Theoretical and applied aspects of avocado yield as affected by energy budgets and carbon partitioning

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SYNOPSIS
Average avocado yields are low compared to other fruit crops because of the high energy cost of producing fruits with a high oil content and a large seed. Other major factors are the evolutionary history and early stage of domestication of this crop, and the ravages of Phytophthora root rot. Implications for breeding and certain aspects of orchard management are discussed.

INTRODUCTION
Average yields of avocado orchards are low when compared with those of other fleshy fruits, although higher than those of nut-bearing trees. Fruit yield in tree crops is affected by many complex, interacting factors, but the final analysis is determined by seasonal photosynthetic efficiency, and more particularly by the 'harvest index'. The latter is a measure of the proportion of photosynthate which is partitioned to the fruit. Cannell (1985) states that it is now a truism that man has increased yield mainly by increasing the harvest index of crops.

This paper is a limited review, in part theoretic of the presumed avocado yield problem, the reasons for low yields, and implications for yield improvement. The approach is to attempt a broad, conceptual perspective, with emphasis on the subtropical avocado industry, assuming good orchard management practices.

AVERAGE AVOCADO YIELDS
Avocado yields are obviously affected by cultivars, rootstock, environmental (including edaphic) factors, cultural practices and tree age. They can be expressed as national (or state) averages, which are especially low as they include the full spectrum of grower capability, bearing and non-bearing trees, and often unreliable obsolete statistics. It can be calculated, for example, that the California average since 1981 was about 4,5 t ha^{-1} (Anon, 1985). The state average per bearing ha for a 10-year period to 1972/73 was 5,8t (Rock, 1977). Kotze (1986) referred to a South African average of below 5 t ha^{-1}, while average industry yields in Israel have been given at around 10tha^{-1} (Ashkenazi, undated).

A more useful concept is that of a good commercial yield. This should be qualified for cultivar and for tree age (eg mature trees), and must be a realistic average ideally based on at least five years' data and a reasonably large block of land (say > 10 ha). Gustafson (1979) stated that good growers in southern California expect between 6,7 and 11,2 t ha^{-1} for Fuerte, and 7,8 to 13,4 t ha^{-1} for Hass. Commercial production varied

between 5,6 and 16,8 t ha^{-1}. Bergh (1986, pers comm) gave good grower averages for the same area as 5,6 t ha^{-1} for Fuerte, 9 t ha^{-1} for Hass, 11,2 t ha^{-1} for Pinkerton and 13,4 t ha^{-1} for Reed.

In South Africa, a conservative yield for Fuerte of 10 t ha^{-1} has been used for planning purposes. In SE Queensland, an orchard of mixed cultivars could be expected to average 12 t ha^{-1} with reasonable management (Whiley, 1987, pers comm). A recent economic analysis in the climatically favourable Tzaneen district, South Africa, used a mature orchard average of 18 t ha^{-1} for growers with 'intermediate' management capabilities (Toerien *et al*, 1984).

Average yields are also available for the best growers, and constitute target yields based on the best available technology in intensively managed orchards in favourable localities. Toerien *et al* (1984) used a figure of 21,6 t ha^{-1}; Ashkenazi (undated) referred to over 20t ha^{-1} for Hass in Israel, and Gustafson (1979) stated that excellent orchards can produce over 16,8 t ha^{-1}. Occasional reported yields of 30 or more t ha^{-1} are possible in some seasons, but are certainly not average yields as defined earlier.

MAIN REASONS FOR LOW YIELDS
Bergh (1977) discussed factors affecting avocado fruitfulness. The writer's approach is to take a broader perspective, emphasizing evolutionary history, *Phytophthora* and energy costs of fruiting.

Evolutionary history and stage of domestication
Centres of origin - Some disagreement exists over the centres of origin and nomenclature of the cultivated avocados. Bergh (1975, 1977) retained the 'horticultural race' concept (Mexican, Guatemalan, West Indian) of earlier workers, but also elevated them to three botanical varieties of *Persea americana* (var *drymifolia*, var *guatemalensis* and var *americana* respectively).

