

The Fruit Tree as an Integrated Unit Implications for Management

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Introduction: The fruit tree can be viewed as a small company that has limited resources for allocation to root growth, shoot growth and fruit growth. When trying to understand the physiological needs of a tree, carbon is typically used as the tree's currency. Fruit production is the tree's main measure of profit, because from an evolutionary perspective, a plant species will become more numerous than their neighbors if they produce more offspring that also survive to reproduce. Nonetheless, because fruit trees are generally long lived, it was generally a better strategy to forgo reproduction in stressful years (high pest pressure, drought) so that the tree could survive and reproduce new offspring in more favorable years during the species evolutionary past. Trees generally have evolved a conservative strategy regarding the amount of energy or carbon allocated to fruit production. Vegetative growth (root and shoot) and carbohydrate storage normally takes precedence over reproductive (fruit and flower) growth when the tree is stressed. Only when the carbon needs for survival are met (adequate roots, leaves and storage), will the surplus carbon be used for fruit production.

Why is there so much focus on carbon? Although one can use other resources (e.g., nitrogen), carbon is particularly effective as a measure of currency because it is nearly always limiting. Suppose trees are growing in what would be considered optimal conditions. Water and nutrients are supplied so that they are never limiting growth, light interception is maximized, all pests are completely controlled and yet the tree is still under stress. The tree is not under water or nutrient stress, it is under carbon stress (Fig. 1). Several studies have been conducted in citrus on the effects of elevated carbon dioxide on growth and carbon assimilation (Koch et al. 1986; Downton et al. 1987; Idso et al. 1991). These studies have demonstrated that plant growth is normally enhanced 20 to 100% by twice ambient CO₂. In apple, less work has been conducted on the effects of elevated CO₂. In one study (Bunce 1992), York apple seedlings exposed for 34 d to twice ambient CO₂ exhibited from 35 to 95% greater rates of carbon assimilation than those at ambient. In this short-term experiment growth was only enhanced 12% by elevated CO₂. It is likely that fruit trees as a group are particularly responsive to carbon fertilization because other resources such as water and nutrients are usually supplied in surplus amounts and fruit production represents an enormous sink for carbon in a fruiting tree.

Plant allocation of carbon is a major factor affecting yield. When trees become stressed, they tend to allocate less carbon towards reproductive growth and more towards vegetative growth. This is illustrated in a carbon flow diagram where plant parts are simply indicated by leaves, roots and fruit (Fig. 2). Additional complexity can be added by creating boxes for storage and stems. The various organs: leaves, roots and fruit compete for carbon based on the relative importance they have in meeting the needs of the plant. Thus when the tree lacks resources the leaves provide, the tree generally will expend more capital (carbon) to reduce the limitation associated with leaf function (e.g., photosynthate). When the tree lacks resources the roots supply (e.g., water, nutrients), it will generally allocate more carbon to the roots to reduce the limitations associated with root function. Fruit production is a major carbon storage buffer as well as an indication of net profit, i.e., the surplus carbon remaining after all essential survival needs are met. This concept is formalized in what can be termed the "Resource Optimization Hypothesis" which basically states that plants tend to optimize carbon expenditure so that water, nutrients and carbon equally limit growth (Bloom et al. 1985).

In this paper, I will review how certain management practices that affect the roots or shoots have subsequent effects on fruit production. Much of my examples will be based on my previous work in citrus and published work in apple; consequently, in this case I do believe we can compare apples and oranges!

Fertilization: When trees have insufficient phosphorus or nitrogen, the plant senses that its limitations to maximum growth and reproduction are primarily below ground. Thus, there is a reallocation of carbon so that a greater percentage goes into root growth and less into shoot and fruit growth (Fig. 3). The effect of nutrient and water stress on root:shoot ratio is well documented for most plants. For example, the effects of water and nutrient stress in apple were studied by Buwalda and Lenz (1992). One-year-old trees of 'Golden Delicious', 'Cox Orange' and 'Gloster' on M9 rootstocks were planted in lysimeters and in the first year, all trees received a standard nutrient solution. In the second and third season, trees in the low-nutrient treatment received one-tenth the nutrients as those in the high-nutrient treatment. For noncropping trees, root growth tended to be slightly higher in the low- than high-nutrient treatment, whereas shoot growth was considerably greater in the high-nutrient treatment (Fig. 4). In another treatment, Buwalda and Lenz (1992) used 'Golden delicious' on 'M9' rootstock and provided 25, 50 and 100% of the water consumed by the control trees for the first three seasons of growth (=low, medium and high irrigation treatments). They found root growth was highest in the medium treatment, slightly less under high irrigation and least under the low irrigation. Shoot growth in the high treatment (non-cropping trees) was twice that of the medium irrigation and almost four-fold greater than the low-irrigation (Fig. 5). Thus, root:shoot ratios are clearly highest when soil resources (water or nutrients) most limit plant growth (Fig. 6).

