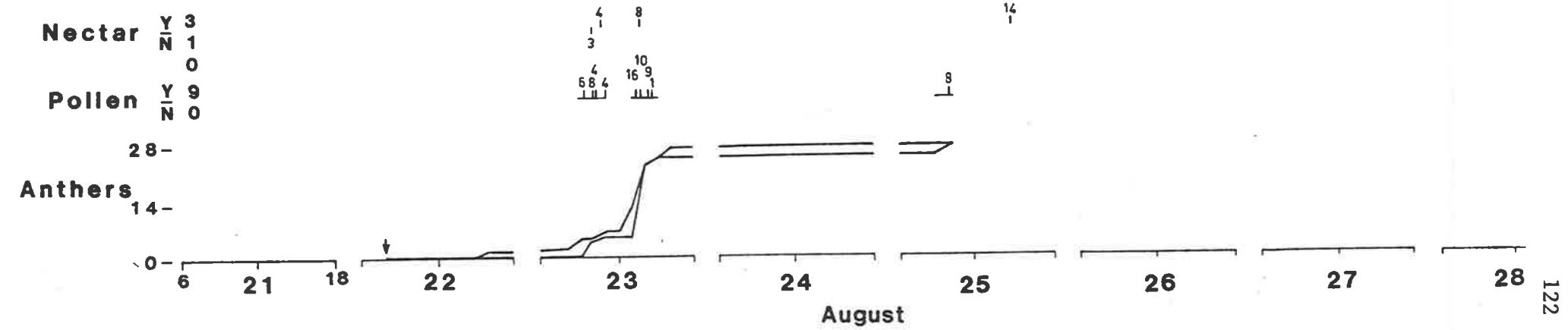
l. Flower 20. Total visits = 10.



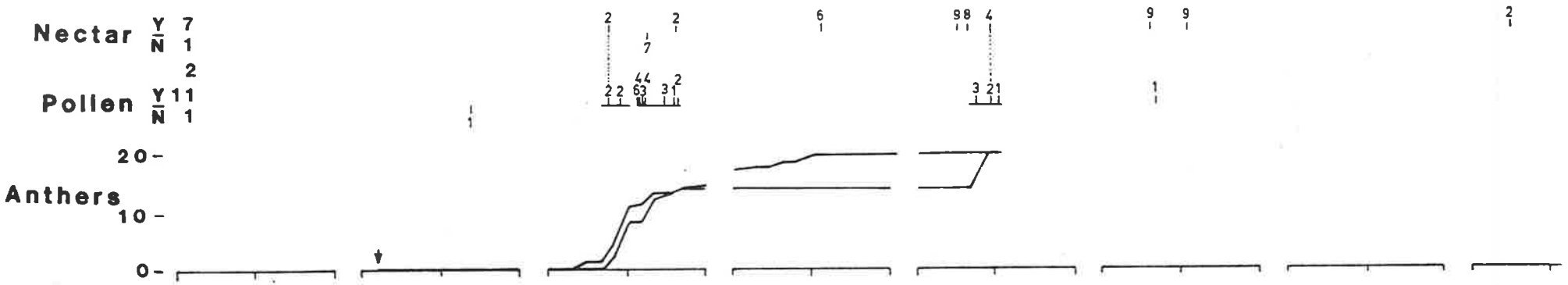
m. Flower 11. Total visits = 13.



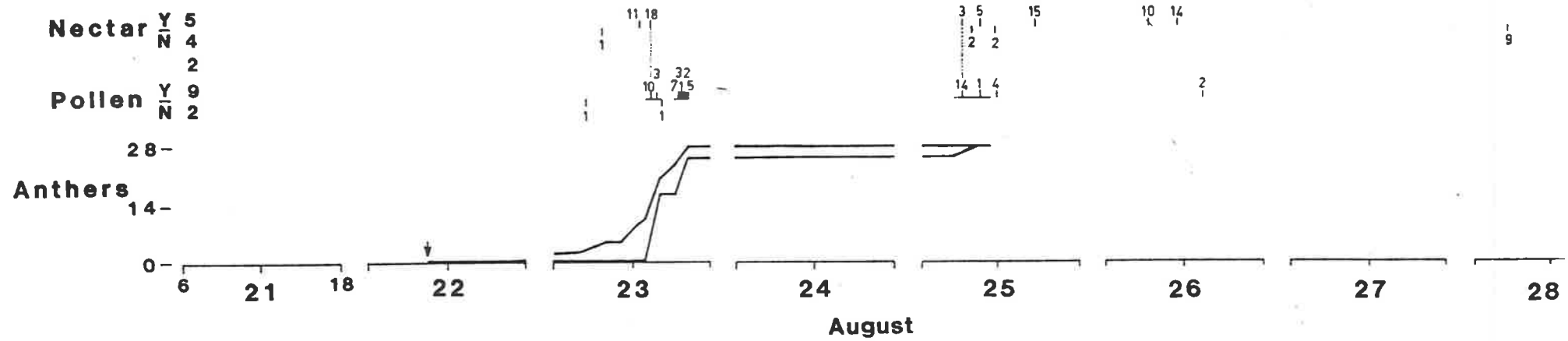
n. Flower 14. Total visits = 13.



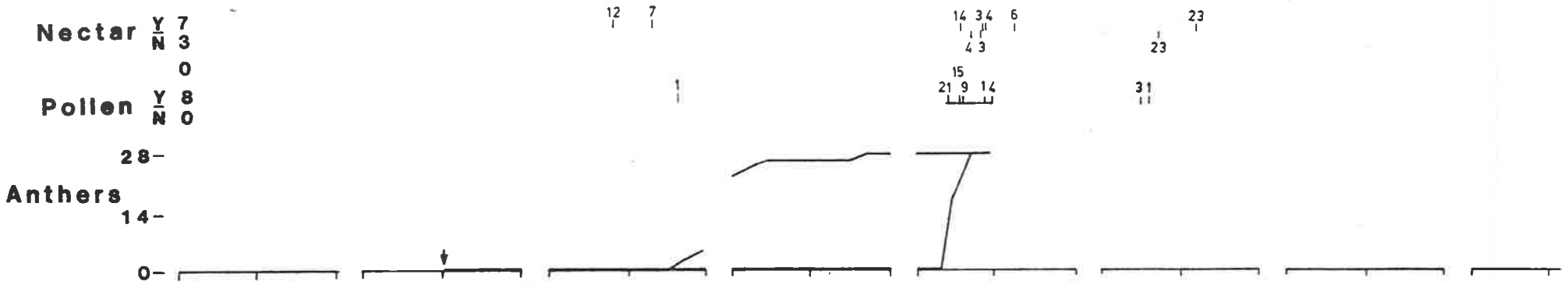
o. Flower 2. Total visits = 22.



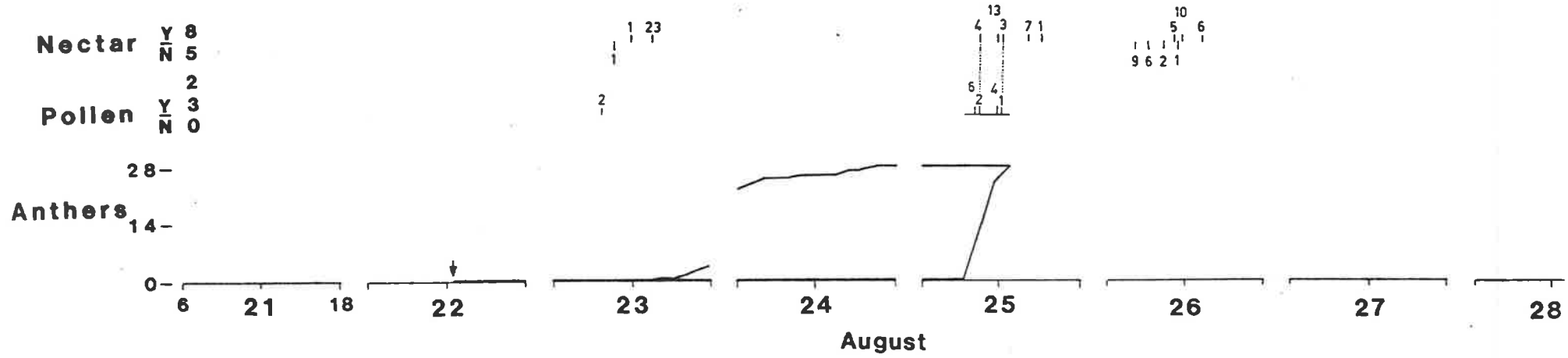
p. Flower 27. Total visits = 22.



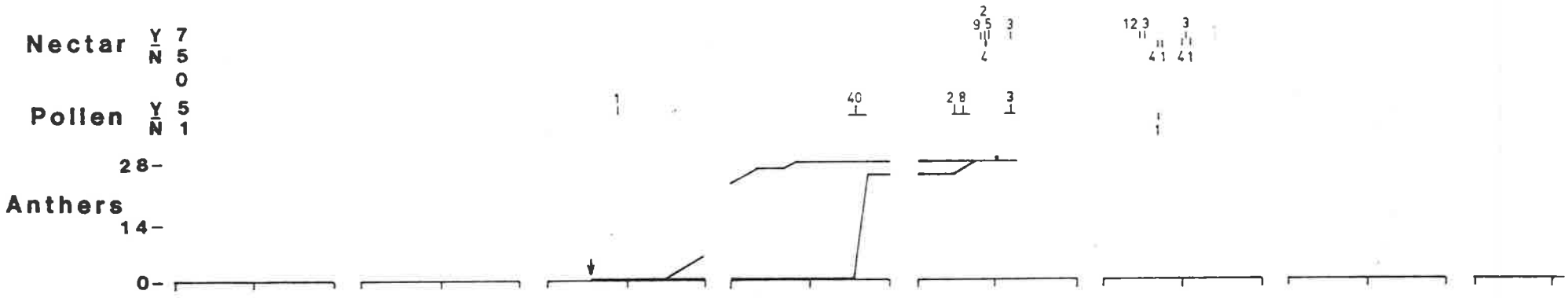
q. Flower 23. Total visits = 18.



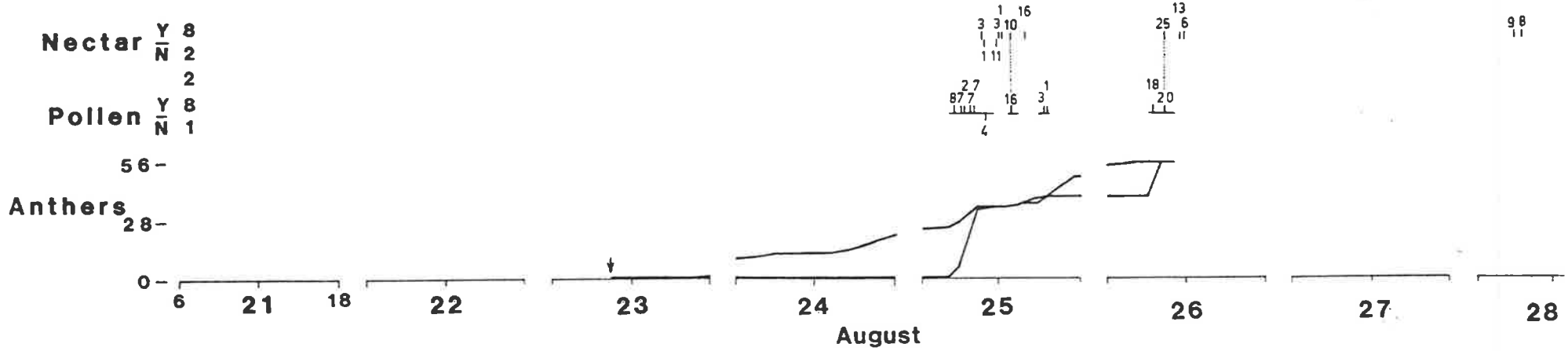
r. Flower 9. Total visits = 18.



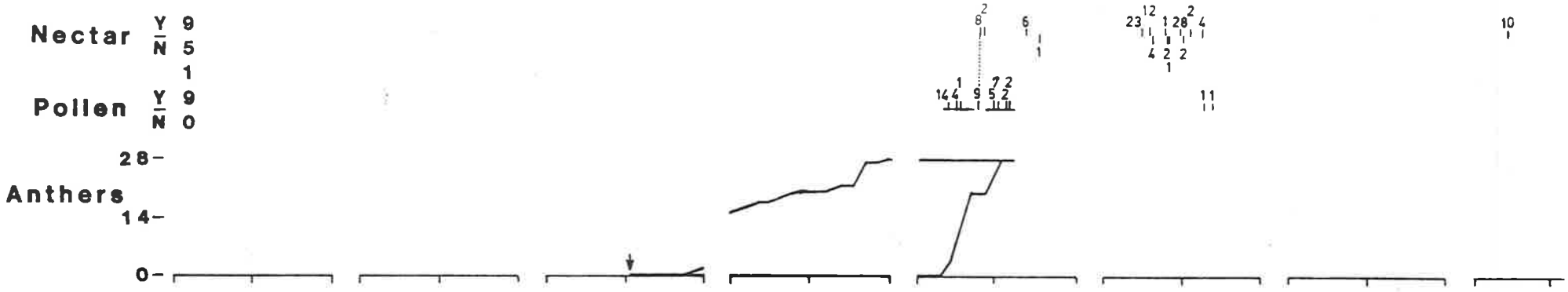
s. Flower 22. Total visits = 18.



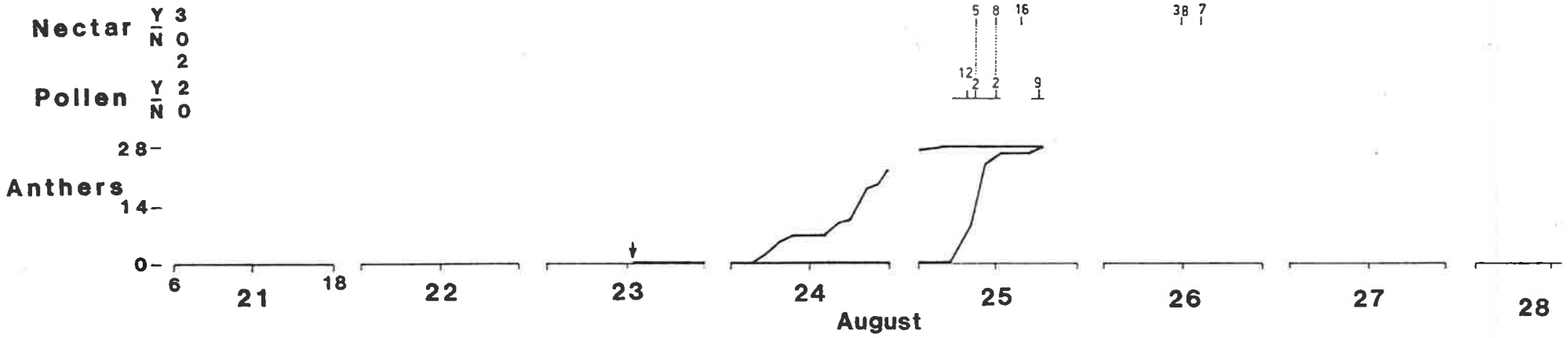
t. Flower 25. Total visits = 21.



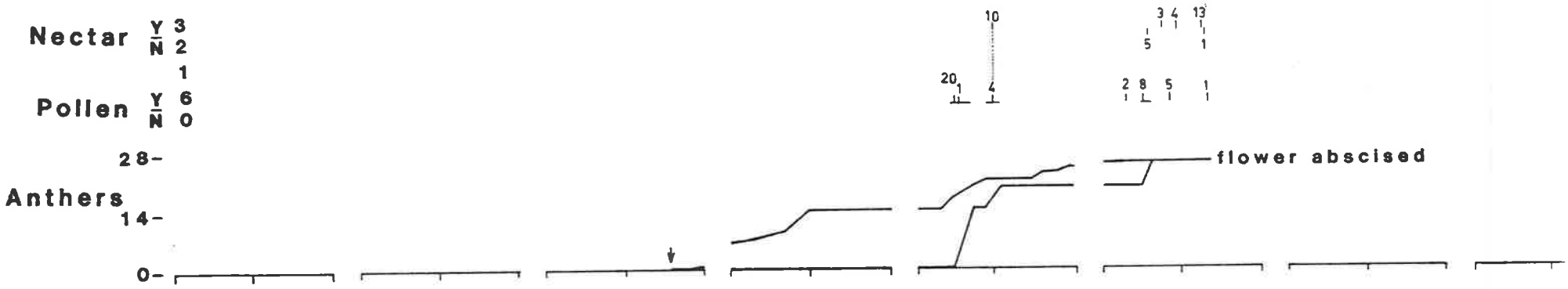
u. Flower 28. Total visits = 24.



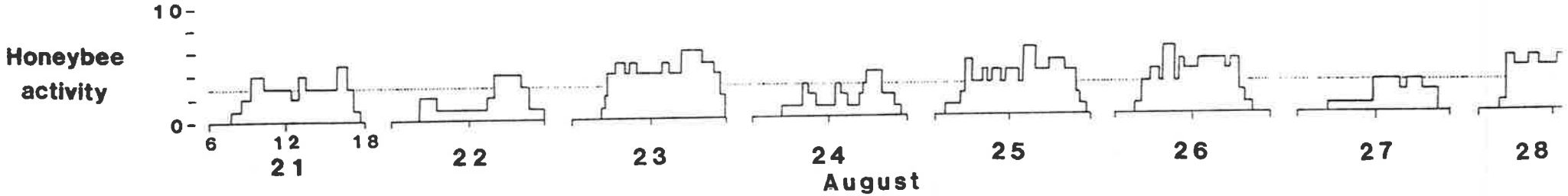
v. Flower 30. Total visits = 7.



w. Flower 13A. Total visits = 12.



x. Honeybee activity



loss are indicated by horizontal lines in the pollen axes of Fig. 6.11. Pollen loss occurred during daylight hours only, and pollen loss per flower often first occurred 24 hours after the first occurrence of anther dehiscence, even though bees were usually active on nearby flowers during the intervening period (Figs. 6.11a-x).

Pollen loss versus honeybee behaviour

Every instance of pollen loss during an interval coincided with at least one visit by a honeybee that exhibited pollen-collection behaviour (see Figs. 6.11a-w). Further, some bees exhibited pollen-collection behaviour when pollen was not available for collection. For example, flower numbers 2, 9, 19 and 22 were visited by pollen-collectors before any anthers had dehisced, that is when there was no pollen available (Figs. 6.11h, o, r, s); so pollen-collection behaviour did not necessarily indicate that pollen was being collected. Perhaps those first bees were scout bees (Section 11.4). Thirteen flowers were visited by pollen-collectors after all pollen had been collected, but the bees may have found some traces of pollen which were missed when flowers were sampled for the presence of pollen (Fig. 6.11a-w).

The number of visits that involved pollen-collection behaviour varied from 4 to 26 visits (flower numbers 11 and 30, and 13 respectively), and the visits lasted a total time of 20, 25, and 95 seconds respectively (Fig. 6.11). The relationship between cumulative time spent on flowers by pollen-collectors versus the number of anthers stripped of pollen, per interval, is shown in Figure 6.12. The relationship was not significant (Fig. 6.12). Honeybees are fast workers, given that they can strip pollen from 28 anthers in only 20 to 95 seconds of visits. In fact, some anthers were stripped at the rate of 7.5 anthers per second, although the average for all flowers and visits was only 0.6 anthers per second (Fig. 6.12).

Individual visits by pollen-collectors ranged from less than one second to about 40 seconds (Figs. 6.11a-w). The longer visits by pollen-collectors were usually to flowers that had pollen available and had not been visited before or had not been visited for several hours (e.g. Figs. 6.11 n, p, q, u, v, w). Moreover, the behaviour of some honeybees suggested that they may have collected traces of pollen that remained after the bulk of the pollen on every anther had been collected.
Pollen-collectors may sometimes leave traces of pollen because the pollen was hidden from their sight. For example, sometimes a bee left a flower

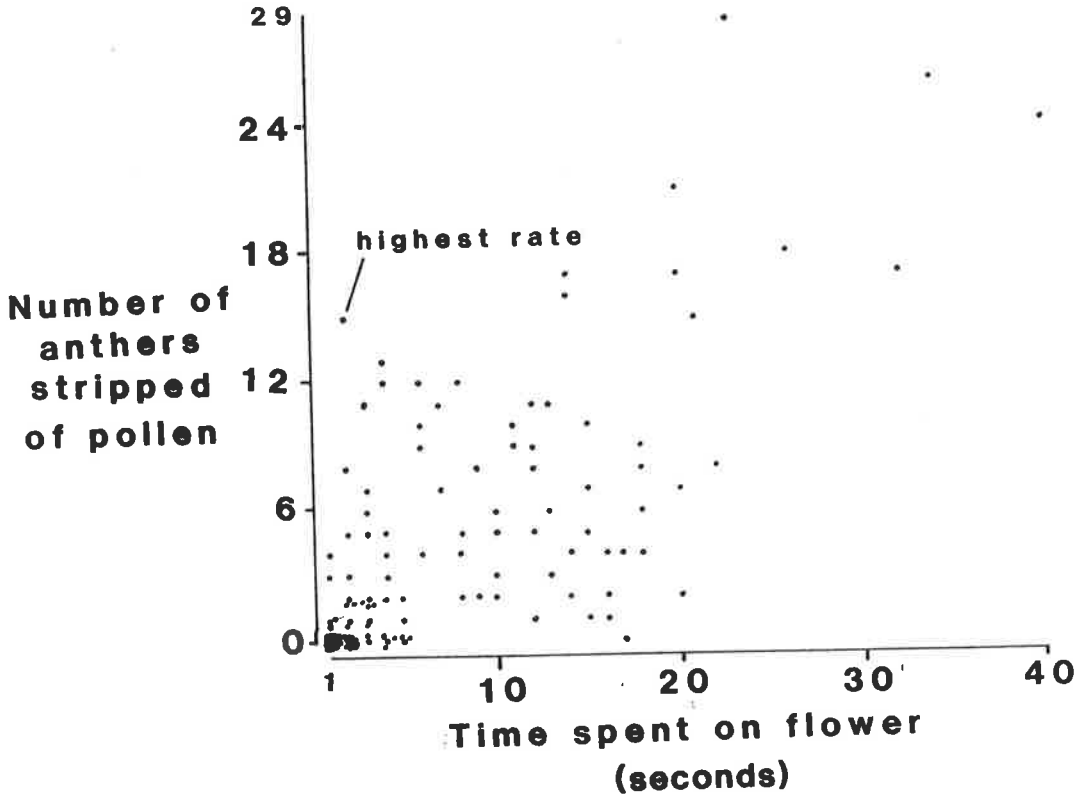
briefly, only to return and gather more pollen after apparently seeing from a new angle of observation that pollen was still available. Traces of pollen may also have been left by honeybees that had a full load. Presumably, the collection of traces of pollen by subsequent visitors involved a similar amount of time to that of the initial collection of pollen. This would explain the broad range of collection rates shown in Figure 6.12.

The comments above suggest that pollen-collectors sometimes do not collect all the pollen that is available on a flower, but pollen is probably left behind only by accident, such as when they do not see the pollen (e.g. see below under "Hovering"); and so the hypothesis that pollen-collectors collect all the available pollen that they see on a flower, may be essentially true.

About 100 flowers are usually visited during a foraging trip by a pollen-collector, and 100 flowers produce between 2 and 8 loads of pollen (Section 10.3.2.4), therefore one would expect each flower to be visited by pollen-collectors no more than between 2 and 8 times. But the observed number of visits per flower ranged from 3 to 22 (Fig. 6.11), so what caused the high number of visits per flower ? Perhaps the efficiency of pollen-collectors to collect pollen was reduced by the conditions of this experiment. Also, the weather was often not favourable to foraging activity, and this can cause an increase in the number of flowers per foraging trip (Section 12.2), which, in turn, can increase the expected number of visits per flower.

An average of between 2 and 12 visits per flower per day were expected to be made by nectar-collectors during the 6 days following anthesis in each flower (Section 10.3.2.4), and nectar-collectors were observed making between 0 and 20 visits per flower per day. The incidence of visitation was erratic and the mean was only about 2.5 visits per day (Fig. 6.11), which was within the range of expectation. As with pollen-collectors, the higher than expected incidences of visitation may have been caused through the foraging areas of nectar-collectors being enlarged by the weather that was not favourable to foraging (Section 12.2). However, that factor may have been counteracted by the fact that nectar production is much lower during such weather (Section 12.4.2), that is, less nectar would have been available for collection.

Figure 6.12: Total time spent per flower by pollen-collectors versus number of anthers stripped of pollen, per interval. Some of the higher points were due to flower number 25 having 56 anthers. The relationship was not significant. The mean for all data points was 0.60 anthers per second. Overlapping points are staggered.



The speed of pollen collection suggests that pollen collection could have occurred undetected during visits which were recorded as being solely by nectar-collectors. Also, some visits lasted much less than a second, and only frame by frame analysis of the video tapes showed that the bees were exhibiting pollen-collection behaviour. This could explain why some authors claimed to have observed bees landing on flowers but without collecting pollen or nectar (e.g. Williams and Brain 1985). Notwithstanding the above comments, whether or not a bee actually did collect pollen was not possible to ascertain from the video tapes.

Honeybee behaviour

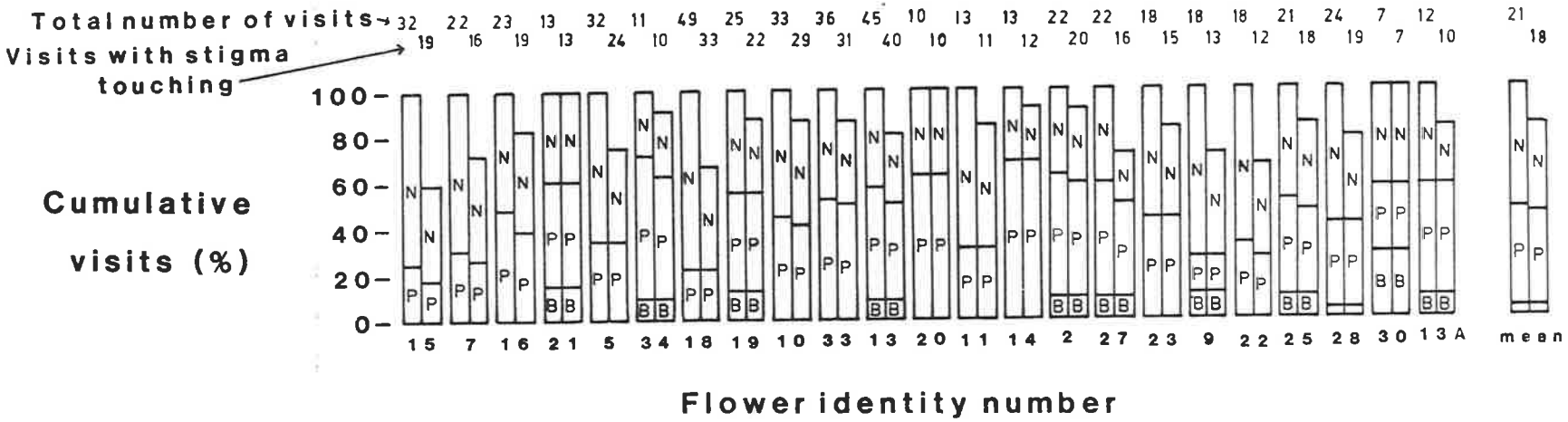
Most flowers were not visited by honeybees until after pollen had become available. Exceptions were for flowers 2, 9, 19, 22, 23 (Figs. 6.11h, o, q, r, s). Generally, the majority of the first few visits to flowers were by pollen-collectors, but nectar-collectors also frequented young flowers, and, after all the pollen had been taken, nearly all visitors were nectar-collectors. Nectar-collectors visited flowers that were at least 7 days old (Fig. 6.11), but effective pollination probably was not achieved by those visits because the effective pollination period was probably much less than 7 days (Section 8.1.2).

The number of observed visits per flower and the incidence of different categories of behaviour per flower is given in Figure 6.13. The number of observed visits per flower varied from 7 to 49 (Fig. 6.13), but more visits to some of the flowers may have occurred outside of the period of the experiment.

Overall, both pollen-collection and nectar-collection behaviour occurred during only 22 visits, which was 4% of all visits. The visits lasted between 3 and 45 seconds, and the proportion of time spent on each sort of collection-behaviour varied greatly (Fig. 6.11). Some of the other visits may have involved the collection of both nectar and pollen, with one or the other behaviour having gone undetected because of the speed with which pollen was collected, or because anthers were sometimes located within, or nearly in, the receptacle of the flower.

Nectar-collection only, accounted for 52% of all recorded visits, but the percentage varied between flowers (Fig 6.13). Individual visits by nectar-collectors lasted for from less than one second to 40 seconds (Fig. 6.11a-x).

Figure 6.13: The percentage cumulative number of honeybee visits for each flower, with the data for each flower being listed from left to right in the order of anthesis that was used in Figure 6.11. The identity number of each flower is given as the bottom axis. The data for each flower is represented by two bars. The left-hand bar shows the proportion of visits by nectar-collectors (N), pollen-collectors (P), and bees that showed both forms of behaviour (B). The right-hand bar gives data for the same categories of bees, but only for visits during which the stigma was touched by the bee. The total number of visits to the flower is given at the top of the left-hand bar, and the number of those visits during which the stigma was touched, is given at the top of the right-hand bar. The means for all 23 flowers are given on the right-hand side of the figure.



Nectar-collection behaviour can usually be put into one of two sub-categories, depending on whether the bee sought nectar by reaching between the bases of the stamens ("side-worker"), or by reaching between the stamens while standing on top of the stamens ("top-worker") (Section 11.2); but the behaviour during many visits prevented such a distinction. For example, some bees landed and maintained a single position while presumably feeding, but other bees moved around the flower, apparently to feed from different parts of the receptacle of the flower. Occasionally a bee left a flower and returned to feed a moment later, presumably because the bee caught sight of some nectar which had been missed.

Constancy of behaviour between flowers

Bees that displayed both nectar- and pollen-collection behaviour on one flower, usually did the same on most subsequent flowers visited in the field-of-view. Similarly, bees that collected either nectar only or pollen only, from a flower, usually maintained that behaviour on subsequent flowers. The exceptional bees usually indulged in the alternative behaviour for at most a few seconds and on one flower only; and most of the exceptional bees were predominantly pollen collectors. Some of the exceptions could have been cases of mis-interpretation of the bees' behaviour, but true exceptions can be explained.

Individual honeybees carry enough sugar energy for about 15 minutes of flying (Scholze *et al.* 1964), which is less than the usual time spent flying to collect one load of pollen (e.g. Free 1970a p396). Consequently, bees may renew their own energy reserve by having an occasional snack of nectar. Moreover, perhaps bees that predominantly collect nectar "need" or "prefer" an occasional snack of pollen.

Density of honeybees

A bee is not deterred from visiting a flower on which another has recently foraged (Darwin 1876; Ribbands 1949; Weaver 1956), and almond flowers are not excepted. Several instances were seen where one bee vacated a flower and a second bee landed on the flower and exhibited foraging behaviour while the first bee was still in the field-of-view. Further, there was one occasion when one bee landed and exhibited pollen-collection behaviour while another bee was exhibiting nectar-collection behaviour on the same flower; and two bees simultaneously probed for nectar on one flower for 45 seconds during a preliminary experiment on Chellaston

flowers. Conflict between bees was noticed but that conflict occurred only when one bee was sited on the flower in such a way that a second bee could not land on the flower without colliding with the first bee.

The probability of seeing more than one bee on a flower was very low during this experiment. For example, the total period of bee activity during this experiment was 52 hours, but bees were present in the field-of-view for only 68 minutes (2.1%), and of that time, 2, 3 and 4 bees were present for only 214, 37 and 4 seconds respectively. Given that the field-of-view contained about 30 open flowers at any given time, and that at least two bees were present in the field-of-view for only 4 minutes of the 52 hour total, then the likelihood of two bees being seen on a flower at the same time should be a rare event. Indeed, this phenomenon occurred during this experiment on only 2 occasions and for a total time of 7 seconds.

Stigma touching

An almond flower is usually only pollinated when the stigma is touched by a bee, but the probability of a stigma being touched by a visiting bee depends on the behaviour of the bee. The relationship, between the incidence of stigma touching and bee behaviour, is summarized by the data in Figure 6.13. The incidence of stigma touching varied, between flowers and categories of behaviour, from 58% to 100% of all visits per flower (Fig. 6.13). The stigma was touched during all visits by bees that displayed both nectar and pollen collection behaviour (B), and stigma touching occurred during 96% and 80% of all visits by pollen-collectors (P) and nectar-collectors (N) respectively (Fig. 6.13). Consequently, the probability of pollination occurring during a visit was good, but the probability appears to have been higher for pollen-collectors (Fig. 6.13).

The distinction between nectar-collectors that are side-workers, from nectar-collectors that are top-workers (Section 11.2), is important because side-workers rarely touch the stigma, whereas top-workers usually do (e.g. Free 1960a, 1960b; Thorp 1979). In this study, many visits could not be placed into one or the other of the sub-categories because the bees moved about the flower so much that their behaviour could be placed in both categories, and this behaviour was the reason for the high incidence of stigma touching by nectar-collectors generally.

The above comments suggest that nectar-collectors had a significant influence on the probability of flowers being pollinated, but,

theoretically, another factor may have restricted the actual value of nectar-collectors for pollination. That factor, known as the effective pollination period (EPP), is the "life-span" of a flower after anthesis, beyond which pollination cannot lead to the production of a nut (Section 8.1.2).

A model of apple pollination (Brain and Landsberg 1981) suggested, in a general sense, that the probability of effective pollination for an apple flower may be close to the limit of one after 5 effective (stigma touching) visits by bees, provided that certain other variables are favourable. In my experiment, flowers were usually 2 or 3 days old before four effective visits had occurred (Fig. 6.11). The EPP in almond may be about 3 or 4 days in favourable conditions (e.g. Griggs and Iwakiri 1964; Micke and Kester 1978b), but if the EPP was less than, say, 3 days, which is possible (Section 8.1.2), then the low number of visits during the EPP, may have been a major nut-set factor during this experiment. Only two flowers in the field-of-view produced mature nuts, although the trees were capable of producing much higher nut-sets (e.g. Section 1.6); so perhaps the EPP was less than 4 days.

Hovering

Many bees that flew through the field-of-view hovered, and some honeybees appeared to examine flowers while flying past, but without hovering. Hovering behaviour consisted of a bee momentarily hovering and orientating its body so that the bee was looking into a flower at an angle that would have allowed the bee to determine whether or not pollen or nectar was present. Hovering lasted typically about 0.2 seconds, but a few instances of up to one second were noticed. Some bees repeated the hovering behaviour up to 5 times within a second, and so the behaviour was not easy to observe except by slow motion replay of the video tapes. Foragers only occasionally landed on flowers that apparently had no pollen or nectar (Fig. 6.11). Such behaviour appears very efficient with respect to time and energy spent collecting pollen and nectar.

Hovering behaviour has been reported by other authors (e.g. Jones and Buchmann 1974; Thorp *et al.* 1976; Jones 1978; Thorp 1979), but detailed studies have not been made. The data were not analysed further because the three-dimensional behaviour was difficult to interpret on a two-dimensional video screen.

6.6 General discussion

Anther dehiscence in almond in this study was not like Percival's (1955) study on peach (Prunus persica). For example, half the anthers per flower dehisced during the first 24 hours following anthesis in peach (Percival 1955), whereas in this experiment, few anthers dehisced in the 24 hours following anthesis. This study shows that the rate and timing of anther dehiscence depends on several variables, especially temperature (Fig. 6.5), and so studies made under limited conditions (e.g. Percival 1955) probably only apply to a very limited range of circumstances and may not be applicable at all in some regions. Furthermore, the data in Figure 6.5 suggest that little or no anther dehiscence occurs when the air temperature is below 8°C, and anther dehiscence occurred overnight (Fig. 6.4), so authors who thought that anther dehiscence did not occur at night (e.g. Micke and Kester 1978b; Webster et al. 1985) may have worked in areas that had overnight temperatures of less than 8°C. Threshold temperatures, below which anther dehiscence does not occur, have been noted for other plant species, and the threshold temperature can be higher on dull days than on sunny days (Percival 1955).

The temperature range of 8.5 to 16.8°C, which occurred during this study, was narrower than had been anticipated. Lower and higher temperatures may have had a significant effect on the examined variables. For example, honeybee activity did not reach the peak that is possible (i.e. Fig. 6.3c) because the temperatures were not high enough (Section 14.1).

Rate of flower visitation by insects has been used as a measure of the insects' ability to pollinate flowers (e.g. Free 1970a p396). However, rate of flower visitation is too simple to be a useful measure of the efficiency of insects to visit and pollinate flowers, because many factors affect either the rate of flower visitation or the probability that a given visit will result in effective pollination (e.g. Section 13.1).

Most visitors to flowers, after all pollen had been lost, were nectar-collectors; but nectar-collectors also visited younger flowers and touched their stigmas (Figs. 6.11, 6.13), and so the belief that nectar-collectors are not important for pollination (e.g. Todd and McGregor 1960) probably was not true during this experiment.

The importance of the effective pollination period (EPP) was highlighted by the last experiment. In essence, if the first one or two visits by honeybees to a flower are made after the EPP has expired, then

all other factors of pollination and nut-set are irrelevant. EPPs for other crops vary greatly between cultivar combinations (i.e. flower cultivar and pollen cultivar) and between years, but very little is known about EPPs in almond, and so more work is required on this subject. EPPs are discussed further in Section 8.1.2.

PART B

"Old maids keep cats. The more old maids, the more cats. Cats take mice. The more cats, the fewer mice. Mice dig out bumblebee nests. The fewer mice, the more bumblebees. Bumblebees are necessary for the production of red clover seed. The more bumblebees, the better seed-setting. In other words: The more old maids, the more clover seeds."

from Faegri and Pijl (1979), after Charles Darwin

Chapter 7: Flowers that cannot produce nuts

7.1 Female-sterile flowers

Many almond flowers are incapable of producing nuts because they lack mature ovules. Such flowers may be referred to as "female-sterile flowers". The occurrence of significant numbers of female-sterile flowers is not unusual amongst the flowers of fruit trees generally (Howlett 1926; Dorsey 1930; Jones 1968; Socias i Company 1976; Postweiller et al. 1985; Rallo and Fernandez-Escobar 1985). For example, up to 8% of flowers are female-sterile in some peach cultivars (Randhawa et al. 1963). Indeed, female-sterility has been claimed to be an important factor of fruit set in apple (Howlett 1936, 1938; Hartman and Howlett 1954; Williams and Sims 1977), and up to 99% of flowers are female-sterile in some European almond cultivars (Almeida 1945, 1948; Pejovics 1963; Dhatt and Dhillon 1981; Socias i Company 1983); but despite this evidence, most of the almond literature ignores the existence of female-sterile flowers, and the exceptional literature usually makes only a passing acknowledgement of the existence of such flowers.

There was not enough information available to determine the importance of female-sterile flowers to almond production in Australia, so I conducted some experiments which are described in Chapter 4. A brief summary follows.

