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Avocado Rootstocks*

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I. INTRODUCTION

A. General

The avocado (*Persea americana* Mill.) is a relatively new commercial fruit crop (Popenoe 1920). Until the present century it was planted mainly in home gardens in its countries of origin, from Mexico, through Central America, to Colombia and Ecuador. Large orchards consisted of seedlings. With the introduction into California in 1911 of a selection from Mexico called 'Fuerte', the avocado became a commercial crop. Since then the avocado has developed rapidly and became an important fruit crop in the United States (California, Florida, and Hawaii), Puerto Rico, Mexico, Dominican Republic, Brazil, Chile, Australia, South Africa, Indonesia, Israel, and Spain.

Tree development, health, and productivity in fruit crops are very dependent on rootstock type. According to Webber (1926), "no factor of the avocado industry is more important than rootstocks, and there is no problem that we know less about, or which requires a longer time to solve." But for some reason, avocado rootstock research developed very slowly and became a main subject of research in California only when root rot disease incited by *Phytophthora* became important. Moreover, although more than 500 articles deal directly with the subject of avocado rootstocks, this subject has not previously been reviewed. The present review includes the history of the avocado in different countries, a review of rootstock research and development, and a summary of the rootstocks used currently.

B. Ecological Factors Related to Rootstocks

Originating in the tropics, the avocado is very sensitive to climatic factors prevailing in the subtropics, especially drought and extreme temperatures. Extreme temperatures result in low productivity and sometimes even in severe damage to the tree canopy (Bergh 1976; Oppenheimer 1978). Avocado is also sensitive to soil stress.

Avocado is extremely sensitive to salinity (Bernstein 1965), particularly the Mexican race (Cooper 1951; Kadman and Ben-Ya'acov 1976). The main factor in the salinity sensitivity is chlorine toxicity (Haas and Brusca 1955), but sodium adds to the problem. Resistant rootstocks do not translocate sodium to the foliage (Ben-Ya'acov 1970). Thus leaf burn can be eliminated, but a negative effect on productivity remains (Ben-Ya'acov et al. 1979). Avocado is also sensitive to alkaline conditions and sensitive to lime-induced chlorosis (Kadman and Ben-Ya'acov 1982). Both factors induce a chlorotic appearance to the tree, due to a lack of iron absorption. Resistant rootstocks have the ability to absorb iron under conditions in which sensitive rootstocks cannot (Halma and White 1951; Kadman and Ben-Ya'acov 1982). Avocado is also sensitive to lack of aeration, which is prevalent in all growing regions. Lack of aeration could be caused by heavy soils, soils with poor structure, or light soils when a hardpan eliminates internal drainage. Poor aeration occurs more often in valleys than on slopes. Heavy, continuous rains can severely affect the avocado tree, even on relatively well drained soils, especially where such rains are not common. Mexican rootstocks are more resistant than West Indian to poorly aerated soils (Ben-Ya'acov et al. 1979).

A very common soil stress factor is root rot disease, caused by the fungus *Phytophthora cinnamomi*, which is usually associated with lack of aeration. Poor drainage, shallow soils, and low pH are conditions preferred by the fungus (Zentmyer 1972, 1980; Coffey 1992). No rootstocks are resistant to *P. cinnamomi*. Some rootstocks are tolerant because they are able to produce new active feeder roots rapidly to replace those attacked by the fungus.

In most cases, combinations of stress factors are present. In arid areas combinations between salinity, alkalinity, and lime, or salinity and poor aeration, are common and these are difficult to solve by appropriate rootstocks. Climate and soil factors may also interact. Thus, an excess or deficit of rainfall induces soil stress and harms the root system. Extreme temperatures that injure the foliage also damage the root system, which reduces the ability of the tree to withstand the climatic conditions that retard growth. It is possible that the generally poor reaction to soil stress is caused in part by lack of root hairs in avocado (Burgis and Wolfe 1945; Ginsburg and Avizohar-Hershenson 1965).

C. Genetic Resources and Taxonomy as Related to Rootstocks

Avocado belongs to the genus *Persea*, subgenus *Persea*, and includes botanical varieties or subspecies (Bergh 1975b). Subspecies have clear differences in their phenological appearance, which make it easy to identify them. They also have clear differences in their characteristics as rootstocks that will be mentioned later.

In the most recent classification, *Persea americana* has three subspecies: ssp. *drymifolia*, the Mexican highland avocado; ssp. *guatemalensis*, the Guatemalan highland avocado; ssp. *americana*, the West Indian lowland avocado; and *P. nubigena*, the primitive highland avocado. We believe that four other species (*P. floccosa, P. steyermarkii, P. tolimanensis, and P. zentmyerii*) are so close to the avocado that they should be considered subspecies of *P. americana*. *P. schiedeana* a member of the subgenus *Persea*, differs greatly in its phenology and should remain a separate species.

In the genus *Persea* there is a second subgenus, *Eriodaphne*, with about 80 species. All these species are distantly related to the avocado and produce small olive-sized fruits; at the present time they cannot be grafted to or hybridized with the avocado. Some of them are resistant to avocado root rot and some are very sensitive. Because of its sensitivity, *P. indica* is used as an indicator plant for the presence of *Phytophthora cinnamomi* in the soil.

Taxa belonging to the subgenus *Persea* already serve as avocado rootstocks. In California (Bergh et al. 1988) *P. nubigena* selections were used as seedling rootstocks. In Israel, rooted cuttings from two seedling trees of *P. nubigena* were used as rootstock under root rot conditions (Zilberstaine et al. 1992). *P. schiedeana* has been introduced into California a few times (Schroeder 1974; Coffey et al. 1988), but slight resistance to *P. cinnamomi* was found. Trees grafted on *P. schiedeana* in Honduras (Fiester 1949) failed to develop but proved to be a desirable rootstock in South Africa (Schroeder 1974); where it tolerated heavy soils and persistent flooding. Many *Persea* species were introduced and investigated in California during the search for rootstocks resistant to root rot. Sixteen species of *Persea* were grafted onto *P. americana* (Frolich et al. 1958), and vice versa, but only six of them, all belonging to the subgenus *Persea*, have large edible fruit and are sensitive to root rot, were found to be compatible. (Zentmyer and Schroeder 1958). The use of avocado relatives as rootstocks (Zentmyer and Schieber 1987) included the G755 group of three resistant rootstocks from

Coban, Guatemala, which were shown by isozyme study, to be natural hybrids between *P. americana and P. schiedeana* (Ellstrand et al. 1986).

During the last 5 years avocado germplasm has been collected in the countries of origin (Ben-Ya'acov 1992b). The main aim was to conserve the avocado gene pool rather than being directed at solving any immediate problem. Gene pool plots have been established in Mexico and in Israel (Ben-Ya'acov et al. 1992d).

D. Propagation of Avocado Trees Grafted on Seedling and on Clonal Rootstocks

The avocado industry is based on seedling rootstocks. In most cases seedling rootstocks were chosen according to their ease of propagation and the horticultural value of the rootstock was not studied. The propagation process changed over the years. Until the end of the 1950s, Californian nurseries rootstocks were planted in the open field and budded after 1 year. Later, seeds were sown under protected conditions and seedlings were tip-grafted very early, when the rootstocks were juvenile. This method, with some variation, is the main method used by avocado nurseries on seeded rootstocks at the present time. It is very easy to employ, relatively cheap, and the transfer of trees to the orchard is convenient. For both methods, rootstocks were chosen for their rapid and uniform germination. Thickness of the shoot is also very important, as thick shoots of the rootstocks can be grafted earlier and better adapted to the scion. A general survey of the commercial nurseries in Israel (Ben-Ya'acov and Sela 1975) revealed that the success in propagation from seed to a complete grafted plant varied greatly with the nursery (43 to 74%) and with the rootstocks (40 to 90%).

The nonuniformity of seeded rootstocks and the necessity to overcome various soil problems gave impetus to the search for a clonal propagation method that can produce known uniformity. However, it is very difficult to propagate avocado vegetatively. Brokaw's version (1987a) of Frolich's method (Frolich and Platt 1972) has become the leading propagation technique. Frolich claimed that rejuvenation by etiolation is necessary to force the avocado to root. Juvenile material roots easily and is also easy to graft. In the Brokaw version the clonal material is first grafted on a nurse rootstock. A few days later the entire plant is moved to a darkroom, where etiolation takes place and a metal ring is placed above the nurse rootstock. Then the entire etiolated branch and the grafted union are covered by rooting medium. When the etiolated shoot emerges, the plant is moved to the light. This new growth is ready for the second graft, this time with a commercial cultivar. The entire plant grows in the nursery for about 1 year, and during this period the ring induces rooting from the previously etiolated portion. Later the portion below the ring disintegrates and the rooted plant separates from the nurse rootstock.

Two other propagation methods will be mentioned briefly. One is the intermediate (sandwich) graft, used experimentally to control tree size by an interstock with a dwarf avocado type (Barrientos et al. 1987), as recommended for other fruit trees (Rogers and Beakbane 1957). The other method is the inarch graft, developed in California by Burns et al. (1964) to replace a rootstock sensitive to root rot by a more resistant one. In Israel this method was used successfully to cure chlorotic avocado trees (Ben-Ya'acov and Kassas 1966; Bergh 1975a; Ben-Ya'acov 1977b) by improving iron absorption of the tree through additional, more efficient rootstocks. The same method was used to reduce salinity damage and to improve productivity.

Some terms should be clarified. When an avocado cultivar is grafted on seedling rootstocks, the seeds are taken from either a known cultivar or the nongrafted "mother" tree, which is also a seedling. When larger quantities of seeds are required from a certain seedling mother tree, it can be propogated by grafting. Each one of the seed supplier trees, be it a lonely seedling, a grafted type, or a known cultivar, is considered a roostock type or just rootstock.

In the case of clonal propagation seedlings that serve as nurse rootstocks are eliminated.Only the identity of the clonal rootstocks and the cultivar source are preserved.

II. COMMON ROOTSTOCKS AND ROOTSTOCK SELECTION

The actual use of avocado rootstocks in various countries will be described as far as information is available. Breeding research for avocado rootstocks is rare and limited primarily to one main problem, avocado root rot. In many countries seed-propagated rootstocks are still chosen according to availability and nursery performance rather than as to orchard performance.

A. Australia

The avocado was introduced into Australia around 1850, but introduction of commercial material, such as known cultivars, began in 1928 (A. W. Whiley, pers. comm.). The planted area is approximately 2000 ha, about 10% of which was planted during the last 5 years. During recent years 'Hass' has became the dominant cultivar, but 'Fuerte' remains important. 'Shepard' is a favorite cultivar in the more tropical area, the Tableland, but is unsuccessful in colder regions. 'Reed', 'Wurtz', and 'Sharwil' are included in commercial orchards (Whiley et al. 1990).

The main soil problem is the presence of the *Phytophthora* root rot. Most of the soils in southern Queensland and northern New South Wales are acid (pH 4.5 to 5.8) and infertile (Young 1992). Drainage is good, but sometimes the soils are heavily saturated for extended periods during the wet season.

The main seedling rootstocks are local selections of the Guatemalan race or Guatemalan hybrid types (e.g., 'Plowman' and 'Velvick'). Mexican race rootstocks were introduced from California due to their success there and have been indexed for Sunblotch viroid but are unsuccessful in Australia.

At present only 2% of new plantings are on clonal rootstocks, mainly 'Duke 7' and 'Velvick'. 'Duke 7' is reliable and if managed correctly will give uniform trees of good performance. According to Whiley et al. (1990), trees grafted on cloned rootstocks are generally more difficult and slower to establish in the field than those on seedling rootstocks. Wolstenholme (1988) believes that the unpopularity of clonal rootstocks in Australia is short sighted and a cause for concern. The relatively small area of avocado grown in the Sunraysia area (the Murray river basin) is subjected to salinity problems (Downton 1978).

