Toxicity and Nutrient Constraints on Root Growth

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Soil acidity, salinity and alkalinity, anthropogenic additions of toxic elements, and deficiencies in soils lead to elemental-induced constraints on root growth and development. Acid soil occupies 3.95 billion ha of the world's ice-free land area (von Uexkull and Mutert, 1995). Poor plant productivity on acid soils is due to combinations of toxicities of Al, Mn, Fe, and H and deficiencies of N, P, K, Ca, Mg, and some micronutrients, e.g., Fe, Zn. The total area of salt-affected soil has been estimated at 952.3 million ha (Szabolcs, 1979). Saline soils contain predominantly chlorides and sulfates of Na, Ca, and Mg, and alkaline soils contain excesses of NaHCO_3 and exchangeable Na. Elements commonly occurring in toxic concentrations in alkaline soils include Na, Mo, B, Se, and bicarbonates (Gupta and Abrol, 1990). Widespread elemental deficiencies (N, P, K, Ca, Mg, B, Fe, Cu, Mn, Mo, Si, Zn) and toxicities (Al, Mn, Fe, S, B, Co, Mo, Cr, Cl, Na) in the world soil are well documented (Baligar and Duncan, 1990; Clark, 1982).

Heavy metals (Cd, Cr, Ni, Pb, Cu, Zn) in soils are usually derived from weathering of underlying parent materials, glacial till or fluvial and other sediments (Table 1). Natural process (gases from volcanic eruption, rain and snow, marine aerosols, continental dust, forest fires) are major contributors of atmospheric inputs of heavy metals (Adriano, 1986; Alloway, 1995a, 1995b, 1995c; Kabata-Pendias and Pendias, 1992). In recent decades, enhanced anthropogenic activities, such as burning of fossil fuel, industrial activities, mining and smelting, automobile exhausts, agricultural amendments (fertilizer, organic manures, lime, slags, sewage sludge), and pesticides, have contributed to the atmospheric deposition of heavy metals to the soil ecosystem (Table 1). Coal-fired power plants generate large quantities of ash and residues. These contain variable levels of heavy metals (Co,

Cr, Cu, Mn, Zn, Cd, As, Pb, Ni). Currently the coal-fired power plants in the United States generate more than 84 million t of residue (Brendel et al., 1997).

During the last century, worldwide use of fertilizers, lime, pesticides, organic manure, sewage sludge, and compost, all of which contain heavy metals, has increased. Disposal of sewage sludge on agricultural soil is now an alternative to land filling. Nitrogen fertilizers lower soil pH and increase the potential for toxicity by naturally occurring Al. Interest in application of sewage sludge to crop lands and in mine reclamation areas has increased considerably in the past few decades. Sludge is a valuable source of plant nutrients (N, P, Cu, Fe, Mn, Zn) and organic matter, but it also contains heavy metals (Cd, Cr, Ni, Pb) that are potentially hazardous to plants, animals, and humans (Alloway, 1995b; Henry and Harrison, 1992; Juste and Mench, 1992). Use of town waste compost, because of heavy annual application rates ($\geq 30 \text{ t ha}^{-1}$) on a yearly basis, leads to a greater accumulation of heavy metals in soil than use of sewage sludge ($\leq 2.5 \text{ t ha}^{-1}$). Under such additions, Cd, Zn, Cu, Ni, Cr, and Pb heavy metals are of primary concern as potential toxicants to plants.

The degree of mobility and bioavailability of heavy metals in soil is influenced by pH, temperature, redox potentials, cation exchange capacity, anion ligand formation, and composition and quantity of soil solution (Alloway, 1995b). At a given pH, the relative mobility of heavy metals in acid soils decreases in the order: $\text{Cd} > \text{Ni} > \text{Zn} > \text{Mn} > \text{Cu} > \text{Pb} > \text{Hg}$. Worldwide, soil acidification has tended to increase as a result of acid precipitation, heavy use of nitrogen fertilizers and organic manures, loss of bases because of increased crop yields, and leaching of bases by nitrate from surface soil. With increased soil acidification, mobility and bioavailability of metals increases. Heavy metals of anthropogenic origin are usually more soluble than those naturally present in soils. Elements such as Pb, Cr, As, and Hg form stable complexes with organic matter and thus accumulate in the top organic layer of soil. Mobility of heavy metals, especially Co, Cd, and Zn, is increasing due to soil acidification.

