ECOPHYSIOLOGY OF THE AVOCADO (*Persea americana* Mill.) TREE AS A BASIS FOR PRE-HARVEST MANAGEMENT

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SUMMARY

In spite of selection for thousands of years, the avocado is still a poorly domesticated tree in the early stages of adaptation to an orchard environment. Cultivars based on Guatemalan and Mexican germplasm, for the subtropics and Mediterranean climates, have only been available since the 1920's, and even in the best growing conditions the yield barrier of 30 t·ha^{-1} is hard to breach. Tropical "West Indian" (lowland) avocado cultivars and production technology is less well developed. Orchard performance is therefore still largely influenced by evolutionary hangovers and constraints. For "subtropical" types, we have to deal with the residual survival strategies of a late-successional, K-selected, small-gap colonizing mountain cloud forest tree. These include potentially vigorous vegetative growth in flushes, counter-productive to flowering and fruiting; delayed and typically irregular (mast) fruiting; unnecessarily profuse flowering in late winter synchronized by winter cold and drought; short-lived shade-adapted leaves borne increasingly further from the trunk on the tree periphery; energy-expensive fruits for large dispersal agents, hence the exhaustive nature of cropping on reserves, especially in large trees; and the tree's strategy to efficiently hoard, store and recycle carbohydrate and mineral reserves (hence "mineral-cheap" fruiting). Physiological attributes include potentially rapid C assimilation, but reduced photosynthesis under shade, water of Phytophthora stress; reasonable drought tolerance which however is at the expense of C assimilation and leaf efficiency; and the poorly researched dependence on perseitol rather than sucrose as the main translocation sugar. Manipulation implications center around canopy/tree size/light management and the alleviation of stress at critical times, to optimize C gain and allocation to fruiting on a sustainable basis. The prime need remains breeding for more manageable scion and rootstock combinations.

KEY WORDS: *Persea americana*, evolutionary ecophysiology, management strategies

INTRODUCTION

There is archaeological evidence that the Mexican ecotype of avocado was used and selected in Puebla, Central Mexico as early as 7000 - 8000 BC (Smith, 1966). Avocado fruits were therefore used by one of the earliest civilizations. There is little doubt that Meso-American people selected improved types from the diverse genepool of the genus *Persea*, subgenus *Persea*, and especially from amongst what is now known as *Persea americana*

and its botanical varieties (subspecies). Smith *et al.* (1992) thus noted that avocado "was domesticated several thousand years ago in Central America". They also state that the apparent early emergence of three distinct "races" of avocado suggests that avocados were "brought to cultivation from genetically diverse and widely separated wild populations". Undoubtedly, early selection by man would have been for improved fruit size and flavor, and a better fruit flesh to seed ratio, *inter alia*.

However, it was only in this century that the avocado became an important commercial orchard crop. Grafted trees of 'Fuerte', the "first generation standard of fruit excellence", were planted in California from 1911 - the start of the pace-setting "subtropical" (as opposed to "tropical") industry worldwide. There has been considerable progress in selecting other cultivars, now dominated by the second generation 'Hass'. Third generation cultivars are in prospect for the new millennium, plus advances in rootstock research and management technology - especially in the subtropics. Nevertheless, Wolstenholme and Whiley (1998) believe that according to modern criteria, cultivar (and rootstock) selection is still in its infancy, and that the tree has many residual features counter-productive to the needs of modern orcharding. In this sense, then, the avocado is still poorly domesticated. This is reflected in the yield problem and in the various approaches, with little standardization both within and between countries, to management and manipulation of the tree for higher and more consistent yields of quality fruit.

Continued selection and breeding, both of scion and rootstock cultivars, will in time contribute to more acceptable orchard performance to offset increasing production costs. Increases in our ecological, physiological and morphological (architectural) understanding of the tree will underpin technology advances. Of these, physiological research has progressed faster in the past two decades, as recently summarized by Whiley and Schaffer (1994). Excellent progress is being made in understanding the physiology of fruit growth (Cowan *et al.*, 1997, Moore-Gordon *et al.,* 1998), with further studies on the role of hormones, sugars and perseitol underway in Cowans laboratory at the University of Natal (Cowan *et al.*, 1998). Tree growth parameters are better understood since the studies of Thorp and Sedgley (1993) and Thorp *et al.* (1993, 1994). We believe that, for a tree in the early stages of orchard domestication for the imperatives of modern fruit growing, ecological and evolutionary constraints must also be appreciated. Little such information, apart from the anecdotal, has been printed. An ecological evaluation for pecan nut (Wolstenholme, 1979a, b) and for mango management (Wolstenholme and Whiley, 1995) proved helpful in explaining low yield constraints.

The main objectives of this mini-review are to summarize current knowledge on avocado evolutionary ecology, ecophysiology and growth habit. Where literature is scarce or lacking, we utilize current ecological theory to suggest possible explanations for tree responses. We attempt to highlight future research needs to improve our basic understanding, emphasizing avocado production in subtropical environments. Our approach is to attempt a broad ecophysiological perspective, sometimes speculative, to stimulate improved orchard management and meaningful research.

