

AVOCADO BREEDING AND SELECTION

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So far, successful avocado breeding has been primitive (2, 4). The leading cultivars around the world originated as chance seedlings-not even the female parent is known. This seems likely to change in the years ahead since procedures involving the known parentage of both sex cells are now available and are considerably more efficient. The use of such procedures is likely to markedly increase the chances for obtaining superior new cultivars by breeding.

The Flower and Its Behavior

The avocado flower is rather typical, but it functions in a peculiar manner. Intelligent breeding requires a clear knowledge of the unusual functioning, which can only be understood in terms of the structure (Fig. 1) (2, 3, 4).

Flower Structure

The perianth includes both sepals and petals. This grouping is especially appropriate in the case of the avocado, since its sepals (often green in other plants) and petals (often brightly colored) are almost identical. There are 3 of each, alternating, about 5 mm long, pale or greenish-yellow.

The stamens are 9 in number, arranged in an outer circle of 6 and an inner circle of 3. The inner 3 have a basal pair of nectar-secreting "nectaries" and alternate with 3 nectar-secreting "staminodes". Each stamen has 4 pollen sacs which release the mature pollen through valves hinged at the top. The pistil is in the center of the flower. It has an enlarged tip (stigma) on which the pollen germinates, then grows down through the long, slender style to reach and fertilize the egg inside the enlarged base (ovary). The fertilized ovary grows into the distinctive, delicately-flavored fruit prized around the world as the avocado.

The flowers are grouped in compound inflorescences of a few to several hundred flowers each. Unlike some plants, the avocado cannot possibly produce a fruit from each flower. In fact, if as few as 1% of the flowers mature fruit, the crop may still be too heavy for the tree.

Flower Function

Each normal avocado flower has both male and female organs. Most such plant species readily self-pollinate, *i.e.*, pollen from a given flower can fertilize the egg of that flower. However, the avocado flower performs in such a way that self-pollination is highly unlikely within a given flower and is difficult within a given tree or even a given cultivar. This is because each cultivar is functionally male one part of the day and functionally female another part of the day.

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Female flower. The first time an avocado flower opens, the pistil is alone in the center, with the stamens and other flower parts close together at an angle of 45° or more away from the pistil (Fig. 1). The stigma is then receptive to pollen so that the egg can be fertilized. The flower is female in function but it is not functionally male since the stamen valves remain tightly shut and no pollen is or can be shed. The flower remains open in this female stage for perhaps a couple of hours, then closes for the rest of the day and that night.

Male flower. The flower opens for the second and last time on the next day, but it is then functionally male, as the stamen valves open and pollen is released (Fig. 1). The stigma is commonly discolored or withered and is no longer receptive, so that the flower can no longer function as female. The flower remains open in this male stage for several hours, then closes again, permanently.

A and B flower types. Nearly all avocado cultivars (and seedlings) fall clearly into 1 of 2 contrasted categories conventionally designated A and B (16). A-type cultivars have their first or female opening in the morning, perhaps about 9 AM to noon. The second or male opening is the afternoon of the following day, perhaps noon to 6 PM. So, for a particular flower, the total time span from first opening to final closing is about 34 hours. B-type cultivars first open in the afternoon, perhaps 1 to 4 PM. The second opening is the following morning, perhaps 8 AM to 1 PM, so the total time span is about 24 hours.

Daily synchronization. 'Hass' is an example of an A flower type, 'Fuerte' of a B. There may be a thousand 'Hass' trees, with perhaps a million flowers opening (first, female stage) each morning in the blooming season in a given climatic area. All of them will open at about the same time and close at about the same time—like a million reasonably accurate clocks. Similarly, each afternoon perhaps a million flowers will have their second or male opening, and will do so again about synchronously. Hence, opportunity for self-pollination will be very limited (but see the article by Gazit on pollination, p. 88). A thousand adjoining 'Fuerte' trees would behave the same way, but with the times of the male and female stages reversed.

Consequences of Avocado Flower Behavior

Cross-pollination is the inevitable result of the flower functioning described above. In our examples, 'Fuerte' is functionally male, *i.e.*, is shedding pollen over the entire period that 'Hass' is functionally female, *i.e.*, its pistils are receptive and must be pollinated if fruit is to set. The converse is true of 'Fuerte' set. Thus, A and B trees provide complementary cross-pollination.