Mineral excess and deficiency affect growth (dry mass, root : shoot ratio) and morphology (length, thickness, surface area, density) of roots and root hairs. Nutrient deficiency leads to much finer roots, and heavy metal toxicities

Table 1. Source of major heavy metals in soils.¹

Source	Heavy metals
<i>Natural</i>	
Soil pedogenic (Lithogenic)	Most heavy metals
Weathering of underlying parent materials	Cd, Cr, Ni, Pb, Cu, Zn
Glacial till or fluvial sediments	
Gases from volcanic eruption	Cd, Hg, Zn, Cr, Cu, Mn, Ni
Rain and snow	Pb, Cd, Cu, Zn
Marine aerosols (spray/mist)	Cu, Mn, Ni, As, Cd
Continental dust	Mn, Ni, Cr, Fe
Forest fires	As, Cd, Cu, Ni, Pb, Zn, Hg
<i>Anthropogenic</i>	
Fossil fuel combustion	Zn, Cd, Cu, Co, As, Ni, Pb
Fuel oil combustion	Ni, Cu, Pb
Industrial stacks and domestic chimneys	Cu, Ni, Pb, Zn
Automobile (emission, wastes)	Cd, Cr, Hg, Ni, Pb, Zn
Mining and smelting	
Lead industry	Cd, Cu, Pb, Zn
Zinc industry	Cd, Cu, Pb, Zn
Cu/Ni industry	Co, Cu, Mn, Ni, Pb, Zn
Fertilizers	Cd, Cr, Ni, Zn
Pesticides	Cu, Hg
Liming materials	Cu, Mn, Zn
Basic slags	Cd, Ni, Pb
Organic manure	Co, Cu, Zn
Sewage sludge	Cd, Cr, Ni, Pb, Zn, Cu, Mn

¹From Adriano (1986), Alloway (1995a, 1995b, 1995c); Kabata-Pendias and Pendias (1992); Seaward and Richardson (1990).

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stimulate initiation and growth of second- and third-order lateral roots, while the tap roots and first order laterals (seminal/basal) are suppressed (Breckle, 1991).

In this review, the effect of elemental toxicity (Al, Cd, Ni, Pb, Cu, Mn, Zn) and deficiency (N, P, K, Ca, Mg, micronutrients), low soil pH, and salinity stress on root growth and morphology are discussed. No attempt will be made to cover extensive literature published in these areas; our objective is to present an overview of the subject.

ROOT MORPHOLOGY

Root growth and morphology (biomass, number, diameter, length, surface area, and distribution in soil) of tap roots, basal roots, lateral roots, and adventitious (shoot-borne) roots differ between and within species. Monocotyledonous plants have a "fibrous" root system composed primarily of adventitious (nodal) roots that arise from the base of the stem and lateral roots. Roots initiated on the mesocotyl are termed basal (seminal) roots, with the tap root being the first root to emerge from the seed. Each of these three types of roots has lateral branches that in turn may have second or third order branching. Dicotyledonous plants possess a taproot (radicle), basal roots, and often shoot-borne adventitious roots. The basal roots arise from the basal portion of the hypocotyl. These roots have lateral roots and branch into secondary and tertiary roots. Esau (1977), Klepper (1992), Leskovar and Stofella (1995), O'Toole and Bland (1987), and Zobel (1975, 1991a, 1991b) have dealt extensively with various types of monocotyledonous and dicotyledonous roots and root hairs, and their growth and morphology.

