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Soil Water and Root Growth

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Healthy, functioning root systems are critical to survival and productivity of land plants. Roots serve the combined functions of anchorage, support, and water and mineral nutrient uptake. Root growth, development, and function are largely determined by genetic information, but respond, often substantially, to available carbohydrate supply and local environmental conditions encountered during growth. Soil attributes that affect the extent and morphology of growing root systems include water content, strength or mechanical impedance, thermal regime, and structural development. The extent and function of plant root systems, in turn, directly or indirectly modify these soil conditions.

Weaver (1919, 1920) performed intensive characterizations of plant root systems in the field that, in many respects, remain unequalled to the present day. That roots exhibit sometimes profound morphological responses to environmental factors (Weaver, 1919, 1920; Weaver and Clements, 1929), and that "...the ideal root system is...one that fully occupies the soil to an adequate depth and throughout a radius sufficient to secure at all times enough water and nutrients" (Weaver and Clements, 1929), were clearly recognized by these and other early workers.

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Despite early and continued efforts, there is growing need for better knowledge and understanding of root growth and root function as related to soil water status. Intensive management of soil-plant systems is required in many cases to enhance resource use efficiency and to minimize potentially harmful effects of inappropriate water or chemical inputs. Despite considerable progress in some areas, however, knowledge of root growth and function is seldom applied directly to management of farms, nurseries, and other plant production enterprises (van Noordwijk and van de Geijn, 1996). Increasingly stringent statutory policies in some European countries may well portend stricter controls on agricultural inputs in the United States, as public concern for environmental quality continues to grow. Intensive water and fertilizer nutrient management, and improved predictions of the fate and transport of soil-applied chemicals, emphasize a need for more detailed information concerning root system responses to soil water status. Increasingly sophisticated computer simulation models, including the ability to provide 2- or 3-dimensional characterization of transient soil water and chemical distributions, require accurate knowledge of how growing root systems react with the soil environment if they are to be truly useful management tools.

We will not attempt to reiterate the accumulated knowledge concerning soil water effects on plant root growth in this paper. Our emphasis will be on how spatial and temporal characteristics of soil water may impact root growth and hence root function, and the importance of knowledge concerning the local

root growth and root function responses to soil water in enhancing our ability to effectively manage plant, soil and water resources.

THE SOIL ENVIRONMENT FOR ROOT GROWTH

Soils are complex amalgamations of physical and biological components, properties and processes, many of which are highly variable in space and time. Although the distributions of many soil physical properties and/or processes are seemingly random, they often have identifiable spatial and temporal structures at some scales of observation. Substantial variation in soil water and other attributes is also a direct result of plant activities (Hook et al., 1991; Jackson and Caldwell, 1993). Considerable progress has been made in characterizing and accommodating soil environmental heterogeneity during the past decade, particularly with respect to stochastic (rather than deterministic) representations. Some of this information is finding its way into computer models that simulate the space and time distributions of water and chemicals in the soil-plant-atmosphere continuum (e.g., Ma and Selim, 1997). A substantial limitation of these models at present is the relative lack of comparable information concerning root system growth and behavior in response to variable and transient conditions in the soil environment (Klepper and Rickman, 1990).

The increased tendency toward reduction of cultural practices, such as tillage, favors development and persistence of aggregates, and of structural voids and biopores in the zone of highest root activity. Water and dis-

solved chemical flow through highly conductive "preferential flow pathways," particularly during brief intervals of high water content following rainfall or irrigation, contributes to unanticipated occurrences of chemicals in groundwater (Beven and Germann, 1982; Ma and Selim, 1997). These same soil pathways, the results of adjacent structural units, biological activity, cultural practices, or other factors, may also provide greatly enhanced opportunities for root growth and proliferation (Wang et al., 1986). The soil water status, and hence the fate and transport of soil chemicals, is impacted perhaps more by the distribution and activities of plant root systems than by any other single factor, save local climate and human activities. Improved understanding of the interrelationships between soil water and root growth (and function) should therefore lead to opportunities for better management.

Many soil environmental factors that potentially affect root growth or root function are intimately interrelated. These include water status, aeration, mechanical impedance, nutrient availability, compaction, temperature, structure, and texture. This greatly complicates unequivocal interpretation of cause and effect. For example, increasing the soil water content may decrease both mechanical impedance and rates of gas diffusion, increase or decrease soil nutrient availability, and modify the soil temperature regime, depending on specific circumstances. Many of these individual changes may have contrasting or even competing effects on root system physiological responses. Soil strength has long been recognized as a primary potential impediment to root growth (Greacen and Oh, 1972). For a given soil, mechanical impedance to root growth may be increased through compaction (i.e., higher bulk density) or decreased water content, among other factors. Dehydration increases the mechanical impedance of soils through its effects on increased interparticle cohesion (particularly in the case of clay fractions), increased frictional resistance, and negative pore water pressures that act to hold adjacent particles together (Marshall et al., 1996). Figure 1 illustrates typical relationships between soil wetness and soil strength (for a given bulk density), and for soil wetness and root elongation rate. Superposition of these relationships is consistent with the commonly reported near-linear decreases in root penetration with increasing mechanical impedance (e.g., Gerard et al., 1982; Taylor and Gardner, 1963; Taylor and Ratliff, 1969; Voorhees et al., 1975).