The Yield Problem and Its Causes

We have previously discussed the avocado yield problem and its causes, *inter alia* at two previous World Avocado Congresses (Wolstenholme, 1985, 1987, 1988; Wolstenholme and Whiley, 1992, 1998). We believe that it is still true to state that good growers in the cool, semi-arid winter-rainfall subtropics average 8-12 t·ha^{-1} (best growers 12 to 15 t·ha^{-1}). Israel's national average in the early 1990's was around 7.5 t·ha^{-1} (Homsky, 1995), which although fair was considered inadequate in view of the costs of production and trade situation. Prospective figures in the warmer, humid summer-rainfall subtropics are 12 to16 and 20 to 25 t·ha^{-1}. A target average yield of >30 t·ha^{-1}, over a period of at least 5 years and on a reasonably large scale, has been suggested and may well be attainable in the humid subtropics with high density planting and tree manipulation. There is little evidence that tropical avocado orchards, using predominantly West Indian (Lowland) germplasm, attain such yields, in spite of shorter fruit development periods and less "energy-expensive" fruits. Why are yields relatively low, are what can we learn from evolutionary ecophysiology?

Avocado Indigenous Habitat

The origin, indigenous range and distribution of the avocado have been widely discussed. Key names in this ongoing saga include Popenoe, Kopp, Williams, Schieber, Zentmyer, Bergh, Storey, Smith, Furnier, and Scora. The taxonomic problem is aggravated by a large diversity of germplasm, spread over a large area of diverse climate and soil due to mountain ranges and ancient volcanoes; and a long history of attempted domestication so that the modern avocado is a cultigen unknown in the wild. Some key articles leading to the modern synthesis include Popenoe (1935), Kopp (1966), Williams (1977) Bergh and Ellstrand (1986), Storey *et al.* (1987), Scora and Bergh (1990; 1992) and Bergh (1993). Nevertheless, avocado taxonomy is still in dispute, and Smith *et al.* (1992) note that the true status of "wild" trees is often questionable - some "wild avocados" may be seed discards from people and therefore feral. Taxonomic lines continue to be blurred by gene flow between the cultivated forms and the wild types.

For the purposes of this paper, we use Scora's interpretation, to be published in Whiley *et al.*'s (2000) definitive text on avocado. The key feature is that *Persea americana* is polymorphic, consisting of several taxa which are considered botanical varieties or subspecies. These include the three original "horticultural races", viz. var. *americana* (Lowland, formerly West Indian avocado), var. *drymifolia* (Mexican avocado), and var. *guatemalensis* (Guatemalan avocado) - regarded as geographical ecotypes. However additional recognized types are var. *nubigena*, var. *steyermarkii*, var. *zentmyeri*, var. *tolimanensis* and var. *floccosa*, and probably also vars. *constaricensis* and *tillaranensis*. Scora (in Scora and Wolstenholme, 2000) currently considers the *P. americana* species aggregate to consist of two groups, viz. vars *drymifolia* and *floccosa* allied with var. *steyermarkii*; and var. *nubigena* closely allied with var. *tolimanensis* and close to vars *americana* and *costaricensis*. Var. *guatemalensis* links these two groups, and is considered a hybrid between vars *steyermarkii* and *nubigena*.

The California Avocado Society Yearbook carries numerous articles on avocado exploration

in Mexico, Guatemala, Honduras, Costa Rica, El Salvador etc, in which the names Popenoe, Zentmyer and Schieber, *inter alia*, feature prominently. The over-riding impressions are of great diversity in topography, environment and vegetation, and of rapid forest clearing and loss of germplasm. However, all botanical varieties which are believed to have contributed to the modern avocado gene pool are indigenous to neotropical forests, mostly (with the exception of the Lowland ecotype) at considerable altitude on the slopes of mountains and volcanoes. The ancestral Mexican avocado is the most subtropical in terms of latitude (ca 20 to 23 N), being typical of the central highlands of Mexico, from many localities over 1000 m in altitude, and in northern Guatemala at altitudes of 1600 m, and even 2000 m to 2600 m (Schieber *et al.*, 1974; 1983). Wild Mexican type trees reach a height of 15 m.

Guatemalan avocados represent (along with their hybrids, especially with the Mexican ecotype) the most advanced selection for fruit quality at least for "subtropical" avocados which form the bulk of world trade and are popular for "western" palates. Their origin is from the highlands of Central America, mainly Guatemala, further south (more tropical latitude) and also at relatively high altitudes, i.e. cool, moist "highland tropical" climates. Primitive forms were reported by Popenoe at altitudes of 2600 to 3000 m in fast-receding woodland cloud forest. However, wild specimens are also known from rainforests at lower altitude, with trees up to 30 m tall. Both its supposed progenitors, var. *steymarkii* (tree up to 15 m tall) and var. *nubigena* (up to 40 m tall) are "cloud forest" types at moderate to high altitude, mostly on acid, infertile soils.

The lowland (W. Indian) avocado is now believed to have a Meso-American origin, mainly from the western coastal areas of El Salvador and Costa Rica (Storey *et al.*, 1987) and possibly also in northern S. America. It is a large tree (to 30 m tall) of lowland, hot and humid forests with a short dry season. Scora believes there are two distinct subtypes, viz. Central American and South American types, as supported by the numerical taxonomic study of Rhodes *et al.* (1971) and other evidence.