B. California

1. History. The avocado was introduced from Mexico in 1871, but a grafted tree industry developed only after the discovery and introduction of 'Fuerte' (1911). By 1970 the avocado area reached 33,000 ha after steady and prosperous development. The California avocado industry is one of the leaders in world production, and it is in first place in regard to knowledge, research, and organization. A Californian seedling 'Hass', later replaced 'Fuerte' as the main cultivar because the productivity of 'Fuerte' was erratic. Nevertheless, the average yield of Californian orchards remained low (± 8 tons/ha).

2. Avocado Rootstock Breeding Research. Avocado rootstock breeding research received high priority at the University of California from the very beginning of the industry (Reuther 1961) and a wide-scale rootstock experimental system was established by F. F. Halma during the 1940s (Halma 1954). At that time decline of avocado trees was a known phenomenon in California, but *P. cinnamomi* was discovered to be its casual agent only in 1942. Salinity was no concern at the time. Halma therefore concentrated on productivity as influenced by Mexican and Guatemalan rootstocks, and discovered differences in sensitivity to lime-induced chlorosis and *Verticillum* wilt. Halma's huge project included about 50 orchard plots, but the results were not summarized due to the large losses of plots from *Phytophtora* root rot and other causes. Later, when the root rot agent was discovered (1942), a new era began for rootstock breeding research aimed at discovering rootstocks resistant to this disease. Zentmyer searched for material in the countries of origin and selected some clonal rootstocks which can tolerate root rot and are now in commercial use in California and elsewhere (see Section III).

In addition, Wallace et al. (1955) studied the salt resistance of *Persea floccosa*; Bergh and Whitsell (1962) had a candidate dwarfing rootstock that later failed; Storey et al. (1984) hybridized Mexican and West Indian parent trees and tested the resulted seedlings as rootstocks and cultivars; Bergh et al. (1988) tested 'Hass' grafted on four rootstocks, including the clonal 'Duke 7'; Arpaia et al. (1992, 1993) established a clonal rootstock production trial in soils not infected with root rot in order to study the horticultural characteristics of the rootstocks selected for root rot resistance (this experiment is still under way); Lovatt (1989) is trying to accelerate the initial screening of avocado rootstocks for stress conditions by developing biochemical indices.

3. Common Rootstocks. During the first decades, Guatemalan and Mexican seedlings were used as rootstocks. In many cases scions on Guatemalan looked better, but in others they suffered from lime-induced chlorosis; the use of Guatamalans was therefore discontinued. Later the Mexican cultivar 'Topa-Topa' became the main source of seeds for rootstocks. Its advantages were mainly in the propagation process: Seeds were cheap and available, germinated uniformly, and produced a relatively thick shoots. Thick shoots was especially important when the avocado propagation method was changed from budding in the field to tip-grafting under protected conditions. However, the orchard characteristics of 'Topa-Topa' were rarely investigated and never proved to have any advantage for the grower. Moreover, 'Topa-Topa' is susceptible to root rot and salinity.

West Indian avocado rootstocks were very rarely used in California, although they are known in Israel (Oppenheimer 1947) and Texas (Cooper 1951; Cooper et al. 1957) to resist salinity much better than the Mexican rootstocks. The fact that the West Indian race is much more sensitive to low temperatures, inspired Halma's conclusion that the West Indian was too tender for California conditions.

Clonal propagation of avocado rootstocks became practical in 1977 after some changes were made by Brokaw (1987a) in Frolich's method (Frolich and Platt 1972). Only a few thousand trees grafted on clonal rootstocks were distributed in California before this development, even in Halma's experimental plots. However, when the new method became available, propagation began on a large scale and hundreds of thousands of trees grafted on root rot-tolerant rootstocks, especially 'Duke 7', were planted. 'Duke 7' now comprises a large part of California orchards, but long-term performance of this rootstock has been proven mixed, with many instances of failure (Coffey 1992). Other rootstocks belonging to the period of the discovery of 'Duke 7', such as 'Duke 6', 'G6' and'G22' have already disappeared and at present 'G755' (Martin Grande), 'Thomas', 'D9' and 'Barr Duke' are under investigation. Three rootstocks of the 'G755' group (a,b,c) developed chlorosis and failed to produce normal yields (Arpaia et al. 1992, 1993); the other three, 'Thomas', 'D9' and 'Barr Duke', which may withstand the root rot infection longer, are susceptible to salinity, as they belong to the Mexican race. A new era of rootstock breeding began recently when new hybrids were produced and dozens of them showed resistance to *P. cinnamomi* under controlled conditions (Menge 1993).

C. Florida

Avocado was introduced into Florida a few years before its introduction into California. The climatic conditions in Florida are more tropical than in California, which prevented the establishment of the Mexican or Mexican hybrid cultivars such as 'Fuerte', but West Indians from the Caribbean Islands were successful. Some Guatemalan cultivars were grown successfully as well. Over the years, hybrid cultivars of Guatemalan x West Indian became important.

West Indian and hybrid cultivars were used as rootstocks. After 'Lula' (hybrid) failed, due to its sensitivity to lime-induced chlorosis and wind, the West Indian cultivar 'Waldin' became the main source of seeds for rootstocks. As a typical West Indian, 'Waldin' seedlings are efficient in iron absorption, and hence the grafted trees are not chlorotic. On 'Waldin' seedlings, trees suffer less from other deficiencies and withstand the strong wind better.

In recent years the Florida avocado industry has suffered from many climatic problems and following Hurricane Andrew, the industry has been in regression. In the past, rootstock experiments in Florida were not continued long enough to draw any conclusions. Recently, Ploetz et al. (1989) investigated seven rootstocks developed in California for root rot resistance under Dade County conditions. The primary determinant was found to be the rootstock's adaptation to alkaline soil.

D. Israel

1. History. The avocado was introduced into Israel (then called Palestine) during the 1920s, although a few trees were known there from an earlier period, probably from the last decade of the nineteenth century. Commercial orchards have been planted since 1954 and on a larger scale since 1960 (Oppenheimer 1978).

The introduction of avocado into Israel included grafted trees, seeds, and graftwood material. In this way, seedling trees were established together with grafted ones. The seedling trees became the main source of rootstock seeds for the newly established nurseries. Most of the seedlings were Mexican but some were West Indian. The Israel main source for Mexican seeds was the avocado orchard of the Miqwe Yisra'el Agricultural School, while West Indian seeds were collected from the Rupin Gardens, established at Kibbutz Deganya 'A', and at Nahlat Yehuda. Later many other avocado seedlings were planted in home gardens and became a source of seeds for propagation. Concomitantly, seeds were taken from grafted cultivars such as 'Northrop', 'Mexicola', 'Duke', and 'Caliente' (Mexican race) and 'Winslowson' and 'Lula' (West Indian or hybrid types).

The Ministry of Agriculture's farm advisor, A. Yoffe, attempted to control the use of different seed sources to eliminate the spread of the Sunblotch viroid and made periodic visits to each mother tree. In 1969, 630 different avocado types of rootstocks were in use in Israel, of which about 50% were Mexican seedlings and cultivars; the rest were West Indian seedlings and cultivars. 'Nabal' was the only Guatemalan source of seeds at that time (Ben-Ya'acov 1976b).

2. Information on Seedling Propagated Rootstocks. As early as 1937, while planting a new experimental plot at Deganya 'A', Oppenheimer (1947) found that trees grafted on West Indian rootstocks could survive the relatively saline water of Lake Kinneret (Sea of Galilee), whereas trees on Mexican rootstocks suffered greatly and finally died. This was the first discovery of the West Indian avocado's resistance to salinity.

Convinced of the importance of rootstocks for the development of avocado in Israel, Oppenheimer established the first rootstock trial at Qubeiba in 1949 (Oppenheimer 1963). He managed to collect yields for 10 years and found that trees on Guatemalan rootstocks were more productive than on Mexican or hybrid roostocks (for more details, see Section IV).

During the years 1960-1964, when additional avocado orchards were planted in Israel, growers became more aware of the importance of choosing the right seedling rootstocks, and some of them kept planting maps in which rootstock and scion sources were recorded. These growers subsequently collected yield data per tree for at least five crops. An example is that of data collected by the author (Ben-Ya'acov 1973, 1976a).

Encouraged by information from these "nonexperimentally designed" orchards, Ben-Ya'acov instituted a new experimental system in 1968. This led to a comprehensive, wide-scale, long-term research project on avocado seedling rootstocks and sources of scion, planted until the year 1978, with data collection for an additional 10 years. As a result (see Sections III and IV), the number of the seedling rootstock types decreased from 630 to 30. As an additional benefit of the research, all Sunblotch-infected trees were eliminated, and new orchards were established to supply seed and scion wood from the best selected types and from viroid-indexed trees.

3. Information on Rootstocks in the Clonal Propagation Era. A new rootstock clonal propagation method was developed in California by Brokaw in 1977 (Brokaw 1987a) based on Frolich's ideas (Frolich and Platt 1972). When this method was introduced into Israel, wide-scale selection of clonal rootstocks became possible. Previously, propagation of green avocado cuttings under mist spray was developed in Israel, but this method never became commercial. The number of rootstocks propagated clonally during this early stage was small, mainly from seedlings resistant to salinity, but none of the West Indian race rootstocks could be propagated by this method.

The new propagation method made possible wide selection from trees included in the seedling rootstock experimental system. The variability found among avocado trees, even of one stionic combination, especially in regard to productivity, was large. Such variability had been described earlier by Gillespie (1954) for 'Fuerte' grown in California. Yield data from individual trees in Israel, indicated that many of the trees produced much less than the average yield of the plot, often not enough to cover minimum orchard expenses. Yield data collection therefore became important in eliminating unproductive trees that occupy space needed by better, neighboring trees. Further, there were often one or more outstandingly productive trees. It was apparent that clonal propagules of rootstocks from these outstanding trees should be tested.

Candidate trees were chosen according to many criteria, and after scion material was conserved, vegetative material was obtained from the rootstock. The entire process of clonal rootstocks selection was described in detail by Ben-Ya'acov (1985) and is reported in Section IV.

At this time, 160 different clonal avocado rootstocks developed in Israel are under investigation. Twenty clonal rootstocks have been released for commercial use. Seedling rootstocks for three commercial cultivars, 'Ettinger', 'Fuerte', and 'Horshim' are no longer recommended, as clonal rootstocks were found to induce higher productivity. There are too few data to justify the same recommendation for 'Hass', 'Reed', and 'Nabal'.

E. Mexico

For thousands of years avocado has been produced and consumed in huge quantities in Mexico. During the last two decades or more, a new avocado industry was developed, especially in the state of Michoacan. This new industry is based on one grafted cultivar, 'Hass', which occupies more than 120,000 ha, with production about 800,000 tons in 1993.

Soil problems are important factors in some parts of Mexico; root rot, for instance, is responsible for the disappearance of avocado from some lowland areas in the state of Vera Cruz. However, where 'Hass' is planted on high-elevation slopes, none of the soil stress factors was noted. Most of the soils are of volcanic origin, fertile, and aerated. Hence it is understandable that the Mexican growers pay little attention to which rootstocks are used. The nurserymen look for any available seeds, and in Michoacan they are available from Mexican seedling trees. In the state of Nayarit, mostly West Indian seeds are available, so 'Hass' is grafted on West Indian rootstocks. Rootstock research is very limited, and clonal propagation of avocado rootstocks is in the early stages.