Female-sterile flowers can be placed into several categories, depending on their morphology (Table 4.1). The proportion of flowers that were female-sterile varied between days from 10 to 90%, and over the whole 1984 season, 22 to 31% of flowers were female-sterile; so female-sterility is an important factor of nut-set. The percentages mentioned above may be shown, by microscopic examination, to be higher (e.g. Pimienta and Polito 1983), and the incidence of female-sterility may depend on several factors (Chapter 4). Flower sterility must be a crucial factor in experiments that use nut-set as a measure of productivity because measurements in terms of nut-set cannot indicate the potential of the tree to produce nuts if those measurements were taken during only part of a flowering season when the incidence of female-sterility was high.

7.2 Losses through damage to buds, flowers and developing nuts

Frost

Frost has been accused of being a major factor of nut-set in almond (e.g. Tufts 1919a; Quinn 1930a, 1930b). Frost usually effects buds, flowers

and developing fruits by freezing the ovules and embryos. Generally, almond flower-buds are not affected by temperatures as low as -40°C until two weeks before anthesis. Beyond that time, the ability of frost to kill almond buds, flowers and developing nuts depends on the stage of development, the temperature range, the duration of frost, and the cultivar; and the flowers of most almond cultivars are killed when exposed to an air temperature of -2°C for three hours (Dorsey 1919a; Taylor 1919; Field 1942; Wood 1947; Griggs 1949; Buyukyilmaz et al. 1976; Micke and Kester 1978b; Cary 1985).

Usually only the lower parts of trees are affected by frost because those parts are more likely to be situated in a pool of cold air, and air temperature tends to increase with increasing height above the ground (Seaton and Kremer 1939). Pools of cold air often accumulate in basins between dunes in the districts near the River Murray in South Australia and Victoria. Frost can kill all flowers and developing nuts within such pools of air; while buds, flowers and nuts only millimetres above the top of the pool of cold air remain unaffected. Growers have learnt to avoid growing almonds in high risk areas. Nevertheless, significant losses can occur in some districts and years, and the loss of whole crops is a risk in some districts (Witcombe 1981) (e.g. Fig. 7.1).

The risk of yield reduction through frost can be reduced by careful selection of the orchard site, improving air drainage, the use of irrigation (Phillips et al. 1983), and by the use of static wind-machines, helicopters or fires to mix cold air with the overlying warm air.

Birds

Many species of Australian birds damage or eat buds, flowers and developing nuts. Damage usually occurs during the period between bud-swell (two weeks before flowering) and harvest. Sometimes branches at the tops of trees are stripped of buds so that the ground beneath becomes strewn with flower buds (Fig. 7.2). Birds also chew holes in flower buds and eat the gynaecea and nectaries. Such buds usually open and abcise during the first few days of the flowering period. They cannot produce nuts but they still pose a useful source of pollen. Many birds eat or chew holes in developing fruits to get the soft, young kernels; and large parrots crack and eat mature nuts.

Figure 7.1: Almond trees covered by icicles near Mildura, Victoria in mid-July 1982, which was two weeks before the trees flowered. Nut-set the following summer was high, so the frost probably did not harm the flower buds. The icicles developed because overhead sprinklers were used in an attempt to reduce the effect of the frost on adjacent *Citrus* trees.

Figure 7.2: Flower buds strewn across the ground in Keane's orchard after birds had stripped the buds from some branches at the tops of the trees. Keane's orchard is described in Chapter 2.

Attempts to keep or drive birds away from almond trees meet with varying success, and some orchardists accept that they may lose 5% of their potential crop to bird damage, although a loss of more than 1% in large orchards seems rare. Generally, the significance of bird damage to nut-set depends on the size of the orchard; orchards of 100 hectares or more experience little damage compared to much smaller orchards.

Rain and hail

Heavy hail can strip trees of buds, flowers and nuts to the extent of total crop loss, but this rarely occurs in Australia. Bird-damaged and female-sterile flowers, which would eventually fall off, may be knocked off prematurely by rain and strong wind, but female-fertile flowers are not easily broken off trees. Heavy rain and hail can strip most petals from flowers, but the remainders of the flowers usually stay on the trees, and honeybees continue to visit and pollinate such flowers (Section 3.7).

Mechanical damage

Buds, flowers and nuts may be rubbed or knocked off by passing machinery and by strong winds that cause considerable movement of branches, but such damage is probably insignificant except in very localized parts of trees.

Pruning

Almond flower-buds are initiated in late spring - early summer (Chandler and Brown 1951), so the removal of branches after that time reduces the number of flowers produced the following spring. Almond trees are pruned during the first few years of the trees life in order to shape the tree. Trees are also pruned occasionally in winter to keep the orchard corridors free of intruding branches.

Chapter 8: Flowers and flowering

8.1 Flower longevity

8.1.1 The concept of effective pollination

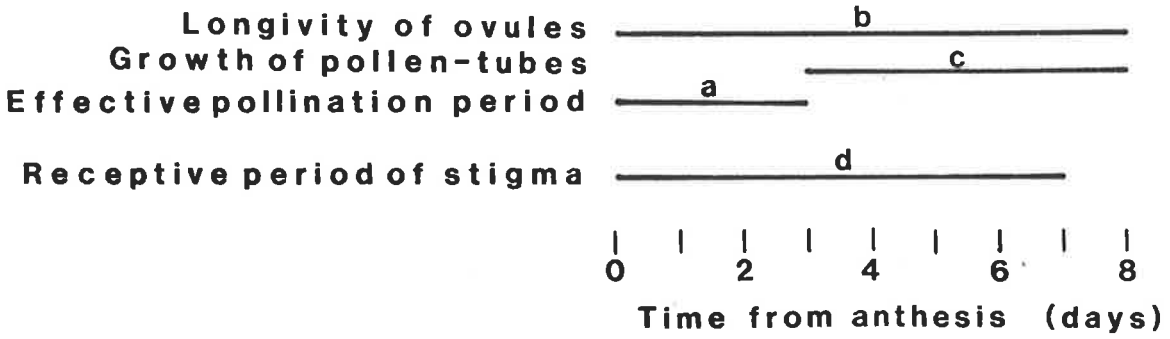
Pollination is defined as the movement of pollen from anthers to a stigma, but not every instance of pollination leads to the production of a fertilized fruit or nut, even when pollination is followed by the most favourable set of circumstances possible. Consequently, I find the term "effective pollination" useful, and I use it to refer to any instance of pollination that can lead to the production of a fertilized fruit or nut in circumstances that would "normally" be expected at the site of the flower in question. Whether or not a fruit or nut does develop depends on the circumstances subsequent to pollination, but that is not important to the concept of effective pollination. Also, effective pollination does not require a certain set of circumstances for it to occur. For example, effective pollination in almond would usually require that the pollen be viable and compatible, but pollen "viability" depends on the tests used to define it (Section 8.4.1), and "incompatible" pollen can lead to the development of a fertilized nut in some circumstances (Section 8.5.4). Whether or not effective pollination has occurred cannot be measured absolutely except when a nut is produced, but the probability of effective pollination occurring may be estimated.

8.1.2 Effective Pollination Period (EPPs)

Every flower has a limited life beyond which pollination cannot lead to the fertilization of an ovule. Williams (1965, 1966a, 1970b) referred to this time limit as the Effective Pollination Period (EPP), and defined it as the period determined by the longevity of the ovules minus the time necessary for the pollen-tubes to grow to the ovules. Occasionally, however, the receptive period of the stigma is less than the calculated EPP, and so the actual EPP is then equal to the receptive period of the stigma (see Fig. 8.1) (Dorsey 1929; Griggs and Iwakiri 1964, 1975; Weinbaum et al. 1980; Stosser and Anvari 1983).

Pollen cannot move to a stigma unless the flowers are open, and almond stigmas are receptive to pollen at anthesis (Free 1970a; Micke and Kester 1978). So the only time during which effective pollination can occur in almond is the time from anthesis to the expiration of the EPP.

Figure 8.1: The effective pollination period (EPP) (a) is equal to the longevity of the ovules (b) minus the time required for the pollen-tube to grow to the ovules (c); but if the receptive period of the stigma is less than the calculated EPP, then the EPP equals the receptive period of the stigma (d) (adopted from Wilson and Williams 1970, and Williams 1970b).



Each flower has its own EPP, but it is more convenient to refer to an EPP that is a mean for a group of flowers of a particular cultivar, the flowers having been pollinated with pollen of another particular cultivar; that is, a particular EPP usually refers to a particular pair of cultivars. But often only the identity of the recipient flowers is known, and the estimate of an EPP can be subject to considerable error when the source of pollen is unknown. The mean EPP is usually delimited by the time when nut-set becomes significantly less than the nut-set of newly-opened flowers, and so some flowers can be effectively pollinated after the EPP for the tree has expired (e.g. Williams 1965; Stosser and Anvari 1983).

The time when a flower's EPP ends is usually not obvious, and many authors either performed experiments without considering the EPPs of the flowers they used, or assumed that flowers could be effectively pollinated until petals abcised or there were signs of senescence on the stigmas (e.g. Tufts 1919a; Tufts and Philp 1922; Griggs 1958; Kester and Griggs 1959a; Nauriyal and Rana 1965; Thorp et al. 1967); and some authors may have reached different conclusions if they had considered EPPs. For example, some experiments on man-aided pollination may have worked, contrary to the authors' conclusions (Section 9.5.4).

EPPs for trees of apple, apricot, sweet cherry, plum, peach, and pear, vary between pairs of cultivars, and between years within pairs of cultivars, within the range of a few hours to at least 12 days (Hartman and Howlett 1954; Eaton 1959, 1962; Williams 1966; Toyama 1980; Vitanov 1983; Stosser and Anvari 1983; Postweiler et al. 1985; Guerrero-Prieto et al. 1985). The EPPs for pairs of almond cultivars probably vary to a similar extent, but the only EPP calculated for almond was 4 days for the cultivar-pair Nonpareil and Jordanolo (Griggs and Iwakiri 1964). That 4 day EPP was assumed by some authors (e.g. Micke and Kester 1978;Weinbaum et al. 1980) to be applicable to all pairs of almond cultivars, but that assumption is likely to be false because the time required for pollen-tubes to grow to the ovules varies from hours to days, depending on the cultivars and weather (Griggs and Iwakiri 1975; Dhaliwal et al. 1979; Godini 1981a). Indeed, the experiments of Griggs and Iwakiri (1964) were performed during warm weather so the EPPs of many pairs of almond cultivars may often be less than 4 days during cooler weather. On the other hand, Weinbaum et al. 1980 obtained 32 and 36% set after hand-pollinating 6-day-old almond flowers, and so EPPs may be more than 4 days in some circumstances.

In the experiment reported in Section 6.5, many flowers were not visited until 2 or 3 days after anthesis, although usually many visits occurred soon after the first visit (Fig. 6.11). Only 2 out of the 39 flowers produced nuts, so the EPP of the flowers in the experiment may have been only 2 or 3 days.

EPPs can be estimated by hand-pollinating flowers at a variety of times after anthesis and calculating the EPP from the gamma distribution curve that describes the EPPs for the tree's population of flowers (Williams 1970b; Brain and Landsberg 1981); but this procedure is time consuming and inaccurate because large samples are required to accurately detect the decline in nut-set.

Another method of measuring EPPs is the morphological examination of ovules and pollen-tubes in hand-pollinated flowers preserved in an age sequence (Williams 1965, 1966, 1970b). Newer methods of measuring EPPs involve direct measurements of pistil receptivity, pollen-tube growth, and ovule longevity. Pistil receptivity may be determined through the measurement of callose accumulation in the stigma (Dumas and Knox 1983). Pollen-tubes can be measured by staining hand-pollinated stigmas that have been maintained _in vitro_ or _in vivo_ and sampled in an age sequence (Martin 1959; Griggs and Iwakiri 1975; Socias i Company _et al._ 1976). Ovule viability can be assessed with a fluorescence-microscope (Anvari and Stosser 1978; Stosser and Anvari 1982, 1983; Bernhardt and Knox 1983; Postweiler _et al._ 1985).

Ovule longevity and pollen-tube growth, and hence EPP, vary greatly between dates and cultivars. Generally, ovule longevity decreases, and the rate of pollen-tube growth increases, with increasing temperature (e.g. Mellenthin _et al._ 1972; Stosser 1980; Jefferies and Brain 1984a, 1984b; Vasilakakis and Porlingis 1984; Postweiler _et al._ 1985), but there may be an optimum temperature above and below which the EPP, and nut-set following open-pollination, decrease (e.g. Marcellos and Perryman 1987). Furthermore, pollen-tube growth can be slowed by the presence of viruses (Marenaud 1974; Marenaud and Saunier 1974). Flower position may also be important; for example, ovules of Delicious apple tend to degenerate later in the terminal flowers than in the lateral flowers of clusters, which may be why the fruit-set of terminal flowers is often superior (Hartman and Howlett 1954). Apple cultivars with a tendency to biennial bearing often have longer EPPs in years of higher yields, but the significance of this coincidence is unknown (Williams 1970b).

Ovule longevity and the rate of growth of pollen-tubes, and hence the EPP and fruit-set, may be increased by the application of nitrogen fertilizer in summer or autumn (Dorsey 1929; Howlett 1936, 1938; Murneek 1937; Hartman and Howlett 1954; Williams 1963, 1965; Hill-Cottingham and Williams 1967); but Weinbaum *et al.* (1980) disagreed, stating that the EPP and fruit-set were not influenced, but that the nitrogen fertilizer increased both the number of fruit per tree and the weight of fruit per tree, by increasing both the number of flowers per tree and mean fruit size.

8.1.3 Pollination may end the EPP

The EPP of flowers of some plant species may be terminated prematurely when senescence is initiated by the presence of pollen on the stigma, whereas the flower may remain receptive for much longer if it is not pollinated (Stead 1985). Also, the process of senescence can be accelerated when the amount of pollen on the stigma is increased (Stead 1985). This reaction would not be important to fruit-set if effective pollination had occurred, but if the pollen was incompatible, then this process would be an important factor of fruit-set because subsequent effective pollination could not occur.

This form of flower behaviour has not been investigated or reported in flowers of *Prunus*, but the stigmas of some, and sometimes many, almond flowers begin to senesce 1 or 2 days after anthesis; that is, the stigmas darken, shrivel, and eventually abcise, leaving behind an ovary that may or may not be developing into a nut. This senescence of stigmas in young flowers has been reported in other plant species and it is considered in the determination of their EPPs (Section 8.1.2), but the nature of this senescence has not been investigated. My frequent sightings of senescent stigmas in young almond flowers suggest that this phenomenon should be investigated further.

8.2 Flowering periods

8.2.1 Coincidence of flowering periods

Almond flowers cannot be effectively pollinated until they have opened and the anthers in the flowers of another, compatible cultivar, have dehisced; that is, two compatible cultivars need to flower coincidentally. Further, the maximization of nut-set requires every flower to be

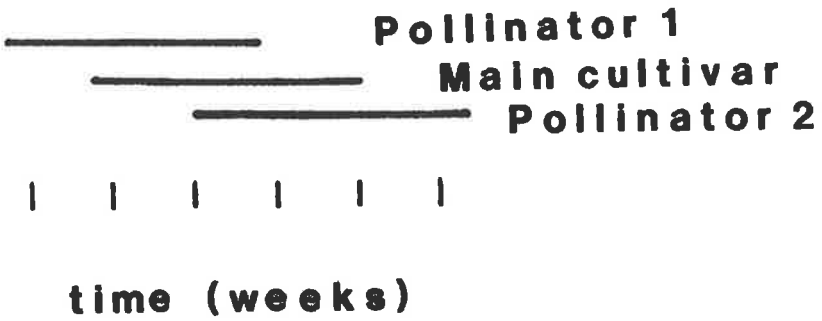
effectively pollinated (Section 1.8), so the flowering periods of the cultivars should coincide to within the EPP, otherwise early and late flowers may not be effectively pollinated. The EPP for fruit trees varies greatly between cultivar-pairs, orchards and years (Section 8.1.2), so specific recommendations for the minimum overlap of flowering periods cannot be made unless one takes the approach of allowing "for the most unfavourable circumstances likely to be encountered" (H.E.A.F.C. 1961).

Australian almond growers usually think of almond production in terms of one "main" cultivar which is pollinated by one or more "pollinator" cultivars, the pollinator cultivars being of lesser importance, with respect to the nuts they produce, than the main cultivar. Having only two cultivars per orchard is efficient for orchard management, but the inclusion of more cultivars is aimed at reducing the risk of insufficient cross-pollination when there are few flowers on the trees of one cultivar or when the overlap of the flowering periods is poor (H.E.A.F.C. 1961; Baker and Gathercole 1977; Hill et al. 1985). Consequently, orchards often contain three cultivars which are selected so that one pollinator cultivar flowers slightly earlier, and the other pollinator cultivar flowers slightly later, relative to the main cultivar (see Fig. 8.2). This arrangement ensures that the main cultivar is usually "adequately" pollinated; but the ability of the main cultivar to pollinate the pollinator cultivars is usually ignored, even though the pollinator trees comprise 30 to 50% of the trees in modern almond orchards. Many flowers on pollinator trees are open when compatible pollen is not available, but this need not be so because better overlapping of cultivars can be achieved through either selecting cultivars that flower coincidentally to within their EPPs, or by manipulating the flowering periods of some trees. Methods of doing this are given below.

8.2.2 Defining the flowering period of a cultivar

The definition of the term "flowering period" (of a tree) varies between authors. One can say that the flowering period begins when the first flower-bud undergoes anthesis, and ends when the petals have fallen from the last flower, but usually a few flowers open long before or long after the majority of flowers, and the combined period when the first and last 5% of flowers open can be double the period through which the remaining 90% of flowers open (e.g. Hill et al. 1985 - Appendix 3).

Figure 8.2: Diagram of overlapping flowering periods (from Baker and Gathercole 1977). The lines indicate the flowering periods of three cultivars.



Moreover, the presence or absence of petals is not an indication of the presence of pollen or of stigma receptivity (Section 8.1.2), and the date of petal fall can be altered by factors such as wind. So petal fall should not be used to delimit the flowering period. Perhaps the best way to delimit the flowering period is to use the date when 5 to 10% of the flowers are open, and the date when 5 to 10% of the flowers are still closed (e.g. Kester 1965).

The date when about 50% of the flowers are open has been referred to as the "date of full bloom" (Beakbane et al. 1935; Jackson 1975; Rattigan and Hill 1986) or the "date of flowering" (Irwin 1931), but the term is loosely defined because "date of full bloom" has also meant the date when 80% of apple flowers were open (e.g. Williams and Sims 1977). Several authors (e.g. H.E.A.F.C. 1961) decided that the date of full bloom was possibly more important than the length of the flowering period because on that day the tree offers the greatest opportunity for cross-pollination. However, that opinion is not applicable to crops that cannot achieve optimum fruit-set on one day of the flowering period; thus it is not applicable to almond to which the whole flowering period is important, especially given that the flowering period of a cultivar usually lasts several weeks (Hill et al. 1985 - Appendix 3). Also, fruit-set achieved on the date of full-bloom may usually be lower than on other days because, for example, the likelihood of a forager visiting flowers of different cultivars is less on the date of full bloom than on other days (Sections 12.2, 14.3.4).

Flowering curves of almond often approximate a normal distribution in relation to time, and the date of full bloom is approximately the peak of the curve (e.g. Kester 1965; Hill et al. 1985 - Appendix 3); therefore the mean and standard deviation of the flowering curve could be used to compare flowering periods.

Index numbers, based on the date of full bloom (50%) of particular reference cultivars, have been used to put cultivars into groups, the cultivars within a group being suitable for cross-pollination with respect to their flowering periods (Kester 1965). This grouping of cultivars presupposes that flowering periods of cultivars, relative to each other, do not change significantly between years and regions; but they do not change significantly, and this is discussed below.

8.2.3 Variation in the date of flowering and the period of flowering

The need for cross-pollination, and hence the need for cultivars that flower coincidentally, has been recognized for at least a century (Section 1.5), but the methods for determining the most suitable cultivars, with respect to coincidental flowering, are unsatisfactory for almond, although the methods may be adequate for crops that have a lower optimum fruit-set.

Most recommendations of suitable combinations of cultivars have been based on an average of several years of flowering data that were collected in a limited number of districts. Those averages were applied to every almond-growing district in the author's state or country (e.g. Tufts and Philp 1922; Wood 1947; Griggs 1953; Moss 1962; Kester 1965; Nauriyal and Rana 1965; Moss and Cowley 1970; Monastra 1982) on the justification that "actual flowering dates vary from district to district and from year to year but the relative times between cultivars remains fairly constant" (Baker and Gathercole 1977). Two cultivars were considered satisfactory for pollination if their average dates of full bloom were not more than 1 week apart (e.g. Griggs 1970; Baker and Gathercole 1977; Micke and Kester 1978). But this technique for the selection of cultivars does not result in satisfactory pollination in every year. Dates of full bloom vary differently for different cultivars and in different years and districts (Crandell 1924; Griggs 1949, 1958; H.E.A.F.C. 1961; Hill et al. 1985; Guerrero-Prieto et al. 1985), so one fruit tree cultivar is not always earlier or later than another by a constant number of days. Significant yield losses can occur in almond and apple in some years and districts when the relative flowering dates deviate greatly from the means. In such years and districts some cultivar-pairs, which usually flower coincidentally, still coincide favourably, whereas other cultivar-pairs do not, although the latter cultivars may appear favourable on an average-year basis (Wood 1946; Williams and Sims 1977; Hill et al. 1985). Furthermore, the flowering periods for some cultivars in some years are less than two weeks (e.g. Wood 1946; Hill et al. 1985), and so a difference of one week between average bloom dates could prevent many flowers from being effectively pollinated, especially if the weather was often poor for pollination and the EPPs were short. Consequently, the selection of suitable combinations of cultivars should be determined by comparing flowering periods on an annual basis and over several years, and by using only data collected within the district (e.g. Wood 1946; H.E.A.F.C. 1961; Williams and Sims 1977; Hill et al. 1985). However, an alternative approach may be to use a model that uses

temperature records to predict the date of flowering for each cultivar (e.g. Rattigan and Hill 1986 - Appendix 4). If successful, this method would overcome the need for flowering data from existing trees in the district concerned, and overseas cultivars could be evaluated, with respect to flowering, before being imported.

Flowering periods within cultivars and orchards can vary between trees and between branches within trees, and young trees can bloom later than older trees by up to three weeks; therefore perhaps only flowering dates of trees of the same age and in similar circumstances, should be compared exactly (e.g. Wood 1946; Section 2.4). Reasons for these variations in flowering are discussed in the next section.

Some cultivars usually have much longer flowering periods than other cultivars (Wood 1946; Hill et al. 1985), and cultivars with longer flowering periods may be more desirable. For example, adverse weather during a short flowering period limits the time during which effective pollination can occur and may prevent some flowers from being effectively pollinated (Sections 14.1, 14.2). Also, the probability of a flower being effectively pollinated may be higher during longer flowering periods because foragers are more likely to visit the flowers of two cultivars when fewer flowers open per day (Section 14.3.4).

Later-flowering cultivars are usually more desirable than early-flowering cultivars because poor weather for pollination is likely to occur less often in early spring than in late winter. However, in some areas and years, late flowering cultivars may not flower at all if their chilling requirement is not met during winter (see below).

8.2.4 Causes of variation of flowering dates

Flowering dates of almond trees are determined by genetic interaction with winter and spring temperatures. The subject is reviewed by Saure (1985). Trees of Prunus generally require several months of low temperatures followed by a few weeks of higher temperatures. The required amount of chilling and warming varies between cultivars and species (e.g. Ruck 1975). The relationships between dates of almond flowering and daily air temperatures are explained by a model that may allow the forecasting of flowering dates for specific almond cultivars to within an accuracy of a few days (Rattigan and Hill 1986 - Appendix 4). The model produced predictions that were within 5 days of observed dates in 59 out of 72 instances, and within 3 days in 46 instances; and there are several ways in

which the model can be improved. This model may enable the prediction of flowering dates in areas where cultivars are not present, which means the overseas cultivars can be evaluated, with respect to date of flowering, before they are imported. The robustness of the model is being investigated, and unpublished data from Nangiloc in Victoria, and from Nimes in France, indicate that the model is equally applicable to those two areas (Rattigan and Hill - unpublished data).

Temperature controls the duration of flowering for individual cultivars, the sequence of flowering for consecutive cultivars, and the length of the season between the first and last cultivar to flower. The following comments, derived from the observations and comments of Wood (1946), Brown (1952), H.E.A.F.C. (1961), and Griggs (1958, 1970), refer to almond trees in a Mediterranean type of climate.

If winter is relatively warm, flowering is late or may not occur at all. The colder the winter, the earlier the chilling requirement is met, but flowering does not occur until sufficient heating has occurred. So if the weather remains cold after the chilling requirement has been met, flowering is delayed. If low temperatures prevail after the first cultivar has started flowering, then the flowering succession of cultivars is spread over a long period. However, if winter temperatures stay low enough to keep all almond cultivars dormant until most or all the cultivars have fulfilled their chilling requirement, and then warm weather prevails, the cultivars flower relatively close together. If winter chilling is inadequate, many buds may fail to open and eventually the buds may fall off the trees.

Flower-bud temperature is the most fundamental of the known factors of date of flowering (Chapter 5), and bud temperature is influenced by the air temperature, the air flow past the bud, the intensity and duration of solar radiation (and shade), and evaporative cooling. Evaporative cooling depends on evapotranspiration, rain, chemical sprays, air flow, and humidity. The influence of those factors on bud temperature and, hence, date of flowering, can be affected by the structure, size, and position of trees; and they can account for differences in date of flowering with tree age and position. For example, the structure of young trees is more open and thinner compared to older trees, and so wind speed tends to be higher within younger trees, and more flower-buds can be heated by direct solar radiation. For similar reasons, trees on the edges of orchards or adjacent to breaks in the rows, may flower differently to the rest of the orchard (e.g. Section 2.4), and the flowering differences between the opposite

sides of a row of trees can be attributed to differences in solar radiation (i.e. shaded versus sunny sides of trees). The importance of solar radiation and bud temperatures to date of flowering is discussed further in Chapter 5.

Differences in flowering dates between the tops and bottoms of trees have occurred when there are temperature gradients with increasing height above the ground, and usually flowering occurs at the tops of trees before it occurs at the bottoms of the trees (Seaton and Kremer 1939). This phenomenon is common in orchards at Willunga (40 km. south of Adelaide) where cold air frequently flows from the adjacent hills and through the orchard, and elsewhere in orchards that are situated in air pockets between dunes (also see Section 7.2).

8.2.5 Controlling the flowering period.

Date of flowering in almond is determined by many genes (Kester 1965; Grasselly and Gall 1967; Kester and Asay 1975; Socias i Company *et al.* 1976), and breeding and selecting trees for particular flowering dates in *Prunus* can be achieved relatively easily. For example, Tardy Nonpareil, which is a bud sport of Nonpareil, flowers 10 to 14 days later than regular Nonpareil, and the major phenotypic change in Tardy Nonpareil appears to be the mutation of a single gene that affects time of flowering (Kester 1965). There is also an early flowering sport of Royal apricot (Lammerts 1941), and two mutants of Fascionello almond, which flower 15 to 20 days later than the parent tree, were induced by Gamma radiation (Monastra *et al.* 1983). A late flowering apricot cultivar is being sought through breeding in Italy (Fideghelli *et al.* 1979).

Many traits of cultivars need to be considered by almond growers when cultivars are being selected for a new orchard, and so almond growers may select cultivars that do not flower coincidentally to within a desirable tolerance every year. Consequently, methods of altering the date of flowering may be useful. Also, it may be financially desirable to make whole orchards flower earlier or later than normal, thus allowing the harvesting of nuts to be staggered and, when fruit trees are concerned, extending the time of supply of fresh fruit to markets.

Many methods of altering the date of flowering of fruit trees have been reported. Most authors have aimed to reduce the probability of flowers and developing fruits being destroyed by frost by delaying flowering to a less risky date. Date of flowering depends on a period of chilling followed

by a period of heating, which is explained in Section 8.2.4, and so the date of flowering can be altered by changing the accumulation of the chilling and heating requirements. Summaries of published experiments are in Tables 8.1, 8.2, and 8.3. The techniques include evaporative cooling (Table 8.1), shading (Table 8.2) and the white washing of trunks (Eggert 1944). Fruit maturity is usually delayed by a similar period (e.g. Chesness et al. 1977). Date of flowering can also be altered by the use of chemicals (Table 8.3) but apparently more is involved than the accumulation of chilling and heating units. Perhaps there is an effect on the mechanism behind the principle of chilling and heating requirements; for example, flowering may be controlled by changes in concentrations of plant hormones, which, in turn, are influenced by temperature (e.g. Saure 1985; Powell et al. 1986). The results of some of the chemical experiments listed in Table 8.3 may have been produced by the evaporative cooling effect of the chemical sprays and not by the influence of the chemicals (e.g. Chandler et al. 1937; Soni and Yousif 1978). Management practices can also effect flowering. For example, severe pruning of fruit trees encourages the growth of long shoots which show delayed flowering (Chandler and Tufts 1933; Hill and Campbell 1949), and nitrogen applied to apple and peach trees delayed bloom by 5 and 3 days respectively (Hill-Cottingham and Williams 1963; Reeder and Bowen 1977a, 1977b, 1978). In Indonesia, apple trees that are manually defoliated within one month of harvesting, flower four weeks later; but if defoliation is not performed, the trees become permanently dormant because of a lack of chilling to end dormancy (Saure 1971). The flowering date of apple and peach scions can be altered by using different rootstocks (Visser 1973; Young and Olcott-Reid 1979; Young and Houser 1980), and droughting trees induces early dormancy and early flowering (Hill and Campbell 1949).

8.3 Pollen production

8.3.1 Flowers that lack viable pollen

Flowers that have no pollen or contain only non-viable pollen occur in some peach cultivars (Knowlton 1924; Percival 1955; Fogle and Dermen 1969;

Table 8.1: Summaries of experiments in which dates of flowering were changed by evaporative cooling. All except 2 authors delayed flowering. The methods used involved the intermittent overhead spraying of water either (A) during the chilling requirement stage only, or (B) during the heat requirement stage only.

Crop	Delay	Method	Author
Apple	7 day	B	Baktir and Bearce 1978
Apple	8-9 days	B	Crassweller et al. 1981
Apple	9 days	B	Stang et al. 1978
Apple	14 days	B	Pisani and Anderson 1977
Apple	17 days	B	Alfaro et al. 1974
Apple	17 days	B	Hamer 1980
Apple	17 days	B	Anderson et al. 1974, 1975
Apple	18 days	B	Hewett and Young 1980
Apricot	10 days	B	Hewett and Young 1980
Cherry	3 to 6 days	B	Dennis 1980
Cherry	15 days	B	Alfaro et al. 1974
Nectarine	advanced 11 days	A	Gilreath and Buchanan 1981a
Nectarine	advanced 14 days	A	Erez and Couvillon 1983
Nectarine	14 days	B	Buchanan et al. 1976, 1977
Peach	13 days	B	Hewett and Young 1980
Peach	14 days	B	Buchanan et al. 1976, 1977
Peach	14 days	B	Chesness et al. 1977
Peach	14 days	B	Lipe et al. 1975, 1977
Peach	15 days	B	Barfield et al. 1977
Peach	15 days	B	Bauer et al. 1976
Pear	8 to 15 days	B	Collins et al. 1978

Table 8.2: Summaries of experiments in which dates of flowering were changed by shading.

Crop	Delay	Methods	Author
Peach	advanced 12 days	Shade cloth in winter	Buchanan et al. 1977
Nectarine	advanced 12 days	Shade cloth in winter	Buchanan et al. 1977
various	various results	Natural effect of winter fog	Chandler et al. 1937

Table 8.3: Summaries of experiments in which dates of flowering were changed by the use of chemicals.

Crop	Effect	Chemical	Method	Reference
Apple	advanced 14 days	nitrate of soda	spray in winter	Ballard and Volck 1914
Almond	delay 6 days	ethephon	spray after leaf drop	Browne et al. 1978
Almond	delay 6 days	gibberellic acid	spray in autumn	Hicks and Crane 1968
Almond	delay 6-8 days	potassium bromide	spray in summer	Blagonravova 1975
Almond	delay 6-8 days	malic acid hydazide	spray in summer	Blagonravova 1975
Almond	delay 6-8 days	IAA	spray in summer	Blagonravova 1975
Almond	delay 6-8 days	alpha-naphthyl acetic potassium	spray in summer	Blagonravova 1975
Almond	delay 7 days	alar (daminozide)	spray in winter	Ryugo et al. 1970
Almond	delay 12-15 days	alar (daminozide)	spray in autumn	Gil and Yarrazaval 1974
Apple	unknown	DNOC	spray at the end of chilling	Erez and Lavee 1973
Apple	advanced 14 days	linseed oil	spray in spring	Black 1936
Apple	advanced 21 days	dinitrocresol	spray in spring	Samisch 1945
Apricot	delay 4 days	ethephon	spray in autumn	Kaska 1978
Apricot	delay 5-11 days	malic hydrazide	spray just before flowering	Soni and Yousif 1978
Apricot	delay 5-11 days	succinic acid	spray just before flowering	Soni and Yousif 1978
Apricot	delay 5-13 days	narengenin	spray just before flowering	Soni and Yousif 1978
Apricot	delay 11 days	coumarin	spray just before flowering	Soni and Yousif 1978
Cherry	delay 3-5 days	ethephon	spray in autumn	Proebsting and Mills 1973
Cherry	delay 4 days	ethephon	spray before leaf fall	Dennis 1976
Nectarine	delay 8 days	SADH	spray at end of chilling	Guerriero and Scalabrelli 1978
Peach	delay several days	gibberellic acid	-	Bowen and Derickson 1978
Peach	delay 5 days	SADH	spray at end of chilling	Guerriero and Scalabrelli 1978
Peach	delay 5 days	potassium gibberellate	autumn spray	Stembridge and LaRue 1969
Peach	delay 7 days	ethephon	spray in autumn	Gianfagna et al. 1986b
Peach	delay 11 days	gibberellic Acid	spray in previous supper	Brown et al. 1968
Peach	delay 14 days	gibberellic acid	spray before end of chilling	Corgan and Widmoyer 1971
Peach	-	DNOC	spray at the end of chilling	Erez and Lavee 1973
Peach	advanced 1 day	potassium gibberellate	winter spray (mid-chilling)	Stembridge and LaRue 1969
Peach	advanced flowering	gibberellic acid	spray before end of chilling	Donoho and Walker 1957
Peach	terminated rest	thiourea and potassium nitrate	-	Wolak and Couvillon 1976
Pear	advanced 14 days	linseed oil	spray in spring	Black 1936
Plum	delay 4 days	ethephon	spray before leaf fall	Dennis 1976
Various	hasten bloom	dinitro-o-cyclohexylphenol	spray just before bloom	Chandler et al. 1937

Fogle 1977), but such flowers have not been reported in almond. Many authors have tested almond pollen for viability (Section 8.4.3), but no one reported finding individual flowers that contained only non-viable pollen. So male-sterile almond flowers, if they do exist, are unlikely to be a significant factor of pollination for almond.

8.3.2 Pollen production per flower

Almond flowers usually contain 28 stamens, but flowers that contain fewer stamens, or have filaments with underdeveloped anthers, are common (Section 1.3). Variation in number of stamens per flower has not been investigated, but the incidence of such flowers may vary within and between cultivars because the amount of pollen per flower varies within and between cultivars (e.g. Hill *et al.* 1985 - Appendix 3). Pollen production per flower in fruit tree crops generally differs between cultivars and years (Webster *et al.* 1949; Oberle and Goertzen 1952; Stanley and Linskens 1974).

The importance of these differences in pollen production is unknown, but one can speculate on several aspects. Pollen-collecting honeybees may make fewer visits to flowers with less pollen, than to flowers with more pollen because the number of foragers is usually proportional to the amount of pollen and nectar available (Section 10.3.2.1), and fewer visits means fewer chances of effectively pollinating the flowers (Section 13.4.4). On the other hand, the number of visits per flower may not be reduced if the period of anther dehiscence within a flower is independent of pollen production, such as is suggested in Section 6.3; and less pollen may improve the chances of effective pollination occurring because individual foragers may need to visit more flowers to obtain a load of pollen, which means there would be a greater chance of individual foragers visiting the flowers of two cultivars (e.g. Section 12.2).

8.3.3 Times of anther dehiscence within flowers

The little information contained in the literature on anther dehiscence in fruit trees is discussed in Section 6.1. Virtually no information was available on the dehiscence of almond anthers, so I performed some experiments which are described in Chapter 6. A brief summary is given below.

The timing and rate of anther dehiscence is an important pollination factor because a flower is unlikely to be visited by a pollen-collector

when there is no pollen available for collection (Williams and Brain 1985; Section 6.5), and almond pollen becomes available for collection by honeybees only when anthers dehisce. So, the sooner anther dehiscence occurs after anthesis, the more likely the flower will be visited and effectively pollinated by a honeybee before the EPP expires.

Anther dehiscence in almond can occur anytime day or night, but the rate of anther dehiscence depends largely on temperature, and the rate of dehiscence is usually higher during the hours of daylight because temperatures at night are usually lower and there is probably a threshold temperature, perhaps 7°C, below which anther dehiscence does not occur. Anther dehiscence appears to be independent of solar radiation except that solar radiation can affect the temperature of anther tissue.

Anther dehiscence within flowers did not occur until 6 to 48 hours after anthesis, and the last anther dehisced after another 2 to 74 hours. Anther dehiscence may occur sooner during warmer weather, and anther dehiscence may occur before anthesis during hot weather (Snyder 1942). Free water on anthers prevents dehiscence and can cause dehisced anthers to close.

If the EPP is only 2 or 3 days (Section 8.1.2), then flowers may not be effectively pollinated if anther dehiscence does not occur until 1 or 2 days after anthesis, because pollen-collectors rarely visited flowers before anthers had dehisced (Section 6.5; Fig. 6.11).

8.4 Pollen viability

8.4.1 Methods of assessment

The most common method of assessing the viability of pollen has been the *in vitro* pollen germination test on agar or on the surface of hanging drops. The results of such tests, however, vary to extremes and depend on the range and concentration of substances in the media (Kandasamy and Vivekanandan 1983). Sugar, usually as sucrose, is the main ingredient of the media, and the sugar concentrations used range from 5 to 20%. Good germination is usually obtained in 15% sucrose solution, but better germination occurs when glucose is used instead of sucrose, fructose or maltose (e.g. Kandasamy and Vivekanandan 1983). Germination and pollen-tube growth may be improved by the addition of boron and calcium to the media (Thompson and Batjer 1950; Vasil 1964; Kwack 1964, 1965; Brewbaker and Kwack 1965), and boron may prevent the bursting of pollen-tubes in sugar

solutions (Lewis 1979). Pollen germination and pollen-tube growth can also be affected by adding amino acids, proteins, and phenolic compounds, to the media, and changing the pH of the media (Stanley and Linskens 1974; Kandasamy and Vivekanandan 1983a, 1983b; Kobayashi *et al.* 1984).

The results of *in vitro* germination tests can also depend on errors in the techniques used. For example, pollen grains are mutually stimulated when crowded together on synthetic media or on the tissue of stigmas (Savelli 1940; Almeida 1945; Kwack 1965b; Linskens and Kroh 1967), and counts of germinated pollen grains on hanging drops may be biased by ungerminated pollen moving to the side of the drop (Stanley and Linskens 1974).

