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ROOT SYSTEM REGULATION OF WHOLE PLANT GROWTH*

R. M. Aiken
Great Plains Systems Research, P.O. Box E, 301 South Howes, Room 353, Fort Collins, Colorado 80522; e-mail: Aiken@gpsr.colostate.edu

A. J. M. Smucker
Crop and Soil Sciences, Michigan State University, East Lansing, Michigan 48824; e-mail: smucker@ajms.pss.msu.edu

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ABSTRACT

New evidence confirms earlier postulates that root signals to shoots, including abscisic acid, nitrate flux, and cytokinins, modify whole plant growth processes including leaf expansion, stomatal behavior, and biosynthesis of photosynthetic enzymes. Root signals are thought to reflect soil water, nutrient, and mechanical attributes, as sensed by roots. Meristematic activities in root tips initiate changes in root architecture, modifying the soil volume subject to root uptake, and may provide multiple sensory and signaling capabilities. Knowledge of root signals regulating whole plant growth processes suggests new analytical and experimental tools for integrated analysis of plant phasic development, optimal growth, and ecological fitness.

INTRODUCTION

The function of roots as sorptive organs for water and nutrients is well known, yet incompletely understood. Though root functions affect plant responses to water, nutrients, and pests, knowledge of mechanisms governing root function is obscured by limited direct measurement of mature root systems (9). The dynamic properties (48, 70) and extensive branching of root networks, coupled

with numerous interactive spatial and temporal fluctuations in soil properties, confound in situ investigations of rhizosphere dynamics (58). Thus, much of our knowledge of root function is gained from studies of seedlings or inferred from the consequences of root function observed in the plant canopy and soil profile (19, 21, 39, 42).

Conceptual models bridge knowledge gaps between individual root behavior and collective root effects on soil and canopy processes (4, 11, 23, 34). Alm & Nobel (1a) used laboratory measurements of individual root respiration and water uptake, at 15 age classes, to compute the respiratory cost of water supply for a desert succulent, predicting the total daily water uptake and respiration within 5% of measured values. They demonstrated that knowledge of individual root behavior can be scaled to predict function of an intact network of roots. Numerical models provide investigative tools for analyses of model sensitivities, identifying critical exogenous factors for experimental manipulation (10). Analysis of predictive failure (19) also provides insight to complex phenomena where multiple interactions among parameters confound direct experimentation. Conceptual and numerical models capable of scaling individual root behavior for root systems can help formulate and evaluate critical hypotheses regarding the role of root function in plant growth responses to fluctuating environmental conditions.

Knowledge of root function can guide investigations of pathogenic rhizoflora that modify these functions (57). Soil fumigation under field conditions demonstrated a host of rhizosphere interactions with beneficial as well as deleterious effects on maize (*Zea mays*) growth (37). The full scope and impact of rhizosphere interactions, implicit in the conception of root health (13), remain unclear. An understanding of root contributions to whole plant growth and development can guide proactive soil and plant management practices that enhance root health and effective function.

A growing body of evidence confirms the earlier postulate (65) that roots affect plant growth by processes beyond the functions of supplying water and nutrients (9). Biochemical signals such as cytokinins and abscisic acid (ABA), transmitted from roots, are thought to serve as active regulators of many physiological processes affecting growth and development of both shoots and roots (40a). Critical experiments indicate that root systems signal water and nutrient availability, modulating shoot growth and activity. We relate these findings to a postulated role of root tips as determinants of root architecture and subsequent function, illustrating with in situ observations of root system development under water deficits. Finally, we consider the implications of a root signaling system for whole plant growth regulation, relating these mechanisms to emerging theories of ecological fitness.

ACTIVE ROOT REGULATION OF PLANT GROWTH

Brouwer (8) described a functional equilibrium in root and shoot growth. This postulated equilibrium can be tested by manipulating initial shoot : root ratios and observing subsequent growth. Despite initial shoot : root ratios of 1 : 1, 1 : 2, and 1 : 3, consistent shoot : root ratios of 11 : 1 at maturity indicate the relative growth of root and shoot for a given set of environmental conditions (56). This equilibrium can be attributed to compensatory growth of shoot when supplied with water and nutrients of multiple root systems. However, balanced growth could also result from effects of growth-regulating hormones, synthesized in root and shoot tissues, and translocated to complementary organs. The relative growth of root and shoot organs appears interactive. Balanced growth may result from supply of water, nutrients, and assimilates, from translocation of growth regulators, or of their combined effects.

Distinguishing roles of root and shoot in growth response to fluctuating environmental conditions is confounded by dynamic interactions among plant functions. White & Castillo (69) undertook grafting studies to find the origins of plant growth response to water deficits. A complete set of reciprocal cleft grafts of roots onto shoots were made for four common bean cultivars (*Phaseolus vulgaris*) differing in growth response to drought. Whole plant growth under drought, at two experimental sites, varied with gene expression in root rather than in shoot organs. The authors inferred drought adaptations could result from direct root effects, including differential root architecture, osmotic adjustment, or interaction with soil organisms. However, adaptive mechanisms could also include indirect root system effects on shoot attributes including leaf size, capacity to orient leaves, or stomatal conductance. The former attribution suggests heritable root traits enhance supply of water. The latter inference, of indirect root effects on shoot activity, invokes whole plant growth regulation effected by root systems. Critical investigations provide the evidence required to discern direct and indirect effects of root function on whole plant growth.

