

Avocado Flowering¹

T. L. Davenport

University of Florida, Tropical Research and Education Center,
Homestead, FL 33031

I. Introduction	257
II. Floral Biology	258
A. Floral Induction	259
B. Floral Anatomy	261
C. Flower Behavior	267
III. Pollination	272
A. Pollen Tube Growth and Fertilization	272
B. Insect Pollination	275
C. Pollination and Fruitfulness	278
IV. Conclusion	283
Literature Cited	284

I. INTRODUCTION

The avocado (*Persea americana* Mill.) has increased in importance over the years in many countries around the world. The United States, Mexico and Brazil lead in world commercial production, while Israel, South Africa, Australia, New Zealand, the Philippines, Spain, Cyprus, Canary Islands, Chile, Ecuador, Venezuela, Greece, and the Caribbean area are actively increasing commercial production (B.O. Bergh, personal communication; Gustafson 1976). The history of the avocado has been detailed by Gustafson (1973, 1975, 1976) and others (Bergh 1975b, Knight 1980; Popenoe 1924; Ruehle 1958; Schroeder 1958; Williams 1976). Several reviews have been published on various aspects of the avocado, including its botany (Knight 1980; Purseglove 1968; Williams 1976), breeding (Bergh 1975b), horticulture (Hodgson 1930b; Ruehle 1958; Ryerson *et al.* 1924), cultivars (Campbell and Malo 1976), and pollination (Gustafson and Bergh 1966). A recent collection of papers discussing the horticultural aspects of avocado production is found in Sauls *et al.* (1976).

The more than 200 cultivars of cultivated avocado are classified into three distinct races: West Indian, Guatemalan, and Mexican. Each race has unique ecological adaptations and identifiable characteristics (Bergh 1975b; Knight 1980), although interracial hybrids do occur. All three races share many similar growth and flowering behavior characteristics. Unless otherwise noted, the examples given generally reflect the behavior of most avocados, although some

¹Florida Agricultural Stations Journal Series No. 6668.

variations are likely due to cultivar, racial differences, and environmental conditions prevalent in each avocado growing area.

The various sources of research information on avocado reproductive biology are sometimes conflicting and have contributed to a general confusion concerning issues of pollination, fertilization, and, ultimately, fruit set. Part of this confusion is likely derived from the fact that avocados are grown commercially in vastly different climates, ranging from the humid tropics to arid subtropics. The objective of this chapter is to review the biology of avocado flowering, to emphasize the important influence of environmental conditions on avocado reproduction, and to point out areas of research that may resolve the many questions still outstanding.

II. FLORAL BIOLOGY

Growth of avocado branches takes place in distinctive vegetative flushes, which generally occur two or three times throughout the year. These flushes of vegetative growth do not necessarily include the whole tree (Davenport 1982; Scholefield *et al.* 1985; Venning and Lincoln 1958). Some cultivars maintain growth in some portion of the tree even though most of the tree branches are in rest at any given time. Others may at times exhibit distinctly phasic growth; that is, they extend new shoots throughout the tree two or three times during the year. Reproductive growth occurs following a rest period only once per year in nearly all cultivars. During development of lateral inflorescences, the apex elongates in vegetative growth. In the meantime, the inflorescences continue to develop toward anthesis. In nearly all cases, inflorescences develop laterally with no new leaves evident except in the newly emerging apical bud as noted above. One notable exception is 'Topa Topa' which produces terminal, leafy inflorescences (Schroeder 1944a). Salomon (1984), on the other hand, recently reported that avocado trees, under certain conditions that promote vegetative growth, may produce leafy inflorescences; his findings suggest that determination of inflorescence morphology is at least in part influenced by environmental conditions.

The last vegetative flush prior to inflorescence development has been reported to take place during late September to early October on Florida grown avocado cultivars (Davenport 1982) and during February on 'Fuerte' grown in Australia (Scholefield *et al.* 1985). Terminal buds typically return to a state of rest following vegetative growth. This period of rest lasts from October to late November or January in the northern hemisphere and from February to April in the southern hemisphere (Scholefield *et al.* 1985), depending upon when development of inflorescences begins within each cultivar (Davenport 1982; Reece 1942). Unless modified by recent pruning or heavy shading, virtually all terminal buds and many lateral buds on mature trees are triggered to develop once the flowering process begins. Lateral buds, however, seldom develop beyond the bud stage, abscising from the tree instead.

Inflorescence development becomes apparent during early fall in many cultivars of the Mexican race and Mexican-Guatemalan hybrids (B.O. Bergh, personal communication). Cultivars of West Indian and Guatemalan races and hybrids of West Indian and Guatemalan races, on the other hand, begin to develop floral buds from late November to late January in the northern hemisphere (Davenport 1982; Reece 1942). Floral development of 'Fuerte' has been reported to begin in April or May in the southern hemisphere (Kotze 1982; Sedgley *et al.* 1985; Scholefield *et al.* 1985). Full, flowering bloom occurs in March and April in the major growing areas throughout the northern hemisphere (Bergh 1967; Davenport 1982; Blumenfeld and Gazit 1974; Hodgson and Cameron 1937; Schroeder 1951) and in August to October in southern latitudes (Alexander 1975; Kotze 1982; Sempio 1974; Scholefield *et al.* 1985; Toerien 1979). At least three notable exceptions are 'Kosel', 'Fuerte', and 'Pinkerton', which may flower under certain conditions more than once during the year. The time required for inflorescence

development in Florida cultivars was reported to range from 2 months in late-initiating cultivars to about 3.5 months in the earliest-initiating ones (Davenport 1982).

A. Floral Induction

Floral induction evidently takes place sometime during the period between the last autumn vegetative flush and the time when initiation of inflorescence buds is apparent. Induction is here defined as that event triggering transcription and expression of flowering genes. It must occur prior to initiation, which shall be defined as the first physiological and histological expression of the induced state. Primordial lateral buds buried beneath bracts are formed at the termination of each flush of growth during the year. It is thus possible that floral development, as well as vegetative growth in subsequent flushes, is determined at the time when these bud initials are laid down at termination of each flush. It is also possible that induction takes place during the subsequent period of rest. Finally, induction of individual nodes may occur sequentially in an acropetal direction at the time of inflorescence development. The three possibilities have not as yet been critically examined.

Because of the similarities in the flowering seasons of avocado cultivars grown throughout the world, some factor common to the growing areas such as daylength or temperature is likely involved in the floral induction process. Buttrose and Alexander (1978) investigated the effects of daylength and temperature on the flowering potential of small, grafted avocado plants. Six-month-old seedlings from an unnamed source were grafted to the Mexican-Guatemalan hybrid 'Fuerte' and allowed to grow 4 months before they were pinched back and placed in growth chambers maintained at prescribed temperatures. The plants required a flush of vegetative growth before initiation of flowering panicles occurred, and flowering occurred 4-6 months after placing the plants in the chambers. Low daytime temperatures (20°C) and nighttime temperatures (5-15°C) promoted floral induction. Daylengths of 9 hr reduced the time to flower compared with 15-hr daylengths, but the number of flowers produced on plants growing with shorter daylengths was less than on plants with longer day lengths. Daytime temperatures of 25-30°C completely inhibited floral induction. Even a short, 1-hr exposure to 30°C each day was sufficient to inhibit flowering severely. The night temperature appeared to have little effect. Further supporting the observation of high-temperature inhibition of flowering, Sedgley *et al.* (1985) reported arrested inflorescence bud growth and, in many cases, unusual development of vegetative, lateral buds when some Mexican-Guatemalan hybrids were subjected to 33°C during the day and 23°C at night.

The results of Buttrose and Alexander (1978) are interesting for several reasons. First, they provide a stimulus for future research studies on the physiology of avocado floral induction. One may use this experimental approach to determine if induction takes place at the end of the last vegetative flush or during the interim rest period by proper timing of exposure to the inductive condition. This study also raises questions concerning the relative importance of daylength vs. temperature effects on flowering. For example, the results indicate that induction occurs regardless of daylength when the daily temperature does not exceed 25°C. A 25-year record of monthly average temperatures in the avocado growing areas of Florida demonstrates that the maximum mean daytime temperature rarely goes as low as 25°C in any month of the year (NOAA 1976). The temperature drops to well below this level only when cold fronts pass, and these periods are only transitory. The average maximum daytime temperature in October and November, when many avocado cultivars are presumed to be induced to flower, rarely goes below 27°C because cold fronts typically lack the strength to reach South Florida during that period. Similar conditions exist in Israel (A. Blumenfeld, personal communication). It is possible that several days at 20°C or lower without a constant daily high-temperature interruption are sufficient to induce flowering. Alternatively, at these higher temperatures, daylength may be the more dominant mediator of floral induction. Furthermore, the West Indian and West Indian-

Guatemalan hybrids, which are better adapted to warm climates than Mexican types, are the typical cultivars grown in South Florida. These cultivars may not exhibit the high-temperature inhibition that was demonstrated for 'Fuerte'. The amount of flower production may be temperature-mediated once induction events are set in motion by short daylengths. The results presented by Buttrose and Alexander (1978) unfortunately are unable to resolve these questions.

Other influences of internal origin appear to affect flowering. Hodgson and Cameron (1935) reported that a heavy crop in the previous year delays the time of bloom as well as reduces the quantity of flowers produced. B.O. Bergh (personal communication) has made similar observations. Personal observations in Florida indicate, however, that even though alternate bearing is apparent in some cultivars, the amount of flower production does not seem to be affected. Popular opinion suggests that modification of the tree carbohydrate status may play a role in alternate bearing (Murneck 1941; Scholefield *et al.* 1985); however, although there are numerous reports of an increase in fruit set resulting from girdling branches (Coit 1921; Hodgson and Cameron 1937; Homsy 1974; Lahav *et al.* 1971; Malo 1971; Ulman and Ben-Ya'acov 1966) its effects on flowering specifically are not clear because girdling was performed during the flowering period. In trees girdled before flowering, only the timing of floral expression seems to be altered, not the number of flowers or inflorescences (Ibrahim and Bahlool 1979; Ticho 1970), and in some cases, girdling seems to have no apparent effect on flowering (Lahav *et al.* 1971). The slight shift in the timing of flowering caused by girdling may be a reflection of a change in growth rate rather than induction of flowering *per se*.

B. Floral Anatomy

Davenport (1982) defined the morphological development of avocado panicles in 10 discreet stages (Table 7.1 and Fig. 7.1). These defined developmental stages are referred to in the following discussion to relate histological details to the readily observable flowering bud. The time required for inflorescence development from stage 1 to stage 9 varies among cultivars. Furthermore, the rate of development also varies among cultivars, each one demonstrating a unique pattern of growth (Fig. 7.2). It is likely that temperature plays an important role in panicle development behavior, but the cultivars shown in Fig. 7.2 were all exposed to similar environmental conditions but exhibited different growth patterns.