Genetic variability within the individual is the inevitable result of cross-pollination. This means that any individual seedling or cultivar has different hereditary options at many different gene locations and can be expected to produce an almost unlimited assortment of sex cells for the next generation. Hence, avocados are more like humans than they are like tomatoes or other plants in which pure breeding lines produce any number of seedlings genetically identical to the parent. This means that in avocado breeding, we do not have to hybridize cultivars in order to obtain segregating variability from which to select—each cultivar has immense genetic variability.

Self-pollination. Our analysis of flower functioning showed self-pollination to be difficult, but it is by no means impossible. Although self-pollination within a flower practically never occurs, pollination among flowers of a single cultivar occurs more readily. There is a little variability in time of flower opening or closing due to differences in location on tree (in terms of sun or wind exposure *etc.*), or other causes of differences in internal physiology. Adjoining trees of the same cultivar would be expected to have this variability accentuated, plus possible effects from rootstock differences. Finally, weather changes can affect the timing of some flowers more than others. It is usually possible to obtain ample breeding progenies from self-fertilization.

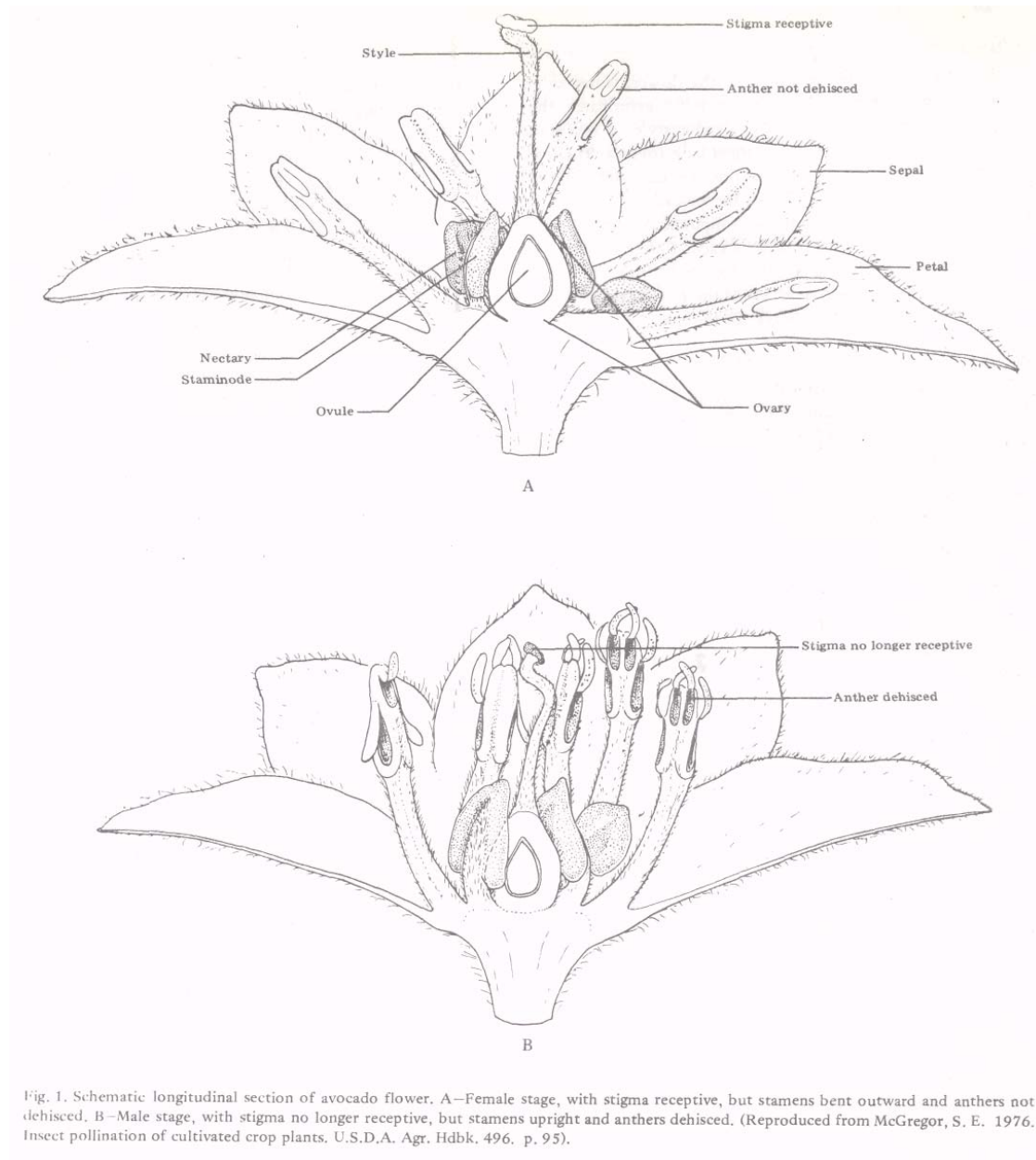


Fig. 1. Schematic longitudinal section of avocado flower. A—Female stage, with stigma receptive, but stamens bent outward and anthers not dehisced. B—Male stage, with stigma no longer receptive, but stamens upright and anthers dehisced. (Reproduced from McGregor, S. E. 1976. Insect pollination of cultivated crop plants. U.S.D.A. Agr. Hdbk. 496. p. 95).

