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SOIL ENVIRONMENTAL MODIFICATIONS OF ROOT DYNAMICS AND MEASUREMENT

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INTRODUCTION

Morphology of root systems is directed by genetic codes and attenuated by historical and contemporary environmental conditions. Plant growth and survival rely upon continuous alterations by the root system, in response to the varied soil environments they inhabit. Net root-system geometry results from the combined expressions of dominant apical root meristems that successfully compete for plant photosynthates. Soil environmental conditions control the rates of extension and respiratory activities associated with root function. Soil water, nutrient, temperature, gaseous composition, microbial inoculum and activities, mesofaunal interactions, carbon, and additional energy inputs control the net geometry and function of a specific plant root system. There is great diversity among root architectures; some of these diferences may be explained, in part, by adaptive responses although the agroecological significance of functional root architectures remains obscure.

Healthy and functional root systems are essential for the production of numerous resources used by animals, people and civilizations. To this end, the root-soil interface can be classified as one of the most important sites for inorganic and organic exchanges in support of life on this planet. Therefore, our knowledge of root health and function needs to move beyond contemporary single-parameter approaches, i.e. absorption along the total length of a uniformly distributed root system. Such single-parameter approaches greatly

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limit our understanding of the complexities of ion and water absorption by root systems. Similarly, root infection occurs at multiple sites along the root axis. Consequently, the description of root diseases, often rated as an index of infection or symptoms, needs to be expanded to include the intensity or the comprehensive nature of the invasion of host root systems. A description of root function and disease needs to include recent knowledge of dissimilar absorption and infection rates for each root segment within each soil horizon across both time and space. Unfortunately, these parameters of root function and disease have not been evaluated due to the paucity of quantitative methods for describing root-system geometry within the soil for the lifetime of each root segment. The absence of methods for nondestructively observing the biotic and abiotic conditions that promote root diseases has placed large constraints on our description and understanding of infection processes and associated losses of root function. Recent advances in nondestructive and quantitative evaluations of root morphology, discussed in this review, should improve future evaluations of the functional responses by roots to soilborne plant pathogens and their associated environments.

ROOT DISTRIBUTION PATTERNS

Root systems are seldom distributed uniformly within any given soil horizon of the root zone. Plant competitiveness and tolerance to stresses depend upon the sustained growth rate and maintenance of viable roots into multiple soil locations rich in water and nutrients and not already occupied by living roots. Rapid growth of functional roots into unoccupied regions of soil increases the competitive and tolerance traits of plants due to their greater acquisition rates of biogeochemical resources (26). Roots frequently grow into planes of weakness, between soil aggregates, or into biopores (pores left by other roots or soil animals), or other areas in the soil with lower mechanical resistances. Roots from the same or different plants often compete for similar volumes within the soil, thereby resulting in the clustering or grouping of roots in the root zone (20, 34, 49). Factors that cause roots to congregate within certain regions of the root zone include: preferential horizontal growth, resulting from root geotropisms within each soil horizon; frequencies of branching along primary and secondary parent roots; root accumulations at planes of weakness within the bulk soil matrix; duration of plant growth; and above- and below-ground environmental conditions. Root clustering spatially limits root access to nutrients and water stored in adjacent soil volumes and increases exposure to soilborne plant pathogens through greater concentration of root exudates supporting growth of host-specific root pathogens (56). Therefore, root clustering increases the potential for greater abiotic and biotic stresses.

Spatial and temporal distributions of roots can be quantified during the

growing season by statistically analyzing root intersections at the soil-wall interface of permanently installed horizontal minirhizotron (MR) tubes at multiple times during the growing season (2). Computations of weighted averages, derived from a semivariogram of at least 80 "windows" (2.14 cm^2) and calculated at a resolution of 0.05 × 0.05 cells located along MR tubes buried horizontally at depth-intervals of 20 cm, were used to obtain the root distribution patterns for maize (Figure 1). Spatial patterns of the maize roots appeared to be dominated by accumulations below each row of maize plants. Root extension, during the vegetative growth stage, primarily occurred below rows of maize plants resulting in fewer roots between plant rows. As the season progressed, more roots explored the soil profile, thereby reducing distances between adjacent roots. However, clusters of roots below the rows of plants persisted through the grain-fill growth stage. Root separation distances (RSD) appear to be exponentially related to time at a given horizontal plane in the soil,

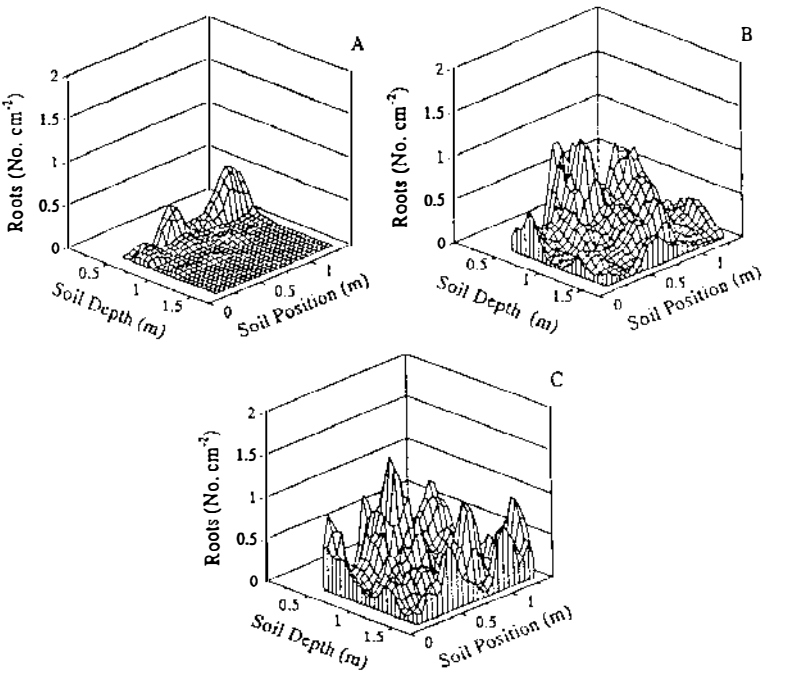

Figure 1 Root distributions of maize (*Zea mays*) at different growth stages in a Spinks sand soil during water deficits. Graphs were derived from exponential trend and semivariograms of roots intersecting horizontal minirhizotron tubes (soil position). Water deficits occurred during both the vegetative and reproductive growth stages. Root distributions are for (A) the eight-leaf growth stage on day 194, (B) anthesis-growth stage on day 217, and (C) the grain fill-growth stage on day 238 (from Ref. 2).

especially during early stages of plant growth. Values for RSD averaged 0.14, 0.05, and 0.03 m at soil depths from 0.50 to 0.72 m for 50, 73, and 94 days after planting, respectively (2). Spatial distances between clusters of roots, which ranged from 0.79 m at the eight-leaf growth stage (Figure 1A) and continued through anthesis (Figure 1B), approximate the distances separating rows of plants (Figure 1A). Confirmation of horizontal and vertical root clustering suggest these highly nonuniform distances influence the diffusive resistances to soil water and solute flow to root surfaces, thereby confounding the cylindrical empirical solutions frequently used to develop models for predicting water uptake by roots (29, 63, 68). Unfortunately, these equations have not accurately predicted root activity or function (51).