Plant access to nutrients including N and P is closely dependent on soil wetness. Root growth (Barracough et al., 1991; Vegh, 1991) and overall plant water relations may be enhanced through favorable mineral nutritional status. Indeed, some reported improvements in water uptake, transpiration, and photosynthesis of host plants in response to infection by vesicular-arbuscular mycorrhizal (VAM) fungi may be explained by the indirect effects of phosphorous nutritional status (Graham, 1987; Puppi and Bras, 1989) rather than by direct influences of VAM in increasing soil water uptake (Baker et al., 1992).

Fig. 1. Typical relationships among relative soil strength (dashed line) and relative root elongation rate (solid line) as functions of soil wetness expressed in terms of relative saturation. Soil strength was calculated as $s_{max} \cdot (1 - \theta)^3$ based on results of Gerard (1965) as fitted by Clausnitzer and Hopmans (1994), where s_{max} is soil-specific maximum strength and θ is relative soil water saturation. Root elongation is based on results of Westgate and Boyer (1985) as presented in Chen and Lieth (1993).

ROOT GROWTH AND SOIL WATER STATUS

Root distribution

Selectively adjusting the root distributions of crop or nursery plants might be a useful strategy in increasing water uptake from the lower soil profile, and, coincidentally, to improve resource efficiency through uptake of fertilizer salts that might otherwise move toward groundwater. Jordan and Miller (1980) claimed that root length density of sorghum (*Sorghum bicolor* L.) in the lower rooting zone was insufficient to meet evaporative demand in the Great Plains region of Texas. Increasing root length density to $2 \text{ cm} \cdot \text{cm}^{-3}$ below 50 cm depth, they predicted, would increase annual water uptake by 6 cm and reduce water stress during the moisture sensitive grain-filling stage. Similar root length densities in the upper half meter, but greater root length densities from 0.5 to 1.2 m were found in two drought-tolerant soybean (*Glycine max* L.) cultivars under water-limited conditions, with no root proliferation below 0.8 m in drought-sensitive lines (Sponchiado et al., 1989). Greater total allocation to root biomass and greater allocation over the 60–120 cm depth were associated with drought tolerance among contrasting wheat (*Triticum aestivum* L.) cultivars (Hurd, 1974). Drought resistance was also associated with high root length density at greater depth for tall fescue (*Festuca arundinacea* Schreb.) (Carrow, 1996).

Comparison between shallow-rooted, cultivated lettuce (*Lactuca sativa* L.) and its deeper-rooted, wild relative *Lactuca serriola* L. nicely illustrates the advantage of deeper root distribution under conditions of surface drying (0–20 cm) accompanied by optimal supply of water to lower soil depths (20–80

cm) (Gallardo et al., 1996). After withholding water for 2 d, leaf water potential, net photosynthesis, and stomatal conductance of cultivated lettuce were significantly less than values for well-watered controls, while surface drying had no effect on *L. serriola* leaf water relations or shoot biomass production. Contrasting responses were associated with different root allocation patterns. Under well-watered conditions, 20% of wild lettuce biomass was allocated to roots with 50% of total root length between the 20 and 80 cm depth, whereas cultivated lettuce allocated only 9% of total biomass to roots, with 35% of their length in the 20–80 cm increment. At the onset of surface drying, *L. sativa* and *L. serriola* distributed 78% and 58%, respectively, of total root length to the upper soil layer. These contrasting patterns of root allocation suggest that wild lettuce germplasm could be used to improve utilization of applied water and nutrients by cultivated lettuce (Gallardo et al., 1996).

Root growth plasticity

Generally, plant morphological plasticity is the ability of plant organs to grow in different ways upon encountering different environments (Hutchings, 1988). Specifically, root morphological plasticity may allow plants to efficiently forage in heterogeneous soil environments (Jackson and Caldwell, 1996). While proliferation of root systems in nutrient-rich microsites is well-documented (Crick and Grime, 1987; Drew et al., 1973; Drew and Saker, 1975, 1978; St. John et al., 1983), plastic responses to nonuniform soil water have been studied less, despite their seemingly obvious importance.