Special effort is devoted to the search for dwarfing rootstocks (Barrientos-Priego and Lopez Jimenez 1987; Lopez Jimenez and Barrientos-Priego 1987; Barrientos-Perez and Barrientos-Priego 1990; Barrientos-Priego et al. 1992) and also to the use of the dwarfing interstock technique (Barrientos-Priego et al. 1987). Another team used in vitro technique to select avocado rootstocks tolerant to chlorides (Gonzalez-Rosas et al. 1992).

F. South Africa

Avocado was introduced into South Africa in the last decade of the nineteenth century and is now grown mainly in eastern Transvaal and Natal. During the last 10 years the planted area increased greatly, as has production. The planted regions in Transvaal are tropical highlands, whose climate is very suitable for the avocado; in Natal the temperatures are moderate. However, some soil factors cause difficulties in growing trees and justify rootstock breeding research. *P. cinnamomi* root rot is distributed in all avocado soils, and although it has been controlled for the present by fungicide injections, this is only a temporary solution, and resistant rootstocks are needed. Soil is acid in Natal, which induces manganese and aluminum toxicity. Relatively frequent droughts cause soil dryness, and in many cases water is unavailable for irrigation. Hence rootstocks resistant to drought are needed.

For many years seeds were taken from Mexican seedlings and used as rootstocks. Later, most of these mother trees were found to be infected with the Sunblotch viroid and were symptomless carriers. Growers tolerated this since they did not see the immediate effect of the viroid. Later, seeds of the Guatemalan cultivar 'Edranol' became the main source for rootstocks. The latent type of Sunblotch viroid infects every seed taken from infected tree (while the virulent type infects only 5 % of them), and when the symptoms finally appear, many trees are already degenerating. Korsten et al. (1987) conducted a general screening of South African mother trees, and most sources of infection were eliminated.

The South African avocado industry was one of the first to adopt Frolich's ideas in regard to clonal propagation of rootstocks by using Brokaw's version (1987a) or other local improvements made by South Africa nurserymen (Ben-Ya'acov 1985). Rootstock propagation material of that time, namely 'Duke 6', 'Duke 7', 'G6', 'G22', 'G755' (Martin Grande) and others were introduced from California. After local selection, clonal 'Duke 7' became the major rootstock in use in South Africa and at the present time it comprises a large portion of South Africa's avocado orchards.

Until recently, rootstock breeding efforts in South Africa were relatively small and trials did not produce sufficient yield data (Ben-Ya'acov 1985). In recent years, Westfalia Estate farm took on the task of record keeping as one of its main research activities, and by keeping yield records per tree, in a few years they will be able to select their own rootstock candidates, propagated from outstanding trees under their local conditions (Smith and Köhne 1992; Smith et al. 1993). This is a better system than introducing rootstocks from other countries, such as California and Israel, which differ considerably in climate and soil types. Together with the search for rootstocks among the local outstanding productive trees, they evaluate introduced rootstocks (Köhne 1992; Kremer-Köhne and Köhne 1992; Smith 1993). The Nelspruit Institute for Tropical and Subtropical Research conducted some limited research on avocado rootstocks in the past. Recently, the activity increased. Bower and Nel (1982) determined selected enzyme activities as influenced by rootstock-scion interaction; they found that the rootstock plays a role in the final expression of biochemical activity in the scion. Moll et al. (1985) described the lethal stem pitting of 'Duke 6' avocado rootstocks. This Institute now has a comprehensive breeding program (Bijzet et al. 1993), including cultivar and rootstock breeding. Different aspects in the search for rootstocks resistant to root rot are being investigated in the Department of Microbiology and Plant Pathology at the University of Pretoria (Lonsdale et al. 1988a, 1988b; Botha et al. 1990, 1992; Merwe et al. 1990; Merwe 1992). Schroeder (1974) described an orchard in northeastern Transvaal where avocado is grown successfully on *P. schiedeana* rootstock.

G. Spain

Avocado probably was first brought to Spain from the Americas. Very old trees are found in continential Spain and in the Canary Islands. It is logical to consider (as did Galan-Sauco 1976) the time of introduction to be decades after the European encounter with the New World. The first primitive avocados in the Canary Islands belong to the West Indian race and can be found mainly on La Gomera Island (Galan-Sauco and Fernandez-Galvan 1983). The types in southern Spain are difficult to identify as to group or race.

The modern avocado industry of Spain is relatively young; a few orchards were established earlier in the Canary Islands, where many trees have died from root rot, especially in the wetter part of the Islands of La Palma and Tenerife, less so in the dry parts of the islands and in Gran Canaria. Rootstock selections for root rot resistance are being made in the Canary Islands (Gallo-Llobet 1991). The water is saline, but the West Indian rootstock can still be grown successfully (Galan-Sauco 1976).

In southern Spain only one commercially grafted orchard (Rancho California) is known from the past. The orchard suffered from lime-induced chlorosis, and Wilson Popenoe himself (L. Sarasola, pers. comm. 1981) brought seeds from West Indian trees grown on La Gomera Island so as to replace the sensitive trees with resistant ones. Many of the new trees, grafted with the 'Hass' cultivar, degenerated. Many years later southern Spain became a center of avocado planting, and during the last 15 years Spain has become large producer of avocado with about 7000 to 8000 ha.

H. Other Countries

In most other countries, nurseries use seeds from locally available seedlings as rootstocks and clonal procedures are not used. The relatively large avocado industries of Brazil and the Dominican Republic use mainly local West Indian seedlings, as do most other Carribean countries, including Cuba. In the Carribean, avocados often are produced on seedling trees. In Ecuador and Chile, seeds from local Mexican avocado types are used for rootstocks. In Ecuador they are called "Nacionales," and the general impression is that they can tolerate alkalinity, typical of some soils. In Peru, different rootstocks are used in different regions. In the central coastal region they are of the Mexican race (Bederski 1972), and in the tropical highlands of Chanchamayo Valley they are West Indian (Rivadeneyera and Franciosi 1972). In Hawaii, Guatemalan seedlings are generally used as rootstock. Where soils have low pH and most of the cultivars are Guatemalan, such as 'Sharwil', Guatemalan rootstocks could be the best choice. On Cyprus, a tiny industry developed early in the Morpho region and later near Paphos. As calcareous soils are common in the latter region, rootstock trials were established in which chlorosis and yields were analyzed over a long period (Gregoriou 1992).

III. SELECTION OF ROOTSTOCK FOR RESISTANCE TO SOIL STRESS FACTORS

A. Salinity

The very high sensitivity of the avocado to saline conditions made the search for resistant roostocks the top priority in some countries. In two regions in Texas and in the Murray River area in Australia (Cooper et al. 1957; Downton 1978) the research was discontinued, as the avocado is no longer of importance. In Israel, water used to irrigate most of the avocado orchards is expected soon to be saline. The salinity problem is serious in California. An effort was made to solve the salinity problem there by rootstocks (Haas 1950a,b, 1952; Haas and Brusca 1955).

In Israel (Oppenheimer 1947) and in Texas (Cooper 1951) the West Indian race was found to be more resistant to salinity than is the Mexican race. Years later this finding was applied in Israel, when it became possible to enlarge some plantations by using West Indian rootstocks where saline water was the only source for irrigation. Major differences were found between the West Indian rootstocks and many were eliminated because of chlorosis sensitivity of the presence or Sunblotch viroid. Later it was found that some of the rootstocks were sensitive to poor aeration and the trees degenerated in a few years, and many of them produced poorly relative to Mexican rootstocks irrigated with water of good quality (Ben-Ya'acov et al. 1979). In 1982, a new selection program was started in which outstandingly productive trees were identified under saline conditions, and from these trees clonal propagation of the rootstocks were made. Such propagules were true to type and trees produced from them were able to produce satisfactory yields under saline conditions (Ben-Ya'acov et al. 1992a). Approximately 50 clones of West Indian rootstocks were developed (Ben-Ya'acov 1992a) from very productive trees under saline conditions. Well-aerated soils are prerequisite for West Indian rootstocks under saline conditions.

The salinity problem of avocado should and could be solved by using resistant rootstocks; but the only major research dealing with the problem is the selection project described above. In some other industries the root rot problem is of top priority and salinity is considered of secondary importance.

Part of the salinity problem is sodium translocation. Ayers et al. (1951), Haas (1952), Kadman (1964), Ben-Ya'acov (1968, 1970), and Kadman and Ben-Ya'acov (1976) found that sodium is accumulated in the root system and little accumulates in the leaves. Oster and Arpaia (1992) found an increasing level of sodium in the new growth following an increase of salinity in the growth medium. Of the experiments mentioned, clonal rootstocks were used only in the last one. The fact that the root system is adventitious in clonal rootstocks may explain the absence of a sodium barrier in these plants.

Oster and colleagues (Oster et al. 1985; Oster and Arpaia 1992) investigated the salt tolerance of root rot-resistant rootstocks. In their experiments salinity level did not affect sodium and chlorine levels in the roots.

There is a higher content of chlorine in the leaves of trees grafted on Mexican rootstocks than on Guatemalans (Embleton et al. 1961, 1962; Oppenheimer and Kadman 1961; Ben-Ya'acov 1968), which is correlated with leaf salt damage. Differences among representatives of each race are notable. In some plots Embleton found that a Guatemalan rootstock induced more Cl accumulation than a Mexican rootstock. When used as the rootstock, the Guatemalan cultivar 'Anaheim' seedlings induced a greater accumulation of Cl in the leaves than did other cultivars. When 'Anaheim' was used in Israel as a seedling and cloned rootstock, it behaved the same way. Among the Mexican rootstocks, 'Topa-Topa' accumulated more Cl and 'Duke' less Cl than other rootstocks. 'Duke' was known also to be more tolerant to root rot, but these results did not induce any change in the use of rootstocks in California.

The degree of leaf damage in the avocado is related to Cl content of the leaves, a fact that can assist rapid selection (Hass and Brusca 1955; Cooper et al. 1957; Kadman and Ben-Ya'acov 1976; Diaz et al. 1984) but some differences in tissue sensitivity can change this relationship. Mexican and Guatemalan seedlings suffer more and West Indian seedlings less than would have been expected from their leaf Cl content (Ben-Ya'acov 1968, 1970). Increase in salinity induced better development of the root system of the West Indian rootstock, while Mexican rootstocks declined. West Indian and Guatemalan rootstocks took up more nutrients than Mexican rootstocks under saline conditions, inducing greater uptake. The increase in uptake was primarily in Ca, while Mexican rootstocks reacted to salinity by increasing potassium uptake and translocation.

1. Mexican Rootstocks. During the search for resistant rootstocks for saline conditions, trees of the Mexican avocado race were also investigated as candidates. Under saline conditions certain Mexican rootstocks looked better than others (Kadman and Ben-Ya'acov 1976). These experiences encouraged the search for saline-resistant rootstocks among the less resistant Mexican race, especially in view of its better adaptation to cold climate and heavy soils.

The present Israeli list of clonal rootstocks includes 14 Mexican rootstocks selected for salinity tolerance (Ben-Ya'acov et al. 1988). But disappointingly, when reinvestigated in commercial orchards planted in an experimental design, most of the trees grafted on these rootstocks were less productive than were trees on other rootstocks in the same experiments, mainly of the West Indian type. This means that the sensitivity to salinity of the Mexican rootstocks was expressed by reduced productivity rather than by leaf burn. Moreover, these rootstocks could not withstand the higher salinity of irrigation water predicted for the future.

2. West Indian and Hybrid Resistant Rootstocks. This group includes early selections for high salinity based on a survey of tree appearance, mainly leaf burn. Two of these clonal rootstocks, 'Fuchs-20' (Kadman and Ben-Ya'acov 1981) and 'Maoz' (Kadman and Ben-Ya'acov 1980), were described in the literature. Although these rootstocks are highly salinity resistant, trees grafted on them were not sufficiently productive, very typical of many West Indian seedling rootstocks under saline conditions (Ben-Ya'acov et al. 1979). Some of the clonal rootstocks failed to withstand adverse soil conditions other than salinity; for instance, 'Maoz' is sensitive to poorly aerated soil and 'VC 30' is sensitive to lime-induced chlorosis.