However, Williams (1977) on the basis of field experience, recognised two species, each with two botanical varieties, and only two centres of origin, viz eastern and central Mexico (Mexican and West Indian avocados) and central Guatemala (Guatemalan avocado). Cultigens have subsequently arisen from crossing amongst the two species (eg Fuerte). The unfortunately-named 'West Indian' avocado is believed to have arisen from the Mexican avocado, although it has subsequently acquired genes adapting it to the tropical lowlands.

The centres of origin of both of Williams' species were highland, montane 'cloud' forests or rain-forests, essentially subtropical highland in Mexico and tropical highland in Guatemala. The Guatemalan progenitors were often gigantic trees.

Stage of domestication - Williams (1977) cites evidence that Mexican avocados have been used as food for 9 000 to 10 000 years, the 'West Indian' avocado for over 4000 years, and Guatemalan avocados for perhaps 2 000 years. They were therefore undoubtedly improved by primitive man, probably for larger fruit size in Mexican

avocados, for smaller seed size, and for eating quality. It must however be stressed that modern man has only exerted purposeful selection on avocados for some 100 years, The avocado is therefore only a partially domesticated tree according to the criteria for commercial orchard culture.

Ecophysiological consequences of a rain-forest origin have been summarised by Possingham (1986) and Kriedemann (1986). Those applicable to avocado trees include a shallow, extensively suberized, relatively inefficient root system with low hydraulic conductivity, a low frequency of root hairs, and vesicular-arbuscular mycorrhizal associations. Leaves have a high stomatal density but a limited vascular network; high quantum efficiency but limited photosynthetic efficiency; light saturation at 20-25 per cent of full sunlight (C3 pathway) and a low light compensation point. These features are typical of shade-adapted plants. Leaves can also store large amounts of carbohydrates and minerals. Episodic growth flushes result in leaves of varying age and efficiency.

Flowering tends to be profuse but first set low, often< 0,001 per cent. It is controlled by strong environmental cues leading to synchronized growth cessation (Verheij, 1986), but there is no physiological dormant period. Cropping is often biennial or irregular.

These evolutionary adaptations were necessary for competitiveness in native rain-forests, but many are counterproductive in the orchard situation. The same applies to the unique flower behaviour of avocados, apparently an adaptation to unknown pollinators and to promote outcrossing, but fortunately with a fail-proof system for self-pollination (Davenport, 1986).

Infection with *Phytophthora cinnamomi*
There is no doubt that *Phytophthora* infection of avocado roots, even when seemingly mild and under control, has been a major cause of poor yields. The fungus is not native to the Americas (Zentmyer, 1985), so that avocado progenitors were not subjected to *Phytophthora* selection pressure. Evidence from Australian rain-forests suggests that biological control is possible (Broadbent & Baker, 1974). It is perhaps unfortunate, therefore, that this highly susceptible plant did not have the opportunity to acquire resistance during its evolutionary history.

The physiological effects of *Phytophthora* infection are severe. Infected trees have lower leaf xylem water potentials, reduced stomatal openings and therefore lower photosynthetic rates, and disturbed mineral uptake patterns (Sterne *et al*, 1978; Whiley *et al*, 1986). Root:shoot balances are disturbed, loss of roots leading to compensatory loss of foliage, severely aggravated by fruiting (Wolstenholme, 1981). The dramatic effect on yield is hardly surprising.

Energy cost of fruiting
Most of the dry mass of plants consists of carbon compounds, with over 90 per cent derived from photosynthetic carbon fixation. The different plant parts ('sinks') compete for assimilates, which *inter alia* are energy sources for growth and respiration.