In cotton (*Gossypium hirsutum* L.), Klepper et al. (1973) found high near-surface root densities, and declining root density with depth,

under well-watered conditions, but after a drying cycle maximal root density was in the deepest portion of the root zone (i.e., 1.8 m). This reversal of root depth distribution was due to loss (decay) of root matter in the dry upper profile and proliferation in the wet lower meter. Taylor and Klepper (1974) found that young cotton plants had much deeper root systems with gradual drying of a deep and initially moist soil than with frequent application of water to the soil surface. In contrast to these results showing root morphological plasticity in cotton, Carmi et al. (1993) found little root redistribution in cotton in response to changes in soil water distribution. Following 85 d of drip irrigation concentrated in the top 30 cm of the soil profile, the soil was wet to one meter. Three weeks of subsequent surface drying produced a 3-fold decline in thin root density in the 0–30 cm depth increment with no significant root penetration to wetted layers below. In a similar container study, Plaut et al. (1996) found cotton roots grew through a partially wetted soil layer (40% of column-capacity) to a water source at 45 cm depth, but were unable to penetrate an upper layer at 20% of column-capacity.

Lupin (*Lupinus cosentii* Guss. cv. Eregulla) displays extremely efficient utilization of localized water sources. When soil columns were hydraulically separated into three layers, drying of the upper two layers for 21 d combined with adequate watering of the basal layer had no effect on shoot or root biomass production. In response to drying, a large shift in root allocation was observed, with 52% of root length occupying the well-watered basal layer. Where the entire soil column was adequately watered, only 23% of root length was found in the basal layer with 61% and 16% in the upper and middle layers (Gallardo et al., 1994). Roots of perennial bunchgrass [*Bouteloua gracilis* (H.B.K.) Lag. ex. Griffiths] plants that were forced to rely on water supplied to a laterally isolated soil compartment showed high capacities for fine root proliferation and water uptake, and root length and water use were similar to values observed directly under plants watered in central compartments (Hook and Lauenroth, 1994). On a smaller scale, addition of water to soil microsites for 40 d under a mixed hardwood forest increased both production of fine roots and their longevity (Pregitzer et al., 1993). Eissenstat (1991) found a positive correlation between specific root length (root length per unit root biomass) and root growth rate ($\text{cm} \cdot \text{cm}^{-3}$ per week) among eight different citrus rootstocks proliferating in moist, disturbed soil. Increased water uptake by roots with greater specific root length suggested that they were better able to exploit enriched soil microsites.

Thus, many plants seem to be able to fairly rapidly exploit zones of water enrichment through plastic growth responses, although this ability does not appear to be universal. Adaptations to environments having greater or lesser climatic and soil resource stability is probably a key factor in these observations.

Root morphological plasticity may also

play an important role in structuring plant communities. Grime (1994) found an inverse relationship between dominance of British grasslands and the precision with which roots exploit environmental heterogeneity. He argued that the ability to dominate a community is not related to plasticity, but depends on a high relative growth rate and proliferation of a massive architecture both above and below ground. This strategy involves coarse-grained foraging of a large soil volume, but does not allow exact placement of roots in local patches of the soil matrix. Within this framework, the contrast between dominants and subordinates in a grassland community represents a trade-off between the scale (high in dominants) and precision (high in subordinates) of resource foraging. This trade-off may be very important in establishment of multi-crop agroecosystems designed to fill more below-ground niches or to understanding weed infestations where niche differentiation is observed (Sheley and Larson, 1994, 1995).

Hydrotropism

The propensity of plant roots to grow toward wetter areas was recognized at least as early as the 19th century (Darwin, 1880; Knight, 1811). Recent work in this area has involved study of single root responses to air humidity gradients established in closed chambers, partly to avoid potentially confounding effects of

related soil environmental properties that vary with wetness. Takahashi (1994) and coworkers used an agravitropic pea (*Pisum sativum* L.) mutant to separate hydrotropic responses from closely related gravitropism. The roots of this mutant exhibit a positive growth response to relative humidity gradients of less than 1%/mm (Takahashi and Suge, 1991). Also noted was a hydrotropic-like response to osmotic stimulation by sorbitol agar (Takano et al., 1995). Oyanagi et al. (1995) reported differences in growth responses of wheat roots to air humidity gradients. Humidity gradients of this magnitude may persist in soils, but are likely only at very low water contents (Fig. 2). The combination of large differences in relative humidity resulting from realistically modest spatial changes in soil water content, with low hydraulic conductivity that would effectively limit the tendency for the gradients to diminish through water flow, may provide stimuli in dry soil consistent with conditions in experimental chambers. This implies, however, that 1) root growth would have to be supported in soil volumes below the wilting point; and 2) in practice such conditions are only likely to be encountered near the soil surface, perhaps the upper 0.3 m or so. Near-surface soils are subject to intensive drying by direct evaporative water loss, as well as by root water extraction, and may commonly reach soil water levels between the lower limits of plant uptake and air dry status if not