In vitro tests have been used as the only evidence to determine the suitability of particular almond cultivars for cross-pollination (e.g. Serafimov and Dzheneva 1980), even though the validity of *in vitro* methods as a simulation of *in vivo* germination has been questioned. For example, the amount of growth of pollen-tubes grown *in vitro* is usually small when compared with the distance the tube must travel in the plant in order to effect fertilization (Brink 1924). Furthermore, pollen may not germinate *in vitro* but it may germinate *in vivo*, and the reverse can also be true (Stanley and Linskens 1974; Parfitt and Almehdi 1984). One can argue that pollen *in vitro* cannot be in circumstances that are as favourable, or as natural, as the *in vivo* situation; however, the *in vivo* situation may not always be the most favourable situation for pollen germination whereas *in vitro* methods may be developed so that the method is reliable, repeatable, and favourable to pollen germination.

A compromise test which has the convenience of *in vitro* tests and the accuracy, or validity, of an *in vivo* test, is to use excised flowers *in vitro*, because the results are similar to *in vivo* germination (Stosser 1980). This test, however, does not overcome the need to consider the variation in pollen viability that may be caused by factors related to flower age, time of day, temperature, humidity, time allowed for germination, the recipe of the media or stigmatic fluid, the age, origin and storage treatment of the pollen, and the genetic interaction between the stigma and pollen (Thompson and Batjer 1950; Griggs *et al.* 1953; Thakur and Thakur 1972; Micke and Kester 1978b; Garcia and Egea Ibanez 1979; Parfitt and Almehdi 1984; Weinbaum *et al.* 1984). Rehydration of pollen before testing seems to be a particularly important factor (Brink 1924; Griggs 1958; Visser and Oost 1981; Montalti and Filita 1984; Corbet and

Plumridge 1985). Moreover, pollen collected by honeybees is generally less viable than hand-collected pollen, even within hours of being collected (Kremer 1948, 1949; Singh and Boynton 1949; Griggs *et al.* 1952, 1953; Vansell and Griggs 1952; Johansen 1956; Romisondo *et al.* 1972), although honeybee-collected fruit-tree pollen can remain viable for many months if it is quick frozen and kept in dry-ice (Griggs *et al.* 1950; Free 1960a). In contrast, hand-collected apple, pear, plum, and cherry pollen can produce viable seeds after up to 4 years of storage (King and Hesse 1938; Nebel 1939), even after being subject to short periods of temperatures up to 90°C (Marcucci *et al.* 1982). Perhaps the viability of honeybee-collected pollen is affected by the liquid added to almond pollen by honeybees, the subsequent growth of microbial organisms, and the decrease in the pollen's protein content (Stanley and Linskens 1974; Standifer *et al.* 1980; Klungness and Peng 1983).

Non-germination assays may be better that germination tests. Seed-set has been used as a measure of pollen viability, but too many other factors can be involved for those tests to be definitive (Knox 1984). Other tests, which involve the use of stains to detect chemical differences between viable and non-viable pollen, may be very reliable, but they destroy the pollen sample (Alexander 1969; Hoekstra and Briunsma 1975; Heslop-Harrison *et al.* 1983, 1984; Rajora and Zsuffa 1986). A non-destructive test involving nuclear magnetic resonance technology has been developed but its accuracy has not been proven (Dumas *et al.* 1983).

8.4.2 Factors of pollen viability

The pollen in the first flowers of the almond flowering season was not as viable as pollen in the flowers that open later (Tufts and Philp 1922; Tufts *et al.* 1926). Rain can burst pollen, but apparently that is not a significant problem in almond (Griggs 1958; Micke and Kester 1978b). However, the presence of free water on stigmas of *Brassica oleracea* can prevent or reduce pollen germination, and this effect may last after the water has disappeared (Zuberi and Dickinson 1985). If this problem occurs in almond then the incidence of wet stigmas could be an important factor of nut-set because almond flowers are often wetted by rain and fungicide sprays.

Viruses can reduce *in vitro* pollen germination and slow the rate of pollen-tube growth (Marenaud 1974; Marenaud and Saunier 1974), and several forms of air pollution can have similar effects (e.g. DuBay and Murray 1983).

Many fungicides kill pollen as easily as they kill fungal spores, and usually naked pollen from dehisced anthers is affected much more than pollen in non-dehisced anthers (Eaton 1961, 1963; Rui and Mori 1963; Cristferi et al. 1966; Shawa et al. 1966; Lockhart 1967; Eaton and Chen 1969; Gentile and Gallagher 1972; Ramina 1974; Legge and Williams 1975; Ries 1978; Fell et al. 1983; Marcucci and Filita 1984; Mayer and Lunden 1986; Section 3.5). However, not all pollen may be killed by fungicides, so fruit-set may not be reduced if "enough" viable pollen is left or deposited on each stigma to ensure that effective pollination has occurred (Church and Williams 1977). Methods of testing fungicides for their toxic effect on pollen are discussed by Church et al. (1983).

A single spray of some fungicides can kill most exposed pollen on anthers, stigmas, and honeybees; and so there may be a day or more, following the spraying, during which few or no flowers are effectively pollinated. When the EPP is only 2 or 3 days (Section 8.1.2) and flowers are effectively pollinated only on the second or third day (Section 6.5), then a single application of a fungicide could preclude many flowers from being effectively pollinated. Several applications of fungicides during the flowering season would compound the problem, and this may be a major factor of nut-set in Australia because several fungicidal sprays are applied during the almond season for the control of the fungus "shot-hole", which is also known as "Coryneum blight" and which is described by Cook (1975).

8.4.3 Viability of almond pollen

The viability of almond pollen is usually over 60% and it is rarely below 20% (Tufts 1919a; Tufts and Philp 1922; Griggs et al. 1952, 1953; Nauriyal and Rana 1965; Thakur and Thakur 1972; Garcia and Egea Ibanez 1979; Dhaliwal et al. 1979; Serafimov and Dzheneva 1980; Parfitt and Almehdi 1984). The number of "effective" pollen grains that must be deposited on an almond stigma to ensure that effective pollination has occurred, is unknown (Section 13.4.4). However, between 60 and 125 pollen grains may be deposited on each almond stigma when it is hand-pollinated (Tufts 1919a). Given that the viability of almond pollen is usually very high, between 60 and 125 pollen grains should be more than enough to ensure that pollination has been effective, or at least as effective as it can be. Furthermore, about 80 to 100 pollen grains may be left on each apple stigma after several visits by foragers (Free et al. 1974), which is also probably enough to ensure effective pollination; but this may not be true for a

single visit by a forager, and also higher densities of pollen may enhance the subsequent growth of pollen-tubes. The points raised in this section are discussed further in Section 13.4.4.

8.5 Pollen-stigma compatibility

8.5.1 Introduction

The presence of viable pollen on a stigma does not necessarily mean that effective pollination has occurred. The pollen grains and the style can interact in a way that prevents the pollen-tubes from reaching an ovule. When there is little or no likelihood of the pollen and ovule producing a zygote, the pollen and ovule, and the cultivars that produced them, are said to be incompatible.

Williams and Wilson (1970) defined several categories of pollen-stigma incompatibility on the basis of the physiological nature of the event in apple flowers. Three of those categories of incompatibility have been found in almond (Lewis 1944; Almeida 1945; Crow 1964; Socias i Company 1976), and those categories were described by Williams and Wilson (1970). Briefly, one category was characterized by the failure of pollen grains to penetrate the stigma or grow more than 2 mm into the stigma; and the other two categories are characterized by most pollen-tubes penetrating the stigma but with growth stopping somewhere in the stigma, the place of cessation of growth being the distinguishing feature between the two groups. Callose deposits are usually associated with the pollen-tube ends in all three categories. A fourth category of incompatibility in almond may be indicated by the failure of stigmas to retain many incompatible pollen grains (Pimienta *et al.* 1983).

Whether or not a pollen grain and a stigma are incompatible depends largely on the genetics of the pollen grain and stigma. Specific incompatibility genes, known as "S" genes, have been identified in *Prunus* (Crane 1925; Crane and Brown 1937), and incompatibility exists when the specific S gene in the pollen grain matches one of the two S genes carried by the tissue of the stigma (Way 1968). Proteins associated with the S genes can be identified by using gel electrophoresis (Li and Linskens 1983).

Incompatibility relationships in almond are usually discussed in terms of self-incompatibility and cross-incompatibility.

8.5.2 Self-incompatibility and self-pollination

The terms "self-incompatibility" and "self-pollination" refer to the situation where the pollen and ovule are of the same genotype, which in almond means that the pollen and ovule are from trees of the same cultivar (Section 1.3). Two forms of self-pollination are recognized. They are termed "unaided self-pollination" and "aided self-pollination", and they refer to self-pollination without, and with a vector, respectively. The former is also known as autogamy. Unaided self-pollination relies on wind, gravity and flower mechanisms to move pollen to the stigma, and aided self-pollination relies on the fore-mentioned mechanisms as well as honeybees and other animals, such as man (i.e. hand-pollination), to move the pollen. Fruit-set following aided self-pollination is usually much greater than fruit-set following unaided self-pollination (e.g. Laere 1957; McGregor 1976; Weinbaum 1985).

Aided self-pollination tests have been performed for many almond cultivars, but nut-set was usually less than 5% (e.g. Tufts 1919a; Tufts and Philp 1922; Reinecke 1930; Almeida 1945, 1948; Griggs et al. 1952; Cambra 1954; Nauriyal and Rana 1965; Grasselly and Oliver 1976; Godini 1977; Dhaliwal et al. 1979; Vasilakakis and Porlingis 1984; Uppal et al. 1984; Weinbaum 1985; Hill et al. 1985); and nut-set following unaided self-pollination was usually less than 2% (e.g. Reinecke 1930; Griggs et al. 1952; Cambra 1954; Godini 1977; Weinbaum 1985). A few cultivars managed to achieve up to 80% nut-set after aided self-pollination but those cultivars are deemed commercially unacceptable (e.g. Almeida 1945, 1948; Nauriyal and Rana 1965; Bright 1970; Griggs 1970; Grasselly and Oliver 1976; Godini 1977; Dhaliwal et al. 1979; Baker 1980; Uppal et al. 1984; Vasilakakis and Porlingis 1984). An exception may be the cultivar Truoito, which achieved up to 56% set after unaided self-pollination (Vasilakakis and Porlingis 1984).

An almond cultivar that is self-compatible and commercially acceptable should be able to achieve consistently higher nut-sets than the present self-incompatible cultivars because pollen transfer for self-compatible cultivars need only occur within flowers. Further, orchards could comprise only a single cultivar, which would overcome the harvesting problems that are due to the presence of two or more cultivars in the same orchard (Socias i Company et al. 1976; Micke and Kester 1978). Despite these advantages, orchards with several cultivars to ensure cross-pollination may still be desirable because self-compatible trees tend to increase their

fruit-set when visited by honeybees and when cross-pollinated (e.g. Lane 1979; Langridge and Goodman 1979, 1981; Matheson 1982).

The transfer of self-compatibility genes from peach and other species of Prunus has been an objective of almond breeding programmes in France, Israel, California and the Soviet Union (e.g. Kostina and Ryabov 1959; Pandey 1968; Kester and Asay 1975; Kester 1978; Grasselly 1979). Such programmes take many years because fruit trees usually require several years to mature and be tested, so commercially acceptable self-compatible almond cultivars may not appear in commercial orchards for at least several decades.

8.5.3 Cross-incompatibility and cross-pollination

Cross-incompatibility refers to pairs of cultivars that are incompatible when they are mutually cross-pollinated. Usually they produce nut-sets of only a few percent, and often no nuts are produced. Cross-incompatibility tests for a particular pair of cultivars usually produce similar results, regardless of which cultivar supplies the pollen. Pairs of cultivars that are known to be cross-incompatible are listed in Table 8.4. Usually cultivars within cross-incompatible pairs are closely related. Furthermore, many almond cultivars are cross-compatible with cultivars of other species of Prunus (e.g. Gagnard 1954).

8.5.4 Variable incompatibility

Incompatibility is not absolute in Prunus and Malus, that is, most cultivars or cultivar-pairs that are normally self- or cross-incompatible respectively, can produce significant fruit-sets when subjected to certain conditions; and temperature is a particularly critical factor (e.g Bowman 1939; Williams and Maier 1977; Raff and Clayton-Greene 1983; Weinbaum 1985; Hill et al. 1985). The variation in incompatibility appears to be due to variation in the race between the incompatibility reaction, which is working to stop the growth of the pollen-tubes, and the pollen-tubes, which are growing to the ovules. The incompatibility reaction seems to need a certain period before it stops the growth of the pollen-tubes; so the pollen-tubes have a time limit within which they must reach the ovules, otherwise incompatibility occurs.

Table 8.4: Pairs of cultivars that are cross-incompatible.

Cultivar	Authors
Brandis Jordan and Joses Jordan	Bowman 1939
Britz late-flowering and Britz early-flowering	Thiele 1968
Jordan Hardshell and Large Papershell	Bowman 1939
Jordanolo and Harpareil	Wood 1947; Kester 1963; Griggs 1970
Long IXL and Profuse	Griggs 1970
Mission (Texas) and Ballico	Kester 1963; Griggs 1970
Mission (Texas) and Languedoc	Tufts 1919a; Wood 1947; Kester 1963; Griggs 1970
Nonpareil and Cressey	Griggs 1970
Nonpareil and IXL	Tufts 1919a; Wood 1947; Thiele 1968; Griggs 1970
Nonpareil and Profuse	Kester 1963
Nonpareil and Tardy Nonpareil	Griggs 1970

Generally, the rate of pollen-tube growth is increased by increasing temperatures, so if incompatibility can be overcome, it is more likely to occur at higher temperatures (e.g. Lewis 1942; Griggs and Iwakiri 1975; Socias i Company et al. 1976). Conversely, some cultivar-pairs that are normally classed as cross-compatible, may be cross-incompatible at low temperatures, the result of which may be confused with the situation in which the growth of pollen-tubes is slowed by lower temperatures so that the ovules die before the pollen-tubes reach them (i.e. EPPs - Section 8.1.2).

The speed at which pollen-tubes grow in a stigma differs between cultivar-pairs, and the differences appear to be unrelated to any of the incompatibility reactions mentioned above. Generally, the fastest growth of pollen-tubes in almond occurs when the temperature is between 18 and 30°C, and below 15°C the pollen-tubes often fail to reach the ovary, regardless of the cultivars involved (Griggs 1958; Socias i Company et al. 1976; Weinbaum et al. 1984). This information has been used to support the suggestion that orchard temperatures generally should be kept above 13°C by supplementary heating and the use of windbreaks to reduce the wind-chill factor (Anon 1980). The growth of pollen-tubes is probably an important factor of nut-set in Australian almond orchards because daily maximum air temperatures in most districts are usually below 13°C during the first half of the almond flowering season.

Techniques of overcoming self-incompatibility are available (Lewis and Crowe 1958; Linskens et al. 1960; Ascher and Peloquin 1966; Hopper and Peloquin 1968; Nakanishii et al. 1969; Shivanna and Rangaswamy 1969; Callan and Thompson 1986, but few of the techniques are commercially acceptable for almond compared to the selection of compatible cultivars. However, "pioneer", or "mentor" pollen, which is discussed in Section 13.4.4, may be used to overcome incompatibility in special circumstances, such as in hand-pollination experiments. The pioneer pollen effect may be common in orchards, albeit undetected, and so it may be overcoming some compatibility problems that normally occur in orchards.

Chapter 9: Carriers of pollen

9.1 Introduction

Almond flowers must be cross-pollinated, and carriers are needed to transfer pollen between flowers. Almond trees flower in late winter - early spring, so the carriers must operate in the low temperatures that are common at that time. Several carriers have been thought important for almond pollination and they are discussed below. Information on the transportation of pollen between almond flowers is scanty, but the pollen of other species of fruit trees (i.e. Prunus spp., Malus spp.) are similar morphologically to almond pollen, and apparently they are transported similarly, so the general literature on fruit trees is referred to in this thesis.

9.2 Wind pollination

Fruit-set due to wind-borne pollen is usually insignificant and the pollen of fruit trees can only be transported by very strong winds (e.g. Wood 1937; Free 1970a p384; Langridge 1969; Langridge and Goodman 1973, 1979, 1981), perhaps because the pollen of most deciduous fruit trees are sticky and hence difficult for wind to dislodge unless the pollen is dried by high temperatures and low humidity (Vansell and Griggs 1952; Crane 1985). Wild bees and other insects probably caused the setting of almond crops said to have been set through wind pollination (Wood 1937). Pear pollen is different from the pollen of trees of Prunus and Malus in that it is lighter and less sticky and so it is more likely to be transported by wind (e.g. Stephen 1958; Free 1970a p384).

9.3 Animals as vectors of pollen

Insects are the only animals that feed in sufficient numbers on the flowers of fruit trees to achieve an acceptable incidence of effective pollination, and many species of the insect orders Hymenoptera, Lepidoptera, Diptera, Coleoptera and Hemiptera visit flowers in orchards (e.g. Free 1970a p387; Kendall 1973; Langridge and Goodman 1979, 1981; Boyle and Philogene 1983, 1985). Even self-fertile trees can benefit from insect visits because insects can transfer pollen within a flower from the anthers to the stigma (Drescher 1976; Fogle 1977; Lane 1979; Langridge and Goodman 1979, 1981; Matheson 1982). However, wild populations of insects have been reduced by the intensive cultivation of land, so few wild insects

are available for pollination in orchards (Free 1970a p388; Romisondo et al. 1972; Langridge and Goodman 1979, 1981). Consequently, insects must be introduced into orchards to ensure adequate pollination.

Many species of solitary bees have been suggested as commercially acceptable vectors of pollen, particularly species of the genus Osmia (Batra 1979). For example, Osmia lignaria may be an efficient pollen vector for almond and the bee can be managed easily by orchardists, but thoughts that Osmia lignaria may be better than honeybees (Apis mellifera) for almond pollination (e.g. Torchio 1976, 1978; Phillips and Klostermeyer 1978; Thorp 1979; Klostermeyer 1979) are unfounded because the experiments in question achieve similar results when done with honeybees (see Erickson et al. 1977). Also honeybees are active at low temperatures when Osmia spp. are not active. Osmia lignaria are not available anywhere in sufficient numbers for commercial almond pollination but they may be available within a few years in California (Thorp 1979; Baker 1980).

The domestic honeybee (Apis mellifera) is the only insect available for commercial pollination services in Australia. There are few other insects suitable for the pollination of almond flowers because the honeybee flies at lower temperatures than most of the other insects that are found in orchards (e.g. Romisondo et al. 1972); so only the behaviour of honeybees (Apis mellifera) is discussed in this thesis.

Suggestions have been made of a need for another insect pollen-vector that is more active than the honeybee during inclement weather, the reason being that active insects at low temperatures could achieve pollination, even though at such times anthers may not be dehiscing, stigmas may not be receptive, and pollen tubes may not grow. The idea is that pollen would then be on the stigmas when the conditions favoured stigma receptivity and pollen tube growth (e.g. Free 1967; Traynor 1966; Williams 1970; Taber 1985). The idea is, however, untested, and it can be opposed by speculating with some known facts; for example, at such times, very little pollen may be on dehisced anthers (Section 6.3), pollen may not adhere to unreceptive stigmas (Pimienta et al. 1983), and insects are unlikely to forage during chilly weather if there is no food for them to collect (Free 1970a p87; Section 10.3.1).

9.4 The domestic honeybee (Apis mellifera)

There are several races of honeybees, and some races appear to be better than others for pollination; but most apiarists have selected bees for honey production, not pollination ability, so the honeybees that are available may not be efficient compared to what may be possible (Green 1934; Gary et al. 1978a; Bailey 1982). Only four races of honeybee are thought important by Australian apiarists. They are Italian, Caucasian, Carniolan, and Black (Green 1934; Bailey 1982).

Black bees are particularly useful for the pollination of fruit trees that flower early because Black bees fly at low air temperatures while other races remain hive bound (Green 1934; Bailey 1982). However, Black bees are poor honey producers, difficult to handle, and have an unpredictable temper, the last problem making them unsuitable for populated areas (Bailey 1982). Consequently, Black bees are not readily available for pollination in Australia although they appear to be the most suitable race of honeybees for almond pollination.

Breeding programmes to select bees for their pollination ability have been instigated (e.g. Conner and Cale 1979; Brother 1983; Taber 1985; Hellmich et al. 1985, 1986). One strain of bees, which is known as Hy-Queen, was thought better than Italian bees for pollination, but Gary et al. (1978a) decided that there was little if any advantage in using Hy-Queen bees for almond pollination. Africanised honeybees may be more suited to pollination than other races of honeybees because Africanised bees may have lower temperature thresholds for foraging, and at higher temperatures they may be more active than other honeybees (DeJong 1984); but Africanised bees are unlikely to be allowed into Australia because of the difficulties created by their aggression. Breeding programmes may also breed bees that favour the collection of pollen from particular crops; for example, honeybees that favour the collection of lucerne pollen have been bred (Nye and Mackenson 1970).

Most of the research on honeybees and pollination has been done with Italian, Caucasian and Carniolan bees; especially the Italian bees because they are the most common race. However, much of the information on the behaviour of honeybees of various races has been mixed because many authors did not state the specific race of honeybees used in their experiments. Also, bee behaviour varies between and within races, and interbreeding between races is apparently common (Bailey 1982). Consequently, I have disregarded the existence of races of honeybee in the remainder of this thesis.

9.5 Man-aided pollination

Some orchardists have turned to artificial methods of pollination to overcome either a lack of insects or a lack of suitable pollen-donating cultivars. Most methods require the collection of pollen by hand and many methods of collecting pollen have been described (e.g. Howlett 1927; Snyder 1942, 1946; Barrett and Arisumi 1952; Griggs 1953; King 1956; Free 1970a p410).

9.5.1 Direct pollen application

Methods of applying pollen directly to the stigmas of fruit trees include hand-pollination (MacDaniels 1930b; Overley and Overholser 1938; Snyder 1942, 1946; Overley and Bullock 1947) with bellows (Overley and Bullock 1947), spraying pollen by ground based machinery as either a solution (Overley and Bullock 1947; Blasberg 1951) with sugar (MacDaniels 1930b; Griggs and Vansell 1949) or as a dust (Overley and Bullock 1947; Williams and Legge 1979), from aircraft as a dust (Overley and Bullock 1947), and by bombs filled with pollen and exploded in the orchard (Bullock and Snyder 1946; Overley and Bullock 1947; Bullock and Overley 1949). Only hand pollination and dusting without using talc were shown to be significantly effective (Overley and Overholser 1938; Overley and Bullock 1947). Hand-pollination can be done efficiently by using a bee stick, which is a tooth pick with the thorax of a honeybee glued to the end (Williams 1980).

Pollen has also been applied directly to the flowers of fruit trees using helicopters and ground blowers with the intention of providing additional pollen for redistribution by pollinating insects, and not to transfer pollen directly to the stigmas of the flowers; but the treatments did not increase yield (Thorp *et al.* 1967).

9.5.2 Pollen inserts

Pollen "inserts" or "dispensers" were designed by several people (e.g. Burrell and King 1932; King and Burrell 1933; Kremer 1948; Antles 1953) to apply pollen to the bodies of bees as they leave the hive, the idea being that the bees are carrying suitable pollen for cross-pollination when they arrive at the first flower. The design and use of pollen inserts is reviewed by Legge (1976), and some aspects that he did not mention are discussed below.

Theoretically, fruit-set should be improved by the use of pollen inserts, but there is some contention as to whether or not pollen inserts do improve fruit-set, mainly because definitive experiments have not been done. Pollen inserts have been tested in orchards of apple, almond, and sweet cherry, but many authors decided that the inserts were not worth using, although perhaps slight increases in apple yield were obtained (Burrell and King 1932; King and Burrell 1933; Overley and O'Neill 1946; Webster et al. 1949; Griggs et al. 1950, 1952; Griggs and Iwakiri 1960). The inserts usually failed because some bees carried pollen back into the hive while other bees fanned the mixture away, hence a way was soon cleared so that the bees could leave the hive with little or no contact with the prepared pollen. Pollen was usually placed in the pans too infrequently to overcome this problem. Furthermore, bee-collected pollen loses its viability rapidly so the pollen placed into some pollen inserts may not have been viable (e.g. Kremer 1948, 1949; Singh and Boynton 1949; Griggs and Vansell 1949; Griggs et al. 1950, 1952, 1953; Vansell and Griggs 1952; Johansen 1956; Romisondo et al. 1972).

Several authors claimed to have produced satisfactory fruit-sets by the use of pollen inserts (e.g. Kremer 1947; Griggs and Vansell 1949; Karmo and Vickery 1954; Johansen and Degman 1957; Townsend et al. 1958; Jaycox and Owen 1965), but usually either insufficient information was given to evaluate the results, or the experiments were poorly designed. For example, Townsend et al. (1958) commented that other authors achieved only poor fruit-set because their pollen inserts were poorly designed. But Townsend et al.'s (1958) experiments were also poorly designed because they lacked adequate controls and most were done with pear, the pollen of which is not comparable to the pollen of apple or Prunus species, because pear pollen is much lighter and not sticky (Section 9.2). Further, the results of the experiments of Townsend et al. (1958) and Johansen and Degman (1957) with sweet cherry and apple, can be interpreted as showing that fluorescent powder is easily spread by honeybees and that high fruit-set can be achieved when a tree is enclosed in a cage with a hive, because self-fertile trees caged with a hive without an insert could also get a high fruit-set (see Erickson et al. 1977). Also, caged trees are an unrealistic portrayal of an orchard because bees within the cage have a restricted foraging area; and so the value of pollen inserts for apple and sweet cherry was not tested. Furthermore, Johansen and Degman (1957) replaced the pollen in the pollen insert hourly for three days, a procedure

which is commercially impractical because it requires a very large amount of pollen and labour.

Good evidence to show that pollen inserts increase fruit-set in orchards of apple and Prunus spp. does not exist, and most of the evidence that does exist was produced by the workers who designed the inserts (Legge 1976). Furthermore, pollen inserts are relatively expensive because they require frequent attention and a continuous supply of pollen (Todd and McGregor 1960; Traynor 1966; Free 1970a; Ferrari 1985). Nevertheless, pollen inserts are still advertised in magazines and journals and are used for pollinating flowers of plum, apple, pear, cherry and almond in the United States of America.

9.5.3 Bouquets.

A few almond orchards are largely or completely comprised of trees of a single cultivar because of either ignorance of the need for cross-pollination, preference for the advantages of having a single-cultivar orchard, or a temporary shortage of suitable "pollinator" trees. Bouquets of flowers of compatible cultivars have been recommended for those orchards as a temporary measure to overcome the lack of suitable sources of compatible pollen (e.g. Phillips 1930; Oppenheimer 1948). Bouquets may increase fruit-set only within a few metres of the bouquets (MacDaniels 1930a, Free 1962a), and honeybees tend not to visit bouquets on the ground, therefore authors have recommended that a bouquet be hung in every tree (Free 1970a p410; Briggs et al. 1983), preferably on the sunniest side of each tree (Snyder 1946; Free 1960a).

Generally, the use of bouquets is not practical because cutting and replacing bouquets every two days requires considerable labour, and a large orchard involves considerable destruction of the trees from which the bouquets are obtained (Brittain 1933). Consequently, most authors recommend the use of bouquets only as a temporary measure until a better system of pollination can be established.

9.5.4 Summary of man-aided pollination

Most of the methods of man-aided pollination did not demonstrate statistically significant increases in yield. However, most of the techniques should be reexamined because many authors appeared to be unaware of some of the critical factors of nut-set. For example, some authors (e.g. Thorp et al. 1967) applied pollen once only, but yield cannot be significantly increased by only one application of pollen when the EPP is only a small fraction of the flowering period, hence the small increases obtained may have been significant, although not detectably so. Moreover, the amount of pollen sprayed onto plants was probably often inadequate to ensure that a sufficient amount of pollen was deposited onto every stigma, because the surface area of stigmas is minute in comparison to the total surface area onto which pollen can land (Lotter 1960; Williams and Legge 1979). Also, the pollen in some experiments may have been macerated by explosions (e.g. Bullock and Overley 1949), by immersion in water (e.g. Overley and Bullock 1947), and by pumps and spray nozzles (e.g. Blasberg 1951; Williams and Legge 1979), and most experiments were not designed or suitable for statistical testing (e.g. Overley and Bullock 1947; Townsend et al. 1958), so the ideas should be retested.

Overall, most forms of man-aided pollination require a considerable labour input compared to the efficient use of honeybees, and so the efficient use of honeybees may be the better option of achieving good pollination. Nevertheless, man-aided pollination may be useful when honeybee activity is low. Indeed, several forms of man-aided pollination are used commercially in the United States of America (Griggs 1970), and many companies supply pollen for man-aided pollination (Stanley and Linskens 1974).

Chapter 10: Putting hives into the orchard

10.1 Introduction

The need for honeybees as pollen vectors in almond orchards was established in Chapter 9, but some orchardists do not acknowledge the importance of honeybees and so they use few or no hives. Orchardists who do use honeybees are confused by the varied recommendations, some of which are given in Table 10.1 (see the table). For example, the most recent information available to Australian almond growers states that "at least 3 hives a hectare are recommended - 6 to 8 hives a hectare are better" (Baker and Gathercole 1977). This confusing advice occurs because hives are extremely variable units, and the optimal number of honeybees per orchard varies greatly between orchards and between years within orchards. This variation is discussed below.

10.2 Hive strength

10.2.1 Measures and measurements of hive strength

The population per hive, often referred to as the hive "strength", varies greatly between hives and with time within hives. "Large" or "strong" colonies are often recommended for pollination, but the definition of such colonies varies between authors and is often vague and confusing, if indeed it is given at all (e.g. Table 10.1). The confusion can be attributed to different terms of measurement, different definitions of the terms of measurement, and different recommendations that are defined in a given term of measurement.

Generally, two measures are used to define the strength of a hive: number of bees and amount of brood; but several different terms of measurement have been used, including frames of brood (e.g. Phillips 1930b; Rea 1940; Webster *et al.* 1949; Coggshall 1951; Griggs 1953; Todd and Reed 1970), combs of brood (Goebel 1984), square inches or centimetres of brood (Purdie and Winn 1965; Sheesley and Poduska 1968a, 1969b; Stanger and Laidlaw 1974), frames of bees (Phillips 1930a; Sheesley and Poduska 1970a; Meith *et al.* 1977; Waller *et al.* 1985), and thousands of bees (Todd and McGregor 1960).

Even the definition of a given measure can differ between authors. For example, a frame of bees or brood is often thought by apiarists to be a hive frame with the comb on both sides being about 70% covered with

Table 10.1: Hive density recommendations by various authors. All the density data are expressed in terms of hives per hectare. A dash indicates that the missing information was not given by the author.

Crop	Density	Minimum hive size	Reference
Almond	2.5 or less in good weather	-	Quinn 1941; Wood 1947
Almond	2.5	-	Taylor 1919; Tufts 1919a; Gayford 1947
Almond	4	-	Gagnard and Griessinger 1954
Almond	2-4 minimum for good weather	-	Gary et al. 1976
Almond	2-7	-	Stanger and Thorp 1972
Almond	2.5 - 7.5	strong	Griggs 1953
Almond	3, but up to 8 better	-	Baker and Gathercole 1977
Almond	3.5 to 7.5	6-8 frames of bees	Meith et al. 1977
Almond	5 to 7.5	5,100 cm^2 brood plus many bees	McGregor 1976
Almond	5 or more	4 frames bees + active queen	Baker 1980
Apple	2 - 4	30-35,000 bees, 4-9 brood frames	Goebel 1984
Apple	2.5 or more	-	Brittain 1933; Green 1934
Apple	over 6.5	-	Kelty 1948
Trees to 12 years	1 per 3-4 hectares	-	Dickson 1942
Young trees	2.5 per 3-4 hectares	-	Howlett 1927
Young trees	2.5 per 3-5 hectares	minimum of 25,000 bees	Murneek 1930
Older trees	2.5	minimum of 25,000 bees	Murneek 1930
Fruit trees	2.5	-	Jackson 1947
Fruit trees	5	12 frames bees at 18.5°C	Traynor 1966

honeybees (e.g. Traynor 1966; Waller et al. 1985), but researchers often regard a frame as being the equivalent of 100% coverage (e.g. Sheesley and Poduska 1970; Baker 1980; D.A. Maelzer and P.H. Mew - unpublished paper). Maelzer and Mew recommended 100% coverage as a standard definition for a hive frame, which in Australia means that a frame consists of 1,780 square centimetres and 3,500 bees. This is in contrast to the use of 1,200 square centimetres and 1,500 bees as the definition of a frame (Waller et al. 1985). Measurements in square centimetres are precise, but such measurements require more time than, say, counting frames of bees. However, in a controlled experiment, apiarists usually over-estimated the number of frames of bees, often by over 100% (D.A. Maelzer and P.H. Mew - unpublished paper), and so visual estimates of hive strength may be unreliable. Regardless of the measure used, not all the bees of a colony may be present at the time of measure, and so time of day, weather, and amount of foraging activity should be considered when hive strength is being estimated (Todd and McGregor 1960).

Recommendations of a minimum hive strength, using a particular term of measurement, also differ greatly. For example, recommendations, in terms of number of frames of brood, vary from 4 frames to 7-8 frames (Free 1970a p397). Furthermore, many authors state a minimum hive strength, and then they recommend hives that are stronger than the recommended minimum strength, because those authors believe the number of foragers per colony is proportional to the size of the colony; that is, larger colonies may have more foragers and, if so, fewer hives are needed to provide the same pollination service (e.g. Phillips 1930a, 1930b; Farrar 1931, 1937; Brittain 1933; Rea 1940; Free 1960a, 1967; Todd and Reed 1970; Erickson et al. 1975; Gary 1979; Thorp 1979; Rinderer et al. 1984; Waller et al. 1985). There are good arguments to support the belief that larger colonies have more foragers than do smaller colonies, but the experiments that supposedly show that the number of foragers does, or does not, vary with colony size, were poorly designed and analysed, and the differences between some treatments in some experiments were probably not statistically different (e.g. Woodrow 1932). Many experiments were based on incorrect assumptions, such as "nectar-collectors are not important for pollination because they rarely pollinate flowers" (e.g. Sheesley and Poduska 1970a), which is probably not true for many cultivars of almond and other crops (Section 13.1). Also, the experiments would have been complicated by other factors; for example, the number of pollen-collectors and nectar-collectors in a

colony varies during and between days, depending on the needs of the hive (e.g. Sections 11.3, 12.3), the amount of pollen and nectar available (Section 10.3.2.1), the weather (Section 14.1), and the amount of brood present (Sections 10.3.2.3, 12.3). Generally, 30 to 50% of a colony's population usually have foraging duties (Bodenheimer and Ben-nerya 1937).

Larger colonies may not be proportionally more valuable for pollination in Australian almond orchards. For example, the extra foragers in a larger colony may not contribute to pollination when the nearest available food source is further than the foragers may be prepared to fly when the weather is marginal for flight (Section 14.2); and the weather is often marginal during the Australian almond flowering season. Perhaps the finding of Sheesley and Poduska (1970a) that colonies larger than 12 frames of bees collected no more pollen, showed the limit of foraging distance which was imposed by the weather during their experiment.

Nevertheless, there may be other advantages in having very strong colonies. For example, larger colonies may have a better chance of survival in cold areas because a larger colony is more able and more efficient at keeping the hive warm. Also, honeybees fly at lower ambient air temperatures from strong colonies than from weak ones, which means foragers from larger colonies may spend more time per day foraging (e.g. Sharma and Sharma 1950; Coggshall 1951; Eckert and Shaw 1960; Free and Preece 1969; Thorp et al. 1973, 1974; Erickson et al. 1975; Harbo 1983). Colonies of less than 10,000 bees risk extinction in winter, and an optimum autumn population may be less than 18,000 bees because colonies with an autumn population above 18,000 do not have a proportionally greater spring population (Jeffree 1955; Jeffree and Allen 1956; Free and Racey 1968).

The Californian State Beekeepers Association stipulates a minimum standard hive strength of four frames of bees (i.e. about 12,000 to 14,000 bees) with an active queen at the beginning of the flowering season; and many apiarists provide stronger hives with developing brood (Baker 1980). This standard is probably suitable for Australian almond orchards because it seems to satisfy the limits and problems discussed in this Section. Discussions in sections below (e.g. Sections 10.3.2, 14.2, 14.3) suggest that larger colonies may not be more useful than smaller colonies to many Australian almond growers.

10.2.2 Use food supplements to increase hive strength

Colony populations normally decline during autumn and winter because there is little, if any, brood when pollen is not available, and adult bees cluster together during winter and consume stored honey for warmth. The almond flowering season starts in late winter, and so honeybee colonies are at their lowest population levels when almond trees flower. This does not worry most apiarists because the hive populations increase during spring, but that can be too late for much of the almond flowering season, and so many colonies are below the recommended minimum strength of four frames of bees per hive at the beginning of the flowering season (Section 10.2.1).

The strength of hives can be increased in preparation for the almond flowering season by feeding the colonies during autumn and winter. Colonies that are fed supplements throughout winter may attain a population of 30,000 to 35,000 bees, whereas the same hive without supplements may have only 8,000 to 12,000 bees in spring (Grout 1949; Stanger and Laidlaw 1974). The feeding of supplements must be started early because a brood cycle of honeybees takes 21 days to mature (Sheesley and Poduska 1969a; Stanger and Laidlaw 1974).

Both pollen and nectar must be given if brood rearing is to begin, and brood rearing continues only if pollen is available (Doull 1972; 1975a). A common supplement is syrup with pollen added (Todd and Vansell 1942; Free 1958; Spencer-Booth 1960; Sheesley and Poduska 1969a, 1969b). Alternatives to pollen have been sought but every pollen substitute is less acceptable to honeybees than is pollen (e.g. Haydak 1953, 1957, 1970; Spencer-Booth 1960; Standifer *et al.* 1970; Atallah *et al.* 1983). Even supplements that contain some pollen are not eaten readily by honeybees (Doull 1974b, 1975a; Zaifert and Shafir 1978; Burgett and Fisher 1979; Margalith *et al.* 1984).

Orchardists should benefit from the larger colonies that are produced by supplementary feeding, but apiarists may also benefit through their hives producing more honey (Gary 1979).

10.3 The honeybee population requirement of almond orchards

10.3.1 Introduction

"Estimates of the number of colonies necessary to pollinate a given area of orchard are based on the experiences and assumptions of growers and apiarists, rather than on experimental results" (Free 1970a p7). Moreover,

recommended hive densities for orchards are confusing because the recommendations are over simplified, in that specific recommendations of hive densities for specific crops merely provide an estimate of populations that are needed in average situations (e.g. Table 10.1) (Gary 1979). The factors that need to be considered when determining a suitable hive density for a particular orchard are discussed generally by Free (1970a pp7, 66, 397), but useful methods for the determination of the optimum hive density for almond orchards have not been published, and so three methods are presented and discussed below.

The strength of hives varies to extremes (e.g. Section 10.2.1), so the following discussion refers to numbers of honeybees instead of numbers of hives or colonies. The ratio of foragers to non-foragers in a colony is assumed to be independent of colony size, an assumption which may or may not be true (e.g. Sections 10.2.1, 14.2).