Pruning/Hedging: When leaves are lost such as by hedging or pruning the tree normally responds to the imbalance in root:shoot ratio by allocating more carbon to shoot growth and less to root and fruit growth (Fig. 7). This was demonstrated in citrus when the upper third of the canopy was removed in a study using 'Valencia' orange trees on 'rough lemon' rootstock (Eissenstat and Duncan 1992). Root growth, which was examined nondestructively with minirhizotrons over a four-month period, tended to be less seven days after pruning and this difference was significant from 14 to 49 d after pruning (Fig. 8). By 30 d after pruning, at least 20% of the roots of the pruned trees at a soil depth of 9 to 35 cm apparently died. By 63 d after pruning, root length density had recovered to that of unpruned trees. Nine to 11 months after pruning, fine root and leaf biomass had completely recovered from the pruning treatment (Table 1). Indeed, there was evidence of overcompensation. The additional carbon for root and shoot growth came at the expense of reproduction. Compared to unpruned trees, heavy pruning of citrus in August caused a 76% reduction in fruit biomass.

Similar results have been obtained with temperate deciduous fruit crops. Weekly or biweekly measurements in plum and apple trees indicated that pruning or defoliation induced diminished root growth within one to three weeks (Head 1967, 1969). Pruning black currant caused diminished root growth within a week (Atkinson 1972).

Other factors such as the timing the trees are pruned and the amount removed can strongly influence the extent the root:shoot ratio is altered and the amount of carbon that is reallocated to reestablishing the canopy (e.g., Maggs 1959; Kikuchi et al. 1989).

Deblossoming/Defruiting: Fruit trees invest an enormous amount of carbon each year in fruit. Citrus for example, can have as much biomass in fruit as in leaves and fine roots combined (Eissenstat and Duncan 1992). Similar or higher proportions of total tree biomass allocated to the fruit have been found in apple (Maggs 1963; Buwalda and Lenz 1992). Thus, when fruiting in abruptly curtailed in a given year, such as by a late spring frost killing blossoms, there is removed an extremely large sink of current photosynthate (Fig. 9). This carbon is reallocated to enhance vegetative growth of the roots and shoots as well as increase carbohydrate storage in the tissues (e.g., starch concentrations). In a defruiting study using 'Valencia' orange on 'rough lemon', root growth was enhanced to a greater extent than shoot growth, causing an increase in root:shoot ratios (Fig. 10) (Duncan and Eissenstat 1993). Starch concentrations in the fine roots was increased 60%. Deblossoming 'Golden delicious' on 'M9' rootstock also caused a large increase in growth of roots as well as stems but only a small increase in leaf area (Schupp et al. 1992). Since carbon is much less limiting in a tree with no fruit, it is understandable that there would be much less allocation to increasing the potential for capturing more carbon (i.e., leaves).

Conclusions: Trees allocate more carbon to the roots under nutrient stress, water stress and loss of reproductive potential. If trees are optimally managed they will have good root development but proportionally greater biomass in leaves and fruit. This will lead to sustained high fruit yields. Poor root development is a

serious problem. Sometimes it is caused by poor light interception and thus the tree is particularly carbon stress. More often, it indicates that although the tree is allocating carbon belowground so as to minimize the restriction to growth and reproduction caused by lack of water and nutrients, some environmental factor (e.g., pathogen, poor aeration) is still preventing good root growth and survival.

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Table 1. Dry weight of fruit, fine roots and leaves in 13-yr-old 'Valencia' sweet orange on 'rough lemon' rootstock 8 to 11 months after a third of the canopy was removed (Eissenstat and Duncan 1992).