Growth under Deficits

The significance of root effects on plant growth under deficits is demonstrated by grafting studies (69) of common bean cultivars under drought. Growth response varied with gene expression in root rather than shoot organs. Do critical root attributes relate strictly to water supply functions, or do roots signal adaptive growth responses in shoots? Torrey (65, p. 443), in a review of root hormones, outlined recognition of active growth regulation by roots: “Although the detailed mechanisms remain to be worked out, in many cases it seems that changes in the root environment modify the hormone production in the root,

change the export of hormone via the xylem sap to the shoot, and thereby elicit changes in the shoot."

Sorting out the interactions of substrate supply and hormone signals confounds research in growth regulation. We review experimental evidence of active root regulation of shoot process under deficits. By deficits, we refer to relative substrate supply, scaled to the minimum or critical nutrient concentration in plants at which growth is near maximal (66). The particular value of growth substrate sufficiency is dependent upon supply of other nutrients and numerous environmental factors (6, 67).

BEYOND HYDRAULICS Plant water deficits are commonly thought to restrict many plant growth processes (17) i.e. reducing turgor pressure driving cell expansion in roots (28). Gowing and colleagues (27) reported split-root experiments that extend water deficit effects beyond the hydraulic growth model. These studies demonstrate reduced shoot growth in the presence of root but not leaf water deficits. An ample supply of water was maintained for only one half of clonal apple (*Malus* × *domestica*) root systems while the soil of the other half was permitted to dry. Root water deficits in the dry soil resulted in reduced shoot growth, relative to growth with adequate water supplied to the entire root system, though water supply was sufficient to avoid leaf water deficits in all cases. Shoot growth rates recovered either with rewatering or by excising roots in the dry soil. Results were attributed to chemical inhibition of leaf initiation and expansion that appeared to emanate from roots in the dry soil.

Further evidence for root signals, beyond known hydraulic processes, relates to stomatal regulation, critical to water loss and photosynthesis. Gollăn and colleagues (25) demonstrated root effects on stomatal regulation that are not explained by hydraulic models of leaf water status. High leaf turgor was maintained independent of low soil matric potentials by supplying positive pneumatic potentials to the soil water in sealed soil chambers. This condition affected limited water supply without loss of leaf turgor. Stomatal responses to soil desiccation were virtually identical to those observed for water deficits at atmospheric pressure. The similarity of stomatal responses, independent of leaf turgor, was attributed to chemical signals from roots. Depressed growth of wheat (*Triticum aestivum*) seedlings in soil with increased mechanical impedance was also attributed to a hormone signal induced in wheat roots (45).

These experiments provide clear evidence for root signals regulating shoot activity by demonstrating shoot responses to root water deficits when water supply to the shoot is not limiting. Plausible mechanisms are proposed for synthesis and transport of hormones known to induce stomatal closure and growth inhibition.

Davies & Zhang (17) described a positive root signal involving abscisic acid (ABA) synthesis and accumulation in roots that was postulated to be a sensitive measure of root water status. Abscisic acid transport via the transpiration stream to sites of evaporation in epidermal cell walls, adjacent to stomatal guard cells, could effectively modify stomatal conductance and cell wall extensibility. Xylem sap, collected from sugarcane (*Saccharum* spp.) of increasing size, altered stomatal conductance of excised leaf strips (46). Delivery of K^+, Ca^{2+}, ABA, and zeatin riboside (a cytokinin) decreased with plants of increasing size. Patterns of cytokinin and K^+ delivery are consistent with a role in size-dependent regulation of stomatal conductance. Cornish & Zeevaart (15) suggested ABA also regulates plant water status by altering hydraulic conductance of roots and ion flux via direct action on membranes. Other chemical signals emanating from roots could include other cytokinins and strong ion differences, which could regulate diffusion of ABA sequestered in leaf chloroplasts by altering pH of leaf tissue (17).

The case for active root regulation of whole plant growth under water deficits is clear. Controlled experiments demonstrate that root water deficits diminish shoot growth (27) and stomatal conductance (25), despite full leaf turgor. A mechanism postulated for root signals of water deficits involves root tip synthesis of ABA, in proportion to turgor pressure, and translocation to epidermal cells adjacent to stomatal guard cells, the action site for stomatal closure (17). This postulate predicts that the ABA content of root tips represents a signal or "forecast" of water availability (51a), with subsequent regulation of shoot activity.

NUTRIENT PATCHES Nutrient deficits alter plant use of assimilated carbon in favor of root growth, while resulting in diminished specific nutrient uptake capacity (55). These plant processes could simply represent consequences of diminished nutrient supply on constitutive growth processes. However, recent evidence demonstrates that nutrient uptake and use are subject to a high degree of active regulation. Root signals appear linked to regulation of active nutrient uptake and of sink strength for nutrient utilization.

Regulation of active transport processes in sorptive roots appears to involve substrate supply and gene expression. Active uptake of nitrate by initially N-starved maize roots was induced by a minimum of six hours' exposure to substrate (32). Induction is apparently dependent upon nuclear DNA–coded RNA synthesis and appears to be subject to feedback regulation by root N-concentration. The involvement of gene expression in N uptake is supported by heritability among seven inbred lines of maize; activity ranged from 44 to 88 μmol NO_3^- g^{-1} fresh weight for six-day-old corn seedling roots (49). Differences among genotypes were not correlated with observed differences

in root morphology. The requirement for gene expression is a particularly significant indicator of active regulation (40a), discussed in the next section.

Active uptake of growth limiting nutrients appears to be regulated at multiple sites, subject to substrate supply, plant nutrient status, and involving gene expression. Hommels and coworkers (33) investigated macronutrient uptake and growth responses of two *Taraxacum* microspecies differing in adaptations to nutrient supply. Ion accumulation beyond the critical nutrient concentration, or "luxury" consumption, was related to regulation of uptake and storage capacity. Nitrogen uptake appeared regulated by growth requirements, with luxury consumption ranging from 10 to 20% for a microspecies adapted to infertile soils. The adapted microspecies exhibited a greater degree of luxury consumption of P and K, exceeding 70%. Genetic differences in physiologic adjustment of uptake capacity suggest that nutrient uptake is subject to active regulation, perhaps in proportion to nutrient deficiencies.