Root functions include the absorption of nutrients and water, respiration of photosynthates, production of plant growth regulators, and the maintenance of a balance between the above- and below-ground plant biomass. New knowledge of below-ground dynamics and the functional morphologies of individual roots could provide additional objectives for plant breeding programs, including the design of cultivars with ability to tolerate specific stresses through the use of rDNA technologies as projected by Schiefelbein & Benfey (70). Plant breeding can be enhanced by the availability of genes controlling novel and fundamental physiological and biochemical mechanisms that control plant responses to environmental stresses (31). However, one of the unknown yet paramount questions relative to plant root responses to environmental stress is: How are single or multiple stresses transduced to response mechanisms within individual root cells, especially pericycle cells that initiate lateral branches? The geometric linkages at nodes, internodal distances, and distances behind each apex of the different levels of branching by the root system at multiple soil depths have many functional implications that should be explored before sustainable single and mixed-crop production systems can be achieved.

Plasticity of Root Branching

Although lateral root development is genetically directed, augmentations in the numbers of lateral roots is a common compensatory response to many environmental stresses (69). For example, root laterals initiated at selected pericycle cells and their associated structures are principal means for overcoming nutrient and water deficiencies. Drought appears to cause abscission of most lateral roots in dry soil and the induction of secondary lateral roots in regions of the soil containing higher soil water contents. Structural changes of root laterals in dry soils, e.g. formation of cortical voids or lacunae, cause roots to shrink forming air gaps between roots and adjacent soils (59). Additional lateral root branching in the wet regions of drying soils promote the efficient absorption of water, while water losses from roots subjected to

drying soils appear to be greatly reduced by these reported root-soil air gaps that disrupt the continuity of water flow at the root-soil interface (58).

Root systems consisting of mostly very fine roots develop greater surface areas at lower relative carbon costs to the plant (24). Plants with greater "specific root surface area," i.e. those that require less carbon per unit of root surface area (cm^2 per mg of root), are more efficient and opportunistic absorbers of ions and water than plants with root systems with fewer fine lateral roots (8). Species with higher specific root-surface areas also produce greater root densities (cm root per cm^3 of soil) than species with lower specific root-surface areas. Roots with higher specific root surface areas have greater absorption potentials and use less carbon. Plants whose root systems have greater specific root-surface areas also appear to be more competitive in single and mixed plant communities (25). Additionally, highly efficient root types respond more rapidly to heterogeneous and localized soil conditions, e.g. localized enrichments of nutrients and/or microorganisms and temporarily wet soil regions (24, 78).

Lateral root branching appears to be stimulated by wetter regions of the soil during periods when plants are subjected to soil water deficits. Accelerated root branching leads to compensatory root responses, which increases plant tolerance to drought (25, 62). Extensive root-branching responses of maize to drying soils in greenhouse and field studies appear to be the result of localized and whole-plant signals that initiate cell division at the pericycle and modify carbon allocation (6, 18, 62, 78). The greatest number of root laterals appear to be initiated in transition zones between wet and dry soil. Although the soil-water potentials that promote root branching are not known, best estimates indicate that most maize-root branches of stressed plants develop in regions where soil-water potentials range between -0.05 to -0.15 MPa (Figure 2). The rate of root development and soil-water potentials adjacent to branching roots appear to be altered by evapotranspirational demands on the plant. The range of soil-water potentials that promote root branching appear to result from recent environmental and carbon-allocation histories (1).

Symbiotic vesicular-arbuscular mycorrhizae (VAM) also increase secondary and tertiary root branching of some plants in drying soils. Thus, the number of laterals per unit length of poplar roots increased up to 600% when colonized by VAM, suggesting that VAM alterations of root system morphology may not be due entirely to improved host-plant nutrition (36). These observations suggest both above- and below-ground environmental conditions cause gradients of water potential to develop within the plant and in the soil volume adjacent to the roots. As thresholds of water gradients interact, additional biochemical changes in the pericycle promote rapid division of pericycle cells and hence formation of root initials at certain regions within the root system.

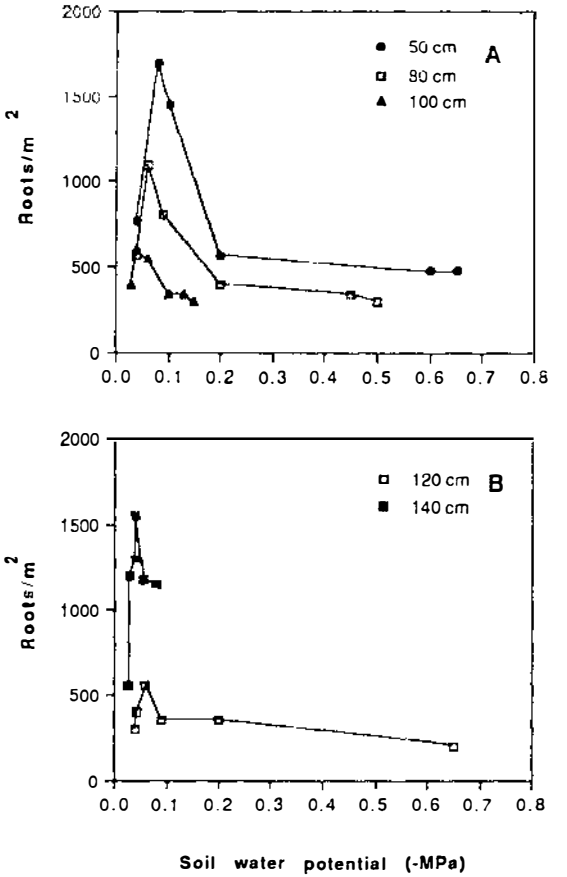

Figure 2 Influence of soil water potential on root density (branching) for maize (*Zea mays*) at soil depths of (A) 50–100 cm and (B) 120–140 cm during 32 days of soil-water deficits and vegetative growth. Maximum root branching occurred between −0.05 and −0.15 MPa for all soil depths

Spatial variabilities of root branching during soil-water deficits confirm reported spatial variability of soil-water potentials within the root zone of a drying soil (4, 73).

It is unknown why all root initials in the pericycle do not develop into functional root branches. Apparently chemical signals are initiated in response to environmental stimuli and accumulations of these signals activate individual pericycle cells. An activated cell may recruit an adjacent cell or multiple cells may be activated by the same signal. Once the meristem of an emerging branch root is formed, it expands, forcing its way through the cortical and

epidermal tissues, emerging as a functional lateral root. One possible chemical signal responsible for activating lateral root development could be the phosphoinositide-associated transduction pathway. Many signal transduction pathways that regulate cell growth and differentiation have been identified for animal cells and evidence is accumulating for the existence of these transduction pathways in plant cells (66). Perhaps root-specific nucleotides similar to the near full-length cDNA clone (pZRP3), which corresponds to a mRNA specific to the cortical ground meristem regions of maize roots (41), are responsive to specific signal transductions within certain cells in the pericycle. The possibility of organ-specific gene expression in response to a specific stress offers exciting opportunities for investigating the effects of environmental and disease stresses on signal transduction pathways, especially those phosphoinositide signals that promote nucleotide activities within root cells.