The climate of selected areas in the presumed native habitat of avocado was summarized by Praloran (1970). Three stations in Mexico averaged 15.4 C M.A.T., but varied from 12.8 C at 2675 m to 17.5 C at 1399 m. The hottest locality averaged 19.8 C and 14.2 C for the hottest and coldest months respectively, the coldest station 15.6 C and 9.7 C. Rainfall varied from 1562 mm to 665 mm, with a pronounced summer-autumn peak and a 6 to 8 month winter-spring dry period. Two localities in Guatemala, at 1502 m and 2350 m, had M.A.T's of 19.6 C and 14.9 C respectively, and rainfall of 1394 mm and 671 mm. Temperatures were similar to the Mexican stations, but with lesser extremes. A cool, moderate climate without marked temperature extremes is typical, with frost only likely above ca 1500 m altitude. In contrast, tropical lowland climates may have year-round monthly means between ca 25 and 29 C, in which the high rainfall is far less effective, especially in the dry season.

Features of Highland, Mountain Cloudforests
Space does not permit a detailed discussion of the features of tropical rainforests, a

seasonal rainfall lowland version of which is the presumed evolutionary habitat of the Lowland avocado, and mountain versions for the Mexican and Guatemalan avocados. Richards *et al.* (1996) discuss tropical rainforest types in detail, the closest to the avocado indigenous habitat being the lowland and mountain rainforests of Costa Rica. Heaney and Proctor (1990) describe the structure and floristics of the forest at five altitudes, incorporating four of Holdridge's 'life-zones' (lowland, premoutain, lower mountain, mountain). Already in the premoutain belt, the canopy trees are less tall (30 to 40 m) than in lowland forests (45 to 55 m), while above 1500 m lower mountain forest trees reach ca 20 to 30 m. On highest mountains, above ca 2500 m, mountain forest emergent trees are ca 25 to 30 m tall, with small rounded crowns, unbuttressed trucks, and smaller sclerophyllous leaves.

It is generally accepted that with increasing altitude, tree size and species diversity decline, along with productivity. Decreasing air temperature and increasing cloudiness are probably ultimately responsible for limiting growth of tropical mountain forests (Grubb, 1977). However, Tanner *et al.* (1998) believe that many lowland forests are limited by P, and many mountain forests by N. Bruinzeel and Veneklaas (1998) review the different structure (including small and tough leaves) and functioning (including low nutrient-cycling rates) of tropical mountain forests, and highlight the effects of frequent low cloud. Although leaf photosynthetic capacity is not particularly low, canopy photosynthesis probably is. Light climate and leaf structure and longevity result in relatively low LAI, and productivity is further limited by substantial investment of carbon in growth of comparatively large root systems due to unfavorable soils. Ben-Ya'acov and Michelson's (1995) review of avocado rootstocks also discusses soil stress factors relevant to tree performance.

Therefore both low photosynthetic C gain, and high maintenance and constructive costs lead to low above ground biomass production. We believe that such features of the indigenous habitat of avocado trees, at least in part, are helpful in understanding the orchard performance of this comparatively undomesticated tree.

Avocado Tree Architecture and Growth Habit
Understanding tree architecture and growth habit is necessary as a basis for manipulation and yield-enhancing orchard management. In the broadest sense, avocado trees conform with Rauh's architectural model (Halle *et al.*, 1978). Key features are a monopodial trunk with rhythmic growth to develop tiers of branches morphogenetically identical with the trunk. By definition, flowers/inflorescences are lateral due to a terminal vegetative bud which may grow out simultaneously with flowering. Branch development, closely correlated with rhythmic growth of the axis, can be proleptic or sylleptic. Avocado inflorescence position is actually pseudoterminal in that the flowers are the first part of the renewal shoot to expand, their lateral position becoming evident when the terminal bud grows as a leafy shoot. The success of this model lies in its ability to regenerate rapidly (reiteration) if the trunk meristem is damaged - unlike the mango (Scarrone's model) with terminal meristems and therefore "loss" of vegetative growth axes. In this sense, vegetative growth potential in avocado is more plastic and, especially in predominantly indeterminate flowers, potentially more vigorous.

Strictly speaking Rauh's model applies only to indeterminate inflorescences. A minority of inflorescences is determinate, without a terminal vegetative growing point. It is generally accepted that early and vigorous growth of the vegetative flush on indeterminate inflorescences, as in trees excessively high in N, reduces fruit set (Biran, 1979; Blumenfeld *et al.*, 1983; Whiley and Schaffer, 1994), especially in vigorous cultivars such as 'Fuerte'. Whiley (1994) showed that the sink: source transition in 'Hass' leaves occurred at ca 80% of full leaf expansion, and that whole shoots attained their CO_2 assimilation compensation point some 27 days after bud break. During the sink phase, 86% of initially set fruits abscised, suggesting a C shortage. Zilkah *et al.* (1987) indicated that this early shoot growth, however, is not due to competition for N. On the other hand, flowers on determinate shoots have a higher fruit set, and Whiley's (1994) studies suggested that they developed into large fruits in 'Hass'. However, anecdotal evidence from South Africa suggests that excessive fruit set on such shoots can lead to smaller fruit size, and furthermore that the reduced leaf cover results in a higher percentage of sunburn fruit in warmer climates.

Avocado tree form has been related to branching type by Thorp and Sedgley (1993), Their architectural analysis accounted for varying growth habits of various cultivars. Thorp *et al.* (1994) presented evidence for preformation of node number in avocado vegetative and reproductive proleptic shoot modules, but not in sylleptic shoots. Thus the mean number of nodes on terminal (dominant) shoots was 14 for vegetative shoot modules and 21 for reproductive modules, irrespective of cultivar, rootstock, location and climate. Axillary shoot modules were less vigorous and more variable. This node preformation results in rhythmic growth and appears to be under strong endogenous control. Both shoot and inflorescence development was dominated by the apical bud, especially on vigorous shoots.