Rapid physiologic adjustment of root uptake activity in the presence of a local supply of a limiting soil nutrient (PO_4) for three desert perennial species was attributed to adjustment of the potential capacity (V_m) for a phosphate carrier (36). Plant nutrient status appears to play a significant role in regulation of vesicular arbuscular mycorrhizal infection (47). Infection of P-deficient sudangrass (*Sorghum vulgare*) coincided with reduced root membrane permeability and increased root exudation (29).

Preferential root growth under nutrient deficits appears to be subject to active growth regulation. Simpson and colleagues (56a) observed a high degree of N cycling among roots and shoots of N-deficient wheat during exponential vegetative growth. This observation contradicts a common hypothesis that roots make first use of growth-limiting nutrients, with surplus nutrients exported to shoots (55). Using mass balance techniques, Simpson and coworkers (56a) concluded 79% of net N uptake by roots cycled from shoots to roots prior to incorporation in shoot growth. The dynamic pool of N accounted for up to 18% of total plant N. The high proportion of mobile N, despite deficiencies, suggests rates of nutrient utilization in root and shoot apices are regulated by factors beyond the supply of substrate.

Regulation of shoot sink strength for N is thought to involve root synthesis and transport of cytokinin via the transpiration stream (42). Partial excision of bean roots led to a decrease in shoot cytokinin content and suppression of shoot growth (12). Exogenous cytokinins delayed the growth retardation induced by N deficiencies (41). Samuelson and coworkers (55) observed transient increases in root and shoot cytokinin (zeatin riboside) levels upon changes in N supply or with luxury consumption, and postulated a role for cytokinin in establishing relative sink size. Increased synthesis of cytokinin, induced in

part by use of NH_4^+-N, is thought to effect N-enhanced tillering in wheat (68). Sugiharto and colleagues (58a) verified a role for cytokinin in establishing shoot utilization of N. Exogenous cytokinin was required for N-dependent accumulation of mRNA for biosynthesis of the C_4 photosynthetic enzymes phospho*enol*pyruvate carboxylase (PEPC) and carbonic anhydrase (CA) in excised maize leaves. Cytokinins enhance gene expression for other proteins, including the small subunit of the photosynthetic enzyme Rubisco (58a). Cytokinin regulation of N-dependent biosynthesis of critical photosynthetic enzymes provides a mechanism for root hormonal regulation of shoot growth response to N, as roots are thought to be a primary site of cytokinin synthesis (67a). Active root regulation of whole plant growth response to N is suggested by a role of cytokinin in establishing shoot sink strength for N. Excised maize leaves required exogenous cytokinin to induce N-dependent biosynthesis of critical photosynthetic enzymes (58a). Cytokinin synthesis is thought to occur primarily in root tips (67a). Active regulation of carboxylase activity in C_3 and C_4 systems, in response to nutrient supply, can modify whole plant growth rates. Root regulation of carboxylase activity is particularly significant, for these photosynthetic enzymes are important determinants of assimilation capacity and stomatal function (16, 20). Nitrogen-dependent regulation of photosynthetic enzymes by cytokinin, originating in root tips, provides a mechanism for growth regulation by roots that links transport of nitrogen, carbon, and water in the soil-plant-atmosphere continuum.

Growth Regulation and Control Systems

Sufficient evidence exists to identify an active role for root systems in whole plant growth regulation in the case of water and nitrogen deficits. The evidence indicates that regulatory mechanisms operate at multiple structural scales: from transcriptional control of photosynthetic enzyme biosynthesis to root signals modulating stomatal resistance to CO_2 and H_2O fluxes. This evidence supports an expanded view of root function that includes supply of "information" as well as water and nutrients for whole plant growth. Features of hormonal growth regulation are illustrated in the case of photosynthetic enzyme biosynthesis.

Regulation of enzyme biosynthesis and stability is a significant form of metabolic control (40a). The potential capacity (V_m) of an enzyme system, subject to degradation, can be regulated by net rates of biosynthesis and degradation. Sugiharto and coworkers demonstrated that biosynthesis of the photosynthetic enzymes PEPC and CA is regulated by nitrate and cytokinin (58a) in detached maize leaves. Both nitrate and the cytokinin zeatin enhanced the stability of mRNA required for synthesis of PEPC and CA. Nitrogen-dependent induction of mRNA transcription resulted from application of either zeatin or benzyladenine, a synthetic cytokinin. The pool size of mRNA, subject to

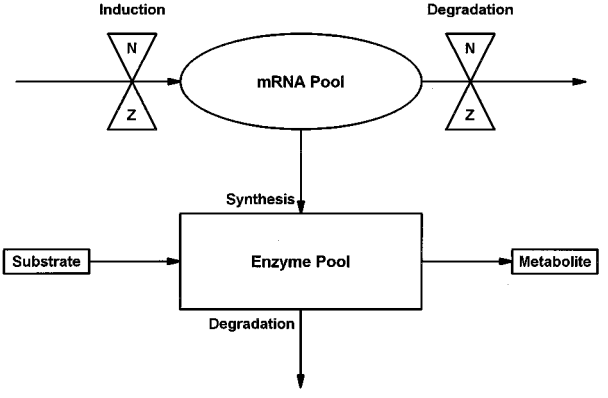

Figure 1 Regulation of enzyme potential by induction and degradation of mRNA regulator pool. Nitrate (N) and zeatin (Z) induce transcription and enhance stability of mRNA for the C_4 photosynthetic enzymes PEPC and CA (58a). Synthesis of PEPC and CA is thought to be proportional to the size of the corresponding mRNA pools (after Kramer & Boyer, 40a).

induction and degradation, serves as a regulator of enzyme capacity (Figure 1). Regulatory control is amplified when enzyme capacity is also subject to degradation. Dynamic regulation of metabolic activity can result from signals acting on biosynthesis and stability of constituent enzyme systems.