Plant Organ	Unpruned	Pruned
Fine roots (kg)	6.31	7.29
Leaves (kg)	8.82	9.88
Fruit (kg)	15.85	3.84
Fine root/Leaf Ratio	0.715	0.738

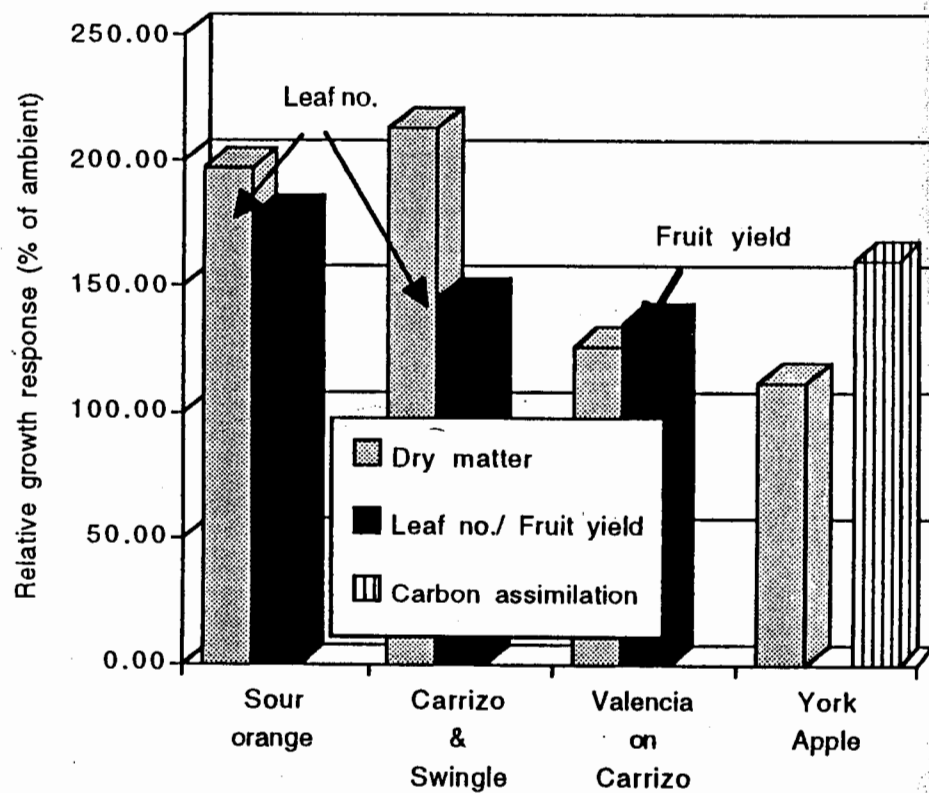


Fig. 1. The effects of twice ambient CO₂ on total tree dry matter, leaf number, fruit yield and carbon assimilation (sour orange, Idso et al. 1991; Carrizo and Swingle citrus root stock seedlings, Koch et al. 1986; Valencia orange on Carrizo rootstocks, Downton et al. 1987; York apple seedlings, Bunce 1992).

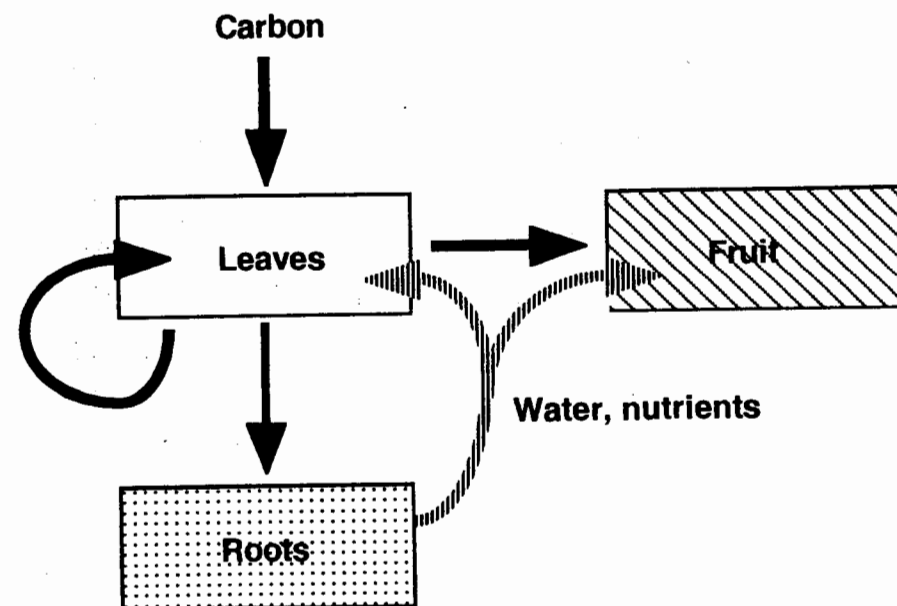


Fig. 2. Carbon and nutrient flows in a fruit tree.