The influence of shoot age on floral development in avocado was studied by Thorp *et al.,* (1993). In seasonal (subtropical) climates, the spring growth flush is typically followed by a summer flush in warm, humid climates (Whiley *et al.*, 1998), but often also by an autumn flush in semi-arid Mediterranean climates at greater latitudes, as in Israel (Adato, 1990) and California. Semi-tropical (lowland) areas are characterized by more periods of rapid shoot growth separated by relatively quiescent periods (Venning and Lincoln, 1958; Davenport, 1982). The spring flush usually involves most terminals; subsequent flushes do not involve fruiting shoots - the resultant canopy consists of cohorts of leaves of varying age. However, Whiley and Schaffer (1994) note the comparatively shoot life of avocado leaves, viz 10 to 12 months, which is much shorter than that of other evergreen fruit trees such as citrus and mango.

Thorp *et al.* (1993) found that floral initiation in late autumn was only in the last-formed shoot modules, i.e. most peripheral, mostly in terminal buds. Thus later flushes (summer and, if present, autumn) were more liable to flower and set fruit than spring flush terminal shoots, provided the shoot was sufficiently vigorous. This suggests that position in the canopy (peripheral/terminal) and vigor were more important than shoot age, and indirectly that light was also a key factor. This has profound significance for pruning - "outside"

shoots will flower in spring if sufficiently vigorous and if they have had sufficient time after pruning to mature and harden, provided that they are not excessively invigorated (waterspouts). Thorp *et al.* (1994) found that sylleptic shoots were invariably vegetative.

Adaptive Strategies of Avocado Trees

There is strong evidence for evolution of Guatemalan and Mexican avocados in cool, mesic mountain cloudforest environments, largely in tropical and near tropical environments but at high altitudes, with high summer-autumn rainfall but relatively dry winter-spring weather. The presumed adaptive growth strategies of avocado progenitors are given in Table 1, with the proviso that considerable variability exists and that the cultivated avocado arose form a rich and diverse gene pool.

Table 1. Adaptive vegetative and reproductive strategies of avocado progenitors resulting from evolution in seasonably wet mountain cloudforests.

Vegetative
Tree architecture adapted to competition with climax forest trees
Potentially vigorous growth in 2 to 4 flushes per season
Large, dark green bicolored (Guat., Mex.) to light green (W.I.) leaves
Fairly shade-tolerant but short-lived leaves (if excessively shaded)
Self-mulching trees due to accumulation of litter
Shallow, relatively inefficient fibrous feeder roots with high O_2 requirement
Efficient interception, hoarding and recycling of scarce nutrients
Reproductive
High light requirements for flowering
Very heavy peripheral flowering synchronized by cold and drought stress
Carbon, mineral and water "expensive" flowering
Small, inconspicuously colored flowers pollinated by small bees
Synchronized dichogamy favoring obligate outbreeding, with female/male anthesis evolved in response to pollinators
Very low fruit set during critical "bottleneck" phase
Crop load adjustment during spring and summer drops
Mast or irregular fruiting
Energy expensive but comparatively mineral cheap fruits
Large chemically protected seeds with concentrated food reserves
Fruit softening only after physical separation from tree

In Table 2 we summarize some key features of avocado tree physiology, which make possible the growth adaptations listed in Table 1.

Discussion of Adaptive Features

There is no doubt that excessive vigor, under favorable mesic growing conditions, can be problematical in avocado and counter-productive to fruiting. In fact, management of vigor is fundamental to good orchard management, especially at critical periods such as fruit set (Biran, 1979; Blumenfeld *et al.*, 1983; Adato, 1990; Wolstenholme and Whiley, 1990; Whiley *et al.,* 1991; Whiley and Schaffer, 1994). It is also true to say that tree vigor is reduced by grafting, and orchard tree shape is less upright that in seeding trees. Cultivars however vary in tree form (Thorp and Sedgley, 1993) and there is greater appreciation of the need to select cultivars for a more dwarfed, compact growth habit. It has been suggested that manipulating tree structure to increase sylleptic shoot growth will improve yield efficiency, as in the productive cultivars 'Reed' and 'Gwen', where high rates of syllepsis occur without excessive shoot vigor (Thorp and Sedgley, 1993). What is certain is that some growth features which are adaptive in the indigenous forests of Central America may be counter-productive in orchards - including vigor, and require careful management *inter alia* through fertilization, irrigation and growth regulators.

Table 2. Some key features of avocado physiology mediating growth adaptations.

Photo-assimilation and carbon budget
Potential for rapid C fixation under mesic conditions
• Potentially high field A max of well-lit leaves
• Low photosynthetic light compensation point
But whole-tree C budget often compromised
• Few well-lit leaves
• High photosynthetic light saturation of whole canopy
• Multiple stresses
Potential for high C reserve accumulation especially under stress
C reserves easily run down
Water relations
Sensitive to atmospheric moisture deficit
Considerable drought tolerance
• Physiological adjustment to control water loss
• Stomata sensitive to moisture status and light
Very flood sensitive/saturated soil sensitive
Salt-sensitive
Miscellaneous
Significant dependence on perseitol for C translocation
Significant investment in secondary compounds

Succession and seed dispersal aspects

The literature is surprisingly deficient in discussing the place of avocado in ecological succession. The tree undoubtedly has more features of climax (equilibrium) species than

pioneer (colonizer) species. Swaine and Whitmore (1988) summarize tropical rainforest dynamics, and in particular the character syndromes of pioneer (r-selected) and climax (K-selected) species, in relation to forest gap size and gap-phase replacement. These represent the two extremes, and variation within them is continuous, and quantitative rather than qualitative.