Table 7.1 Description of Various Stages in Avocado Reproductive Development. ^a

Stage	Description
0	Bud in rest, bracts closed with no sign of growth
1	First indication of bud development, bracts show signs of opening
2	Obvious bud growth, bracts open showing development of inflorescence bud
3	Bud assumes spherical shape as inflorescences begin enlarging
4	Bud becomes angular, continued enlargement of inflorescences
5	First observable elongation of primary peduncles
6	Continued elongation of primary peduncles. First observable elongation of secondary peduncles
7	Continued elongation of inflorescence and development of flowers
8	First opening of flowers
9	Maximum flower opening

^a From Davenport (1982).

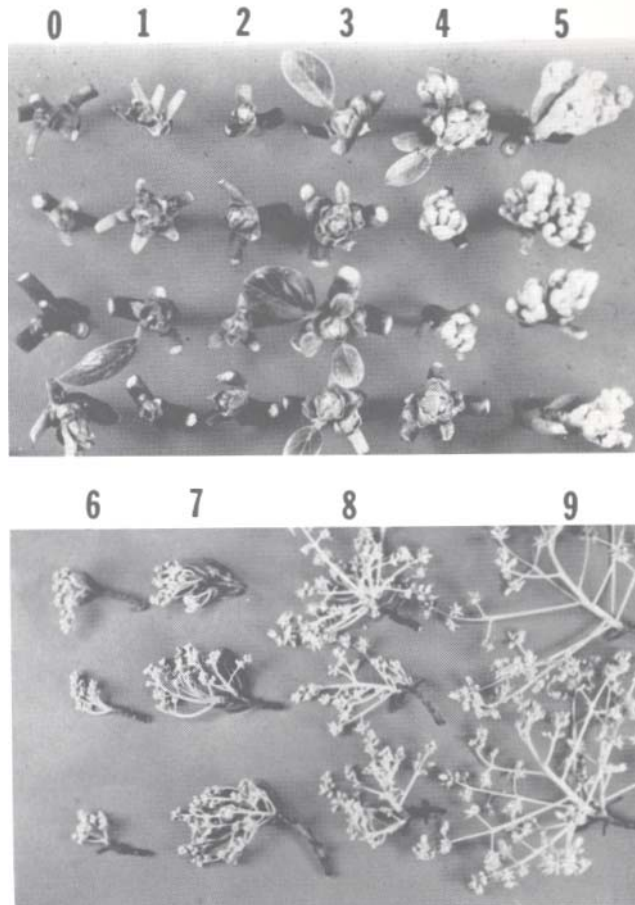


Fig. 7.1. Developmental stages of avocado inflorescences. See Table 7.1 for description of each stage (from Davenport 1982).

Inflorescence development was briefly reviewed by Valmayor (1967). Histological sections of terminal buds at various times from rest to flowering (Reece 1939, 1942) reveal that the buds are initially composed of lateral and apical undifferentiated meristematic areas protected by bud scales (stage 0). Growth commences (stage 1) in the most proximal axils of the bud scales and proceeds acropetally (stage 2). The developing axils expand, forming bractlike structures, which increase the volume of the developing bud, causing it to assume a spherical shape (stage 3). Reece (1942) referred to these developing, lateral axils as secondary axes [primary peduncles according to Davenport (1982)]. Further development of the bud consists of continued elongation of the secondary axes (primary peduncle) and initiation of cell division in the meristems of tertiary axes (secondary peduncles), which are located alternately in the axils of the elongating primary peduncle. It should be noted that because the sequence of evocation of bud growth is toward the apex, each bud has progressed to a different level of development in stage 3, ranging from initiation and elongation of secondary peduncles in the most proximal to undifferentiated lateral buds near the apex. The first sign of floral development in the most proximal lateral buds occurs in late stage 3. Continued development proceeds as lateral buds differentiate and elongate within the bud, causing it to swell into an angular shape (stage 4). An excellent histological description of individual flower development can be found in Schroeder (1952). Macroscopically, the developing lateral axils (peduncles) first become apparent in stage 5 and proceed to elongate through developmental stages 6 and 7. Anthesis of the first initiated

flowers occurs in stage 8 followed by full flowering in stage 9.

Each secondary peduncle generally develops an apical and two lateral flowers. Each generative structure then is composed of a number of cymose inflorescences (Reece 1942). Unlike the acropetal development of primary and secondary peduncles, floral differentiation and anthesis of the cymules is basipetal. Thus, the terminal flower opens first, followed generally the next day by the lateral two flowers. Several flowers open each day in the cluster of inflorescences. The average number of lateral inflorescences that develop on branches from year to year is relatively constant, but varies among cultivars ranging from about 6 to 12 (Davenport 1982).

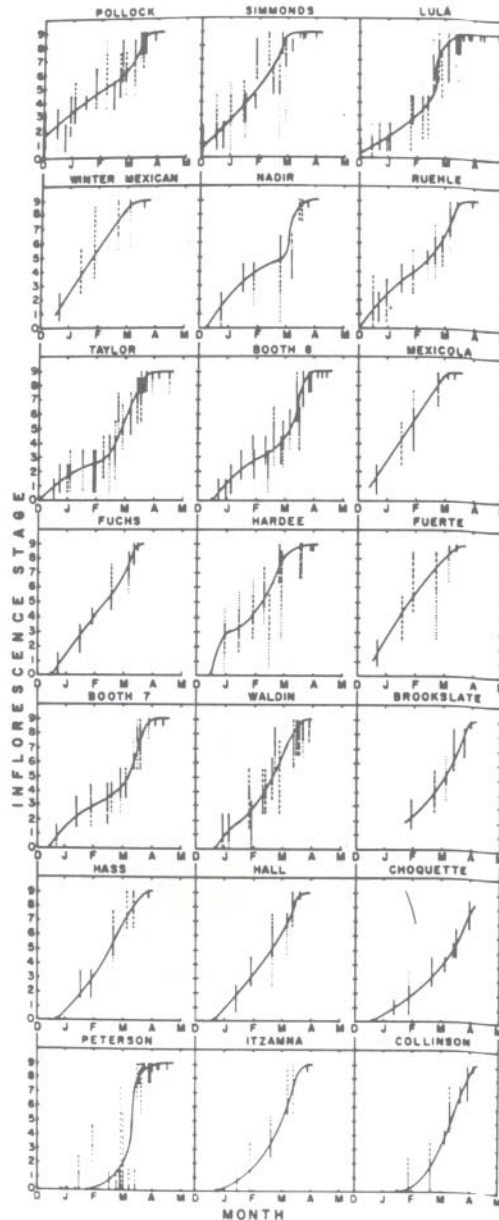


Fig. 7.2. Transition of avocado inflorescence buds through stage 0-9 during flowering season. Each cultivar was observed one to three seasons. Each vertical line represents the range and percentage of each stage observed at the indicated time (..... = 20%; ---- = 20%-40%; _____ = >40% (from Davenport 1982).

The avocado flower (Figs. 7.3 and 7.4) is perfect, with minor variations among cultivars (e.g., presence or absence of trichomes on the pistil and stamens). Each flower normally has three pale greenish-yellow petals alternating with three similarly colored sepals. Aligned with each petal is one stamen and one nectar-secreting, yellow staminode. Similarly, two stamens are aligned with each sepal, the interior one having a pair of nectaries at its base. Thus, each flower normally has a total of nine stamens, each one bearing four pollen sacs each with a pollen-releasing valve hinged at the distal end of the anther. Each anther may contain 500-700 pollen grains depending upon cultivar and environmental condition (Schroeder 1955). The pistil, which has a slender style and small stigmatic surface, is located in the center. Structural details of the stigma and style have been reported by Sedgley and Buttrose (1978). The stigma and style are asymmetrical, with a distinct groove, which extends the 3.5-mm length of the style and is lined with transmitting tissue. The stigmatic surface is composed of elongated papilla cells, giving it a coarse texture. The stigma and transmitting tissue secrete a substance containing lipids and carbohydrates that is assumed to promote pollen germination and tube growth. The open flower is approximately 1 cm in width and 6-7 mm in length from the base of the ovary to the stigma. Further details of avocado flower anatomy may be found in Tomlinson (1980), Scholefield (1982), and other articles cited in Section II.C.

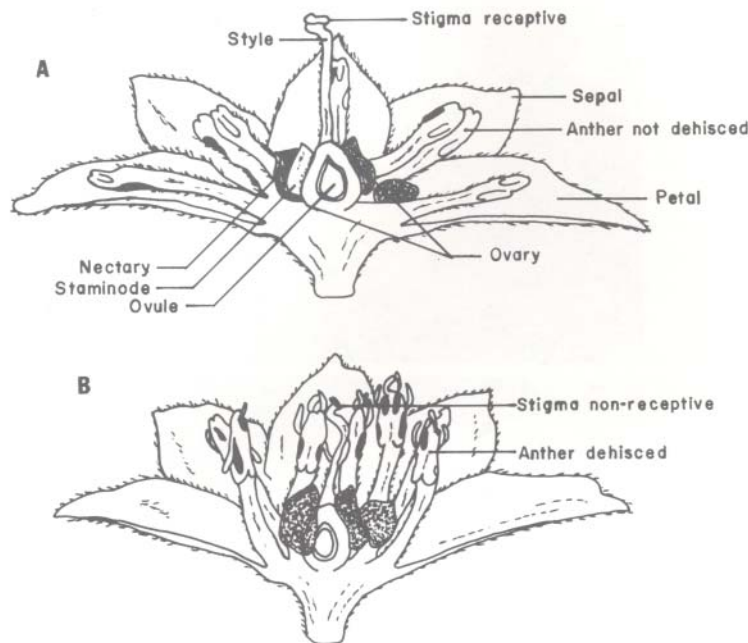


Fig. 7.3. Schematic longitudinal section of avocado flower. A-Female stage, with stigma receptive, but stamens bent outward and anthers not dehisced. B-Male stage, with stigma no longer receptive, but stamens upright and anthers dehisced (from McGregor 1976).

Abnormalities in avocado floral structures are common. Schroeder (1940) reported that the most common abnormality was staminoidy, the conversion of other flower parts to stamens. He found that the number of stamens ranged from 4 to 19. Less frequent, but still common, are flowers exhibiting pistilloidy, i.e., the conversion of other flower parts to pistils (Kadman *et al.* 1974; Schroeder 1940,1944a). Less common abnormalities included fused stamens, stamens fused with staminodes, irregular nectaries, modified perianth parts, naked ovules, double pistils with naked ovules, and modified perianth number. Tomer and Gottreich (1978), Tomer *et al.* (1976), and Sedgley (1980) observed several abnormalities in ovule development, including

double embryo sacs, embryo sac degeneration, lack of the embryo sac, and compartmentalization (i.e., development of voids in the tissue).