The molecule capable of inducing changes in biosynthesis or degradation of either a regulator pool, such as mRNA, or an enzyme pool, such as PEPC or CA, constitutes an effective "signal" in the regulatory system (40a). The signal function of hormones is clear. However, nitrate, a growth substrate, also serves as a signal molecule regulating metabolic activity. Nitrate enhances the stability of mRNA for PEPC and CA, providing a positive feedback signal for biosynthesis. Nitrate is capable of inducing biosynthesis of nitrate reductase, an enzyme mediating a necessary reduction reaction prior to amine formation (40a), and is thought to be capable of inducing active uptake processes in roots as well (32). The nitrate reductase system appears responsive to substrate flux rather than tissue concentration (40a), indicating root uptake and transport of substrate constitutes a signal for shoot metabolism.

Kuiper (42) proposed a coordinated phytochrome-cytokinin growth regulation system responsive to a variable supply of nutrients and light. In this model, mineral sufficiencies promote root growth; subsequent cytokinin synthesis in roots promotes protein and chlorophyll synthesis in shoot. Phytochrome induction of nitrate reductase and mediation of nitrate transport from storage to metabolic pools (3) provides a mechanism for feedback signals regulating

nutrient cycling and metabolism. Conclusive evidence of hormone regulation of N-mediated growth responses requires further investigation to identify factors regulating N cycling between root and shoot under N-limited growth (14). The role of cytokinins in establishing sink strength and the effects of root synthesis of cytokinin on shoot synthesis and subsequent responses can only be understood in the context of signal transduction within whole plants (40a, 55).

Systems regulated by feedback control, illustrated in the case of enzyme biosynthesis, exhibit stability in the face of fluctuating external conditions. Feed-forward control, demonstrated by root signals of soil-water deficits (51a), prior to shoot deficits, conveys further stability to systems regulated by feedback control. It is noteworthy that evidence of feed-forward control is clearer in the case of growth response to water deficits, whereas feedback control appears to dominate growth responses to nutrient deficits. Hommels and colleagues (33) proposed nutrient uptake is regulated relative to a "set point" or plant nutrient status intermediate between critical and toxic nutrient concentrations. Further investigation of regulatory mechanisms, including threshold conditions, signal processing, and the dynamic response of the regulated process to signal inputs, is required at scales ranging from molecular to whole plant to describe the structure of growth response to water and nutrient deficits.

DEFICITS, NETWORKS, AND SIGNALS

A growing body of evidence indicates root signals convey "information" to shoots that can modulate whole plant growth processes. The signaling system appears to involve known shoot responses to growth regulators, thought to originate in meristematic tissue of growing root tips. A dynamic distributed network of roots is thought to sense soil attributes and provide growth regulating signals to shoots. We review current knowledge of root function that is relevant to the root signal hypothesis.

First, we review the conventional model of root function: diffusive flow of water and solutes to and from a sorptive root segment (10, 50). Next, we consider root tips as dynamic sensory organs whose growth trajectories define the time and duration of root segments occurring within the soil profile. Finally, we illustrate the problem of analyzing dynamic root growth and activity using in situ observations of root system development under water deficits.

Cylindrical Flow

Root sorptive function is typically quantified as diffusive flow of water and solutes from a cylinder of soil to the surface of a root segment, proportional to gradients in water and ionic activity. The inner cylinder corresponds to the root surface, with characteristic diameter, permeability, thermodynamic state, and

active uptake capacities. The outer cylinder corresponds to the porous media, with characteristic diameter, diffusivity, distribution of thermodynamic states, and supply capacities. The cylindrical diffusion model indicates water uptake per unit of carbon is maximized for small root diameters, because assimilate requirements of root synthesis and maintenance decrease more rapidly than sorptive capacity as root diameters decrease. Field sampling of irrigated corn roots corroborates this view, as the frequency of roots with progressively larger diameters decreased beyond the smallest 140 μm size class (RM Aiken & HJ Farahani, unpublished observations). Radial permeability of roots decreases with age (48) as impermeable suberin is deposited in the endodermal cell walls during secondary development (50). Active uptake of ions by chemiosmotic pumps (42) and carrier mechanisms maintain low ion activity at the soil-root interface, driving diffusive flow from the bulk soil solution to the root surface. Discontinuities between aging roots and the walls of root channels in soil alter radial resistances to fluxes of ions and water, exacerbating uncertainties of root uptake (50, 51).

Root maps and spatial analysis of roots in field environments invalidate simplifying assumptions of uniform root distributions common to many models. Clustered root distributions result from preferential root growth along pedon faces and biopores (43), and from restricted root growth in regions of compacted soil (59). Heterogeneous root distributions reduce the fraction of soil subject to depletion by root activity. Tardieu (60) found that horizontal gradients in soil water, resulting from differential rooting intensities, exceeded vertical gradients between soil layers, limiting the utility of one-dimensional models of root water extraction.