Breeding Techniques

The technique to be used will depend on whether the breeder wishes to hybridize or self. Hybridization is the only way to obtain progeny with 2 or more desirable traits that are not present in an available breeding line. This is also true when one needs a trait intermediate between available superior lines, such as season of maturity or ecological adaptation. Indeed, the major cultivars being grown in Florida, Hawaii and some other areas with similar climates are first or later generations from hybridization of Guatemalan and West Indian races. The major cultivars being grown in California, Israel, South Africa, Australia and similar less tropical climates are hybrids of the Guatemalan and Mexican races. These latter 2 races are also the hybrid source of promising new cold-hardy selections for central and northern Florida (13).

Hybridization has 2 major disadvantages when compared with selfing: 1) obtaining positive hybrids is far more difficult and expensive and 2) the breeding worth of each parent tends to be obscured by the contribution from the other parent. Nevertheless, a technique is described later for obtaining at low cost a considerable proportion of hybrid seedlings for situations where hybridization is indicated.

The avocado breeding program of the University of California at Riverside is using both approaches. Selfing has proven to be generally much more efficient, as seedlings can be obtained from isolated or buffered trees at a cost no higher than that of the fruits.

Breeding worth has proven to be only poorly correlated with commercial worth. For example, 'Fuerte' was used as the chief parent in extensive hybridizing during the early years of the California program. Not 1 commercial cultivar has resulted from all this work. Had the wrong lines been chosen as the other parent? Several hundred 'Fuerte' selfs quickly showed the true situation: they were a remarkably poor lot (7), indicating that 'Fuerte' is a highly undesirable breeding parent for California and similar regions.

'Hass', on the other hand, has proven to be an exceptionally good parent (6). Its selfed seedlings have averaged as superior in terms of productivity and quality as the 'Fuerte' selfs were inferior on both counts. From about 400 trees of each, there were no 'Fuerte' selections and 18 'Hass' selections.

Further selfing of 'Hass' selections has further increased the proportion of seedlings worth selecting. More than a quarter of the seedlings in one line were actually considered to merit commercial testing by the third selfed generation—a remarkable 6-fold increase over the impressive first generation of 'Hass' selfs. Unfortunately, while larger fruit size and green color have been obtained, none of the selections so far has appeared to achieve the outstanding 'Hass' standards of flavor, long season and unblemished surface.

Hybridization by Hand

This approach may be prohibitively expensive in terms of human labor (2), since about 99% of the flowers will fail to mature fruit and there is currently no way to differentiate those that are going to make it. However, methods for increasing the

success proportion will be suggested in a later section. Avocado pollen is not collectable by the usual suction methods. Flowers in the male stage may be picked off and the pollen clumps daubed onto female-stage stigmas directly or a fingernail can be used to remove the pollen and transport it. Emasculation of the female flower is unnecessary (2).

In a greenhouse. A few dozen avocados have matured on such trees growing in large containers or directly in the soil. Tree care costs are greater, but conditions can be made much more conducive to fruit set. Since bloom is usually considerably earlier indoors, one can hybridize lines with discrete blooming periods by establishing the later-blooming parent under glass.

In sleeves. Sleeves made of plastic (usually) 1 x 0.5 m are useful to enclose a flowering branch. The material should let in as much light as possible. Sleeves can also be used to protect the male parent's pollen from bees.

In field cages. Instead of enclosing a flowering branch, field cages enclose the whole tree. Plastic screening on wooden frames of convenient size are bolted or otherwise fastened together to form the walls and a loose screen is put over the top and tied down. A zippered or hinged entrance-way should be provided.

Hybridization by Bees (or Other Pollinating Insects)

Seedlings produced here will probably be both selfs and hybrids in a varying and unknown mix. The majority should be hybrids with the preferred parental choice of 1 A and 1 B flower type. Also, the very different parental types that are usually present when hybridization is desirable should make it possible to segregate selfs from hybrids—at least in the fruiting stage. Hybrids produced by insects cost a tiny fraction of those produced by hand. The honeybee accounts for the majority of avocados set in California but other insects apparently predominate in more tropical areas.