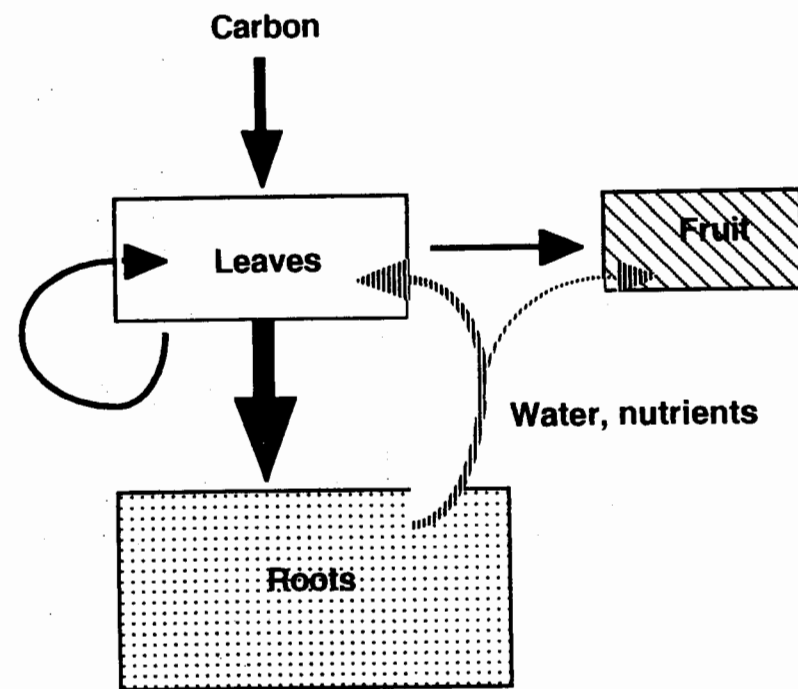


Fig. 3. Carbon and nutrient flows in a fruit tree under conditions of water or nutrient stress.

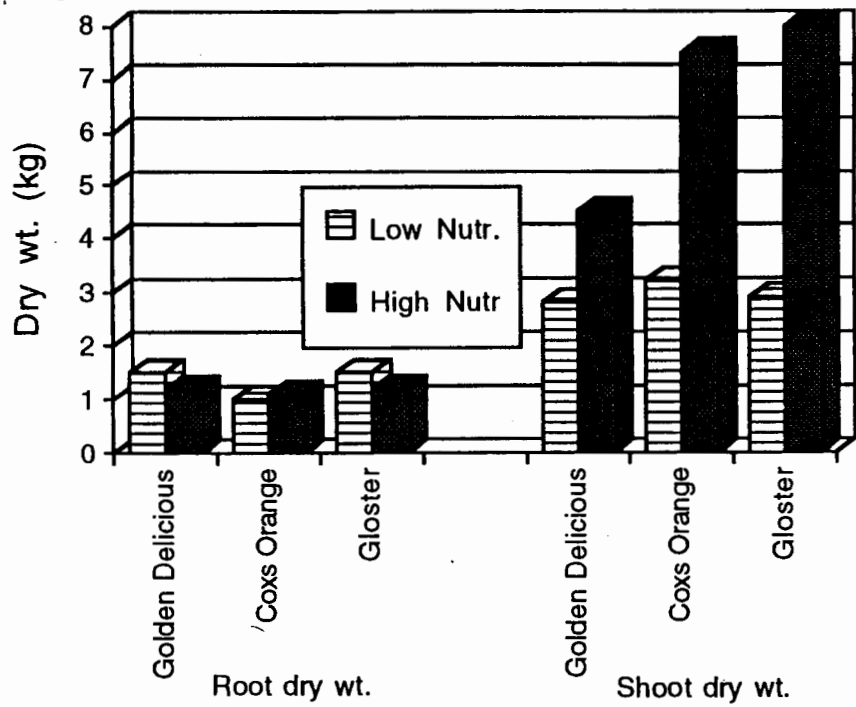


Fig. 4. Root and shoot dry wt. of 3-yr-old apple cultivars on M9 rootstock (redrawn from Buwalda and Lenz 1992)

