PHYSIOLOGICAL ASPECTS OF CITRUS WATER RELATIONS

JAMES P. SYVERTSEN
University of Florida, IFAS,
Citrus Research and Education Center,
700 Experiment Station Road,
Lake Alfred, FL 33850

Water generally is considered to be the most important factor limiting plant growth. There is no doubt that plant water deficits can limit productivity, yield, and the quality of all crops. Therefore, it is important that we understand how water stress impinges upon plant production systems through time. The understanding of the relationships between water and carbon budgets should be an essential long-term goal in horticultural research. This discussion will focus on whole-plant water relations and how they interact with carbon budgets to modify vegetative growth and fruit yield. The references cited are not intended to be comprehensive but rather to serve as a starting point to gain more specific information.

Water and Carbon Budgets

Two of the most important materials entering plant systems from the environment are water and CO_2. From 60 to 90% of plant fresh weight is water and up to 95% of plant dry weight is composed of carbon in the form of structural carbohydrates (wood) and nonstructural carbon compounds (starches and sugars). The remaining 5 to 10% of plant dry weight is mineral nutrients. In addition, carbohydrates from photosynthesis supply energy for growth and other plant processes. Thus, water and carbon budgets are inextricably related in plant systems.

The two major contact points between plants and their external environment are: 1) between the root and the soil where water, mineral nutrients, and oxygen enter the system and carbohydrates, amino acids, other exudates, and CO_2 can leave the plant and enter the soil; and 2) between shoot tissues and their aerial environment where CO_2 and oxygen are exchanged and H_2O vapor inevitably diffuses out of stomata. Thus, plants that fix the most carbon and produce the most dry weight also transpire the most water. These plant/environment interfaces are critical control points where environmental factors and physiological mechanisms interact to regulate exchanges of energy (heat and radiation) and materials.

When available soil water is limited, water movement through the plant system is regulated primarily by soil water supply and conductivity of the roots. When soil water is adequate, water movement is controlled by root conductivity and transpiration. This water movement through the tree is regulated by both stomatal aperture and evaporative demand. Plant water deficits can be caused by an inadequate water supply or by high evaporative demand.

Soil Water Supply

Water input into the soil is determined by precipitation, the canopy's tendancy to deflect rainfall, and irrigation frequency (Chaney, 1981). Available soil moisture is determined by the moisture-holding capacity and the hydraulic conductivity of the soil (Table 1) which are largely a function of bulk density and pore size distribution. As irrigators, we use the soil as a water reservoir. How water moves in the soil is defined as its hydraulic conductivity which, in turn, depends on soil water content, temperature, and salinity (Cary and Taylor, 1967). Excess salinity from poor quality irrigation water or from salt accumulation in the soil can decrease soil water availability (Syvertsen et al., 1989).

On the other hand, excess soil water reduces oxygen availability or increases anaerobic toxins and is another form of water stress that is important in tree water

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Table 1. Summary of contributing factors that influence water movement into the plant system at the soil-root interface and out of the plant system at the leaf-air interface.

Soil to root (supply)	Leaf to air (demand)
Rain, irrigation	Tissue capacitance
Canopy interception	Plant water status
Soil water content, conductivity, salinity	Stomatal conductance
Root distribution, density	CO_2 concentration
Root conductivity	Radiation
Genetic (rootstock)	Temperature
Temperature, aeration	Humidity gradient
Nutrition	Plant growth regulators
Plant growth regulators	

relations (Syvertsen et al., 1983). Furthermore, the depth to water table can influence the health and size of trees by limiting root growth.

Roots

The wide variation in root distribution patterns in the soil profile can affect a tree's capability to utilize available water (Castle and Krezdorn, 1977; Kriedemann and Barrs, 1981). Root density in the soil profile usually increases as trees grow, but root growth ceases as the soil dries (Bevington, 1983). Small soil water deficits, however, may actually increase the root density relative to shoot growth if shoot growth is more greatly affected than root growth. Such a relative increase in root density, in effect, can reduce effects of subsequent drought stress (Table 1) by reducing transpirational demands on individual roots (McCoy et al., 1984). The root system's capacity to transport water (conductivity) to the shoot also depends on the water extraction efficiency of individual roots (Castle and Krezdorn, 1977; McCoy et al., 1984). If root temperatures are above or below optimum, water conductivity of roots may be reduced. This may indirectly affect stomatal conductance in leaves and, hence, CO_2 assimilation and subsequent translocation of carbohydrates (Kadoya et al., 1981). Citrus roots growing in cool soil can have higher conductivities per unit root length of individual roots (Syvertsen et al., 1983) than roots growing in warm soil. This may partially compensate for reduced root growth at cool soil temperatures. Soil salinity can decrease both root growth and hydraulic conductivity through osmotic effects and the presence of toxic ions in soil (Syvertsen and Yelenosky, 1988).