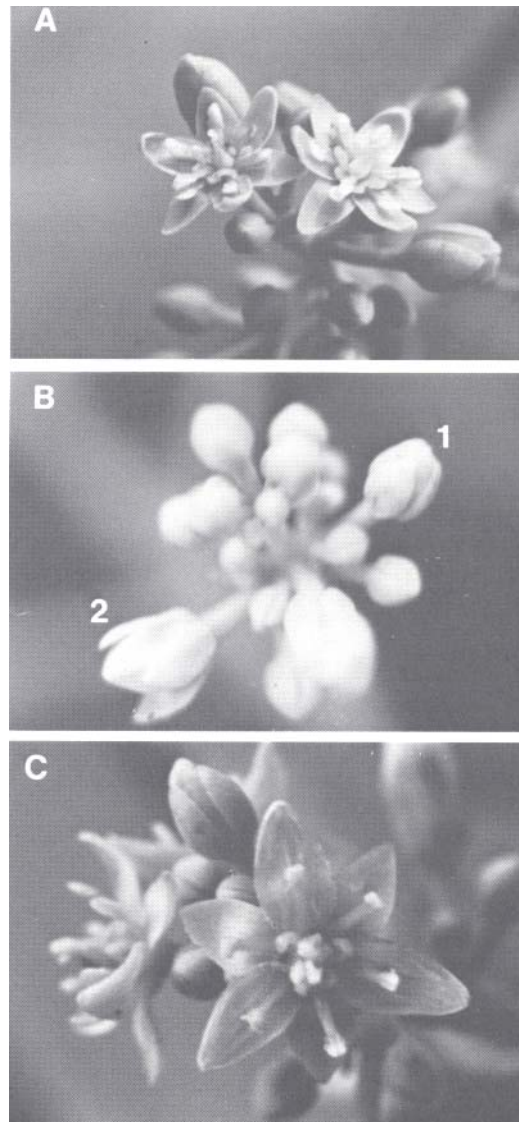


Fig. 7.4. Different stages of avocado flowers. A-Stage I, functional female. B-Post-stage I, closed flower (B-1); post-stage II, closed flower (B-2). C-Stage II, functional male.

As lateral inflorescences develop, new leaf primordia begin to emerge from the terminus. These differentiate, giving rise to a distal vegetative flush that occurs during and after flowering. Thus, inflorescence development occurs at the same time as induction of vegetative growth. The coincidence of these two events suggests that floral induction may occur in all nodes of a bud at some time before the onset of inflorescence initiation. Because flower differentiation occurs late in the development of individual inflorescences, it is likely that induction, regardless of when it occurs, is responsible for initiation of the primary peduncle; and the events that follow, including flower expression, are a consequence of a cascading, developmental sequence.

C. Flower Behavior

Groups of avocado flowers begin to open in unison throughout a tree as the inflorescences reach developmental maturation. Those flowers borne on inflorescences that developed first, i.e., the most proximally located ones, are the first within panicles to undergo anthesis. Flowering continues on a daily basis as more distal inflorescences mature. Flowering persists for several weeks, the length of time required being dependent upon cultivar and climatic conditions.

1. Synchronous Dichogamy. Avocado flowers are perfect, bearing functional male and female parts. They do, however, exhibit a unique mechanism for alternation of sexes that enhances the opportunity for outcrossing. Nirody (1922) first recognized that avocado flowers were dichogamous, i.e., they first have a distinctive female period with receptive stigma and a subsequent male period when the stigma is generally considered no longer receptive and the anthers dehisce to expose pollen. The anatomical differences between the two stages are illustrated in Figs. 7.3 and 7.4. Stout (1923) described the unique dianthesis and synchronously dichogamous nature of avocado flowering behavior. Later reports by Stout (1924, 1927, 1933), Stout and Savage (1925), Robinson and Savage (1926), Peterson (1955b), and Bergh (1976) confirmed the early studies and discussed the implication of this behavior on fruit set.

Each avocado flower opens twice: the first time (stage I) as a functional female and the second time as a functional male (stage II). The openings, separated by one overnight period, last up to half a day and occur during either the morning or afternoon hours. Flower opening is synchronous, i.e., flowers open and close in near unison throughout a tree. The petals and sepals bend outward into a plane more or less perpendicular to the axis during both openings but have been noted to open further at the second opening (B.O. Bergh, personal communication). During the first open period, the nine stamens reflex outward against the perianth, and the pistil stands erect with the stigmatic surface receptive to pollen (Figs. 7.3A and 7.4A). There is no dehiscence of anthers at any time during the first opening. At the end of the opening period, the perianth recloses tightly and stays closed overnight (Fig. 7.4B-1). The time required for opening and closing is short, usually taking substantially less than 1 hr. The second opening the next day exposes an easily recognizable functional male flower (Figs. 7.3B and 7.4C). The nine stamens are noticeably larger and somewhat longer than on the previous day; the inner three stamens stand erect adjacent to the pistil, while the outer six stand out at an angle of about 45°. The stigmatic surface of the pistil may begin to desiccate and darken before or during this opening, which led to the early conclusion that the pistil was not receptive during the second opening (Nirody 1922; Stout 1923). Dehiscence of the anthers generally occurs 1-2 hr after the second opening of the flower. Four valves on each anther fold back to expose sticky pollen within spoon-shaped pockets and on the recurved inner valve surfaces. The flowers later close and either set small developing fruitlets or abscise within hours or days (Davenport 1983; Sedgley 1977a,1980).

Stout (1923) classified avocado cultivars into two types, A and B. Type A cultivars exhibit the first opening of functional female flowers during the morning hours; these flowers close near midday and reopen in the functional male stage the afternoon of the following day. Thus, if one observes avocado flowers of an A cultivar in the morning only functional female flowers in their first opening will be seen. If, on the other hand, the flowers are observed in the afternoon, only functional males, which had been functional females the previous morning, will be seen. The reverse is true for type B cultivars. In these, the first opening, showing female flower, occurs in the afternoon, and the second (male) opening occurs in the morning of the following day.

Because of the synchronously dichogamous nature of its flowering and the existence of type A and B cultivars, the avocado affords interesting opportunities for cross-pollination. Thus, in the morning, type A cultivars showing functional female flowers could be crossed with B types showing functional male flowers to provide pollen. Alternatively, in the afternoon, B types

showing functional females could be crossed with A types showing functional male flowers. If the stigma is nonfunctional during the second opening, the possibility of selfing within flowers or within the same cultivar is nil. More on this subject is discussed in Section III.C. It is obvious that the opportunity for cross-pollination is maximized when type A cultivars are planted in close proximity to type B cultivars to facilitate pollen transfer by insects. A recommendation to interplant cultivars to maximize pollination and fruit set was made by Nirody (1922) and has been supported by many subsequent publications. A number of reports are available listing the flowering types of local cultivars (Abrams *et al.* 1957; Alexander 1975; Bester 1975; Gogolashvili 1980; Ito and Fujiyama 1980; Knight 1971; Peterson 1956; Seiglie 1976).

2. Environmental Effects. The synchronously dichogamous nature of dianthesis in avocado flowers is extremely sensitive to environmental conditions. With optimum climatic conditions, daily flower openings are uniform and remarkably predictable. Nirody (1922) noted in his original report on avocado flowering that cool weather or overcast days typically delayed flower opening from several minutes to about an hour. Stout (1923) commented: "Cool, cloudy days makes opening of flowers irregular and retarded. Fog at night and rainy weather affect regularity and continuity and sequence of bloom." This phenomenon has been observed wherever avocados are grown-California (Stout 1923), Florida (Stout and Savage 1925; Robinson and Savage (1926), Australia (Sedgley 1977b; Sedgley and Annells 1981; Sedgley and Grant 1983), Israel (Argaman 1983), and France (Lichou and Vogel 1972); however, there has been no in-depth, systematic study of the effect of light intensity on avocado flowering behavior other than casual observations. Some workers have questioned whether shading by enclosures during pollination studies modifies flowering behavior (Clark and Clark 1926). Whether light intensity plays a direct role in behavior modification or whether these modifications are a manifestation of cooler temperatures usually associated with cloudy, overcast, and rainy weather is not known. The more basic question of the interplay between daylength and control of flower opening was recently studied by Sedgley (1985). The cultivar 'Hass' was found to be more sensitive than 'Fuerte' to various daylengths ranging from 1 to 12 hr. Shifts in flower opening were observed in both cultivars. Continuous darkness prevented male-stage opening in 'Hass' and disrupted the floral cycle of both cultivars suggesting that day-night cycles were important in the control of floral anthesis.

The sensitivity of flowering behavior to temperature varies greatly among cultivars. Notwithstanding the popularity of 'Fuerte' in dry, subtropical areas such as California and Israel, its flowering behavior is radically affected by subtle changes in temperature. Nirody (1922) noticed that 'Fuerte' was the only cultivar out of 12 studied in Florida whose flowering behavior changed under cool weather conditions such that functionally male flowers remained open through the period of female opening. He commented that 'Fuerte' was the "only variety in which the chances of pollination are not decreased for want of interplanting," due to overlap of the female and male stage within the same inflorescences. Indeed, this cultivar is so sensitive to temperature shifts that stage II (male) opening has been observed to be retarded 2 hr or more in trees located at opposite ends of a grove due to temperature gradients (Stout 1923).

Opening and closing of stage I and II flowers under optimum temperature conditions is such that there is little opportunity for transfer of pollen from functionally male, stage II flowers to stage I, functionally female flowers on the same tree or within the same cultivar regardless of the flowering type (A or B). Under low-temperature conditions, both female and male openings in type A cultivars may be retarded so much that they become reversed. Thus, instead of morning-opening flowers being female and afternoon-opening flowers being male, the reverse is observed, i.e., morning flowers are male and afternoon flowers are female, a behavior that is typical of type B cultivars under more favorable weather conditions. Type B cultivars are apparently even more sensitive to lowered temperatures than A types (Sedgley and Grant

1983). Some cultivars often respond to low temperatures by failing to open in stage I (Stout 1923; Stout and Savage 1925), although there is a range in this response. Lesley and Bringhurst (1951) found that when the daily maximum temperatures were 12-21°C, the flowers of type A cultivars were delayed in female opening to early or late afternoon, if they opened at all. Flowers of type B cultivars had no fully open females, or they opened so late in the day that pollination during stage I was unlikely.

Although no experiments have been conducted to test the hypothesis, it is likely that shifts in flowering behavior are quantitatively correlated with temperature. In other words, the low-temperature-mediated delay in the first flower opening in type A cultivars probably is offset by the gradually increasing temperature throughout the day. Flowers of type A cultivars, therefore, are likely to open in the afternoon as the temperature rises, but on those days that remain cool type A cultivars probably produce no functionally female flowers. Type B cultivars do not have the advantage of a rising temperature at the time of stage I anthesis. Low afternoon and lower night temperatures may extend the first opening time beyond its physiological ability to open in normal stage I. Sedgley and coworkers obtained such results using plants maintained at daytime and nighttime temperatures of 17 and 12°C, respectively (Sedgley 1977b, Sedgley and Annells 1981, Sedgley and Grant 1983). All type A cultivars had normal but extended floral cycles, whereas five out of the six type B cultivars studied had few or no female flowers. The type B flowers could therefore miss the opportunity for female opening, but the time for male opening the following morning coincides with the rising daytime temperature, resulting in delayed but functional male flowers. Under low-temperature conditions, flowers of both type A and B cultivars are delayed in closing once they have opened. This delay may last through two or more photoperiods in the case of type B functionally male flowers (Sedgley and Grant 1983).