3. West Indian Rootstocks from Productive Trees. Rootstocks of the West Indian race, were expected to tolerate salinity without a reduction in productivity and became the main source of selection (Ben-Ya'acov et al. 1992a; R. Steinhardt, pers. comm. 1992). Clonal West Indian rootstocks selected and propagated from highly productive trees are currently being evaluated. There are approximately 50 rootstocks in this group and 10 of them have been released for commercial use. More details about this group are presented in Section IV.

B. Calcareous and Alkaline Soils

In its native lands, avocado grows on acidic soil (pH 3.5 to 5.5). Lime-induced chlorosis and other alkaline problems are known in Florida, Spain, Israel, and Cyprus, and to a lesser extent in California. Guatemalan avocado was found to be the most susceptible to chlorosis (Halma and White 1951), and this was subsequently corroborated in Israel (Ben-Ya'acov and Kassas 1966; Ben-Ya'acov 1977b; Kadman and Ben-Ya'acov 1982) and other countries. Guatemalan race rootstocks of avocado were completely eliminated in California and Florida. It is in use to a limited extent in South Africa, Australia, Hawaii, and Israel in sandy loam soils of low pH. On the other hand, the West Indian seedling rootstocks are resistant to lime-induced chlorosis, and some of them are highly resistant. Hybrids between the two botanical races, such as 'Lula', 'Hall', 'Colinson', and 'Booth 8', behave more or less like their Guatemalan parents and their use was discontinued in Israel (Ben-Ya'acov et al. 1979) and in Florida. Similar conclusions were reached in Cyprus (Gregoriou 1992). Selection of rootstocks resistant to lime-induced chlorosis is continuing in southern Spain. Seedlings of the Mexican race are of intermediate sensitivity. During the last 15 years, selection of clonally propagated rootstocks did not include chlorosis resistance as its main aim, but has eliminated rootstocks selected for other characteristics when they turned out to be chlorosis sensitive. This was the case with some salinity-resistant rootstocks selected in Israel (Ben-Ya'acov et al. 1979) and with 'G755' selected for root rot in

California (Coffey and Guillemet 1987b; Menge et al. 1992). In Florida (Ploetz et al. 1989) adaptation to alkaline soils is the primary determinant of the performance of new rootstocks in Dade County.

There is very little information, if any, on the mechanism involved in resistance to lime-induced chlorosis or why avocado trees grafted on one rootstock look green even if the $CaCO_3$ level in the soil reaches 60%, and trees grafted on others are chlorotic at 3% $CaCO_3$. Another important factor is the type and form of the lime in the soil and the size of its particles.

C. Acidity

Very low pH induces certain toxicities (Mn and Al) and encourages root rot. There are known agrotechnical means to treat this problem, but special selection of adapted rootstocks is unknown.

D. Poorly Aerated Soil

Poor aeration is very hazardous to avocado and is conducive to root rot infection. Avocado has almost disappeared from most sites where aeration is limited, and it seems that soils rather than rootstocks should be selected to overcome this problem. In Israel, a few seed-propagated clonal rootstocks were selected for poorly aerated soils, but they did not stand up when reevaluated. The most resistant rootstocks for salinity are the most sensitive to poor aeration, and some of them should not be used any further for this reason (Ben-Ya'acov et al. 1979). Mexican rootstocks can tolerate such conditions better than the West Indian rootstocks. Large differences in the susceptibility were found among rootstocks of each race (Ben-Ya'acov et al. 1979).

E. Root rot Disease

Root rot caused by *P. cinnamomi* is the most hazardous soil factor for the avocado. The search for resistant rootstocks began soon after it was identified in California. This subject has been reviewed by Zentmyer (1972, 1980) and Coffey (1992). There have been extensive studies, including a search for resistant rootstocks in Latin America (Zentmyer 1957; Zentmyer and Schieber 1987), selection techniques in vitro (Zentmyer 1972 1980; Bergh et al. 1976) and new screening techniques (Kellam and Coffey 1985; Dolan and Coffey,1986; Gabor and Coffey 1990; Merwe et al. 1990; Merwe 1992), field evaluation (Zentmyer et al. 1962; Coffey and Guillemet, 1987a, b; Guillemet et al. 1988; Gabor et al. 1990; Menge et al. 1992, Menge 1993), evaluation of the rootstocks for horticultural purposes (Brokaw 1982 1986; Oster et al. 1985; Arpaia et al. 1992, 1993; Oster and Arpaia 1992), as well as various studies outside of California: (Lonsdale et al. 1988a,b; Botha and Kotze 1989; Ploetz et al. 1989; Botha et al. 1990; Merwe et al. 1990; Botha 1991; Köhne 1992; Kremer and Köhne 1992; Merwe 1992).

Many of the rootstocks selected (e.g., 'G22', 'G6', 'Huntalas', 'Duke 6') failed over the years for different reasons. The present status of some of the remaining rootstocks has been evaluated by Whiley et al. (1990). They recommend continued use of clonal 'Duke 7', although it has only mild tolerance and is sensitive to waterlogging conditions. The clonal rootstocks 'Toro Canyon' and 'Thomas' should be investigated, and 'Martin Grande' appears to be nonproductive.

Efforts are continuing at the University of California-Riverside to find resistant rootstocks; there are still about 10 rootstocks from past selections under evaluation (Menge et al. 1992). In a survey of 16 orchards infected by the disease, three clonal rootstocks look better than 'Duke 7': 'Thomas', 'D9', and 'Barr Duke'. New collections were brought in from Central America. Seeds are collected and screened from a new breeding program consisting of 10 rootstock types (Menge 1993). Field evaluation is continuing as well. At the same time an effort is being made to develop resistant rootstocks by nonconventional means, including exploitation of somaclonal variation (Kurtz and Tolley 1989),

In other countries, California selections are also under evaluation and independent selection projects are under way. In South Africa (Bijzet et al. 1993) 105 seedlings were selected from 6000 seeds collected and grown from six rootstock cultivars known to have some root rot tolerance. This is a large, comprehensive study which is in its first stages. In the Canary Islands, Gallo Llobet (1992) selected West Indian root rot-resistant rootstocks from four sources. Approximately 29% of the seedlings survived the screening. West Indian rootstocks are preferred by local nurseries and can solve the salinity problem (Galan-Sauco 1976).

In Israel, although root rot is restricted at the moment to only a few locations, a selection process began immediately after the discovery of the problem (1982). Local selections and introduced germplasm were evaluated under root rot conditions. Fifteen clonal rootstocks passed the preliminary evaluation successfully and eight of them look promising (Zilberstaine et al. 1992). This group of rootstocks was introduced into California and South Africa for further evaluations. Most of the rootstocks selected in Israel belong to the West Indian race; in Israel and the Canary Islands, two places where selection is concentrated on this race, the percentage of resistant rootstocks is much higher in West Indian than in the Mexican and Guatemalan populations.

At present a holistic approach is recommended for root rot control in various countires because none of the rootstocks selected can fulfill all the requirements (Coffey 1992). Rootstocks play the main role in this approach, but other means are also necessary, including a very careful selection of soil, hygiene, biological control, and fungicides.

Other soilborne diseases are known to attack avocado roots and shoots, but they are much less important. Halma et al. (1954) found Guatemalan rootstocks to be more sensitive than Mexican rootstocks to *Dothiorella* and *Verticillium* wilt. Ben-Ya'acov and Frenkel (1974) found significant differences in sensitivity to *Verticillium* wilt among different West Indian rootstocks. One of the rootstocks, 'Degania 12', is extremely sensitive and its use was eliminated. On the other hand, Barchilon et al. (1987) found seedlings of 'Stewart' resistant to *Verticillium* wilt. Symptoms did not appear on most of the 'Stewart' seedlings after inoculation. The pathogen population remained low in the stem parts, and an investigation should be conducted to study the trees grafted on this rootstock.

Dematophora necatrix is harmful to avocado roots in Israel and is a serious problem in Spain (J. M. Farre, pers. comm.). Differences in sensitivity to this fungus among rootstocks are not known. *Phytophthora citricola* has become a serious pathogen of the avocado in recent years. Tsao et al. (1992) found that some rootstocks that are tolerant to *P. cinnamomi* are sensitive to *P. citricola.*

F. Combinations of soil stress factors

Frequently, soil stress factors act together, sometimes synergistically, such as root rot and poor aeration or root rot and salinity, or sometimes antagonistically, such as root rot and lime. The breeder should take into account actual combinations of factors and select rootstocks for them, and not for one individual factor. The most frequent combinations are root rot and salinity, salinity and lime-induced chlorosis, salinity and poor aeration, root rot and poor aeration, and root rot and acidity.

Productivity is important in avocado cultivation. Any rootstock tolerant or resistant to stress or to any combination of stresses should not be considered resistant if it fails to induce high productivity regardless of the presence or absence of stress.

IV. ROOTSTOCK-SCION RELATIONSHIPS

A. Tree size and vigor

Avocado is a vigorous evergreen tree. The large size of the trees of most commercial cultivars causes excessive expenses for orchard management and overcrowding in the orchard. Bergh and Whitsell (1962) cited growers' opinions that shorter trees would reduce picking costs.

In avocado, dwarfness could be achieved by growing dwarf cultivars. However, at present small-sized cultivars (e.g., 'Wurtz', 'Colin V-33', 'Gwen') are not commercially successful enough. For large-sized cultivars, dwarfing rootstocks would be the best means of size control (Hodgson 1947; Bergh 1976; Brokaw 1982). Rootstock effect on tree size and vigor is strongly related to tree productivity; this interaction includes "tree efficiency," discussed in Section IVC.

Numerous methods for estimating tree size in fruit crop have been proposed (Cummins and Aldwinckle 1983). Trunk size, either above or below the graft union or at both locations, is very common. Either trunk diameter or circumference is measured (Warneke et al. 1972; Ben-Ya'acov 1976a; Bergh et al. 1988; Gregoriou, 1992; Köhne 1992; Oster and Arpaia 1992) but circumference is preferred because the cross section is never a complete circle. Cross-sectional area can be calculated but does not add any additional information (Gregoriou 1992). Trunk measurements do not correlate well with the actual dimensions of the tree, so investigators measure tree height (Oster and Arpaia 1992; Barrientos-Priego et al. 1992) or canopy diameter.

Arpaia et al. (1992) calculated canopy volume by measuring tree height and width. To compare orchards of different ages, Menge et al. (1992) divided trunk diameter measurements (2 cm above the bud union) by the tree's age in years and calculated tree volume growth per year by measuring the height and diameter of the canopy, estimating canopy size and dividing it by tree age. Data obtained by this method are related to tree growth rate rather than tree size.

A completely different calculation was made by Ben-Ya'acov et al. (1993a) to study tree efficiency (see Section IVC). They related yield to unit area occupied by the tree rather than to tree volume. The area occupied by the avocado tree was measured by aerial photography (Ben-Ya'acov 1978; Edelbaum et al. 1988). The correlation between area determined by aerial photography and ground measurement was high (r = 0.9), but a coefficient was necessary to adapt the laboratory measurements to the actual situation in the field (Kadman et al. 1976).