One could take the approach of recommending a honeybee population that is large enough to meet the requirement of any orchard under any conditions, but such an approach is not realistic because of several reasons, the foremost reason being that there are not enough honeybees available to supply every orchard with more than enough honeybees to ensure optimum pollination (Free 1958; McGregor 1976). Moreover, honeybees are sometimes scarce in California because some colonies are killed by pesticides, and apiarists are reluctant to expose their honeybees to pesticides by supplying honeybees for pollination (McGregor 1976). The impact of pesticides on honeybees and other insects, with respect to pollination and for various crops, is discussed by Crane and Walker (1983). There is not a shortage of hives in Australia, but a shortage could occur in future if the demand for hives increases as progressively more orchardists realize the value of hives for pollination. Also, some apiarists are reluctant to supply hives for pollination because they find it unprofitable, hence almond growers must ensure that the supply of honeybees for pollination is a profitable exercise for apiarists (Section 10.7).

Nevertheless, some orchardists may be able to get more honeybees than they need, and having more than enough honeybees to ensure adequate pollination has been recommended as a way of improving pollination through providing extra competition between honeybees so that individual honeybees forage over a larger area (Butler 1943, 1945b; Grout 1949; Butler and Simpson 1953; Ribbands 1953; Thorp 1979; Baker 1980). But this effect has

not been demonstrated conclusively, and attempts to demonstrate it conclusively have failed (e.g. Free 1966a), apparently because there is a limited density of foragers beyond which more honeybees cannot be made to forage on flowers unless the amount of food in the flowers is increased. This limit to the density of foragers is discussed further in the next Section. Moreover, too many hives means unnecessary expense to the orchardist when pollination fees are being paid, and the apiarist may also lose through the colonies suffering and losing strength if there is insufficient food to meet their requirements. Consequently, the value of oversupplying orchards with honeybees is questionable.

On the other hand, too few honeybees may reduce the amount of effective pollination. For example, when the honeybee population is too small, many flowers may not be visited by foragers until several days after anthesis (e.g. Section 6.3), by which time pollination may not be effective because the EPP of the flowers has expired.

So there must be an "optimum honeybee population density" that suits the target crop and perhaps the colonies, and hence also satisfy the orchardists and the apiarists. The following sections are a discussion of methods of estimating the optimum honeybee population for almond orchards. The methods depend on the concept of an "optimum forager density".

10.3.2 Optimum forager density

10.3.2.1 Introduction

The number of honeybees foraging on a food source is almost always proportional to the amount of food available, even when flowers are scarce and there are many colonies nearby (e.g. Bonnier 1906; Butler *et al.* 1943; Butler 1945a; Grout 1949; Brown 1951; Griggs *et al.* 1952; Roberts 1956; Free and Spencer-Booth 1963; Free 1966b; Mommers 1966; Langridge and Goodman 1979; Nunez 1982). In other words, there is a limited or "optimum forager density" for any given source of food. Exceptions to this optimum density occur when too many foragers are sent to the food sources during the first two or three days after hives have been placed into the orchard, perhaps because the colonies or individual foragers need some time to establish foraging territories. This situation is discussed elsewhere (Section 12.6) because it is a separate issue from the current discussion in that the effect may be induced irrespective of the population of honeybees in the target crop.

The optimum forager density probably changes hourly and daily throughout the flowering season and in unison with the number of flowers and the amount of pollen and nectar they produce (e.g. Synge 1947; Percival 1955). Consequently, the optimum forager density probably peaks in the middle of the flowering season when the rate of flowering peaks, and the curve of optimum forager density versus time may be similar to the flowering curve (e.g. see the flowering curves in Fig. 2 of Hill et al. 1985 - Appendix 3). Air temperature and sunshine are important factors of honeybee activity, nectar secretion and anther dehiscence (Chapter 6). Therefore the optimum forager density may remain steady only during days when the weather is optimal for foraging, nectar secretion and anther dehiscence, such as on warm, sunny days.

This variability introduces the problem of choosing between at least two strategies. Either a particular "optimum honeybee population" could be maintained throughout the flowering season so that the population is adequate to supply enough foragers to fully exploit food sources at the peak of pollen and nectar production. Alternatively, the honeybee population could be adjusted throughout the flowering season so that it usually matches the current rate of pollen and nectar production. The latter strategy should, theoretically, suit both orchardists and apiarists, because orchardists would save some of the cost of pollination fees (Section 10.7), and the apiarists could ensure that their hives were not being starved. However, the advantages would need to outweigh the cost of frequently moving hives in and out of orchards; so the latter strategy may only be feasible in orchards that have a long flowering season. Ultimately, the choice of strategy would need to be made by the orchardists and apiarists, and the methods of estimating both the optimum forager density and the optimum honeybee population, which are given below, should be easy to use for both strategies.

Three methods of estimating the optimum honeybee population are discussed below. I have used the specifications of Keane's orchard, which is described in Chapter 2, to produce a description of an "example almond orchard", and which is used below to illustrate the three methods of estimating the optimum honeybee population. The example orchard is ten years old and the trees were planted at a density of 173 trees per hectare. Each tree produces 10,000 flowers during its flowering season, and there is a peak of about 2,000 flowers that are producing pollen and nectar on a given day. The number 2,000 flowers was obtained by assuming that flowers

produce significant amounts of pollen and nectar during only 2 and 6 days of their life respectively (Sections 6.5, 8.1.2), and that 20% of all the flowers open over the 2 day peak of flowering (e.g. Fig. 2 of Appendix 3).

10.3.2.2 Method 1 - Trial and error to get a uniform distribution of foragers

The honeybee population can be altered until a uniform distribution of foragers occurs throughout the orchard (e.g. Filmer 1941; Free 1970a p66; Gary et al. 1976; Goebel 1984). When the honeybee population is below the optimum density, the density of foraging bees tends to decrease with increasing distance from the hives (Hutson 1926; Free and Spencer-Booth 1963; Free 1970a p75). This trend is also dependent on weather (Section 14.2), but the effect of weather can be negated by ensuring that hives are evenly distributed throughout the orchard so that the trees that are most distant from any hive can still achieve the optimal forager density during poor foraging weather (Section 14.3.7).

Forager density can be measured by counting the number of foragers per tree, but such measurements are not accurate for orchards that do not have a uniform flower density, and so a better method may be the measurement of the forager density relative to the flower density, such as in units of foragers per 100 flowers. A measurement in terms of honeybees per 100 flowers can easily be converted to honeybees per hectare of orchard by using estimates of the number of flowers per tree and the number of trees per hectare.

Goebel (1984) suggested an optimum forager density in apple orchards was 1 foraging bee per 1,000 flowers; but between 1.8 and 2.0 foragers per 100 flowers may be a more accurate estimate of the optimal forager density for apple (Mommers 1977; Hagley 1983; Danka et al. 1985), except that the density may rise to 8 foragers per 100 flowers when food supplies in the flowers have accumulated during a period of non-exploitation (e.g. Butler 1945a).

A density of 2.0 foragers per 100 flowers means that a tree in the example orchard (i.e. a tree with a peak of 2,000 flowers) may have 40 foragers on it during a peak period of flowering. These estimates of forager density correspond to the measurements that were obtained on "mature" trees of almond and apricot of 20 to 40 foragers per tree when the temperature was over 20°C (e.g. Griggs et al. 1952; Langridge and Goodman 1981; Loper et al. 1985).

Using these data, the example orchard (i.e. 173 trees per hectare) would require 7,000 foragers per hectare during peak flowering. Given that about 30 to 50% of the honeybees of a colony are foragers (Bodenheimer and Ben-nerya 1937), then colonies with up to between 14,000 and 22,000 bees would be needed for each hectare of orchard during peak flowering.

10.3.2.3 Method 2 - Food production of flowers versus the requirements of colonies

This method relies on the assumption that the optimum honeybee population is equal to the maximum honeybee population that can be satisfied by all the pollen and nectar produced by the flowers. The method requires (a) an estimate of the amount of pollen and nectar consumed by the colonies, and (b) an estimate of the amount of pollen and nectar produced by the target flowers. Presumably, the optimum forager density occurs when the two estimates are equal.

(a) Estimates of the pollen and nectar requirements of colonies

Pollen is essential food for honeybee larvae, and adults consume only negligible amounts (Section 12.3). Each larva requires about 100 mg pollen to reach the adult stage (Haydak 1935b; Todd and Bishop 1940, 1941; Ribbands 1953; Rashad 1957), and the lifespan of the average honeybee during early spring may be about 40 days, and can be much less (Free and Spencer-Booth 1959; Seeley 1982; Nowogrodzki 1984; Winston and Furgusson 1985). So, a colony with a population of 10,000 bees would need to raise 10,000 larvae every 40 days just to maintain the population, and therefore the colony would need 1,000 gms pollen during a 40 day almond flowering season. The colony population would increase if either more larvae were raised or the average lifespan of workers were increased.

Adult honeybees in small experimental groups consumed 34 and 9.5 mg of sucrose per day at ambient temperatures of 10 and 35°C respectively (Free and Spencer-Booth 1958), but adult honeybees in larger groups (i.e. viable colonies) probably require less energy to maintain the temperature of both their bodies and their hive to the optimum range of 32 to 36°C (Seeley and Heinrich 1981). Maximum air temperatures of 10 to 15°C are common during flowering in Australia's almond orchards. So let us assume that each honeybee requires 20 mg sugar per day, and that a colony of 10,000 bees would require 200 gms sugar per day, or 8 kgs sugar during a 40 day flowering season.

(b) Estimates of the pollen and nectar production of the flowers

Pollen production per 100 flowers varied between almond cultivars in the range 29 to 126 mg pollen per 100 flowers (Hill et al. 1985). A tree in the example orchard (i.e. 10,000 flowers per tree) may produce between 2.9 and 12.6 gms pollen, which is 500 to 2,200 gms pollen per hectare for an orchard of 173 trees per hectare.

The nectar production of almond flowers is difficult to estimate because there are few data available. Other species of Prunus and of Pyrus produced between 80 and 550 mg of nectar per 100 flowers per day (Free 1970a p391; Mommers 1977), but nectar production per flower varies greatly within trees and between species, depending on factors that are discussed in Section 12.4.2.

Let us assume that almond flowers produce similar amounts of nectar to those mentioned above, that is, between 100 and 500 mg nectar per 100 flowers per day. Visits to almond flowers by nectar-collectors suggest that almond flowers may produce nectar for 6 days after anthesis (Section 6.5). Therefore, 100 almond flowers may produce between 600 and 3,000 mg of nectar during their 6 day lifetime. The value of nectar to bees depends on the combination of quantity and energy content. Almond nectar is usually 20 to 40% sugar (Section 12.4.2), so 600 to 3,000 mg of nectar may contain 120 to 1,200 mg of sugar. A tree of 10,000 flowers may produce between 12 and 120 gms sugar, and so the example orchard (i.e. 173 trees per hectare) may produce 2 to 20 kg of sugar per hectare during a flowering season.

(c) Comparisons of the estimates

The example orchard may produce between 500 and 2,200 gms pollen per hectare, depending on the cultivars involved. This would be enough pollen to raise between 5,000 and 22,000 larvae, and given the assumptions made above in (a), this would be enough pollen to maintain a population of 5,000 to 22,000 bees per hectare.

The sample orchard may produce between 2 and 20 kg sugar per hectare per flowering season. A figure midway in the given range is probably appropriate because the sugar concentration of nectar tends to be inversely related to the amount of nectar produced (Section 12.4.2). This compares favourably with the 8 kg sugar estimated to be needed by a colony of 10,000 bees during a 40 day period, and sufficient sugar may be produced by a hectare of orchard to supply up to 25,000 bees.

10.3.2.4 Method 3 - Pollen and nectar loads collected by foragers

Method 2 examined the food requirements of whole colonies whereas this method examines the food collection requirements of foragers by producing an estimate of the number of foragers that would be satisfied by the loads of nectar and pollen that are produced by the trees. The optimum forager population can be estimated by comparing (a) estimates of the number of loads required or obtained by foragers, with (b) estimates of the number of loads produced by the trees.

(a) Loads per forager

The size of a load depends on the distance between the hive and the flowers. Honeybees that forage closer to the hive visit fewer flowers per flight, and return to the hive with smaller loads, compared to honeybees that forage further from the hive; and the mean load size increases to a maximum for distances of greater than 1,000 metres between the hive and food source (Nunez 1982). Presumably the fore-mentioned behaviour occurs because a honeybee expends more energy carrying a heavy load from flower to flower than through returning to the hive and making a second trip (Robinson et al. 1984; Schmid-Hempel et al. 1985). The variation in size of loads and number of flowers per load is probably not important here because bees that collect smaller loads tend to make more flights per day (Nunez 1982), so the total pollen or nectar collection per bee per day is likely to vary little between foragers.

As an aside, one could argue that placing hives at a distance of at least a few hundred metres from the target crop may increase the mean size of loads and hence increase the number of flowers per trip and the likelihood of pollen being transferred directly from tree to tree; but this is unlikely to occur in Australian almond orchards because the weather usually prevents honeybees from flying more than 100 or so metres from their hive, and often the distance is less (Section 14.2).

Estimates of the number of flower visits required to obtain a pollen or nectar load are given in Table 10.2. The observation of a honeybee during a complete foraging flight is a difficult feat, and so some observers have stated the observed number of visits and not the total number of visits per flight (see Table 10.2). The actual number of flower visits necessary for a load may vary greatly as the pollen and nectar production of the flowers varies greatly (Sections 6.3, 12.4.2), but the

data in Table 10.2 suggest that an average of 100 flower visits may be necessary for a forager to collect a load of pollen or nectar.

Foragers tend to specialize by collecting only either nectar or pollen (Section 11.2), so one would expect one of each foraging type to forage on a single group of 100 flowers; that is, one would expect a density of 2 foragers per 100 flowers. This concurs with the observed forager densities of 1.8 to 2.0 honeybees per 100 flowers (Section 10.3.2.2).

Observers of a wide range of crops found that 5 to 10 trips per day are made by foragers in average flight weather (e.g. Dyce 1929; Brittain 1933; Zander 1936; Singh 1950; Karmo and Vickery 1954; Lindauer 1976), but up to 20 trips per day may be made on the most favourable days (Park 1928; Betts 1931; Grout 1949) such as when the nectar supply is richer or the rate of supply of pollen or nectar increases (Nunez 1982).

(b) Loads per tree

The number of nectar and pollen loads that are produced by trees can be calculated by dividing estimates of the pollen and nectar production per tree by the size of the average pollen and nectar load.

Almond trees produce 29 to 126 mg pollen per 100 flowers (Hill et al. 1985). The weight of pollen loads varies greatly, depending on factors such as the ease that honeybees have in collecting the pollen, and the species and cultivar of the pollen; but an average pollen load in orchards that are similar to the example orchard, may be 15 mg (e.g. Park 1922; Parker 1926; Grout 1949; Percival 1950; Maurizio 1953; Free 1970a p19). So, 100 almond flowers may produce between 2 and 8 pollen loads, and a tree with 10,000 flowers may produce a total of between 200 and 800 pollen loads. A tree with a peak of 2,000 flowers may produce 20 to 80 pollen loads per day during the peak of flowering.

Data on the nectar production of almond flowers have not been published. Other species of Prunus produced between 80 and 550 mg of nectar per 100 flowers per day (Free 1970a p391; Mommers 1977), and nectar production per flower varied greatly within trees and between species, depending on the influence of factors that are discussed in Section 12.4.2. If the mean load of nectar weighed 40 mgs (e.g. Grout 1949; Free 1970a p17; Gary et al. 1978; Lindauer 1976; Rinderer et al. 1985), then 100 flowers could produce between 2 and 14 nectar loads per day. If each 100 flowers produces that much nectar for 6 days, then a tree of 10,000 flowers may produce a total of between 1,200 and 8,400 nectar loads.

Table 10.2: The number of flowers visited by single foragers to obtain a load of pollen (a) or nectar (b), as reported by several authors.

(a) Pollen

Crop	Flower per load		Author
Apricot	89	A	Free (1960b)
Garden flowers	7 to 120	B	Ribbands (1949)
Pear	84	B	Vansell (1942)
Pear	38	A	Free (1960b)

(b) Nectar

Crop	Flowers per load		Author
Apple	53 and 61	A	McColloch (1914)
Apple	100	C	Webster (1947)
Pear	84	B	Vansell (1942)
Pear	76	A	Free (1960b)
Sweet Cherry	82	A	Free (1960b)

A Number of visits observed during part of a flight.

B Number of visits observed during a whole flight.

C Number of visits estimated per flight.

Each example tree may have 3,500 to 5,000 flowers that are between 0 and 6 days old, and which are producing nectar during peak flowering. Such trees may produce between 70 and 700 nectar loads per day during peak flowering.

(c) Comparisons of the estimates

In the example orchard, a tree of 10,000 flowers and a peak of 2,000 flowers may produce between 20 and 80 pollen loads per day and between 70 and 700 nectar loads per day, during peak flowering. Given that pollen-collectors and nectar-collectors collect between 5 and 10 loads per day, then this would be enough pollen to satisfy between 2 and 16 pollen-collectors and between 7 and 70 nectar-collectors. One hectare of the example orchard would satisfy between 350 and 2,800 pollen-collectors and between 1,200 and 12,000 nectar-collectors. Given that 30 to 50% of a colony consists of foragers (Bodenheimer and Ben-nerya 1937), then perhaps one can use the above estimates to say that the foragers in colonies with a total population of between 6,300 and 45,000 bees would be satisfied by the pollen and nectar produced by one hectare of example orchard during peak flowering.

10.3.2.5 Conclusion

The three methods of estimating the optimum forager density produced estimates that are broadly similar to each other. Given the specifications of the example orchard, the orchard was estimated to produce sufficient pollen and nectar for between 5,000 and 25,000 honeybees per hectare (Method 2), and between 6,300 and 45,000 bees may be necessary to supply enough foragers to collect all the pollen and nectar as soon as it becomes available during peak flowering (Method 3). This compares favourably with the observed maximum forager densities that would require an orchard population of 14,000 to 22,000 bees per hectare (Method 1).

The variable common to all 3 methods was number of flowers, and so a good estimation of the optimum orchard population per hectare can be obtained by estimating the number of flowers produced by each hectare of trees. The following calculation produces an estimate of the optimum honeybee population per hectare for almond. Estimate the number of flowers produced by a hectare of orchard, divide by 5 (to get the number of flowers at peak flowering), divide by 50 (i.e. 1 forager per 50 flowers), and multiply by 2.5 (assuming 40% of a colony consists of foragers). The

accuracy of the estimate may be improved by making adjustments for the cultivars present because pollen and nectar productivity per flower differs between cultivars. The amount of pollen and nectar produced per flower may also depend on other factors, including flower density per tree, tree density, weather variables, and orchard management practices such as pruning, irrigation and fertilizer use (e.g. Sections 8.3.2, 12.4.2).

Variations of these methods have been used to produce recommendations of hive density, but most such recommendations are only suitable for the orchard and conditions in which the measurements were obtained because the authors referred only to numbers of hives per hectare (e.g. Gary et al. 1976). Hive strength and flower density should be stipulated if an estimate of the optimum honeybee population is to be suitable for extrapolation to other orchards.

Weather influences both the behaviour of honeybees and some physiological aspects of the plants, and these relationships will be discussed in greater detail in Sections 14.1 and 8.3.3. For many crops, a particular population of honeybees may result in too much effective pollination when the weather is ideal, but may produce too little effective pollination during unfavourable weather (Quinn 1941; Philp and Vansell 1944; Webster et al. 1949; Grout 1950). So some authors give a range of hive densities, with a higher density being recommended in areas where the weather was likely to be poor for foraging during the flowering season (e.g. Wood 1947; Baker and Gathercole 1977; Erickson et al. 1977).

Notwithstanding variables such as the number of hives available for distribution (Section 14.3.7), the observed differences in amounts of effective pollination (i.e. fruit-set) between times of favourable and unfavourable weather (Free 1970a p397) are probably not due primarily to differences in honeybee population, but instead may be a reaction by honeybees to the influence of weather on other factors of pollination, especially on the rate that pollen and nectar becomes available (Sections 8.3.3, 12.4.2). Indeed, the optimum honeybee population depends largely on the rates of flowering, pollen production, and nectar production, all of which are lower when the weather is not favourable to honeybee activity (e.g. Sections 8.2.3, 8.3.3, 12.4.2). So a lower honeybee population may be all that is necessary during less favourable weather for foraging activity, contrary to the opinion of many authors (e.g. Quinn 1941; Gary et al. 1976). Also, too much effective pollination (i.e. too high a fruit-set) is not a problem for almond (Section 1.8).

Optimum forager density is only a measure of whether or not the orchard is saturated with honeybees. The optimum forager density is not a good measure of effective pollination, contrary to the belief of some authors (e.g. Goebel 1984), because whether or not a flower is effectively pollinated depends on other factors which are described elsewhere in this thesis.

10.3.3 Honeybee population of the surrounding area

Foragers are more likely to stay within the target crop when the flowers outside the target crop are saturated by foragers from hives that are sited outside of the target crop. If adjacent crops lack sufficient honeybees, then neighbours may gain as much from the honeybees as the hirer (Brittain 1933; Grout 1949; Jay and Jay 1984). Consequently, the distribution and number of colonies should be determined for large districts rather than on a field by field basis, and perhaps the surrounding area of several kilometres radius should be considered when the optimum honeybee population for a target crop is calculated (Brittain 1933; McGregor 1976; Gary 1979; Thorp 1979).

Perhaps pollination districts could be formed to promote collective planning for the distribution of hives, thus benefiting orchardists and apiarists alike (Gary et al. 1976). Orchardists could equally share the cost of a minimal number of hives, while individual orchardists could obtain additional hives to meet any extra requirements they may have (Gary et al. 1976).

10.4 Date and time of hive introduction to the orchard

Some authors recommended that hives be put into crops a few days before any flowers open, so that the bees have ample time to make orientation flights before visiting the flowers (e.g. Howlett 1934; Zander 1936; Free 1970a p72), But foragers start visiting non-target flowers and do not forsake those flowers when target flowers open, so hives should not be put into crops until after flowering has commenced (e.g. Stapel 1934; Menke 1951; Smith 1952; Townsend and Burke 1952; Jones et al. 1953; Roberts 1956; Dickson and Smith 1958; Free 1970a p72). Evidence for the latter strategy at first consisted of the observations of apiarists (e.g. Wadey 1944; Moore-Ede 1947) but later experiments showed that there were more bees on the target crop when hives were placed after flowering had commenced (e.g. Free 1959; Free et al. 1960). Some authors supported the

latter strategy because they wanted to reduce the risk of bees being killed by pesticides, by restricting the period hives are in the orchard to the period during which the bees have the most effect on nut-set (e.g. Thorp and Mussen 1978; Thorp 1979). The difference between the two strategies decreases with time, probably because foragers in the target crop find non-target flowers while foragers on non-target flowers find the target crop (Free et al. 1960). The delay before colonies establish their territories may have important effects on both strategies (Section 12.6).

The latter strategy may not be the best because it may prevent the first flowers of the season from being effectively pollinated, especially if their EPP expires before hives are put into the orchard. However, many of the first flowers to open may be female-sterile (Section 7.1), so their pollination may not be important. Furthermore, there may be sufficient honeybees and other pollinator insects already present to effectively pollinate the few flowers that open during the first two or three days of the flowering season. Indeed, the early flowers may have a better chance of being effectively pollinated than later flowers because the sparse distribution of flowers should ensure that many foragers fly between flowers of different cultivars, assuming, of course, that flowers of different cultivars are present (Section 8.2.1).

10.5 Effect of the hive's history on it's suitability for pollination

There may be some advantage in obtaining hives with particular histories. For example, the temperature regime at the hive's previous site may determine the threshold temperature above which bees forage, in that a colony from a relatively warm area may have a threshold temperature for foraging which is higher than for a colony from a cooler area (Section 14.1). Another consideration is that when a colony is moved, the bees tend to forage on the same plant species as before (Eckert 1933; Free 1959, 1963), which may be advantageous if the foragers are fixed on the target crop species, but may be disadvantageous if the foragers are fixed on non-target species and the non-target species is present near the new site. Perhaps the latter problem may be overcome by placing the hives deep within the orchard so that the prior species is not within flight range for at least several days after the placement of hives, by which time the bees may become fixed on the target crop (Section 12.6).

10.6 Landmarks for navigation, and drift of bees between hives

Honeybees apparently need landmarks for navigation. For example, proponents of the bee dance language theory suggest that honeybees use the sun as a sole navigation aid (Section 11.5), but when the sun is hidden by cloud, experienced foragers use local landmarks as navigation aids (Dyer and Gould 1981). Also, bees tend to return to the wrong hive and become attached to that colony when many hives are located together, and sometimes many bees drift from one particular group of hives to another. For example, when hives are arranged in repetitive patterns, bees drift to hives in similar positions in other rows; and when hives are arranged in single rows, the bees drift towards the end colonies (Free 1970a p71; Robinson 1979b). Furthermore, bees drift to colonies nearest the direct line of flight from the food source (Free 1970a p71). The incidence of drift can be reduced by facing colonies in different directions and painting the hives different colours (Free 1970a p71).

The significance of drift to pollination efficiency is not clear. There is not a loss of foragers from the orchard's bee population, but honeybees that have navigation difficulties may expend more energy in foraging. If true, then apiarists may obtain an increase in honey production if the navigation problems of honeybees are eliminated, perhaps by placing obvious landmarks throughout the orchard. On the other hand, a lack of landmarks may improve pollination if foragers enlarge their foraging area because the cannot always find their particular patch of flowers (e.g. Gary et al. 1977; Gary 1979).

10.7 Rental charges for hives

Some Australian apiarists want to be paid for pollination services while others do not. The opinion of the apiarists generally depends on whether or not they have access to alternative sources of nectar during the almond flowering season. If they do, then they often argue that rental charges for hives are justified because almond blossom does not produce surplus honey, and so there is no value to the apiarist in placing hives in almond orchards (e.g. Oertel 1939; Free 1960a). However, colonies are usually very small at the beginning of the almond flowering season and so the colonies increase their population instead of storing honey (Section 10.2.2), but large colonies that have a surplus of honey from autumn do store almond honey (Murneek 1930). Furthermore, alternative sources of

nectar are limited during the almond flowering season, and so apiarists who do not have access to better food sources are eager to use almond orchards, especially when other nectar-producing flowers, such as the weed Salvation Jane (Echium spp.), are due to flower profusely in neighbouring fields towards the end of the almond season (e.g. Section 2.3). The latter apiarists are willing to place hives into almond orchards for little or no charge.

The increased demand for good hives for almond pollination has reduced the supply of available hives, so many orchardists need to pay pollination fees to prevent apiarists from exploiting alternative sources of pollen and nectar. However, hives that are put into almond orchards are often arguably of little value for pollination because there is no brood to stimulate the collection of pollen, and the colony is too small to be a significant source of foragers (Section 10.2.1). Hives do improve once placed into almond orchards, but there is a delay of several weeks before the hives reach a desirable standard. Some orchardists are aware of this problem, and they realize that pollination fees are a way of persuading apiarists to stimulate the production of brood and increase the strength of the colonies, by feeding the colonies with supplements (Section 10.2.2). Other costs encountered by apiarists include distributing hives throughout the orchard (Section 14.3.7), and placing the hives at densities greater than may be optimal for efficient honey production (Doull 1972; McGregor 1976).

Although pollination fees can be justified, apiarists must realize that if they receive a fee, the orchardist is justified in complaining when the hives are not of a suitable standard or are not managed in a way that provides maximum foraging activity throughout the flowering season (Doull 1972). Some apiarists complain that the pollination fees are usually low and often uneconomic; but this is often regarded as the fault of the apiarists because they either supply sub-standard hives regardless of the pollination fee, or they consider pollination fees as supplementary to income from honey production, or they feel that higher pollination fees would invite competition with other apiarists (McGregor and Levin 1970; McGregor 1976). Nevertheless, low fees provide little inducement for apiarists to supply hives that are the most useful for pollination.

Contracts, known as pollination agreements, overcome many of the complaints that can develop. Several examples of pollination agreements have been published (e.g Shuel and Pedersen 1953; McGregor 1976; Baker 1980; Anon 1981; Chetaikin 1982; Lacey 1984; Monson 1985). Usually there is

a set rate per hive for a particular period, but sometimes there is also an incentive to the apiarists in the form of a percentage of the additional yield that is due to the presence of the hives (e.g. Shuel and Pedersen 1953). This overcomes the problem of hives being rented on a flat-rate basis with little regard to their condition, in that populous colonies are worth more to the orchardist because they apparently supply more foragers to the field (Section 10.2.1).

Set rates per hive are common, but the fees vary tremendously, depending on the circumstances. Charges of $5 to $10 are common for almond in Australia (e.g. Section 2.3), but up to $70 has been suggested when the apiarist needs to forfeit a good return from a major honey flow (Rhodes 1985). Suggested pollination fees per hive include $2 to $10 per season (Murneek 1930; Phillips 1930a), $2 per week (Langridge 1956), and $5 to $15 per season (Baker 1980); that is, the pollination fees generally have not increased for at least 55 years. Hives are usually rented on a flat rate basis, but perhaps fees should be based on a measure of hive size instead of a flat rate per hive because this may induce apiarists into supplying hives with larger colonies (Gary et al. 1978a).

Pollination agreements solve some problems, but there is a need to police the agreements. Most almond growers do not like touching bee hives so they often pay for substandard, and sometimes empty, hives. Although such deception may not be done intentionally by the apiarists, the grower is not going to know about it unless someone looks into the hives. This problem is overcome in California through the use of brokers who act on behalf of both orchardists and apiarists (Baker 1980). Such an organized service does not exist in Australia, but orchardists who are aware of this problem organize independent inspections of hives (e.g. Section 2.3). Inspections should be done carefully because, no matter how strong the colony is, its pollination ability and honey production can be reduced if, for example, smoke is used during the hive inspection (Taber 1963b).

10.8 Packaged bees (Disposable pollination units).

Packaged bees, which are known as disposable pollination units (DPUs), were produced for Californian orchardists to overcome hive shortages and to allow orchardists more control over the use of honeybees (Kauffeld et al. 1970; Erickson et al. 1977). DPUs are artificial colonies consisting of 1.4-2.7 kg of honeybees housed in a light-weight, biodegradable container with either a drone-laying queen (a virgin treated with carbon dioxide), or

a caged queen, or without a queen (Erickson et al. 1974, 1975, 1977).

The value of DPUs has been expressed in terms of pollen-collection because most authors who worked with DPUs thought nectar-collectors were unimportant for pollination, an attitude which is discussed in Section 13.1. With respect to the amount of pollen collected and the number of foragers present, queenless DPUs are not as good as DPUs with queens, which, in turn, are not as good as hives of a similar size (e.g. Woodrow 1934; Jaycox 1970; Robinson 1979b). However, the DPUs tested usually did not contain brood when foraging activity was measured, and one would expect the demand for pollen to be less for a DPU without brood than for a hive with brood (Thorp et al. 1973, 1974); but, after a week or two of brood rearing, the flight activity of DPUs increases greatly (Filmer 1932). Therefore DPUs are not as valuable as hives of a similar size, with respect to their ability to collect pollen, until the DPUs have a laying queen and have been established for several weeks.

Although effective, DPUs are usually not commercially feasible replacements of hives because the cost is greater than the rental of a conventional hive. Also twice as many DPU bees may be required to do the work of the bees of a normal overwintering colony (Erickson et al. 1977; Baker 1980). However, DPUs are useful for the pollination of some crops, such as cranberries, in which case DPUs are air dropped onto the cranberry bogs because ground transport is usually impractical during the flowering season (Cantwell et al. 1971, 1972). Canadian apiarists rely on packaged bees to replace colonies that die in winter (Winston et al. 1985).

Much of the cost of DPUs is due to the cost of supplying queens. If the effect of the queen and brood can be replaced by artificial pheromones, then DPUs may become an economical proposition (Showers 1967; Jaycox 1970a, 1970b). Synthetic 9-oxodecenoic acid is an effective substitute for a queen in stimulating foraging activity (Jaycox 1970a), but DPUs with that hormone instead of a laying queen gathered less pollen and nectar than DPUs with queens (Kauffeld et al. 1970).

Chapter 11: Types of foraging honeybees

11.1 Introduction

The work that is done by individual worker-honeybees depends on their age. Honeybees usually start foraging when about 15 to 20 days old; but if a colony loses many foragers, other workers begin foraging at a younger age (Free 1970a p55-57; Stanley and Linskens 1974; Seeley 1982; Nowogrodzki 1984; Winston and Fergusson 1985). Juvenile hormone analogue can induce young bees to forage before they otherwise might (Robinson 1985).

There are several types of behaviour which a foraging bee may adapt. An individual honeybee may be consistent to one form of behaviour, or the bee may change from one form of behaviour to another. Four broad categories of foraging behaviour distinguished herein are pollen collection, nectar collection, water collection, and scouting.

11.2 Collectors of nectar and pollen

Five classes of nectar and / or pollen collection behaviour are recognized on fruit trees (Free 1960b; Williams and Brain 1985), and I distinguished 2 more classes of behaviour in almond trees. The classes of behaviour are described in Table 11.1.

The ratio of pollen-collectors (Table 11.1 - class a) to nectar-collectors (classes b and e) differs greatly between and within days, depending on nectar availability, pollen availability, and the food requirements of the colonies (Shaw *et al.* 1954; Johansen 1956; Free 1970a p395; Romisondo *et al.* 1972; Gary *et al.* 1978; Langridge and Goodman 1979, 1981; Section 6.5). Changes in the ratio of pollen-collectors to nectar-collectors are mostly due to individual honeybees changing with one type of behaviour to another, and are not due to bees with a particular type of behaviour deserting the crop (Section 13.2).

Few authors have distinguished between top-workers (Table 11.1 - class b) and side-workers (class e). The importance of this distinction is discussed in Section 13.1. The essential difference is in the probability of effective pollination occurring during a visit by a forager.

Free (1960b) mentions the two classes of nectar-collector, but he did not use the distinction in his experiments. Thorp (1979) found that most nectar-collectors collected from the side on almond flowers, but he examined behaviour on only a few cultivars, and other authors found that top-collectors are common on almond flowers (Section 13.1).

Table 11.1: Descriptions of the classes of behaviour for honeybees on the flowers of fruit trees.

(a) Pollen collectors scrabble over the anthers to obtain pollen and do not attempt to collect nectar (Fig. 11.1).

(b) Nectar (top) collectors (top-workers) obtain nectar by standing on the stamens, and sometimes also the petals, and pushing their tongues and front part of their bodies down among the stamens to reach the nectary (Fig. 11.2). This includes the "spreaders" of Robinson (1979a).

(c) Nectar (top) and pollen collectors behave as in 'b' but scrabble over the anthers afterwards.

(d) Nectar (top) and pollen collectors behave as in 'b' but scrabble over the anthers for pollen first.

(e) Nectar (side) collectors (side-workers) obtain nectar by standing on the petals and pushing their tongues between the filaments (Fig. 11.3).

(f) Nectar (side) and pollen collectors behave as in 'e' but scrabble over the anthers afterwards.

(g) Nectar (side) and pollen collectors behave as in 'e' but scrabble over the anthers first.

Figure 11.1: A pollen collector on an almond flower.

Figure 11.2: A nectar (top) collector on an almond flower.

Figure 11.3: A nectar (side) collector on an almond flower. Note the thick stigma which ends well above the body of the honeybee.

Robinson (1979c) noted that the proportion of side-workers to top-workers differed greatly between apple cultivars; for example, on trees of 5 non-Delicious cultivars, 94% of nectar-collectors were top-workers and only 6% were side-workers; but on trees of the cultivar Delicious, only 13% were top-workers while 87% were side-workers. He suggested that nectar-collectors may prefer to collect nectar from the side of the flower (i.e. Fig. 11.3), but that they can only do so easily when the "basal" gaps between the stamens are big enough to allow a honeybee's glossa to reach the nectaries; so the ratio of top-workers to side-workers may depend on the incidence of basal gaps, which differs between cultivars (Robinson 1979a, 1979c, 1981). However, another hypothesis is that nectar-collectors prefer to collect nectar from the top of the flower (i.e. Fig. 11.2) and the behaviour of the foragers depends on whether or not the stamens are short and flexible enough to allow foragers to approach the nectaries from the top of the stamens (Roberts 1945b; Preston 1949; Brown 1951; Loken 1958; Free 1960b; Free and Spencer-Booth 1964b). The experiments of Kuhn and Ambrose (1982, 1983) suggest that the latter theory may be correct. Foragers may find one class of behaviour more efficient than another class of behaviour on some cultivars, but when they move to another cultivar, they usually continue the behaviour although another class of behaviour may be preferred by more experienced foragers.

A significant number of honeybees collect both nectar and pollen (Table 11.1 - classes c, d, f, g) (e.g. Shaw et al. 1954; Free 1960b). Observations suggest that each foraging honeybee is predominantly either a pollen-collector or a nectar-collector, but occasionally lapses to the alternative behaviour for a snack. These lapses exclude the occasions when foragers change their behaviour in response to changes in the demand or supply of pollen or nectar (e.g. Free 1970a p62). Honeybees store enough sugar in their blood for about 15 minutes of flying (Crane 1955; Scholze et al. 1964), but foraging flights may sometimes last longer than 15 minutes, especially if the flowers are far from the hive (Free 1970a p396); therefore, pollen-collectors may need to obtain nectar periodically for their own energy needs. Pollen-collectors may also take an occasional sip of nectar in hot weather and use the water to cool themselves by evaporative cooling (Section 11.3). On the other hand, nectar-collectors can become dusted with so much pollen that they may clean themselves by putting the pollen in their corbiculae. Furthermore, and for reasons that are unknown, nectar-collectors may take an occasional snack of pollen.

11.3 Water-collectors.

Each colony has some foragers that collect water, and which are referred to as water-collectors. Water is used to dilute honey (Seeley and Heinrich 1981), for feeding directly to the brood and queen (Robinson et al. 1984), and for keeping the hive cool (Free 1970a p62).

Honeybees tend to keep the temperature of the core of their hive to about 32-36°C, even when the air temperature outside is below 0°C (Bodenheimer and Ben-nerya 1973; Seeley and Heinrich 1981; Szabo 1985). Honeybees use their body-heat to warm the hive, and the cooling effect of evaporating water to keep the hive cool. When the ambient air temperature rises above about 25°C, many foragers turn to water-collection. The diversion of foragers to water-collection occurs first in hives that are situated in direct sunlight; and occurs in shaded hives only after the temperature has risen further. The number of water-collectors increases with increasing temperature (Bodenheimer and Ben-nerya 1937; Lindauer 1955; Owens 1959; Todd and McGregor 1960). The diversion of foraging bees to water-collection can be minimized by shading the hives, using heat reflective paint, and making water readily accessible to the hives (Owens 1959; Todd and McGregor 1960). Water troughs should be placed near the hives so that the bees do not have to travel far to collect water. Small pieces of wood or water-soaked sponge should be placed in the troughs so that the bees can alight on them and drink without risking drowning (Baker 1980).

Nevertheless, the diversion of most pollen-collectors to nectar-collection or water-collection may be unavoidable when the air temperature is over 30°C because pollen-collectors cannot constrain their thoracic temperature by evaporative cooling, unlike water-collectors and nectar-collectors which are able to cool themselves with the water they collect; and pollen-collection may cease altogether when the air temperature is over 40°C (Cooper et al. 1985). Nectar-collectors can continue to forage for nectar when the air temperature is over 40°C, but they may turn to water-collection if the needs of the hive are great enough (Schaefer et al. 1979; Cooper et al. 1985).