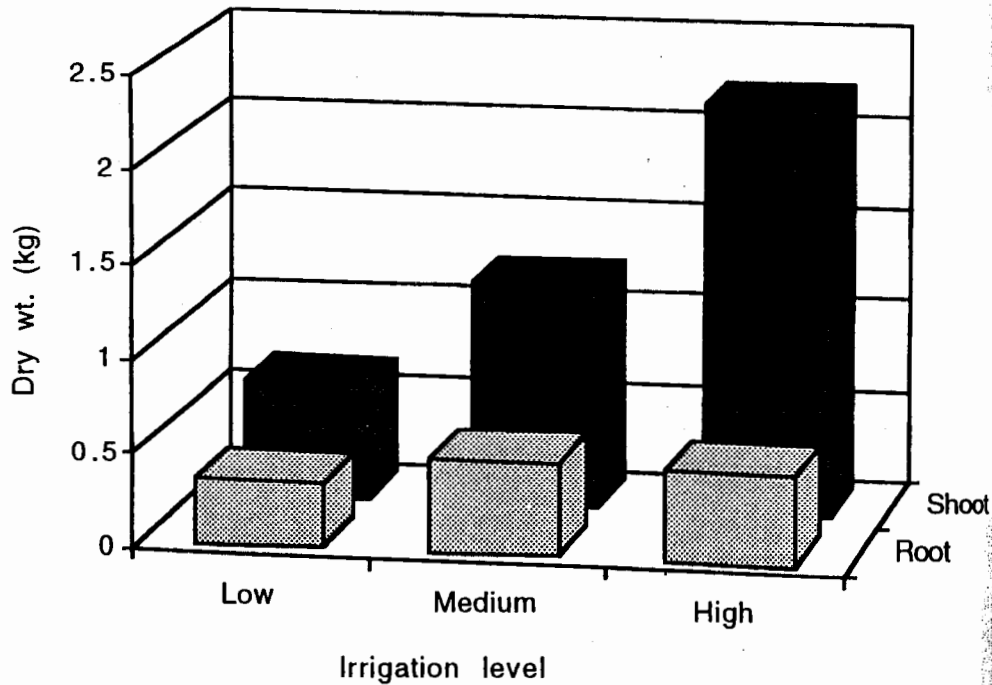


Fig. 5: Shoot and root growth of 3-yr-old 'Golden Delicious' on 'M9' rootstocks

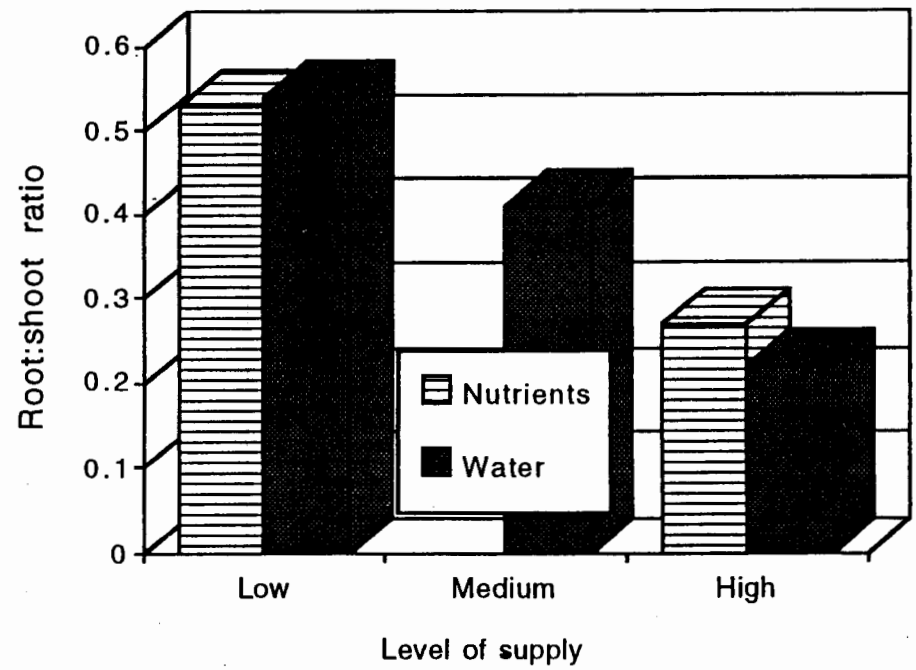


Fig. 6. The effects of supply of water or nutrients on root:shoot ratio (redrawn from Buwalda and Lenz 1992).