In field cages. These can be made longer in order to include 2 adjoining trees that one wishes to hybridize or there may be only 1 tree with branches of the second parent worked into it. A hive of bees is placed inside the cage with a source of water after both parents have started to bloom.

In isolation. This approach is not at all expensive. Indeed, it can be as simple as harvesting the fruits from adjoining branches of 2 desired parents in the field. They may be from contiguous trees, or grafts of the complementary parent may be worked into established trees in a solid grove. No third parent should be closer than perhaps 100 m, although considerably closer distances appear safe under California conditions.

Selfing Techniques by Hand

Situations where selfs would be worth the cost in human labor must be exceedingly rare—no such situation has arisen in the University of California program. They could be obtained if field selfs were impractical and if selfs were that valuable or labor that cheap. One would want to increase the likelihood of male-female overlap by treating part of the tree or a second tree differently, such as by shading or by reflected light or heat. In the absence of bees, pollen would be more likely to hang on the valves into the next female-flower opening. The flower could be

protected in greenhouse, sleeve or cage, as in the case of hybridizing.

Selfing Techniques by Insects

In a cage. A tree is caged and a hive of bees placed inside, as described for hybridizing. Fruit set has been variable to heavy. Evidently the strict sex alternation has had appreciable exceptions under these conditions, or possibly the closely contained bees have forced open flowers that were near enough to maturity to function sexually.

Isolated trees. This is perhaps the most desirable method for most avocado breeding because of its ready availability and low cost. The source can be lone avocado trees or trees that are isolated from other genetic lines by buffer trees of the line to be selfed. Out-crossing should be practically nil with 100 m or more isolating distance.

Maximizing the Breeding Set

General Procedures to Increase Seed Yield

There are various means to increase the number of breeding fruits obtained from selfing and hybridizing.

Heavy-setting cultivars should be selected as the seed parent in hybridizing. Desirable traits may thus be efficiently introduced into highly productive lines by using their light-bearing carriers as the male parent. In selfing, it may be necessary to use lines with less fruit set in hope that better setters will segregate out with other virtues intact or that more genetically uniform lines for use as male parents as described above will be obtained.

The productive ("on") year can make a light bearer set well and a heavy bearer set very heavily. Nearly all avocado lines are subject to alternate bearing. If the natural pattern of alternation does not fit in with the breeder's convenience, he can usually create an upcoming "on" year by removing all set fruits by midsummer or earlier.

An optimum location in terms of climate and other factors may make the difference between a breeding program with plenty of material from which to select and one that suffers from the fatal flaw of insufficient controlled-parentage seedlings. Breeding avocados is indeed a long-range program. It may be best to delay its start if to do so makes possible a location that ensures an adequate number of progeny.

Optimum care is important to permit the realization of the above potentialities. The breeder should understand and apply sound principles and practices of horticulture, soil science, irrigation, fertilization, wind and frost protection, disease and insect control or have his trees looked after by someone else. Fruit set is poor when trees are in stress situations.

Maximum light availability is important to maximize avocado fruit set. Southern exposure is very helpful in more-northerly avocado regions and the reverse is true south of the equator. The breeder can often select his particular breeding trees with this in mind. Adjoining avocado or other less valuable trees can be cut back

as needed. The materials used for sleeves and cages should transmit as much light as is consistent with safety from pollinating insects. Increased cooling capacity in the greenhouse may be a good investment to permit less roof shading.

Girdling often increases fruit set, and it increases fruit number more than total weight (14). Hence, it offers more of an advantage to the breeder than to the commercial grower. Girdling may be an excellent investment, especially with light-setting lines or with a major cost undertaking such as in hand hybridization.

Specific Means to Increase Seed Yield in Hybridization

Different large-scale hand-hybridizing programs have had success rates (in terms of pollinated flowers that mature fruit) ranging from less than 0.04% to about 5% (3). The later remarkably high order of magnitude is made-possible in part by the general procedures described above. Further increases in percentage take are attributable to techniques involving the hybridization process itself.

Optimum weather is worth waiting for. Hot and dry conditions can cause desiccation of both the pollen and the pistil. Cold weather may inhibit proper sex cell functioning. A climate (like California's) that is generally cooler than optimum during the blooming period delays most fruit set until the latter part of the blooming season so the breeder should concentrate his efforts accordingly.