In Israel, a West Indian tree called 'Maoz' (Kadman and Ben-Ya'acov 1980), with pronounced dwarf characters, was found to be a consistent source of dwarfing. 'Maoz' was selected from a group of "Nachlat" seedlings, planted at Kibbutz Maoz-Haim in the Bet-Shan Valley. When grafted on its seedling or clonal rootstocks of 'Maoz', different cultivars are smaller than on any other rootstock, with clonal rootstocks more dwarfing than seedlings. 'Maoz' is sensitive to poor soil aeration but highly tolerant to lime and saline conditions. 'Maoz' is representive of a group of West Indian rootstocks called in Israel the Nachlat group, which have been grown as seedlings over many years and are characterized by tolerances and sensitivities similar to 'Maoz' (Ben-Ya'acov 1977a; Ben-Ya'acov et al. 1979, 1993a). A grafted orchard on Nachlat-type rootstocks can easily be identified by typical cracks on the trunk under the bud union. These cracks resemble those caused by the Sunblotch viroid (Wallace and Drake 1972) but are more regular and easily distinguishable from the viroid cracks. The degree of dwarfing by Nachlat rootstocks in terms of projection area is about 25%.

Rootstock dwarfing can be attributed partly to unfavorable conditions for a given rootstock. In the case of Nachlat rootstock, however, growth is limited even under the best growing conditions. Rootstocks belonging to this group are still the favored ones where soil is well aerated, and salinity and lime-induced chlorosis are the limiting factors; no other avocado rootstock can withstand such conditions. Moreover, as a rootstock the Nachlat group induce productivity (Ben-Ya'acov et al. 1992c).

The Nachlat group is not homogeneous, and various rootstocks that are in use in Israel are considered more or less typical of the group. The so-called less typical are stronger, although still dwarfing, less sensitive to soil aeration, and are preferred now for planting under saline and lime conditions. The 'Zrifin 99' rootstock is the best representative of this group among the seedling rootstocks (E. Tomer, pers. comm.). 'Nachlat No. 2' represents the other extreme characteristics, with its significant dwarfing effect, which varies from one cultivar to another (Bergh and Whitsell 1962). The upright-growing 'Ettinger' lost apical dominance when grafted on rootstocks of this group (Ben-Ya'acov et al. 1979, 1993a), and 'Hass' declined in many cases.

There are some West Indian seedling tree populations around the world that resemble the Israeli Nachlat type, such as many trees in La Antigua, Vera Cruz, Mexico. A comprehensive description of such populations was published by Galan-Sauco and Fernandez-Galvan (1983, 1985) in regard to the avocado of La Gomera, of the Canary Islands. They describe typical characteristics of dwarf trees, such as short internodes. In general, the trees were found to be of much smaller size than would be expected for their age.

Dwarfing rootstocks have also been found in Israel among Mexican seedling rootstocks. Compared with three other Mexican rootstocks, 'Benjamina', for example (Ben-Ya'acov et al. 1993a) significantly reduced the projection area of grafted 'Hass' trees. The average area occupied by 'Hass' trees grafted on 'Benjamina' and on 'Zofit No. 2' rootstocks was 18.6 and 24.5 m^2, respectively.

Usually, dwarfing is not the main aim of avocado rootstock breeding but a by-product. In Mexico, Barrientos-Priego et al. (1992) investigated the reduction in tree size that can be achieved by using a dwarfing cultivar ('Colin V-33') as seed source. The seedlings were grafted with various cultivars and measured 6 years after grafting. Taking the height of the tree as the criterion, the rootstock dwarfing effect varies from 32% to 68% (percent reduction relative to the highest tree of the same cultivar) for the various cultivars. Canopy diameter was reduced from 27% to 67% by the rootstocks relative to the largest tree canopy. The rootstock inducing the smallest tree should be evaluated as clonal rootstocks for their productivity and other characteristics.

To obtain a better understanding of characteristics involved in dwarfness, Lopez-Jimenez and Barrientos-Priego (1987) studied the trunks of seedlings from the same group and found that a higher proportion of transversal bark area occurred in dwarf trees than in tall trees. Tree size as influenced by rootstocks of different horticultural races was studied in Cyprus by Gregoriou (1992) in a long-term experiment. Trunk cross-sectional area was unaffected by rootstock type when the grafted cultivar was 'Fuerte', but with 'Ettinger' a large and significant difference was found between the same rootstocks. The cross-sectional area of the trunk 20 years after planting for the rootstocks 'Topa-Topa', 'West Indian', 'Duke', and 'Mexicola' was 791, 508, 383, and 289 cm^2, respectively. Warneke et al. (1972) compared trunk cross-sectional area of 'Bacon' trees on 'Ganter' (Mexican) rootstock propagated by seed and vegetative methods and observed that seedling rootstocks induced faster development.

In California and South Africa clonal rootstocks that had been developed previously for root rot resistance (see Section IIIE) were investigated for other characteristics, including growth and vigor. Oster et al. (1985) found that under low saline conditions 'Duke 7' was the most vigorous, but the order of vigor changed with salinity. Under highly saline conditions, 'Borchard' and 'G755' were more vigorous than 'Duke 7'. The development of 'Borchard' and 'G755' were unaffected by the salinity level. In another experiment (Oster and Arpaia 1992) the order of the rootstocks changed; 'Duke 7' was found to be the most vigorous under saline conditions and 'Parida' and 'G755B' the least.

Arpaia et al. (1993) compared eight root rot-resistant clonal rootstock selections and two sensitive rootstocks in the absence of *P. cinnamomi*. 'Hass' trees grafted on the 'Borchard' rootstock were found to be the most vigorous followed by 'G755A' and 'Topa-Topa'; on 'G755C', 'Toro Canyon', and 'D9' trees were smaller than the others, and 'Duke 7' produced trees average in size.

Menge et al. (1992) studied the performance of the same rootstocks, included in 16 field experiments with root rot present. As the orchards varied in age, trunk diameter and canopy volume were divided by years. A tree's dimensions depend on the sensitivity of its rootstock to root rot; hence the trees grafted on sensitive rootstocks such as 'Borchard' and 'UCR 1033' were smaller than 'Duke 7' and those on tolerant rootstocks ('Thomas', 'D9', and Barr Duke') were larger than 'Duke 7'.'D9', expected to be a dwarfing rootstock, did not dwarf trees on it.

Bergh et al. (1988) included clonal rootstock 'Duke 7' and three seedling rootstocks ('G6', 'Topa-Topa', and *Persea nubigena*) in a 7-year experiment with 'Hass' and 'H670'. Tree size was measured as trunk circumference above the graft union. *P. nubigena* rootstocks induced vigorous growth and larger trees, which reduced tree efficiency as yield was not increased.

In South Africa, Köhne (1992) evaluated three Californian root rot-resistant rootstocks; 'Duke 7', 'G6', and 'G755C'. Trunk circumference was measured 20 cm above ground level. 'G755C', a relatively nonproductive rootstock, induced the largest of trunk size.

In Israel, clonal rootstocks were developed. Some Israeli clonal rootstocks, such as 'Maoz', demonstrated a very significant dwarfing effect, which sometimes results in decline. Some clonal rootstocks obtained from productive trees (Ben-Ya'acov 1985, 1986) demonstrated size control and they will be discussed in reference to tree efficiency. One of these rootstocks, 'VC 68', showed a clear dwarfing effect and its trunk diameter was smaller than the diameter of the grafted vigorous cultivar 'Horshim' (Ben-Ya'acov et al. 1993a).

A general discussion in regard to dwarfing rootstocks was included in a paper of Bergh and Whitsell (1962). The consensus had been that a semidwarfing rootstock might be advantageous for vigorous cultivars (Hodgson 1947) and that such rootstocks may be associated with precocity and higher yield (Bergh and Whitsell 1962). Dwarfing rootstocks were considered to have disadvantages, including shallower roots requiring frequent irrigation and thus intolerance of mismanagement. We admit today that the Israeli avocado dwarfing rootstocks of the Nachlat type suffer from these problems. As the orchards get older they start to decline and feeder roots are hard to find. Stronger rootstocks can more easily withstand complex stresses, and most avocado-growing countries face such a situation. The possibility of selecting new avocado rootstocks resistant to root rot or rootstocks that tolerate salinity and lime and at the same time are dwarfing and productive is realistic only on very well aerated soils. Nevertheless, the search for dwarfing rootstocks in the well-aerated volcanic soils of the Mexican highlands has a much better chance for good results and should be continued.

B. Compatibility

There are no known compatibility problems within the *P. americana* species. This statement covers any graft relationship between and within the three different races, also known as botanical varieties or subspecies. In some cases rootstock overgrowth or undergrowth was noted and even described in the literature. The explanation for such phenomena is that one part of the grafted tree, either the rootstock or the scion, is much more vigorous than the other (Ben-Ya'acov et al. 1993b, c). In some cases a certain rootstock was not well adapted to a certain cultivar, and vice versa. Sometimes this results in the death of many young trees, up to 50% of the population of a given combination (Ben-Ya'acov et al. 1979). Even such cases could not be identified as noncompatible as long as the reason for the failure is not known.

Among trees of different *Persea* species, avocado is compatible only with species belonging to the subgenus *Persea*, and not to those of the subgenus *Eriodaphne*. This was demonstrated clearly by Frolich et al. (1958), during investigations conducted to solve the root rot problem in California (Schroeder and Frolich 1955). *P. schiedeana*, as a species of the subgenus *Persea*, can easily be grafted on avocado, but the reciprocal combination did not survive long in Honduras or in California. Zentmyer (Sauls et al. 1976) mentioned that success varies with the source of *P. schiedeana* collection. In Honduras 'Fuerte' was growing very poorly on *P. schiedeana* as the stock had overgrown the scion, but in another planting growth was successful (Schroeder 1974).

C. Precocity and Yield

According to Cummins and Aldwinckle (1983), precocious fruiting may be a conspicuous rootstock effect and may occur independently of a dwarfing influence. They present data in support of this declaration from various fruit species. In regard to production, they preferred "tree efficiency" as the best criterion, with yields calculated according to different expressions of tree size. Rootstock experiments in citrus and in deciduous trees indicate a significant influence of rootstock on precocity and productivity. In avocado, the history of rootstock experiments is short, and until the end of the 1960s most rootstock experiments were planned on a short-term basis, not aimed at obtaining yield data.

1. Seedling Rootstocks. Halma's experimental system (Halma 1954) was aimed at collecting yield data for enough years on a significantly large field scale of approximately 50 plots in California. Unfortunately, Halma lost most of his experimental plots relatively early (see Section IIB), and from the data collected, he was unable to draw any conclusions in regard to yield. Nevertheless, Halma had the impression (G. Goodall, 1970, pers. comm.) that productivity does not depend on the horticultural race of the rootstock-Guatemalan or Mexican-but on the specific rootstock involved. Thus rootstocks belonging to each race could be found among the best producers and the worst producers in some of his experimental plots.

Oppenheimer (1963) established a seedling rootstock x variety experiment at Qubeiba, Israel in 1949. It included five rootstocks and four cultivars and is the only known experiment that was able to provide 10 years of yield data during that early period. For the four cultivars included, the Guatemalan seedling rootstocks 'Nabal' and 'Benik' improved productivity by approximately 30% relative to the Mexican rootstocks and to 'Fuerte' hybrid rootstock. The Qubeiba experiment was the first to show that improved production can be achieved in avocado by using the right rootstock at a site where no particular stress factor was identified. Growers who applied conclusions from the Qubeiba experiment under different soil conditions, especially where lime was present, failed, as the Guatemalan rootstocks were sensitive to chlorosis, a fact known from Halma's data (Halma and White 1951).

The effect of rootstock on productivity was then studied in some orchards planted between 1960 and 1964 and not designed as experiments (Ben-Ya'acov 1973, 1976a). An important and applicable conlusion of this was that West Indian rootstocks are not poor producers, and in most cases trees grafted on them produced normal yields, even better yields than on Mexican rootstocks in the same plot. Until 1969, planting under the saline conditions prevailing in many parts of Israel was not recommended or supported, and the results above enabled such plantings.