ELEMENTAL TOXICITY CONSTRAINTS

Low pH

Plant roots are subjected to a wide range of soil pH, and the effects of pH on roots are often confounded with those caused by other chemical properties of soil (Baligar and Duncan, 1990). Depending on the type of soil and climatic conditions, low pH (below 5.0 in water) frequently causes toxicity (Al, Mn, H) and induces elemental deficiencies (P, Ca, Mg, Zn, Mn, Fe, Mo). Low pH reduces root

mass, length, and root hair formation (Table 2). In Brazilian Oxisols, maximal dry mass of rice (see Table 3 for scientific names of all species cited) roots was produced at pH 4.1, with a significant tendency toward reduction in mass as pH increased (Fig. 1). In wheat and common bean, root mass increased with increasing soil pH to 6.0, then decreased as the pH increased to 7.0. A low pH (4.8) reduced mass and volume of grape roots, and such effects have been reported worldwide (Himelrick, 1991). At a pH below 4.5, watermelon exhibited short or no taproots, and the number of lateral roots increased as the pH increased to 5.0 and above; however, root dry mass decreased with increasing pH from 4.0 to 5.5 (Liu et al., 1994). Stoffella et al. (1991) reported that mass of taproots and all roots of bell pepper seedlings was greater at pH 5.9 than at 4.1 or 7.3; however, pH had no effect on basal or lateral root morphology. Root growth may be directly or indirectly inhibited by high pH (5.0–7.5) depending on plant genotype. In alkaline soils, $\text{NH}_4\text{-N}$ toxicity is a major cause of severe root inhibition (Marschner, 1995).

Aluminum toxicity

Aluminum toxicity is an important root growth-limiting factor in acid soils. Symptoms of Al rhizotoxicity include: stunted roots; poor root hair development; swollen root apices; stubby and brittle roots; less branching; fewer primary and secondary roots; and coraloid, dense and compacted root systems (Table 2) (Foy, 1992). Both species and cultivars within species differ widely in root response to Al toxicity.

Lin and Myhre (1990) reported that root density of sour orange was twice as great when the concentration of Al was $9.14 \text{ mg}\cdot\text{L}^{-1}$ of soil saturation extract (pH 3.7) than when it was $0.13 \text{ mg}\cdot\text{L}^{-1}$ (pH 5.1). Higher Al concentrations ($18 \text{ mg}\cdot\text{L}^{-1}$, pH 3.7) reduced root density, as well as the number of primary and secondary roots and the length of primary roots. In nutrient culture, Lin and Myhre (1991) reported that citrus root growth was retarded at $308 \mu\text{M}$ Al or higher; fewer new laterals and fibrous roots appeared, and root tips become thickened. The root system as a whole appeared coraloid.

Alva et al. (1986) demonstrated that the

sum of the monomeric Al species $[\text{Al}^{3+}, \text{AlOH}^{2+} + \text{Al}(\text{OH})_2^+ + \text{Al}(\text{OH})_3^0 + \text{AlSO}_4^-]$ best predicted root length of soybean, subterranean clover, alfalfa, and sunflower. Application of Ca can ameliorate Al toxicity (Foy, 1992). Such effects are attributed to a reduction in Al activity because of an increase in ionic strength of solution or a direct physiological effect of Ca at root surface. Increasing Ca also reduces Al-induced interference in Ca translocation in soybean (Foy et al., 1969). Adding SO_4^{2-} with Ca to the growth medium may reduce the phytotoxicity of Al in less sensitive species.

Huang and Grunes (1992) reported that increasing the K : Mg ratio from 0.1 to 2.3 on a $\text{mol}\cdot\text{L}^{-1}$ basis at $50 \mu\text{M}$ Al significantly decreased root dry mass, length, and tolerance index for the Al-sensitive wheat cultivar Scout-66, but had no effect on Al-tolerant 'Atlas 66.' Increasing levels of Si ($0\text{--}3560 \mu\text{M}$) at toxic levels of Al ($300\text{--}600 \mu\text{M}$) increased root dry mass and length in sorghum genotypes (Galvez and Clark, 1991). Low concentrations of Al may be beneficial to plants; for example, Al reduces Fe and Cu toxicity (Foy, 1992).