Pollinate few flowers per cluster. Each cluster can mature only a very small proportion of its flowers. Thus, excess hybridization is not only time-wasting, but can actually lead to reduced set via excessive fruit drop resulting from competition among the developing fruits. However, one should hybridize more than the number of flowers estimated to be the maximum that the cluster can mature, as defective ovules (18) and other problems will reduce the theoretical set. It has been suggested that the excess flowers should be removed a few days prior to hybridizing to increase chances of set by reducing flower competition. Statistical advantage has, to my knowledge, never been shown and it would seem uncertain that the limited gain would be worth the labor involved.

Pollinate at the first opening only. Occasional stigmas look fresh and receptive at the second (male) flower opening, but no second-day pollination has proved successful, to my knowledge—the stigma may be less receptive than it looks, or the internal egg apparatus may be degenerating.

Never pollinate an abnormal pistil. A considerable proportion of the female organs are deformed or otherwise aberrant to varying degrees. Some stigmas are darkened or withered or otherwise unhealthy looking, even at the first flower opening. The odds against successful hybridization are high enough for the best of flowers without wasting time on inferior ones.

Pollinate by mid-afternoon. This applies especially to a climate like that of California where the temperature, especially toward evening, is well below optimum for avocado flowers. Later pollination will cause temperature-induced slower pollen tube growth. Instead of reaching the egg in about 3 hours (Shmuel Gazit, personal communication), the sperm may not arrive until the egg has broken down. Other parts of either sex cell may degenerate in the meantime.

Breeding Objectives

Avocado breeding objectives (Table 1) vary somewhat on some points among the different producing regions and there is not full agreement on some points, even among the avocado people of a given region.

Table 1. Avocado breeding objectives.

Fruit quality	
Medium size	Thick ovate shape
Uniformity	Pulp
Skin	Proper softening
Medium thickness	Appetizing color
Readily peelable	Absence of fibers
Insect, disease resistance	Pleasing flavor
Free from blemishes	Long shelf life
Attractive color	Slow oxidation
Long tree storage	Chilling tolerance
Seed	High oil content
Small	High nutritional value
Tight in its cavity	
Shoot qualities	
Spreading habit	Tolerant of chlorosis
Easy to propagate	Tolerant of other stresses
Strong grower	Short fruit maturation period
Tolerant of pests and diseases	Precocious
Tolerant of wind	Regular bearing
Tolerant of cold	Wide adaptability
Tolerant of heat	Heavy bearer
Tolerant of salinity	
Rootstock qualities	
Conducive to high quality fruit	Easily grafted
Conducive to healthy, productive trees	Tolerant to <i>Phytophthora</i> and other organisms
Free from sun-blotch	Tolerant of salinity
Dwarfing or semi-dwarfing	Tolerant of chlorosis
Genetically uniform	Tolerant of drought
Hardy and vigorous	Tolerant of other adverse soil conditions
Easily propagated	

Fruit Qualities

Medium size. The markets in which most California avocados are sold prefer a size about 260 g. The optimum range might be 200-300 g (Jack Shepherd, private communication). Israel's European markets like a slightly larger fruit (5). The markets for fruits grown in more tropical regions where the West Indian race is

adapted have come to favor considerably larger fruit size. The breeder will need to give careful consideration to present and potential size preferences of the markets for which he is breeding.

Thick ovate shape. While a round shape may be more efficient, most avocado markets have come to associate the fruit with a somewhat pear or at least ovate form. New selections would have to have outstanding compensating traits to be able to disregard this established market preference.

Uniform size and shape. Variation in both traits among available cultivars may help to meet individual consumer preferences and identify for the consumer individual differences in flavor and other qualities. Variation within a given cultivar should be minimized. Moreover, fruit variation increases marketing problems. Seedlings and cultivars vary in the degree to which shape is altered by climatic differences and to which size is altered by fruit clustering differences.

Medium skin thickness. The skin should be thick enough to provide good protection under normal shipping and handling and to permit good peeling. Too thick a skin is undesirable (11) as it may make the detection of ripeness difficult and represents more wastage.

Skin peelability. The importance of peelability depends on how the fruit is eaten. Peeling doesn't matter when the flesh is scooped out of the skin—for example, eaten in the half-shell or smaller segments. However, avocados are eaten in various ways that involve pre-peeling (11). Thus, peeling reduces flesh attractiveness, as in salads, and always means more wastage.

Resistance to pests and diseases. These problems vary greatly in severity among the world avocado-growing regions, so the breeder's concerns will vary accordingly. A thicker fruit skin is desirable where fruit flies are a problem. I do not know of reported genetic differences in resistance to other fruit insects. Fungal diseases are of little concern in California but they are a serious consideration in more tropical areas (16) and potential breeding lines differ markedly in resistance.

