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 stress 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. Meanwhile, because fruit trees are generally long lived, it was generally a better strategy for reproduction to be established in stressful years (high pest pressure, drought) so that the tree could survive and reproduce new offspring in more favorable years facing 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 (flower and fruit) 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; Nowak et al., 1991; Den et al., 1996). 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 et al., 1992), York apple seedlings exposed for 34 to twice ambient CO₂ exhibited from 35 to 95% increase in 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 freezing 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 stress. The various organs: leaves, roots and fruits are then linked with carbon based on the relative importance they have in fueling the tree's needs. Thus when the tree lacks resources the leaves tend to reallocate carbon to the root, reduce the flow of carbohydrates to the fruits and increase the flow of carbohydrates to the leaves or roots. This is the basic concept of the Resource Optimization Hypothesis which states that the plant begins to optimize carbon expenditure to that water, nutrients and carbon equally limit growth (Blum et al., 1981).

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 to oranges.
Fertilization: When trees have insufficient phosphate or nitrogen, the plant leaves that suffer its limitations to maximum growth and reproduction are primarily below. Thus, there is a reallocation of carbon on that greater part going into root growth and less into shoot and fruit growth (Fig. 3). The effect of water and nutrient stress in apple was studied by Bawduls and Less (1992). Gusiner and Ns12111211\(^{*}\) rootstock were planted in lysimeters in the first year. All trees received a standard nutrient solution. In the second and third season, trees received one-tenth the nutrients that those in the high-nutrient-low-water treatment. For low-nutrient-low-water treatment, where shoot growth was considerably greater in the high-nutrient-low-water treatment (Fig. 4). In another treatment, Bawduls and Less (1992) water consumed by the control trees for the first three seasons of growth (Fig. 5). Those trees received only sufficient water to maintain the highest soil resources (water or nutrients) most limit plant growth (Fig. 6).

Pruning/Hedging: When leaves are lost such as by budworm or pruning the tree normally responds to the removal of a shoot by allocating more carbon to shoot growth and less to root and fruit growth (Fig. 7). This was demonstrated in a series of experiments where the loss of shade to citrus when the upper third of the canopy was removed in a 9 Experiment on oranges on 'July-late' rootstock (Eisnerat and Duncan 1992) Root growth, which was examined nondestructively with microtome sections, showed a significant increase in the number of roots per plant. The number of roots at a soil depth of 9 to 13 cm appeared to be reduced by 53% 14 months after Pruning. The root and leaf biomass had completely recovered from the pruning treatment (Table 1). Indeed, there was evidence of overcompensation in the number of roots and shoot growth came at the expense of reproductive growth. Compared to unpruned trees, heavy pruning of citrus in August caused a 76% reduction in fruit biomass.

Similar results have been achieved with temperate deciduous fruit crops. Weekly or biweekly measurement in plum and apple trees indicated that pruning on three weeks (Head 1967, 1969).

Pruning black currant caused diminished root growth within a week (Akinbode 1972).

Other factors such as the timing of the treestrained, the amount of pruning and the number of trees removed were not considered in this study (e.g., Maggs 1979 philosophically).

Dobloosming/Defoliation: Fruit trees invest an enormous amount of carbon each year. For citrus, for example, can have as much biomass in fruit as in leaves. Thus, the removal of fruiting spurs by the late spring bud-fall burning, there is no removal of the excess foliage, and the growth of the roots and shootless as well as increase carbohydrate 'Valencia orange on 'Monument' variety. In a defoliation study with three treatments, root growth was enhanced to a greater extent than shoot growth, causing an increase in root/shoot ratio (Fig. 2). Dobloosming 'Golden Delicious' on 'M9' rootstock also caused a large increase in root growth of as well as some shoot growth. There is no damage to the trees in the area (Schupp et al. 1992). Since carbon is much less limited in a tree with no fruit, it is understandable that there would be much less allocation to the increasing potential for capturing more carbon (i.e., leaves).

Conclusions: Trees allocate more carbon to the roots under nutrient stress, water stress and less reproductive potential. If trees are optimally managed they will have good root development but proportionately greater biomass in leaves. 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 trees do not allocate carbon efficiently. 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 nutrient stress (e.g., pathogens, poor aeration) is still preventing good root growth and survival.

References:
- Koch KE, Jones PR, Aigner HJ, and Dickson. Growth, dry matter partitioning, and climatic activities of PEP carboxylase in citrus seedlings maintained at two levels of CO2. Physiologia Plantarum 77:417-446.
Table 1. Dry weight of fruit, fine roots and leaves in 10-year-old 'Valencia' sweet orange on 'Tangelo', sweet orange and 'Carrizo' in 8 to 11 months after a third of the canopy was removed (Esparza and Duance 1992).

<table>
<thead>
<tr>
<th>Plant Organ</th>
<th>Unpruned</th>
<th>Pruned</th>
</tr>
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<tbody>
<tr>
<td>Fine roots (kg)</td>
<td>4.31</td>
<td>2.70</td>
</tr>
<tr>
<td>Leaves (kg)</td>
<td>8.82</td>
<td>9.38</td>
</tr>
<tr>
<td>Fruit (kg)</td>
<td>15.45</td>
<td>13.84</td>
</tr>
<tr>
<td>Fine roots/Leaf Ratio</td>
<td>0.735</td>
<td>0.728</td>
</tr>
</tbody>
</table>

Fig. 1. The effect of twice ambient CO2 on total tree dry matter, leaf number, fruit yield and carbon assimilation (sour orange, Jones et al. 1991; Carrizo and Swingle trees on rootstock seedlings, Knops et al. 1986; Valencia orange on Carrizo rootstocks, Dowson et al. 1991; 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 Bewald and Lea 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 Bewald and Lea 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 5 and 35 cm after removal of a third of the canopy in 10-yr-old 'Valencia' sweet orange trees on 'rough lemon' rootstock. Root length is expressed as a proportion of initial root length. One standard error (SE) of each treatment (n=8) is indicated (from Eisersen and Duques 1995).

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

Fig. 10. Biomass partitioning (top) and root/leaf ratio (bottom) 8 to 11 months after defruiting in 'Valencia' orange on 'rough lemon' rootstock (after Duques and Eisersen 1993).