Night temperature appears to be important in determining the extent of delay in flower opening. Bringhurst (1951) observed normal flowering behavior in avocado plants placed in a temperature-controlled (16°C minimum) greenhouse overnight and placed outside (21°C maximum) during the day. Conversely, if the plants were placed in the greenhouse during the day and outside during the night, they behaved the same as plants left outside continuously. These results are understandable considering that a substantial difference in greenhouse and outside temperatures (minimum 16 and 7°C, respectively) occurred only during the night.

As a result of the shifts that occur in avocado flowering behavior during periods of cool weather, both functional male and female flowers may be present at the same time on individual trees. This situation creates an opportunity for pollinating insects to transfer pollen directly from stage II flowers to receptive stage I flowers within the same inflorescences or between trees of the same cultivar, a self-pollinating process that shall be referred to as close pollination (Peterson 1955a). The opportunity for close pollination may enhance fruit set during these periods; however, Sedgley and co-workers (Sedgley 1977b; Sedgley and Annells 1981; Sedgley and Grant 1983) and (Argaman 1983) have found that events subsequent to pollination are also affected by adverse temperature conditions.

Sedgley (1977b) exposed small trees of 'Fuerte', a type B cultivar, and 'Hass', a type A cultivar (Sedgley and Annells 1981), as well as other cultivars (Sedgley and Grant 1983), to high (33°C day/28°C night), medium (25°C day/20°C night), and low (17°C day/12°C night) temperature regimes during flowering. The high-temperature regime caused precocious abscission of flowers, buds, and fruitlets of all cultivars tested; furthermore, fertilization of 'Fuerte' did not occur under these conditions. Similar responses, as well as ovule damage, were observed by Argaman (1983) in 'Fuerte'. 'Ettinger', 'Hass', and 'Reed', on the other hand, were less affected by the high-temperature regimes. Of the three temperature regimes tested by Sedgley, the midrange was optimal. All cultivars tested at this temperature range exhibited normal flower behavior, including synchronous dichogamy. Flowering behavior in the low-temperature regime

was altered as already described, i.e., delayed flower openings. Although pollen tube germination on 'Fuerte' stigmas appeared normal in the low-temperature regime, tubes rarely grew beyond the style, markedly reducing the potential for fertilization. This response was also observed in plants that were transferred to the low-temperature regime only 1 hr before pollination. Thus, pollen growth appears to be affected by lower temperatures directly rather than as a result of a predisposed physiological state of the flowers at the time of pollination. Other type B cultivars demonstrated similar responses to low temperatures (Sedgley and Grant 1983). Pollen tube growth and ovule penetration occurred at all temperatures tested in all type A cultivars; however, a lower percentage of embryo sacs was penetrated under the low-temperature regime. Thus, even though low temperatures may promote close pollination by causing overlapping of flower openings on the same tree, the fecundity of the pollen and ovule may at the same time be adversely affected. A better understanding of the complex, quantitative interplay of temperature and total flower functionality is needed.

III. POLLINATION

The avocado produces hundreds of flowers in the lateral inflorescences of each branch, but only a fraction of 1% of these flowers may set fruit. A better understanding of the pollination and fertilization processes may lead to improved fruit set and increased yield in avocado.

A. Pollen Tube Growth and Fertilization

The storage and viability of avocado pollen have been studied (Schroeder 1942; Sedgley 1981) because of the importance of these characteristics in breeding programs (Bergh 1976; Sedgley and Alexander 1983) and to our understanding of pollination. Pollen has been shown to remain viable for up to 6 days under ambient temperatures of 20.6-32.8°C at relative humidities of 57-63% (Papademetriou 1975a). These conditions are typical of those during the flowering period in the humid Caribbean tropics in South Florida. Schroeder (1942) claimed to have stored viable pollen for several months at 15°C successfully. More recent evidence, however, suggests that this result may be in error (B.O. Bergh, personal communication). In these studies, viability was considered synonymous with germinability of the pollen, but germinability may not ensure fecundity. Sedgley (1981) reported storage of avocado pollen at 4°C at 1 or 23% relative humidity (RH) for up to 1 month without loss of germinability or ability to penetrate the ovule. In contrast, pollen grains stored at 25 and -15°C at a range of relative humidities germinated on avocado stigmas, but they were unable to penetrate the ovule. Germinability of pollen could be maintained for at least a year under storage conditions of 4°C with less than 50% RH, but the germinated grains could not penetrate the ovule. Apparently, relative humidity is important since pollen stored at 4°C and 55-75% RH did not germinate. Storage of pollen at -196°C and 0% RH for one year resulted in pollen that would germinate and penetrate the ovule. In all cases, thawing and refreezing the pollen destroyed viability. Thus, under proper conditions, pollen can be stored until the following year for breeding purposes. Furthermore, pollen viability is not likely to limit natural pollination of avocados since it has the potential to remain functional for at least 6 days under ambient conditions (Papademetriou 1975a; Schroeder 1942). This period is more than enough time to pollinate flowers on the same or following day of anther dehiscence.

Germination of avocado pollen is not well understood at the present time. Although attempts have been made to germinate pollen in artificial media, generally composed of sucrose solutions (Furon 1963; Schroeder 1942), they have not met with success. More recently, however, Sahar and Spiegel-Roy (1984) successfully germinated avocado pollen *in vitro* by suspending the pollen in a 15% sucrose plus mineral solution followed by transfer to a solid support of the same solution with agar. Germination took place only if the pollen was first

suspended in the solution before being placed on the agar medium. Differences in germination rates among the tested cultivars were noted. Optimum germination temperature was 25-27°C, and addition of calcium to the medium appeared beneficial to germination. The best in vitro germination, however, was not as good as has been reported for direct pollination of stigmas (Papademetriou 1975a,b; Schroeder 1942; Sedgley 1981). The reasons for this difference are not at present known. Secretions by the papilla cells of the stigma are known to contain a complex of carbohydrates, lipids (Sedgley and Buttrose 1978), and possibly proteins and minerals. Any one or all of the components may regulate pollen germination on the stigmatic surface; yet neither the pollen nor the stigma is specific in its ability to germinate or to stimulate germination. For example, Schroeder (1942) showed that avocado pollen would germinate on stigmas of apple (*Malus domestica* Borkh), passion fruit (*Passiflora edulis* Sims.), papaya (*Carica papaya* L.), carnation (*Dianthus caryophyllus* L.), and Sterculia (*Sterculia apetala* L.). Conversely, pollen from apple, feijoa (*Feijoa sellowiana* O. Berg.), passion fruit, boysenberry (*Rubus ursinus* var. *loganobaccus*), and papaya freely germinated on avocado stigmas.

Once pollen is placed on a receptive stigmatic surface, it germinates within a few minutes, sending a rapidly elongating tube intercellularly through the transmitting tissue (Sedgley 1979c). Tube elongation begins in the matrix between the cell wall and the cuticle of the papilla cells, and proceeds through the lipid-laden intercellular spaces of the transmitting tissue lining the stylar groove, conforming to the shape of the intercellular space as it grows (Sedgley and Buttrose 1978). Consistent with the results of Papademetriou (1975b), who reported pollen tube penetration of the ovary within 1 hr under conditions prevailing in Trinidad, Sedgley (1977b) reported ovary penetration (pollen reaching the base of the style) occurring within 2.5 hr under controlled temperatures of 25°C day and 20°C night.

Despite an abundance of pollen germination at the stigmatic surface, great variation in the rates of growth has been noted (Papademetriou 1975b; Sedgley 1976; Tomer and Gottreich 1975). Only one pollen tube typically reaches and penetrates the ovule. Papademetriou (1975b) reported that some of the slower growing tubes had swollen tips and suggested that an inhibitor was present in the pollen grains giving rise to short tubes. Sedgley (1976) reported that half of the pollen tubes developed swollen tips and had stopped moving at the base of the stigma in hand-pollinated stigmas, bearing an average of 66 germinated pollen grains. Tomer (1976) made similar observations and confirmed that the number of persistent tubes decreased with distance until only one pollen tube persisted at a point one-half to three-fourths of the way down the style. Sedgley (1976) reported that two pollen tubes proceeded to the ovule in 9% of 'Fuerte' flowers. Only those flowers that contained two ovules in the pistil (approximately 50% of the observed flowers) had two pollen tubes reaching the ovules. Later observations, however, indicated that the occurrence may be common in flowers containing a single ovule as well (Sedgley 1979a).

Changes occur in the stigmatic and stylar tissue during the stage I flower opening (Sedgley 1979c). These changes include a marked decrease and near complete loss of starch in papilla and transmitting cells within 18 hr after flower opening. These changes take place in both pollinated and nonpollinated pistils. It is presumed that the readily available soluble sugars are a source of energy for all of the cells involved including pollen tubes. Accompanying the loss in cellular starch is an increase in callose, an amorphous polysaccharide associated with the cell walls. Pollination tends to increase the rate of callose formation. Furthermore, ultrastructural deterioration of the papillae and transmitting tissue occurs only after passage of the pollen tubes. Nonpollinated pistils showed no deterioration up to more than 18 hr after closing of the functional male flower.

After reaching the ovarian tissue at the base of the style, the pollen tube grows through the ovarian wall, entering a cone-shaped space formed by the ovarian wall on the sides and the

ovule on the bottom (Sedgley 1979b). The pollen tube continues growing along and down the inner surface of the ovarian wall finally proceeding around the funicle to the oblique micropyle. It further proceeds between the papillate cells at the apex of the nucellus and enters the embryo sac via a synergid. The time after pollination required for the pollen tube to penetrate the ovule was 18-24 hr under the temperature regime imposed in the study by Sedgley (1979b). Another 6-24 hr was required for the pollen tube actually to penetrate the embryo sac. Sedgley (1979b) suggested that the slow progress of the pollen tube in the ovary compared to its rapid extension through the style may be due to arrested elongation as a result of a period of synthesis or lack of embryo sac maturation.

Fusion of the sperm and egg nuclei probably takes place about 48 hr after pollination (Sedgley 1979b). The first cell division of the zygote takes place 5 or 6 days following pollination. Details of these and other fusion events associated with the reproductive cells of the embryo sac can be found in Schroeder (1952), Sedgley (1979b), and Tomer and Gottreich (1976).

B. Insect Pollination

The pollen of avocado is coated with a sticky substance, which causes the grains to adhere together and prevents it from being windborne (Furon 1963). This tenacity also dictates that some pollen-transferring agent such as a large, flying insect is required for pollination of avocado flowers. Clark (1923), Lammerts (1943), and Peterson (1955a) demonstrated the need for pollinating insects with caged avocado trees in southern California. The most likely candidate for such a purpose in less tropical regions is the honeybee, *Apis mellifera* (Bergh 1975a,b; Gazit 1976; Lecompte 1961; Lesley and Bringhurst 1951; McGregor 1976); however, the activities of bees do not always fit avocado pollination requirements (Bergh 1967; Lecompte 1961).