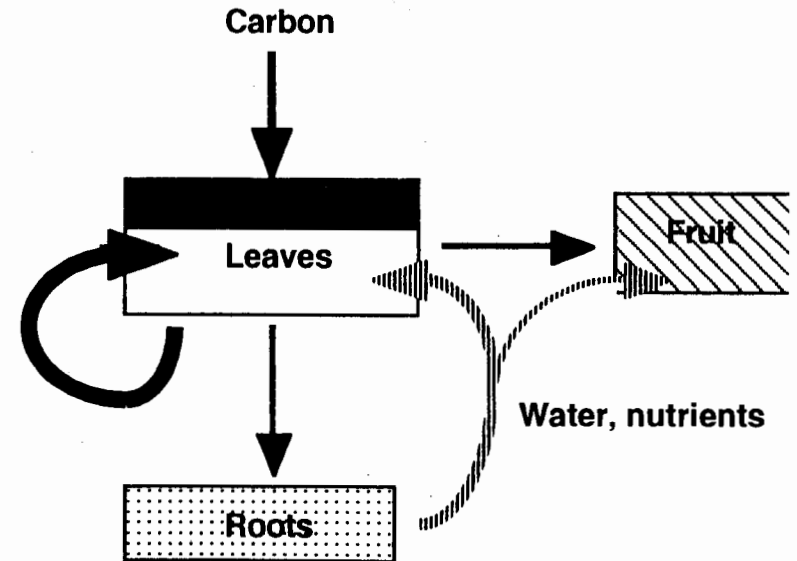


Fig. 7. Carbon and nutrient flows of a fruit tree following hedging, pruning or other form of canopy loss.

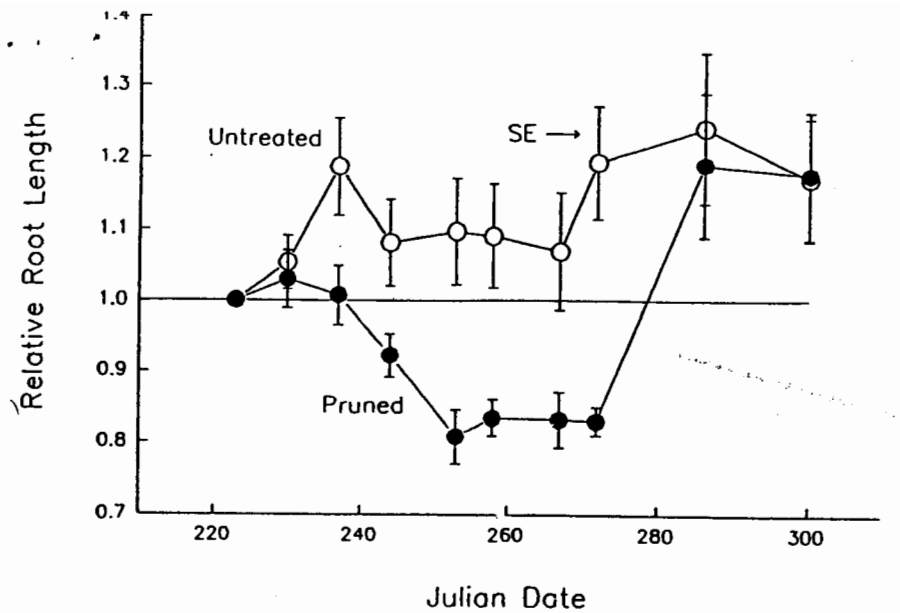


Fig. 8. Relative root length between depths of 9 and 35 cm after removal of a third of the canopy in 18-yr-old 'Valencia' sweet orange trees on 'rough lemon' rootstock. Root length is expressed as a proportion of initial root length. One standard error (\pm) of each treatment ($n=8$) is indicated (from Eissenstat and Duncan 1992).