Complex communication between roots and surrounding environments generate a range of diverse responses in root-system development. Many feedforward and feedback networks that promote natural root-system diversity have been suggested (18, 64). Signals from the roots appear to affect shoot function and growth, which modify plant activities for the life of the plant (65, 85, 92, 93). Highly synchronized responses between the shoot and root occur at the onset and during environmental stresses, yet little is known regarding the mechanisms of these communication networks. However, rapid and excessive root-growth responses are expensive investments by plants whose carbon assimilation is finite. Additionally, maximum and sustainable plant productivity are at risk when extraordinary quantities of photosynthates are allocated to root systems by plants subjected to short- and long-term environmental and disease stresses (35, 62, 71).

CARBOHYDRATE UTILIZATION

Large root systems require relatively large quantities of carbohydrate to produce and maintain functional root tissue. Root production and maintenance costs range from 20–47% of all plant photosynthates. This consumption rate is even greater when plant roots are subjected to environmental stresses (30, 43, 46, 57, 71). Plants with root systems consuming such high rates of carbon are at risk. Excessive consumption of carbon by root systems will certainly interfere with attempts to augment biomass production above ground. Roots with larger diameters require more carbon for growth and maintenance respiration, because of the greater number of cortical cells. Additionally, the larger root diameters present greater radial resistances to the flow of ions and water. One of the most efficient approaches for overcoming the contradiction of conserving photosynthesized carbon while producing more root surface area is to genetically program root systems to produce greater numbers of

smaller second- and third-order laterals in regions of the soil relatively rich in nutrients and water (24, 78). In other words, the high cost of root production and maintenance can be offset by preferential growth of fine roots into soil volumes where there is greater absorption of water and nutrients for each unit of carbon invested. Proliferation of fine roots appears to occur in some nutrient-rich zones and in the wetter regions below drying soils (21, 25, 78).

Because they contain only a few layers of cells (70, 87), the surface areas of fine roots are much greater for each unit of carbon invested e.g. cm^2 of root per unit of biomass (24). Smaller diameter roots of *Arabadopsis,* having a thickness of less than 0.1 mm, contain two cell layers between the endodermis and epidermis (70). These fine roots penetrate into finer soil pores and remove greater quantities of stored water (4, 24) and ions (8) from within soil structural units than larger roots. Short and thin lateral roots can also bridge the discontinuities that develop between larger roots and adjacent soil walls during periods of soil and plant water deficits, resulting in subsequent root shrinkage. Mechanisms responsible for root branching and the photosynthate costs associated with the production and maintenance of these branches are essentially unknown. One approach for determining root branching mechanisms and associated with absorption is to quantify the carbon required for the development and subsequent absorption by each order of root branching. Then compare alterations in these carbon requirements when plants are subjected to disease and other stresses.

A second approach for conserving carbon consumption by root systems is to alter the biosynthesis and catabolism of starch and soluble sugars in roots. Sucrose metabolism, which reflects the balance between synthesis and use in both source and sink tissues, could be altered. The potential also exists for modifying the activities of key enzymes using recombinant DNA technologies, thereby altering carbohydrate composition of plant parts. Key enzymes of metabolic pathways that have been targeted for manipulation include ADP-glucose pyrophosphorylase (starch synthesis), sucrose-phosphate synthase (sucrose synthesis), and galactinol synthase (raffinose saccharide synthesis) (39). A wide range of genetic modifications in root morphology, physiology, and biochemistry offer nearly unlimited opportunities for improving the functional efficiencies of root systems.

Root Deposition of Carbon

A significant proportion of plant photosynthates is released into the rhizosphere via exudation, respiration, tissue deposition, root death, and other processes. Carbon released by root exudation and respiration, as determined by the pulse-labeling of shoots with $^{14}CO_2$ and ^{14}C accumulations in the root chamber, represented 20–39% of the labeled carbon allocated to the roots by dry edible beans (*Phaseolus vulgaris*) (71). Carbon released by roots of barley

(*Hordeum vulgare*) and wheat (*Triticum aestivum*) represents 20% or more of the photosynthetic C and appears to be a function of the stage of growth, aging, and environmental conditions of the root system (6, 30, 43, 52). Additions of NO_3^-
from wheat roots by increasing these losses to nearly 40% of the current rate of photosynthesis (9). The amount of carbon lost by living roots also appears to be a function of the size of the root system, since highly variable quantities of soluble low-molecular-weight carbohydrates exuded by roots have been correlated with root length. However, the quality of monosaccharides lost is not correlated with total length of the root system (16).

Root respiration is essential for the production of metabolic energy. Since nitrogen sources greatly influence the quantities of carbon dioxide respired by a root system, it is necessary to quantify the contributions of HCO_3^-
NO_3^-
the amount that enters the root system. Nitrate salts caused a transient increase (40–50%) in both oxygen uptake and carbon dioxide released by roots (9). These greater respiration rates accounted for 66% of the dry weight changes for roots of barley fertilized with nitrogen (47). Slower-growing roots of barley without nitrogen fertilizer appeared to lose considerably more organic carbon per unit weight of root than did the faster-growing roots.

Plant uptake of carbon in the soil by roots appears to be independent of the photosynthetic rate and, in most cases, may be predicted by transpiration rate and carbon concentrations in solutions surrounding the roots. Independent relationships between root uptake of soil carbon and current photosynthetic rates, regardless of ambient carbon dioxide concentrations, suggest that recent increases in atmospheric carbon dioxide concentrations (which also increase the allocation of photosynthates to plant root systems) may not have a direct effect upon the root uptake of soil carbon. On the other hand, anaerobic conditions within the root zone increase carbon uptake by hypoxic or anoxic roots (5), resulting in greater root respiration rates (75). Since the rate of root respiration responds to the demand for respiratory energy and the carbohydrate supply, greater rates of carbon dioxide evolution following anoxia may result from accumulations of adenylates (e.g. ADP) and not necessarily greater supplies of carbohydrates (46). Carbon respiration via the cyanide-resistant alternative respiratory pathway is often associated with anoxic conditions and has been reported to be a luxury consumption process for removing excess quantities of photosynthates during short-term accumulations by some root systems. The alternative respiratory pathway appears to be a more wasteful process than the cytochrome-oxidase pathway and should be removed from the metabolic pathways of aerobic root respiration (46).

Root decomposition may contribute large quantities of carbon to the soil carbon pool (88). Although the importance of root death and decay relative

to carbon cycling is not well understood, either during crop growth or following harvest, nearly half of the root carbon appears to be released as carbon dioxide during a 90-day period following the harvest of winter wheat, with 24% of the root carbon transferred to soil organic matter during the 18 months following harvest (14).