Vigorous rootstocks have greater root densities (Bevington, 1983; Castle and Krezdorn, 1977) and intrinsically higher potential hydraulic conductivity of roots (Syvertsen, 1981) than less vigorous rootstocks. Relatively vigorous rootstocks, however, usually produce more leaf area, so that leaf water potentials of rootstocks with different conductivities may not necessarily differ very much.

Inadequate soil moisture not only limits water supply to the roots, but also reduces root conductivity directly (Wiersum and Harmanny, 1983), perhaps because of increased suberization of roots. Any stress-induced change in the root system's capacity to supply water to the shoot can influence the tree's tolerance to low temperatures (Wilcox et al., 1983) and flooding (Syvertsen et al., 1983), and affect the quality of fruit produced (Kriedemann and Barrs, 1981). Tree nutrition interacts with soil water supply, but the relationship can be complicated by vegetative growth responses and internal redistribution of minerals.

Adequate mineral nutrients can enhance root growth (Radin and Eidenbock, 1984) and hence surface area contact with soil. This becomes especially important when soil moisture is limiting. Some improvements in plant water relations can be attributed to improved phosphorous nutrition (Graham and Syvertsen, 1985). Mineral nutrient deficiency can also limit the hydraulic conductivity of roots (Radin and Eidenbock, 1984). Citrus rootstocks with higher root conductivities also tend to have higher concentrations of mineral nutrients in their leaves than rootstocks with lower conductivities (Syvertsen and Graham, 1985).

Competition between roots and shoots for carbohydrates is also important since canopy shading, drought, severe defoliation, or heavy crop load can all lead to decreases in root growth of citrus (Kriedemann and Barrs, 1981). Since the source of carbohydrates is in the leaves and shoots, shoots typically compete better for photosynthates than roots. This is an important factor when considering how a tree recovers from partial defoliation caused by drought, salinity, or freezes.

WATER DEMAND

Shoots and Leaves

Most estimates of the efficiency of water transport in the xylem come from measurements of leaf water status at different transpiration rates (Cohen and Cohen, 1983). The conductivity of water by xylem can be a factor in the development of plant water deficits in citrus (Jones et al., 1985; Kriedemann and Barrs, 1981). In most cases, however, leaf water status does not regulate stomatal conductance until extremely high drought stress occurs (Syvertsen, 1982a).

Tissue Capacitance

In large trees, stored water (capacitance) in the trunk can provide a significant water source that is available to augment transpirational requirements (Chaney, 1981). Seasonal and diurnal variations in sapwood water content can, therefore, be used as estimates of transpirational demand. Diurnal and seasonal dimensional changes in leaves (Syvertsen and Levy, 1982), fruit, stems (Hilgeman, 1963), and branches have been used as quantitative estimates of tissue water changes (Kozlowski, 1972). Water status of various plant tissues quantitatively reflect internal competition for water. Redistribution of water is a function of both water status (Table 1) and resistance to transport (Cohen et al., 1983). Thus, daily changes in tissue water content, relative thickness of leaves (Syvertsen and Levy, 1982), and fruit diameter (Cohen and Goell, 1988) are indicative of interactions in the water transport system (Kadoya et al., 1981; Kozlowski, 1972; Syvertsen and Levy, 1982). Since these factors are linked by way of leaf transpiration, which is a function of both conductivity and vapor pressure gradients, their relationship may not always be simple (Levy and Syvertsen, 1981).

Tree growth (Levy et al., 1978b) and leaf expansion are inhibited by water stress, and leaf senescence can be hastened or delayed by water deficits. Since cell expansion requires turgor pressure, cell turgor is inextricably linked to both shoot and root growth. The leaf area that intercepts radiation can be modified by drought-induced wilting, curling of leaves, solar tracking, and leaf shedding (Fereres et al., 1979). During extreme drought, leaf loss can enhance tree survival by decreasing the evaporative surface. Although leaf shedding may be an important drought avoidance mechanism, such vegetative losses are generally detrimental from a horticultural point of view, especially for broad-leaved evergreens.

Cessation of new leaf growth is a means by which the tree can acclimate to drought stress conditions (Syvertsen, 1982a). Young leaves lose turgor and wilt during water stress before mature leaves. Thus, initiation and growth of new leaves is very sensitive to water deficits. In subtropical citrus, leaf age is more important than environmental conditions in determining physiological responses over a season (Syvertsen, 1982a).

Evaporative Demand

Interactions between internal plant water status, stomatal conductance, and vapor pressure deficit (Kadoya et al., 1981; Sinclair and Allen, 1982) make it difficult to characterize adequately the negative effects of water deficits without integrating such interactions over time. Furthermore, citrus leaves subjected to alternate drying and irrigation cycles become physiologically hardened to drought stress and thereby enhance their tolerance to subsequent drought (Levy, 1983).