A few years after Oppenheimer concluded his experiment, and based on his conclusions, Ben-Ya'acov (1972) established a new long-term large-scale rootstock scion field research project in commercial orchards. The aim was to find the best rootstocks, scions, and rootstock-scion combinations for each set of climatic and soil conditions prevailing in Israel and for each commercial variety (Ben-Ya'acov 1987). The propagation material had been chosen from commercial sources. A comparison of rootstocks was possible by grafting them with the same source of scion, and a comparison of sources of scion, by grafting them onto the same rootstock. Each experiment included a certain number of rootstock-scion combinations, for comparison purposes. The experimental orchards were planted in a randomized block design in which the number of blocks in each experiment, and the number of trees representing each stionic combination per block, varied from experiment to experiment. The data collected were yield (kg/tree-year, as reported by the growers), area occupied by the tree (in m^2, as calculated from aerial photography), and tree condition in regard to chlorosis and leaf burn (by survey). From these data a cumulative yield per unit area (kg/m^2) and alternate bearing degree (%) were established. Analysis of variance was applied for each experiment. The entire project with seedling avocado rootstocks included about 350 experiments, in 70 settlements, incorporating 100,000 trees. It consisted of about 400 different rootstocks types and 400 different scion sources.

Data collected from this large experimental system served immediately for negative selection. Many rootstocks (and sources of scion) were found to be less productive, or more sensitive to soil stress or to *Verticillium* wilt, or they were infected by Sunblotch viroid. All these sources of propagation material were eliminated after which positive selection was carried out for the best rootstocks. Some experimental results are listed below.

At Ofir orchard (Ben-Ya'acov et al. 1979; Ben-Ya'acov 1987), four Mexican rootstocks were grafted with one source of scion 'Fuerte'. Up to the ninth year, the trees grafted on the four rootstocks produced 273, 254, 240, and 152 kg/tree cumulative yield. The fourth rootstock differed significantly from the other three, which did not differ significantly from each other. The fourth rootstock was 'Northrop', a Mexican cultivar, introduced from California, used to supply thousands of seeds to nurseries every year. However, as trees on this rootstock produced only about 55% of the yield of the leading rootstock, it was eliminated. Trees on 'Northrop' were unproductive in other experiments as well.

Different sources of scion of the 'Fuerte' cultivar were found to vary in their productivity. The yield reduction by a poor source relative to the best source in a given experiment ranged between 20 and 90%. There is evidence that graftwood was collected at Atlixco, Mexico, from different "identical" seedling trees under one name, 'Fuerte'. This can explain the difference in productivity. 'Hass' cultivar combinations resulted in 370, 313, and 236 kg/tree cumulative yield for 'Lula' and two Mexican rootstocks, respectively (differences were statistical significant).

At Bene-Deror (Ben-Ya'acov et al. 1992b), 'Fuerte' trees grafted on 'Nabal' (Guatemalan), 'APAM 23' and 'APAM 22' (Mexican) rootstocks produced 237, 155, and 149 kg/tree cumulative yield, respectively, for the first 7 years. These results agree with Oppenheimer's results (1963) in regard to the better productivity on Guatemalan rootstocks on sandy-loam soils.

At Qevuzat Schiller, 'Ettinger' combinations (Ben-Ya'acov et al. 1993b) included one Mexican rootstock ('Schiller No. 1') and one West Indian ('Schiller No. 10') of the dwarfing West Indian group, described earlier. The 6-year cumulative yield per tree was 205 kg for the Mexican rootstock and 233 kg for the West Indian; for the respective trees, leaf burn was 1.45 and 0.24 (ranking from 0 = no leaf burn to 5 = severe damage), and the coefficient of variation (CV) was 35% and 22%. This experiment showed that the West Indian rootstock 'Schiller No. 10' produced 14% more yield per tree (significant difference), significantly smaller trees, very little leaf burns, and a greater uniformity of the tree population. 'Schiller No. 10' is now one of the recommended dwarfing rootstocks used in Israel for the 'Ettinger' cultivar.

Two West Indian rootstocks were found to induce significantly different cumulative yield: 384 kg for 'Degania 117' and 324 kg for 'Acre'. The average area under the tree was 35.4 and 29.4 m^2, respectively, a significant difference as well. Dividing the cumulative yield by the area we found that the two rootstocks became equally efficient: 11.1 kg/m^2 for the first and 11.4 kg/m^2 for the second.

The 10-year cumulative yield of the 'Hass' cultivar on four Mexican rootstocks was 297a, 292a, 262b, and 223b kg/tree (Ben-Ya'cov et al. 1993a; different letters indicate mean separation). The respective projection area was 24.5a, 18.6c, 21.3b, and 21.7b m2. Hence the second rootstock ('Benjamina') became the most efficient, with 16.3 kg/m^2 relative to 10 to 12 kg/m^2 for the other rootstocks (Horshim orchard, planted in 1976). The difference was significant at the P = 0.01 level for all the data presented here.

The conclusions were as follows:

1. Rootstock type affects avocado productivity in all cultivars investigated.

2. Rootstock effect was significant in most cases, although variability within each group of trees was very large due to the rootstocks seed origin.

3. The ranking of productivity of rootstocks on the basis of yield per tree can change when they are evaluated according to yield per unit of occupied area.

4. Dwarfing and productive rootstocks as well as vigorous and nonproductive rootstocks can be found in each of the three horticultural races of avocado.

5. Productivity as influenced by rootstock, scion, and rootstock-scion combination was consistent over the years.

6. A scion effect was found mainly in the 'Fuerte' cultivar. 'Fuerte' may be genetically variable.

7. Rootstock-scion combination is important and certain combinations may be unproductive.

The results changed rootstocks and scions use in Israel. The number of rootstocks was reduced from 600 in 1970 to 30 in 1990. Mother plantations have been established to supply seeds of the best types, and only this material may be used. The sources of scion was also changed. The use of nonproductive sources of scion has been eliminated. Only the best sources of scion are in use now and they are grown mainly in mother plantations. Viroid identification was instituted. Almost all sources of propagation material in Israel today are free of the Sunblotch viroid. A Center for Coordination of New Plantings was established and it chooses the best of the material selected for each grower according to local conditions.

The only known avocado seedling rootstock experiment outside Israel in which yield data were recorded for a long-term period is Gregoriou's (1992) experiment in Cyprus. Both 'Fuerte' and 'Ettinger' cultivars were grafted on three Mexican and one West Indian rootstocks. Yields are presented from the second 10 years of the tree's life, as no differences were found in the first 10 years. Good and consistent yields were recorded for both cultivars grafted on the leading rootstocks. For 'Fuerte', the best rootstock was 'Mexicola' and the poorest one was 'Duke' (585 and 373 kg/tree cumulative yield, respectively); 'Ettinger' produced best on a West Indian rootstock, followed by 'Topa-Topa', and much less on 'Mexicola' and 'Duke' (619, 567, 345, and 337 kg/tree, respectively). In 'Ettinger', large differences in tree size, as measured by cross-sectional area, probably explain the large difference in productivity. Generally speaking, the larger trees produced greater yields, but the West Indian rootstock induced better productivity than could be expected on the basis of tree size.

Some conclusions from Gregoriou's experiment are in agreement with the Israeli results. Trees on West Indian rootstocks can produce as good yields as those on Mexican rootstocks (at least for one of the cultivars); rootstock performance depends on the cultivar. 'Mexicola' rootstock was the best for 'Fuerte' and the worst for 'Ettinger'. In Israel, 'Mexicola' was a low-grade rootstock and is no longer used. Gregoriou's results should be considered a classical case of rootstock-cultivar interaction.

2. Clonal Rootstocks. Seedling rootstocks are still widely used, but clonal avocado rootstocks are the rootstocks of the future (Wolstenholme 1988). In Wolstenholme's opinion, the only place for seedling rootstocks in the 1990s will be as "temporary interplanted trees among clonals." Whiley et al. remind us (1990) that "cloned elite rootstocks have revolutionized many fruit industries providing precocity, control of vegetative vigour, salt tolerance, lime tolerance and disease resistance." According to Hartman and Kester (1975), "clonal rootstocks are desirable not only to produce uniformity but, and this is equally important, to preserve special characteristics and specific influence on scion cultivars such as disease resistance, growth, and flowering habits." It should be mentioned that long before the idea of any clonal propagation method for avocado was even a thought, Webber (1926) wrote the following: "The great problem before us is to locate the one [avocado] seedling among thousands, be it Mexican, Guatemalan or West Indian, the progeny of which will give us the best results with a certain fruit variety on a certain soil. This is a problem of such magnitude that only by united effort can it be attacked with any great hope of solution within a reasonable time. To reach a final solution every grove planted must, in a sense, be an experiment, and be so definite as to stock and bud as to furnish exact data that may ultimately be used in solving the problem."

Avocado clonal rootstocks can be selected for one or more soil stress factors and then evaluated for other characteristics, particularly productivity. Using this procedure, root rot-resistant clonal rootstocks were selected at the University of California (Zentmyer 1972, 1980), and salinity- and lime-resistant rootstocks were selected in Israel (Ben-Ya'acov 1985; Kadman and Ben-Ya'acov 1976, 1980). The possibility of improving the low fertility of avocado through this system is unlikely, but there is a chance of eliminating unproductive types (Whiley et al. 1990). An alternative procedure is to select avocado trees based on productivity and then evaluate their rootstocks adaptability to different soil conditions, including those that stress growth and productivity, (Gillespie 1952, 1954; Brokaw 1972; Ben-Ya'acov 1985; Ben-Ya'acov et al. 1992a).

Avocado orchards are not uniform either in tree behavior or in productivity. They are probably the most nonuniform of all fruit trees. The principal explanation for such a phenomenon is the rootstock variability resulting from seed heterozygosity.

The first to take advantage of avocado tree variability was Gillespie (1952), who found that various 'Fuerte' trees from the same source of propagation material, and planted under very uniform growth conditions, varied in average annual yield btween 12 and 500 kg in the Casper orchard at Yorba Linda, California. One out of eight trees was excellent and 1 out of 23 trees was really outstanding. Gillespie did not manage to propagate the rootstocks of his productive tree as he aimed to do.

Around 1977, Brokaw's addition (1987a) to Frolich's method led to new efforts in avocado rootstock propagation. Rootstocks selected for resistance to root rot (Coffey 1987; Zentmyer 1980) or to lime and salinity (Ben-Ya'acov et al. 1979; Kadman and Ben-Ya'acov 1976, 1980, 1981, 1982) were widely distributed and evaluated in California and Israel. However, there were no good rootstock candidates to improve productivity. To choose such candidates, a follow-up was made in existing orchards (Ben-Ya'acov 1985) included in the seedling rootstock research project. All 100,000 trees included in the long-term project became subject to screening to select the most promising ones for duplication (Ben-Ya'acov et al. 1992a). After summarizing data from many orchards, we came to the general conclusion that outstanding individual trees of 'Fuerte' and 'Hass' produce 100% more than average trees of those stionic combinations and outstanding 'Ettinger' produced 40% more yield. This yield advantage is large enough to justify cloning the most productive rootstock (Ben-Ya'acov 1986).

Additional selection criteria were applied for the selection of outstanding trees rather than just "total yield per tree." "Tree efficiency," based on the projected area of the tree alternate bearing, based on annual deviations from the average yield, and precocity were taken into account as well as leaf burn and chlorosis. After the candidate trees were chosen, their rootstocks were induced to sprout by complete removal of the tree down to the graft union (Ben-Ya'acov et al. 1992a). The sprouting rootstock and the scion were grafted in a graftwood orchard and in pots. The trees were indexed for viroid. In some cases it was difficult to determine whether the sprouting branches were from the scion or from the rootstock. In Israel isozyme technique was used to differentiate between the two (Degani and Ben-Ya'acov 1983).

