South African Avocado Growers' Association Yearbook 1981. 4:27-29

ROOT, SHOOT OR FRUIT?

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OPSOMMING

Die belangrikste wortelfunksies is om die plant te anker, water en minerals op te neem, en om sekere metaboliete en hormone te vervaardig. Omrede hulle interafhanklikheid, is 'n ekwilibrium tussen die wortels en die bogrondse dele van die plant gevestig. Wortelgroei en die wortel:stingel verhouding is deur baie faktore beïnvloed. Vruggroei benadeel die verdere ontwikkeling van die boomraamwerk, en veral wortelgroei. Die uitwerking van Phytophthora op die wortel:stingel en blaar:vrug verhoudinge, en die moontlike implikasies vir bestuursbesluite is bespreek.

SUMMARY

The most important functions of roots are anchorage, water and mineral uptake, and manufacture of certain essential metabolites and hormones. An equilibrium between the root and aerial tree parts is established due to their inter-dependence. Many factors affect root growth and the root: shoot ratio. Fruiting is at the expense of further growth of the tree framework, and particularly of root growth. The effect of Phytophthora *on the root: shoot and leaf: fruit interactions, and the possible implications on management decisions, are discussed.*

INTRODUCTION

The root system of a plant is both dependent on and essential for the normal functioning of the aerial plant parts. There is in fact strong feedback control between these two dependent partners (root and top or "shoot"). Any factor affecting one will directly or indirectly affect the other.

The root system is difficult to study. Because we cannot directly observe it, we tend to take it for granted. It is surprising how little has been published on avocado roots and root: shoot interactions — in spite of the devastating effects of *Phytophthora cinnamomi.*

It is at this stage premature to report on preliminary root studies initiated by the author during 1980. This paper is a general popular discussion on the functions and importance of roots and their relationship to aerial plant parts. It is hoped that it will help to stimulate research on avocado root: shoot and root:shoot:fruit interrelationships. This is a currently fashionable field closely associated with "assimilate partitioning" or "resource allocation" between the various plant organs.

The more serious reader is referred to several excellent books and reviews on the subject, in particular Wilson (1970), Russell (1977), Bohn (1979) and Atkinson (1980).

FUNCTIONS OF ROOTS

Apart from anchoring the plant, the most obvious root functions are water and mineral element uptake. Roots also manufacture many essential metabolites needed by the whole plant, e.g. they incorporate nitrogen into amino acids essential for protein and nucleic acid synthesis.

In recent years the importance of roots as suppliers of growth hormones has been recognized. They are major sources of cytokinins and gibberellins, in some situations exclusively so in the case of cytokinins (Goodwin *et al.,* 1978; van Staden & Davey, 1979; Wareing, 1980).

To a varying extent, especially in deciduous trees, roots store a significant proportion of the tree's food reserves. The avocado is known to be intermediate between typical evergreen trees such as citrus, and deciduous trees such as apple in the amount of food stored in the tree framework.

By their very nature roots must be continually replaced or undergo growth to perform their absorption functions. It is only the young, white unsuberized portions of roots that efficiently absorb water and minerals. Furthermore, avocado roots do not have root hairs which aid absorption in most plants. Suberization, the formation of a corky protective layer, occurs faster under stress conditions such as drought or cold.

Thus roots must keep growing and proliferating, because only in this way can they come into contact with new (or previously "tapped") sources of water and minerals. Albert (1975) has stated that perhaps the most important function of roots is growth. The relevance of this to avocado growers is obvious.

FACTORS AFFECTING ROOT GROWTH

Important *environmental factors* affecting root growth are soil moisture and aeration, soil CO_2 content, pH value (including aluminium and manganese toxicity in very acid soils), mineral elements, salt concentration, and soil temperature.

In avocado growing the importance of exceptional soil drainage and aeration has been emphasized *ad nauseum.* Avocado roots are intolerant of water saturated soils, even for short periods and in the absence of *Phytophthora.* Many of our orchards are monuments to careless choice of soils and nurseries.

The mineral elements more important for healthy root growth are phosphorus, calcium and boron. Of these, calcium has received the most attention in avocado orchards. It also helps to counteract aluminium toxicity, and improves soil structure and therefore drainage and aeration.