ROOT DEPOSITION OF NITROGEN AND PHOSPHORUS

There is also an appreciable flux of nitrogen from roots into the soil. Nitrogen losses by the exudation of amino acids and peptides from root systems are sometimes quite high. Carbon to nitrogen ratios in root exudates have been observed to range from 2.0–2.7 (44). Net deposition of nitrogen by the root systems of wheat was determined by pulse-labeling shoots with gaseous $^{15}NH_3$ and determining ^{15}N in the soil for the entire growing season. Nitrogen in the soil was 8 and 25 mg per plant for low and high nitrogen fertility, respectively. These amounts represented 18 and 37% of the total nitrogen accumulated by the wheat plants (40). Much of the root-deposited nitrogen appears to be highly labile since one third of all nitrogen originally present in the organic form of these studies was mineralized to plant-available nitrogen. Root exudation of soluble proteins was not influenced by root numbers but was highly correlated with the particulate materials lost by living roots (16, 76).

Roots of perennial ryegrass (*Lolium perenne*) lose substantial amounts of phosphorus within a few weeks of detachment from the plant. Roots with high phorphorus contents will lose up to 70% of the phorphorus within 21 days following death. The amount of phorphorus lost by roots deficient in phorphorus is reduced to approximately 30% during the same period of decomposition (22). Earliest losses of phorphorus are in the lipid form, with nearly 75% of the lipid-P lost during the first week following root death. Losses of water-soluble phorphorus from dying roots require up to three weeks. Greater water-soluble phorphorus appears to be lost by plants with greater phorphorus contents, and essentially no water-soluble phorphorus is lost by plants low in phorphorus content. Lipid-P losses from roots low in phosphorus comprise nearly 50% of the total phorphorus lost (23). Competition for nitrogen and phorphorus by the pathogenic and nonpathogenic microbial populations in the rhizosphere is often intensified when the host becomes infected as root diseases enhance root turnover and nutrient release into the soil.

Decomposition of Carbon and Nitrogen in the Roots

In natural ecosystems, certain portions of living root systems are always under attack by associated organisms. Each incremental change in the environment of adjacent soil microsites within the root zone causes roots to become more vulnerable to biotic factors, accelerating decomposition rates of cells and

tissues within the root system. We have observed extensive invasions of root surfaces by fungi, and possibly bacteria, on all roots, immediately before they turn dark and disappear from view at the surfaces of minirhizotron tubes (73). Death of plant roots during the growing season introduces large pulses of carbon, nitrogen, and other nutrients into the soil system. These nutritional pulses are frequently intensified during periods following each stress. Abiotic and biotic stresses causing root death and turnover and influxes of soil-borne pathogens promote the release of more root-based nutrients into the cycles of each nutrient. Root decomposition following physiological maturity of each plant may contribute the greatest pulse of nutrients into soils, to depths as deep into the root zone as the deepest root. Decomposing plant roots are a rich source of nutrients, which augment populations of selected soil microbes and mesofauna on soil walls of root channels. Therefore, greater knowledge of root growth, death, and disappearance could contribute to the development of successful root-disease models.

Relative decomposition rates of above- and below-ground plant parts appear to be a function of the plant type and associated soil conditions. Decomposition rates of roots have been reported to be approximately one half the rate of shoots for a desert pepperweed (*Lepidium lasiocarpum*) (61) and 133% of straw residues for winter wheat (14). Maize roots intersecting minirhizotron tubes at depths greater than 0.8 m may not decompose until well into the next growing season of succeeding crops (A. J. M. Smucker, unpublished data). Dead roots appear to stimulate microbial activities by attracting fungal-consuming mesofauna, e.g. Collembola (80), resulting in mineralization rates of carbon from dead roots. Nitrogen mineralization of dead roots appears to follow fungal invasions with subsequent immobilization of nitrogen occurring primarily in the soil organic fraction adjacent to the decomposing roots (61). Controlled losses of carbon, nitrogen, and phorphorus by the exudation of soluble forms of these nutrients as well as scheduled root-death rates and subsequent root decomposition appear to maintain the delicate balance between efficient retention of C, N, and P and the many beneficial effects of their deposition in the rhizosphere. When root losses are too low, beneficial effects of the rhizosphere suffer. When root losses are too great, absorption efficiencies are lowered. A moderate mutualistic balance of nutrient cycling between the root and associated microbial populations of the rhizosphere appear to benefit plant root-soil interactions the most.

SOIL ENVIRONMENT, ROOT HEALTH AND FUNCTION

Plants attain maximum and sustainable productivity when optimal quantities of carbon are allocated to and most carbon- and nitrogen-compounds are retained by absorptive portions of healthy and highly efficient root systems.

Greater retention of carbon and nitrogen by the root produces more efficient absorptive surfaces, which are more resistant to soilborne plant pathogens. Therefore, a reduction in the frequencies of abiotic soil stresses reduces the loss of these compounds. The negative effects of root and vascular diseases in plants are exacerbated by accompanying abiotic soil stresses (3). Although inoculum densities of soilborne plant pathogens are relatively low, ranging mostly from 0.2 to 10^2 propagules per gram of soil (10, 17), these concentrations make an enormous difference to the incidence of root infection, severity of root disease, and plant productivity, especially when susceptible cultivars are replanted in conducive soil environments without benefit of crop rotation (3). The highly competitive soil microbiota continuously depletes soil niches of readily available energy sources (42, 45, 48), even causing excessive leakage of nutrients from adjacent microorganisms. Continuous recropping (monoculture) of susceptible plants in the same soil produces ideal nutritional conditions in the root zone and increases the inoculum potential of host-specific pathogens (42). Monoculture has also been observed to increase the numbers of roots occupying root channels developed by the previous crop, especially in nontilled soils (A. J. M. Smucker, unpublished observations for maize root interceptions of horizontal minirhizotrons).

The greater incidences of root diseases in monoculture systems could result from occupation of old root channels by successive susceptible crops. Continuous monoculture appears to reduce the diversity of root-associated fungi, with concomitant reductions in net root growth (56). Therefore, the greater yields associated with crop rotations, often referred to as the "rotation effect," can be partly or largely explained by lower incidences of root diseases as roots of different varieties explore fewer rhizosphere niches developed by the previous crop. This may be one mechanism explaining how crop rotations are routinely used to control root pathogens. Although crop rotation sequences influence levels of microbial biomass in soil, soil enzymes, and soil physical properties, the effects of crop rotations on the diversity and biocontrol of rhizosphere microbial populations, particularly pathogenic organisms, need further examination (55).

Biocontrol of root diseases has been reported in response to soil or seed inoculations by certain strains of fluorescent pseudomonads (50, 90, 91). However, a major limitation to the commercial use of these agents is their lack of consistent disease control in the field. These inconsistencies result, in part, from the variable colonization of plant roots by introduced bacteria (91). Colonization of root surfaces by different strains of pseudomonads appears to be influenced by fungal infections of the same root. Co-colonization of roots by fungal pathogens appears to either increase or depress populations of fluorescent pseudomonads, with different strains of pseudomonads reacting differently to a multitude of root pathogens (53). It

is projected that these multiple root colonizations by pseudomonads and fungal pathogens in the rhizosphere may have resulted from nonuniform occupancies of the same microniches of the soil by roots of wheat plants. These data demonstrate the importance of quantifying root distribution and activities during the assessment of root disease and interactions of root pathogens with biocontrol agents.