Fig. 2. (top) Relative humidity of soil air in equilibrium with soil water potential based on the relationship $\psi_a = RT/V_m \ln(e/e_s)$, where ψ_a is soil water potential (kPa), R is the ideal gas constant ($8.314 \times 10^{-3} \text{ kPa} \cdot \text{m}^3 \cdot \text{mol}^{-1} \cdot \text{K}^{-1}$), T is Kelvin temperature, V_m is molar volume of water ($1.8 \times 10^{-5} \text{ m}^3 \cdot \text{mol}^{-1}$), e is water vapor pressure, and e_s is saturation water vapor pressure at the same temperature. (bottom) Typical hydraulic conductivity-soil water potential relationships for two representative soil textures.

rewetted. Extremely sharp but transient humidity gradients across a wetting front may be encountered during infiltration of water into dry soils; these would seemingly favor upward root growth in response to hydrotropic stimulus, although the duration of such conditions near a single root would ordinarily be quite brief. Roots may also exhibit tropistic responses to thermal gradients, electric and magnetic fields, and mechanical force (Takahashi and Scott, 1991).

Root architecture

While the overall form or architecture of root systems varies widely between species (Weaver, 1919, 1920), most researchers deal with root systems at a fairly coarse scale, measuring attributes such as total mass or length and their distribution in space and time. In an architectural approach largely advocated by A.H. Fitter, whole root systems are described in terms of their branching structure, or topology.

In a strictly mathematical sense, plant root systems are rooted trees, a classification including other natural branching structures, e.g., arterial networks, neurons, and river systems. In this formalism, a "link" is a segment of root between two nodes. The "magnitude" of a root system is its number of exterior links. Trees of equal magnitude can have very different topologies ranging from a "herringbone" structure, where branches arise from a single axis, i.e., segmental branching (Fig. 3), to dichotomous structures where branches arise from the ends of links, i.e., terminal branching (Fig. 3). Topological differences between trees of equivalent magnitude can be quantified by their pathlength characteristics. The "altitude" of a tree is the longest individual pathlength from an exterior link to the tree's base. The herringbone tree in Fig. 3 has an altitude of eight, the dichotomous tree an altitude of four. Given a collection of trees, the slope of a log-log plot of altitude vs. magnitude, or "topological index," reflects the branching rule generating the observed trees. A topological index of 1 corresponds to herringbone or segmental branching, a slope of 0.59 corresponds to random branching. Smaller values are indicative of dichotomous branching (Fitter, 1986). Application of this formalism to plant root systems allows calculation of costs and benefits of different root architectures, description of plastic responses to changing soil environments, and comparison of taxonomically and ecologically distinct species (Fitter et al., 1991; Fitter and Strickland, 1991, 1992).

Fitter et al. (1991) developed a computer simulation model to explore relationships between different root architectures and exploitation efficiency (the ratio of soil volume occupied by root depletion zones to root tissue volume). High exploitation efficiency was associated with a herringbone topology and the authors suggest that this branching pattern might be optimal where soil-derived resources limit growth or in plants characteristic of nutrient- or water-poor habitats. Red clover (*Trifolium repens* L.) grown under a limited water

Fig. 3. Two extreme root topological types each having magnitude 8. (right) Herringbone, altitude = 8; (left) dichotomous, altitude = 4. Adapted from Fitter (1986).

supply produced herringbone root systems while increasing application rates generated random topologies, followed by dichotomous branching (Fitter, 1986). Assuming that species with low relative growth rate were characteristic of infertile soils, Fitter and Strickland (1991) found an inverse relationship between topological index and mean relative growth rate in 13 dicotyledonous species, supporting the prediction that more herringbone-like topologies should be found in plants characteristic of less productive soils. No similar trend was found among eight grass species, all had high topological indices regardless of relative growth rate. Berntson (1994) combined a topological approach with more conventional measures of root system size, and found that a fast-growing herbaceous annual, *Senecio vulgaris* L., produced a larger root system and more random branching topology under moist conditions than when water-limited. Using measured architectural parameters to generate simulated root systems, the author also found an inverse curvilinear relationship between the exploitation potential and the efficiency of root foraging. Large root systems were clustered at high exploitation potential (cm^3 of soil depletion zones) where the rate of change of exploitation efficiency was small, while small root systems had high exploitation efficiencies where variation in exploitation potential was limited. Thus, simultaneous measurement of root system size and size-independent topological properties revealed a trade-off between the scale and precision of root foraging, supporting Grime's hypothesis as discussed above.

Architectural descriptions *sensu* Fitter have also been supplemented with methodologies from fractal geometry (Mandelbrot, 1983), revealing that root systems have a fractal structure within a finite range of scales (Tatsumi et al., 1989). Differences in root fractal dimension, a measure of root branching, have been documented among soybean genotypes (Lynch and Van Beem, 1993) and under nutrient stress (Eghball et al., 1993). Nielsen et al. (1997) found a log-linear relationship between spatial

dimension and fractal dimension, suggesting that the three-dimensional fractal dimension of root systems could be derived from more easily measured linear and planar fractal dimensions.