Salinity stress

A saline (accumulated salts) environment imposes osmotic and ionic stress on roots. In osmotic stress, high salt concentration leads to lower water potentials in the soil and eventually causes water stress in roots (Maas and Nieman, 1977). Ionic stress in saline soil is due to high concentrations of Na^+ , Mg^{2+} , Cl^- , and SO_4^{2-} and, in some soils, a toxic concentration of B (Kafkafi, 1991). Salinity reduces root growth and permeability, and consequently reduces water and nutrient uptake. Snapp and Shennan (1992) reported that excess salinity reduced root growth of tomato plants; extensive lateral root die-back occurred in sensitive lines. Crop species show a spectrum of response to excess salt; however, growth and economic yields are reduced in all species when exposed to the same level of salinity. The degree of plant response to salt is influenced by seasonal and climatic variation, and is related to salt uptake and transpiration, as affected by light, temperature, and saturation vapor deficit (Yeo and Flowers, 1992). In general, salinity leads to reduction in mass and length of roots and dieback of laterals (Table 2).

Table 2. Toxicity constraints and their effects on root morphology and growth.^a

Toxicity constraints	Crop species	Effects on roots
Low pH (H)	Grape, pepper, watermelon, sorghum, maize, broadbean	Reduction in mass, length, and volume. Short or no tap roots, reduction in root hairs. Increase in laterals. pH < 4.0 or > 7.0 reduces basal and lateral roots
Aluminum	Cereals, potato, peanut, legumes, cotton, onion, tomato, marigold, sweet potato	Decrease in root length, specific root length, and root mass. Inhibition of elongation of main axis and lateral roots. Stubby and brittle roots. Root tips turn brown. Thickened laterals. Lack of branching. Coraloid root system. Dense and compound root architecture. Increase/decrease in root density. Fewer primary and secondary roots, smaller primary root hairs.
Salinity/alkalinity	Tomato, wheat, barley	Reduction of root mass and length. Die-back of laterals. Reduced root system.

^aFrom Foy (1992), Kafkafi (1991).

Table 3. Common and scientific (Latin) names of plants.

Alfalfa	<i>Medicago sativa</i> L.
Barley	<i>Hordum vulgare</i> L.
Bean-common	<i>Phaseolus vulgaris</i> L.
Beech	<i>Fagus sylvatica</i> L.
Broad bean	<i>Vicia faba</i> L.
Bush bean	<i>Phaseolus</i> spp.
Cabbage	<i>Brassica oleracea</i> (L.) Capitata
Carrots	<i>Daucus carota</i> L. var. <i>sativas</i> (Hoffm.) Arcang.
Clover-subterranean	<i>Trifolium subterraneum</i> L.
Clover-white	<i>Trifolium repens</i> L.
Cotton	<i>Gossypium hirsutum</i> L.
Cowpea	<i>Vigna unguiculata</i> L. Walp.
Gladiolus	<i>Gladiolus</i> sp.
Grape	<i>Vitis</i> sp.
Lupine	<i>Lupinus</i> sp.
Marygold	<i>Tagetes erecta</i> L.
Maize	<i>Zea mays</i> L.
Oats	<i>Avena sativa</i> L.
Onion	<i>Allium cepa</i> L.
Orange-sour	<i>Citrus aurantium</i> L.
Peanut	<i>Arachis hypogaea</i> L.
Pea	<i>Pisum sativum</i> ssp. <i>arvense</i> (L.) Poir
Pepper-bell	<i>Capsicum annuum</i> L. var. <i>annuum</i>
Potato-Irish	<i>Solanum tuberosum</i> L.
Potato-sweet	<i>Ipomoea batatas</i> (L.) Lam.
Radish	<i>Raphanus sativus</i> L.
Rape	<i>Brassica napus</i> L.
Rice	<i>Oryza sativa</i> L.
Ryegrass	<i>Lolium perenne</i> L.
Sorghum	<i>Sorghum bicolor</i> L. Moench
Soybean	<i>Glycine max</i> L.
Spinach	<i>Spinacia oleracea</i> L.
Squash	<i>Cucurbita</i> sp.
Sunflower	<i>Helianthus annuus</i> L.
Tomato	<i>Lycopersicon esculentum</i> Mill.
Watermelon	<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai
Wheat-common	<i>Triticum aestivum</i> L.
Wheat-durum	<i>Triticum durum</i> L.