In short, to keep an agricultural system sustainable and profitable, diverse plant types and microorganisms need to be considered for stabilizing the soil, controlling soil erosion, providing nutrients, and reducing root diseases. Multiple root occupancies of preestablished root channels reduce microbial diversity, enhance root diseases, and reduce functional efficiencies of roots, thereby exacerbating the adverse effects of associated environmental stresses and contributing to the yield declines associated with monocultural practices. Root clustering in soils could be reduced by deep soil tillage, crop rotations, and the planting of bridge or other crops with different root-system geometries. Root exploration of soil areas not previously inhabited by roots may dramatically reduce the potential for root disease as well as abiotic stresses. Therefore, knowledge of root-system clustering is essential for each cultivar and soil type before complete knowledge of the epidemiology of root diseases can be determined and disease control can be improved.

QUANTIFICATION OF PLANT-ROOT SYSTEM MORPHOLOGY

Knowledge of spatial and temporal root geometry is essential before we can fully describe root function and root disease epidemiology. Below-ground bioprocesses are generally ill defined because measurement of relevant variables at the soil-root interface is difficult. This paucity of quantitative approaches, available for repeatedly measuring complex interactions between plant roots and associated soil organisms, should motivate scientists from more disciplines to improve our investigative potential for exploring many largely unknown activities of below-ground interactions. Fundamental knowledge of the *in situ* interrelationships between roots and associated soil activities frequently limit the expansion of many disciplines within the plant and soil sciences. We need additional quantitative methods for more belowground processes.

Quantum increases in our knowledge of below-ground dynamics will occur on the heels of significant improvements in methodological approaches that can be used to measure relevant bioprocesses below ground. In contrast to other disciplines such as physics, engineering, or the medical sciences, soil biology is substantially underdeveloped with respect to both measurement and manipulation. Most *in situ* measurements are physical (e.g. soil water, gas

concentrations, temperature) or chemical (e.g. ion concentrations, pH, redox potential) rather than biological. Biologically relevant variables (e.g. energy exchange, respiratory capacity) are generally more complex. Additional requirements that can be restrictive include: (*a*) Repeated observations of the rhizosphere; (*b*) Continuous capacity and rate measurements; (*c*) Stable and reliable measurements over time and space; (*d*) Noninterference with below-ground activities, capacities or rates.

Fortunately, recent advances in microchip and video technologies provide new opportunities for accessing and repeatedly observing the dynamic "hidden half" (89) of the plant-soil-atmosphere continuum. Recent developments, which complement other reviews of root biology, are reviewed in this publication (11, 15, 72, 74). Special attention is devoted to the application of image processing of plant-root morphologies extracted from destructive and nondestructive images. Appropriate methods for quantifying root morphology are a function of the experimental objectives and can be grouped into (*a*) destructive sampling where soil and root samples are extracted from the site, roots are separated from the soil, and associated debris and root morphologies are quantified; and (*b*) nondestructive observations of root and associated organism activities such as image processing.

Destructive Sampling

Destructive samples are useful for quantifying root disease, biomass, ion contents, length, diameter, surface area, and volume at each sampling time. However, destructive methods preclude repeated sampling of the same plant, thereby resulting in large variations among successive destructive samples of additional heterogeneous plant-root and soil conditions.

SPATIAL VARIABILITY Heterogeneous distributions of plant roots in the field must be considered when selecting the most appropriate method for evaluating root-system dynamics. Spatial variability in the planes of weakness among soil aggregates, soil horizons, pore and biopore geometries, and the distribution of microbial, nutrient, water, insect, disease, and allelopathic "hot spots" are a few of the environmental factors directly influencing patterns of root development, function, and death. Temporal differences in soil-nutrient concentrations, water contents, temperature, gaseous concentrations, microbial populations, and mesofaunal activities that modify phenologic development and competition within or between root systems should all be considered when deciding where, when, and how often to sample. The variability among samples governs the number of replications. The universal approach to core sampling ranges from 5-cm diameter cores, taken to depths of several meters (11), to larger profile samples (e.g. 23 × 7.6 × 91 cm), which can be

fractionated into smaller subsamples and analyzed separately (81). Variations among root and soil samples can be greatly reduced when sampling protocols are based on the depths of each horizon and horizon interfaces within individual soil types rather than specific depth intervals. Currently, our best approach is to obtain large numbers of replications and statistically analyze them for significant differences at an acceptable degree of probability.

The number of replicated, destructive core samples needed for quantifying root dynamics in a field experiment also depends upon the sample size. For core samples with diameters of 6.5 cm, five to nine random replications within the row appear to be necessary for obtaining significant results between cultivars of plants at $P = 0.05$ by the Duncan's Multiple Range Test (11). Greater heterogeneity of tree roots requires 9–30 replications for statistical comparisons of root samples taken from orchards and forest ecosystems (11). The minimum number of samples for statistically comparing root systems in surface horizons of row crops or grassland is five replications of soil cores 7 cm in diameter (11). In our experience, 8–12 replications are needed for each treatment before significant differences can be obtained using nontransformed data. The number of replications can be reduced somewhat when subsamples are combined or when data are log or sine transformed.

Classical methods for separating roots from soils include varying the water pressures applied directly to root and soil samples on screens of different mesh sizes. Although these methods may use inexpensive equipment, they yield mostly larger roots since many of the finer and more active roots are broken and forced through the separation screen by water. This method of extraction does not provide the accuracy necessary for evaluating active root absorption surfaces. Separation of roots by hydropneumatic elutriation will retain up to 99.4% of all roots > 0.05 mm, with attached root hairs and nodules, as well as some propagules of fungal pathogens (72, 79). This system rapidly provides excellent root samples and has been widely accepted (15). A high-energy water vortex is generated in the separation chamber of this enclosed system. Quantitative separation of roots from mineral soils, including compacted clays, and the roots plus associated plant residues, weed seeds, and other organic matter, less dense than the mineral fraction, is accomplished by elutriation and flotation in the separation chamber. Floating roots and associated materials are transferred to and retained on low-energy separation screens submerged in water (72, 79). Multiple screens may be stacked to separate roots and residues of different diameters. Large numbers of root and soil samples from replicated multifactorial field experiments can be processed in a few days. Roots can be video recorded and quantified immediately or preserved in 15% methanol and stored at 4°C for quantification at a later date.

Nondestructive Sampling

RHIZOTRONS Nondestructive evaluation of root dynamics can be achieved by observing root intersections of transparent surfaces adjacent to the soil. Historically referred to as rhizotrons, these facilities generally are large soil bins containing as much as 12 m^3 of soil with one side of the soil bin equipped with large reinforced glass or plastic windows (11). The large transparent walls are covered to exclude light. Light covers are removed periodically for measuring root intersections at the wall. Large soil bins with transparent walls have distinct advantages for observing greater areas of the soil. However, the edge or wall effect of these observation facilities can dramatically influence water, soil, root, pathogen, and perhaps ion interactions. A disadvantage of the large rhizotrons is their initial cost and the limitation to a single soil type when using nondisturbed soil profiles. Other types of observation systems include temporary field rhizotrons, where smaller windows are installed adjacent to undisturbed soil profiles in soil trenches at random locations within a field or forest (37). Temporary rhizotrons are relatively inexpensive and are useful for observation of certain root-organism interactions, but have the disadvantage of large wall effects similar to those described above.