The study of roots from an architectural perspective allows exploration and quantification of the complexities of root growth in the heterogeneous, 3-dimensional soil medium. Combined with increasingly sophisticated computer simulation techniques, this methodological advance should improve our understanding of functional relationships between root architecture and efficient resource acquisition, particularly under suboptimal soil conditions (Lynch, 1995).

Absciscic acid and physiological responses to soil water deficit

A common response to soil water deficit is disparate inhibition of shoot growth relative to root growth, often producing an increase in the root : shoot ratio. The growth regulator abscisic acid (ABA) appears to play a key role in the relative maintenance of root extension. Saab et al. (1990) examined the effect of low endogenous ABA levels in maize mutants deficient in ABA biosynthesis and in wild-type seedlings exposed to fluridone [1-methyl-3-phenyl-5-[3-(trifluoromethyl)phenyl]-4-[1H]-pyridinone], an inhibitor of ABA synthesis. In vermiculite with low water potential that completely inhibited shoot growth, root elongation rate of fluridone-treated and nontreated seedlings was reduced 83% and 55%, respectively (Fig. 4). Similarly, ABA-deficient mutants exhibited greater declines in root elongation rate than did wild-types (Fig. 5). Creelman et al. (1990) also found differential inhibition of shoot vs. root growth in soybean seedlings. Hypocotyl growth was inhibited while root elongation was not affected upon transfer of well-watered seedlings to increasingly lower water potentials. Root growth at -0.3 MPa produced a nearly 10-fold increase in the concentration of ABA in mature root segments

Fig. 4. Effect of fluridone (FLU) on primary root elongation of maize seedlings growing in -0.03 MPa (high ψ) and -1.60 MPa (low ψ) vermiculite. Data points represent the mean $\pm$ SD of 20 to 40 roots. Adapted from Saab et al. (1990).

Fig. 5. Primary root elongation of wild-type and ABA-deficient (mutant) maize seedlings growing in -0.03 MPa (high ψ) and -1.60 MPa (low ψ) vermiculite. Data points represent the mean $\pm$ SD of 4 to 22 roots. Adapted from Saab et al. (1990).

and root tips increased nearly 10-fold when grown at -0.3 MPa, while application of 10^{-3} M ABA to well-watered seedlings reduced growth to a rate identical with that in the low water potential treatment.

An increase in cell wall extensibility may explain the maintenance of root extension at low water potential and indicate a regulatory role for ABA. In primary roots of maize growing in vermiculite at low water potential, root elongation rate was reduced nearly 3-fold relative to that of well-watered control plants through reduction of the length of apical elon-

gation zones (Spollen and Sharp, 1991). Additionally, turgor pressures in individual cells of the apical cortex and stele of well-watered controls were on the order of twice the values found at low water potential. Although longitudinal growth in the apical 2 mm was the same in both treatments, roots growing in low water potential media had a smaller diameter. The authors interpreted continued extension of thinner roots at lower cell turgor pressures as evidence that low soil water potential causes an adjustment in cell wall yielding properties. Investigating the metabolic basis for apparent

cell wall loosening in maize, Wu et al. (1994) found increased activity of xyloglucan endotransglycosylase (XET) in the apical portion of roots growing at a water potential of -1.6 MPa. Other workers propose that XET increases cell wall extensibility by cleaving and reconnecting xyloglucan molecules that bind adjacent cellulose microfibrils (Fry et al., 1992). An apparent regulatory role for ABA in this response to low water potential was indicated by the inhibition of XET activity following treatment with fluridone and subsequent restoration of XET activity following application of exogenous ABA (Wu et al., 1994).

While ABA appears to mediate continued root extension at low soil water potential, its proposed role as a root-to-shoot signal of soil drying has been debated over the past decade. In the late 1980s, researchers observed reduced stomatal conductance in lupin preceding measurable decreases in leaf water potential, but coinciding with increased leaf ABA concentration (Henson et al., 1989a, 1989b). Absciscic acid had been known to cause stomatal closure since the late 1960s (Mittleheuser and van Stevenick, 1969; Raschke, 1975), and subsequent studies demonstrated a correlation between xylem ABA concentration and leaf conductance (Tardieu et al., 1992; Waringer et al., 1990) in maize and almond [*Prunus dulcis* (Mill.)]. Zhang and Davies (1991) found that removing most of the ABA from maize xylem largely eliminated antitranspirant activity. However, evidence implicating ABA as a root-to-shoot signal is equivocal. Munns and King (1988) found that inhibition of wheat stomatal conductance was maintained even after ABA was removed from xylem sap, while Trejo and Davies (1991) observed drought-induced stomatal closure in bean (*Phaseolus vulgaris* L.) before leaf water deficit or an increase in xylem ABA levels was detected. Subsequently, a large molecular weight compound with antitranspirant activity was found in the xylem stream of wheat and barley, although its exact structure has not yet been determined (Munns, 1992; Munns et al., 1993; Turner, 1997).