Root uptake efficiency is influenced by the spatial arrangement of root segments. The depletion zone for water or solutes surrounding a root segment is proportional to the effective diffusivity of water or solutes and to time (10). Overlapping depletion zones, reducing the catchment area for individual roots, are more likely to occur for roots clustered in biopores or along pedon faces than for isolated depletion zones surrounding uniformly distributed roots. Passioura (50) inferred from flow geometries that the time constant for soil-water depletion increased as constraints to root growth, imposed by soil structure, shifted from cubic to prismatic or slab or biopore geometries. Ehlers and colleagues (19) verified in the field that theoretical root water uptake, assuming simplified flow geometries, substantially overestimated observed uptake rates.

The soil environment sensed by root systems is circumscribed by the spatial coordinates and the temporal occurrence of active root segments: the dynamic soil-root interface. We have seen that preferential growth of roots along pedon faces and biopores is a strong determinant of root distribution and subsequent

uptake activity. Since root-branching networks result from meristematic activity of root tips, we turn to intriguing features of this dynamic root element.

Spherical Signaling System

The growth activity of root tips is critical to dynamic root function, as spatial and temporal changes in root distribution are defined by the growth trajectories of root tips. Critical parameters of the cylindrical flow model of root sorptive properties are conditioned by root tip characteristics: diameter, position in the soil matrix, and initial permeability. Subsequent root functions can be inferred from these factors as permeability declines over time with suberin deposition, and driving gradients across the soil-root interface and along root axes are spatially dependent. Root growth capabilities augment dynamic root responses to changes in the spatial distribution of water and nutrients.

Multiple soil factors influence lateral root initiation, growth rates, and trajectories [see Lucas (44) for review]. Lateral root growth is favored by nitrate availability (55), can be stimulated by slight mechanical pressure (20 to 50 kPa; 26), the but is restricted by ABA (7). Turgor-driven cell elongation is proportional to the hydric status of adjacent soil (28), but is reduced several-fold by soil mechanical resistance (5, 18, 51). Tardieu & Pellerin (61) observed an eightfold variation in the horizontal component of maize nodal root trajectories. Mean soil temperature at 100°C-days after emergence accounted for variation associated with effects of location, year, mulch, and sowing date on growth trajectories. Root proliferation, led by meristematic activity of root tips, is subject to a host of environmental factors.

Root tips are endowed with a host of sensory functions as well as growth capabilities. The well-known gravitropic sensory system is reviewed by Lucas (44). Fortin & Poff (22) demonstrated a thermotropic system in maize seminal roots, with gravitropic response offset by thermal gradients of $4.2^{\circ}C\ m^{-1}$. The hydric status of root tips is closely coupled with the adjacent soil sphere, insulated from the sorptive regions of young root segments by axial resistance imposed by cross-walls of early metaxylem vessels (23). Mucilage, formed at root tips from decomposed statolyths of epidermal cells, enhances root continuity with soil water while buffering potentially toxic ion concentrations (44). Hypothesized functions of mucilage include mediating extracellular recognition processes with rhizoflora, and generating surfactants that enhance water uptake capacity (50). Chemical sensing capability of root tips is proposed as an integral form of iron nutrition (53). Root tips are also thought to be capable of synthesizing growth regulators including ABA and cytokinin (65, 67a); combined with abundant sensory function and a strategic role in dynamic change in root distributions, root tips appear to form the nexus of a root sensing system conveying signals the soil environment capable of regulating whole plant growth.

A Root Chronosequence under Water Deficits

Detailed observations of root systems over the growing season illustrates the dynamics of root system function (1). Advances in micro-videography permit nondestructive video-recording of root intersections with clear polybutyrate tubes (minirhizotrons), installed in the soil matrix (2). Repeated observation of roots and collateral measure of soil water, by neutron thermalization, permit in situ quantification of root growth and soil water uptake.

The timing of water deficits alters the spatial pattern of root system development. Maize root distributions, at mid-vegetative growth (eight mature leaves), are depicted for two growing seasons when controlled water supply was deficient (Figure 2*a*) or sufficient (Figure 2*b*). Vertical root proliferation directly below crop rows (0.4 and 1.1 m soil position) was evident at the 0.5 m soil depth when developed under water deficits (Figure 2*a*). Few roots occur directly under furrows (0.0–0.3 m, 0.6–0.8 m soil position). This distribution is thought to result from a form of apical dominance exerted by seminal roots, inhibiting lateral root initiation. Elevated ABA levels in roots, a likely consequence of soil-water deficits, can inhibit lateral root initiation (7, 65). Preferential root proliferation in the vertical direction could enhance ecological fitness under water deficits as lower soil layers may be more likely to retain residual water supplies than upper soil layers. A more homogeneous root distribution, relative to soil position, occurred under water sufficiency (Figure 2*b*), with rooting depth extending to 0.9 m. Presumably this reflects a number of widely dispersed lateral roots growing vertically into soil layers at similar growth rates.

Geostatistical tools extend the spatial analysis of root distributions beyond the limiting assumption of random distributions. These tools quantify the scope and magnitude of spatial autocorrelation, e.g. the likelihood of observing similar

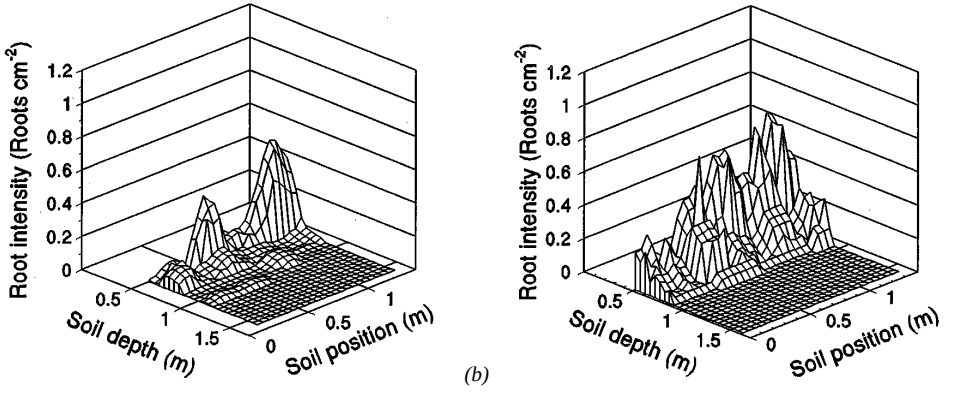

Figure 2 Spatial distributions of maize rooting intensity at mid-vegetative growth stage, grown with deficient (*a*) or sufficient (*b*) soil water supply.