By screening commercial and experimental orchards in Israel, a few hundred candidate trees were identified. About 160 new promising clonal rootstocks were obtained; approximately 100 of them were from under outstanding grafted trees of commercial cultivars, and the remaining 60 from trees resistant either to lime, salinity, or root rot. About 50 other clonal rootstocks were obtained from trees in the Israeli avocado germplasm bank for evaluation on a small scale. All clones serving as rootstocks were given "VC" numbers (for being vegetative clones for the Volcani Center research program). A guide to the Israeli avocado clonal rootstocks was published in Hebrew (Ben-Ya'acov et al. 1988). Numbers between VC 1 and 200 are reserved for the rootstocks developed in Israel; from VC 201 to 300 for rooted rootstocks from the germplasm bank; and from VC 801to 831 for rootstocks selected locally for resistance to root rot. Altogether, 228 rootstocks are included in the list.

Evaluation in the orchards began when the first rootstocks developed were available in minimum quantity, enabling the nurseries to produce sufficient number of trees for comparison study. The trees were distributed in orchards with differing ecological conditions. The plantings were in commercial orchards but planned as experiments in a randomized block design. The planting system and follow-up methods were identical to those described earlier (Ben-Ya'acov 1972, 1985, 1987) and in this review for the seedling rootstocks experiments.

During the period 1979-1987, approximately 350 field plots were established to evaluate the selected rootstocks, the different scion sources of scion, and the specific stionic combinations. About 70,000 trees were included in this evaluation system, of which one-third were grafted on Mexican rootstocks and the remaining two-thirds on West Indians rootstocks.. The evaluation includes trees duplicated from the outstanding trees (i.e., copy trees), new combinations of rootstock and scion, and a test of adaptibility of rootstock under various cultivars.

Data collected resulted in the elimination of some new rootstocks. Trees on some rootstocks were unproductive at most evaluation sites, or only where detrimental factors were found. Rootstocks were eliminated for general or specific purposes.

Most yield data show that good to high productivity can be achieved from duplicated trees, but as can be expected, the best trees are not the same in every location and depend on different ecological conditions. Sometimes a rootstock produces best with a different scion selection of the same cultivar and not the one originally discovered scion with this rootstock, or even with another cultivar.

Not many experiments were conducted in which the new rootstocks are compared with traditional seedling rootstocks, as the main purpose of the evaluation system was to select the best rootstocks (and stionic combination) for a given local condition and cultivar. Some examples were published for the 'Ettinger' cultivar (Ben-Ya'acov 1992a).

At Kibbutz Horshim, Mexican clonal rootstocks 'VC 40' and 'VC 13' were compared with a Mexican seedling rootstock, 'Ometz 18/4'. The cumulative yield up to the ninth year for these three rootstocks was 371, 295, and 227 kg, respectively, a highly significant difference. 'VC 40' was selected from an outstanding productive 'Ettinger' tree, while 'VC 13' was propagated from a resistant tree. It is notable that the CV for these tree rootstocks was 17%, 17%, and 34% respectively, which means that the trees grafted on the clonal rootstocks were much more uniform. 'VC 13' was propagated by cutting from the 'Ometz 18/4' tree, which was the source of the seed for this experiment.

At Kibbutz En haHoresh, an 'Ettinger' experiment was planted in 1982. Until the eighth year the Mexican rootstocks VC 57 (clonal), VC 51 and 'Schmidt' (seedling) induced productivity of 230, 237, and 161 kg/ tree, respectively. Trees on clonals yielded approximately 45% more; CV values were 22%, 27%, and 35%, respectively.

Due to the salinity of the irrigation water, Mexican rootstocks are not going to be planted in Israel in the foreseeable future, even if they are very productive (see Section IIIA); hence we concentrated on West Indian rootstocks from highly productive trees. To find productive tree with West Indian roots is more difficult than with Mexican roots because West Indian rootstocks are more uniform in productivity (Ben-Ya'acov 1976a; Ben-Ya'acov et al. 1993b), and hence do not appear at the extreme edges of the distribution curve, where outstanding productive (and nonproductive) trees can be found. Searching for productive trees was especially difficult with the 'Ettinger' which is less variable than other cultivars. Hence our list of clonal rootstocks drawn from very productive trees includes only 11 West Indian rootstocks grown under 'Ettinger' trees, and even these were discovered very late in the research period.

To replace West Indian rootstocks originally taken from 'Ettinger' trees, we included more rootstocks selected earlier for their resistance to lime and salinity, such as 'Maoz' ('VC 43') and 'En Harod' ('VC 28'). Trees on some of them found to be productive on heavy soils when irrigated with water of medium salinity. They produced more than selected West Indian seedling rootstocks and clonal Mexican rootstocks selected earlier. The resistant group includes 'VC 26', 'VC 27', 'VC 28', and 'VC 44'. Later, some West Indian rootstocks propagated from 'Fuerte' trees were found to induce better productivity than rootstocks from the resistant group when used with 'Ettinger' as scion, and this includes 'VC 6' and 'VC 65'.

'VC 51', a clonal rootstock, originated from an 'Ettinger' is probably a West Indian x Guatemalan hybrid, with excellent performance in heavy to light soils where lime content is low. Productivity is good to very good at different salinity levels and should be considered the most universally adapted rootstock found (Ben-Ya'acov 1992a; Ben-Ya'acov et al. 1992a. R. Steinhardt, pers. comm.).

There are more clonally selected rootstocks and more evaluation experiments with 'Fuerte' than with 'Ettinger'. Many 'Fuerte' orchards were uprooted or topworked in Israel during the research period, due to extreme climatic events and mismanagement.

Among the Mexican rootstocks, 'VC 31' is an excellent producer where growth conditions are not limiting. At Metzer, 'VC 31' and 'VC 39' and two Mexican resistant clonal rootstocks produced yields of 374, 271, 105, and 84 kg/tree, respectively, up to the age of 12 years. The increased yield was negatively correlated with defoliation in the blooming season (Zilkah, 1988). The 'VC 31' rootstock originated from an offshoot of Mexican seedling rootstock. The original 'Fuerte' tree grafted on this rootstock yielded 500 kg in its first 5 years of productivity, while the group of trees to whom it belonged produced 253 kg/tree average yield.

Twenty-four West Indian clonal rootstocks were obtained from 'Fuerte' trees, but only about half of them have been reevaluated to date. 'VC 7' induced high productivity on heavy nonaerated soil where lime is not present. A few rootstocks ('VC 6', 'VC 54', 'VC 65', and 'VC 68') were superior to 'VC 7', where lime is present. Only a few experiments with the 'Hass' cultivar have been summarized. Elimination of alternate bearing in 'Hass' by duplication of rootstocks from consistently bearing trees seems to be the main aim, as nonalternating trees produce, theoretically, bigger fruits. (In Israel, about 50% of 'Hass' production is unmarketable because of small fruit size).

With 'Horshim', some 'Fuerte'-originated rootstocks look promising. So far they improve productivity, control tree size, and reduce alternation, a negative factor in this cultivar. Promising rootstocks are 'VC 6', 'VC 65', and 'VC 68'; the last one has an especially pronounced dwarfing effect.

During the 15 years since Brokaw's (1987a) clonal propagation method became available, most of the effort has been devoted to propagation of root rot-resistant rootstocks which were later evaluated for their productivity (Bergh et al. 1988; Köhne 1992; Arpaia et al. 1992, 1993). In Israel, where the root rot problem did not seem to be very serious, selection for better productivity under stress conditions was of high priority. To adopt the Israeli approach, yield records are being collected at Westfalia Estate in South Africa (Smith and Köhne 1992; Smith et al. 1993). As the researchers there identify trees that perform consistently well and trees that perform consistently poorly. When they calculated the annual yield of the best trees, they found it to be between 36 and 60 tons above the industry mean yield of 12 ton/ha (1992). In the following year (1993) they found a tree that yielded 1100 kg. To improve productivity, they have already made attempts to duplicate trees of the best-producing group.

3. Productivity of Resistant Clonal Rootstocks. Avocado clonal rootstocks production trials related mainly to rootstocks selected for resistance to root rot, were initiated in California in 1981 (Bergh et al. 1988) and in 1986 (Arpaia et al. 1992, 1993) on soils where *P. cinnamomi* was absent. Little has been done to evaluate horticultural attributes such as tree productivity, vegetative vigor, and fruit quality of the selections prior to these experiments (Arpaia et al. 1992). Bergh et al. (1988) had to terminate a 'Hass' experiment early, but the results show some advantage to the clonal rootstock 'Duke 7' relative to the seedling rootstocks of 'Topa-Topa' (equal-sized trees) and *P. nubigena* (larger trees). Low productivity was observed for 'Hass' trees grafted on 'G6' seedling rootstock.

Arpaia et al. (1992, 1993) also worked with 'Hass'. For 'Hass', eight groups of trees on clonal rootstocks were planted in 1986 and two in 1987. Up to the sixth year, 'Duke 7' and 'Borchard' were the best rootstocks, while the three representatives of the 'G755' group were very disappointing. 'Topa-Topa', 'Toro Canyon', and 'D9' induced medium productivity, while 'Thomas' and 'G1033' could not be rated. Comparing the two favorite rootstocks, 'Duke 7' is preferred since it produces the same yield on smaller trees (53 m^3 tree canopy volume) than 'Borchard' (63.4 m^3) and it has some tolerance to root rot, which is missing in 'Borchard' (Menge et al. 1992).

Evaluation of three rootstocks from the same group was initiated in South Africa by Köhne (1992) in 1987. 'Hass' grafted on clonal rootstocks produced the first commercial yield in 1990. 'Duke 7' performed best (33.5 kg/tree), 'G755C' performed worst (5.5 kg/tree), and 'G6' was intermediate (14.5 kg/tree).

Whiley et al. (1990) concluded that 'Duke 7' is the best rootstock. It is a reliable and if managed correctly will produce uniform trees of good performance. However, Coffey remarked (1992) that long-term performance of 'Duke 7' has been mixed, with many failures. On *Phytophthora*-infected soils 'Duke 7' cannot be considered a highly productive rootstock.

Uniformity of clonal rootstocks is important economically. In Israel (Ben-Ya'acov et al. 1992a) field experiments include tree variability, and in one experiment the CV of clonal rootstocks was 17% compared to 34% for seedling rootstock where the same rootstock tree was used for seeds and clones. In this comparison the rootstock was Mexican type, which we consider more variable than the West Indian (Ben-Ya'acov 1976b) when used as seedling. In a comparison of the CV of seedlings and clonal rootstocks, Steinhardt (pers. comm. 1992) also found a significant uniformity for clonal rootstock.

As clonally propagated trees are genetically identical, how could they vary more than is caused by soil variability? If variability among trees really exists, it might be explained by differences induced in the nursery, especially by the fact that each tree propagated has its own seedling nurse rootstock (Brokaw 1987a).

Biennial bearing pattern is of great economic importance in the avocado. For selection purposes, we prefer to calculate alternate bearing per tree, according to a formula developed by the statistician A. Genizi at the Volcani Center. The alternate bearing formula is based on calculation of the deviation of each yield from the biennial average, and summing up the deviation over the years.

Hodgson (1946) determined that alternate bearing is not transferred from rootstock scion. However, it is unknown if the rootstock can control alternate bearing of the grafted tree. Studies to determine this are under way.