11.4 Scout bees

A popular concept is that each colony maintains a force of "scout" or "wandering" or "searcher" bees which fly around in the surrounding area and

bring back "news" of available food. The scouts then communicate with other bees so that no more foraging bees are recruited than are sufficient to collect all the nectar and pollen from the newly discovered food source. Such a feed-back process would improve the energy efficiency of the hive because if foragers cannot readily find new food sources then the drain on the colony's food store can be minimized by preventing many foragers making unproductive trips (Doull 1971; Seeley 1983).

Three distinct categories of scout bees have been postulated. A scout bee may be:

(1) A young bee which has left a hive to search for food for the first time, and has not been stimulated by foragers that have already found food (e.g Oettingen-Speilberg 1949; Singh 1950; Lindauer 1952; Doull 1971; Seeley 1983). This description excludes the majority of new foragers which are recruited to crops by successful foragers or scouts. The scout bees continue to search when food sources are not found, and while searching they may visit the territories of other foraging honeybees (Butler 1943, 1945b, 1951; Butler and Simpson 1954). When they find food they become either foragers or scout bees of type 2 (below).

(2) A bee whose source of forage has failed, perhaps because of competition with other bees, and which is searching for a new source of forage (e.g. Butler 1943, 1945b; Butler and Simpson 1954; Singh 1950; Weaver 1957; Seeley 1983). Such a bee may inspect a source of food to which it is already conditioned, but if that food supply is not adequate then the bee also searches for other sources of food, usually through visiting the territories of other honeybees. Butler (1945b) suggested that the factor which determines whether or not such a bee will settle down in any given area and become a member of the fixed population, is the length of time the bee takes to collect a stomach-full of nectar, and that if the bee gets a load within a particular length of time, she takes orientation flights and becomes fixed; otherwise, she moves on to the next area.

(3) A bee that is dedicated to searching for new sources of food, and reports the food sources that it finds, but the bee then continues to search for unexploited sources of food. Such a bee may feed from colony food stocks or from flowers (Ribbands 1953; Doull 1971).

There is some evidence for the existence of bees that exhibit scouting behaviour (e.g. Oettingen-Speilberg 1949; Seeley 1983), and some foragers

may specialize in scouting behaviour (Seeley 1983). Young honeybees, and perhaps scout bees of type 1, stay close to the hive during their first few days of foraging, and progressively move away from the hive (Levin 1959). Such bees are unlikely to find flowers that are not utilized by other bees, so they are likely to visit many flowers before they find an unutilized food source. The behaviour of these bees may account for much of the cross-pollination that occurs in orchards (Butler 1945b; Singh 1950; Butler and Simpson 1954; H.E.A.F.C. 1961); but the fruit-set attributed to these bees can also be explained by secondary pollination (Section 8.3).

11.5 Communication between bees

Scout bees must be able to quickly communicate the location and quantity of their newly discovered food to other bees, because new food sources, such as bowls of sugar solution, become fully exploited within an hour of being discovered by a bee (e.g. Ribbands 1955); and the number of foragers that exploit the food is usually proportional to the amount of food available (Section 10.3.1). The communication of information about food sources, by scout bees to potential foragers, should make the colony more efficient at collecting food, compared to each bee finding its own food source, but this may not always be true (Seeley 1983).

Certainly honeybees do communicate precise details, but how they do so is debatable. Several forms of communication within the bee sub-family Apinae have been proposed or described (Kerr 1960; Michelsen *et al.* 1986a, 1986b), but only two principal theories of communication are popular with people who work with honeybees (*Apis mellifera*).

The most popular theory is the "bee dance language", which refers to the dance that some foraging honeybees perform when they return to the hive after foraging (e.g. Grout 1949; Chalifman 1950; Frisch 1967, 1974; Free and Williams 1972b; Gould 1975, 1976; Nunez 1982; Seeley 1983; Robinson 1986; Michelsen *et al.* 1986; Schneider *et al.* 1986a, 1986b). Various characteristics of the dance supposedly relate to the location and size of a new food source (e.g. Free 1970a p26-30).

However, other authors (e.g. Rosin 1978, 1980a, 1980b, 1984; Renner and Heinzeller 1979; Takeshi 1983; Wells and Wells 1984) claim that although the dance does occur, the information contained within the dance may not be used as a form of communication, and there is little evidence to show otherwise (see Barnard 1983 p269). The latter authors claim that another theory, which is based on odours, can account for all the results

obtained as evidence for the "dance language". Furthermore, they criticized the evidence that supports the dance language because of poor experimental design, such as a lack of replication, failure to publish contrary results, and a lack of consistency between the results of different experiments, especially between different authors. Also, there is evidence that contradicts the dance language; for example, if the dance language was the only precise method of communication, then one would expect foragers to retain their orientation to a point a certain distance and direction from their hive after their hive is moved, but they do not do this (e.g. Levin 1960). Furthermore, honeybees need landmarks when the sun is masked by cloud, so the sun is not the sole "landmark" used in communication and navigation (Dyer and Gould 1981). Also, most of the "evidence" for the dance language was based on observations of honeybees that were collecting syrup from bowls of syrup, and this may not be valid if honeybees regard bowls of syrup as food sources to be robbed, instead of regarding them as the equivalent of flowers, because honeybees behave very differently when robbing compared to when collecting from flowers (Taber 1986).

Several authors claimed to have performed experiments that show the dance language to be the correct theory (notably Gould 1975, 1976), but such experiments have been successfully criticized, and a definitive experiment has not been performed. Furthermore, a definitive experiment may be difficult to perform because the language of communication, whatever it may be, appears to vary between colonies, and suitably replicated experiments, using colonies as units, are difficult to organize.

Further discussion on this subject is beyond the scope of this thesis, except to say that there is some form of precise communication between bees within hives. A better understanding of the language may be valuable in inducing bees to effectively pollinate flowers.

Chapter 12: Getting bees to the target flowers

12.1 Introduction

Almond pollination is essentially the accidental transfer of pollen by honeybees that are visiting flowers to collect food in the form of pollen and nectar. Merely having honeybees near the target flowers is not necessarily adequate to ensure that the flowers will be visited by honeybees, because the bees may not be attracted to the target flowers, or the bees may decide that other flowers are preferable to the target flowers. The attractiveness of target flowers, relative to other flowers, can vary with time, and bees from adjacent hives may differ with regard to what they find attractive, perhaps because of different nutritional requirements (Free 1970a p31). Particular strains of bees can have innate preferences for particular species of plants (Free and Williams 1973), and honeybees that favour the collection of lucerne pollen have been bred (Nye and Mackenson 1970). Even when apparently suitable food sources are located near the hive, many bees fly beyond the target crops to other flowering species, some of which may be quite distant (e.g. Butler et al. 1943; Grout 1949; Free and Williams 1974; Gary 1979). Such behaviour appears maladaptive energetically but may well be adaptive nutritionally because of the great variation in nutritional value of pollen and nectar sources (Gary 1979). Preferences of bees for particular flowers may be explained by optimal foraging models (e.g. Waddington and Holden 1979; Waddington 1983), but those models may not be valid because they were constructed by using artificial flowers which may be treated differently from real flowers by honeybees (Taber 1986).

12.2 Foraging areas and the fidelity of honeybees to plants

The foragers of a colony may visit the flowers of many species of plants, but individual foragers usually forage only on one species or cultivar, and many forage on only one plant for as long as the plant carries enough flowers to satisfy the forager's pollen and nectar needs (Betts 1920, 1935; Brittain and Newton 1934; Moffett et al. 1974; Lindauer 1976). Individual foragers, after their hive is moved, continue to collect pollen and nectar from the same species of plant, if it is available, and even from the same plants, if the hive is still within flight range of the plants (Eckert 1933; Levin and Bohart 1957, 1959; Free 1963), and

regardless of whether or not richer sources of nectar are available (Wells and Wells 1984).

Notwithstanding secondary pollination (Section 13.3), bees that keep to one tree during a trip are usually considered valueless as cross-pollinators because the bees are unlikely to carry a significant amount of pollen for cross-pollination, and so information on the foraging areas of individual honeybees is thought important. Behavioural mechanisms that are related to the fidelity of honeybees to plants, and the efficiencies of that behaviour, are reviewed by Grant (1950), Bateman (1951), Free (1963, 1970a), Lindauer (1976), and Waser (1986). A brief summary follows.

Each forager usually make several foraging trips per day (Section 10.3.2.4), and usually the same patch of flowers is visited on each flight until the patch of flowers ceases being a source of pollen or nectar (Free 1970a p42; Moffett et al. 1974; Gary et al. 1977). The size of a forager's foraging area probably depends on the number of flowers that are necessary to provide the forager with a load of pollen or nectar within a certain fixed time, because the number of foragers at a food source is usually proportional to the amount of food present (Section 10.3.2.1).

Theoretically, the foraging areas of individual foragers should be larger during the beginnings and ends of flowering seasons because fewer flowers are open during those periods; and so nut-set may be higher for flowers that opened during those times, relative to flowers that opened during the peak of the season. For similar reasons, flowers of cultivars that have long flowering seasons, or low flower densities, may have a better chance of being effectively pollinated, than flowers of cultivars with short flowering seasons or high flower densities.

Foragers usually visit 100 flowers per foraging trip and make 10 trips per day during good weather (Section 10.3.2.4). However, adverse weather decreases the forager density, and the remaining foragers make fewer trips per day through increasing the time required to collect a load and not through decreasing the time each forager spends foraging (e.g. Wilson 1926, 1929; Free 1960b, 1970a). Obviously the number of flowers does not change, so the number of flowers available to a forager must be higher during cooler weather, therefore each forager may visit more than 100 flowers to obtain a load; that is, the foraging areas of foragers may be larger during adverse weather for foraging.

Other possible causes of an increase in foraging area include a lack of landmarks to ensure precise navigation by honeybees (Section 10.6), and disturbance by wind or other honeybees (Singh 1950; Free 1960b).

The foraging areas of individual foragers usually overlap, that is, each flower may be visited by two or more foragers, and the low density of foragers on flowers ensures that the accidental meeting of two or more foragers on one small flower is a rare event (Section 6.5). Nevertheless, competitive aggression between bees has been reported, although several bees can feed peacefully on one flower, especially if the flower is large (e.g. Ribbands 1949; Weaver 1956, Kilkuchi 1963; Section 6.5). Whether or not a forager is disturbed by another forager may depend on whether or not the first bee can see the second bee; so nectar-collectors, which usually have their head facing into the flower cup, are usually not disturbed (Weaver 1956).

The frequency and importance of the fidelity of foragers to foraging areas is illustrated by the types of pollen loads that are collected by pollen-collectors. Individual pollen-collectors may collect one of several types of mixed pollen load, and the type of load may indicate the behaviour of the honeybee and the circumstances at the time (Grout 1949; Singh 1950; Free 1970a p34). Individual honeybees usually visit the flowers of two or more species of plant either when there are an inadequate number of flowers of a single desirable species to fulfill the food requirements of a single honeybee, or when the flowers of several species are growing together (Free 1963; Klungness and Peng 1983). Generally, less than 10% of the pollen carried into hives are as mixed loads (Betts 1920, 1935; Percival 1947; Maurizio 1953; Free 1963), but many mixed loads may go unnoticed because pollen from some plant species, especially within Prunus, are difficult to distinguish without using a scanning electron microscope (Hodges 1952; Fogle 1977a, 1977b, 1979; Thorp 1979; Iezzoni and Hancock 1984; Marcucci et al. 1984; DeGrandi-Hoffman et al. 1984).

Populations of foragers, especially nectar-collectors, shift from one plant species to another at different times of the day, presumably because either certain species of plant are more attractive at certain times of the day (Brittain and Newton 1934; Lutze 1934; Percival 1947), or plants produce pollen and nectar only at certain times of the day (Section 6.1); but there is little evidence to show that individual foragers shift between species. An alternative idea is that most foragers return to the hive where they remain until "their" species, or food source, is again producing food;

that is, the foragers learn to react to the daily fluctuations of nectar and pollen production (Beling 1929; Grabensberger et al. 1934; Kleber 1935; Korner 1939; Park 1949; Frisch 1967, 1968). The individual honeybees change to another food source and another set of routines only when the original food source becomes unproductive.

Fidelity of honeybees to species could explain the common phenomenon of good nut-set in isolated almond trees which are more than 1 kilometre from the nearest source of compatible pollen. Individual bees may fly large distances between trees of the same species in order to keep to one species of plant. However, an alternative explanation is that secondary pollen transfer accounts for the high nut-sets (Section 13.3).

Foragers can be constant to a single cultivar in some circumstances, and such behaviour may be a problem in crops that require cross-pollination (Hutson 1926; Brittain and Newton 1933; Filmer 1941; Shaw and Turner 1942; Karmo 1958; Free 1970a p37), but the importance of such behaviour to almond pollination is unknown.

12.3 The food requirements of honeybees

Honeybee food is pollen and nectar collected from flowers, and small quantities of fungal spores are also eaten (Percival 1947). Honey, including nectar, the raw material from which it is made, is the sole essential food of adult honeybees, and honeybees store honey without limit in order to survive non-food periods (Grout 1949). Nectar is largely comprised of water and several sugars, but small amounts of other substances, such as organic acids, volatile oils, polysaccharides, proteins, enzymes and alkaloids, contribute to its aroma and the characteristics of the honey prepared from it (Beutler 1953; Shuel 1955a; Percival 1965; Baker and Baker 1975, 1983).

Honeybees carry their collected nectar in the honey-stomach. Nectar within the honey-stomach can be digested or regurgitated by the bee. The average load of nectar is 40 mg, and large loads can weigh 70 mg, which is heavy compared to the 82 - 93 mg that is the weight of worker honeybees (Grout 1949; Willmer and Unwin 1981). About 10 mg of the nectar load may be digested by the bee while flying (Grout 1949), but the actual amount depends on the circumstances; and the blood sugar of a bee, excluding the contents of the honey-stomach, lasts only about 15 minutes of flight (Crane 1955; Scholze et al. 1964).

Pollen provides bees with proteins, fats, carbohydrates and vitamins and is essential for brood rearing in honeybee colonies (Maurizio 1951; Percival 1955; Spencer-Booth 1960; Stanley and Linskens 1974; Standifer et al. 1980; Klungness and Peng 1984). Pollen is not required, but may be eaten, by adult bees, and it may be utilized, but is not necessary, in wax production (Green 1934). Almond pollen is one of the more nutritious pollens of those tested on honeybees (Cooper and Berdel 1980b; Standifer et al. 1980).

The two pollen pellets collected by a bee during its foraging trip are referred to as a pollen load. Reported weights of pollen loads vary from 8 to 29 mg, and 15 to 20 mg is common (Park 1922; Parker 1926; Todd and Bishop 1941; Grout 1949; Percival 1950; Maurizio 1953). Most pollen is eaten by brood as soon as it is collected, and so the demand for pollen depends largely on the amount of brood present, which, in turn, depends on the size of the colony, the time of year, and the quality and quantity of nectar and pollen available (Louveaux 1950; Fukuda 1960; Free 1967; Doull 1971, 1972). Colonies with similar amounts of brood may differ widely with respect to foraging activity and pollen collection (Filmer 1932; Synge 1947; Braun et al. 1953; Louveaux 1958; Moriya 1961).

Honeybees store very little pollen relative to the amount they collect. For example, the amount of pollen stored by colonies with populations that peaked at 24,000 bees, averaged only 75 gms and peaked at about 650 gms (Jeffree and Allen 1957), which is much less than the 20 to 30 kg pollen that may be collected by a colony in a year (Section 10.3.2.3).

12.4 Factors that make flowers attractive to bees

12.4.1 Introduction

The attractiveness of target flowers depends on factors related to the target flowers, any nearby non-target flowers, and the needs and preferences of the honeybees. The factors may include flower shape, flower colour, nectar volume, sugar concentration, types and proportions of the various sugars in nectar, fragrance, flavour, ease of getting to the nectar (flower morphology), and flower density. Some factors, such as flower colour, may be ignored by bees that are foraging on the flowers of some plant species, but not ignored by bees foraging on the flowers of other plant species (Darwin 1876; Mather 1947; Grant 1950; Wells and Wells 1985).

The flowers of some plants respond to pollination or age by rapidly changing their characteristics and become inconspicuous, unattractive, or inaccessible to pollinators (Gori 1983); but this has not been observed in almond flowers.

12.4.2 Nectar quality and quantity

The attractiveness of a source of nectar is dependent on the amount of nectar, its odour, its sugar concentration, and the range of sugars present.

The quantity and quality of nectar varies, depending on species, cultivar, flower age, maturity, plant nutrition, and climatic variables of the macro- and micro-environments (Shuel and Pedersen 1953; Free 1970a pp84, 390; Battaglini and Battaglini 1974; Loper *et al.* 1976). Even within a single flower, and especially with shallow open ones such as are common in *Prunus*, the nectar quality and quantity is subject to considerable fluctuations as a result of concentration by wind, high temperatures and low humidities, and dilution by dew and rain (Scullen 1942; Shuel 1952, 1955; Roberts 1956; Free 1970a p390). So the attractiveness of particular flowers may differ at different times of the day, from day to day, and at different stages of flowering.

Generally, there is little nectar in a flower at anthesis (Percival 1961), and so nectar-collectors tend not to visit newly opened flowers (Section 6.5). However, nectar production and concentration usually peak during the first day or two after flowering (Shuel 1961), except in flowers of apple and cherry, in which nectar may be most concentrated in old flowers about to wither (Ewert 1940). Nectar production may cease soon after a flower is pollinated, and nectar secretion may persist for longer in unpollinated flowers. Nectar secretion ceases when the air temperature is above or below certain limits, and those temperature limits differ between species (Behlen 1911; Shuel 1955a; Free 1970a p390). Irrespective of temperature, nectar secretion is greater on a sunny than a dull day, reflecting the fact that nectar sugars are products of photosynthesis (Shuel 1955a). Plants that receive too much water (Doull 1972), or too little water (Shuel and Shivas 1953; Shuel 1955a, 1955b), may produce less nectar, the latter perhaps being true for almond (Traynor 1966). Fertilizers may improve nectar production, diminish it, or have no effect at all (Plass 1952; Ryle 1954; Shuel 1955a, 1955b). The collection of nectar by nectar-gathering insects and by man can stimulate flowers into

producing more nectar (Pedersen and Todd 1949; Wykes 1953; Bogoyavlenskii and Kovarskaya 1956), and an increase in the production of nectar coincides with a decrease in the sugar concentration of the nectar, although there is an increase in the total amount of sugar present (Beutler 1949; Wykes 1953; Bogoyavlenskii and Kovarskaya 1956; Mommers 1966).

Nectar for analysis can be obtained from flowers and the honey-stomachs of honeybees. Early authors questioned the use of nectar from honey-stomachs because the nectar may be concentrated in flight; but later authors (e.g. Park 1932, Simpson 1964; Free and Durrant 1966b; Sylvester et al. 1983) found that the volume and concentration of nectar collected by honeybees was decreased only slightly while a forager was en route to its hive. Nevertheless, errors of measurement may occur on warm days because foragers use the evaporative cooling effect of regurgitated nectar to keep their thoracic temperature within an optimum range while flying (Cooper et al. 1985). Most published measurements of sugar concentration were obtained with a refractometer, but non-sugar constituents in nectar can enter into the refractive index and cause errors of up to 13% (Inouye et al. 1980). Furthermore, errors may occur through the use of different units of measurement for sugar concentration (Bolten et al. 1979). Modern methods of measuring sugar concentration are discussed by Severson and Erickson (1983).

The number of bees working a species of plant is proportional to the quantity of nectar available (Section 10.3.2.1). Also, honeybees prefer to forage on the richest source of nectar available (Kleber 1935; Wykes 1952a; Mommers 1966; Free 1970a p17, 43; Loper et al. 1976; Wells and Wells 1984), and they can discriminate approximately 5% differences in sucrose concentration (Jamieson and Austin 1956; Waller 1972). However, the absence of competitive nectar sources does not mean that flowers with low-sugar nectars will receive the undivided attention of the foragers. Honeybees prefer nectars that contain 20 to 50% sugar, and rarely collect nectar of lower concentrations, perhaps because dilute nectar needs an excessive amount of energy to remove the water and produce honey (Vansell 1934; Roberts 1956; Jamieson and Austin 1956; Waller 1972; Gary 1979).

The ranges of average sugar concentration recorded by authors are: almond 20-40%, apple 25-55%, apricot 5-25%, nectarine 20-25%, peach 20-38%, pear 2-37%, plum 10-40%, sour cherry 15-40%, and sweet cherry 21-60% (Free 1970a p390). These ranges suggest that almond nectar is probably always attractive to honeybees; therefore the importance of the concentration of

almond nectar probably only depends on whether or not the almond nectar is the most concentrated nectar available and hence the most attractive to honeybees.

Sugars that occur in nectar are not equally attractive to bees, and the proportions of the various sugars in the nectar differ greatly between species and cultivars within Prunus, although the proportions of different sugars are usually consistent between flowers within cultivars (Wykes 1952a, 1952b; Bailey et al. 1954; Percival 1961; Waller 1972; Barker and Lehner 1973; Baker and Baker 1983). The main sugars in nectar are sucrose, fructose and glucose, and the minor sugars include maltose, raffinose, melibiose, trehalose and melezitose. Honeybees can distinguish between syrups containing only slight differences in the ratios of sugars (Vansell 1934; Frisch 1934; Battaglini and Battaglini 1972, 1974). Nectar from flowers of Prunus, including almond, are low in sucrose and rich in glucose and fructose (Battaglini and Battaglini 1974), and sucrose may be the most attractive sugar to honeybees (Wykes 1952a, 1952b; Waller 1972; Barker and Lehner 1973, 1984a, 1984b), so almond nectar may not always be as attractive as the nectar of other plant species. Dicotyledonous plants show trends of different sugar proportions in different evolutionary lines, so perhaps plants that produce very attractive nectars can be bred (Percival 1961).

Bees have a highly developed sense of smell and can associate forage with a particular scent or mixture of scents, and the bees can be attracted or repelled by those scents (Frisch 1919, 1965; Clements and Long 1923; Butler 1945a, 1945b, 1951; Ribbands 1955; Lacher and Schneider 1963; Lacher 1964; Wells and Wells 1985). Droughts, and a related lack of odour from flowers, have been blamed for poor almond yields, and so a lack of odour or nectar may affect the attractiveness of bees to flowers. Many chemicals occur in nectar (Baker 1977b), but only some have been studied in relation to honeybee behaviour. Honeybees can detect the presence and concentration of amino acids in solution, and so amino acids in nectar may affect the attractiveness of nectar (Inouye and Waller 1984). Methods of characterizing almond nectar, such as by using high-performance liquid chromatography, may help determine differences and similarities among almond cultivars in relation to the foraging behaviour of honeybees (Thorp 1979; Erickson et al. 1979; Williams 1983). Compounds in the aroma of pear flowers are known to be attractive to insects (Williams and Smith 1979).

12.4.3 Preferences for certain pollens

Honeybees collect some pollens in abundance and other pollens are collected rarely or not at all, and different pollens are collected at different times of the day (Synge 1947; Percival 1955; Levin and Bohart 1955; Boch 1982). Preferences for particular pollens may depend on traits such as nutrition, colour, and the presence of specific chemicals.

The nutritional value of pollen varies greatly, there being effects on longevity and brood development (Todd and Bretherick 1942; Maurizio 1950, 1951; Haydak 1958; Wahl 1966; Loper and Berdel 1980a, 1980b), but there is little evidence to show that bees select pollen for its nutritive value. Perhaps the number of bees reared in a hive depends more on the amount of pollen consumed than on the nutritional value of pollen (Campana and Moeller 1977). Doull (1966) commented that bees work more slowly, take longer to collect a load, and collect smaller loads, when collecting the apparently less attractive pollens. The intensity of the yellow pigment in pollen can be a factor of attraction (Boch 1982), and several authors have demonstrated that a benzine extract of some pollens contains materials that are responsible for the attractiveness of pollen to bees (e.g. Louveaux 1959; Hugel 1962; Taber 1963; Robinson and Nation 1968; Robinson *et al.* 1968; Lepage and Boch 1968; Hopkins *et al.* 1969; Hohmann 1970; Loper and Berdel 1980).

Almond pollen is a highly nutritious and attractive pollen (Loper and Berdel 1980; Webster *et al.* 1985), so the attractiveness of pollen to honeybees is probably not a problem for almond pollination.

12.4.4 Flower morphology

Honeybees readily fly to flowers that do not have petals or stamens, so petals and stamens are not necessary to attract honeybees to almond flowers (Section 3.7). Nevertheless, several aspects of flower morphology influence the behaviour of honeybees.

Honeybees can distinguish between flowers of different colours in the ultraviolet-blue-green-yellow spectral range (Kevan and Baker 1983). Individual bees may visit flowers of one colour only, even when flowers of a different colour offer more concentrated nectar, and other individual bees may readily change between flowers of different colours, especially if the flowers are of the same species (Darwin 1876; Frisch 1919; Mather 1947; Grant 1950; Marden and Waddington 1981; Wells *et al.* 1983). White is the dominant colour of almond petals, but some cultivars have distinct pink and

purple hews, therefore bees could distinguish between some cultivars on the basis of flower colour.

Nectar-guides, also known as honey-guides, which occur on the petals of flowers, are patterns of lines that converge on the nectaries. They supposedly enhance the attractiveness of flowers and are more pronounced in flowers in which the nectaries are harder to find (Free 1970b). Bees fly just as often towards model flowers without honey guides as to model flowers with them, but the bees alight more often and hover longer over the latter (Manning 1956b). Honeybees can discriminate between artificial nectar guides with lines differing in width by less than 1 mm (Anderson 1977). Relationships between the colour of nectar guides, and the pollination strategies of the flower, are discussed by Penny (1983). Nectar-guides vary between almond cultivars with respect to prominance, pattern, and colour, so honeybees could use nectar-guides to distinguish between almond cultivars.

Honeybees can learn the general shape of flowers and the general form of plants (Darwin 1876; Manning 1956), and they may remember flowers as low resolution pictures (Gould 1986). Some bees forage only on flowers of particular shapes and sizes, but other bees readily move between tall and stunted plants of the same species, and between flowers at different stages of opening (Free 1970a, 1970b). The shape and size of almond flowers do not vary greatly between cultivars, so flower shape and size may not have a significant bearing on the attractiveness of almond flowers.

Floral structure can influence the behaviour of visiting foragers. For example, the behaviour of nectar-collectors depends on the accessibility of the apple nectar, which, in turn, depends on the stiffness and spacing of the anthers (Section 11.2); and the different forms of behaviour affect the probability of effective pollination, as discussed further in Section 13.1.

12.5 Improving the attractiveness of flowers

Honeybees may not visit the target crop if the target crop is not attractive to bees or if the bees consider other flowers to be a more attractive food source (Section 12.4), so methods of making flowers more attractive to honeybees have been investigated.

Many authors have tried methods of directing bees to particular flowers (Free 1970a p81), but there has been much contention as to whether or not the methods worked. Some experiments were poorly designed, and

different colonies standing side by side can vary considerably in the proportion of the pollen they collect from different crops. So experimental data that supposedly show bees to have been directed to a particular crop may be the result of chance variation. Free (1958a) claimed that there is a tendency for experiments of this sort only to be published if they have given positive results. Also, directing honeybees to a particular flower species is difficult when the bees are already obtaining ample nectar and pollen from other species (Frisch 1943; Free 1958a). Aluminium strips may attract honeybees to adjacent flowers (Wolfenbarger and Moore 1968), but the other methods rely on various types of chemicals, and their value in improving pollination has not been established.

Honeybees have been induced to visit certain species of flowers by providing, inside or outside their hive, sugar syrup to which the odour of the target flowers had been imparted; and increases in honey production, pollen collection, seed yield, and rate of bee visitation, were claimed (Bretschko and Bullmann 1966; Free 1970a p82; Hohmann 1970; Johnson and Wenner 1970; Goodwin 1986). Odour in the stored honey may also influence the foraging behaviour of the colony's bees (Free 1969). Another method of redirecting honeybees to target crops has been the spraying of the target crop with sugar syrup (Frisch 1967; Crane et al. 1955; Free 1970a p83), but critical experiments have shown little or no beneficial effect (e.g. Stephen 1958; Free 1965b, 1965c), although astounding claims have been made (e.g. Antles 1953). Roberts (1956) and Free (1965c) did succeed in getting more bees to the trees, but few of the extra bees would have transferred pollen onto stigmas because the sugar solution was all over the trees and not just on the flowers. Indeed, some bees that would have pollinated flowers were diverted to other parts of the tree, and so fruit-set was probably reduced by the treatment (Free 1965c).

"Beelure" and "Beeline", which are reputed bee attractants, did not increase yield, or attract more honeybees, when tested in Californian almond and apple orchards (Zaifert and Shafir 1978; Burgett and Fisher 1979; Thorp 1979; Rajotte and Fell 1982; Margalith et al. 1984; Tew and Ferree 1984). Also, attempts to condition honeybees to forage on almond trees or creosote bushes by feeding them on the respective pollen for six weeks, failed to alter the behaviour of the honeybees (Boelter and Wilson 1984).

An alternative approach to attracting honeybees to crops is to use chemicals that repel honeybees from non-target flowers, the theory being

that the repelled bees then switch to the target crop (Free 1958a; Woodrow et al. 1965; Simpson 1966; Anderson and Atkins 1968; Atkins et al. 1975; Johansen 1977; Ayers et al. 1984; Free et al. 1985). Most of the fore-mentioned authors were aiming to prevent the killing of foragers by pesticides. Pesticides and fungicides can repel honeybees (Todd and Reed 1969; Praagh and Ohe 1983), so the use of fungicides in almond orchards during flowering may decrease the amount of effective pollination immediately after fungicides are sprayed. This is apart from the ability of fungicides to kill pollen (Section 8.4.2).

Honeybees may produce substances (e.g. Nasonov pheromones) that attract or repel other honeybees. Such substances may be used in relation to poor or exhausted food sources, but the literature is confusing and contradictory (e.g. Ribbands and Speirs 1953; Renner 1960; Nunez 1967; Frisch 1967; Wells and Wenner 1971; Free et al. 1984). Attempts to attract honeybees to crops by using synthetic Nasonov pheromone did not succeed (Waller 1970); perhaps because only water-collecting bees regularly expose their Nasonov gland whereas nectar-collectors and pollen-collectors normally do not expose their Nasonov gland except, perhaps, at rich sources of nectar (Free 1968; Free and Williams 1970, 1972a, 1972b, 1983). Nevertheless, Nasonov pheromone is comprised of several chemicals, some of which may alone be attractive to honeybees (Free 1962c, 1979, 1984b; Waller 1970; Williams et al. 1981; Free et al. 1981; Ladd and Tew 1983). Two of those chemicals, citral and geriol, apparently improved apple yields by masking the repellency of fungicides (Ohe and Praagh 1983; Praagh and Ohe 1983). Other chemicals, which are not known as pheromones, may be attractive to honeybees (Ladd and Tew 1983; Praagh and Ohe 1983).

Some of the confusion mentioned in the previous paragraph may be explained by the theory that foragers may be able to detect the presence or absence of food in flowers by sight while hovering (Section 6.5; also Thorp et al. 1975, 1976; Kevan 1976), that is, pheromones alone cannot explain the behaviour of foragers. Another theory is that bees may be able to detect changes in the electrostatic charge of flowers, which may be caused by visiting bees and which may take 5 to 40 minutes to disappear (Erickson and Buchmann 1983).

12.6 The use of limited flight range immediately after hive placement

Honeybees tend to forage in and dominate the food sources in the area nearest to their hive, but the territory of a colony, or group of colonies,

may extend up to several hundred metres from the hive, and the majority of foragers in a territory originate from the respective hive or group of hives (Gary et al. 1978; Gary 1979; Guerrero-Prieto et al. 1985). The territory of a colony does not exclude bees from other colonies; that is, a territory is only an area in which the majority of bees are from the colony to which the territory belongs (see Free 1970a p41). Perhaps, though, individual flowers are the exclusive domain of a particular colony. Large colonies may or may not have larger territories than smaller colonies (Beutler 1954; Levchenko et al. 1968; Olifir 1969), but the evidence for either alternative is scanty.

Colonies apparently require several days to establish their territory, and the foraging range of honeybees is limited to the vicinity of their hives during the first three days after hive placement (e.g. Kremer 1948; Free 1970a p75; Section 3.6). For example, colonies placed in a blueberry patch gradually extended their foraging range to 135 metres on the first half-day, to 540 metres on the second day, and to 675 metres or more on the third day (Karmo 1958).

This behaviour may be useful in target crops, such as pear, that are not very attractive to bees. For example, hives can be placed in the middle of the target crop so that bees will not fly outside of the crop for 2 or 3 days, by which time the bees may have become "fixed" on the target crop (Free and Smith 1961). Further, exchanging hives between distant orchards every 2 to 4 days, could maintain a high population of foraging bees within the target orchard (Karmo and Vickery 1954; Karmo 1958), especially if the hives are interchanged between crops of the same species, because bees which have been moved tend to forage on the same crop as before, if it is available (Eckert 1933; Levin and Bohart 1957; Free 1959, 1963). A similar advantage may be gained by progressively introducing more and more hives into the target crop as the flower density increases, thus keeping the hive density in proportion to the food supply (Todd and Vansell 1952). A long term prospect is the breeding of strains of bees that have a limited flight range (Gary and Witherell 1977; Witherell and Laidlaw 1977).

A secondary advantage of the progressive introduction of hives may be that too many foragers are sent to the flowers during the 2 or 3 days necessary for a colony to establish its territory. This idea is theoretical, and it is based on casual observations of excessive densities of foragers on flowers for 2 or 3 days after hive introduction. Normally, no more bees are sent to a food source than are necessary to fully exploit

the food source (Section 10.3.2.1), but before hive territories are established, each colony may send an adequate number of foragers to exploit the food source, so that, collectively, too many foragers are sent to the food source. During that time, the excessive competition at the food source should force foragers to fly further to collect a load of pollen or nectar, and hence those foragers are more likely to effectively pollinate flowers because they are more likely to visit the flowers of two or more cultivars (also see Section 14.3.2) (Butler 1943, 1945; Butler et al. 1943).

Another method of fixing bees onto particular crops is to confine the bees until there is a time of day when there are no food sources to compete with the target flowers, but colonies can be damaged by confining the bees to their hives (Free and Nuttall 1968; Crane and Walker 1983).

12.7 Weed control - reducing the competition

Honeybees forage on the most attractive flowers available, and so weeds, which are often more attractive than target crops, may need to be destroyed (Brittain 1933; Karmo and Vickery 1954; Griggs 1970). Competition between almond trees and other plants, for honeybees, is not a great problem in Australia because when almond trees flower, few other plants flower in sufficient profusion and proximity to almond orchards to provide competition for honeybees. The weeds Soursob (Oxalis pesaprae) and Salvation Jane (Echium spp.) are two noteworthy exceptions in Australia. Salvation Jane begins its flowering season late in the almond flowering season, and it is very attractive to honeybees (Corbet and Delfosse 1984). Indeed, at Angle Vale, South Australia, hives are left in the almond orchards after the almond flowering season so that the bees can forage on the Salvation Jane in neighbouring fields (e.g. Section 2.3). Soursob flowers during the almond flowering season, and sometimes honeybees find soursob flowers more attractive than almond flowers, but soursob flowers open for only a few hours per day and only during sunny weather, so they are not a great distraction to bees (Purdie and Winn 1964, 1965). Nevertheless, soursob flowers are usually destroyed by almond growers to eliminate the competition for bees.

Chapter 13: Interaction between bees and flowers

13.1 Importance of the different foraging behaviours

An almond flower is usually pollinated only when pollen moves from the body of a forager to the stigma when the forager's body incidentally touches the stigma. Only nectar-collectors and pollen-collectors visit flowers, so only those bees can pollinate almond flowers; but the probability of pollination occurring during a single visit depends on the behaviour of the forager, and the most desirable behaviour is likely to be that which yields the most stigma touching during the EPP.

The actual transfer of pollen to the stigma is a difficult event to observe or measure. However, stigma touching is observable, and the electrostatic forces between the forager, pollen grains, and stigma, may ensure that pollen is transferred to the stigma whenever pollen on a forager's body is close to a stigma (Corbet et al. 1982; Erickson and Buchmann 1983). Furthermore, most foragers may always carry an "adequate" amount of pollen for transference although the amount of pollen on a forager may depend on the forager's behaviour (Section 13.4.2). So perhaps the value of each type of foraging-behaviour to pollination may be assessed by measuring the incidence of stigma touching. Certainly the incidence of stigma touching is important because, no matter what the influence of other factors is, the probability of effective pollination (i.e. P1 in Figure 1.2 and Section 1.2) approaches the limit of unity as the incidence of stigma touching increases (Brain and Landsberg 1981).

The probability of a forager touching the stigma during a flower visit apparently depends on the position of the stigma. Usually the stigma and stamens within flowers of fruit trees are at about the same height above the flower cup, but in the flowers of some apple and almond cultivars, the stigma can be well below, or well above, the platform of stamens (Section 3.4; Fig. 3.5). The probability of flowers with short stigmas being pollinated by a forager may be lower for pollen-collectors, which usually stay on the stamen platform (Fig. 11.1), than for top-workers which delve between the stamens and adjacent to the stigma (Fig. 11.2).

Generally, and notwithstanding stigma length, side-workers rarely contact the stigma, but pollen-collectors and top-workers usually do (e.g. Roberts 1945a, 1945b; Free 1960a, 1960b; Thorp 1979; Robinson and Dell 1981; DeGrandi-Hoffman et al. 1985; Section 6.5). For example, pollen-collectors and top-workers contacted apple stigmas during 86-100%

and 83-100% of visits respectively, depending on cultivar, but side-workers contacted apple stigmas during only 0-33% of visits (Robinson 1979a; 1981). In other words, top-workers and pollen-collectors appear very effective at pollinating stigmas, while side-workers appear to be largely ineffective; but this may not always be true.

Foragers that visit flowers after their EPP has expired are useless for pollination. Pollen-collectors predominantly visit newly-opened flowers whereas nectar-gatherers favour older flowers. For example, 258 (84%) of 305 visits by pollen-collectors were to apricot flowers that contained anthers with pollen, compared to 9 of 266 visits by nectar-collectors (Langridge and Goodman 1981). This tendency was also observed in almond (Section 6.5). Consequently, nectar-collectors tend to visit older flowers and so are less likely than pollen-collectors to effectively pollinate flowers that have very short EPPs (i.e. 1-3 days). Also, nectar-collectors that visit flowers that have lost all their pollen, cannot incidentally obtain pollen from such flowers for subsequent pollination elsewhere, so the bodies of nectar-collectors tend to carry less pollen than the bodies of pollen-collectors (Free 1966a).

The importance of the different behaviours must also depend on the frequencies of the behaviours. The ratio of top-workers to side-workers depends on several factors, which are discussed in Sections 11.2 and 13.2.