It was observed in the early 1920s that bees prefer other plants to avocados (Clark 1923). Eisikowitch and Melamud (1982) observed that the presence of avocado pollen in hive traps in Israel was rare, even when the hives were near avocado trees. This observation was especially apparent whenever citrus flowers, which are preferred by bees, were within 3 km. In the absence of citrus flowers bee pollination of avocado increased. The presence of wild flowers also appears to divert the activity of bees away from avocado flowers (Clark 1923; H. Melamud, personal communication). Relatively little bee activity has been observed in avocado groves located in South Florida. Free and Williams (1976) made hourly pollen counts in beehives in Jamaica that were located adjacent to an avocado planting of type A cultivars. Another set of hives placed next to a planting of type B cultivars several miles away was also observed. They found the percentage of avocado pollen to be 0% from dawn to 10 A.M., 9.1% from 10 A.M. to 2 P.M., and 0.4% after 2 P.M. in the hives adjacent to the type A cultivars. They observed 0.2-0.7% avocado pollen before noon and 1.0-2.2% after noon in hives near the type B cultivars. The incongruous peaks of avocado pollen in the hives at times other than those of pollen shed in the orchards led the authors to speculate that the bees were gathering pollen from orchards of complementary avocado cultivars possibly growing nearby. Bees found visiting the female, stage I flowers in these solid plantings had less avocado pollen on their body hairs than those actively gathering pollen during stage II. Thus, although the honeybee is known to be an effective pollinator, other characteristics of bee behavior suggest that it may not be the sole pollinator of avocado in tropical areas.

Field bees are known to divide up duties so that some only gather pollen, others gather nectar, while hive workers conduct tasks necessary for the survival of the colony, e.g., defense and hive maintenance (McGregor 1976). Because of this separation of duties by field bees, it is unlikely that a pollen gatherer would visit functionally female flowers (Lecompte 1961). The nectar gatherers, on the other hand, might wander from pollen-shedding, stage II flowers of one cultivar and transfer pollen, inadvertently attached to body hairs, to another cultivar bearing

functionally female flowers. However, bees have been consistently observed to visit only one tree before returning to the hive to deliver their load (Bergh 1966). For this reason, Bergh (1967) concluded that relatively few California avocado trees are close enough to suitable pollinizer trees for cross-pollination to occur on a commercial scale. Clark (1923) conducted an experiment in which trees of complementary cultivars spaced about 10 m apart were enclosed with beehives. The bees were active on both trees, but they never flew from tree to tree at any time. They flew from the hive to the tree of choice, worked that tree, and then returned directly to the hive. Thus, unless branches of complementary cultivars are interlaced, giving the bee the illusion of working a single tree, the likelihood of cross-pollination is relatively small (Bergh 1967). More recently, Torres and Bergh (1978a) obtained electrophoretic analysis results indicating that some bees may transfer avocado pollen over 100 m or more. A Blumenfeld (personal communication) has also observed bees flying from tree to tree in avocado orchards located in Israel. Finally, it has been observed that bees are sensitive to weather conditions (Bergh 1967; Lesley and Bringhurst 1951; Peterson 1955a). One may observe a high level of bee activity on warm days, but cold or cloudy, rainy weather markedly reduces their activity.

Bees are clearly the primary pollinators of avocado in California (Bergh 1967, 1976) and Israel (Bergh 1975a; Gazit 1976), since few other flying insects have been reported to visit avocado (Clark 1923) in these areas. However, the principal insects visiting avocado flowers in Jamaica, Trinidad, and Florida are *Polistes* wasps (Free and Williams 1976; Papademetriou 1976; Stout and Savage 1925) and *Metabolybia sigulata* (Papademetriou 1976). Seven species of *Forcipomyia* and several species of *Atrichopogon* were reported to visit avocado flowers in the northern Transvaal of South Africa (De Meillon and Wirth 1979), and honeybees rarely frequented avocado flowers in these areas. Similarly, few honeybees are found in avocado orchards in Florida (Robinson and Savage 1926), although we have found some cultivars such as 'Booth 7' may be more attractive to honeybees than others. A number of different flying insects, including *Polistes* wasps, mirids (*Dagbertus* spp.), and flies (*Musa domestica* L.), can be found in greater numbers than bees.

Flower thrips (*Franklimella* spp.) have been found in great numbers in avocado orchards of South Florida. Virtually every flower has at least one thrips, which freely roams the stamens and pistils. Their numbers have been observed to reach a half a dozen or more in each flower, and they are large enough to easily transfer pollen grains across the submillimeter distance from the anther to the stigmatic surface during their constant roaming about the flower. Thrips are known to be effective pollinators of many plants (Lewis 1973). Peterson (1955a) questioned the possibility of thrips-mediated pollination of avocado flowers. In this respect, Schroeder (1954) reported an interesting study, which is seldom cited. Flowers in panicles that had been enclosed in cloth bags for several days were inspected for pollen grains on the stigmatic surface. Of 61 flowers observed, 51% had been pollinated with an average 4.9 pollen grains/stigma, whereas 88-94% of the stigmas in open inflorescences had been pollinated. The rate of pollen grain germination in the enclosed panicles was 31%. These observations provide evidence that pollen is transferred to the stigma either mechanically or perhaps by some locally mobile agent such as thrips. Others have noted a lack of, or difficulty in, establishing a correlation between the number of visiting bees and fruit set (Clark and Clark 1926; Bergh 1967).

The relative importance of potential pollinating agents is not at all clear. The literature is rife with conflicting information, much of it anecdotal. Bees undoubtedly play an important role in avocado pollination at certain times in some areas, but other insects may play a far more important role than previously suspected in the fruitfulness of avocado.

C. Pollination and Fruitfulness

The primary aim of crop management is to maximize yields. In some circumstances,

pollination can be a limiting factor in avocado fruit production (S. Gazit, personal communication), but there is ample evidence of situations where pollination is not the limiting factor. This point is especially evident in cultivars exhibiting the type I fruit-setting habit described by Davenport (1982). This habit is characterized by heavy initial set of fruitlets followed by gradual loss of most of the fruitlets throughout the following months until they reach horticultural maturity. A type II fruit-setting habit is one in which relatively few fruitlets are initially set, but these generally remain on the tree to maturity. These two definitions of the extremes consistently apply to some cultivars. Some cultivars exhibit intermediate fruit-setting habits, and some alternate bearers, such as 'Booth 8', may exhibit the type I habit in "on" years and type II habit in "off" years. In all cases, the fruitlets contain a developing seed, indicating that successful fertilization took place. It remains to be unambiguously determined whether fruit set of type II cultivars is limited by pollination.

One observation suggests that pollination is not limiting in type II cultivars grown in Florida. In 1984 and 1985, flowers of 'Booth 7', a typical type II fruit-setting cultivar, were visited by bees as well as other insects in both the female and male stages. The initial set of small fruitlets was much greater than normal for this particular cultivar, but within 1 week after anthesis, fruitlets abscised before they grew more than 2 mm in diameter, and the final yield was similar to other years. Although ample pollination likely took place, as indicated by the unusually heavy initial set, the cultivar still exhibited an overall type II fruit-setting habit due to the early loss of fruitlets. That pollination may not be the rate limiting step in fruit production is also supported by observations and conclusions of others located in more subtropical areas (Argaman 1983; Lahav and Zamet 1976; Sedgley 1977b). The fact that hand pollinations have consistently resulted in low yields also supports this view (Lammerts 1943, 1945; Sedgley 1980).

The elegant, flowering design discovered by Stout (1922), along with the original observations made by Nirody (1922) that the stigma becomes shrivelled soon after the second opening, led early researchers to conclude that outcrossing is the most likely mode of pollination of avocado. It was, however, noted that some cultivars were self-fruitful because they produced well in solid plantings (Robinson and Savage 1926; Clark 1923, 1924). It was suggested by Robinson and Savage (1926) that these cultivars were likely self-pollinated because the pistils appeared still to be receptive in the second opening when pollen became available following anther dehiscence, a condition rarely found in drier climates (B.O. Bergh, personal communication). It was recommended that avocado orchards be interplanted with complementary type A and B cultivars to facilitate effective cross-pollination by flying insects, thus maximizing the potential for good fruit set. Growers in Florida soon followed this recommendation, and the practice is still followed today in virtually all orchards despite grower complaints of poor fruit set in many cultivars. During the early production years in Florida, Robinson (1933) noted that even though Florida growers were interplanting complementary cultivars, some growers were getting good fruiting from solid plantings or on isolated trees (Cintron 1947); nonetheless, interplanting continued to be recommended (Davis 1939). This practice is still followed today.

California growers continued to plant trees in solid blocks. The reason for the difference in planting style was primarily due to the results of Clark (1923,1924) and Clark and Clark (1926), who demonstrated that caged, self-pollinated trees produced as much fruit as those that were left to open pollination. Furthermore, the modifications in flowering behavior to which avocados are susceptible in California due to frequently cool temperatures was also cited as an alternative mechanism by which close pollination could commonly occur (Hodgson 1930a,b; Lesley and Bringhurst 1951; Robinson 1931). Hodgson (1935), however, noted that 'Fuerte' fruit set sharply declined when the average temperatures were less than approximately 15°C. Sedgley (1977b) later confirmed this observation in this cultivar and others (Sedgley and Annells 1981; Sedgley and Grant 1983) using controlled temperature conditions. Thus, the opportunity for fruit

production as a result of close pollination appears to be restricted to those temperatures that alter flowering behavior to such an extent as to cause overlap of stage I and stage II flowers on the same tree but are not low enough to inhibit fertilization of the otherwise receptive flower.

In the late 1950s, Bergh and Gustafson (1958) revived the concept that cross-pollination may play an important role in avocado fruit set in California. They observed that rows of 'Fuerte' (type B) trees planted next to 'Topa Topa' (type A) yielded significantly more fruit than the rows of 'Fuerte' trees comprising the rest of the grove, which were not adjacent to 'Topa Topa'. The branches of the trees of the complementary cultivar had to be touching for bees, the likely pollinating insect, to transfer pollen effectively (Bergh 1966) and for higher yields to result. 'Fuerte' trees located in the second row from 'Topa Topa' yielded no more than the trees in rows distantly separated from the pollen parent rows (Bergh *et al.* 1966), supporting Clark's (1923) observation that bees visit only one tree per flight and seldom will cross a space to reach another row of trees. Usually 'Fuerte' was found to have higher yields when interplanted with other cultivars as well, but the results were inconsistent and reasons were suggested to explain the exceptions. (Bergh and Garber 1964). In 2 out of the 6 observed years yields were higher in the presumed selfed portions of the grove than in the interplanted portions (Bergh *et al.* 1966). Furthermore, many individual trees in the presumed selfed section of the grove performed better than some trees adjacent to the pollinizer row even when the presumed cross pollinated trees performed better on average (Bergh 1966), reflecting the exceptionally large tree-to-tree variation in avocado fruit set.