Plant water deficits routinely occur during the day, not only in response to an inadequate water supply or an insufficient water transport system, but also in response to normal increases in evaporative demand. Daily increases in vapor pressure deficits increase the difference between the absolute humidity of leaves and air, and stomatal conductance generally decreases (Levy and Syvertsen, 1981; Jones et al., 1985). Overall, it is important to recognize stomatal conductance is a function of several environmental factors such as CO_2 concentrations, VPD, and light and, secondarily a function of leaf water status which is determined by water supply and demand.

Internal Factors Affecting Stomatal Behavior

As mentioned previously, extremely low leaf water potentials can decrease net CO_2 assimilation by lowering stomatal conductance or by affecting photosynthetic or respiratory processes. Given adequate leaf water status to maintain turgor, stomata may respond directly to CO_2 concentrations, resulting in the rate of CO_2 photosynthesis affecting stomatal conductance rather than the reverse (Farquhar and Sharkey, 1982). Thus, stomatal limitations on photosynthesis are probably not as great as is generally believed until extreme drought stress causes leaves to wilt.

Reductions in leaf area by decreased growth and accelerated leaf drop caused by water stress can reduce photosynthetic capacity by reducing the leaf area. Remaining leaves can partially compensate for leaf area losses by enhancing CO_2 assimilation rates. Such changes influence carbon budgets through carbohydrate production, loss, and allocation to leaf and fruit growth.

Reproductive Growth

Differentiation of vegetative or reproductive tissue is directly affected by water deficits (Kaufmann, 1972; Morshet et al., 1983) and indirectly affected by the availability and distribution of photosynthates and plant hormones (Kriedemann and Barrs, 1981). Decreases in vegetative growth and flower bud initiation due to drought stress can hasten fruit growth of remaining fruit by decreasing competition for water and carbohydrates, but water deficits also can delay fruit maturation (Kaufmann, 1972). Water loss directly from flowers can be quite high (Syvertsen et al., 1981). Flower petals and fruit can have functioning stomata (Kaufmann, 1972), although the importance of water loss from oranges diminishes as fruit mature (Syvertsen and Albrigo, 1980). Leaves and fruit compete for a limited water supply diurnally as well as seasonally. Early fruit abscission of weak young fruit ("June drop") has been related to drought stress. Limited soil water usually results in yield losses but may enhance water use efficiency (Bielorai, 1982; Morshet et al., 1983).

Reproductive yield usually is adversely affected by inadequate soil moisture. High temperatures and evaporative demand during flowering and fruit set can be disastrous (Kaufmann, 1972). Moderate drought stress can increase percentage of flower abscission and, thus, reduce fruit yield (Morshet et al., 1983). Yield usually is decreased by inadequate soil moisture (Levy et al., 1978b) but moderate drought stress can enhance fruit quality by decreasing the size of citrus fruit (Bielorai, 1982), and decrease dilution effects in citrus (Levy et al., 1978a). Changes in fruit volume or dry matter content may be of use in scheduling irrigations (Cohen and Goell, 1988).

Post-freeze Water Relations

Defoliation freezes have become relatively common in the past decade such that the water relations of partially or totally defoliated trees is of interest. Since defoliated trees have a decreased evaporative surface and a relative abundance of roots, drought stress is not a problem unless the soil is extremely dry. Surviving leaves after a freeze were under less daily water stress than they would have been if there had been no defoliation (Syvertsen and Smith, 1982). Leaf loss reduced internal competition for water.

Large losses of photosynthetic area can upset the carbon balance between shoots and roots. Carbohydrate reserves in woody tissues are likely to be depleted by the large post-freeze flush of leaves. Leaves do not become net exporters of carbon until about the time they reach full expansion (Turgeon, 1989). Regrowth leaves are often relatively small which is probably a reflection of this depletion of carbon reserves as well as high water demands by the large new flush (Syvertsen, 1982a). During the period following a defoliating freeze, it is likely there is no new root growth while existing fibrous roots continue to die naturally. Soil temperatures below the top six inches probably do not get cold enough to directly kill roots. The finest roots will likely starve and die before larger roots do. Continued root death will eventually reestablish a new balance between shoots and roots. This can be a prolonged process for there can be twig dieback, after apparent freeze recovery, that may be attributed to this reestablishment of the functional balance between roots and shoots. Water loss through the peel (Syvertsen, 1982b) of freeze damaged fruit can also contribute to post-freeze tree water relations.

SUMMARY

Leaves that fix the most carbon also lose the most water. Greater productivity and yield, therefore, require increased water consumption. An important potential strategy for maximizing water use efficiency is to maximize the use of water input from irrigation (Sinclair et al., 1984).

Brief day to day stresses probably have little or no measurable effect on yield, since even well-irrigated citrus trees are seldom in a completely optimum condition. The extent to which prolonged drought or flooding stress decreases crop yield and quality depends on the condition of vegetative and reproductive growth. Often, tree response is a subtle change in carbon reallocation between shoots, roots, and fruit. Nevertheless, research on interactions between water, carbon and nutrient budgets in whole-plant systems should lead to a better understanding of how to manage horticultural plant productivity.

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