If we accept a continuum from true pioneer to true climax species, the seral position of wild avocado trees appears to be late succession, but not true climax. This is supported by their large tree size; long juvenile period (delayed reproduction); large, quality fruits with large seeds; mast or irregular fruiting; the relatively small seed crop; recalcitrant seeds (quick loss of germinability on drying); seeds capable of germinating and seedlings establishing in shade; leaves apparently chemically well-defended and not very susceptible to herbivory; and long life - all these features being typical of climax forest species.

However, avocado trees do have some characters that are listed as typical of pioneer tree species in tropical rainforests by Swaine and Whitmore (1988). These include relatively short-lived leaves (10 to 12 months, Whiley and Schaffer, 1994); superficial rooting; rapid height growth; high seedling carbon-fixation rate (under favorable conditions); and pale, low density, non-siliceous wood.

If the strict division of forest tree species into only two clearly defined guilds is accepted (*sensu* Swaine and Whitmore, 1988), then the weight of characters places avocado in the climax group. They believe that "late seral" is an ill-defined term which should be abandoned. However, it could be applied to more light-demanding, faster-growing climax species with light-colored as apposed to dark hardwood, of which we suggest avocado is typical. In terms of Denslow's (1987) three resource partitioning groups of rainforest trees in relation to treefall gaps, the avocado is clearly a small-gap specialist. Such trees have seeds which can germinate in shade but which require a gap to grow into the canopy, in contrast to light-demanding large-gap specialists (pioneers) and shade tolerant understory specialists. We suggest that the large, carbohydrate-rich seed of avocado provide a competitive advantage, quickly giving rise to large-leafed seedlings which can persist in "idling mode" in shaded environments for a long time. In fact, Westoby *et al.*'s (1992) review of the evolutionary ecology of seed size concludes that the major observable pattern is that species whose seedlings can establish in the shade under forest canopies tend to have larger seeds. In other words, selection pressure for fewer, larger seeds is because these have a better chance of producing an established plant.

Whiley (1994) notes the large seed (40 to 80 g) of avocado, and the large fruit size (300 to 700 g in selected cultivars, but probably mostly smaller in wild trees). Light environments of understory strata have irradiant levels of 0.4 to 3% of full sunlight (Chazdon and Fletcher, 1984). Permanent understory plants have a light saturation level for photosynthesis of ca 3 to 4 µmol quanta $\cdot m^{-2} \cdot s^{-1}$, and a photosynthesis rate of saturating PPF's of 3 to 4 µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Chazdon, 1986). Whiley (1994) pointed out that as a light compensation point for photosynthesis in avocado is ca 30 µmol quanta$\cdot m^{-2} \cdot s^{-1}$, there would
be insufficient light (in the absence of a gap) to sustain seedling growth once seed reserves

are depleted.

The high quality, energy-rich pulp (Wolstenholme, 1986, 1987) of avocado fruits undoubtedly evolved to facilitate seed dispersal by specialist mainly ground-dwelling frugivores after falling to the forest floor. However fruit (and pulp) size in wild avocado was smaller, and the seed was large in relation to flesh (Smith *et al.*, 1992). Dispersal of the large seeds of small-gap specialists is often poor, and the high quality fruits are eaten by animals and birds which either ignore or are able to cope with and disperse the large seeds (Howe and Smallwood, 1982; Howe *et al.*, 1985). A very large proportion of rain forest trees have fruits or seeds attractive to mammals and birds (Richards *et al.*, 1996).

Little has been written on avocado seed dispersal. Most Lauraceous fruits are dispersed by birds (Ridley, 1930). Schieber and Zentmyer (1973, 1979) refer to the quetzal bird which eats fruit of some of the smaller-fruited *Persea* types - a bird of the trogon family. Toucans are also mentioned. Hallwachs (1986) noted that the agouti (*Dasyprocta punctata*), a large rodent, also disperses *Persea* seeds in neotropical forests, with these seeds probably chemically protected against most mammal seed predators (avocado seeds are sometimes loosely described as "poisonous"). Janzen and Martin (1982) draw attention to a rich fauna of now extinct megaherbivores about 10 000 years ago in new world neotropical lowland forests. They point out that frugivory by extinct horses, gomphotheres, ground sloths etc offers a key to understanding reproductive traits in Central American lowland (and probably also highland) forests. When the megafauna died out, *Persea* spp. did not go extinct because other dispersal systems were adequate, as long as seeds were not all eaten, e.g. water, gravity, monkeys, birds and not least people.

Certainly *Persea* spp. have seeds and fruits with at least some of Janzen and Martin's (1982) megafaunal dispersal syndrome characteristics - large, indehiscent fruits containing energy-rich pulp; seeds obviously not abiotically dispersed; fruits and seeds similar to African fruits eaten by large mammals; and fruits that fall from the tree before ripening ("behavioural presentation of fruits to earth-bound dispersal agents"), etc. We suggest that the well-known delayed flesh softening of avocado fruits until physically separated from the tree (dropped onto the litter layer) is a dispersal mechanism allowing time for presentation of the pulp "reward" to *inter alia* large herbivores with high energy requirements, in some cases ingesting whole fruits and excreting undamaged seeds at some distance. In this regard Chadwick (1992) postulates that mango fruits (*Mangifera indica*), which are today so appreciated by African primates and African elephants, also evolved with primates and elephants in mind - in this case Asian - a striking case of convergent evolution. The mango seed, protected by a stony, fibrous endocarp, survives passage through the gut and germinates in a fertile pile of dung. Could this be a reason for the germination recalcitrance (inability to withstand drying out, Storey *et al.*, 1986) of avocado seeds?