Some examples from the experiment in Israel based on Genizi's formula for alternate bearing follow. For 'Hass' cultivar grafted on two seedling rootstock, 'Sarid' and 'Barkai 25/2' at HaOgen, the values were 61% and 81%, respectively. For 'Fuerte' grafted at Yad Mordechai on seedlings rootstocks 'Ashdot 17' and 'Nachlat 2', the values were 54% and 74%. For 'Ettinger' grafted on two clonal rootstocks, 'VC 5' and 'VC 14' at En haHoresh, the values were 28% and 43 %. For selection purposes of outstanding productive trees we compared the mean value of a group of trees to individual trees. At Qeuvatzat Shiller the mean value for 'Ettinger' treees grafted on the West Indian rootstock 'Shiller 10' was 47%, but for the most productive tree it was only 17%.

D. Rootstock Effect on Fruit Quality

Quality characteristics are known to be affected by rootstock in citrus. In avocado only a few characteristics have been studied: fruit size, fruit shape, seed size, oil content, dry weight, and postharvest performance.

In California (Arpaia et al. 1992, 1993), 'Hass' fruit size was the same on both productive and nonproductive rootstocks. In Cyprus (Gregoriou 1992), fruit size of 'Fuerte' and 'Ettinger' cultivars was unaffected by any of the four seedling roostocks. Köhne (1992) studied rootstock influence on 'Hass' fruit and found that 'Duke 7' produced shorter and rounder fruits with larger seed than did the two other rootstocks. The postharvest performance of fruit from trees grafted on all three rootstocks was equal and excellent. In another research project, in South Africa (Smith and Köhne 1992; Smith 1993), fruits from highly productive and from unproductive trees, which probably differ in their rootsocks were examined for typical fruit disorders known in South Africa. The fruits from the nonproductive trees ('Fuerte') were much more sensitive to both external and internal damage. 'Fuerte' fruits from very productive trees are known to be of better storage quality than those from low-yielding trees also in Israel.

In avocado, maturity is determined by oil content. Oil content for 'Fuerte' and 'Ettinger' in Cyprus (Gregoriou 1992) was unaffected by any of the one West Indian and three Mexican rootstocks involved. However, Kadman and Ben-Ya'acov (1976) found that oil percentage of fruits from trees on Guatemalan and hybrid rootstocks was higher than when on Mexican roots. In California (Arpaia et al. 1993), dry weight was little affected by any of the five rootstocks included in the test. In Australia, Young (1992) claims that there is a consistent effect of rootstock race on avocado maturity in southeast Queensland, where the Mexican rootstocks induce maturity 2 to 3 weeks earlier for 'Fuerte' and 6 to 8 weeks earlier for the 'Hass', relative to Guatemalan hybrid rootstocks. According to Young, (1992) Mexican avocado rootstocks from indexed trees introduced from California are unadapted to the local conditions of southeast Queensland. This explains the stress symptoms found on the grafted trees, which results in early fruit maturity.

In Israel, rootstocks were found to affect the length of the harvest period of 'Ettinger'. 'Ettinger' usually has a short picking season, and when it is grafted on Mexican rootstocks it must be picked by the third week of November. Later, the fruit loses its brightness, the seeds become free in their cavity, and through the ripening process fruit quality decreases considerably. When the 'Ettinger' is grafted on 'Nabal' (Guatemalan) its fruit is of good quality until the end of January without any of the above-described symptoms, but the shelf life becomes short, thus eliminating the possibility of picking the fruits in January (G. Zauberman, pers. comm. 1980).

The rootstock can affect fruit quality through its influence on the uptake of nutrients. Bingham and Nelson (1971) found that a high soil sodium absorption ratio increases sodium content of the leaves, resulting with higher oil content of the fruit, which is a sign of faster maturation. They generalized this phenomenon to extend to other salt-stress conditions. In many cases the rootstock affects Zn absorption and that can affect fruit shape; rounder fruit is known to be typical sign of zinc deficiency.

E. Rootstock Effect on Climatic Adaptation

The three avocado horticultural races (or subspecies) differ widely in their cold sensitivity (Bergh 1975b, 1976) due to their different origins. For this reason the above ground part of the sensitive West Indian rootstock should be very well protected in frost-hazard conditions, as recommended in Texas (Law et al. 1948), California, and Israel. In regard to the effect of the rootstock on the top's sensitivity to frost, , Halma (1954) found West Indian rootstocks to be too tender for Californian conditions, probably because of low soil temperatures (Sauls et al. 1976). Krezdorn (1974) said that a frost-resistant rootstock could not help a sensitive cultivar. Ben-Ya'acov et al. (1979) came to the same conclusion upon surveying orchards in February 1973 following a heavy frost in December 1972. In two 'Hass' avocado orchards, the frost injury was rated the same when the trees were grafted on Mexican or on West Indian rootstocks.

In Texas (Cooper et al. 195 7) attempts have been made to solve the two main problems of the avocado industry, salinity and frequent frosts by developing intraracial hybrids found in the state of Tamaulipas in Mexico (Schroeder 1954). Under such conditions and according to our present knowledge, it seems better to select West Indian rootstocks for salinity and Mexican or hybrid cultivars for cold hardiness. The use of West Indian rootstocks was recommended by the Texas growers committee at that time (Law et al. 1948)

F. Nutritional Effect of Rootstock

Many examples of nutritional effects of rootstocks are known in the literature for various fruit species.. However, with the exception of clear deficiencies and toxicities, most of these cases do not explain any effects of the rootstock on tree development and productivity. This also holds true for avocado. We shall mention a few studies, excluding the effect of saline conditions, which were described earlier.

Haas (1950b) found calcium to be the element most affected by rootstock; the leaf calcium content of the grafted cultivar was higher on a Guatemelan rootstock than on Mexican rootstock. Embleton et al. (1962) and Ben-Ya'acov (1968, 1970; Ben-Ya'acov et al. 1992b) found consistent differences between Mexican and Guatemalan rootstocks in regard to cation absorption. On Guatemalan rootstocks grafted trees had more calcium and magnesium in the leaves, and on the Mexicans rootstocks more potassium. Embeton et al. (1962), Ben-Ya'acov (1992b), and Oppenheimer et al. (1961) found more nitrogen in the leaves of trees grafted on Mexican than on Guatemalan rootstocks. Ben-Ya'acov (1968) found the West Indian rootstocks to behave like the Guatemalan in respect to nutrient uptake. Labanauskas et al. (1978) compared two Mexican rootstocks and found more N, P, and Cu and less Mn in leaves of 'Hass' grafted on 'Duke' rootstock than on 'Topa-Topa'. Arpaia et al. (1993) found significant differences among 10 different clonal rootstocks in regard to leaf content of 13 elements in the grafted 'Hass' trees. No correlation between the element content and other variables was mentioned. The values were relatively high for all elements on all the rootstocks. In contrast, Menge et al. (1992), in a survey of 16 groves, found relatively low values of P, Zn, and Cu leaf content on all four rootstocks included. No correlation was found between rootstock performance and leaf element content, nor with mineral element levels in the soil. The only significant correlation was found between tree development and soil manganese. Nutrients in the different parts of the root system can also vary according to the rootstock type. Zilberstaine et al. (1991) found higher potassium uptake in the roots of the Mexican rootstock 'Topa-topa', than in those of the West Indian 'Degania 117'. Ben-Ya'acov (1968) found that most of the elements examined in the experiment (Mg, K, Na, Cl, P, N, and F, but not Ca and Cu) were more concentrated in root systems of Guatemalan and West Indian rootstocks than in those of Mexican origin.

G. Sunblotch Viroid

The Sunblotch viroid is a unique phenomenon of avocado. It is important that elimination of the viroid be included in every breeding program during the negative selection steps. Through registration programs, the viroid was almost completely eliminated from the propagation material in California (Wallace and Drake 1972) and in Israel. Once a tree in the field is infected, it is impossible to free it of the viroid. 'Huntalas', a promising rootstock for its root rot-resistance characteristics, was eliminated from the Riverside (California) breeding program when it was found to be a Sunblotch carrier.

In Australia and especially in South Africa, a symptomless type of the viroid was found. Many Mexican seed-mother trees used to supply nurseries in South Africa, were identified as viroid carriers and eliminated (Korsten et al. 1987). It has been found (Smith and Köhne 1992; Smith 1993) that 72% of nonproductive 'Fuerte' trees were infected by the Sunblotch symptomless viroid. It should be remembered that the latent-symptomless carrier type of the viroid produces 100% infected seeds, whereas the virulent type produces only 5 to 6% (Wallace and Drake 1972). As the viroid can be transmitted through root grafts, an orchard with more than 10 to 20% infected trees should be uprooted.

In Israel, the identification of infected sources of propagation material, whether seeds, clonal rootstocks, or scion, is an integral part of the rootstock-scion breeding project; when different sources of propagation material were chosen to be planted in foundation plots in order to supply the best material to nurseries, every item was indexed by the Agricultural Research Organization's Department of Virology. In the last 15 years very few cases of Sunblotch contamination were discovered in new plantings, possibly due to the use of seedling nurse rootstocks for clonal propagation.

V. FUTURE OF AVOCADO ROOTSTOCK BREEDING

In 1926, Webber claimed that "no factor of the avocado industry is more important than rootstocks, and there is no problem of the industry that we know less about, or which requires a longer time to solve." Although about 70 years have passed, the avocado rootstock problem still exists. For many years, people used to germinate any available avocado seeds and grow them as seedling trees and later as rootstocks to be grafted. Avocado horticultural races were known to the habitants of Mexico even before the European discovery of America, but only in the present century were seeds chosen for propagation according to their race. Athough produced by open pollination, avocado seedlings were found to be mostly true to type and especially to race.

The next step after the choice of seedling rootstocks according to race was the identification of specific seed-mother trees, either known as cultivars or of trees propagated from selected seedlings. A registration scheme was used in some countries, as part of Sunblotch viroid elimination, and horticultural knowledge became available.

Clonal propagation of avocado rootstocks became a practical method only about 16 years ago, and the clonal rootstocks are considered to be the rootstocks of the future (Wolstenholme 1988; Ben-Ya'acov 1989). Today, over 1 million such trees have been planted. In Israel, approximately 160 different clonal rootstocks are being carefully monitored and evaluated for different soil conditions; 20 of them have already been release commercially. On other countries, the 'Duke 7' is the primary clonal rootstock in use. The clonal orchards show good vegetative development and precocity. In most cases they bear more fruit than do regular (seedling rootstocks) orchards.

There is enough evidence to conclude that the two most important advantages of clonal propagation-increased uniformity of the trees and the conservation of important characters-have been proven in avocado. Therefore, selection of clonal rootstocks for different purposes should be continued, taking into account that improvement of productivity should not be neglected, while looking for resistance to biotic and abiotic factors.

The main line in new breeding projects for root rot-resistant rootstocks is a wide-scale selection among seedlings, resulting from open pollination of known-tolerant rootstock trees (Menge 1993; Bijzet et al. 1993). The newly developed rootstocks should withstand variable forms of the fungi. Disappointment with the 'G755' series, found to be unproductive rootstocks, induced retreat from intraspecific hybrids. In other breeding projects the procedure is to select rootstocks from very productive trees under stress conditions (Ben-Ya'acov 1992a; Smith et al. 1993).

Reevaluation of each rootstock is necessary to determine its ecological limitations. This is especially important for the elimination of damage resulting from the uniformity of trees with adverse characteristics (Ben-Ya'acov et al. 1992a,b).

Controlled hybridization and a genetic engineering approach cannot be profitably applied to avocado breeding, including rootstock breeding until better genetic information is available and assessment of the present variability is completed. In the meantime, there is a huge treasury of characteristics as well as a tremendous diversity among the avocado tvnes and its relatives to be studied.

Selected rootstocks are a key factor in solving any soil stress problem, but complete resistance is still only a goal and cannot be achieved in the near future. For this reason, agrotechnical means should be applied parallel to the use of resistant rootstocks. Moreoever, good productivity of a cultivar or productivity induced by the best productive rootstock can be achieved only if the essential factors are present at optimum levels.

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