Physiological Effects of Incomplete Root-zone Wetting on Plant Growth and Their Implications for Irrigation Management

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The application of water to a portion of a plant's root system is now a common practice in tree fruit production areas throughout the world. Microirrigation systems have increased water use efficiency and production efficiency in comparison to flood and over-tree sprinkler application (Bucks, 1995; Phene, 1995). Early workers demonstrated that high frequency trickle irrigation of a portion of the root system reduced vegetative growth but not yield or fruit quality (Levin et al., 1979; Middleton et al., 1979; Proebsting et al., 1977). However, there are limits to the minimal root volume that can be adequately irrigated without severely depressing growth and yield potential (Proebsting et al., 1989; Tan and Buttery, 1982). The purpose of this review is to identify root processes that limit plant productivity when only a portion of the root system is wetted. Split-root studies are reviewed to evaluate the potential to manipulate plant growth and development, emphasizing tree fruit crops.

When only a portion of the root zone is wetted, root growth may be increased in the wetted regions (Gersani and Sachs, 1992; Kosola and Eissenstat, 1994, and citations therein; Levin et al., 1980; Tagliavini et al., 1996), and water absorption by the wetted roots increases relative to the amount absorbed by the same portion when the whole root system is wetted (Michel and El Sharkawi, 1970; Tan and Buttery, 1982). The increased water uptake may be a result of increased hydraulic conductance, as measured by Morizet et al. (1988) or root conductance and root water potential may be changing simultaneously (Brouwer, 1953). Simonneau and Habib (1994) found that both transport of water from nonirrigated roots and stored water can contribute to the water balance without a change in root hydraulic conductance. Thus roots in the nonirrigated soil can actively contribute to the nutrient and water balance of the plant.

Root growth slows or stops in dry portions of the soil, while it continues in the wetted areas because of reduced carbon partitioning to the dry roots (Kosola and Eissenstat, 1994). Root mortality is generally extensive in nonwoody species, but is minimal in citrus (Kosola and Eissenstat, 1994). In woody species, water and nutrients are translocated from wetted and fertilized portions of the root zone to dry roots occurs (Caldwell and Richards, 1989; Coutts and Philipson, 1980; Ferrier and Alexander, 1991; Glenn and Welker, 1993). Associated with the translocation of water and nutrients is an increase in the osmotic potential of the root tissues in drying soil (Hsiao and Acevedo, 1974). Conversely, water may be translocated from roots in contact with high water quality to roots in zones with high salinity (Zekri and Parsons, 1990). If water stress is sufficient to cause root death, N is retranslocated from the dying root, but transport is less efficient than from leaves during their senescence (Ferrier and Alexander, 1991). The reduced N retranslocation efficiency of roots compared to leaves may reflect the random and rapid onset of severe water stress that occurs locally in roots, compared to the more environmentally cued and genetically programmed process of leaf senescence.

Not all nutrients are easily translocated from root tissues, whether healthy or dying. Calcium is not translocated (Gergely et al., 1980; Nable and Loneragan, 1984), while K, Mg, and P are translocated to a limited degree from zones of adequate or excess availability to depleted zones (De Jager, 1979; Jeschke and Wolf, 1988; Scott and

Robson, 1991). Roots in dry soil are also capable of nutrient uptake from the root zone (Nambiar, 1976, 1977). Kirkham (1983) and Xu and Bland (1993) presented models of water movement that adequately describe the movement of water and solutes in similar split-root systems based on the development of gradients favoring movement to roots in drying soil. These processes are key survival mechanisms for woody plants with or without benefit of irrigation. Under drought conditions, plants use these mechanisms to "mine" water and nutrient resources held in the subsoil and to survive periodic drought (Caldwell and Richards, 1989). These mechanisms are important for nonirrigated plants but for irrigated plants they probably contribute little to the water or nutrient balance.