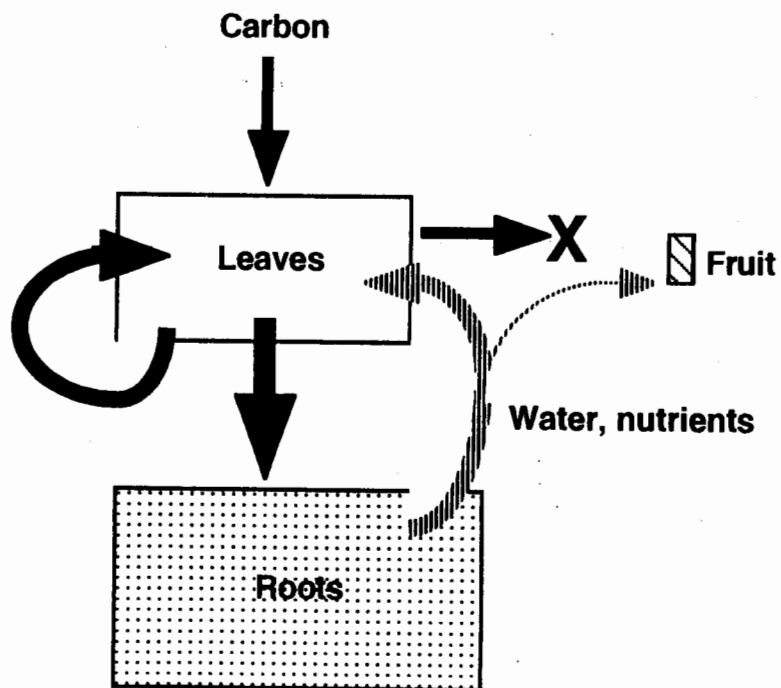


Fig. 9. Carbon and nutrient flows in a fruit tree after loss of blossoms or fruit.

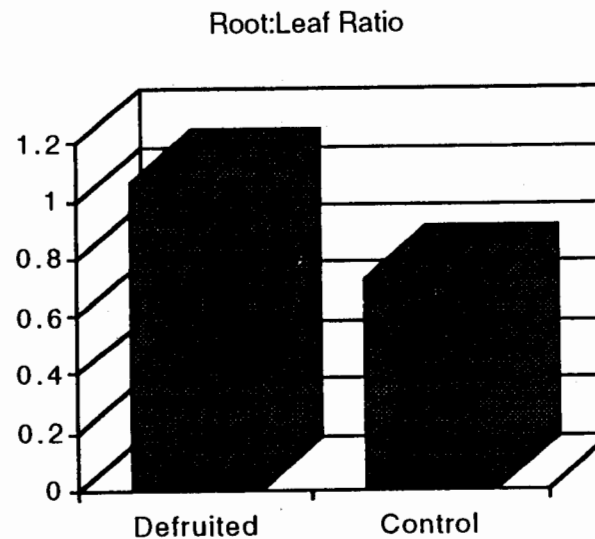
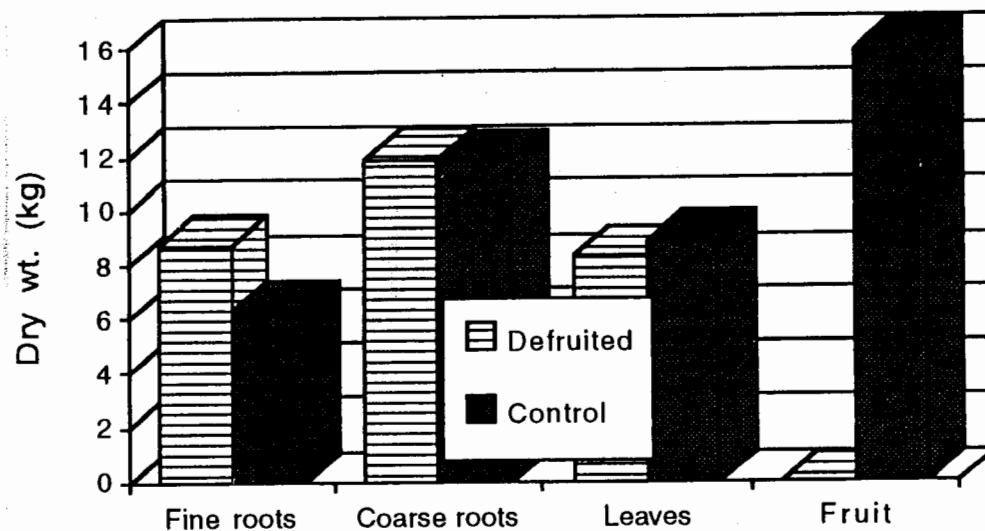


Fig. 10. Biomass partitioning (top) and root:shoot ratio (bottom) 8 to 11 months after defruiting in 'Valencia' orange on 'rough lemon' rootstock (after Duncan and Eissenstat 1993)