The concept that cross-pollination increases fruit set was supported by research conducted in Israel (Bergh 1975a) showing that crosspollination promoted increases in yield of 'Fuerte' and possibly 'Hass'. Pollen parents such as 'Tova' tended to produce greater fruit set than others. Fruit set of 'Fuerte' was also higher using 'Hass' pollen than when selfed even though 'Hass' pollen was found not to germinate well on 'Fuerte' stigmas. More recently, Argaman (1983) found that fruit set was greater when 'Ettinger' or a West Indian cultivar were the pollinizers than when 'Hass' was. Thus, pollen source may be an important factor in fruit set. Sedgley (1979a), using ovule penetration as the criterion for compatibility, reported no evidence of sexual incompatibility in 10 cultivars studied. She also found that the female parent exerted more control than the pollen source on pollen tube growth and ovule penetration.

Knowledge of the relative ability of avocado cultivars to cross pollinate and self-pollinate is important not only to the grower, who is trying to maximize yields, but also to the fruit breeder, who needs to know the pollen source of progeny derived from open pollination or from caged pairs of trees. Self-pollination can occur in both of these planting arrangements. However, the use of electrophoretically separated isozymes of certain enzymes as single gene markers partially to define the enzymatic phenotype of vegetatively propagated avocado cultivars has enabled the unambiguous identification of hybrids (Torres, *et al.* 1978; Torres and Bergh 1980). Using this method Torres and Bergh (1978a) evaluated the isozyme patterns derived from seedlings of 'Pinkerton' planted in a solid block but unprotected from pollination by other nearby cultivars. Their data suggest that 'Pinkerton' seedlings, resulting from self-pollination, accounted for 2-69% of the total seedlings, depending upon the heterozygosity in isozyme patterns of the pollen parents. Using similar methodology, Degani and Gazit (1984) examined seedlings derived from caged pairs of six complementary cultivars and found that the percentage of seedlings that were a product of self pollination ranged from 8 to 93%. Four of the 6 cultivars tested demonstrated a tendency to self-pollinate, and there was no apparent correlation between percentage selfing and fruit set.

There is a possibility that the ability of a fruit to remain on the tree to maturity may be greatly influenced by the pollen parent (Argaman 1983; S. Gazit, personal communication). Thus, the percentage outcrossing, as determined by electrophoretic patterns of the siblings, may be

skewed by the survivability of the developing fruits depending upon the genotype of the pollen parent. Another possibility that must be recognized in studies using open-pollinated orchards is that what is assumed to be a unique, clonal cultivar may be a mixture of clones containing a mixture of isozymes, each with a different set of isozyme patterns. Indeed, this phenomenon has been demonstrated in 'Duke' avocado (Torres and Bergh 1978), where its seedlings were mistakenly identified as the parent. Gan *et al.* (1981) found similar anomalies in some cultivars of mango. If such heterozygosity exists within what is thought to be a clonal cultivar, it is possible, based on isozyme evidence, to conclude incorrectly that crosses between a complementary cultivar occurred when in fact the cross was between trees of the same cultivar. An isozyme analysis of a number of representative parent trees in the planting should be conducted to ensure clonal homogeneity as well as to serve as an appropriate control in such investigations. One possible example of this type of situation is in the report by Torres and Bergh (1978a), where it was concluded that the most likely potential crosses of 'Pinkerton', a type B cultivar, were with B types ('Bacon', 'Fuerte', and 'Edranol'). If the seedlings were true hybrids rather than selfs, then cross-pollination should only have occurred during cool weather when overlapping of flower opening might have occurred, or perhaps by transfer to stage I flowers of morning-collected pollen, retained through the day on pollinating insects. A third possibility is that the 'Pinkerton' pistil was still receptive during the second flower opening. In any case, self-pollination would seem to be much more likely than cross-pollination with these cultivars.

An interesting observation was made in Florida during experiments designed to compare pollination rates of cultivars exhibiting type I and type II fruit-setting habits (Davenport 1985). Regardless of fruit-setting type, avocado pollen was found on stigmas at the close of stage I flowers in only 1-2% of the flowers, despite the fact that much higher fruit-set counts were occurring. This observation was especially noticeable in 'Simmonds', which began flowering approximately 2 weeks before any other cultivar in the area. Pollen counts were made on stigmas of closing stage II flowers as well, and it was found that the pollination rates ranged from 10 to 35% in three of the four cultivars examined. Few flying insects were found in the groves at any given time, and overlap of flower openings did not occur. Furthermore, the stigmatic surface of all flowers remained white throughout the second opening, although receptivity of the stigma and style to pollen germination and fertilization has not yet been determined.

All of these lines of evidence are inconclusive at the present time, but they suggest to us that self-pollination during the second flower opening may be an important mechanism of pollination of avocado flowers in some of those cultivars grown in South Florida. The opportunity for selfing in these cultivars also suggests that pollen can be transferred from the closely adjacent anthers to the stigmas by small, insects, such as flower thrips or ants. This mechanism could explain why fruit set takes place when few flying insects are about. Indeed, any insect visiting the flowers during the post dehiscence period of the second opening could thus become a potential pollinator of the flowers and contribute to fruit set potential if the stigma and ovule are receptive to the pollination and fertilization process. This possibility does not, however, rule out the opportunity for cross-pollination of flowers, as is evidenced by the fact that 'Collinson', a male-sterile cultivar, produces fruit in a mixed planting (Stout and Savage 1925).

The consensus of opinion in recent years concerning self-pollination has been that it can occur only on flowers in the first opening when the stigma is receptive. Thus, it can only occur during periods when the weather is sufficiently cool to cause flower overlap so that pollen can become available for close pollination. Pollen may also be transferred after being retained on insects through the day in the case of type B cultivars or overnight in the case of type A cultivars (Papademetriou 1975a). This concept is based on repeated observations that the stigmas are often found to be shriveled during the second opening, that hand pollinations during the second

opening rarely produce any fruit set, and that the rate of pollen tube growth in stage II flowers is slower than that in stage I flowers (Sedgley 1977a), even though the pistils show little cytological change until 48 hr after first opening (Sedgley 1979c). There is, however, circumstantial evidence to suggest that self-pollination within flowers may occur more often than had previously been considered.

The early work of Stout (1923, 1933) suggested that cultivars such as 'Trapp' were self-fertile. Numerous observations already cited indicate that solid block plantings and individual trees with no reasonable source of complementary pollen can set consistently good crops each year. Clark (1923) concluded that 'Fuerte' pollination must occur in the forenoon during pollen shedding because receptive flowers opened too late in the day for bees to function as pollinators. Papademetriou (1975a) observed good fruit set in plantings of 'Pollocks' trees located in the humid tropics of the Caribbean with little chance of cross-pollination or overlapping of flowers. Peterson (1955a) observed excellent fruit set in both 'Zutano' and 'Hass' trees when they were individually caged with bees, but flower overlapping was not observed and so it is not clear how much self- or close-pollination may have been occurring.

For pollination in the second opening of the flower to effect fertilization and potential fruit set, it is necessary that the stigma and the ovule still be receptive. Receptivity in this case refers not only to the condition of the stigma in that it has not shriveled, but also it must support pollen grain germination and fertilization of the ovule. Papademetriou (1976) noted that in many cultivars growing in the humid tropics, the stigma remained receptive throughout the male opening. Similar observations have been made in South Florida; however, we have also noted that the condition of the stigma appears to be highly dependent upon relative humidity. When the breezes are out of the west and north quadrants, conditions that are usually associated with low relative humidity, stigmas shrivel before or during the second opening. Easterly breezes bring humid air from the ocean, and drying of the stigma generally does not occur during the second opening. There are, however, some cultivars that appear to be more sensitive to the desiccating environment than others; for example, 'Topa Topa' stage II flower stigmas readily shrivel while nearby 'Simmonds' stigmas remain white throughout the second opening. Peterson (1955a) also found a similar relationship between relative humidity and longevity of the stigmatic surface, and Bringhurst (1952) reported that the stigmas became shrivelled in stage I in dry, windy conditions. This relationship needs to be investigated more fully.

One major drawback to much of the research on pollination during avocado flowering has been that pollination has not been examined directly. Many workers have used fruitfulness as the criterion to determine whether pollination took place. However, numerous factors that influence the fruit-set process are independent of pollination; this is evidenced by the extremely low and undependable set of fruit as a result of hand pollinations (Lammerts 1943,1945). Schroeder (1954) found that up to 51% of bagged 'Fuerte' flowers were pollinated during the functional male stage. These flowers must have been selfed within the same flowers since flying insects were unavailable. Interestingly, he also found that 79% of the flowers had been pollinated in an area where 'Fuerte' produces little to no crop and that 31% of the pollen grains had germinated on the stigmas. The ratio of self- vs. cross-pollinated flowers could not be determined. Sedgley (1977a) reported that avocado plants placed in controlled conditions of a growth chamber produced flowers that were apparently selfed on their own flowers, with an average rate of five pollen grains per stigma.

IV. CONCLUSION

The events encompassing the induction, flowering, pollination, fertilization, and postfertilization processes in avocado are extremely complex. Much of the published information

is anecdotal, with conclusions sometimes based on results obtained under poorly controlled conditions. There are many opportunities to increase our knowledge of the physiology of floral induction as well as the intricate relationships between temperature, humidity, and the various aspects of floral behavior. The further use of controlled environments will be necessary to understand fully the mechanisms involved in avocado flowering.

The avocado has evolved a unique and elegant mechanism to promote outcrossing. It is being cultivated in environments that are vastly different from its original evolutionary habitats, not only in terms of temperature and relative humidity but also in available pollinators. The evolutionary pressures that were conducive to development of the avocado's mechanism of dianthesis and synchronous dichogamy are unknown, as are the pollinating insects that must have played an important role in that evolution. The domestic honeybee could not have been involved, since it was not introduced to the New World until the arrival of European colonists (Grout 1949). Furthermore, the habits of honeybees are simply not in concert with those of avocado. Clearly, however, the honeybee is an effective pollinator of avocado in many areas of the world, but other insects may be as important in pollen transfer in some areas.

As a result of synchronous dichogamy, cross-pollination clearly has the best opportunity for fertilizing the ovum. Yet, it is plausible that if cross-pollination does not occur, the avocado has evolved, a fail-safe system of self-pollination dependent upon environmental conditions. One unifying factor that could make this possible is the receptivity of the pistil through the second flower opening of some cultivars. That relative humidity may play an important role in the receptivity of the pistil could explain the conflicting results and conclusions prevalent in the literature.