Boron is deficient in many of our high rainfall soils. It is required in minute amounts for root growth, e.g. 0,1 ppm or less. It appears to be necessary for elongation growth of root initials stimulated by auxin in stem cuttings (Albert, 1975). Perhaps we should pay more attention to boron in our avocado soils and irrigation waters. In contrast, California avocados are often subjected to very high and sometimes toxic levels of boron.

Avocado roots are very intolerant of high salt concentration (low electrical resistance values in soil analysis). This is only a factor in low rainfall areas. Very little is known about the effect of soil temperature on avocado root growth. With the expected change to clonal rootstocks such as 'Duke 7', this should be investigated.

Internal factors affecting root growth are many and complicated. The role of hormones is vital, affecting the ability of the roots to compete for photosynthate with the other "sinks" such as shoots, fruits etc.

ROOT:SHOOT INTERACTIONS

The avocado, like most evergreen fruit trees, displays rhythmic growth. Thus there are typically three growth "flushes" alternating with periods of quiescence. Little is known about the timing of root flushes in avocado. The assumption is that active root growth alternates with shoot growth, provided that environmental conditions are favourable. In deciduous trees, most root growth occurs in spring and in autumn.

If we consider a tree as composed of the two major subsystems "root" and "shoot", the interdependence of the two can easily be demonstrated. A flow chart for control of tree growth is given in Fig. 1 (modified from Wilson, 1975).

The fundamental raw materials for growth are CO_2 and light for the leaves, and water and minerals for the roots. Only the leaves can photosynthesize. The type and distribution of growth then depends on how the photosynthate is distributed or partitioned.

Fig. 1 shows that if the shoot system grows faster than the root system for any length of time, compensatory "feedback controls" will be set in motion. The roots will soon become unable to supply enough water, minerals or possibly hormones such as cytokinins. Shoot growth will accordingly slow down and stop, so that more photosynthate will become available for root growth. This feedback interaction between root and shoot is believed to be the basis for rhythmic growth (Borchert, 1976). It restores root: shoot equilibrium to a ratio characteristic of the particular plant types, stage of growth etc.

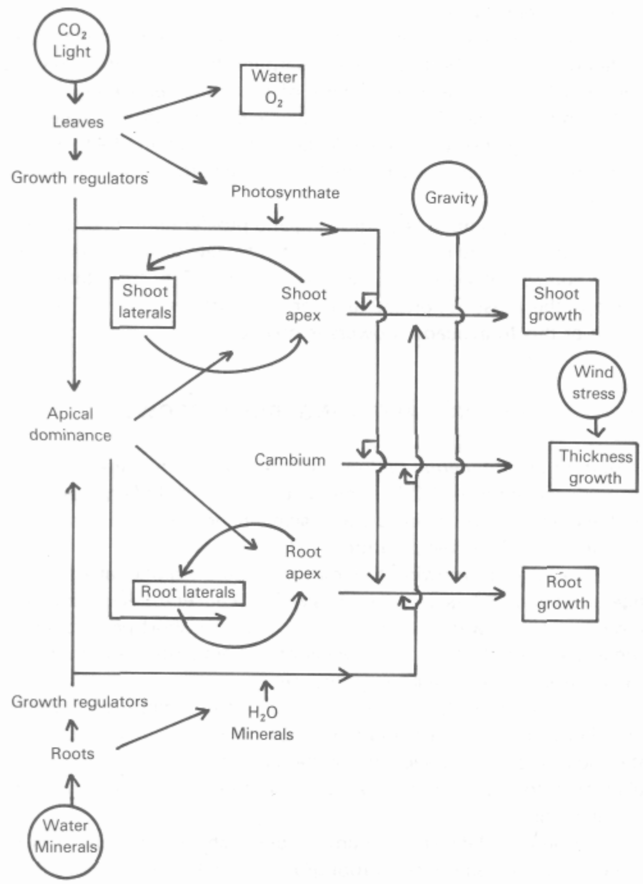

FIG. 1: A flow chart for control of tree growth. Items in circles are environmental *inputs*; those in boxes are outputs to the environment or as growth. The lines from apical dominance cross those from lateral shoots and roots where inhibition occurs.

FACTORS AFFECTING ROOT:SHOOT RATIO

Young plants tend to have higher root: shoot ratios than old plants. As a tree's root system approaches its physical limits of depth and spread, it encounters progressively deteriorating growing conditions. Root growth slows and the less restricted shoots are advantaged. However the lower root: shoot ratio in mature trees will in turn limit the potential for further extension growth in height and spread.