Some authors recognized the importance of nectar-collectors in pollinating some crops (e.g. Bohart 1957; Martin and McGregor 1973; McGregor 1976), but other authors thought that nectar-collectors were of little use for pollination, probably because most of the nectar-collectors that they observed were side-workers (e.g. Phillips 1930a, 1930b; Dirks 1946; Free 1970a p392; Sheesley and Poduska 1970a; Al-Tikrity et al. 1972; Erickson et al. 1975). The latter authors applied their conclusion to cultivars and crops for which the conclusion was probably not relevant because many top-workers were probably present (Free 1958, 1967; H.E.A.F.C. 1961; Free 1970a p84-87; Gary et al. 1978a). Also, some authors looked at ways of increasing the number of pollen-collectors because they believed nectar-collectors to be of little use for pollination (see below).

13.2 Interconversion of pollen-collectors and nectar-collectors

Methods of increasing the number of pollen-collectors, and the amount of pollen collected, have been investigated (e.g. Free 1970a p84). Generally, an increase in the amount of pollen collected, indicates an

increase in the proportion of foragers that collect pollen (e.g. Louveaux 1950; Lindauer 1952, 1953; Fukuda 1960; Free 1967). Changes in the ratio of nectar-collectors to pollen-collectors reflects a change in the behaviour of individual foragers, rather than to foragers with one form of behaviour deserting the target flowers (Free and Spencer-Booth 1964a, 1964b; Robinson 1981).

Pollen-collection increases when the amount of brood increases (Allen and Jeffree 1956; Al-Tikrity et al. 1972) and decreases greatly when colonies are deprived of their brood (Free 1967), because the collection of pollen is initiated and controlled by pheromones which originate in the brood and the queen. Adding the relevant pheromones produced by the queen or brood may increase pollen collection (Butler et al. 1961; Callow et al. 1964; Free 1967), and colonies collect more pollen than they otherwise would when bees are made to leave an entrance that is adjacent to the brood combs (Free and Williams 1976).

Pollen-collection can be increased by feeding colonies with syrup or honey, which may either free nectar-collectors so that they can collect pollen (Goodwin 1986), or it may stimulate the production of brood which, in turn, increases the demand for pollen (Free and Spencer-Booth 1961; Free 1965a, 1965b; Barker 1971).

Pollen traps, which were designed to remove the pollen from the corbiculae of bees as they enter their hive, can make the colony short of pollen. This, in turn, may increase or decrease the amount of pollen collected, the amount of brood rearing, and the number of pollen-collectors; that is, the experimental evidence is contradictory (e.g. Wilson 1923; Fukuda 1960; Stephen 1958; Todd and McGregor 1960; Moriya 1966; Free 1970a p85; Laere and Martens 1971; Shaparew 1985).

Regardless of the comments made above, an increase in the number of pollen-collectors, and the amount of pollen they collect, does not necessarily mean that the incidence of effective pollination has been increased. For example, increased pollen collection does not always mean collection of the target pollen because pollen collected by some foragers may have come from outside of the target crop and thus not have resulted in an improvement of pollination within the target crop (e.g. Free 1965a, 1965b; Waller et al. 1985). Most early authors did not mention whether or not they checked the identity of the collected pollen, perhaps because discerning between species of pollen is difficult, even with the aid of an electron microscopy (Section 12.2). Furthermore, all the pollen in an

almond orchard is probably eventually collected if hives are present (e.g. Sections 6.3, 6.5), so an increase in the number of pollen-collectors may not increase the incidence of effective pollination unless the probability that a flower is effectively pollinated is increased through the flowers receiving more visits before the EPP expires (e.g. Section 13.4.4).

Pollen-collectors may change to nectar-collection when pollen becomes scarce (Free and Spencer-Booth 1964b) and perhaps when the colonies lose their honey reserves to apiarists (Rinderer and Hagsted 1984). Pollen-collectors may also change to nectar-collection or water-collection during warm weather (Section 11.3).

13.3 Secondary pollination

Primary pollen transfer, which refers to pollination where only one bee moves the pollen from anther to stigma and from tree to tree, is often assumed to be the only significant pathway for the movement of pollen from anther to stigma (Williams 1959; Free 1962a; DeGrandi-Hoffman et al. 1984). Individual foragers keep to small foraging areas during single trips, usually visiting no more than 1 or 2 trees, but the total area covered during consecutive trips can be much larger (Free and Spencer-Booth 1964b; Free 1966). However, the large areas that bees visit over consecutive foraging trips, are not large enough to explain why significant pollination usually occurs in crops hundreds of metres from the nearest source of pollen (e.g. Oppenheimer 1948; Singh 1950; Williams 1959; Free 1962a, 1966a, 1970a p46; Free and Spencer-Booth 1964a). Furthermore, isolated trees can produce a good fruit-set although they may be several kilometres from the nearest source of pollen (Free and Williams 1972).

These phenomena can be explained by two theories of secondary pollination, both of which refer to the involvement of 2 or more bees in the pathway for the transfer of pollen between anther and stigma.

Betts (1931) suggested that pollen that has been carried by a bee to a flower can be transferred to another bee with an overlapping foraging area, and eventually be used to pollinate a flower outside the foraging area of the first bee. This process may be repeated by numerous bees so that an appreciable number of flowers may be pollinated far from the pollen source. Fluorescent powder put on bees can be distributed in this way (Townsend et al. 1958; Johansen 1959), but fluorescent powder may be more readily distributed than pollen, and the presence of fluorescent powder on flowers can influence the behaviour of honeybees (Mittler 1962). Furthermore,

Johansen and Degman (1957) were unable to detect a redistribution of foreign pollen that had been placed on some of the flowers of an apple tree which was enclosed in a cage with a hive of bees. Consequently, sound support for this hypothesis has not been produced, and the experiments that have been done were not designed to differentiate between the mechanisms of this theory and the next one.

Another theory of secondary pollination is that foragers unintentionally transfer pollen between their bodies while they are inside their hive (Stadhouders 1949; Karmo and Vickery 1954, 1957; Karmo 1961). The transfer of pollen between bees within the hive does occur because dead bees that were left in hives, and bees that were too young to forage, accumulated thousands of pollen grains on their bodies (Free and Williams 1972; DeGrandi-Hoffman et al. 1986). Furthermore, bees that were departing from their hive were able to cross-pollinate apple flowers with the pollen they carried from the hive (Free and Durrant 1966; DeGrandi-Hoffman et al. 1984, 1986).

Opposition to both the above theories of secondary pollination has occurred, but the claims are not justified. For example, Latimer (1936) concluded that bees transferred little or no apple pollen to stigmas from the flowers that the bees were on two or more days earlier, but the design of his experiment was not adequate to justify such a conclusion, especially since there were no replications of the treatments. Similarly, Butler and Haigh (1956) and Kraai (1962) claimed to have shown that the bodies of foraging bees were thoroughly cleansed overnight of all pollen collected during the previous day, but their conclusions are invalid because they did not show that the bees carried "contaminant" pollen prior to the supposed "cleansing". Nevertheless, the viability of apple pollen taken from bees' corbiculae decreases rapidly within a few hours (Singh and Boynton 1949; Griggs et al. 1950) and this may also happen to pollen from other parts of the body, especially when the pollen dries rapidly (Overley and Bullock 1947). So there may be a limited time for the pollen to reach a stigma via a secondary pollination pathway.

In conclusion, secondary pollination does appear to be a significant factor of pollination; but primary pollen transfer is probably more important than secondary pollination; otherwise fruit-set would not decrease rapidly with increasing distance from a pollen source and across hedgerows (Sections 14.3.1, 14.3.5).

13.4 Number of honeybee visits to ensure pollination

13.4.1 Introduction

Effective pollination does not occur every time a bee visits a flower because, apart from reasons given elsewhere, the bee may not touch the stigma, and if it does, pollen may not move from it to the stigma. On the other hand, if pollen does move to the stigma, the pollen may not be compatible with the stigma. Whether or not a bee touches the stigma depends largely on the behaviour of the bee and the morphology of the flower, as discussed in Sections 11.2 and 13.1. Whether or not pollen moves from the bee to the stigma when the stigma is touched, probably depends on the amount of pollen on the body of the bee, and this is discussed below and in Section 13.1. The compatibility of pollen with the stigma is discussed in Section 8.5, but the probability of the pollen that is transferred being compatible with the stigma depends on the mixture of viable pollen on the bee, and that, in turn, depends on the prior foraging activity of the bee in relation to the particular cultivars to which the visited flowers belong. This is also discussed below.

13.4.2 Amount of pollen per honeybee body

Estimates of the number of pollen grains on the bodies of honeybees, excluding pollen in the corbiculae, vary from thousands to millions (e.g. Murneek 1937; Lukoschus 1957; Skrebtsova 1957; Rozov 1957; Stanley and Linskens 1974). The number of pollen grains seems to depend on the plant species involved. For fruit trees, the number is usually in the thousands (e.g. Rozov and Skrebtsova 1958; Free and Williams 1972; Kendall and Solomon 1973). The bodies of nectar-collectors also tend to carry less pollen than do the bodies of pollen-collectors (Free 1966a).

The identity (i.e. cultivar or species) of the various pollen grains on the body of a forager must depend on the foraging history of the forager, and, if one considers secondary pollination (Section 13.3), the foraging history of other bees in the colony. Presumably, a forager which has flown from one cultivar to another will increasingly dilute the pollen that came from the first cultivar with pollen from the second cultivar as it progressively visits more flowers of the second cultivar. So, theoretically, the probability of effective pollination occurring decreases as a forager continues to forage on the flowers of a particular cultivar (Free 1970a; Waddington 1983).

The incidence of compatible pollen on apple stigmas was examined by DeGrandi-Hoffman et al. (1983). They found that every pollinated stigma, and every forager, carried a wide range of pollen from other apple cultivars, as well as from other species; but the experiment was done in very small experimental orchards, and so the results may not be applicable to larger commercial orchards.

13.4.3 Longevity of pollen on a honeybee body

The viability of apple pollen taken from honeybees' corbiculae decreases rapidly within a few hours, especially when it dries rapidly (e.g. Overley and Bullock 1947; Singh and Boynton 1949; Griggs et al. 1950), but there is sufficient viable pollen on the bodies of honeybees that have been confined for 4 days to allow effective pollination to occur. However, the probability of effective pollination is not as great as for bees that have just been foraging (e.g. Latimer 1934; Karmo 1960, 1961; Free and Durrant 1966).

13.4.4 Number of visits per flower to ensure effective pollination

Effective pollination can occur only during the EPP, and a single visit by a forager is not enough to ensure the effective pollination of a stigma, even if the stigma has been touched (e.g. Section 13.4.1). However, irrespective of the probability of effective pollination during a single visit is, the probability of a flower being effectively pollinated increases towards the limit of unity as the number of visits by foragers to the flower increases (Brain and Landsberg 1981). Furthermore, the number of seeds per fruit in multiple-ovary fruits is also increased when there is more than one instance of pollination (e.g. Kondrat'ev et al. 1972; Panov and Petkov 1975; Wolfenbarger 1979; Visser and Verhaegh 1980b; DeVries and Dubois 1983; Shore and Barrett 1984).

The deposition of compatible pollen on a stigma is not a sign that effective pollination has occurred because, for example, the pollen grains may not germinate. The probability that pollen grains will germinate is increased by multiple pollinations because pollen grains can be mutually stimulated to germinate when crowded on the stigma (e.g. Almeida 1945; Lapins and Arndt 1974), and fruit-set and seed production are increased with increasing density of pollen grains on the stigma (Ter-Avanesian 1978; Shore and Barrett 1984). Moreover, the "pioneer" pollen grains deposited by a first pollination can affect the stigma in a way which allows the pollen

that is deposited by subsequent pollinations to germinate more readily and produce faster growing pollen tubes than might otherwise have occurred (Stettler 1968; Knox et al. 1972a, 1972b; DeVries and Dubois 1983). This interaction may be the reason why plants that are normally self-incompatible can self-set seed after 2 or 3 successive pollinations (Dayton 1974; Visser 1981; Van Tuyl et al. 1982; Visser et al. 1983; Visser and Marcucci 1983; Montalti and Filita 1984; Eenink 1984).

The model of Brain and Landsberg (1981) suggests that visits beyond about 5 visits may have little effect on the probability of effective pollination having occurred. In the experiment reported in Section 6.5, only 2 of 39 flowers produced nuts, perhaps because the EPP was only 2 or 3 days (Section 8.1.2) and because many flowers received between 0 and 2 visits during that time. Methods should be sought of increasing both the EPP and the incidence of flower visitation by foragers.

Chapter 14: Flight activity of honeybees, and orchard design

14.1 Weather and flight activity

Honeybees fly during daylight hours only, but they may fly at light intensities as low as 10 lux if the other weather variables favour foraging (Levchenko 1961). Often, however, weather does not favour foraging, and unfavourable weather for honeybee flight is considered a dominant factor of fruit-set in many crops (Hedrick 1908; Dorsey 1919a; Free 1960b, 1970a; Robinson 1979). Temperature seems to be a particularly important factor (Hambleton 1925; Wafa and Ibrahim 1957b, 1958). There is a minimum threshold temperature below which significant flight activity does not occur; and flight activity, measured as the number of honeybees leaving a hive in a minute, varies with ambient air temperature up to about 20°C, beyond which flight activity is usually at its peak. The threshold temperature for flight varies greatly and has been stated to be 17°C (Corbet and Delfosse 1984), 13°C (Lundie 1925; Brittain 1933; Langridge *et al.* 1977; Langridge and Goodman 1981; Seeley and Heinrich 1981), 10°C (Lundie 1925; Vansell 1942; Louveaux 1958; Thorp *et al.* 1973; Erickson *et al.* 1975; Williams and Sims 1977; Heinrich 1979), 9°C (Burrill and Dietz 1981); 8°C (Bodenheimer and Ben-nerya 1937), 7°C (Rashad 1957; Section 3.6), and 6°C (Parks 1925; Boyle-Makowski and Philogene 1985).

The variation in threshold temperature has been attributed to several factors. The experience of the hive may be important; for example, hives from cooler areas may have a lower threshold temperature than hives from warmer areas, through the colonies being "conditioned" to certain temperature regimes (Free and Spencer-Booth 1960). Similarly, the threshold temperature may vary throughout the year; for example, it may be 12-14°C in early spring, and 13-17°C later in summer (Lundie 1925; Parks 1925). The threshold temperature may be lower for larger colonies than for smaller colonies (Woodrow 1932, 1934; Brittain 1933; Rea 1940; Thorp *et al.* 1973; Erickson *et al.* 1975), or the reverse might be true (Taranov 1952; Free and Preece 1969). This contradiction may be explained by older bees having a higher metabolic rate, and hence a better tolerance of low temperatures than younger bees (Free 1970a p61); that is, the results obtained by an author may have depended on the age structure, and perhaps experience, of their colonies. Moreover, the threshold temperature may be determined by the inability of foragers to maintain the minimum desirable body temperature of an estimated 23 - 25°C (e.g. Cena and Clark 1972;

Heinrich 1979). Then colony size may not be a factor because the body temperature of a foraging bee cannot be influenced by the temperature of the hive after the bee has been away from the hive for more than 1 or 2 minutes (Willmer and Unwin 1981). Certainly body temperature is affected by solar radiation, because the body temperature of honeybees is higher when flying in sunlight than when flying in shade (Digby 1955; Cena and Clark 1972; Heinrich 1979; Willmer and Unwin 1981). Also, honeybees prefer to fly in sunlight and visit flowers in sunlight, and many foragers return home when clouds form overhead (Butler et al. 1943; Percival 1947; Roberts and Struckmeyer 1948; Free 1960b, 1962b; Free and Spencer-Booth 1964a; Thorp et al. 1973; Erickson et al. 1975).

However, honeybees can fly when the air temperature is below the threshold because honeybees have been seen collecting ice-water from pools of melting snow when the air temperature was 0.5°C (Lundie 1925). Progressively more honeybees are required in the hive as the ambient air temperature decreases below 18°C, because the temperature of the brood combs must be maintained at about 32-36°C (Seeley and Heinrich 1981); but some honeybees may still be available for foraging when the temperature is below 5°C because colonies can survive temperatures of -38°C (Szabo 1985). These observations, and the variation in threshold temperatures mentioned above, suggest that honeybees may desist from flying in cold weather for some reason other than because they are unable to do so.

Honeybees seem to be aware of the times when pollen and nectar become available because the maximum number of foragers at a food source is usually proportional to the amount of food available (Section 10.3.2.1). Scout bees (described in Section 11.4) may be the only bees that are outside of hives when food is not available. If true, then the scarcity of foragers in the field when the air temperature is below the "threshold" temperature for flight may be a reflection of the corresponding lack of available pollen and nectar at those temperatures (e.g. Heinrich 1979; Section 6.5). The "responses" of honeybees to fluctuations in solar radiation, which are discussed above, can be explained in terms of the coincidence of foraging activity with pollen and nectar availability; that is, both the rate of anther dehiscence, and the amount of honeybee activity, tend to increase with increasing air temperature, and they have a similar threshold temperature (e.g. Hambleton 1925; Percival 1947, 1955; Wafa and Ibrahim 1957a, 1958). For example, the experiments reported in Sections 6.3 and 6.5 suggest that the threshold temperature of 7°C may be

common to both foraging activity and anther dehiscence in almond. Furthermore, the observation that honeybees tend to forage on the sunnier parts of trees can be attributed to the propositions that (a) anther dehiscence is promoted at times of direct sunlight (Section 6.3), and (b) the flowers that receive direct solar radiation are the flowers most likely to be dry, which aids collection of pollen by pollen-collectors (Percival 1947).

If one accepts these propositions, then orchard management should maximize the number of flowers in sunlight, such as by pruning and shaping trees to allow sunlight to penetrate into the canopy. Row orientation may also be important in that rows orientated north-south may be best because both sides of such rows would receive sunlight during some of each day.

Temperature is not the only weather variable that effects foraging activity. Honeybees do not fly extensively during rainy, cool weather, and pollen is not collected from wet flowers, but honeybees may continue to forage for nectar in drizzling rain (Dorsey 1919a; Legesse 1928; Butler et al. 1943; Percival 1947; Thorp et al. 1973; Erickson et al. 1975). Possible reasons for honeybees not collecting pollen in wet weather are the mechanical difficulty of transferring wet pollen to the pollen basket, and the tendency of anthers to close when they get wet (e.g. Dorsey 1919a). However, relative humidity apparently has little effect on foraging activity (e.g. Boyle-Makowski and Philogene 1985).

Winds below 8 kph have little effect on foraging activity, but foraging activity is low during cool periods with winds of 10 to 20 kph, and few honeybees forage when the wind is over 40 kph, regardless of the temperature (Dorsey 1919a; Hutson 1925; Rashad 1957; Thorp et al. 1973; Erickson et al. 1975). This relationship between wind speed and temperature, with respect to foraging activity, suggests that the wind chill factor of strong winds may restrict foraging activity by reducing the body temperature of bees to below the threshold for flight (e.g. Digby 1955), or the wind chill may effect the availability of pollen and nectar (Sections 6.3, 12.4.2), and so effect foraging activity (Section 10.3.1). Furthermore, honeybees prefer to forage on the lee side of trees and windbreaks, especially when air temperatures are low (MacDaniels and Heinicke 1929; Lewis and Smith 1969). Wind direction influences the direction in which the honeybees forage if the wind is above 16 kph (Dorsey 1919a; H.E.A.F.C. 1961), and wind may increase the foraging areas of individual foragers by blowing the foragers about (Singh 1950; Free 1960b).

14.2 Weather versus distance to foraging areas

Honeybees that work a long way from their hive are more easily deterred from foraging by unfavourable weather than are honeybees that work closer to the hive (Free 1970a p76). At least two theories attempt to explain what happens to the honeybees that are deterred from foraging.

One theory is that deterioration in the weather reduces the distance that individual foragers fly from the hive, that is, the deterred foragers work closer to the hive (Sax 1922; Hutson 1926; MacDaniels and Heinicke 1929; Hootman and Cale 1930; Ribbands 1951, 1952). The other theory is that deterioration in the weather induces the foragers that are working farthest afield to return to the hive and not leave it again until the weather improves sufficiently for them to go back to their foraging areas; meanwhile the honeybees working closer to the hive continue to forage (Butler et al. 1943; Boch 1956). There is no evidence to support the former theory and such behaviour is unlikely because areas close to the hive are likely to be already saturated with foragers, thus leaving no room for more foragers (Section 10.3.1). On the other hand, there is evidence which supports the latter theory (Free 1970a p41), and one can propose a reason for the behaviour suggested by the latter theory. Foragers require more energy to maintain their body temperature in cooler weather than in warmer weather, because the rate of loss of body heat is much greater at cooler temperatures; and foragers must maintain their body temperature above a certain threshold, otherwise they cannot fly (Willmer and Unwin 1981; Cooper et al. 1985). Also, the maximum distance that foragers fly during cool weather is independent of the colony's population size (Gary et al. 1978; Waller et al. 1985). So the distance a forager flies from its hive in cool weather may depend on its energy supply versus its rate of heat loss. The behaviour suggested by the latter theory may be important in Austalian almond orchards because the weather is often unfavourable to foraging activity (i.e. cold, wet and windy). The distance foragers can fly from their hive, or from sources of water, is also restricted when the air temperature is over 30°C because the bees cannot prevent their bodies from overheating unless they use water for evaporative cooling (Cooper et al. 1985). Pollen-collection may stop completely, but nectar-collection usually continues in hot weather because the bees can use the water from the nectar to cool themselves (Section 11.3).

Regardless of the weather, honeybees probably prefer to forage as close to the hive as possible, given that enough food is available, because successful foragers recruit more honeybees when working near rather than distant crops, and the density of foragers decreases with increasing distance from a hive, even in good weather (Hutson 1926; Bodenheimer and Ben-nerya 1937; Francon 1939; Mommers 1948a, 1951; Boch 1956; Wolfenbarger 1954, 1959; Lee 1961; Free and Spencer-Booth 1963; Gary et al. 1976, 1978a, 1978c; Erickson et al. 1977; Gary 1979; Walker et al. 1985; Loper et al. 1985). Moreover, a trend of decreasing yield with increasing distance away from hives is common in orchard and field crops (see the next Section).

14.3 Orchard design with regard to foraging activity

14.3.1 Yield variation within orchards

Yield within field crops and orchards usually varies in relation to several distinct trends. The most obvious trends have been decreasing yield with increasing distance from hives (e.g. Hutson 1926; MacDaniels and Heinicke 1929; Butler et al. 1943; Mommers 1948, 1951; Tzyganov 1953; Wolfenbarger 1954; Nevkryta 1957; Glushkov 1958; Free 1970a p68), and decreasing yield with increasing distance from the nearest source of compatible pollen (e.g. Whiffen 1948; Williams 1959; Williams and Smith 1967; Free 1970a p406; Lapins and Arndt 1974). The latter trend can be observed over very short distances. For example, fruit-set on a tree is often highest on the side of the tree adjacent to the pollinator tree or bouquet (Williams and Smith 1967; Free 1970a p407). These trends can be related to the behaviour of foragers and the probability of effective pollination occurring while a forager is visiting a flower (Free 1970a p67-69), and the trends suggest that the optimal distance between a tree and a source of compatible pollen, and between a tree and a hive, is the shortest distance circumstances allow. However, foraging behaviour and variation in yield with distance also depend on physiological aspects of the orchard (e.g. tree size, spacing, distribution), and this is discussed below.

Primary pollination is probably far more important than secondary pollination (Section 13.3), and so the significance of secondary pollination is conveniently ignored in the following discussion.

14.3.2 Inter-tree flights by foragers

Almond trees must be cross-pollinated, and so foragers must visit the flowers of two or more compatible cultivars. But many foragers are useless for cross-pollination because they do not fly from one tree to another, and instead forage only on the flowers of one tree (e.g. MacDaniels 1931; Singh 1950; Free 1960b, 1966; Free and Spencer-Booth 1964b). For example, in an apple orchard with tree canopies of 6 to 7.5 metres in diameter and planted to a 6.7 metre square grid, 45 foragers visited only the flowers of a whole tree, 16 foragers visited two trees, 2 foragers visited 3 trees, 2 foragers visited 4 trees, and 1 forager visit 5 trees (Singh 1950); that is only 21 of 66 honeybees (32%) were potential cross-pollinators in that they moved between two or more trees. However, not all of those 21 bees would have been effectively cross-pollinating flowers because, in most orchards, only some of the foragers that fly from tree to tree, fly between trees of different cultivars. Consequently, the number of foragers that effectively pollinate flowers depends on the planting pattern of the orchard.

14.3.3 Planting patterns for orchards

Many planting patterns have been recommended for almond and other temperate tree crops, and examples of those patterns are given in Figure 14.1a-p (e.g. Wood 1947; H.E.A.F.C. 1961; Free 1962a, 1966a, 1970a; Williams 1966b; Anon 1980). Some early authors gave a range of planting pattern recommendations, emphasizing that a high degree of cultivar mixing was desirable, but also stating that the selection of a suitable planting pattern depends on the desired proportions of cultivars, suitability for management, and the ease of obtaining the desired fruit-set (e.g. Tufts 1919a; Taylor 1919).

Many Australian almond growers use the pattern of 2 rows of a "main" cultivar to one row of a "pollinator" cultivar (Fig. 14.1d). Usually two "pollinator" cultivars are planted so that each pair of "main" cultivar rows are flanked by a solid row of each of the pollinator cultivars. Recently, the pattern of one row of "main" cultivar to one row of "pollinator" cultivar has become favoured (Fig. 14.1e). These planting patterns were thought adequate to ensure efficient pollination of the "main" cultivar trees (Section 8.2.1), but they do not use honeybees efficiently, and there are better designs.

Figure 14.1: Planting patterns for orchards. Rows go down the page, and "x" represents a tree of the "main" cultivar, and "o" represents a tree of the "pollinator" cultivar. Each planting pattern is composed of replication units. A replication unit is demarcated by a rectangle. For each pattern, the proportion of foragers that fly between trees of different cultivars is given as a percentage of all the foragers that fly from tree to tree (see the text).

a. 1:6 21%

```
o x x x x x x o x x x x x x x o x
o x x x x x x o x x x x x x x o x
o x x x x x x o x x x x x x x o x
o x x x x x x o x x x x x x x o x
o x x x x x x[o x x x x x x]o x
o x x x x x x o x x x x x x x o x
o x x x x x x o x x x x x x x o x
o x x x x x x o x x x x x x x o x
```

b. 1:4 30%

```
o x x x x o x x x x o x x x x o
o x x x x o x x x x o x x x x o
o x x x x o x x x x o x x x x o
o x x x x[o x x x x]o x x x x o
o x x x x o x x x x o x x x x o
o x x x x o x x x x o x x x x o
o x x x x o x x x x o x x x x o
o x x x x o x x x x o x x x x o
```

c. 1:3 37%

```
o x x x o x x x o x x x o x x x
o x x x o x x x o x x x o x x x
o x x x o x x x o x x x o x x x
o x x x o x x x[o x x x]o x x x
o x x x o x x x o x x x o x x x
o x x x o x x x o x x x o x x x
o x x x o x x x o x x x o x x x
o x x x o x x x o x x x o x x x
```

d. 1:2 50%

```
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x[o x x]o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
o x x o x x o x x o x x o x x o
```

e. 1:1 75%

```
o x o x o x o x o x o x o x o x
o x o x o x o x o x o x o x o x
o x o x o x o x o x o x o x o x
o x o x o x o x o x o x o x o x
o x o x o x o x[o x]o x o x o x
o x o x o x o x o x o x o x o x
o x o x o x o x o x o x o x o x
o x o x o x o x o x o x o x o x
```

f. 4:4 19%

```
o o o o x x x x o o o o x x x x
o o o o x x x x o o o o x x x x
o o o o x x x x o o o o x x x x
o o o o[x x x x o o o o]x x x x
o o o o x x x x o o o o x x x x
o o o o x x x x o o o o x x x x
o o o o x x x x o o o o x x x x
o o o o x x x x o o o o x x x x
```

g. 3:3 25%

```
o o o x x x o o o x x x o o o x
o o o x x x o o o x x x o o o x
o o o x x x o o o x x x o o o x
o o o x x x[o o o x x x]o o o x
o o o x x x o o o x x x o o o x
o o o x x x o o o x x x o o o x
o o o x x x o o o x x x o o o x
o o o x x x o o o x x x o o o x
```

h. 2:2 37%

```
o o x x o o x x o o x x o o x x
o o x x o o x x o o x x o o x x
o o x x o o x x o o x x o o x x
o o x x o o[x x o o]x x o o x x
o o x x o o x x o o x x o o x x
o o x x o o x x o o x x o o x x
o o x x o o x x o o x x o o x x
o o x x o o x x o o x x o o x x
```

Figure 14.1 (continued)

i. 2:4 25%

```
o o x x x x o o x x x x o o x x
o o x x x x o o x x x x o o x x
o o x x x x o o x x x x o o x x
o o x x x x x x o o x x o o x x
o o x x x x o o x x x x o o x x
o o x x x x o o x x x x o o x x
o o x x x x o o x x x x o o x x
o o x x x x o o x x x x o o x x
```

j. 1:8 24%

```
x x x x x x x x x x x x x x x x
x o x x o x x o x x o x x o x x
x x x x x x x x x x x x x x x x
x x x x x x x x x x x x x x x x
x o x x o x x o x x o x x o x x
x x x x x x x x x x x x x x x x
x x x x x x x x x x x x x x x x
x o x x o x x o x x o x x o x x
```

k. 1:9 15%

```
x x x x x x x x x o x x x x x x
x x x x o x x x x x x x x x o x
x x x x x x x x x o x x x x x x
x x x x o x x x x x x x x x o x
x x x x x x x x x x x x x x x x
x x x x o x x x x x x x x x o x
x x x x x x x x x o x x x x x x
x x x x o x x x x x x x x x o x
```

l. 1:2 50%

```
x x o x x o x x o x x o x x o x
o x x o x x o x x o x x o x x o
x o x x o x x o x x o x x o x x
x x o x x o x x o x x o x x o x
o x x o x x o x x o x x o x x o
x o x x o x x o x x o x x o x x
x x o x x o x x o x x o x x o x
o x x o x x o x x o x x o x x o
```

m. 1:24 8%

```
x x x x x x x x x x x x x x x x
x x x x x x x x x x x x x x x x
x x x x x x x x x x x x x x x x
x x x x x x x x x x x x x x x x
x o x x x x o x x x x o x x x x
x x x x x x x x x x x x x x x x
x x x x x x x x x x x x x x x x
x x x x x x x x x x x x x x x x
```

n. 1:1 100%

```
o x o x o x o x o x o x o x o x
x o x o x o x o x o x o x o x o
o x o x o x o x o x o x o x o x
x o x o x o x o x o x o x o x o
o x o x o x o x o x o x o x o x
x o x o x o x o x o x o x o x o
o x o x o x o x o x o x o x o x
x o x o x o x o x o x o x o x o
```

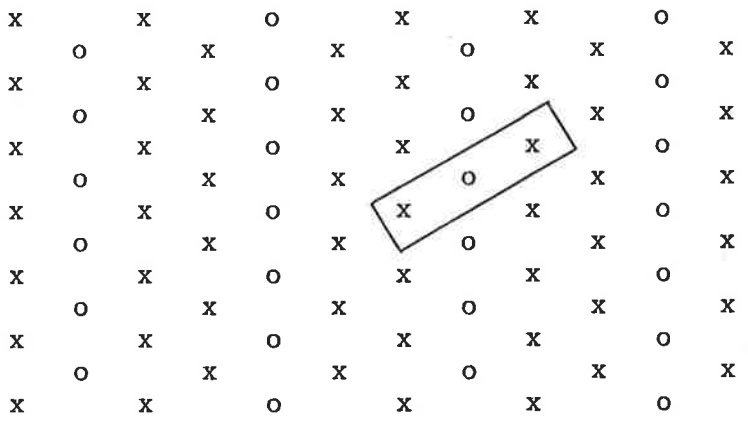
o. Solid orchard with "pillar" trees

```
x   x   x   x   x   x   x   x   x   x   x   x
    o       o       o       o       o       o
x   x   x   x   x   x   x   x   x   x   x   x

x   x   x   x   x   x   x   x   x   x   x   x

x   x   x   x   x   x   x   x   x   x   x   x
o       o       o       o       o       o
x   x   x   x   x   x   x   x   x   x   x   x

x   x   x   x   x   x   x   x   x   x   x   x
```

(continued)

Table 14.1 (continued)

p. Staggered rows of 1:2 (rows go down the page) 44%



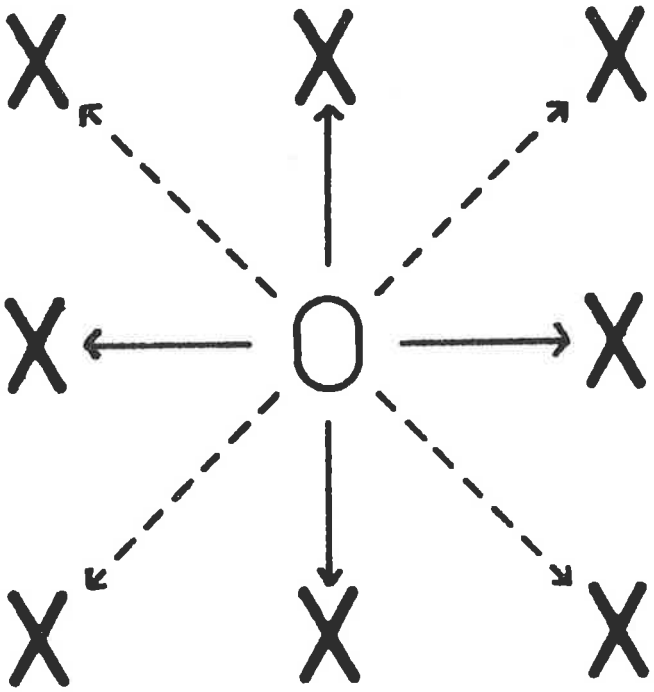
The ability of planting patterns to use honeybees efficiently, with respect to intertree flight, is discussed below.

Consider the common hypothetical orchard where each tree is of a single cultivar, the trees are planted to a square grid pattern, and the tree canopies are spherical and do not touch each other. A forager can move in a straight line from 1 tree to any one of the 8 surrounding trees (see Fig. 14.2), and, for the sake of this discussion, the probability that a given forager will move to a particular tree is the same for each of the 8 possible movements (although this is not true - see below). If we use the data and orchard described by Singh (1950) (Section 14.3.2), then 32% of the population of foragers will move from tree to tree, but only a proportion of those foragers fly to a tree of a different cultivar, and that proportion depends essentially on the planting pattern. My calculations of those proportions for different planting patterns are shown in Figures 14.1a-n. Each planting pattern has been recommended as an optimum pattern for tree crops that require cross-pollination (e.g. Free 1970a p406). Only the 1:1 pattern of Figure 14.1n makes use of all (i.e. 100%) of the foragers that fly from tree to tree. However, the situation is often more complex because other factors influence the incidence of flight from tree to tree.

14.3.4 Tree size

Foragers are more likely to move from tree to tree when there are fewer flowers per tree because each forager is more likely to have to visit two or more trees to find enough flowers to satisfy it's foraging requirement. Larger trees usually produce more flowers, so the probability of a forager being attracted to a flower on the same tree, in opposition to a more distant flower on another tree, is likely to rise with increasing tree size (Robert 1956; Free 1960a, 1966; H.E.A.F.C. 1961); and this may be why fruit-set tends to be less on large apple trees than on smaller trees (Preston 1958). Pruning to keep the trees small could overcome this problem, but pruning may decrease yields more so than the effect of tree size, because flower buds are removed with the pruned wood (Section 7.2) and more fruits are likely to develop when there are more flowers. An alternative solution might be to graft two or more cultivars onto each tree, so that the foragers are more likely to fly to flowers of another cultivar. This solution, however, may produce management problems for the orchardist through, for example, making difficult the separation of nuts of different cultivars.

Figure 14.2: In an orchard planted to a square grid pattern, a honeybee can move directly from one tree to any one of 8 trees. Note that four trees (solid lines) are closer than the other four trees (dotted lines).



14.3.5 Distance between canopies, and the hedgerow effect

Still considering the hypothetical orchard described in Section 14.3.3 and by Figure 14.2, the distance to the 4 trees along the lines of the square grid (i.e. across and along rows) is less than the distance to the 4 trees that are diagonally placed relative to the lines of the square grid (see Fig. 14.2). This is important because the incidence of intertree flight tends to decrease with increasing distance between trees (e.g. Rymashevskii 1956; Free 1960b; Free and Spencer-Booth 1964b). For instance, 123 honeybees flew between trees 3 metres apart while only 59 honeybees flew between trees 4.5 metres apart (Singh 1950). Honeybees fly even less frequently across large gaps such as roadways and other cleared areas (Mommers 1948b; Whiffen 1948). So, referring again to the hypothetical orchard, the 4 trees on the diagonals are less likely to receive a visit by a honeybee, than are the other 4 trees (consider Fig. 14.2). The pattern of fruit-set in apple suggests this behaviour is very important (e.g. Free 1962a). This information, however, is insufficient to explain the behaviour of foragers in many orchards.

Pruning and tree-growth usually ensures that the space between canopies between rows is retained while the space between canopies within rows dwindles so that eventually the canopies of the trees within rows join to form a continuous mass of vegetation, which is often referred to as a "hedgerow". The age of the trees when hedgerows form depends on the planting distance within rows, the growth of the trees, and pruning. Generally, square planted orchards form hedgerows after about 15 years, but modern orchards are usually planted with the trees within the rows planted closer together, so that hedgerows usually form after about 8 years (e.g. Fig. 14.3).

The movement of foragers in orchards of hedgerows is fundamentally different from behaviour in orchards of separated trees, because foragers tend to move along hedgerows and not from hedgerow to hedgerow (Jay and Jay 1984). For instance, only 62 of 611 foragers moved from one hedgerow to another, while the other foragers moved along the hedgerows, usually in one direction (Free and Spencer-Booth 1964b).

Figure 14.3: The canopies of trees within rows have joined to form hedgerows.

Moreover, the reduction in fruit-set that often occurs from one side of a hedgerow to the other side suggests that foragers tend not to pass through or over hedgerows; that is, most foragers tend to forage along one side, or the other, of a hedgerow (Fig. 14.4a). Furthermore, the foragers that do move to a second hedgerow rarely move further than the adjacent hedgerow, and that is usually only to the hedgerow on the opposite side of the inter-row space (e.g. MacDaniels and Heinicke 1929; Roberts 1945; Brown 1951; Singh 1953; Congdon and Woodland 1959; Williams and Smith 1967). This behaviour suggests that the habit of orchardists planting whole rows to only one cultivar, instead of mixing cultivars within rows, reduces the chances of cross-pollination occurring (Figs. 14.4a, 14.4b). Also, each forager confines its foraging to only a few metres of hedgerow during one trip, so pollinator trees should be placed within hedgerows at intervals of only a few metres (Fig. 14.4c) (e.g. Latimer 1930; Burrell and MacDaniels 1930; Free 1962a, 1962b; Free and Spencer-Booth 1964a, 1964b; Smith 1970; Wilson and Williams 1970).