Even if ABA is involved in mediating a root-to-shoot signal, the signal transduction pathway is likely to be more complicated than originally proposed. Guard cell response to ABA is sensitive to xylem sap pH and concentrations of calcium and nitrate (Schurr et al., 1992). Tardieu and Davies (1992) found that maize stomata were more sensitive to ABA at low leaf water potentials. Nonetheless, apparent root-to-shoot signaling reminds us that plants are not merely passive consumers of soil water, but dynamically respond to a changing below-ground environment. This recognition will be important as more precise modeling and manipulation of root systems is attempted.

Resumption of water uptake capacity following drought

Ability to rapidly exploit soil water that becomes available from rainfall or other events may be critical in some situations. For ex-

ample, plant water status in many arid and semiarid areas is dependent on rainfall for replenishment of near-surface soil water. These upper soil layers generally contain the greatest concentrations of both roots and nutrients, but are subject to severe dehydration from the combined effects of root uptake and direct evaporative loss to the atmosphere. A number of factors related to soil drying, including suberization and secondary thickening of endodermal cell walls (Cruz et al., 1992; North and Nobel, 1991; Sanderson, 1983), formation of xylem emboli (Tyree and Sperry, 1989), or loss of root to soil contact through root shrinkage (Huck et al., 1970; Nobel, 1994) may inhibit absorption of soil water that becomes available following periodic rainfall or irrigation. In this situation, the transpiring plant and the evaporating soil surface are competitors for the water added to the system (Wraith et al., 1995). This is particularly true where light or moderate rains may rewet only the upper few centimeters of the profile (Passioura, 1988). Any lag in recovery of root absorptive function favors soil evaporation at the expense of transpiration. In water-limited environments, reductions in transpiration will result in reduced dry matter production.

In addition to renewed conductance of existing root tissues (Lopez and Nobel, 1991; North and Nobel, 1991), new root growth following rewetting is important to rapid resumption of water uptake following soil drought. BassiriRad and Caldwell (1992) reported an increased rate of root growth in prestressed plants relative to controls during the initial 4 d following rewetting. This was largely due to elongation of existing roots, although some new laterals were produced. Stasovski and Peterson (1991) observed a rapid growth response upon rewetting of droughted maize plants. Despite the death of epidermal and cortical cells in the midlength regions of roots, stressed plants resumed growth upon rehydration by elongation of existing seminal, adventitious, and lateral roots and by emergence of dormant lateral root primordia. Lateral root primordia emerged from onion (*Allium cepa* L.) roots despite 200 d of soil drying (Stasovski and Peterson, 1993). Jupp and Newman (1987) subjected perennial ryegrass (*Lolium perenne* L.) to low soil matric potentials (-2.0 to -10.0 MPa) and found that while drought caused substantial death of root cortex and root hairs at a soil matric potential of -1.5 MPa, death of root tips was not detected until soil matric potentials had declined to -10.0 MPa. This apparently greater desiccation-resistance of root tips, due in part to a degree of hydraulic isolation resulting from immature vascular tissues, allowed existing roots to elongate upon rewetting.

The emergence of lateral roots may also increase the permeability of older main roots by disrupting the continuity of suberized tissue. Peterson et al. (1981) found that two apoplastic tracers entered the steles of maize and broad bean (*Vicia faba* L.) along the margins of secondary roots that had recently emerged from the epidermis of primary roots. North et al. (1993) reported that the radial

conductivity of *Agave deserti* Engelm. main root-lateral root junctions increased by 5-fold over 21 d of soil drying.

Wraith et al. (1995) grew barley (*Hordeum vulgare*) plants in soil columns having hydraulically isolated surface and subsoil layers. The upper 0.05 m soil layer was allowed to dry to -1.8 to -3.0 MPa for 10 to 14 d, during which time subsoil wetness was maintained at about -0.6 to -0.7 MPa. The time course of soil water uptake was monitored at 0.5 h intervals following rewetting of the surface layer. Substantial water uptake began 1 d after rewetting following 10 d of water deficit, and 2 to 3 d after rewetting following 14 d of water deficit in separate experiments. Rate of water uptake was substantially more rapid in response to a second rewetting 5 to 7 d later, indicating some restoration of hydraulic function during the interim in response to the initial water addition (Fig. 6). The decline in cumulative water uptake and uptake rate after the initial increases (Fig. 6) is a result of diminishing soil water availability in the isolated surface soil layer. Consistent genotypic responses in terms of cumulative water uptake on a whole plant and leaf area-specific basis were observed during each trial. Root growth was not directly measured in these experiments.