LITERATURE CITED

- ABRAMS, R., W. PENNOCK, G.C. JACKSON, and A. PEREZ LOPEZ. 1957. Flower behavior of different avocado varieties grown in Puerto Rico. *J. Agric. Univ. Puerto Rico* 41:236-241.
- ALEXANDER, D. MCE. 1975. Flowering times of avocados in the Murray Valley. *J. Austral. Inst. Agric. Sci.* 41:264-267.
- ARGAMAN, E. 1983. Effect of temperature and pollen source on fertilization, fruit set and abscission in avocado (*Persea americana* Mill.). M.S. Thesis, Hebrew University of Jerusalem.
- BESTER, A. 1975. Flowering types of avocado cultivars. *Inf. Bull. Citrus and Subtrop. Fruit Res. Inst.* 36:12-13.
- BERGH, B.O. 1966. Avocado tree arrangement and thinning in relation to cross pollination. *Calif. Avocado Soc. Yearb.* 50:52-61.
- BERGH, B.O. 1967. Reasons for low yields of avocados. *Calif. Avocado Soc. Yearb.* 51:161-172.
- BERGH, B.O. 1975a. Avocado research in Israel. *Calif. Avocado Soc. Yearb.* 58:103-126.
- BERGH, B.O. 1975b. Avocados. In: J. Janick and J.N. Moore (eds.). *Advances in fruit breeding*, pp. 541-567. Purdue Univ. Press, Lafayette, IN.
- BERGH, B.O. 1976. Avocado breeding and selection. In: J. W. Sauls, R.L. Phillips, and L.K. Jackson (eds.), *The avocado*, pp. 24-33, *Proc. 1st Int. Trop. Fruit Course*. Univ. of Florida Coop. Ext. Serv., Gainesville, FL.
- BERGH, B.O., and M.J. GARBER. 1964. Avocado yields increased by interplanting different varieties. *Calif. Avocado Soc. Yearb.* 48:78-85.
- BERGH, B.O., and C.D. GUSTAFSON. 1958. Fuerte fruit set as influenced by crosspollination. *Calif. Avocado Soc. Yearb.* 42:64-66.

- BERGH, B.O., and C.D. GUSTAFSON. 1974. Self-pollinated Hass seedlings. *Calif. Avocado Soc. Yearb.* 58:118-126.
- BERGH, B.O., M.J. GARBER, and C.D. GUSTAFSON. 1966. The effect of adjacent trees of other avocado varieties on 'Fuerte' fruit set. *Proc. Am. Soc. Hort. Sci.* 89:167-174.
- BLUMENFELD, A., and S. GAZIT. 1974. Development of seeded and seedless avocado fruits. *J. Am. Soc. Hort. Sci.* 99:442-448.
- BRINGHURST, R.S. 1951. Influence of glasshouse conditions on flower behavior of Hass and Anaheim avocados. *Calif. Avocado Soc. Yearb.* 35:164-168.
- BRINGHURST, R.S. 1952. Sexual reproduction in the avocado. *Calif. Avocado Soc. Year.* 36:210-214.
- BUTTROSE, M.S., and D.M. ALEXANDER. 1978. Promotion of floral initiation in 'Fuerte' avocado by low temperature and short daylength. *Sci. Hort.* 8:213-219.
- CAMPBELL, C.W., and S.E. MALO. 1976. A survey of avocado cultivars. In: J.W. Sauls, R.L. Phillips, and L.K. Jackson (eds.), *The avocado*, pp. 20-24. *Proc. 1st Sub. Trop. Fruit Short Course*. Univ. Florida Coop. Ext. Serv.
- CINTRON, R.H. 1947. Fruit setting and fruit development of avocados in Texas. *Calif. Avocado Soc. Yearb.* 31:62-66.
- CLARK, O. I. 1923. Avocado pollination and bees. *Calif. Avocado Assoc. Yearb.* 7:57-62.
- CLARK, O. I. 1924. Avocado pollination tests. *Calif. Avocado Assoc. Yearb.* 8:16-22.
- CLARK, O. I. and A. CLARK. 1926. Results of pollination and other experiments on avocados at the orchards of the Point Loma Homestead. *Calif. Avocado Assoc. Yearb.* 10:85-94.
- COIT, J.E. 1921. The effect of girdling the avocado. *Calif. Avocado Assoc. Yearb.* 5:69-70.
- DAVENPORT, T.L. 1982. Avocado growth and development. *Proc. Fla. State Hort. Soc.* 95:92-96.
- DAVENPORT, T.L. 1983. Ethylene production in avocado flowers and fruit: its role in senescence and abscission. *Proc. 10th Annu. Meeting. Plant Growth Reg. Soc. Am.*, pp. 213-215. East Lansing, MI.
- DAVENPORT, T.L. 1985. Avocado flowering, pollination and fruit set. *HortScience* 20:589.
- DAVIS, S.J. 1939. Avocado growing in the Redland district. *Proc. Fla. State Hort. Soc.* 52:71-73.
- DEGANI, C., and S. GAZIT. 1984. Selfed and crossed proportions of avocado progenies produced by caged pairs of complementary cultivars. *HortScience* 19:258-260.
- DEMEILLON, and W.W. WIRTH. 1979. Subsaharan Ceratopogonidac (Diptera) II. Ceratopogonidae taken on flowers of avocado, *Persea americana*, in South Africa. *J. Entomol. Soc. S. Afr.* 42:187-189.
- EISIKOWITCH, D., and H. MELAMUD. 1982. A preliminary report on the role of honey bees in avocado pollination. *Alon Hanotea* 37:19-29.
- FREE, J.B., and I.H. WILLIAMS. 1976. Insect pollination of *Anacardium occidentale* L., *Mangifera indica* L., *Blighia sapida* Koenig and *Persea americana* Mill. *Trop. Agric.* 53:125-139.
- FURON, V. 1963. La pollinisation de l'avocatier en Cote d'Ivoire. *Fruits* 18:197-199.
- GAN, Y.Y., Z. SULTAN, and I. ABDOL. 1981. Genetic variation in the grafted vegetatively propagated mango (*Mangifera indica*). *Pertanika* 4:53-62.
- GAZIT, S. 1976. Pollination and fruit set of avocado. In: J.W. Sauls, R.L. Phillips, and L.K. Jackson (eds.), *The avocado*, pp. 88-92. *Proc. 1st Int. Trop. Fruit Short Course*. Univ. of Florida Coop. Ext. Serv., Gainesville, FL.
- GOGOLASHVILI, L.A. 1980. Biology of flowering and fruiting in avocado in Abkhazia. *Tr. Prikl. Bot., Genet. Sel.* 68:53-59.
- GROUT, R.A. (ed.). 1949. *The hive and honey bee*. Dadant & Sons. Hamilton, IL.

- GUSTAFSON, C.O. 1973. The avocado industry in San Diego county. CP226 Univ. of Calif. Coop. Ext. Serv., San Diego.
- GUSTAFSON, C.O. 1975. History of the avocado. Univ. of Calif. Coop. Ext. Serv., San Diego.
- GUSTAFSON, C.O. 1976. World avocado production-1976. In: J.W. Sauls, R.L. Phillips and L.K. Jackson (eds.). The avocado, pp. 1-9. *Proc. 1st Int. Trop. Fruit Short Course*. Univ. of Florida, Coop. Ext. Serv., Gainesville, FL.
- GUSTAFSON, C.O., and B.O. BERGH. 1966. History and review of studies on cross pollination of avocados. *Calif. Avocado Soc. Yearb.* 50:39-49.
- HODGSON, R.W. 1930a. Cross-pollination. *Calif. Avocado Assoc. Yearb.* 14:30-31.
- HODGSON, R.W. 1930b. The California avocado industry. *Calif. Agric. Ext. Serv. Cir.* 43 (Rev. 1947).
- HODGSON, R.W. 1935. Temperature in relation to alternate bearing behavior of the Fuerte avocado variety. *Proc. Am. Soc. Hort. Sci.* 33:55-60.
- HODGSON, R.W., and S.H. CAMERON. 1935. Studies on the bearing behavior of the Fuerte avocado variety. *Calif. Avocado Assoc. Yearb.* 19:156-165.
- HODGSON, R.W., and S.H. CAMERON. 1937. Girdling to induce bearing in the Fuerte avocado. *Calif. Avocado Assoc. Yearb.* 21:149-153.
- HOMSKY, S. 1974. Autumn girdling in avocado Fuerte. *Hassadeh* 55:56.
- IBRAHIM, I.M., and S.E. BAHLOOL. 1979. The effect of girdling on flowering, fruiting and vegetative growth of avocado trees. *Agric. Res. Rev., Hort.* 57:55-56.
- ITO, P.J., and D.K. FUJIYAMA. 1980. Classification of Hawaiian avocado cultivars according to flower types. *HortScience* 15:515-516.
- KADMAN, A., E. TOMER, and M. GOTTREICH. 1974. Some abnormalities observed in avocado fruits and flowers. *Calif. Avocado Soc. Yearb.* 57:115.
- KNIGHT, R.J. 1971. Comportamiento de la floración (clasificación A y B) de cultivares de Aguacate. *Proc. Trop. Reg. Am. Soc. Hort. Sci.* 15:14-18.
- KNIGHT, R., JR. 1980. Origin and world importance of tropical and subtropical fruit crops. In: S. Nagy and P.E. Shaw (eds.). *Tropical and subtropical fruits*. AVI Publ. Co., Westport, CT.
- KOTZE, J.M. 1982. Phases of seasonal growth of the avocado tree. *Citrus Subtrop. Fruit J.* 586:9-11.
- LAHAV, E., and D. ZAMET. 1976. Flower, fruitlet and fruit abscission in avocado trees. *Spec. Publ. Agric. Res. Organ Volcani. Cent. Div. Sci. Publ.* 65:57-63.
- LAHAV, E., B. GEFEN, and D. ZAMET. 1971. The effect of girdling on the productivity of the avocado. *J. Am. Soc. Hort. Sci.* 96:396-398.
- LAMMERTS, W.E. 1943. Progress report on avocado breeding. *Calif. Avocado Soc. Yearb.* 27:36-41.
- LAMMERTS, W.E. 1945. The avocado breeding project. *Calif. Avocado Soc. Yearb.* 29:74-80.
- LECOMPTE, J. 1961. Observations sur la pollinisation de l'avocatier aux Antilles francaises. *Fruits* 16:411-414.
- LESLEY, J.W., and R.S. BRINGHURST. 1951. Environmental conditions affecting pollination of avocados. *Calif Avocado Soc. Yearb.* 35:169-173.
- LEWIS, T. 1973. Thrips: their biology, ecology and economic importance. Academic Press, New York.
- LICHOU, J., and R. VOGEL. 1972. Floral biology of avocado in Corsica. *Fruits* 27:705-717.
- MALO, S.E. 1971. Girdling increases avocado yields in South Florida. *Proc. Am. Soc. Hort. Sci., Trop. Reg.* 15:19-25.
- MCGREGOR, S.E. 1976. Insect pollination of cultivation crop plants. *Agric. Handb.* 496 U.S. Dept. Agric.