The root: shoot ratio is strongly influenced by soil moisture. Moderately dry soils increase the ratio, i.e. favour root growth over shoot growth. Root systems are deeper and more fibrous in such conditions. Competition with weeds has the same effect. Both these factors reduce *overall* tree growth.

On the other hand competition for light, as with close spacing, decreases the root: shoot ratio. Root growth is reduced due to reduction in photosynthate transport to roots. Any reduction in leaf area or efficiency, e.g. defoliation by insects or infection by disease, will have the same effect. High soil nitrogen in particular favours shoot growth, and reduces the root: shoot ratio.

Pruning reduces root growth and increases shoot growth in fruit trees (Head, 1967). The vigorous vegetative growth, which also discourages fruiting, will however set the scene for later recovery root growth.

Once a tree starts fruiting, a new and powerful "sink" for photosynthate complicates the picture. The food resources (the "cake") must now be divided amongst more plant parts. The effect is to drastically reduce. the proportion of photosynthate available for allocation to the vegetative sinks.

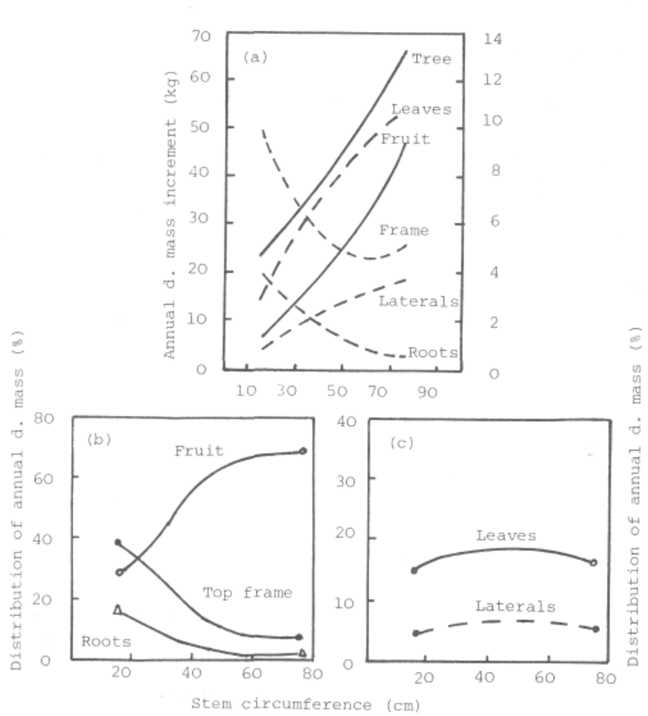

FIG. 2: a) Effect of peach tree size (stem circumference) on annual dry mass increment of the tree and its components. Solid lines refer to left hand ordinate, broken lines to right hand ordinate. b) Effect of tree size on distribution of dry mass between annual increments of ●, tree frame (top); o, harvested fruit; △ tree frame (roots). c) Effect of tree size on distribution of dry mass between annual increments of o, leaves, and ● lateral shoots. Modified from Chalmers & van den Ende (1975)

EFFECT OF FRUITING

Fruits are acknowledged to be the strongest "sinks" for photosynthate. It is not surprising that fruiting has a dwarfing effect on the overall growth of the tree.

Chalmers & van den Ende (1975) studied assimilate partitioning in growing peach trees in Australia. Fig. 2 shows that the percentage of dry matter directed into fruit growth progressively increased from 30% in young trees to 70% in a mature tree. The organs most adversely affected by fruit growth were the tree framework (decline from 40 to 20%) and especially the roots. In young trees roots appropriated 10% of the plant dry mass, but in mature trees this had declined to only 1%. The results of a similar study on apples are illustrated in Fig. 3 (Moore, 1978). Many other workers have found that fruiting strongly reduces root growth (Magga, 1963; Head, 1969; Avery, 1970).