Brady et al. (1995) also used hydraulically isolated regions within soil columns to investigate root responses to transient soil wetting. They reported significant elongation of wheat lateral roots along the top 3 to 40 cm of seminal root axes 2 d after rewetting previously dry surface soils with either water or nitrate solution. New laterals were also initiated near the root tips of primary nodal roots growing into the soil. Interestingly, they compared responses of nodal and seminal roots by imposing a confined nodal root treatment. Only plants with unconfined nodal roots could take up N 1 d after rewetting, presumably because nodal roots had intact, viable epidermis and cortical tissue. However, despite measured increases in root length and nitrogen uptake per unit root length in the upper soil zone, they found plants were still N-deficient and had exploited little of the available N in this soil volume after 4 d.

Genotypic variation infers a potential for development of varieties having superior productivity under conditions of transient near-surface soil water reserves. While most plant breeding programs take a rather more generalized approach, deliberate selection of specific root system traits that favor rapid regrowth of fine roots in response to periodic rainfall or irrigation may enhance water use efficiency in arid or semiarid regions.

Root responses to excess soil water

While access to sufficient quantities of soil water is critical to the growth and development of land plants, many species are not adapted to conditions of excess soil water. Because soil water preferentially occupies pore spaces at the expense of soil air, high water content results in poor continuity and often extreme tortuosity of the remaining air-filled pore spaces. The rate of gaseous diffusion to

and from roots is thus seriously limited by excess water content, and may not be adequate to support metabolic processes in roots or shoots. Portions of the root zone may thus become limiting to oxygen diffusion due to inappropriate water management, even when physical properties are otherwise favorable for adequate aeration.

Excess soil water may lead to formation of aerenchyma, reduced root elongation, and early nodal root emergence (Drew et al., 1979, 1981; Jackson et al., 1979). Insufficient rates of oxygen diffusion to the root system may interfere with water relations and mineral nutrition, and result in hormonal imbalance within the plant (Drew and Stolzy, 1996). The time required for adverse effects in response to transient soil flooding may range from a few hours to a few days, depending on the species, rate of plant growth and metabolism, the extent of excess wetness in the root zone, and the degree to which gas diffusion and other processes are constrained as a result of these combined conditions.

Readers are referred to several excellent review articles (e.g., Armstrong, 1979; Crawford, 1982; Drew and Lynch, 1980; Drew and Stolzy, 1996; Kozlowski, 1984) for further information concerning the impacts of excess soil water on root growth and related plant processes.

Modeling root growth responses to soil water

Considering the state of current computer models is useful and informative because they may be considered as concise repositories of our collected knowledge, assumptions, and speculations. In many areas our ability to develop complex models has outstripped the available experimental evidence for model verification. In the case of plant root systems, this is certainly a partial result of the formidable difficulties associated with direct experimental observation of roots under representative conditions. Such models can also be useful in testing specific hypotheses concerning root-soil interactions, with consistency of predictions often interpreted in light of available observations of root behavioral responses to soil properties or processes. Thus, these models have substantial utility in nurturing our developing abilities to characterize and manage the complexity of the root environment and the myriad interrelated processes that occur in or impinge on the root zone.

For our present purposes, models designed to simulate the growth and activity of plant root systems may be conveniently categorized based on their abilities either to accurately portray one-, two-, or three-dimensional root architecture (Clausnitzer and Hopmans, 1994; Pages et al., 1989), or to estimate the dynamic mean volumetric root mass or root length with respect to time and location (Acock and Pachepsky, 1996; Adiku et al., 1996; Brugge and Thornley, 1985; Chen and Lieth, 1993). The former approach has been termed "developmental" or "architectural," while the latter may be considered a "continuum" strategy

Fig. 6. (top) Cumulative water uptake from upper 50 mm soil by four barley genotypes following 14 d at $\psi_s = -1.8$ to -3.0 MPa. Surface layers were watered on Days 48.5 and 55.4, and uptake was calculated based on measured changes in water content using time domain reflectometry (TDR). Error bars indicate standard error of mean ($n = 4$ or 5). (bottom) Mean water uptake rates from upper 50 mm soil for two barley genotypes following rewatering. Water uptake rates were calculated as the first derivative of data shown in top graph. Data for the two remaining genotypes are not shown in the interest of clarity. Adapted from Wraith et al. (1995).

(Acock and Pachepsky, 1996). Further, or alternative, classifications based on modeling approach may be found in these and other papers (e.g., van Noordwijk and van de Geijn, 1996). Schemes to simulate interactions of a growing root system with the transient soil physical environment may be included in each of these approaches, although the complexity may vary in accordance with model objectives.