MINIRHIZOTRONS Very small (5 cm in diameter) transparent tubes, often referred to as minirhizotrons (MR), have been successfully installed, at 30–45° angles or parallel to the soil surface at random locations throughout fields and forests (2, 13, 33, 83). Generally 12–16 replications are needed when MR tubes are installed at acute angles to the soil surface to satisfactorily compare differences among plant species, crop cultivars, and soil treatments. Additional replications may be necessary when soil conditions or root-growth habits are highly variable. Fewer (e.g. two or three) replications of horizontal MR tubes are needed as the multiple intersections can be counted as replications or can be grouped by geostatistical methods for establishing semivariograms (2).

The MR observation method has many applications for evaluating root dynamics by remote sensing. First, MR tubes can be installed at most locations in the landscape. Second, nondestructive root measurements can be evaluated on location or recorded by microvideo cameras (86) at intervals of minutes or longer without disturbing the rhizosphere. Third, simultaneous and associated soil measurements can be taken, e.g. soil water by the neutron probe using the same MR tubes as access tubes and gas measurements by extracting gases through microtubules fixed to the walls of the MR tubes (2). These consolidated measurements provide opportunities for evaluating root growth, maintenance, function, death, and disappearance (2, 28).

Root intersections of transparent MR tubes are recorded by microvideo

cameras onto video cassettes (77, 86). Attachment of an indexing handle provides additional opportunities for estimating root turnover rates, recording root activities, root disease development, and associated organismal activities at identical soil depths, and visually quantifying these processes or activities at various time intervals (28). Video recordings of roots can be returned to the laboratory where root numbers, root lesions, root branching, and associated mesofauna can be counted manually or by image processing. More detailed root morphology can be determined by image processing video images of crop plants (77) or trees (33). Root dynamics are usually determined by the appearance and disappearance of roots at the upper region of the MR tubes. These data are statistically evaluated, summarized, and presented graphically as in Figure 1. Unfortunately, all background morphologies recorded in MR video recordings cannot be identified by current image processing systems. The current status of this technology is discussed below. Other limitations of the MR method include possiblc disruption of normal root growth at the plastic-soil interface. Much of the interference effects can be overcome by evaluating root morphology and conditions at the upper surface of MR tubes.

In addition to the high portability of MR tubes and associated video recording equipment, labor requirements are low. One technician can video record root intersections to depths of 150 cm for 50 MR tubes daily. The speed and repeatability of nondestructive measurements by the MR and video recording methods, as well as the permanent video records of root and associated rhizosphere activities, provide excellent opportunities to collect necessary information of the many below-ground activities associated with root morphologies and diseases. Additionally, libraries of root dynamics can be collected and electronic databases of rhizosphere activities can be assembled for widespread dissemination.

Quantitative Image Analyses

Image processing offers exceptional opportunities for quantifying individual root and associated components recorded as complex video images in MR tubes. MR images contain multiple levels of root branching, root crossover and overlapping, mesofaunal movements, invasion and infection of roots by microorganisms, development of symbionts, and other activities. Recent developments in flatbed scanners, video cameras, image storage, computer processing speeds, artificial intelligence algorithms, and statistical and graphical programs provide numerous opportunities to automate past laborious and error-prone estimates of root morphology and activities in the rhizosphere.

Until recently, root measurements have been limited to root length as estimated by the line-intercept method, which is based on mathematical relationships between the intersections of randomly distributed roots and a

straight-line grid (84). This approach uses inexpensive equipment but is highly laborious. Technicians can be trained to identify and manually count roots, but human error is common and results obtained by different individuals and laboratories can vary. An alternative method is to interface a high-resolution flatbed scanner and personal computer (PC) equipped with a digitizing board and image processing algorithms that will characterize root length, width, and calculated diameters (60). Although relatively rapid, this approach cannot be used to separate roots from associated residues and it does not record images for future reference. A video camera and PC computer system for digitizing and analyzing video images (32) have been developed for quantifying clean root samples, but errors still result because of associated residues and root overlapping.

Current developments in pattern recognition and image-processing, computer algorithms offer greater opportunities to extract information from complex root and soil images. Increased processing speeds of workstation environments provide improved approaches for segmenting root and associated organic debris and for electronically discarding information produced from unwanted organic debris. Improved computer algorithms have been developed to compensate for root crossover and quantify more morphological parameters from each videoed root image. Improved algorithms for root-image processing quantify root morphologies from video recordings of washed roots and MR tubes are accurate to within 3 and 5%, respectively (38, 77).

AUTOMATED PRODUCTION-LEVEL IMAGE PROCESSING As more root images from the field or laboratory are stored in video cassette libraries, greater computational capacities and image processing standards will be required. When additional root and associated soil information is needed, images, stored as video cassettes in the video library, can be transferred to one of three Vicom image processors (VIP) via video cassette recorders (VCR) and time base correctors (TBC) at Michigan State University. Computer-generated bar-codes, which identify each sample or MR tube, experiment, and sample date, are installed on the video tape at the time of recording. Audio signals can also be generated and placed on the video tape cassettes. The audio signal identifies more than 100 video frames of each root image, i.e. 32 frames per second for at least 3 seconds of continuous recording. Three seconds of continuous recording of each root image provides ample time for manual or machine decisions of associated mesofaunal movements. Enhancement of root images is accomplished by averaging 6–12 video frames of each root image by the TBC. Enhanced images are transferred to the VIP for digitizing, segmentation and quantification. Feedforward and feedback communications among the VCR, TBC, and VIP are received and controlled by the VIP. Video cassettes, containing up to 2500 individual root images, are processed

without human intervention at approximately 24 per hour. Analyzed video cassettes are manually refiled and replaced at approximately four-day intervals. Up to 16 morphological parameters are quantified for each image (e.g. root length, diameter, surface area and volume measurements for each of the first, second and third orders of roots and parameter totals for the entire sample). Some images are compressed and archived in disc storage for additional evaluation. Several root images have been thoroughly analyzed by multiple machines and individuals. These intensely evaluated images have been established as ground truth images that serve as standards. All image analysis data are transferred by electronic networks to PC computers that process and print statistical and graphic information. This information is also available via electronic wide-area networks (Figure 3).

A Root Image Processing Laboratory has been developed at Michigan State University that processes up to 11,800 video images of root samples per week, without human intervention. This analytical system currently accepts standard video images developed by the robotic video camera recordings of washed root samples, described above, and field microvideo-recorded images from