- MURNECK, A.E. 1941. Relative carbohydrates and nitrogen concentration in new tissue produced on ringed branches. *Proc. Am. Soc. Hort. Sci.* 38:133-136.
- NIRODY, B.S. 1922. Investigations in avocado breeding. *Calif. Avocado Assoc. Yearb.* 6:65-78.
- NOAA. 1976. Climate of Homestead, Florida. NOAA Bull. Climatology of the United States 20. National Climatic Center, National Oceanic and Atmospheric Admin., Asheville, NC.
- PAPADEMETRIOU, M.K. 1975a. A study of the viability of avocado pollen under natural conditions. *Calif. Avocado Soc. Yearb.* 58:74-76.
- PAPADEMETRIOU, M.K. 1975b. Pollen tube growth in avocados (*Persea americana* Mill). *Calif. Avocado Soc. Yearb.* 58:99-102.
- PAPADEMETRIOU, M.K. 1976. Some aspects of the flower behavior, pollination and fruit set of avocado (*Persea americana* Mill.) in Trinidad. *Calif. Avocado Soc. Yearb.* 59:106-152.
- PETERSON, P.A. 1955a. Avocado flower pollination and fruit set. *Calif. Avocado Soc. Yearb.* 40:163-169.
- PETERSON, P.A. 1955b. Dual cycle of avocado flowers. *Calif. Agric.* 9:6-7,13.
- PETERSON, P.A. 1956. Flowering types in the avocado with relation to fruit production. *Calif. Avocado Soc. Yearb.* 40:174-179.
- POPENOE, W. 1924. Manual of tropical and subtropical fruits. MacMillan, New York.
- PURSEGLOVE, J.W. 1968. Tropical crops: Dicotyledons 1. Wiley, New York.
- REECE, P.C. 1939. The floral anatomy of the avocado. *Am. J. Bot.* 26:429-433.
- REECE, P.C. 1942. Differentiation of avocado blossom buds in Florida. *Bot. Gaz.* 104:323-328.
- ROBINSON, T.R. 1931. Some aberrant forms of flower mechanism in the avocado. *Calif. Avocado Soc. Yearb.* 15:107-111.
- ROBINSON, T.R. 1933. Pollination and other factors influencing the production of avocados. *Proc. Fla. State Hort. Soc.* 46:109-114.
- ROBINSON, T.R., and E.M. SAVAGE. 1926. Pollination of the avocado. Circ. 387 U.S. Dept. Agric.
- RUEHLE, G.D. 1958. The Florida avocado industry. Fla. Agric. Exp. Stn., Bull. 602.
- RYERSON, K., M.E. JAFFA, and H. GOSS. 1924. Avocado culture in California. Calif. Agric. Exp. Stn. Bull. 365.
- SAHAR, N., and P. SPIEGEL-ROY. 1984. *In vitro* germination of avocado pollen. *HortScience* 19:886-888.
- SALOMON, E. 1984. Phenology of flowering in citrus and avocado and its significance. *Acta Hort.* 149:3.
- SAMPIO, V.R. 1974. The flowering period of avocados. *Rev. Agric.* 49:121-123.
- SAULS, J.W., R.L. PHILLIPS, and L.K. JACKSON (eds.). 1976. The avocado. *Proc. 1st Int. Trop. Fruit Short Course*. Univ. of Florida Coop. Ext. Serv., Gainesville, FL.
- SHOLEFIELD, P.B. 1982. A scanning electron microscope study of flowers of avocado, litchi, macadamia and mango. *Sci. Hort.* 16:263-272.
- SHOLEFIELD, P.B., M. SEDGLEY, and D.M. ALEXANDER. 1985. Carbohydrate cycling in relation to shoot growth, floral initiation and development and yield in the avocado. *Sci. Hort.* 25:99-110.
- SCHROEDER, C.A. 1940. Floral abnormality in the avocado. *Calif. Avocado Soc. Yearb.* 24:36-39.
- SCHROEDER, C.A. 1942. Pollen germination in the avocado. *Proc. Am. Soc. Hort. Sci.* 41:181-182.
- SCHROEDER, C.A. 1944a. The avocado inflorescence. *Calif. Avocado Soc. Yearb.* 28:39-40.
- SCHROEDER, C.A. 1944b. Multiple embryos in the avocado. *J. Hered.* 35:209-210.

- SCHROEDER, C.A. 1951. Flower bud development in the avocado. *Calif. Avocado Soc. Yearb.* 35:159-163.
- SCHROEDER, C.A. 1952. Floral development, sporogenesis, and embryology in the avocado, *Persea americana*. *Bot. Gaz.* 113:270-278.
- SCHROEDER, C.A. 1954. Some aspects of pollination in the avocado. *Calif. Avocado Soc. Yearb.* 38:159-162.
- SCHROEDER, C.A. 1955. Pollen production in avocado. *Calif. Avocado Soc. Yearb.* 39:184-186.
- SCHROEDER, C.A. 1958. The origin, spread and improvement of the avocado, sapodilla and papaya. *Indian J. Hort.* 15:116-128.
- SEDGLEY, M. 1976. Control by the embryo sac over pollen tube growth in the style of the avocado (*Persea americana* Mill.). *New Phytol.* 77:149-152.
- SEDGLEY, M. 1977a. Reduced pollen tube growth and the presence of callose in the pistil of the male floral stage of the avocado. *Sci. Hort.* 7:27-36.
- SEDGLEY, M. 1977b. The effect of temperature on floral behavior, pollen tube growth and fruit set in the avocado. *J. Hort. Sci.* 52:135-141.
- SEDGLEY, M. 1979a. Inter-varietal pollen tube growth and ovule penetration in the avocado. *Euphytica* 28:25-35.
- SEDGLEY, M. 1979b. Light microscope study of pollen tube growth, fertilization and early embryo and endosperm development in the avocado varieties Fuerte and Hass. *Ann. Bot.* 44:353-359.
- SEDGLEY, M. 1979c. Structural changes in the pollinated and unpollinated avocado stigma and style. *J. Cell. Sci.* 38:49-60.
- SEDGLEY, M. 1980. Anatomical investigation of abscised avocado flowers and fruitlets. *Ann. Bot.* 46:771-777.
- SEDGLEY, M. 1981. Storage of avocado pollen. *Euphytica* 30:595-599.
- SEDGLEY, M. 1985. Some effects of day length and flower manipulation on the floral cycle of two cultivars of avocado (*Persea americana* Mill., Lauraceae), a species showing protogynous dichogamy. *J. Exp. Bot.* 36:823-832.
- SEDGLEY, M., and D.M. ALEXANDER. 1983. Avocado breeding research in Australia. *Calif. Avocado Soc. Yearb.* 67:129-135.
- SEDGLEY, M., and D.M. ANNELLS. 1981. Flowering and fruit-set response to temperature in the avocado cultivar 'Hass'. *Scientia Hort.* 14:27-33.
- SEDGLEY, M., and M.S. BUTTROSE. 1978. Structure of the stigma and style of the avocado. *Austral. J. Bot.* 26:663-682.
- SEDGLEY, M., and W.J.R. GRANT. 1983. Effect of low temperatures during flowering on floral cycle and pollen tube growth in nine avocado cultivars. *Sci. Hort.* 18:207-213.
- SEDGLEY, M., P.B. SCHOLEFIELD, and D. MCE. ALEXANDER. 1985. Inhibition of flowering of Mexican- and Guatemalan-type avocados under tropical conditions. *Sci. Hort.* 25:21-30.
- SEIGLIE, R.H. 1976. Study of flowering in avocado (*Persea americana*, Mill). *Centro Agricola* 3:71-83.
- STOUT, A.B. 1923. A study in cross-pollination of avocados in southern California. *Calif. Avocado Assoc. Yearb.* 7:29-45.
- STOUT, A.B. 1924. The flower mechanism of avocados with reference to pollination and the production of fruit. *J. New York Bot. Gard.* 25:1-9.
- STOUT, A.B. 1927. The flower behavior of avocados. *J. New York Bot. Gard.* 7:145-203.
- STOUT, A.B. 1933. The pollination of avocados. *Fla. Agric. Exp. Stn. Bull.* 257.

- STOUT, A.B., and E.M. SAVAGE. 1925. The flower behavior of avocados with special reference to interplanting. *Proc. Fla. State Hort. Soc.* 38:80-91.
- TICHO, R.J. 1970. Girdling, a means to increase avocado fruit production. *Calif. Avocado Soc. Yearb.* 54:90-94.
- TOERIEN, J.C. 1979. An investigation into the successful grafting of avocados after the commencement of flower bud differentiation. *S. Afr. Avocado Gro. Assoc. Res. Rep.* 3:61-62.
- TOMER, E. 1976. The fertilization process in the avocado flower. *Spec. Publ. Israel Agric. Res. Org.* 65:47-48.
- TOMER, E., and M. GOTTREICH. 1975. Observations on the fertilization process in avocado with fluorescent light. *Euphytica* 24:531-535.
- TOMER, E., and M. GOTTREICH. 1978. Abnormalities in avocado (*Persea americana* Mill.) ovule development. *Bot. Gaz.* 139:81-86.
- TOMER, E., M. GOTTREICH, and S. GAZIT. 1976. Defective ovules in avocado cultivars. *J. Am. Soc. Hort. Sci.* 101:620-623.
- TOMLINSON, P.B. 1980. The biology of trees native to tropical Florida. Harvard Univ. Printing Office, Allston, MA.
- TORRES, A.M., and B.O. BERGH. 1978a. Isozymes as indicators of outcrossing among 'Pinkerton' seedlings. *Calif. Avocado Soc. Yearb.* 62:103-110.
- TORRES, A.M., and B.O. BERGH. 1978b. Isozymes of 'Duke' and its derivatives. *Calif. Avocado Soc. Yearb.* 62:111--117.
- TORRES, A.M., and B.O. BERGH. 1980. Fruit and leaf isozymes as genetic markers in avocado. *J. Am. Soc. Hort. Sci.* 105:614-619.
- TORRES, A.M., U. DIEDENHOFEN, B.O. BERGH, and R.J. KNIGHT. 1978. Enzyme polymorphisms as genetic markers in the avocado. *Am. J. Bot.* 65:134-139.
- ULMAN, H., and A. BEN-YAACOV. 1966. Increasing the yields of avocado trees by girdling. *Alon Hanotea* 20:208-209.
- VALMAYOR, R. V. 1967. Cellular development of the avocado from blossom to maturity. *Philip. Agric.* 50:907-976.
- VENNING, F.O., and F.B. LINCOLN. 1958. Developmental morphology of the vegetative axis of avocado (*Persea americana* L.) and its significance to spacing, pruning practices, and yields of the grove. *Proc. Fla. State Hort. Soc.* 71:350-356.
- WILLIAMS, L.O. 1976. The botany of the avocado and its relatives. In: J.W. Sauls, R. L. Phillips, and L.K. Jackson (eds.), *The avocado*, pp. 9-15. *Proc. 1st Int. Trop. Fruit Short Course*. Univ. of Florida Coop. Ext. Serv., Gainesville, FL.