Traits affecting photosynthesis and tree carbon budget
 Compared to evergreen fruit trees such as citrus and mango, the short leaf longevity (10 to 12 months, Whiley and Schaffer, 1994) is noteworthy. The ecology of leaf life span suggests different strategies represent various compromises of the cost-benefit equation.

The avocado tree invests relatively little in each cohort (flush) of large, peripheral, and basically horizontally displayed leaves, but replaces them frequently (two to four flushes per annum), and appears to efficiently salvage and recycle mobile minerals.

In terms of leaf structure in relation to photosynthetic characteristics, only recently has mechanistic evidence been obtained. Smith *et al.* (1997) classify 234 plant species into four groups, based on combinations of high or low sunlight and high or low environmental stress. Avocado (Guatemalan and Mexican ecotypes) conform best to their "low sun, low stress" model, with thin, large horizontal, bicolored and hypostomatous features *inter alia*. Mountain cloudforests will experience relatively low sunlight during the warmer rainy months. In such conditions large, horizontal leaves ("shade leaves") on the tree periphery (tree crown in the forest) have the most efficient sunlight interception. Thin bicolored leaves (distinctly darker and lighter sides) as in Guatemalan and Mexican types in particular have an internally reflective lower epidermis and other features for greater light trapping. Stomata limited to the leaf undersurface are also protected from direct sunlight and have reduced transpiration water loss. We suggest that avocado leaves of these ecotypes were photosynthetically limited more by light than by CO_2 supply during their evolutionary adaptation in cloud forests. Under such conditions also, where reproductive efficiency is compromised, we believe that dark green leaves (high chlorophyll content made possible by adequate nitrogen uptake) are functionally important. Such leaves are more protected against photoinhibition during the dry season and during the critical fruit set period (Whiley *et al.*, 1998). In contrast, the usually smaller, lighter green, and less bicolored leaves with shorter internodes in West Indian (lowland) avocados suggest that light was less limiting in their evolution.

Avocado leaves use the C_3 photosynthetic pathway. The carbon assimilation responses to irradiance, temperature and water stress have been summarized by Whiley and Schaffer (1994). Light saturation of individual leaves of container-grown plants occurs at ca 20 to 33% of full sunlight. For small 'Edranol' plants in containers this value increased to 33% (Bower *et al.*, 1978), consistent with greater leaf shading, while Whiley (1993) unpubl. data), in the only recent study on orchard trees, reported light saturation at 1110 μmol quanta·m^{-2}·s^{-1}, or over 50% of full sunlight. He also noted that the previously accepted A max for container-grown avocados of ca 7 μmol quanta·m^{-2}·s^{-1} was due to unidentified limiting factors, and measured A max of 23 μmol quanta·m^{-2}·s^{-1} in 'Hass' in subtropical, humid Queensland (Whiley, 1994). As previously mentioned, the light compensation point for A in avocado leaves is intermediate, not low enough to qualify as true shade leaves, but indicating considerable shade tolerance.

Whiley (1994) discussed the plasticity of the light response in avocado in the context of a small gap colonizer with short-lived (for an evergreen tree) leaves. It is clear that, in non-stressful, mesic conditions, high photosynthetic rates can be maintained in well-lit leaves, allowing moderate to rapid growth in several flushes. Under similar favorable conditions starch concentrations in trunk wood tissue can build up to ca 6 to 8% of FM (Kaiser and Wolstenholme, 1994; Whiley *et al.*, 1996) in avocado orchards. However, in more stressful environments, including cool, semi-arid south Australia, and Mediterranean climates,

maximum trunk starch concentrations reach ca 18%, and fluctuate more between "on" and "off" bearing years.

Chandler (1958), Whiley (1994) and Wolstenholme and Whiley (1997) point out that reserve starch concentrations in avocado are higher than those in other evergreen fruit trees, but lower than in deciduous fruit trees. Whiley (1994) notes that avocado in stressful environments can be semi-deciduous or "wintergreen". We suggest that high starch reserves in avocado trees, peaking at the onset of flowering, are, as in citrus to a lesser extent (Goldschmidt and Koch, 1996), a buffer against stress. Stress in the avocado context is highest during flowering and fruit set in the indigenous environment - coinciding with the dry season. More prolonged stress, in semi-arid environments, appears to invoke the stress-coping response of greater starch accumulation, along with greater alternate bearing. Wolstenholme and Whiley (1997) speculate that if accumulation of reserve carbohydrates is a high priority in citrus, it is even more so in avocado, which evolved with seasonal stress.

The carbon budget of avocado trees has only been studied in terms of starch cycles. Starch concentrations and amounts in various plant parts (as in van Vuuren *et al.*, 1997) provide useful information for management, although carbon is but one of many potentially limiting factors. The energy costs of flowering and fruiting are high in avocado (Wolstenholme, 1986, 1987; Blanke and Whiley, 1995) and a large crop dramatically runs down starch reserves.