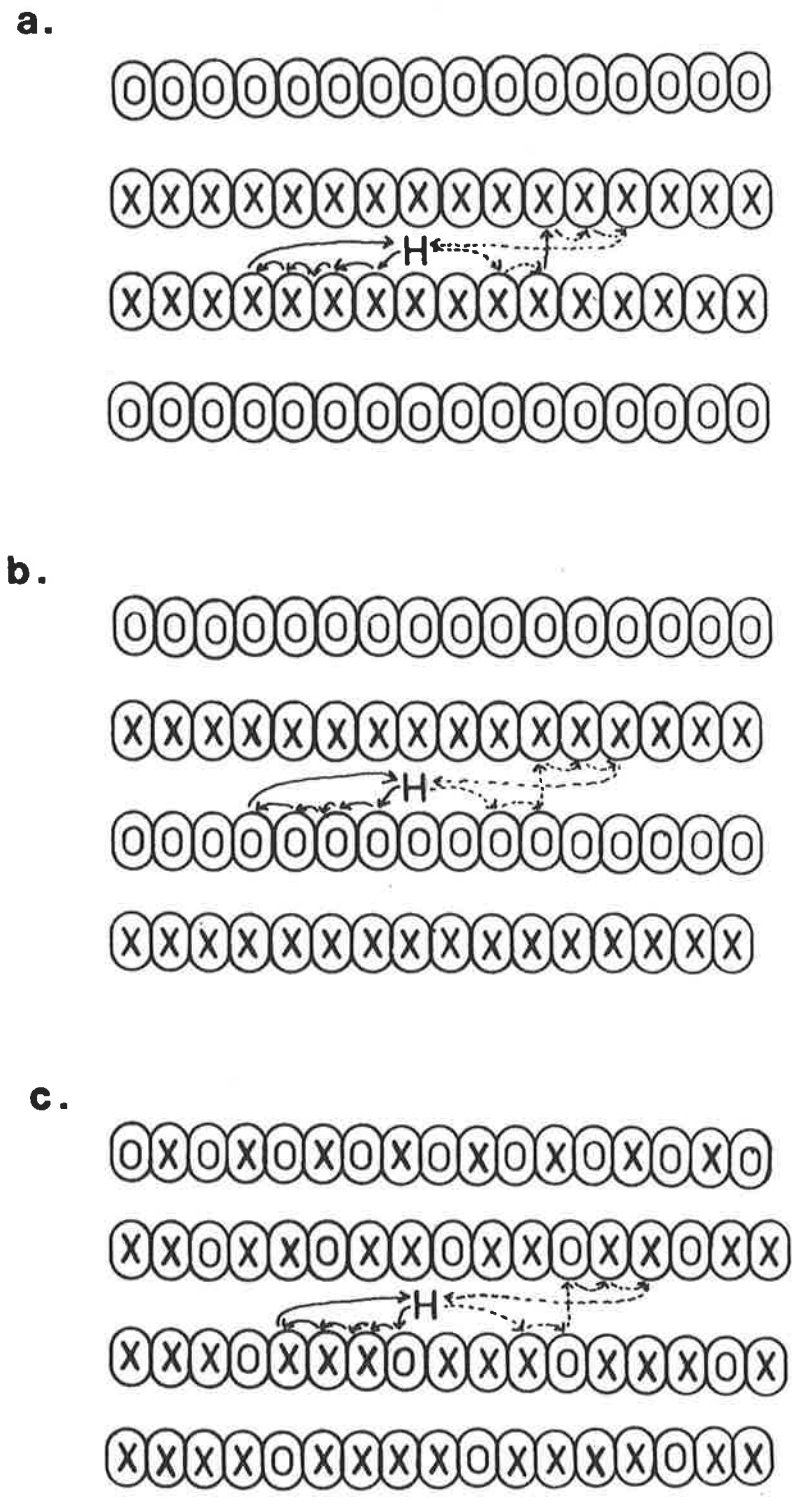
A hexagonal planting pattern has been suggested (e.g. Free 1970a p408), so that each tree is opposite a gap in the next row (Fig. 14.1p), but this pattern may not be better than others because the gaps disappear when hedgerows form.

14.3.6 Planting patterns

Given that foragers rarely cross hedgerows while foraging, nut-set is likely to be higher within the inter-row spaces that are flanked by trees of 2 cultivars, compared to inter-row spaces that are flanked by trees of only one cultivar. Consequently, the 1:1 planting pattern described by Figure 14.4a is likely to produce higher nut-sets than the 2:1 planting pattern in Figure 14.4b; but the planting patterns mentioned so far have been concerned only with trees that are of one cultivar only. Other sorts of planting patterns have been used or suggested.

Pollinators can be planted between the "main" trees and trained as pillars or vertical cordons (Anon 1980; Pheasant 1985) (Fig. 14.1o). Another type of pattern is to plant solid orchards of main cultivar and then top-graft one or two main branches of each tree to a desirable pollinator, so that each mature tree will be 1/6 to 1/3 pollinator (e.g. Tufts 1919a; Schuster 1925; Snyder 1946; Griggs 1954, 1970; Corner et al. 1964; Free and Spencer-Booth 1964b). The main advantages of these planting

Figure 14.4: Planting patterns in orchards of solid rows of hedgerow at (a) 1:2 mixture of pollinator (o) and main (x) cultivars, with one cultivar per row (i.e. Fig. 14.1d); (b) 1:1 mixture of cultivars with one cultivar per row (i.e. Fig. 14.1e); and (c) several different ratios of cultivars with cultivars mixed within rows. Flight paths of foragers from hives (H) are shown. The solid lines indicate a common form of flight path, and the dashed lines indicate an uncommon form of flight path.



patterns are that the proportion of the orchard that consists of the "main" cultivar is high while pollination is usually as good or better than other planting patterns, especially when each tree consists of two cultivars, because foragers are more likely to visit the flowers of two cultivars during a foraging trip.

The planting patterns of existing orchards can be changed by grafting new cultivars onto the butts of established trees, or replacing the trees with new trees. An alternative is to plant new trees between existing trees, but the new trees usually grow very slowly.

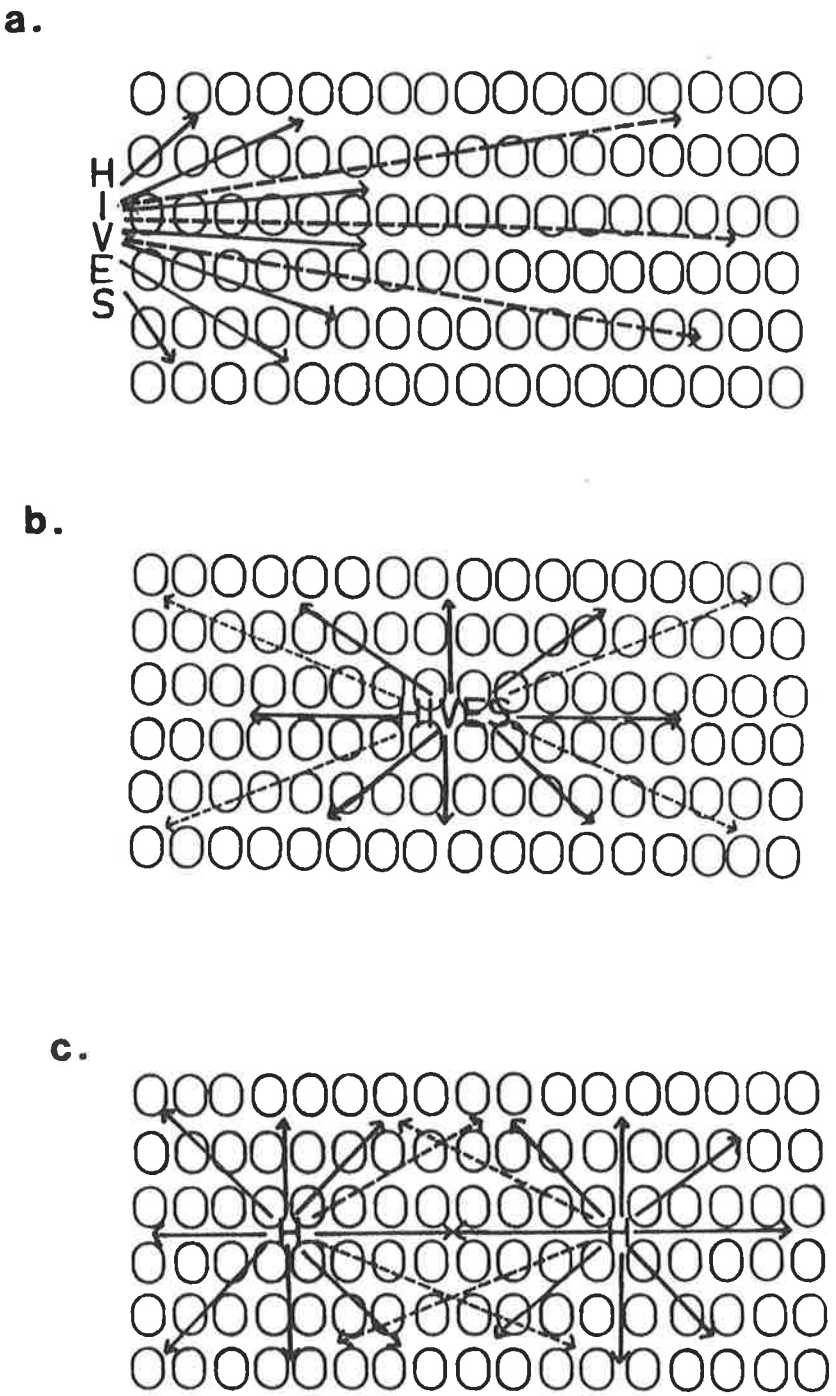
There are disadvantages, from a management point of view, in having two or more cultivars in an orchard, especially if the fruit from the two cultivars cannot be harvested simultaneously and marketed as a mixture. An approach that overcomes these disadvantages is the use of bouquets, which then allow most or all of the orchard to consist of trees of the "main" cultivar; but bouquets are not recommended as a long term provision for cross-pollination because of the reasons given in Section 9.5.3.

14.3.7 Hive distribution and placement

The optimum hive density is discussed in Section 10.3.2. The general recommendation for a hypothetical ten-year-old almond orchard is one to two hives per hectare, with each hive being of the minimum recommended strength of 4 frames of bees. These hives should be distributed so that the maximum pollination potential of the bees is attained. What that distribution should be is discussed here.

Forager densities are usually highest on trees adjacent to hives, and progressively decrease away from the hives, especially when the weather is only marginally favourable for foraging activity (Section 14.2). These trends, combined with the distribution of hives in the orchard, may have a significant influence on the mean nut-set of the orchard. For example, if all the hives are placed at one end of the orchard, as is done in some orchards (Fig. 14.5a), the density of foragers per tree generally decreases with increasing distance away from the hives; so trees at the far end of the orchard may not be visited by any foragers when the weather is marginal for foraging activity. Placing the hives in the centre of the orchard is better (Fig. 14.5b), but many trees on the edges of the orchard may not be visited by foragers during weather that is marginal for foraging activity. The best strategy appears to be the locating of hives singularly and evenly scattered throughout the orchard (Fig. 14.5c), so that every tree is

Figure 14.5: Examples of hive distributions in an orchard. Hives can be placed at one end of the orchard (a), in the middle of the orchard (b), or evenly scattered throughout the orchard (c). Foragers may visit all parts of the orchard when the weather is favourable (dashed lines), but in poor weather, foragers may only visit trees that are close to the hives (solid lines).



within foraging distance of a hive when the weather is only marginal for foraging activity. Such a strategy has been suggested by many authors (e.g. Tufts 1919a; Schuster 1925; Dyce 1929; Hooper 1929; MacDaniels and Heinicke 1929; Green 1934; Karmo 1958; Stephen 1958; Purdie and Winn 1965). Apiarists may also benefit from having as even distribution of hives throughout the orchard because honey production may increase when the energy expended on long flights is reduced (Gary et al. 1976).

However, hives are easier to maintain when they are placed in small groups, hence scattered groups of 5 to 20 hives per group have been recommended (e.g. Brittain 1933; Philp and Vansell 1944; Snyder 1946; Kelty 1948; Menke 1951; Griggs 1953; Dickson and Smith 1958; Sorenson et al. 1958; Thorp 1978). Spacings of 150 metres (i.e. 2.25 hectares per group) between groups of hives, and less in poor flight weather, have also been recommended (Hutson 1926; Murneek 1930; Free and Spencer-Booth 1963; Traynor 1966; Erickson et al. 1977). A reduction of the spacing to 100 metres between groups (i.e. one hectare per group), which may be an optimum spacing in Australia, would result in each group consisting of only one or two hives in the hypothetical ten-year-old almond orchard of Section 10.3.2.1.

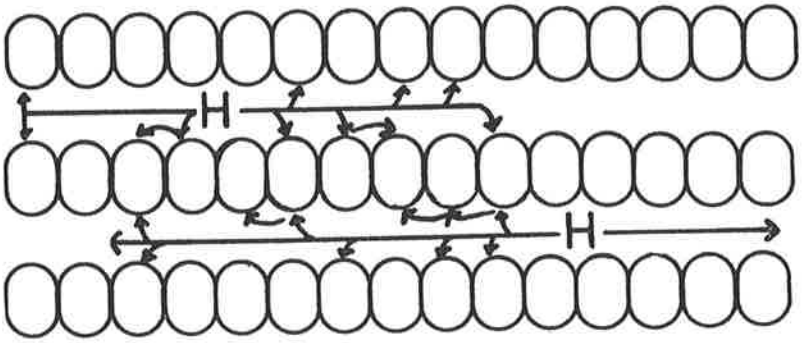
Hive distributions also need to be planned in relation to the distribution of hedgerows. Most foragers move along hedgerows and they rarely cross hedgerows to forage on other hedgerows (Section 14.3.5), so there should be a hive in every corridor between two hedgerows (Fig. 14.6a). There may also be some overall advantage in removing trees, thus creating holes in hedgerows, to encourage foragers to pass through hedgerows during their foraging trips (Fig. 14.6b). Also, if there are not enough hives to place one in every corridor, then a hive that is placed in a hole in a hedgerow may be able to supply sufficient foragers to two corridors. Supposedly, the improved pollination of the remaining trees would compensate for the loss of yield from the removed trees.

14.3.8 Sites for hives

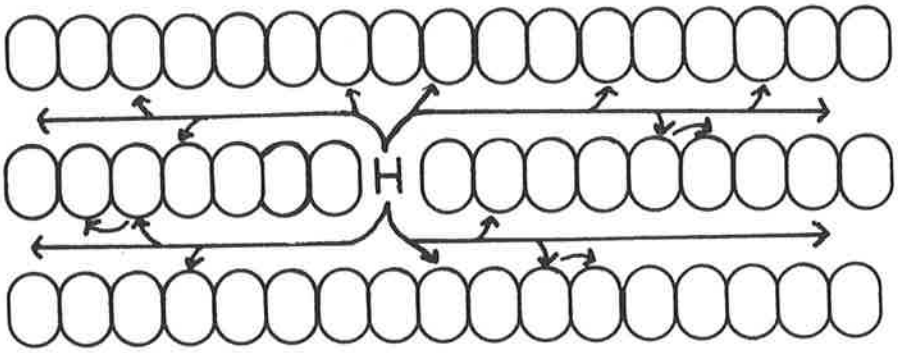
Few or no honeybees forage until the air temperature reaches the threshold for foraging (Section 14.1). Assuming that air temperatures at the hive entrance is the critical factor, then the earlier in the day the threshold is reached, the more time the bees spend foraging; so in winter and spring, the hives should be sited so that the hives warm quickly.

Figure 14.6: The movement of foragers from hives that are placed in orchards of hedgerows. Hives can be placed in the orchard corridors (a), or they can be placed in gaps within the hedgerows (b).

a.



b.



Suggestions include: keeping the hives off the cold ground by placing the hives on blocks or stands (Baker 1980; Jay and Jay 1984); keeping the hive sites free of weeds which may otherwise reduce airflow and allow evaporating dew and transpired water to cool the hive (Purdie and Winn 1965; Baker 1980; Jay and Jay 1984); locating the hives in warm, sunny positions with each hive entrance placed to leeward and facing the morning sun (Overley et al. 1946; Traynor 1966; Baker 1980); placing hives on sheets of black material so that the absorption of heat from solar radiation is increased, the growth of weeds is overcome, and evaporative cooling due to wet ground is reduced (Purdie and Winn 1964, 1965; Traynor 1966); and placing each hive on a mound so that the hive slopes slightly forward and water drains away from the hive (Purdie and Winn 1965). Contrary to the opinion of some people, more bees do not forage on shaded flowers when their hive is placed in shade (Jay and Jay 1984).

Chapter 15: Miscellaneous factors

15.1 Parthenocarpy

Parthenocarpy in almond refers to the development of a fruit that appears normal but which does not have a seed (i.e. kernel). The ultimate aim of almond growers is to produce almond kernels, so parthenocarpic almonds are useless to the growers. Nevertheless, large numbers of parthenocarpic nuts are sometimes produced by the trees of some almond cultivars, perhaps mostly from flowers that opened early in the flowering season (G. Keane, personal communication). Little is known about parthenocarpy in almond and so the significance of parthenocarpic fruit as a factor of nut-set in almond is unknown.

Parthenocarpy has been studied in other crops, and large numbers of parthenocarpic fruit can be produced by spraying trees with giberellic acid. Naturally occurring parthenocarpic fruit are also common on the trees of some peach and nectarine cultivars (Weinbaum and Erez 1983). Parthenocarpic fruit may develop from female-sterile flowers and from fruitlets which had fertile embryos that subsequently disintegrated (Section 7.1).

15.2 Competition between fruits and other sinks, may reduce fruit-set

Plants that carry "too much" fruit often abort large numbers of developing fruit (e.g. Barlow 1975; Bookman 1984; Guardiola *et al.* 1984). The subject is reviewed by Stephenson (1981).

A popular theory is that the developing fruits compete for the nutrients in the plant and that some fruit abcise when there is not enough nutrient to satisfy the needs of all the fruit on the plant. In other words, plants of a given size and in given circumstances can produce a certain maximum crop and no more (e.g. Bradbury 1929; Hill *et al.* 1987). Cytokinins may be a major determinant of the maximum yield that a tree can produce (Stevens and Westwood 1984).

In olive, competition between sinks limits final fruit-set to about 1%, regardless of the amount of initial fruit-set; and cross-pollination experiments in olive have been foiled by this behaviour (e.g. Griggs *et al.* 1975; Fernandez-Escobar and Rallo 1981; Rallo and Fernandez-Escobar 1985). In almond, however, the high nut-sets achieved after hand-pollination suggest that this effect is rare or non-existent (e.g. Section 1.7). So that almond trees with very high nut-sets have not reached their limit of

nut production. Nevertheless, there is evidence for competition between nuts, because mean kernel size per tree decreases with increasing nut density on the tree (Hill et al. 1987), and later flowers may produce smaller nuts than do earlier flowers (Maggs 1975).

Chapter 16: More discussion

16.1 Introduction

The aims of this thesis were to elucidate the factors of nut-set in almond, the long term aim being to supply information to increase the mean nut-set of Australian almond orchards.

Much is known about the factors of nut-set in almond, but knowledge of some important factors is still minimal; for example, little is known about EPPs of almond (Section 8.1.2). Also, almond trees and orchards are dynamic systems; that is, the more important factors of nut-set may differ between seasons and between orchards. So suggestions for the improvement of nut-set appear somewhat speculative. Nevertheless, some factors appear to predominate in most seasons and orchards, and so methods of manipulating those factors to advantage are discussed below.

The philosophy of Traynor (1966) may be apt for Australian almond growers. He stated that

> "Preparing for the worst possible conditions and hoping for the best is a good philosophy to follow in orchard pollination. Growers who have adopted a fussy, perfectionist attitude towards pollination rather than letting nature take its course may not reap any benefits in a good pollination year, but they can gain a great deal in a poor pollination year."

16.2 Recommendations for future orchards

Achieving high nut-sets in Australian almond orchards is largely a race to effectively pollinate flowers before their EPP expires (Section 8.1.2). The probability of a flower being effectively pollinated (i.e. maximization of the probability "P1" in Figures 1.2 and 1.3) apparently depends largely on the number of times the stigma is touched by foragers that are carrying pollen that is viable and compatible. So the best strategy may be to aim to maximise the chances of a forager (a) carrying pollen that is compatible and viable, and (b) visiting a flower during the flower's EPP.

The chances of a honeybee carrying compatible pollen apparently depends on whether or not the forager visits trees of two or more different and compatible cultivars (Sections 8.5.3, 14.3.2), and the probability of a forager carrying compatible pollen may depend largely on the size of trees (Section 14.3.4), the spacing of trees (Section 14.3.5), and the

distribution of trees of different cultivars (Section 14.3.6). So the two most important factors which should be discussed are orchard design and the selection of cultivars, as follows.

Orchard design

For efficient pollination, as many pollinator trees as possible should be scattered within the orchard and within rows, especially if the weather tends to be unfavourable for foraging by honeybees (Sections 14.2, 14.3.1). Perhaps the best planting pattern is the 1:1 pattern with cultivars being alternated within rows (Fig. 14.4c). That pattern maximizes the likelihood of a forager visiting the flowers of two cultivars. It also has the advantage of each tree being of one cultivar only. But it can cause management problems, especially when hedgerows have formed (Section 14.3.5). For example, harvesting is a problem when the cultivars do not mature simultaneously, or cannot be harvested and sold as a mixture. These problems can be overcome by the careful selection of pairs of cultivars that are compatible (Section 8.5), flower simultaneously (Section 8.2.1), mature simultaneously, and can be marketed as a mixture.

The approach of having a "main" cultivar and one or more "pollinator" cultivars needs to be discarded, that is, all the trees of the orchard should be regarded as "first class" producers of nuts. Nevertheless, suitable cultivars may not be available to meet these and other important requirements, so there may be a need for the breeding and selection of cultivars that are more suitable than the cultivars that already exist.

Selection of cultivars

Nut-set may be improved by the selection and breeding of cultivars with certain traits. Cross-compatibility and self-compatibility (Section 8.5), and coincidental flowering periods (Section 8.2) are obvious choices, but the EPP is perhaps the most important trait to consider (Section 8.1.2). The ability of flowers to attract foragers should not be overlooked (Sections 8.3.2, 12.4, 12.5), and the morphology of flowers can affect the probability of effective pollination occurring during visits by foragers (Sections 11.2, 12.4.4). Apparently foragers usually visit flowers only when pollen or nectar is available for collection (Section 12.4.1), and the probability of a stigma being effectively pollinated is increased by an increase in the number of visits by foragers (Section 13.4.4), so flowers (and cultivars) that have prolonged periods of pollen dehiscence and nectar

production may be desirable (Sections 8.3.3, 12.4.2). Also, cultivars that have few female-sterile flowers are desirable (Section 7.1), and the behaviour of bees, and hence the probability of effective pollination occurring, is affected by the morphology of flowers that differs within and between cultivars (Section 11.2).

The attractiveness of flowers to honeybees is very important, but almond flowers are apparently always very attractive to honeybees (Section 12.4) so this factor need not concern orchardists. However, plant breeders should ensure that new cultivars are also very attractive to honeybees. Methods of increasing the attractiveness of flowers are probably not important to almond orchardists (Section 12.5).

Disadvantages can occur in marketing when nuts of different cultivars are mixed together. The breeding and selection of cultivars whose nuts can be mixed together is desirable because the inter-planting of cultivars within orchards is desirable (e.g. Section 14.3.6).

16.3 Recommendations for existing orchards

Almond cultivars that are both self-compatible and commercially viable are unknown (Section 8.5.2). Therefore the commercial production of almond nuts relies on cross-pollination between cultivars.

Orchards that contain trees of only one cultivar, and orchards that contain no or only a few trees of cultivars that are cross-compatible and flower coincidentally (Sections 8.2.1, 8.5.3) need pollen from other cultivars. This pollen can be provided by several means (Sections 9.5, 14.3.6). Some planting patterns are also better than other planting patterns, and existing planting patterns can be changed by grafting and the planting of new trees (Section 9.3).

In young, square planted orchards, which are comprised of rows that contain only one cultivar per row, the orientation of rows may be changed so that cultivars alternate along rows (Section 14.3.5). This may also be done to orientate rows north-south to gain the advantage of sunlight penetration to most flowers (Section 14.1). Bouquets and perhaps pollen inserts can be used while newly planted or grafted trees of alternative cultivars become established (Section 9.5.3).

The ability of almond flowers to attract foragers is apparently not a problem in most circumstances, but a lack of water and nutrients may be important (Section 12.4.2), and those factors may also effect the

receptivity of stigmas and the ability of pollen-tubes to grow down stigmas (Sections 8.4, 8.5).

Selection of the best cultivars with respect to date of flowering may not be enough to ensure that the flowering periods of the cultivars overlap adequately. Dates of flowering can be altered by many methods, but most of the techniques have not been proven in commercial orchards (Section 8.2.5).

Pollen viability is probably not important for almond because pollen viability in almond is usually very high (Section 8.4.3); but fungicides, which are used during the flowering season, can reduce pollen viability and may destroy all naked pollen on flowers and foraging bees, thus restricting the incidence of effective pollination for hours and perhaps days (Section 8.4.2).

Honeybees are the only insects available in sufficient numbers to satisfy the pollination requirements of commercial almond orchards, and very little effective pollination occurs in almond orchards when honeybees are not present (Sections 9.3, 9.4). Races of honeybees, or of other insects, that are specifically suited to the pollination of particular crops, may be bred in future, but currently there are few options when selecting honeybees for pollination (Section 9.4). Hives for pollination may become difficult to obtain for orchardists who do not appreciate the need for pollination fees (Sections 10.3.1, 10.7).

Recommendations of the optimum honeybee population for orchards are usually expressed in terms of number of hives per hectare, but hives vary greatly with respect to the size of the colony contained within; so the number of honeybees per hectare may be a better measure (Sections 10.2, 10.3). Furthermore, recommendations are usually too general, and so a way of determining the optimum honeybee population for each orchard appears desirable. Three methods of doing this are described in Section 10.3.2. Generally, the honeybee population should be proportional to the number of flowers and, more specifically, to the amount of pollen and nectar produced by the flowers (Section 10.3.2.5). Flowers and bees in adjacent areas should also be considered (Section 10.3.3).

The timing of hive placement into orchards may be important, and perhaps the best strategy is to put the hives in a day or two after flowering has commenced (Section 10.4). The swapping of hives between distant orchards every few days, or progressively introducing more hives during the flowering season, may increase the chances of effective

pollination occurring during the EPP, but this has not been proven (Section 12.6).

The weather in Australian almond orchards during the flowering season is often only marginally favourable to foraging activity. On many days, foragers do not fly for much of the day, and when they do fly, they do not travel far from their hive (Sections 14.1, 14.2). But a lack of foraging may not be a problem if hives are put into orchards so that they are evenly distributed throughout them and with regard to their planting pattern (Section 14.3.7), otherwise many trees may not be visited by foragers on some days. The placement of hives in warm places may ensure that the foragers forage for more hours than they might otherwise (Section 14.3.8). Also, foragers prefer to visit flowers in sunlight, so steps can be taken to ensure than many flowers are in sunlight (Section 14.1).

16.4 Problems that may arise in the future

There are about 700,000 hives in Australia (Davey 1983), which is more than enough to satisfy the requirements of Australian almond orchards; but many of the hives are not available to almond growers because they are usually sited well away from almond growing areas, and apiarists believe that the alternatives to almond pollen and nectar are more profitable to them. Consequently, hive shortages can occur in Australia, especially for orchardists who are not prepared to pay pollination fees to offset the cost of transporting hives to and from orchards (Section 10.7). This problem may be overcome by the payment of pollination fees, the organization of co-operative use of hives in each growing region (e.g. Section 10.3.3), and the efficient use of available hives in orchards (e.g. Section 14.3.7). Supplementary feeding may improve the effectiveness of available hives by increasing the size of the enclosed colonies (Section 10.2.2).

Almond growers generally do not use insecticides during almond flowering, but if the need arises in future, such use would cause problems because honeybees may be killed in numbers that apiarists would not tolerate. Insecticides are often used during flowering in Californian orchards and consequently many apiarists refuse to supply hives to almond orchards there (e.g. McGregor 1976; Thorp and Mussen 1978; Thorp 1979; Hagley 1983).

The improvement of nut-set may create marketing problems. Almond ovaries contain two ovules and each ovule can form into a kernel although usually only one ovule forms into a kernel (Section 1.3). Two kernels in

one nut is an undesirable characteristic because the kernels are usually deformed and hence difficult to market. Improved pollination could increase the incidence of "double" kernels, but cultivar selection should be able to overcome the problem should it arise.

Biennial bearing, which is reviewed by Jonkers (1979) and Monselise and Goldschmidt (1982), may become prevalent if nut-set is increased. Biennial bearing is the biennial alternation of light and heavy yields which is attributed to annual alternations in flower density. Presumably trees produce fewer flowers when nut-set was high in the previous year. Biennial bearing causes marketing problems when whole orchards or even countries become synchronized in a biennial bearing cycle. Methods of controlling biennial bearing are needed.

16.5 Future research

Almond trees and orchards are dynamic systems, and so the influence of any one factor can vary greatly between orchards and years. This makes the understanding of factors and their interrelationships difficult to understand without some assistance. Multi-variate analysis may aid the construction of models that explain the interactions between the factors, and perhaps the models can be used to increase nut-set in orchards.

Several models that are applicable to pollination, fruit-set, and honeybee behaviour have been constructed (e.g Brain and Landsberg 1981; Waddington 1983; Jefferies and Brain 1984; DeGrandi-Hoffman *et al.* 1985; Omholt 1986), and they are useful in demonstrating the relationships between some variables, but those models are very simple and require several assumptions to make them work. More knowledge of real systems is needed before models that are reliable and more complex can be constructed. The information in this thesis should enable the construction of better models to describe pollination and nut-set in almond, and perhaps in other crops as well.

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Appendix 1

The major factors of nut-set and pollination for almond are listed below under several headings. The headings represent a time sequence from the time the orchard is planted, through flowering, pollination, fertilisation, and embryo development, to harvest. The headings are related to the probabilities P1, P2, and P3 which are described in Section 1.2. A factor is listed under a heading if the factor is important at that time. The factors are divided into groups which are indicated by equal indentation from the left. Factors within a group are thought to be important to the factor that is immediately above the group. Some factors are listed more than once. Question marks indicate factors that are of unknown, but suspected, importance to almond pollination. Section numbers indicate the places in the thesis where the factor is discussed.

Orchard design

Selection of cultivars 16.2
- Time of flowering 8.2
- Effective pollination periods 8.1.2
- Saleability of nuts when mixed with nuts of different cultivars 14.3.6, 16.2
- Flower production 1.1
- Female-sterility 7.1
- Compatibility of pollen and stigmas 8.5
- Viability of pollen 8.4
- Pollen production 8.3.1, 8.3.2
- Nectar production 12.4.2

Orchard site selection
- Frost risk 7.2
- Risk of damage by birds, rain and hail 7.2

Tree design
- Pruning 7.2
- Shaping of trees 7.2, 14.1
- Tree size 14.3.4
- Hedgerows 14.3.5

Planting pattern 14.3
- Places for honeybee hives 14.3.7, 14.3.8
- Hedgerows 14.3.5

Flowering

Timing of flowering in different cultivars 8.2.1
- Genetics 8.2.3
- Winter temperature regime 8.2.4
- Position of tree in orchard 8.2.3
- Position of flower in tree 8.2.4
- Tree shape (pruning, genetics of scion) 8.2.3
- Tree size (genetics of scion and rootstock, nutrition, water supply) 8.2.3
- Evaporative cooling (rain, wind, irrigation, sprays) 8.2.4
- Solar radiation 8.2.4
- Shading (tree shape, row orientation) 8.2.4

Control of flowering 8.2.5
- Chemical treatments 8.2.5
- Evaporative cooling 8.2.5
- Defoliation 8.2.5
- Shading 8.2.5
- White washing 8.2.5

Abortion of damaged flowers and buds 7.2

Pollination (Probability P1)

Compatibility of pollen and stigma 8.5
- Genetics of pollen and stigma 8.5
- Nutrition 8.4, 8.5.4
- Temperature of stigma 8.5.4
  - Air temperature 8.5.4
  - Solar radiation 8.5.4
  - Shade 8.5.4
  - Supplementry heating 8.5.4
  - Windbreaks 8.5.4

Effective pollination periods 8.1.2
- Flower age 8.1.2
- Date of flowering in flowering season ? 8.1.2
- Ovule longevity (temperature, genetics, nutrition) 8.1.2
- Pollen-tube growth rate (temperature, genetics, nutrition) 8.1.2

Pollen-tube growth and fertilisation (Probability P2)

Temperature 8.1.2, 8.5.4

Genetics (pollen - stigma compatibility) 8.5

Effective pollination period 8.1.2

Nutrition ? 8.4.1, 8.4.2

Parthenocarpy ? 15.1

Damage to flowers 7.2

Development of a mature nut (Probability P3)

Inter-fruit competition (abortion) ? 15.2

Damage to developing fruits (abortion) 7.2

Harvest

APPENDIX 3

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Almond pollination studies: pollen production and viability, flower emergence and cross-pollination tests

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Summary. During 1978–80, flower emergence was recorded on 12 almond cultivars (*Prunus dulcis*) at Angle Vale, South Australia. Early flowering cultivars showed a larger annual variation in flowering period (2–3 weeks) than late flowering cultivars (0–2 weeks). In the same period, pollen production ranged from 30 to 122 mg per 100 flowers and *in vitro* pollen germination ranged from 76·1 to 99·0%. Pollen production and *in vitro* germination differed significantly between cultivars. Hand-pollination of Nonpareil with pollen from each of eight other cultivars resulted in significantly higher nut set than with open-pollinated or self-pollinated flowers. In contrast to Nonpareil, hand-pollination of Chellaston with pollen from five other cultivars resulted in significantly higher nut set compared with self-pollinated Chellaston but not compared with open-pollinated Chellaston. The potential increase in almond yield due to improved pollination is discussed.

Introduction

Several authors have found that from 30% to over 50% of almond flowers can produce mature nuts (Kester and Griggs 1959*a*; Erickson *et al.* 1977; Micke and Kester 1978); yet in commercial orchards percentage set is normally much less and is commonly 5–30% (Tufts 1919; Griggs 1949; Kester and Griggs 1959*a*; Gary *et al.* 1976). While an increase in percentage set decreases the size of individual nuts (S. J. Hill, D. W. Stephenson and B. K. Taylor unpublished data), the net yield per tree is increased, and small nuts are in short supply in Australia (Baker 1980) and California (Kester *et al.* 1963). Fruit setting and presumably pollination are therefore limiting factors for almond nut production.

This is in contrast to crops for which pollination is usually not a significant influence on yield; for example, a maximum apple crop is achieved with only 3–7% fruit set (McGregor 1976) and fruit thinning is required when apple fruit set is higher. While much is known about pollination (Horticultural Education Association Fruit Committee 1960, 1961; Free 1970), not all the information is applicable to almond because of the difference in fruit setting required for commercial cropping.

To obtain a maximum almond crop, essentially 100% of the flowers must be cross-pollinated (Kester and Griggs 1959*a*). Since all almond cultivars in Australia are commercially self-sterile (Moss 1962; Moss and Cowley 1970; Baker and Gathercole 1977), and since Griggs and Iwakiri (1964) found that an almond flower must be pollinated by compatible pollen within 4 days of first opening, flower-

ing periods of compatible cultivars should coincide to within 4 days.

Australian growers have found that a cultivar suitable for use in one area may not be suitable in another because of different relative flowering dates, yet only a single table of flowering periods (Baker and Gathercole 1977) is available to almond growers in Australia, and almonds are grown in a wide range of climates. Furthermore, some of the flowering periods in the table by Baker and Gahercole (1977) are based on Californian, not Australian, data.

Pollination is the transfer of pollen to a stigma. Since relatively few pollen grains are transferred, the viability and compatibility of those pollen grains may determine the probability of a nut developing. No Australian data on viability and compatibility are available, yet overseas studies have shown that much variation exists (e.g., Tufts and Philp 1922; Gagnard 1954; Garcia 1978).

To increase knowledge about almond flowering and pollination in Australia, and as a foundation for further research towards the improvement of pollination efficiency, the following aspects were studied in an almond orchard at Angle Vale, South Australia during 1978–80: pollen production and *in vitro* viability, rate and period of flower emergence of many of the common cultivars, and compatibility of 'pollinator' cultivars with the major cultivars Nonpareil and Chellaston.

Materials and methods

Site

The trees were growing in one orchard at Angle Vale, 40 km north–northeast of Adelaide, South Australia, except for White Brandis which was in a nearby orchard under similar climatic and management conditions. The climate is Mediterranean with average annual rainfall of 460 mm. The trees were drip-irrigated every 3 days during the growing period to give an annual total of 325 mm water. The soil was a deep sandy loam and all trees were 6 years old in 1978. Bees were introduced before flowering for cross-pollination at the rate of about 3·7 hives per hectare.

Pollen production and viability

For each cultivar, two lots of 100 flowers at the 'popcorn' stage were collected randomly from five trees. The anthers were removed and allowed to dehisce at room temperature for 36 hours following which the pollen was shaken through a sieve and weighed. Hanging drops of 15% sucrose were dusted with pollen samples and incubated at 20°C for 72 h. Germinated pollen grains were then counted.

Flower emergence

For every cultivar, five trees were chosen and a straight limb at shoulder height in the north-east quarter of each tree was marked at 1 m back from the furthest growing tip. All flower buds on the limb which were forward of the basal mark were then considered part of that limb.

Growers report that flower emergence can vary according to elevation within the tree but there was no evidence that this occurred at Angle Vale during the experiment.

Flower emergence was recorded by tagging newly opened flowers on the selected limbs with jewellers' price tags at intervals of 2 days. This was repeated on the same trees each year resulting in 180 to 750 tagged flowers per cultivar per year. The cultivars White Brandis, Chellaston, Johnston's Prolific and Bruce were not included in 1978.

Compatibility of pollinator cultivars with Nonpareil and Chellaston

Limbs were selected for pollination treatments in the same way as for flower emergence. In the case of Nonpareil, 10 limbs per tree were selected for individual treatments repeated on five trees in 1978 and 1979, and on nine trees in 1980. For Chellaston, seven limbs per tree were chosen, repeated on five trees in 1979 and on seven in 1980. With the exception of the open-pollinated treatment, a muslin bag was placed over each limb before flowering commenced to exclude bees. All bagged treatments were hand-pollinated with pollen of a single cultivar applied with a fine paint brush to all open flowers that did not have a visually dried stigma. Pollinated flowers were tagged. A sample of the pollen collected for viability measurements was used in these tests. On the open-pollinated limbs, only flowers with receptive stigmas were tagged.

The resultant developing nuts from tagged flowers were counted every 2 weeks until mid-November. In the first year, a further count was made in February before harvest but, since there had been only a small decline in nut numbers over the intervening summer period, pre-harvest counts were not repeated in subsequent years.

Table 1. Pollen production (mg per 100 almond flowers) at Angle Vale, South Australia in each of 3 years

Values are means of two replicates. Within columns, values not followed by the same letter differ significantly ($P<0{\cdot}05$, Duncan's multiple range test). Levels of significance are between collection dates in the same year (n.s., not significant $P>0{\cdot}05$; **, significant at $P<0{\cdot}01$).