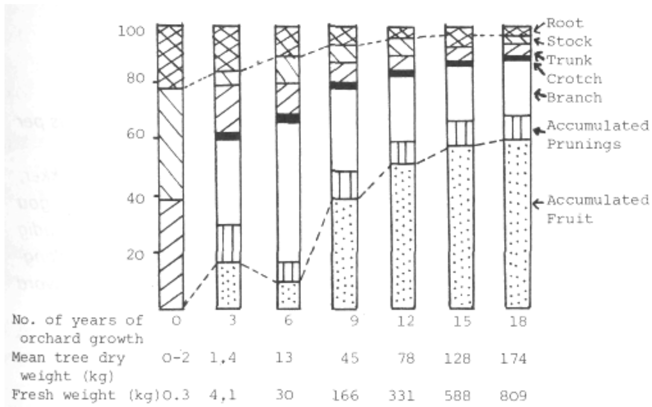

FIG. 3: Percentage distribution of total dry mass of apple tree components at 3-year intervals. (Modified from Moore, 1978)

Clearly, the growth of the fruit, roots and tree frame is competitively interrelated throughout the tree's life (leaf and young shoot growth is more independent). The roots, which are dependent organs, tend to become the poor relations, and the fruits the favoured organs. The photosynthate available for fruit growth is of course inversely related to and controlled by the potential for vegetative growth. It can therefore be concluded that assimilate partitioning between roots, frame and fruit is ultimately controlled by the growth of the roots.

In comparison with sugar-rich fruits such as citrus, peaches and apples, the main storage material of avocado fruits is oil (5 - 40%). To make 1 g of oil requires more than twice the energy as 1 g of carbohydrate. Fruiting in avocado, as in nuts, represents a particularly severe drain on the tree's food reserves, and therefore also on root growth potential.

CONSEQUENCES FOR AVOCADO GROWERS

The avocado grower, like any farmer, is seeking to maximize fruiting and economic returns. His life is however complicated by *Phytophthora* and short tree longevity. Let us now speculate on possible, consequences of the above discussion.

Firstly, the effect of *Phytophthora* is equivalent to root pruning. The result is reduction in vigour of shoot growth, and reduction of leaf area. This reduces the photosynthetic "factory", and a vicious circle of feedback control is instituted as the tree strives to restore the root: shoot equilibrium with reduced "capital" (resources). One of the reasons for the extreme susceptibility of avocado to *Phytophthora* may well be a poor ability to replace roots killed by the fungus. This would apply more to trees under stress due to fruiting, environmental factors etc.

If the root system becomes out of phase with top growth due to *Phytophthora* attack, it seems logical to try and swing the balance back into equilibrium, or even (temporarily) in favour of the roots. Our most powerful tool at present is Ridomil, but there are other options. Reducing the fruit load is perhaps the most effective of these. This would make more photosynthate available for leaf and for root growth. Maybe an occasional "off" year in *Phytophthora* affected trees would benefit tree longevity, in spite of the short-term economic loss of fruit. This is a dilemma for the grower.

To help keep the leaves healthy and to increase vigour, foliar feeding with nitrogen, zinc and possibly boron may be advisable during the recovery phase from *Phytophthora.* There seems to be little point in applying soluble fertilizers to the soil if most of the roots have been rotted away. Emphasis on nitrogen during the recovery phase also makes sense — even intentional over-fertilization of weakened trees. The resulting vigorous shoot growth will soon benefit the roots, especially if fruits are thereby sacrificed for a season.

Pruning has been cited as favouring shoot growth due to an altered root shoot balance. This again will later benefit the root system. Moderate cutting back of trees at the first signs of *Phytophthora* attack is suggested.

I have suggested above that *Phytophthora* infected trees may well have higher nitrogen needs in the recovery phase, provided the grower accepts (probably in his long-term interests) the accompanying temporary loss of cropping. I also believe that leaf analysis standards for trees suffering from root rot should be investigated separately. Norms are usually drawn up for *healthy* trees.

The most critical time in *Phytophthora* infected trees is likely to be in late summer and autumn. Soil temperatures and water status are favourable for the fungus, and rapid fruit growth to maturity is placing the trees under heavy photosynthetic stress. Root growth will be adversely affected at a time when active root growth normally occurs. The stress is likely to persist through winter, with consequent profuse flowering and heavy fruit set. The big crop load in relation to leaf and root can only aggravate the situation.

CONCLUSION

Avocado growers must be mindful of their trees' roots. The condition of the roots will be a mirror image of that of the aerial parts of the tree. A weak runty tree will have a weak root system and vice versa. It is suggested that there is much that can be done to improve root health. If roots do not grow actively, the growth of the whole plant will be checked. A balance of growth between root, shoot and fruit must be maintained. *Phytophthora* complicates these relationships, but there is much the grower can do to manipulate them to his long-term advantage.

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