Free from blemishes. Appearance may be much more important than flavor in determining consumer acceptance. The detrimental effect of surface flaws on retail purchases of avocados has been clearly shown (19). Tendency to skin russetting varies widely at different locations and in different breeding lines (17).

Attractive skin color. Color preferences depend largely on prior familiarity. The green color of 'Fuerte' has been the "right" avocado color in the extensive markets long dominated by that variety and its relative smoothness has made a rough skin less desirable in the same markets. These are 2 reasons that 'Hass' is less acceptable in the French market served by Israel (Shimon Zackai, private communication). In some markets, dark fruit is preferred. Apart from actual color, or skin blemishes, general attractiveness varies considerably and is significant (15).

Long tree storage. The longer edible fruits can be left on the tree without dropping or deteriorating, the more favorable is the marketing potential. The more quickly fruit mature, the shorter the tree storage period usually is. 'Fuerte' is an early-maturing cultivar with an exceptionally long storage period; unfortunately, for other reasons,

it is an inferior parent. 'Hass' passes its long storability on to a high proportion of its seedlings.

Small seed. Cost per edible portion is a frequent criticism of the avocado (11, 15). Seed proportion of total fruit weight varies markedly, but has high heritability in some lines (my unpublished data). Guatemalan race genes can add this desirable trait to the less favored backgrounds of the other 2 races.

Tight seed. The seed should completely fill its cavity. Moreover, the outer coat of loose seeds will often adhere to the flesh, thereby wasting edible flesh and the consumer's time.

Proper flesh softening. The entire flesh should soften simultaneously. In some regions, especially late in the season, 'Fuerte' and other partly Mexican-race cultivars have problems with this (Shmuel Gazit, private communication). A seedling with a marked degree of this weakness should probably be discarded.

Appetizing flesh color. Consumer preferences vary, but most people find less appeal in pulp that is nearly white, or mostly green, or has a dull appearance, or has discoloration under the skin.

Minimal fibers. Flesh is also less appetizing when it is traversed by fibers that are distinct because of a dark or reddish color. Indistinct fibers can be objectionable because of toughness when eaten.

Pleasing flavor. Nothing is more subjective than flavor. Prior familiarity influences present avocado preference, as with size, shape and color preferences. Still, most consumers agree that certain lines have too bland, or too strong, or otherwise too objectionable a taste.

Long shelf life. Once picked, the avocado is much more difficult to store or ship than such fruits as the apple. Some lines ripen (soften) in 3 or 4 days while others at a comparable stage of maturity may take 2 weeks to ripen. Ripe avocados deteriorate much more rapidly at room temperature. Some lines will remain edible only about a day, but others have the advantage of remaining in reasonably good condition for as long as 3 or 4 days.

Slow oxidation. This is another aspect of keeping quality. Cut surfaces of most avocados discolor rapidly— often within minutes. The Israeli cultivar 'Horshim' maintains a fresh appearance much longer. I have seedlings that do not discolor noticeably for several hours.

Chilling tolerance. A final aspect of keeping ability, this refers to proper softening, without flesh browning, following prolonged cold storage. 'Hass' is outstanding and 'Nabal' nearly as good; most West Indian lines and many lines derived from the other 2 races tolerate chilling poorly. This trait is especially important in the avocado because of its generally short shelf life.

High oil content. This is important in California because of a legal 8% minimum limit on fruit grown and marketed within the state. Oil content affects flavor and there are personal preferences as to whether or not high levels are pleasing.

High nutritional values. Higher oil content usually means higher calorie count—which

is desirable or undesirable depending on whether one's problem is obtaining adequate nourishment or avoiding overweight. Higher oil content is correlated with higher content of some vitamins. Other cultivar differences in vitamin content are independent of oil level (10).

Shoot (Tree) Qualities

Spreading tree habit. Tall trees are more difficult and more expensive to pick and to spray and are more susceptible to wind injury.

Easy to propagate. This is a composite of good bud formation, compatibility with the proper rootstocks and good graft-uniting ability. Propagation difficulty may make an otherwise good selection prohibitively expensive (8).

Strong grower. Grafts may take readily enough and yet the resulting trees grow too poorly for commercial success. Several cultivars derived from the Guatemalan race have had this serious drawback.

Tolerant of pests and diseases. These tolerances have so far been a minor consideration in California, but are important in some avocado-growing regions.