Clausnitzer and Hopmans (1994) developed a model of three-dimensional soil water flow and root growth that simulates root system architecture in response to transient local soil conditions. The model is intended primarily as a tool for testing hypotheses on soil-plant interactions, and allows different levels of simulation (and hence input) complexity. Soil and other environmental factors that affect growth of root apices depend on the level of simulation complexity. These include mechanical strength as a function of soil water content, and (optionally) soil temperature and several stress adjustment factors, including stomatal closure in response to soil water deficit. The assumed relationship between soil water content and soil strength is illustrated in Fig. 1. At the most comprehensive level shoot growth is included, and individual growth events respond to allocation of assimilate to shoots and roots. The authors presented favor-

able comparisons of measured and simulated single-plant root systems based on specific sets of local soil conditions. A recent update of this model (Somma et al., 1997) incorporates soluble chemical transport and uptake, root age effects on water and solute uptake activity, and root growth responses to nutrient deficiency or excess.

In continuum models, root proliferation may be generated by either differential equations describing a diffusion-like propagation process from point to point, colonization of finite-sized soil cells by roots from adjacent cells, or changes in root concentration as a function of depth and time (Acock and Pachepsky, 1996). Acock and Pachepsky (1996) reported an approach that relied on developing differential equations for root proliferation as driven by downward convection (geotropism) and diffusion-like, gradient-driven propagation in all directions in response to soil variables and root density. Numerical solutions were generated on the same space and time finite element grid used for simulating soil transport processes, thus potentially facilitating applications to improved water and fertilizer management.

Adiku et al. (1996) also modeled lateral root growth (proliferation) and vertical root extension (front velocity) using a continuum approach. A soil water deficit factor was used

to modify root distribution, assuming that plants act to minimize energy expenditure for root growth based on local soil environmental conditions. The root length at any depth was allowed to approach the maximum species-specific value, such that compensatory increases in root growth at depth could occur in response to water stress or other restrictions in the top layers. Different root distribution patterns were determined by the time and space variations in soil water content, rather than by an assumed decay function with depth (e.g., Borg and Grimes, 1986; Gerwitz and Page, 1974). Based on comparisons with existing data sets, the authors concluded that the model produced plausible results for root growth and distribution. Simulated shifts of root length density to greater depth over time under water-limited conditions resembled those observed in wheat and cotton.

In a two-dimensional model of root growth distribution of potted plants, Chen and Lieth (1993) used a modified Arrhenius equation to modify root growth based on soil matric potential and temperature. Root growth and senescence were proportional to existing root mass or root mass density, and limited by carbohydrate supply. They described total root growth (mass basis) over time as a logistic function, rather than taking an iterative approach based on whole plant carbon balance or similar strategy. Their simulation results were in agreement with root mass density of chrysanthemum [*Dendranthema ×grandiflora* (Ramat.) Kitam.] as measured in 1-L containers, although the authors suggested that more experimentation was needed to improve and/or validate the soil matric potential (based on Westgate and Boyer, 1995) and temperature index functions.

van Noordwijk and van de Geijn (1996) comprehensively reviewed the parameters required for process models of crop growth as limited by soil water or nutrients. They opined that, for models that are designed to simulate the uptake potential of field root systems, most of the underlying processes are already known and research should concentrate on refinement and practical applications. For models which attempt to predict interactions of roots with transient soil environmental conditions, however, they concluded that many processes are based mostly on qualitative information, and hence improved quantitative knowledge of these interactions is urgently needed.

SUMMARY AND CONCLUSIONS

Given the increasing attention to efficient and environmentally sound management of soil water and chemical inputs for plant growth, we must continue to improve our understanding of root growth responses to soil water and other environmental conditions. This need may be intensified by future global climate changes, including increased evaporative demand, altered precipitation patterns, and increased ambient CO_2 concentration. Recent advances in the ability to measure, characterize, and model variability in root zone soil physical and chemical properties and processes requires

additional knowledge of concurrent root system interactions with the soil environment.

The ability of plants to rapidly exploit transient soil resources has not been fully understood or utilized. Improved measurement approaches are needed to aid in acquisition of knowledge concerning root growth responses to soil water status. Primary impediments to progress continue to be difficulties associated with direct root measurements, particularly in their natural state. As is true of some other topics, the ability to develop theoretical constructs or simulation models has generally outstripped our abilities to verify these predictions based on direct measurement of below-ground processes.

Selectively breeding plants to modify root distribution patterns or enhance plastic growth responses may improve plant performance under less than optimal inputs. We are still not able to specify with any certainty (or at least unanimity) the critical parameters that describe an optimal root system for specific sets of soil environmental conditions. We believe these topics, as well as others, will remain increasingly relevant in view of continued scrutiny of modern plant production systems. Opportunities abound for creative scientists and practitioners to make important contributions to our understanding of soil water and root growth, and to improve our abilities to effectively and efficiently manage the soil-root interface.

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