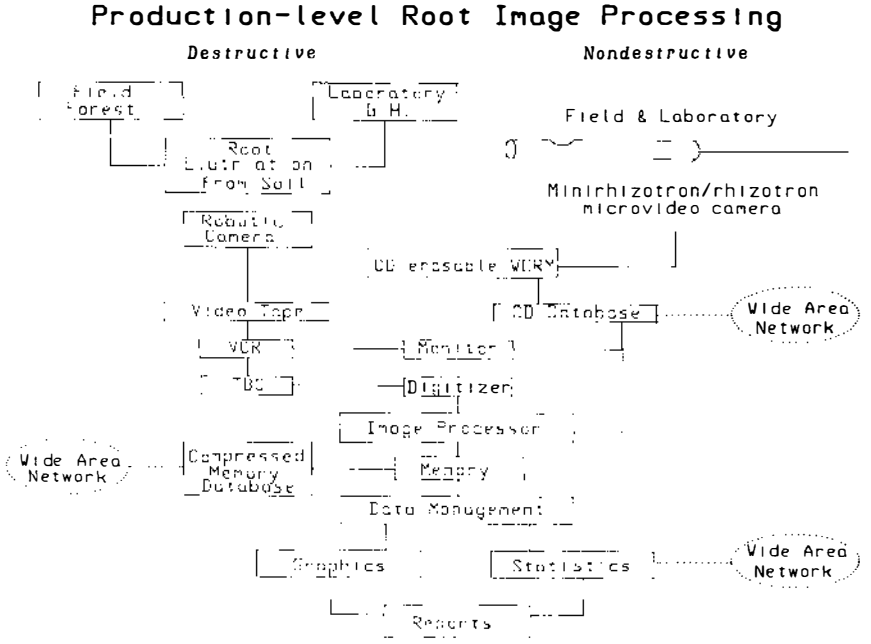

Figure 3 Diagrammatic representation of image collection, processing, data management, and reporting of video root images originating from the field, forest, greenhouse (G. H.) and laboratory by destructive and nondestructive samplings

MR tubes, as outlined in Figure 3, from several laboratories in the USA and abroad.

Two additional computer processing approaches are currently under development between the Departments of Crop and Soil Sciences and Computer Sciences at Michigan State University. The first group of computer algorithms is a ridge detection approach for identifying roots in video recordings from MR observation tubes (27). This image (Figure 4), which has been color enhanced (Figure 5), portrays the complete segmentation of root images by identifying the parallel edges of each root segment and separating the roots from the soil background. Center lines of these segmented root images (Figure

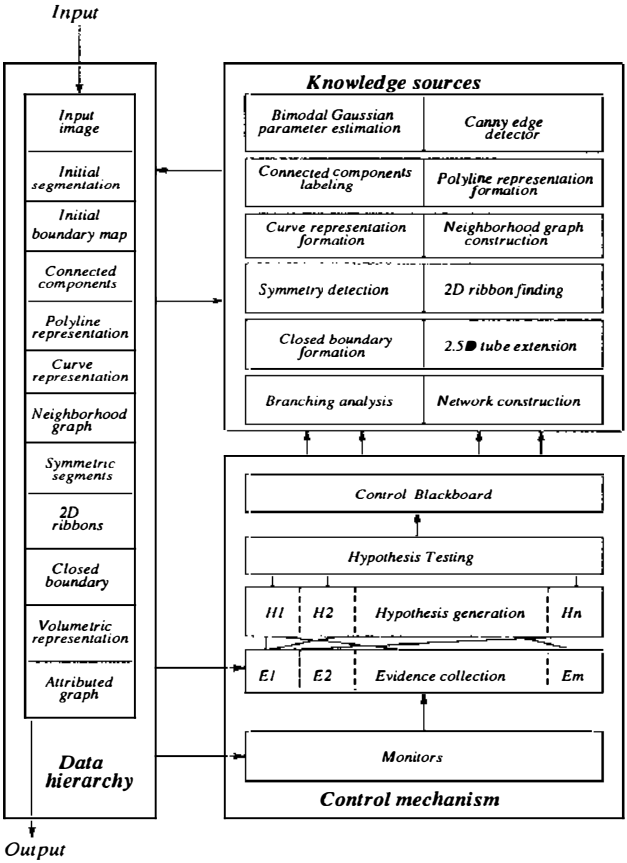

Figure 8 Flow chart of token-based computer algorithms for separating roots from background residues. The knowledge-based feedback approach increases the accuracy and flexibility of root image processing (from Ref. 38).

6) are identified by skeletonization algorithms and root widths are measured at multiple points along each root segment. Surface area and volume are calculated for each root segment. The three orders of root segments in Figures 4 and 5 are identified by root diameter classes. Diameter classes can be adjusted based upon the plant species and the optical magnification by the video cameras. The parallel edges of each root segment in the video image are identified by comparing contrasting pixel intensities across the entire video image. When the intensities of adjacent pixels or matrices of pixels contrast significantly, then root objects are identified in the video image. Parallel lines of these segmented objects are classified into roots and residues (Figure 7) by "intelligent" morphology discrimination algorithms. Center lines are established and roots are identified and summarized into the above-mentioned 16 (or less) root parameters recorded in each MR video image. Currently, we have been able to identify 94–96% of all roots, depending upon the complexity of the MR video image (27). A second and new generation of segmentation algorithms are currently being developed for Sun SPARC workstations (Figure 8). These new segmentation algorithms are token-based groupings applied at multiple levels within the imaging process. Token-based image processing increases the flexibility for identifying roots in a broader range of video images having complex backgrounds, e.g. identification of root disease, death and specific root turnover. As these algorithms are further tested and improved, they will become available to more laboratories.

MODELING THE SOIL-ROOT SYSTEM

Quantitative information on root morphology is essential for the development of functional and mechanistic root models. Quantitative information on root phenology is essential for the evaluation of root growth and root responses to soilborne plant pathogens. Although a thorough discussion of root and rhizosphere modeling is beyond the scope of this review, it is important to briefly describe essential criteria for integrating root-system parameters into root simulation models that accurately predict the dynamics of root growth, root-associated microorganisms and diseases, root function, and root death.

Models of plant roots and root diseases can be formulated at different scales. At the scale of a field or landscape, mega-scale functional models could be used to predict root disease epidemiology and economic losses to specific plant populations whose root systems are negatively affected by abiotic and biotic stresses in areas ranging from 1000 m^2 and larger. At the root-soil interface, meso-scale levels of functional and mechanistic models could be used to predict root infection and host-pathogen interactions. Individual roots, soil aggregates, and microbial "hot spots", as examples, are often modeled

at the meso-scale level of resolution with units of m^{-2}. Mechanistic models describing specific root function, e.g. nitrate or water absorption per unit area of root surface area, and root infection are generally limited to mathematical descriptions at the micro-scale level having units less than m^{-3}.

Current simulations of root growth have been limited to soil-plant-atmosphere models. Above-ground portions of these models emphasize canopy-related processes such as photosynthesis, leaf development, gaseous and water exchange, and phenological development, yet these provide little representation of root and other below-ground processes (51). Root growth in many current root modules is often limited to a root length parameter, which declines exponentially with depth (54, 67).