The order of priority amongst the carbon sinks is usually seeds > fleshy fruit parts > shoot apices and leaves > cambium > roots > storage (Cannell, 1985). Fruiting therefore, has strong priority, is energy expensive, and reduces vegetative and especially root growth (Cannell, 1971; Chalmers & Van den Ende, 1975; Heim *et al*, 1979).

The energy cost of fruiting can be estimated from total annual carbon budgets. Unfortunately, few carbon budgets have been constructed for trees, and most of them suffer from serious limitations. Forestry models have however shown a high annual dry matter (and therefore energy) allocation to fine root turnover and root respiration (Cannell, 1985). The effect of *Phytophthora* on avocado would be to greatly increase this allocation in largely futile attempts to replace rotted roots.

Wolstenholme (1986) estimated the energy content of whole avocado fruits at maturity from published data on total carbohydrate, protein and fat contents. Heat of combustion values of 16,74 kJ g^{-1} of carbohydrate, 16,53 kJ g^{-1} of protein, and 38,91 kJ g^{-1} of fat are used for extrapolations to specific yields per ha^{-1}, ignoring respiratory losses during fruit growth.

It was estimated that Fuerte fruits with 17 per cent oil content and a flesh:seed ratio of 4:1 (fresh mass) contain 8 072 million kJ $tonnes^{-1}$, compared with 2 925 and 2 628 million kJ $tonnes^{-1}$ for Valencia oranges and apples respectively. Adopting a yield target of 100 t ha^{-1} as attainable for intensive apple orchards, the equivalent target (potential) yield for avocados is about 32,5 t ha^{-1}. The fact that the best avocado growers are only achieving two-thirds of this is an indication of the lag in avocado as compared with apple growing technology.

It is also clear that apparently low yields of avocado orchards are due to two main factors, viz the high oil content (oil is 2,3 times more energy-expensive than carbohydrate), and the large seed with concentrated food reserves. In fact, within the assumptions adopted, it was evident that only at oil contents above 17,8 per cent was the edible flesh more energy expensive per unit fresh mass than the seed.

IMPLICATIONS FOR AVOCADO YIELD IMPROVEMENT
Avocado selection and breeding Perhaps of the most immediate concern, based on conclusions reached with other crops (Gifford & Evans, 1981; Cannell, 1985), is altered assimilate partitioning away from wood production towards earlier, heavier and more regular fruiting. This can be attained by semi-dwarfed trees with greater branching and compactness. Cultivars such as Gwen and Whitsell (Bergh, 1986, pers comm) may be capable of average yields of 16,8 and 22,4 t ha^{-1} respectively at appropriate close spacings in southern California, without the benefit of dwarfing rootstocks. Further testing is needed to confirm their early promise.

Traditional breeding methods (Bergh, 1975) may not be fast enough to make the needed impact, for example incorporating dwarfing ability in *Phytophthora*-resistant

rootstocks. Early application of new breeding approaches to avocado problems made possible by biotechnological advances, mutation breeding, etc, is desirable.

In energy terms, selection for small seed size and somewhat lower flesh oil content should increase yield potential. There is however no evidence that the low oil content of tropical West Indian type avocados results in higher yields, possibly due to large seed size, and to higher respiration rates in warm climates. Furthermore, there is evidence from other crops that potential yields are set during the early, intense cell division of fruit growth by the availability of energy reserves at the time.

Phytophthora control
With the advent of chemical control of *Phytophthora* (Darvas *et al*, 1978; Darvas *et al*, 1983; Coffey, 1985 a; Pegg *et al*, 1985; Whiley *et al*, 1987) avocado growers have entered a new era of healthy, vigorous trees. More permanent control should arise with new resistant rootstocks (Coffey, 1985b). Provided that the extra vigour of trees can be satisfactorily controlled, average yields will show marked increases.

Manipulation of the vegetative/reproductive balance
The early onset of a vigorous, competitive spring growth flush is known to be detrimental to fruit-set in vigorous cultivars such as Fuerte and Sharwil. Emphasis is placed on keeping leaf nitrogen levels in Fuerte below 1,8 per cent as a practical means of controlling this vigour.