Table 1 Geostatistical descriptors of maize root spatial structure with controlled growth stage water deficits

Growth stage	Water supply[a]	Semivariance model[b]	Variance[c]			Range[d] (m)	Coefficient of Det. (R^2)
			Nugget	Structural	N/S		
Vegetative	Suf.	Linear	0.142	–	–	–	0.09
Anthesis	Suf.	Spherical	0.232	0.282	0.82	0.45	0.26
Grain fill	Def.	Spherical	0.274	0.362	0.76	0.31	0.68
Vegetative	Def.	Spherical	0.018	0.029	0.62	0.79	0.31
Anthesis	Def.	Exponent	0.086	0.139	0.62	0.30	0.36
Grain fill	Def.	Exponent	0.121	0.243	0.50	0.21	0.78

[a]Sufficient (Suf.) or deficient (Def.) water supply is relative to 50% soil water holding capacity in rooted soil.
[b]A nonlinear model of variance as a function of distance separating observation points.
[c]Nugget and structural variances reflect expected degrees of randomness at small and large spatial scales. The ratio of nugget to structural variance (N/S) is an inverse index of spatial correlation.
[d]Refers to the spatial scale of autocorrelation.

rooting intensities among nearby locations. Spatial distribution of roots developing under vegetative water deficits exhibited autocorrelation with a range of 0.8 m at mid-vegetative growth (Table 1), confirming visual assessment of cyclic row:inter-row variation in rooting intensity. The random, but homogeneous proliferation of roots, given sufficient water supply, indicates more extensive root branching—tending to widely dispersed lateral root growth. Root clustering at anthesis and grain-fill growth stages is indicated for both deficient and sufficient growing conditions by spatial autocorrelation ranging from 0.21 to 0.45 m. A higher degree of root clustering for root systems developing under vegetative water deficits persists through grain fill growth stages, diagnosed by a lower ratio of nugget to structural variance, an inverse indicator of autocorrelation.

Root clustering can reduce the effective volume of soil explored by roots in early proliferation phases (10, 43, 50, 59). The scope of root exploration is quantified as the fraction of soil included in "depletion zones," scaled by the distance separating individual roots (Figure 3). Fourteen days after initial root

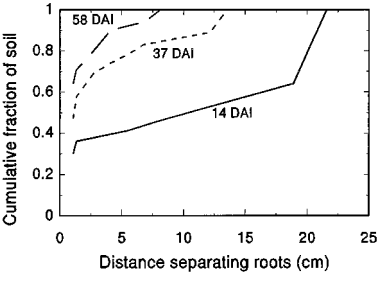

Figure 3 Cumulative fraction of soil subject to root extraction, scaled by distances separating roots. Distributions correspond to observations made 14, 37, or 58 days after the first intersection (DAI) of maize roots with horizontal observation tubes.

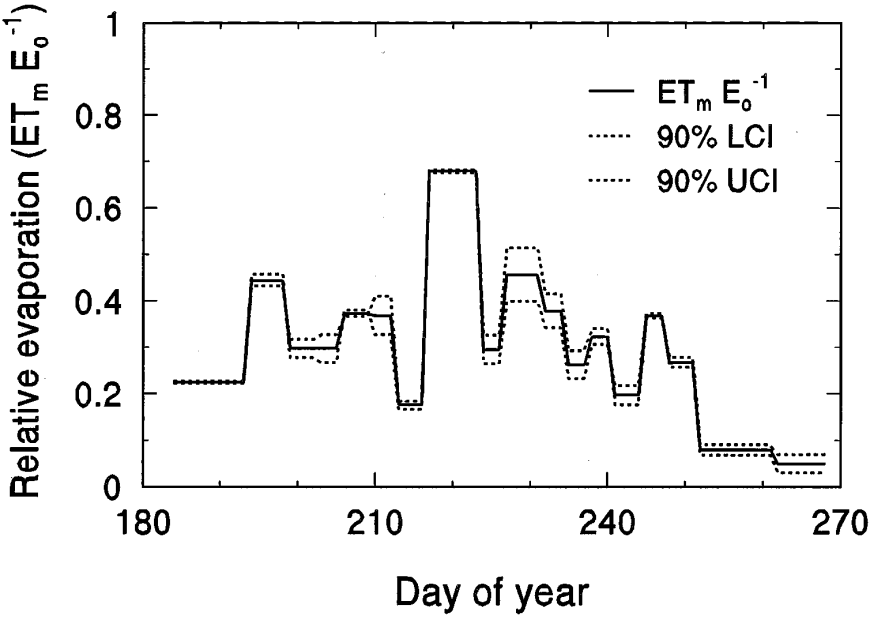

Figure 4 Ratio of mean daily evapotranspiration (ET_m) to mean daily potential evaporation (E_o) for maize growing strictly on stored soil water. Lower and upper 90% confidence intervals (LCI, UCI) refer to ET_m.

appearance, only 40% of the soil volume occurred within 3 cm of a root (root separation distance of 6 cm or less). Consequently, the diffusive path length for 60% of the soil volume exceeded 3 cm, considered the effective limit of root sorption (35). After 37 days of root proliferation, the fraction of soil subject to depletion by roots increased to 75%, reaching 90% by 58 days. Horizontal gradients in rooting intensity limit the effective volume of soil subject to uptake by root networks (60). The timing of seasonal water deficits alters the spatial pattern of root proliferation and clustering, affecting the scope and intensity of soil exploration by the root system, and quantity of water and nutrients available for plant growth.