Tolerant of wind. Wind resistance is advanced by stronger wood and wider crotches in addition to a low, spreading habit as noted above. Strong crotches also minimize limb breakage from heavy fruit set.

Tolerant of cold. This virtue enables the avocado to be grown in colder areas and provides a safety factor against occasional freezes in less rigorous areas. There is some variation in cold tolerance within each horticultural race and wide variation among the races. West Indians may be injured even above freezing while Mexicans may tolerate negative 9°F or more of frost. Knight (12) has used artificial freezing tests in avocado breeding, as have other Florida researchers.

Tolerant of heat. In California, Mexican-race lines have appeared somewhat more hardy to heat than most Guatemalan lines. The West Indian race tolerates much heat where the humidity is consistently high.

Tolerant of salinity. The rootstock is more important than the scion in this regard, but the superiority of the West Indian race as stock has been observed also in racial comparisons of the lops (9).

Tolerant of chlorosis. The rootstock is the major determinant, but, differences in susceptibility have been observed among California cultivars.

Tolerant of other stresses. Differences have been noted among potential breeding lines in terms of resistance to nutritional deficiencies and to miscellaneous environmental stresses.

Short, fruit maturation period. It is desirable for all fruits on a tree to mature about simultaneously in order to permit the picking of all fruits at one time.

Precocious. This aspect of productiveness is important in order to permit an early return on investment. Moreover, earliness and heaviness of fruit yield are partly correlated.

Regular bearing. Perhaps all California cultivars tend to alternate in the amount of fruit set year after year, but they do so to markedly different degrees. Alternation on a regional basis (e.g., 'Fuerte') is especially serious because of the added marketing problems that result from sharply fluctuating crops. Alternation that is mainly on an individual tree basis (e.g., 'Hass') largely avoids this difficulty. Even so, alternate bearing has the weaknesses of added limb breakage, sunburned fruits and branches and overall set that is below the physiological maximum.

Wide adaptability. While factors like tolerance of climatic extremes and other stresses may limit some cultivars to certain areas, there is an additional factor of differing adaptability. Some lines perform and bear well in more diverse locations than do other lines. The more limited is adaptability, the larger the number of cultivars required and so the greater the marketing problems.

Heavy bearer. If this virtue is present, many other weaknesses may be tolerable. If it is absent, all other virtues may be futile.

Rootstock Qualities

Conducive to high-quality fruit. Differential rootstock effects are known in other fruits. Careful study may identify such in the avocado.

Conducive to healthy, productive trees. Major root-stock effects on scion performance have been identified by Ben-Ya'acov in Israel and complex rootstock-scion interactions also exist (1). Cultivars in California have made up to twice the growth on Guatemalan as on Mexican rootstocks (my unpublished data). Rootstocks from seeds of the West Indian 'Waldin' cultivar are proving inferior for California's relatively cool winter soils.

Free from sun-blotch. Genetic resistance to this virus disease is unknown. Hidden carriers of it must be avoided as female parents in rootstock breeding.

Dwarfing (or Semi-Dwarfing). Mexican-race lines have a somewhat dwarfing effect which has not been observed to increase the tree precocity or productivity but has produced trees somewhat less subject to wind injury and easier to pick. Stocks that cause true dwarfing could be a tremendous boon to the industry.

Genetically uniform. Rootstock segregation contributes to variable scion performance to an unknown but probably substantial degree. Complete uniformity can be achieved only by asexual propagation or, theoretically, by doubling the chromosomes of a haploid. Helpful approaches to uniformity should be possible by repeated self-fertilization.

Hardy and vigorous. West Indian rootstocks have major advantages in terms of resistance to salinity and chlorosis, but they are more difficult to grow in the less tropical California climate. Even Guatemalan lines are tender under some conditions, in comparison with the Mexicans. Quite apart from hardiness, some lines produce a much higher proportion of weak, slow-growing seedlings than other lines.

Easily propagated. This refers to the ease with which the rootstock itself can be multiplied. A conflict arises with the desired quality of genetic uniformity noted above, as clonal stocks are the only way to achieve uniformity within a reasonable time, but

they are far more expensive to propagate. There are wide differences in fruit setting ability even among seed-propagated stocks, e.g., 'Duke' selections for superior *Phytophthora* resistance have been shy bearers.

Easily grafted. Some progeny sets grow to graftable size more quickly than others. Some, for unknown physiological reasons, take more readily when grafted. Some Guatemalan cultivars have a failure rate many times as great on healthy, strong Mexican seedlings as on comparable-appearing Guatemalan seedlings.