Spring growth flush vigour can also be manipulated by shoot tipping (Blumenfeld *et al*, 1983), which temporarily reduces the sink strength of the rapidly expanding vegetative shoot tips, giving fruitlets a better opportunity to establish their mobilising ability. In this regard, 'determinate' flower clusters appear to have a better fruit-set than 'indeterminate' clusters. The growth retardant paclobutrazol (Cultar(§) reduced the vegetative vigour of indeterminate flower clusters (Bertling & Kohne, 1986). Significant increases in fruit-set of Fuerte and Hass avocados have also been obtained by strategically timed foliar sprays of paclobutrazol which target the emerging spring shoots (Wolstenholme & Whiley, unpub data).

Avocado yields have been increased by girdling treatments. Israeli (Lahav *et al*, 1971) and Australian (Trochoulias & O'Neill, 1976) workers have reported yield increases of 2 to 5 t ha^{-1}. Further research on vigorous, healthy trees with good shoot systems appears justified.

Canopy architecture management
It is now accepted that small trees in high density plantings are physiologically more efficient as fruit producers, and maximise early yields and yields per unit land area (Chalmers, 1986). However, the problems of translating these concepts to vigorously growing evergreen fruit trees are many, and were a recurring theme at a recent symposium (Cull & Page, 1986).

Accepting the need for close initial spacing, critical decisions on tree thinning programmes arise as crowding sets in. Some aspects of avocado photosynthesis have been researched (Bower *et al*, 1980; Ramasadan, 1980; Scholefield *et al*, 1980). However, further investigation of light relationships in the orchard situation is needed for a more scientific basis for decision-making. We lack a sophisticated understanding of whole-canopy architecture.

Some aspects of flowering and fruiting
Very heavy flowering is characteristic of avocado trees, and is undoubtedly a heavy drain on both energy and mineral resources at a critical time. In a two-year study of mature Fuerte trees in California, abscissed flowers constituted 8 per cent of annual dry matter production (Cameron *et al*, 1952). Trochoulias (1987) found that flowers accounted for 2,7 per cent of the dry mass of a single 13-year-old Fuerte tree sampled in spring. Heavy abscission of young fruitlets in spring aggravates nutrient and energy losses. It appears that in the subtropics, where heavy flowering is usually assured, selection for reduced flowering intensity may have beneficial effects on yield.

Avocado fruits are often left on the tree after attaining minimum legal maturity. The consequent increase in oil content from about 10 per cent, sometimes to over 30 per cent in subtropical cultivars, adversely affects energy partitioning in the rest of the tree. Wolstenholme (1986) estimated that a 30 t ha^{-1} yield at 10 per cent oil content is energetically equivalent to 12,54 t ha^{-1} at 35 per cent oil content. Late hanging, although sometimes economically attractive, therefore severely depletes carbohydrate reserves and correspondingly reduces the following season's crop.

CONCLUSIONS
Seemingly low average avocado yields are partly due to the highland rainforest origin and the early stage of domestication of this crop by modern man. The high energy costs of fruiting limit the potential target yield to somewhat over 30 t ha^{-1}. Best growers achieve two-thirds of this, indicating considerable scope for research improvement.

In the longer term, breeding opportunities are believed to reside mainly in altered dry matter partitioning, particularly from unproductive wood production to fruit production. A range of *Phytophthora*-tolerant, dwarfing rootstocks are also needed.

For the average grower, the greatest short-term gains will come from alleviation of environmental stress, including Phytophthora control. Provision for healthy root growth will also improve water and nutrient supply, which ultimately limit yield.

In the medium term, research on growth retardant manipulation of vegetative/ reproductive balances, girdling, and a better understanding of canopy light relationships in high density orchards hold possibilities. The main gaps in our knowledge are phenological matching of critical developmental phases of root, shoot and fruit to relative source and sink strengths.

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