Roots growing in the wetted portion of the root zone function as the primary tissue of nutrient and water uptake and root hormone production. The island of resources created in the wetted root zone is analogous to a shoot growing into the light and responding by developing lateral shoots and leaves. Root development in the wetted zone integrates the effects of the local environment with the physiological relationships between individual roots and other plant tissues. Generally, roots in a given environment develop more rapidly if other roots on the same plant have less access to resources (Gersani and Sachs, 1992). Generalized responses of roots when they encounter a resource-rich patch of soil include increased nutrient uptake and life-span, and changes in carbon allocation and morphology. Increases in the kinetics of nutrient uptake by roots (Caldwell, 1994; Jackson et al., 1990; Robinson, 1994) generally precede root proliferation. It is not clear, however, if root exudation is reduced in nutrient-rich zones (Caldwell, 1994).

Roots may or may not live longer in response to additions of water and nutrients (Gross et al., 1993; Pregitzer et al., 1993, and citations therein) as a strategy to minimize carbon cost while maximizing nutrient acquisition (Eissenstat, 1991; Eissenstat and Yanai, 1997). The carbon economy of roots can significantly affect root biomass in relation to the cost of foraging for nutrients. Root biomass is reduced when nutrients occur in patches, rather than being homogeneously distributed (Crabtree and Bazzaz, 1992). Numerous studies demonstrate that as little as 15% of the root system can supply the entire plant's N needs (Burns, 1980; Robinson et al., 1991). Acquisition of diffusion- and interception-controlled nutrients, e.g., phosphorus, probably requires more root growth for nutrient foraging than does acquisition of nutrients that move predominantly by mass flow.

Root morphology is affected by the chemistry of nutrient-rich sites. Roots supplied with ammonium have increased total root length and surface area, while those supplied with nitrate have longer laterals (Schortemeyer et al., 1993). These results explain, in part, why nitrate-rich zones have less root biomass and use less water than those in ammonium-rich patches (Feil, 1994). The abundance of nitrate- and ammonium-N often differ in the soil, with ammonium-N localized in the topsoil and nitrate-N leaching to greater depths. The vertical stratification of N-sources can lead to pH differences in the soil. Roots exposed to high levels of ammonium will excrete more protons, acidifying the soil more than do roots exposed to high nitrate levels (Loss et al., 1993, and citations therein).

The size of the aboveground portion of a tree is generally proportional to the volume of the root zone (Glenn et al., 1996; Levin et al., 1979; Ran et al., 1994; Richards, 1977; Richards and Rowe, 1977a, 1977b). The restriction of aboveground growth, in the simplest terms, is generally attributed to reduced nutrient uptake, particularly N, and

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reduced hormone translocation from the root system. Ran et al. (1994) proposed that an equilibrium exists between N and dry matter in peach [*Prunus persica* (L.) Batsch] in which the tissue N concentration is static; any environmental factor that limits N uptake will consequently reduce growth. This is similar to the functional equilibrium concept of Wilson (1988) and Richards and Rowe (1977). Itai and Vaadia (1965) demonstrated that cytokinin production and transport from root tissues were reduced in drying soil and this was associated with reduced growth. Irrigating only a portion of a root system reduces the size of the root system and hence its capacity to produce and transport cytokinins, other plant growth substances, and nutrients to the aboveground portion. This mechanism is generally cited for controlling size in plants (Davies et al., 1994; Davies and Zhang, 1991). Cytokinin levels of roots, shoots and xylem sap are also reduced at low root N levels (Samuelson et al., 1992, and references therein). Recent research has demonstrated that both hydraulic and nonhydraulic signals from the soil-root environment influence stomatal activity and carbon assimilation (Davies et al., 1994; Davies and Zhang, 1991). Depending upon the relative influence of the hydraulic and nonhydraulic signals, measurements of mid-day leaf water potential to evaluate leaf water status may be misleading (Sadras et al., 1993; Turner et al., 1996). Irrigation scheduling strategies based on mid-day leaf water potential may be influenced by the degree of soil drying outside the wetted regions of the irrigation system; however, whether stem and predawn leaf water potentials are affected has not been determined.

CONCLUSIONS

In conclusion, irrigating only a portion of the root zone alters the morphology of the root system, the efficiency and mechanisms of nutrient and water uptake, root hormone production and other signals from the root. Microirrigation provides horticulturists with another tool to regulate plant growth and development to increase yield, yield efficiency, and fruit quality. Understanding and manipulating the configuration and function of the root system should increase the efficiency of water application. Manipulating the frequency and duration of irrigation to the wetted zone will alter the wetting pattern and may be another means to further increase water use efficiency.

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