Tolerant of Phytophthora and other organisms. For California and some other avocado regions, *Phytophthora* resistance is the paramount rootstock *desideratum*. Several lines with some resistance are known, but none has enough resistance to be a commercial solution. Resistance to nematodes and other harmful soil organisms would be advantageous.

Tolerant of salinity. Harmfully high salt concentrations can be present in the soil or brought in with irrigation water. Rootstocks that translocate less salts to the tree top are desirable in California, Texas, Israel and other areas with salinity problems (5). More and more California avocados have been grafted on West Indian seedlings for this reason—but with subsequent problems as noted above. Guatemalan stocks average superior to Mexican, but there is variation within both races.

Tolerant of chlorosis. Iron chlorosis can injure or even kill trees (5) under conditions of high lime content, or of other soil conditions that provide sub-optimal rootstock functioning. Again, West Indian stocks are most resistant; Guatemalans are most susceptible.

Tolerant of drought. Any advantage here would lower production costs, reduce the need for critical cultural care and permit wider distribution of avocado production. Trees have been reported to suffer less water stress on Guatemalan than on Mexican stocks (private communication from 2 growers).

Tolerant of other adverse soil conditions. 'Irving' seedlings have proven especially inefficient in extracting nitrogen from the soil (my unpublished data). Differences in tolerance of diverse soil limitations may prove to be common when critical tests are made. Superior rootstocks could reduce production costs and permit higher yields.

Summary

The avocado flower has both male and female organs, but the female organ functions only on 1 specific day and the male organ of that flower functions only on the following day. Moreover, either all female-functioning flowers of a cultivar are open only in the morning and all male-functioning flowers in the afternoon (A type) or, conversely, the open flowers are female-receptive in the afternoon and shedding pollen in the morning (B type). This makes cultivar self-pollination usually rare. Cross-pollination of 2 A or 2 B cultivars is also difficult, although often to a lesser degree. An A and a B cultivar together provide ideal complementary cross-pollination. Therefore, each avocado cultivar is highly variable (highly heterozygous) genetically. This means that a specific cultivar may itself provide all

of the seedling variability needed for selection of superior cultivars. Self-fertilization is the indicated avocado breeding approach, since it provides the least expensive seedlings and it effectively tests the breeding worth of a parent. Nevertheless, for some breeding and especially for subsequent breeding, hybridization may be desirable.

Hybridization may be prohibitively costly in terms of hand labor, but it can be done in a greenhouse or outside in plastic mesh sleeves or cages. Bees or other pollinating insects will do the hybridizing at a tiny fraction of the cost per hybrid, with the proper setup. However, they will probably simultaneously produce a smaller proportion of self-pollinations, to be differentiated only in the later seedling stage. Hybrids can be obtained from adjoining trees of the 2 parents, or branches of 1 worked into the other. The tree(s) may be isolated, or may be protected from nearby third parents by a cage with bees placed inside.

Self-fertilization by hand will only rarely be desirable, but it can be carried out in a greenhouse, sleeve or cage. Self-fertilization by insects is the heart of an efficient avocado breeding program. As with hybridization, the tree(s) may be isolated or enclosed with bees in a cage.

For any breeding procedure, seedling numbers can be increased by using heavy-yielding parent(s), working in the "on" year in the case of alternate bearing, growing trees in the best location and giving them the best care. The tree should receive maximum light. Girdling may markedly increase the number of fruits. Some additional ways to increase the yield of hybrid seedlings are to pollinate during optimum weather, pollinate few flowers per cluster, pollinate the first or female opening only, avoid any abnormal pistil and avoid late afternoon pollination.

Breeding objectives for the fruit include: medium size (about 260 g for the California markers); thick, ovate shape; uniform size and shape; skin of medium thickness, peelable, resistant to pests and diseases, free from blemishes, with attractive color; long tree storage life; small, tight seed; flesh that softens uniformly, has an appetizing color, a minimum of objectionable fibers, long shelf life, slow discoloration when cut, tolerance of chilling in storage, a high oil content in certain circumstances, high vitamin content and other nutritional values.

Desirable shoot qualities include: spreading tree habit; easy propagation; strong growth; tolerance of pests, disease, wind, cold, heat, salinity, chlorosis, and other stresses; maturing its fruits over a short period; precocity; annual productivity; wide adaptability; heavy yielder.

Rootstock qualities to aim for include: promoting quality fruit on productive trees; freedom from sun-blotch; dwarfing; uniformity; hardiness and vigor; easy propagation and graftability; tolerance of *Phytophthora*, salinity, chlorosis, drought and other adverse conditions.

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