Surprisingly little published work exists on the avocado tree's seeming reliance on the sugar alcohol perseitol, as well as sucrose, for phloem translocation between sources and sinks. Sorbitol is a major photosynthetic and translocation product in the woody Rosaceae (Bieleski and Redgwell, 1985) and mannitol in some other plants. We are aware of current work in California and at the University of Natal. Cowan (1999, pers. comm.) believes that perseitol helps in regulating cell division in young avocado fruits, and may have a role in protecting plants from free radicals generated in growth.

In an evolutionary ecological context, irregular bearing is normal in competitive, light-limited avocado environments. However, is mast fruiting due to carbon starvation, or simply the need for the tree to grow vegetatively after a heavy crop (for example, to re-establish canopy position)?

Another aspect deserving of study is the increasing adverse effect of growth in height on whole-tree carbon budgets. Tall trees have much greater maintenance costs and an increasing percentage of carbon (and intercepted sunlight) is allocated to "balancing the books", i.e. reaching what Givnish (1988) terms the "ecological compensation point". Correspondingly less carbon is then available for fruiting, aside from considerations of inefficient space utilization. Ryan and Yoder (1997), discussing hydraulic limits to tree height and tree growth, propose a feedback loop in which increasing tree size limits carbon assimilation through increased hydraulic resistance. This leads to slower growth, less new xylem, and greater allocation of carbon to respiration and production of additional roots.

Tall trees can never be as energetically efficient as smaller trees.

In management terms, being aware of the limitations imposed by short-lived leaves, with high light and water needs for high A max, are key elements. Avocado canopies and starch accumulation are especially compromised by poor root health, especially Phytophthora infection, where leaf redundancy is not due to shading by new leaf cohorts, but by slow replacement in poor or absent flushing. As long as trees are healthy and environment permits a good fruit set, manipulation of the phenological and ecophysiological growth cycle based on a thorough understanding of tree ecophysiology (Whiley *et al.*, 1988; Whiley *et al.*, 1998) holds the best promise for high yields until better adapted cultivars and rootstocks are released. Growth regulating chemicals, pruning, girdling etc are available as tools. Tree pruning to contain size and improve light interception will be aided by plasticity of the light response, but complicated by the inherent potential for vigorous growth.

Flowering, fruit set and yield
A characteristic of late seral and climax tree species is delayed flowering while the tree establishes its position in the forest canopy in the juvenile seedling phase. Orchard trees of selected, more precocious cultivars grafted onto selected rootstocks and growing in a less light-limited and less stressful environment, can be expected to flower more precociously and regularly. Flowering of cultivated avocado is usually profuse - Cameron *et al.* (1952) estimated that mature trees can produce up to 1.6 million flowers.   Whiley *et al.* (1988) estimated that flowering of 'Fuerte' trees in S.E. Queensland increased the canopy surface area for water loss by ca 90% and that ca 13% of total transpirational water loss was attributable to flowering. The heavy carbon and mineral cost of "wasteful" flowering has also been noted (Wolstenholme and Whiley, 1997). We suggest that this problem is a consequence of the tree's forest adaptation. Orchard trees, except when crowding occurs, experience better conditions for flowering than forest trees and in fact are stimulated to produce what is horticulturally an excessive number of flowers.

Nevertheless, even if bearing potential and regularity is much improved in orchards, alternate bearing remains problematical. Heavy cropping of energy-expensive fruit reduces the number and intensity of shoot flushes in that season (Lahav and Kalmar, 1977; Schaffer *et al.*, 1991). Salazar *et al.* (1998) found that spring vegetative shoots arising from indeterminate inflorescences which held fruit to maturity did not produce summer or autumn flushes. This reduced the number of shoots capable of flowering the following spring. Thus an "on" crop reduces flowering intensity and results in more vegetative shoots in the "off" season. Salazar and Lovatt (1998, 1999) investigated GA_3 application to individual 'Hass' shoots and as winter trunk injection to alter flowering phenology and give adequate annual flowering for more regular bearing, with fairly promising results. Control of flowering however is not yet practical, although highly desirable.

Avocado flowering has been reviewed by Davenport (1986), who emphasized the extremely complex events encompassing induction, flowering, pollination and fertilization, and post-fertilization processes. Chaikiattiyos *et al.* (1994) comparing 'Hass' avocado with other "tropical" fruit trees, clearly demonstrated that low temperature (below about 23/18 C

day/night) decreases growth and induces flowering even in well-watered trees, and were unable to induce flowering by water stress in potted trees (until trees were rewatered). Kubitzki and Kurz (1984) pointed out that most rain forest trees are obligate out breeders, with heavy reproductive constraints due to low population density. Neotropical Lauraceae are either hermaphrodite or dioecious, with the former the basic and the latter the derived state. Hermaphrodite genera (including *Persea*) have the highly evolved alternating protogynous dichogamy, which effectively is a type of temporal dioecy involving two flower morphs with reciprocal stigma receptivity and pollen release. Nectar is provided as a reward for pollinating insects, apparently mostly very small native bees. However, synchronized dichogamy is vulnerable to disturbing influences, especially unusual weather. Temperature in particular influences fruit set (Sedgley and Annells, 1981; Whiley and Winston, 1987) and "B" type flowerers in avocado (e.g. 'Fuerte', 'Edranol') are more disadvantaged by cold weather than "A" type cultivars ('Hass', 'Pinkerton'). Lahav and Gazit (1994), in a world listing of cultivars according to flowering type, also noted that "A" type cultivars have an inherent advantage in cool climates (California, Israel) whereas "B" cultivars predominate in warmer areas of Mexico, Hawaii and Guatemala. Lavi *et al.* (1993) found that group B offspring predominate in avocado hybrids, but it is not known if this is the case in wild avocados.