Cultivar	1978		1979		1980	
	8 Aug.[A]	16 Aug.	19 July	7 Aug.	5 Aug.	15 Aug.
Grant	122 a	—	98 a n.s.	126 a	83 a **	66 a
Mission[B]	—	89 a	—	102[B]	—[B]	—
Chellaston	—	—	89 a	—	60 b	—
Fritz	—	60 b	—	92 b	—	65 a
Somerton	93 ab	—	65 c n.s.	65 c	53 c n.s.	59 a
Baxendale	80 b	—	—	61 c	—	31 d
Ne Plus Ultra	49 cd	—	—	72 c	—	64 a
Bruce	—	—	72 bc	—	67 b	—
White Brandis	—	—	60 c	—	68 b	—
Davey	—	34 b	—	48 d	—	42 bc
Nonpareil	—	33 b	—	42 d	—	43 b
Johnston's Prolific	29 d	—	39 d n.s.	55 d	54 c **	34 cd

[A]Date of flower collection for pollen measurements.
[B]Mission pollen was collected on 17 August 1979, and is not included in the statistical calculations. Mission pollen was not collected in 1980 because of late flowering.

Table 2. *In vitro* germination (%) of almond pollen collected in each of 3 years at Angle Vale, South Australia

Values are means of four replicates. Cultivars not followed by the same letter differ significantly ($P<0{\cdot}05$, Duncan's multiple range test using arcsine-transformed data). There were no significant differences between years, and no significant differences between collection dates in the same year.

Cultivar	1978		1979		1980	
	8 Aug.[A]	16 Aug.	19 July	7 Aug.	5 Aug.	15 Aug.
Grant (abc)	99	—	87	93	99	99
Mission (d)[B]	—	88	—	89[B]	—	—[B]
Chellaston (abc)	—	—	96	—	97	—
Fritz (a)	—	99	—	96	—	99
Somerton (ab)	99	—	97	96	98	99
Baxendale (bc)	98	—	—	96	—	95
Ne Plus Ultra (d)	89	—	—	89	—	84
Bruce (d)	—	—	76	—	89	—
White Brandis (cd)	—	—	83	—	99	—
Davey (c)	—	96	—	94	—	92
Nonpareil (d)	—	76	—	90	—	97
Johnston's Prolific (c)	93	—	89	86	98	99

[A]Date of flower collection for pollen viability measurements.
[B]Mission pollen was collected on 17 August 1979. Mission pollen was not collected in 1980 because of late flowering.

Results

Pollen production and viability

Pollen grain size did not differ significantly between cultivars, so pollen grain number was assumed to be proportional to pollen grain weight per cultivar. For each collection date and year, pollen production per flower varied significantly between cultivars (Table 1). Grant was always the highest producer of pollen and Johnstons Prolific always one of the lowest.

In 1979 and 1980, pollen from Grant, Somerton and Johnstons Prolific was collected twice. There was no significant difference in pollen production per flower between collection dates in 1979, but pollen production of Grant and Johnstons Prolific declined between 5 August and 15 August 1980. The significance of this finding is not clear and no one appears to have monitored pollen viability or production throughout flowering on almond.

All cultivars tested had high *in vitro* pollen germination percentages but significant differences in germination percentages were found between cultivars (Table 2). Fritz and Somerton showed the highest viability, while Ne Plus Ultra, Mission, Nonpareil and Bruce showed the lowest (Table 2). The range of germination percentage (76–99%) is similar to that reported by Porlingh (1956) and Garcia (1978). No significant differences were found between collecting dates within a given year.

Flower emergence

Most cultivars flowered earlier in 1979 than in 1978 and 1980 (Fig. 1). In 1979, the early flowering cultivars flowered 2–3 weeks earlier, while the later flowering cultivars flowered 0–2 weeks earlier than they did in 1978. Griggs (1949) noted a similar trend for early and late flowering cultivars. Flower emergence on Mission, the latest flowering cultivar, did not vary significantly between years (Fig. 2).

In 1979, early flowering tended to spread the bulk of flowering over a longer period, with a lower flowering peak compared with other years (Fig. 2). The ranking of the cultivars did not change between years; there were, however, significant variations in the amount of overlap of the various cultivars (e.g. Ne Plus Ultra and Baxendale; Nonpareil and Davey) (Fig. 1).

In 1979, the rate of flower emergence on cultivars with more than 5% of blossoms opening on 18 July declined until 22 July, then progressively increased (Fig. 2). This may have been due to several days' warm weather followed by a frost on 19 July. This type of weather pattern was reported by Taylor (1919) 'to produce the greatest injury to flowers, while when both day and night temperatures are low, frosts do no harm'. Affected flower buds may have shown delayed opening or dropped off.

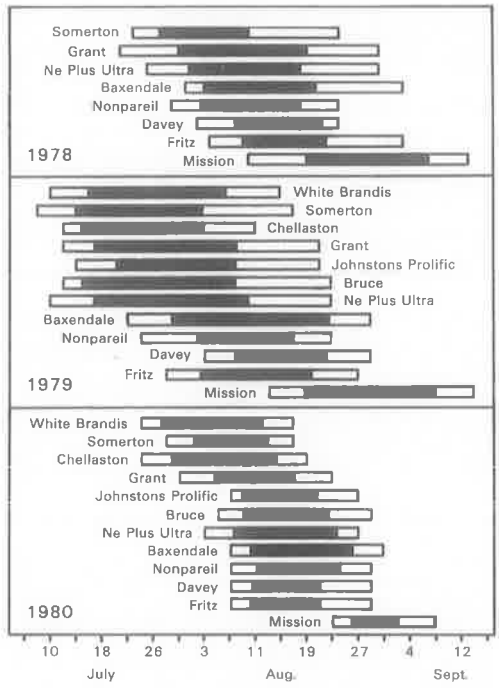

Fig. 1. Flower emergence periods of almond cultivars at Angle Vale in each of 3 years. The shaded central portion of each bar represents the period when 90% of flowers first opened. The unshaded portions represent the opening of the initial 5% and the final 5% of flowers. Because flower opening was recorded on alternate days, some flowers would have been open a full day before being recorded. Each bar is based on the mean of five one-limb-replicates, each replicate being on a separate tree. Data were not collected in 1978 for White Brandis, Chellaston and Johnston's Prolific.

Compatibility of pollinator cultivars with Nonpareil and Chellaston

Nuts on hand-pollinated and open-pollinated limbs were counted in November of each year after most of the natural nut drop should have occurred (see Kester and Griggs 1959*b*; Garcia *et al.* 1980). On average, only 3·3% of the developing nuts were later lost between November 1978 and harvest in February 1979. Results showed that all the 'pollinator' cultivars were compatible with Nonpareil and Chellaston but some gave much higher nut set than others within years (Tables 3 and 4). However, considerable variation in nut set was recorded between years for a given pollen donor.

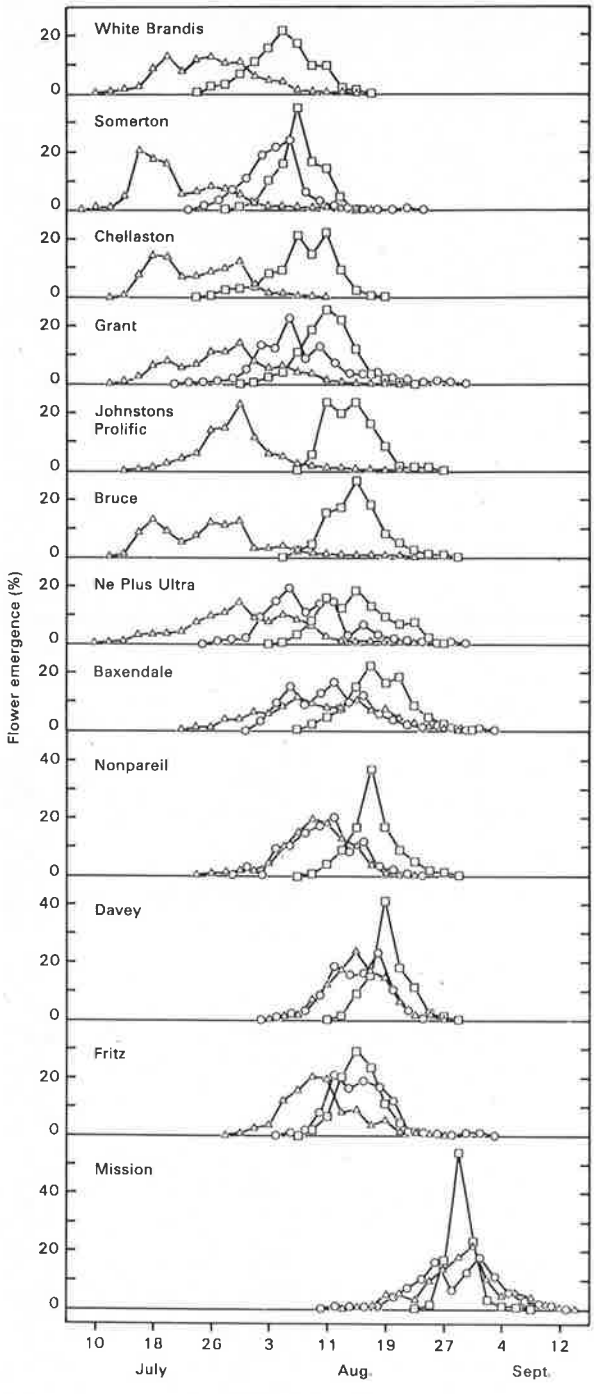

Fig. 2. Recorded flower emergence on almond cultivars at Angle Vale in each of 2 or 3 years of 1978 (○), 1979 (△), and 1980 (□). Each point represents the percentage of flowers that first opened on that day and the previous day, relative to the total number of flowers that opened during the season. Each point is the mean of five one-limb-replicates each on a different tree. Data were not collected in 1978 for White Brandis, Chellaston and Johnston's Prolific.

Table 3. Nut set (%) following hand pollination of Nonpareil flowers

Values are numbers of developing nuts in November as a percentage of total number of flowers pollinated. Values are means of five replicates for 1978 and 1979; and nine replicates for 1980. Within columns, values not followed by the same letter differ significantly ($P<0.05$), Duncan's multiple range test. In 1978, the Fritz, Davey and Mission treatments were done 4 days after the others (18 August) and were subjected to very wet and cold weather in the 4 days following pollination. Those conditions may have reduced nut set.

Pollen-donating cultivar	1978 14 Aug.[A]	1979 20 Aug.	1980 18 Aug.
Grant	49·4 a	45·1 a	60·1 a
Fritz	29·3 bc	50·0 a	56·3 ab
Somerton	54·6 a	40·4 ab	52·6 abc
Ne Plus Ultra	47·8 a	47·5 a	44·6 c
Johnston's Prolific	47·1 a	39·5 ab	51·5 abc
Baxendale	52·0 a	34·4 ab	55·9 abc
Mission[B]	40·7 ab	39·4 ab	—[B]
Davey	30·5 ab	28·1 bc	48·1 bc
Open pollination	17·4 cd	18·0 c	32·7 d
Nonpareil (self-pollination)	3·8 d	0·6 d	4·0 e

[A]Date of hand pollination.
[B]The Mission treatment was omitted in 1980 because of the late flowering of this cultivar.

In 1978, the treatments using pollen from Fritz, Davey and Mission may have suffered reduced nut set because they were done 4 days after the other treatments and were subjected to very wet and cold weather in the 4 days following pollination (Table 3). Such weather may reduce the probability that pollination and fertilization will occur (Gagnard 1954; Free 1970; Griggs and Iwakiri 1975; Socias i Company *et al.* 1976; Meith *et al.* 1977).

Nut set on open-pollinated Chellaston trees was not significantly less than on hand-pollinated trees (Table 4). But fruit set decreases with increasing distance from hives (Free 1962; Wolfenbarger 1979), and it should be noted that beehives were located adjacent to the experimental Chellaston trees each year. The 1979 hand-pollination results were significantly less than the 1980 hand-pollination results (Table 4), due perhaps to the cool wet weather on the days of pollination in 1979.

Nonpareil was reported by Tufts and Philp (1922), Gagnard (1954) and Nauriyal and Rana (1965) to be self-sterile, but results of selfing tests on Chellaston have not been reported previously. In 1979, the

Table 4. Nut set (%) following hand pollination of Chellaston flowers

Values are numbers of developing fruits in November as a percentage of total flowers pollinated. Values are means of five replicates for 1979, and seven replicates for 1980. Within columns, values not followed by the same letter differ significantly ($P<0.05$, Duncan's multiple range test).

Pollen-donating cultivar	1979 31 July[A]	1980 8 Aug.
Johnston's Prolific	42·3 a	57·1 a
Somerton	31·3 ab	55·9 a
White Brandis	22·3 abc	50·0 a
Grant	24·5 abc	43·0 a
Bruce	12·8 bc	55·4 a
Open pollination	29·4 ab	46·4 a[C]
Chellaston (self-pollination)	9·0 c[B]	3·8 b

[A]Date of hand pollination. Collectively, the 1979 results were significantly lower than the 1980 results ($P<0.05$).
[B]In 1979 the muslin failed to exclude bees from the self-pollinated Chellaston flowers.
[C]The high nut set values for open pollination relative to those for hand pollination may have been partly due to bee hives being adjacent to the trees

muslin failed to exclude bees from some of the self-pollinated Chellaston flowers. In 1980, a low level of nut set occurred in two of the seven replicates. In comparison, selfing Nonpareil resulted in a low level of nut set in three out of nine replicates in each of the years 1978, 1979 and 1980 (Tables 3 and 4).

Discussion

Pollen production characteristics for almond cultivars have not been reported by other authors, yet there appears to be a consistent difference in pollen production between cultivars in this study (Table 1). Each year, Grant was the highest producer of pollen per 100 flowers, while Johnston's Prolific produced only 24% to 64% of that produced by Grant, depending on the year and sampling date. Theoretically, these recorded differences could be enhanced or offset by differences in flower density (S. J. Hill, D. W. Stephenson and B. K. Taylor unpublished data), and there is still much to be learnt about the effect of pollen availability and flower density upon honeybee behaviour and fruit set. For example, the importance of variations in pollen production can be argued in two ways. First, larger amounts of pollen per flower reduce the area over which a bee needs to forage to obtain a load of pollen and the probability of visiting two different cultivars is therefore reduced (Free 1970); on the other hand, smaller amounts of pollen may be exhausted before extensive cross-pollination has occurred.

The viability of pollen would not normally be expected to be a significant limitation to pollination unless only two or three pollen grains are left on a stigma by a single effective bee visit — assuming that pollen viability *in vivo* is not significantly different from that found *in vitro*.

Many authors (Tufts and Philp 1922; Wood 1946; Griggs 1953; Moss 1962; Nauriyal and Rana 1965; Moss and Cowley 1970; and Baker and Gathercole 1977) have averaged the flowering dates of separate cultivars for several years for one area and then applied the result to every almond growing area in their respective state or country. Baker and Gathercole (1977) summed up the reason for this by stating that 'actual flowering dates vary from district to district and from year to year but the relative times between varieties remain fairly constant'. However, the results of Fig. 1 show that the variation between years can be significant if, for maximum yield, all of the flowers of a tree need to be pollinated within the 4-day limit.

Many orchards growing Nonpareil have Fritz and Ne Plus Ultra as 'pollinators', and, as an example, the results (Fig. 1) suggests that in 1979, Ne Plus Ultra depending on Nonpareil for pollination, would have lost over 40% of its cropping potential — assuming that at least 5% of flowers on a tree must be open before that tree becomes a significant pollen source for cross-pollination (Kester 1965). Baxendale coincided better with Nonpareil than did Ne Plus Ultra in that year. This situation also occurred in 1983 when both Ne Plus Ultra and Fritz were past 90% bloom when Nonpareil reached 5% bloom, while Baxendale bloomed to within a day of Nonpareil's blooming period. Fortunately, the flowering period of Nonpareil was short and the weather was warm, hence a lot of cross-pollination did occur. Even so, the yield of Nonpareil orchards that relied upon Fritz as a late flowering pollinator were at least 20% less than those orchards that included Baxendale (F. Keane, private communication). Mr Keane also commented that such an event was not unusual.

Growers in the warmer areas of Australia have found that in most years the flowering times of

Mission are as favourable as was shown by Baker and Gathercole (1977), but, in the cooler areas such as Angle Vale, Mission flowers far too late (Fig. 1) relative to other cultivars, especially Nonpareil. Griggs (1953) noted that in California, in years when a cold period occurs during the flowering season, Mission (synonym for Texas) delayed flowering until most of the blossoms of Nonpareil had fallen (Serr and Kester 1953). However, in such years, Mission often still produces a good crop. Note that the 4-day limit for pollination to occur (Kester and Griggs 1959*a*) was obtained by tests of only Nonpareil and Jordanolo flowers. With apple and pear, the limit varies (1–10 days) depending upon the combination of cultivars and, to a lesser extent, weather conditions (Williams 1966). It is therefore unlikely that the 4-day period applies to all combinations of almond cultivars, and further study is needed to determine how well the flowering periods of various cultivars need to overlap to maximize potential nut set.

The weather varies greatly between almond-growing regions and between years in Australia therefore, to determine the value of a given cultivar for cross-pollination, it would be preferable to record the flowering period for each cultivar in each growing region for many years without averaging across years or regions. The annual potential of each cultivar combination could then be calculated to enable a more accurate assessment of their long-term value.

Many pollination factors affect crop yield (Horticultural Education Association Fruit Committee 1960, 1961; Free 1970), but if the flowering period of two almond cultivars can be made to closely coincide each year then yield should be increased significantly. Approaches that can be made to achieve this include the selection of mutually suitable cultivars, the breeding of new cultivars (Kester 1965), and the use of methods such as evaporative cooling to manipulate flowering dates (Alfaro *et al.* 1974; Anderson *et al.* 1975; Lipe *et al.* 1975; Chesness *et al.* 1977). On the other hand, the breeding or chance discovery of a commercially-yielding self-pollinating cultivar would be ideal.

All the 'pollinator' cultivars we tested are compatible with Nonpareil and Chellaston, but some appear to be more so than others. Perhaps the variation is due to variable compatibility between cultivars with respect to temperatures and rates of pollen tube growth (Griggs and Iwakiri 1975; Garcia and Egea Ibanez 1979). In any case, there is sufficient evidence (e.g., Table 4, Erickson *et al.* 1977) to suggest that high nut sets obtained through hand pollination may be attainable throughout an orchard by open pollination.

Neither Chellaston or Nonpareil can be said to be completely self-sterile (Tables 3 and 4). Tufts (1919) held that 'self-incompatibility was not a constant factor in a variety for it may be barren in one locality and self-fruitful in another, and the degree of adaption of a variety to soil and climate had much to do with its ability to fruit abundantly with its own pollen'. This again may be due to weather and pollen–stigma interactions (Socias i Company *et al.* 1976; Weinbaum *et al.* 1980). In any case, the results here confirm that cross-pollination is necessary for commercial production of almonds.

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APPENDIX 4

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elationship between temperature and flowering in mond

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ummary. Records of flowering in 12 almond ıltivars over 7 years, together with temperature :cords from a standard climate station, were used to ;timate the chilling requirement for dormancy break ı flower buds and the heat sum requirements for floral evelopment in each cultivar. Hourly temperatures ere estimated from daily minimum and maximum :mperatures. A continuous function relating hourly temperatures to rate of chilling was used to calculate daily chill unit accumulations.

Requirements of 220–320 chill units were estimated and calculated heat sum requirements ranged from 5300 to 8900 growing-degree-hours above 4·5°C. These requirements were used to estimate the dates of 50% flowering for 1958–84.

ıduction

prediction of flowering date in orchard trees is ırtant for management (Hamer 1981). It is also a ponent in the research task of modelling the whole uction cycle (Landsberg 1977; Nix 1981). Almonds ı crop of potential economic interest in Australia, :h presently imports nearly half its requirements ıglas 1984). Almond tree yield can be increased by ring that two cultivars flower coincidentally, but ive flowering dates vary between years and regions *et al.* 1985). An effective model of flowering date in ion to climate would enable growers to select the most ıble cultivars with respect to flowering date for their ın without the need for time-consuming field trials. ılarly, overseas cultivars could be evaluated before ortation.

ıe relationship of temperature to the development of ers in deciduous fruit trees has been studied for many s (Chandler *et al.* 1937; Anstey 1961; Erez and Lavee l; Richardson *et al.* 1975; Anderson and Richardson 2), but little has been published specifically on almond ın 1971). The purpose of our study was to apply to ond the concepts developed by Richardson *et al.* 4) and Ashcroft *et al.* (1977) on peach. Their models ulate flowering as a two-stage process. In the first stage dormant flower bud accumulates exposure to low peratures (chilling) up to a predetermined level. In the nd stage the flower develops at a rate influenced by perature. Two constants are therefore necessary to lel flowering: the chilling requirement for breaking nancy and the heat sum requirement for floral elopment.

Richardson *et al.* (1974) proposed a function which measured chilling requirement in 'chill units' (*CU*) that express the relative effectiveness of various temperatures in releasing dormancy. Their function is supported by the results of controlled environment studies on the influence of particular temperature ranges on dormancy (Erez and Lavee 1971; Erez *et al.* 1979; Gilreath and Buchanan 1981). The heat sum requirement for floral development was measured as growing-degree-hours (*GDH*): the linear accumulation of hourly temperatures above a threshold temperature (Richardson *et al.* 1974; Hamer 1981). These two functions formed our model which was tested with 7 years of flowering data from an almond orchard at Angle Vale, South Aust. So that the model might be of practical use, we designed it to require only standard climatic data (daily maximum and minimum temperatures).

The application of the results to 27 years of temperature records provided the range of flowering dates to be expected at Angle Vale for these cultivars.

Material and methods

Flowering

The trees grew in one orchard at Angle Vale, 40 km north-north-east of Adelaide, South Aust., with the exception of the cultivar White Brandis, which was in a nearby orchard under similar climatic and management conditions. The climate is Mediterranean with an average annual rainfall of 460 mm. The trees were drip-irrigated every 3 days to give an annual total of 325 mm water. The soil was a deep sandy loam and all trees were 6 years old in 1978.

Newly opened flowers on selected limbs were counted and tagged at 2-day intervals in 1978, 1979, 1980 and 1984. In 1977, 1981 and 1982, days of first, last and peak flowering were recorded. For analysis, flowering date was taken as the day on which 50% of the final number of flowers was open. The dates were obtained directly from the 1978–80 and 1984 records and were estimated for 1977, 1981 and 1982 by assuming a similar pattern of flowering. Not all cultivars were counted in every year (Table 1).

Chill unit calculations

The following equations, derived from Anderson and Richardson (1982), determine the *CU*s associated with a given hourly temperature (T, °C).

$CU = 0{\cdot}0$ for $T < 1{\cdot}0$
$CU = -0{\cdot}4248 + 0{\cdot}4672T - 0{\cdot}0398T^2$, for $1{\cdot}0 < T < 6{\cdot}0$
$CU = 1{\cdot}2852 - 0{\cdot}01026T - 0{\cdot}00575T^2$, for $6{\cdot}0 < T < 19{\cdot}0$
$CU = -1{\cdot}0$ for $T > 19{\cdot}0$

Growing-degree-hour calculations

The following equations, derived from Richardson *et a* (1975) and Jackson *et al.* (1983), determine the *GDI* associated with a given hourly temperature (T, °C).

$GDH = 0{\cdot}0$, for $T < 4{\cdot}5$
$GDH = (T - 4{\cdot}5)$, for $4{\cdot}5 < T < 25{\cdot}0$
$GDH = 20{\cdot}5$, for $T > 25{\cdot}0$.

Temperature

The above functions required the input of hourl

Table 1. Predicted (*p*) flowering dates for almond cultivars at Angle Vale, South Aust., estimated from the chilling and heat su requirements shown, compared with observed flowering dates (*o*), together with the residual mean squares (RMS) deviation betwee predicted and observed dates, where RMS = $[\Sigma(o-p)^2/(n-1)]^{½}$

Cultivar	Chilling requirement	Heat sum requirement	1977		1978		1979	
			p	*o*	*p*	*o*	*p*	*o*
Baxendale	280	7200	10 Aug.	13 Aug.	6 Aug.	10 Aug.	6 Aug.	8 Aug.
Bruce	300	5400	31 July	—	27 July	—	4 Aug.	—
Chellaston	260	5300	28 July	4 Aug.	22 July	—	4 Aug.	25 July
Davey	300	6900	9 Aug.	13 Aug.	6 Aug.	14 Aug.	14 Aug.	14 Aug.
Fritz	240	8200	9 Aug.	20 Aug.	19 Aug.	14 Aug.	6 Aug.	9 Aug.
Grant	240	7100	4 Aug.	10 Aug.	5 Aug.	5 Aug.	29 July	27 July
Johnston's Prolific	300	5600	2 Aug.	5 Aug.	29 July	—	5 Aug.	28 July
Mission	320	8900	19 Aug.	23 Aug.	25 Aug.	28 Aug.	26 Aug.	29 Aug.
Ne Plus Ultra	300	5800	3 Aug.	3 Aug.	30 July	6 Aug.	7 Aug.	29 July
Nonpareil	300	6800	9 Aug.	11 Aug.	6 Aug.	9 Aug.	13 Aug.	9 Aug.
Somerton	220	6800	29 July	3 Aug.	1 Aug.	3 Aug.	20 July	19 July
White Brandis	260	5500	29 July	—	25 July	—	22 July	23 July

Cultivar	1980		1981		1982		1984		RMS (days)
	p	*o*	*p*	*o*	*p*	*o*	*p*	*o*	
Baxendale	19 Aug.	17 Aug.	7 Aug.	6 Aug.	11 Aug.	11 Aug.	21 Aug.	18 Aug.	2·7
Bruce	10 Aug.	14 Aug.	27 July	31 July	3 Aug.	5 Aug.	9 Aug.	7 Aug.	5·9
Chellaston	6 Aug.	7 Aug.	25 July	—	1 Aug.	2 Aug.	8 Aug.	29 July	6·3
Davey	19 Aug.	18 Aug.	5 Aug.	8 Aug.	10 Aug.	12 Aug.	20 Aug.	5 Aug.	7·3
Fritz	19 Aug.	14 Aug.	11 Aug.	3 Aug.	15 Aug.	9 Aug.	25 Aug.	—	7·1
Grant	12 Aug.	10 Aug.	4 Aug.	—	9 Aug.	6 Aug.	18 Aug.	—	3·6
Johnston's Prolific	10 Aug.	13 Aug.	29 July	30 July	4 Aug.	5 Aug.	10 Aug.	7 Aug.	4·3
Mission	30 Aug.	28 Aug.	20 Aug.	—	22 Aug.	—	1 Sept.	26 Aug.	4·3
Ne Plus Ultra	12 Aug.	14 Aug.	30 July	31 July	5 Aug.	5 Aug.	12 Aug.	8 Aug.	5·0
Nonpariel	19 Aug.	16 Aug.	5 Aug.	6 Aug.	10 Aug.	11 Aug.	19 Aug.	18 Aug.	2·6
Somerton	10 Aug.	6 Aug.	31 July	29 July	6 Aug.	—	15 Aug.	10 Aug.	3·9
White Brandis	7 Aug.	4 Aug.	26 July	28 July	2 Aug.	5 Aug.	9 Aug.	5 Aug.	3·1

ıeratures. In order to use standard climate data it was ıssary to derive these from daily maximum and mum temperatures. The suggestion of Richardson (1974) to use linear interpolation is not adequate lers 1975). We used the function of Johnson and ıatrick (1977) in the following form.

r the daytime hours, temperature (T, °C) at N hours sunrise is given by

$$T=(M_x-M_n)\sin 2\pi N/[2{\cdot}0(Y+4{\cdot}0)]+M_n$$

e Y is photoperiod, M_x is the maximum temperature M_n is the minimum temperature.

r the night-time hours, temperature T°C at H h ·essed in 24-h notation) is given by

$$T=TAV+R(X+P)$$

e $TAV=(M_x+M_n)/2{\cdot}0$, $R=M_x-M_n$, $X=0{\cdot}463$ ²+232·63°)+0·121 sin(2B+55·35°)+0·031 sin -73·32°), where $B=15(H+A)$, where $A=(W-S$ ·52) $(H-W)/(24{\cdot}0+S-W)$, where S is the time of se and W the time of sunset and $P=(P_s-P_t)$ $W)/(24+S-W)+P_t$, where $P_s=(M_n-TAV)/$ $(_s$, where X_s is X when $B=4{\cdot}48$, and $P_t=(T_w-TAV)/$ $(_w$, where $T_w=M_n+R$ sin[π(W−S)]/(W−S)+4 Y_w is X when $B=18{\cdot}0$. Sunrise and sunset times were lated from the date and the latitude, longitude and zone of the climate station, using the computer nes of Goodspeed (1975).

ily maximum and minimum temperatures from the ıte stations at Roseworthy Agricultural College m north of the orchard) and Edinburgh (8 km south-west) were used initially in the analysis. No rial difference was found in the results from the two ıns for 1978–80. Roseworthy data were used to uce the results presented here for 1977–84 because were fewer missing data than for Edinburgh and term records were available for calculating expected ring dates.

ıation of chilling and heat sum requirements

stematic trial-and-error approach, based on that sted by Ashcroft *et al.* (1977), was used to estimate ng and heat sum requirements for each cultivar. The edure, incorporated in a computer program, was as ws.

e *CU* total for each day of the year was calculated for years 1977–84. The first day in each year with a ive *CU* total was identified (start day). These days fell ay, the earliest being 2 May 1979 and the latest ay 1984.

e *GDH* total for each day of the year was calculated. sum of daily *GDH* totals for all the days between the day and the day of 50% flowering was recorded for cultivar. The *CU* total of the start day was added to the *CU* total of the next day and the *GDH* sum from that day to the day of 50% flowering was recorded. This process was repeated to create a table of *CU* sum and *GDH* combinations. The initial combinations had small *CU* sums associated with large *GDH* sums and the later combinations (near 50% flowering) had large *CU* sums associated with small *GDH* sums.

The means and standard deviations over 7 years of the *GDH* sums associated with each *CU* sum were calculated. Preliminary analysis indicated that the chilling requirements would be found within the range of 100–500 *CU*. Accordingly, coefficients of variation (100 standard deviation/mean) were calculated for values at 20 *CU* intervals over this range. Coefficients of variation for values less than 160 *CU* and greater than 460 *CU* were high but irregular. Between those values the coefficients tended more or less smoothly towards a minimum for each cultivar (Fig. 1). A quadratic function was fitted to each set of data to determine the *CU* sum with the minimum coefficient of variation (Fig. 1). This *CU* sum is the chilling requirement of the cultivar in question and the *GDH* sum associated with it is the heat sum requirement (Table 1).

Results

The coefficients of variation of each cultivar are shown in Fig. 1. The fitted quadratic curves have regression coefficients (r^2, adjusted for degrees of freedom) greater than 0·79 ($P<0{\cdot}01$), except for the cultivar Bruce ($r^2=0{\cdot}67$, $P<0{\cdot}02$). The selected chilling requirements, together with the corresponding heat sum requirements for each cultivar, are listed in Table 1. Also shown are the dates of flowering, for 1977–84, estimated using these values, compared with the observed dates of flowering. As might be expected from the fitting of only a small number of data points to the complex functions for calculating chill units and heat sums, the residual mean squares values are high for some cultivars.

Table 2 shows the range of estimated flowering dates for 1958–84. These results suggest that in 24 years out of 27 the 50% flowering date will fall within about 10 days either side of the mean date. Results for individual years show that the order in which the cultivars flower is almost always the same, although the number of days between flowering in any two cultivars varies from year to year. It appears from these results that the cultivars Bruce, Chellaston, Grant, Johnston's Prolific, Ne Plus Ultra, Somerton and White Brandis form an early flowering group with mean flowering dates in an 8-day range. The cultivars Baxendale, Davey, Fritz and Nonpareil form an intermediate group flowering on average 1 week later than the latest of the early group. The remaining cultivar, Mission, stands alone, reaching 50% flowering 2 weeks later on average than the intermediate group.

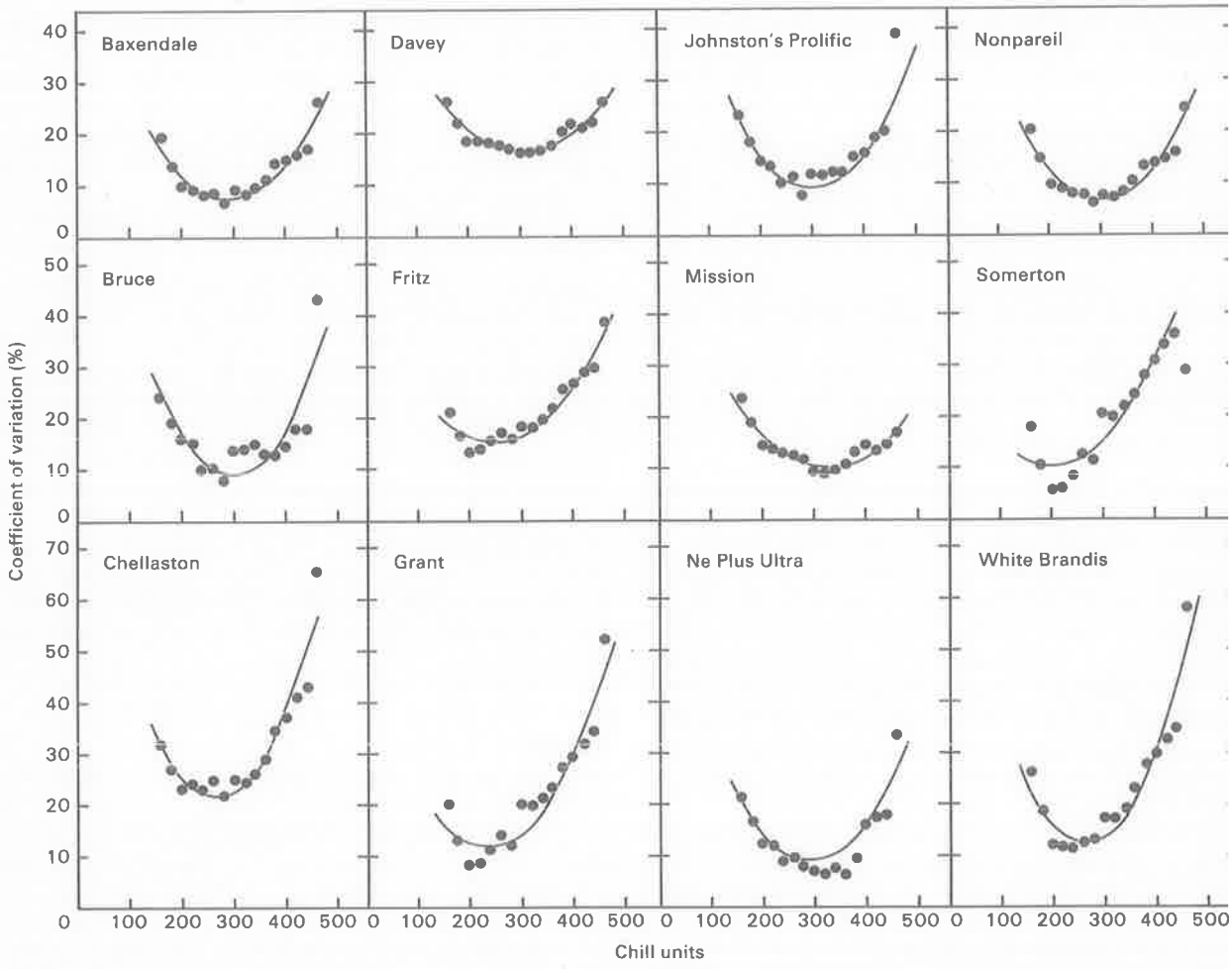

Fig. 1. Coefficients of variation in heat sums to flowering at various chill unit accumulations for 12 almond cultivars at Angle Val South Aust., 1977–84.

Table 2. Mean and 85 percentile dates of 50% flowering for almond cultivars 1958–84 at Angle Vale, South Aust., calculated from estimated chilling and heat sum requirements

Cultivar	Mean	85 Percentile	
Baxendale	11 Aug.	31 July	20 Aug.
Bruce	31 July	22 July	10 Aug.
Chellaston	27 July	13 July	7 Aug.
Davey	11 Aug.	31 July	20 Aug.
Fritz	12 Aug.	31 July	25 Aug.
Grant	4 Aug.	25 July	19 Aug.
Johnston's Prolific	1 Aug.	23 July	11 Aug.
Mission	24 Aug.	17 Aug.	1 Sept.
Ne Plus Ultra	3 Aug.	24 July	12 Aug.
Nonpareil	10 Aug.	30 July	19 Aug.
Somerton	30 July	20 July	15 Aug.
White Brandis	28 July	15 July	8 Aug.

Discussion

The estimated chilling requirements of 220–320 units ar consistent with the accepted view of almonds having relatively low chilling requirement (Chandler and Brow 1951; Granger 1980; Baxter 1981). There are no publishe estimates of chilling based on the 'chill unit' measuremen Aron (1974), reporting studies in a similar climat (California), gave estimates in the range of 255–300 h c chilling for the cultivars Davey, Nonpareil and Ne Plu Ultra.

The heat sum estimates are more difficult to compar with data from elsewhere. Published heat sums are ofte accumulations from an arbitrarily chosen date, an therefore ignore the effect of earlier or later breaking c dormancy (e.g. Weinberger 1967). Such data as there ar for peach, a closely related species, suggest that the hea sums obtained in our study are high (Richardson *et a*

'5; Bauer *et al.* 1976; Ashcroft *et al.* 1977). This may ect the crudity of the linear heat sum function. Perhaps relatively high temperatures at Angle Vale are ıtributing less to floral development than more derate temperatures.

'he predictive value of the estimates obtained is iable among years and cultivars. In particular, the dicted flowering dates for 1977 and 1978 are con-ently earlier than the actual flowering dates, while se for 1984 are later. The cultivars Chellaston and Fritz play several instances of differences of more than 5 's between predicted and actual dates. Possible sources error in the predictions include measurement errors, ;ystematic variations in temperature between the hard and the climate station and factors other than ıperature which may influence the flowering of the es. We have no basis on which to assess the importance hese possible sources of error. Another possible source error is failure of the chill unit and heat sum functions used to represent adequately the relationship of wering to temperature in all circumstances.

Closer definition of the form of the chill unit function uld require controlled environment studies over a ge of temperatures including day/night temperature nbinations. One difficulty of all studies of the chill unit ıction, particularly field studies, is that the end of mancy is not observed directly, but is inferred from ısequent floral development, which is a process with its n relationships with temperature. To overcome this ficulty would require microscopic examination of the al apex during chilling.

The heat sum concept has been used with greater or ser success in the prediction of phenological stages in a de range of crops (Nix 1981), although the concept is her rudimentary in its linear function, with sharply ined upper and lower bounds. However, exploring ıre elaborate continuous functions would require ensive experimentation with environment control.

Pending more fundamental research into the tem-rature–flowering relationship, one must fall back on tistical approaches as suggested by Ashcroft *et al.* (1977) d attempted in this study. The results of Hill *et al.* (1985) gest that predictions of flowering dates which deviated more than 5 days from actual flowering dates would be urate enough to determine whether or not a cultivar s suitable for a particular area and whether or not two or ıre cultivars were suitable pollinators when grown gether. Our results (Table 1) indicate predicted flowering tes within 5 days of observed dates in 59 out of 72 tances (within 3 days in 46 instances). However, our ults were obtained at only one site. Before the chill unit d heat sum estimates we have presented can be used nerally, further information on flowering dates from ner sites with different climates would have to be alysed.

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