The timing of root proliferation appears closely linked to changing water supply and plant response to evaporative demand. Detailed sequential observation of root and water distribution, in situ, under water deficits corroborates controlled experiments demonstrating effects on shoot transpiration activity. Successive water deficits from mid-vegetative through grain-fill growth stages are indicated by water extraction well below atmospheric demand, indicated by the ratio of actual to potential evapotranspiration (Figure 4). Fluctuations in

this ratio illustrate changes in water availability as roots grow into and deplete water in successive soil layers.

The synchrony of root proliferation and water uptake for roots growing strictly on a stored supply of water is depicted with respect to soil depth and soil position (Figure 5). Pre-anthesis water uptake (Figure 5*c*) was limited to the rooting depth of 1.3 m (Figure 5*a*) and predominately occurred at soil positions 0.3 and 1.2 m, where roots and available water were both present. Water uptake during this period was insufficient to meet evaporative demand (Figure 4). Subsequent root proliferation (Figure 5*b*) into wet soil below 1.3 m reduced the water deficiency, with the predominant supply derived from soil below 1.3 m (Figure 5*d*). The tendency of root clustering, observed for vegetative growth

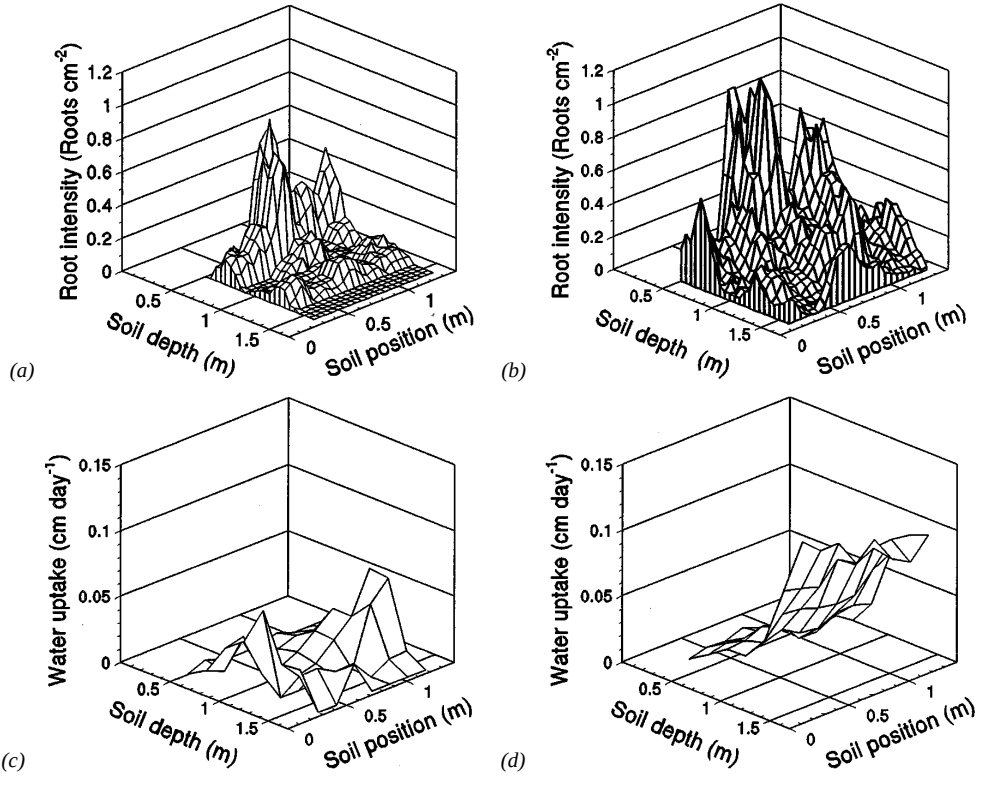

Figure 5 Spatial distributions of maize rooting intensity prior to anthesis (*a*, day 210) and at anthesis (*b*, day 217). Corresponding distributions of main daily water uptake, integrated over seven-day intervals prior to anthesis (*c*, days 210–217) and during anthesis (*d*, days 217–224). The root systems developed in a Spinks sand on stored soil water without supplemental rainfall or irrigation.

under water deficits (Figure 2*a*), persisted through anthesis (Figure 5*b*). Spatial patterns of root proliferation are dynamic, altering supply of growth factors with implications for plant growth and development.

INTEGRATED PLANT GROWTH ANALYSIS

Predicting the fate of assimilates and of subsequent growth of root and shoot in the presence of fluctuating supply of water and nutrients proves to be an elusive task. Root growth responses to nutrient patches and growth signals in the presence of a drying soil may guide answers to questions of plant growth response to deficits. When do specific root and leaf initials form and develop? What is the extent and direction of tissue growth? Does the form of growth enhance the fitness of the organism? We review implications of active growth regulation by roots for whole plant growth and consider the consequences for ecological fitness.

Phasic Plant Development

Developmental models of root growth name root segments according to anatomical origins (54). Klepper and coworkers (39) demonstrated the correlation of wheat nodal root and leaf initiation with a thermal measure of time. The sequential development of nodal and lateral roots of monocots appears to be coordinated by a biological clock marking a thermal measure of time (52). The length of the thermal time interval, or plastochron, between formation of successive plant developmental units, or phytomers (nodes, internodes, leaves, root buds, tiller buds), appears to be regulated by environmental factors such as day length and thermal extremes (31), as well as by the plant genome (38).