The next generation of root models needs to incorporate more information on fundamental mechanisms of root growth, function, disease, and other stress responses. For example, more information on the soil and plant-root variables that control spatial and temporal conditions of the root-soil interface is needed to resolve currently unknown resistances of water flow within the soil-root continuum. Once these resistances (R) to water flow are quantified for the soil (R_s), the root-soil interface (R_{if}) and the root (R_r), as projected by Moldrup et al (53), then the influence of root diseases on water absorption can be quantified by comparing water absorptions for a range of R_s and R_r for specific soil types at multiple soil-water contents. Combining this approach with root quantification procedures described above will provide many opportunities for quantifying the effects of root disease on water uptake by roots. Multidisciplinary modeling efforts that integrate root morphology, disease development, and ion and water fluxes will provide unlimited opportunities to explore mechanisms that modify plant root function during stress. Additional models describing the fundamental mechanisms of root and soil

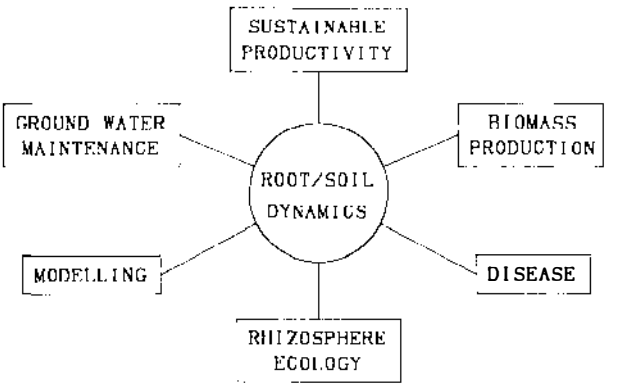

Figure 9 Integrated diagram relating soil and rhizosphere activities to root-soil dynamics

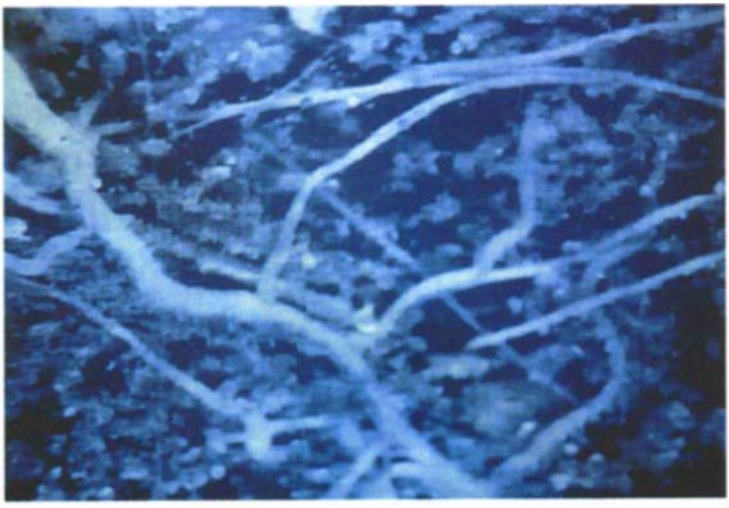

Figure 4 Original video image of alfalfa (*Medicago sativa*) roots in a Kalamazoo loam soil, recorded by a microvideo color camera lowered into a clear plastic minirhizotron tube installed at 45° angle to the soil surface. Root image contains secondary and tertiary root branches located at a soil depth of 85 cm on 20 August, 1991. Complex backgrounds of soil add to the difficulty of segmenting root images from minirhizotron video images

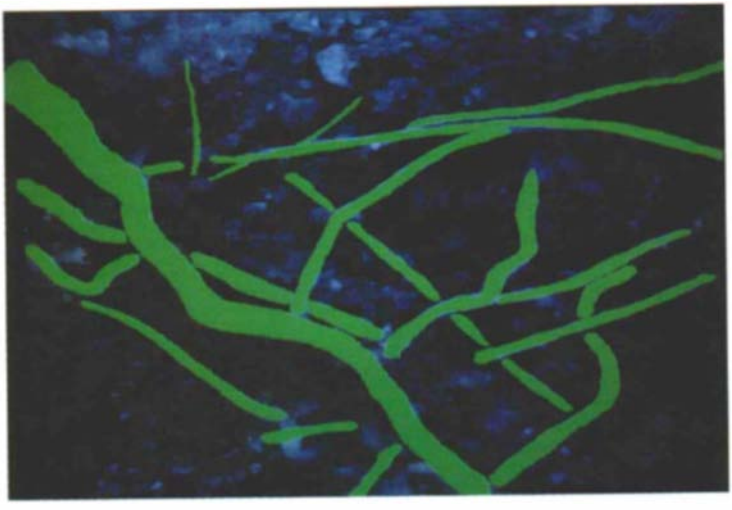

Figure 5 Color-enhanced image of alfalfa roots, from Figure 4, with background diminished

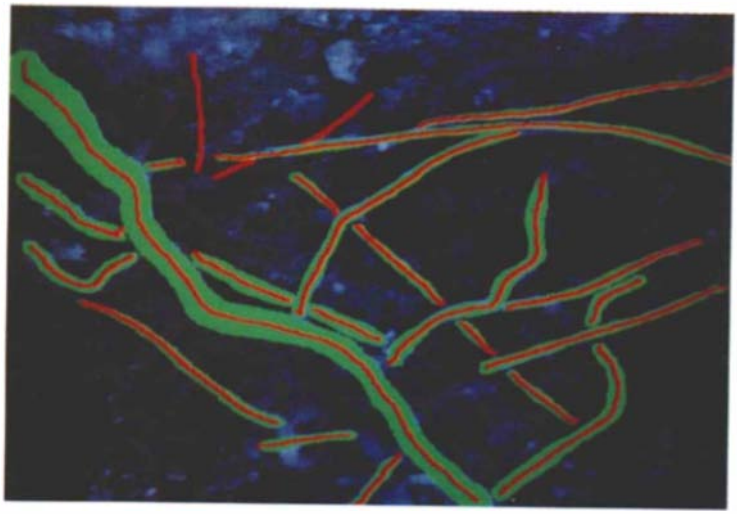

Figure 6 Center lines of color-enhanced root image, from Figure 4, with center lines drawn by skeletonizing algorithms that contain information on root width and length. These values can be used to calculate root surface area and volume

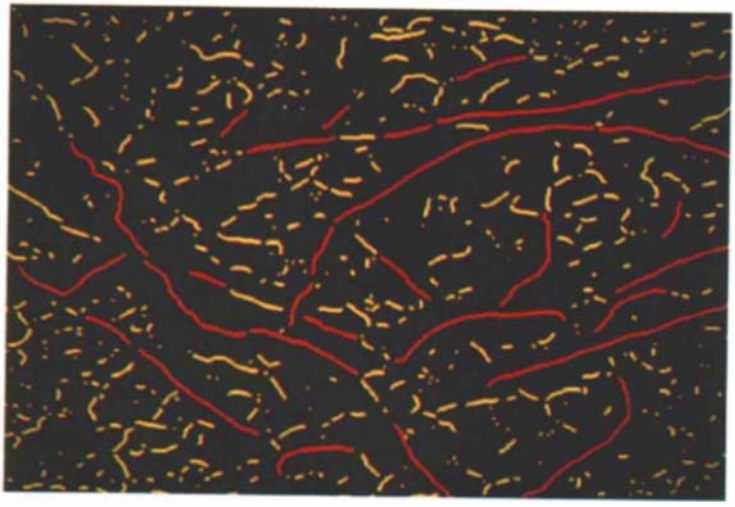

Figure 7 Center lincs (red) of original roots using thc ridge detection algorithms that segment and locate center lines of root images from the original image in Figure 4. Background of residue information (yellow lines) are removed to enhance the original root images. Note high similarities

dynamics could be expanded to address serious environmental questions such as ground water quality and below-ground root competition as summarized in Figure 9. Specific interactions of the dynamic root system are essential before root diseases can be reduced, leading to greater sustainable agricultural productivity.

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