Lauraceous genera which are dioecious have pollen:ovule ratios of 3000 to 8400 and are obligate outbreeders, whereas hermaphrodite genera (including *Persea*) have values of 150 to 500 and could be classified as facultative outbreeders (Kubitzki and Kurz, 1984). This is true for avocado, which is designed for outcrossing but which has evolved a fail-safe system of self-pollination (Davenport, 1986) which at least assures some crop, even though there is now substantial evidence that cross-pollinated fruits have a better chance of maturing (Lahav and Gazit, 1994). Davenport (1986) also points out that cultivated avocados face often very different environments from their evolutionary habitats, including availability of pollinators. The honeybee certainly did not pollinate wild avocados, and the low attractiveness of avocado flowers to honeybees limits fruit set in Israel, with at least five bees per tree during the pistillate flowering stage being needed for a significant initial fruit set (Ish-Am and Eisikowitch, 1998). They also showed that early-blooming as opposed to late-blooming cultivars received fewer bee visits (a temperature effect) and only ca. 5% of their flowers received sufficient visits for fruit set.

The limitations to avocado yield have been extensively discussed, *inter alia* by ourselves (Wolstenholme and Whiley, 1992; 1998), and have included evolutionary constraints. Phenological and phenophysiological models (Whiley *et al.*, 1988; Whiley, 1994) have been useful in guiding tree manipulation to improve yields. A recent example is the testing of GA_3 sprays in winter to induce earlier development of the vegetative apex of indeterminate inflorescences so that the new leaves undergo the sink : source transition earlier and contribute to rather than reduce fruit set (Salazar and Lovatt, 1998). Humid subtropical areas continue to outyield Mediterranean areas, but it remains difficult to achieve 20 t·ha^{-1} average yields on a large scale. Whether new high density planting combined with tree shaping and pruning, and use of growth retarding chemicals such as paclobutrazol (Wolstenholme *et al.*, 1990; Whiley *et al.*, 1991) and uniconazol (Erasmus and Brooks,

1998) will provide practical and economic answers remains to be seen. New cultivars and rootstocks provide the best hope for long-term solutions.

CONCLUSIONS

The various ecotypes of avocado evolved in either cool, mesic mountain cloudforests in borderline subtropical/tropical latitudes, or in lowland tropical forests, in both instances with a winter/spring dry season. The trees appear to be late successional exploiters of small forest gaps, with the potential for rapid growth. However, some earlier seral features such as short-lived leaves and shallow, litter-feeding fibrous root systems exist. We believe that in spite of centuries of selection for larger, better-tasting fruits with more edible pulp and smaller seeds, the avocado tree is poorly domesticated in terms of orchard potential. Residual forest-adaptive features of tree architecture and ecophysiology may not always suit orcharding and are often counter-productive to consistent yields of good quality fruit.

Perhaps one of the most important adaptations relates to leaf longevity, shade tolerance and carbon fixation potential. Adaptation to often low light and competitive forest environments led to frequent replacement of leaf cohorts and early loss of excessively shaded leaves. The need to compete for light appears critical, and only well-lit peripheral buds undergo floral induction in autumn, when rains are diminishing in cloud forests. consequently the tree continues to increase in size, which leads to side-shading in orchards and consequent loss of bearing and inefficient space utilization. Meanwhile the built-in "vegetative growth imperative" (in non-stressed trees) adds new cohorts of short-lived leaves, increasing the shading effect, which while tolerated, reduces the number of well-lit terminals capable of flowering.

Taller trees also require increasing proportions of sunlight just to satisfy their respiration, growth and maintenance carbon demands, i.e. to reach "ecological compensation point" (Givnish, 1988) for the whole tree. This is complicated by a shallow, relatively inefficient feeder root system which performs best with a good decomposing litter layer and is therefore responsive to mulching, (Moore-Gordon *et al.*, 1997); complex flowering and fruit set biology with the potential serious spring fruit set bottlenecks aggravated by attrition of feeder roots, reduced storage reserves and photosynthetically inefficient, sometimes seriously photoinhibited leaves; and the energy expensive fruit requiring a substantial number of well-lit leaves. Two keys to management would seem to be smaller trees with better overall canopy light interception, and good root health in an environment where stress is reduced to a minimum. The avocado's evolutionary adaptations make it remarkably tolerant to stress, but at a severe cost in fruiting and fruit quality terms. A higher percentage of leaves should be given the opportunity to realize the rapid photosyntheis rate of which they are capable. Nor should we be misled by the comparative "mineral cheapness" of individual avocado fruits - high yields especially on infertile soils make substantial demands of nutrients, even if lower than "gross feeders" such as citrus and banana.

Avocado yields have plateau, usually off a low base and much of the blame appears to be

due to evolutionary constraints. We await new research insights to improve the situation, and in the longer term the success of breeding programs is critical. The industry is currently in a phase of uncertainty with regard to key questions of intensification of management, especially planting density, tree shaping and manipulation by pruning and chemicals (e.g. Stassen *et al.*, 1995; Snijder and Stassen, 1998). World markets are becoming more competitive, and the millennium brings huge challenges, not least the impact of global warming. Research remains the key to guiding the quantum leap in grower efficiency which will be necessary in a fast-changing environment.

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