Despite ambiguities, the plastochron suggests a rational basis for predicting the onset and duration of root development, defining the period of time when environmental conditions modify growth processes for individual phytomers. Klepper (40) illustrated the synchrony of first- and second-order lateral root branching, commencing 2.5 plastochrons after root axis emergence. The timing and duration of phytomer development permits morphometric analysis of environmental growth determinants. The influence of soil temperature on the growth trajectories of nodal root axes was limited to the initial 50- to 100°C-days following axis initiation (61). The color pattern of wheat leaves infected, via root axes, with Cephalosporium stripe demonstrates that the activity of a specific root segment is directly connected to a corresponding leaf (40). Effects of environmental stressors on growth of individual phytomers may be assessed with greater precision considering the synchrony of phasic plant development. We infer consequences of growth under substrate deficits from physiological arguments based on optimality.

Optimal Growth

Physiological trade-offs (63) are implicit in the optimality view of growth regulation. Nitrogen limitations can constrain whole plant growth by reduced leaf photosynthetic capacity (67). Increased N supply by root proliferation in N-rich nutrient patches can increase specific leaf photosynthetic capacity. Hilbert (30) postulated that whole plant growth is maximized, or optimized, when the marginal costs of assimilates required for an incremental increase in shoot N concentration is equivalent to marginal gain in assimilation rates resulting from that increment of shoot N concentration. This criterion for optimal growth response to limiting substrate joins the principle of compensatory growth with cost-benefit analysis (24), indicating root proliferation in nutrient hot spots can compensate for reduced leaf expansion by increasing leaf photosynthetic capacity via nutrient supply. As we have discussed, regulation of these growth processes are thought to involve root : shoot signals and internal N cycling.

Proportionate growth regulation, a form of feedback control, is implicit in the optimality view of plant growth response to supply of a limiting nutrient. The growth response to supply of a limiting nutrient is proportionate to both supply intensity and to the magnitude of the nutritional deficit. Physiological adjustment of active nutrient uptake, of symbiotic VAM infection, and of lateral root initiation all represent proportionate growth responses to nutrient supply. The precise role of root signals and hormones in regulation of proportionate growth requires further investigation.

Together, phasic development and optimal growth considerations provide complementary views of whole plant growth and development. Phasic development theory relates the synchrony of leaf and root development to thermal time, indicating when growth of a leaf and root segment may be subject to environmental stressors. Optimal growth theory relates environmental stress effects on leaf or root growth to specific shoot and root uptake activity. An expanded view of root function further postulates active hormonal regulation of growth under deficits, signaled by a root sensing system. An integrated analysis of whole plant growth may yield inference of timing, duration, and magnitude of growth in response to fluctuating environmental conditions. To evaluate improvements in fitness conferred by a particular set of growth responses, we turn to an emerging theory of ecological succession.

Depletion Theory and Ecologic Fitness

Tilman (63) applied the principle of differential growth to the problem of population dynamics in successional ecosystems. Simply put, differential growth of root, stem, and leaf organs stratifies a given set of plant species according to their capacities to absorb critical growth substrates, such as light, water, and

nutrients (62). At equilibrium, the capacity to deplete a critical growth factor beyond the limiting level required by species differing in growth attributes is hypothesized to drive reproductive success among species in nutrient-limiting successional ecosystems. A priori predictions of equilibrium levels of nutrient depletion derive from models, differing in complexity, considering nutrient uptake kinetics, growth response, nutrient partitioning, senescence, and predation (63).

Pairwise competition experiments among prairie grasses demonstrated competitive displacement by species capable of greater soil N depletion, determined in independent monoculture experiments (64). However, Caldwell (10) argued that ecological fitness is conferred by dynamic uptake and growth responses to fluctuating nutrient patches—a preemptive form of resource competition. Equilibrium levels of nutrient depletion and dynamics of preemptive nutrient uptake represent distinct adaptive strategies that may confer ecological fitness. An integrated analysis of whole plant growth should describe the essential features of both growth patterns. Such analysis may guide critical field investigations required to resolve these compelling questions of ecological fitness. Applications to pest management and the stability of managed ecosystems are likely to follow.

Integrated analysis of whole plant growth considers regulated growth response to deficits, at structural levels ranging from molecular to ecosystem. Biological hierarchies occur in temporal as well as structural domains (47a). The growth regulation processes reviewed here differ in the time scale of their constituent rate processes. Transient leaf water deficits induce stomatal closure within seconds, whereas soil-water deficits, which may be forecast by root signaling systems, develop on the order of days. Phasic development appears scripted to a biological or thermal clock, whereas ecological succession is scaled to the life cycles of component species. Behavior observed at the ecosystem scale can represent an integration of processes identified at lower levels of structural and temporal domains (63).

CONCLUSIONS

Regulatory processes condition balanced growth of roots and shoots. These processes share similar features with control systems theory. Controlled experiments provide evidence that root signals regulate shoot growth and activity under water deficits. Root signals are thought to include fluxes of ions and growth hormones capable of regulating stomatal activity and enzyme biosynthesis, affecting shoot sink strength for N, photosynthetic capacity and activity, and transpiration. Root tip meristematic activities initiate changes in root distribution, result in synthesis of plant growth regulators, and apparently sense

and signal information regarding soil supply of water and nutrients. Integrated analysis of whole plant growth responses to deficits, at structural levels ranging from molecular to ecosystem, suggests a new suite of investigative tools that may expand our understanding of rhizosphere dynamics.

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