Heavy metals (Cd, Ni, Pb, Cu, Mn, Zn)

Heavy metal toxicity induces a series of biochemical and physiological alterations in plants. These include damage to the membrane, altered enzyme activities, hormone imbalances, deficiencies of essential nutrients, inhibition of photosynthesis, and alteration in carbon allocations and water relations (Breckle, 1991). Such changes greatly inhibit root growth. Many of the toxic effects of heavy metals are related to replacement of Ca from essential sites on the root cell membrane. Low supplies of Ca and P in soil have a profound effect on metal toxicity. Heavy metals inhibit root extension and interfere with cell division, even at low concentrations, and they also cause root hair collapse and lower density of root hairs (Breckle, 1991). Heavy metal toxicity is associated with browning of roots, collapse and lower density of roots, and a "barbed-wire" appearance of roots (Table 4).

In bush beans, Cd induced structural and ultrastructural changes in the vascular system. The number and size of tracheary elements were significantly reduced (Barcelo et al., 1988). In beech seedlings, Cd in soil reduced growth and extension of primary roots and produced an abnormally compact and branched root system (Breckle, 1991). It reduced the number of first-order laterals, but increased development of second-order laterals. Jalil et al. (1994) reported that increasing the concentration of Cd from 0 to 2 μM reduced root mass

and length of durum wheat. At 14 μM Cd, root growth was reduced by 75%, 65%, 50%, and 40% of control values in white clover, maize, ryegrass, and cabbage, respectively (Yang et al., 1996b).

Excessive Pb inhibits root extension and interferes with cell division, but its main effect is on root cell elongation (Breckle, 1991); Pb also affects root hair density and increases the lengths of second- and third-order laterals (Table 4). Breckle (1991) stated that subtoxic concentrations of Pb appeared to stimulate root growth; in beech seedlings, a Pb concentration of 44 $\text{mg}\cdot\text{kg}^{-1}$ thickened root tips, and concentrations higher than 55 $\text{mg}\cdot\text{kg}^{-1}$ significantly reduced root mass.

Excess Ni causes brown and stunted roots, and reduces root dry mass, length, and root/shoot ratio (Yang et al., 1996a). At 120 μM , root mass was reduced by 26% in white clover and ryegrass, 52% in cabbage, and 70% in maize relative to control values (Yang et al., 1996a).

Barley seedling roots are very sensitive to heavy metals. At 30, 200, and 600 μM Cd, Ni, and Zn, respectively, root biomass was reduced 50% relative to controls (Brune and Dietz, 1995).

Excess Cu and Ni decreased the density of root hairs, coinciding with their earlier collapse (Breckle, 1991; Patterson and Olson, 1983). Increasing concentrations of Mn, Cu, and Zn in the growth medium increased the number of lateral roots and resulted in denser

Fig. 1. Root dry mass of upland rice, wheat, and common bean as influenced by soil pH of an Oxisol (N.K. Fageria, unpublished, 1997).

Fig. 2. Relative dry mass of roots of lowland rice, common beans, corn, and soybean under different N, P, and K fertility treatments in an Inceptisol $N + P + K = 100\%$ (V.C. Baligar and N.K. Fageria, unpublished 1997).

and more compact root systems in legumes (Breckle, 1991). In acid soil, Mn can be toxic to sensitive plants. Manganese can be toxic at higher soil pH (even at pH 7.0) in soils that are poorly aerated or compacted, or both, where reducing conditions favor the production of divalent Mn that plants absorb (Foy, 1992). Unlike Al, Mn seems to affect plant tops more directly than roots, but damage follows when the toxicity is severe (Suresh et al., 1989).

Heavy metals, even at low concentrations, lead to collapse and lower density of root hairs. They inhibit root extension and lead to browning of roots, which is caused by enhanced suberization (Table 4) (Breckle, 1991). Heavy metal toxicities stimulate growth and initiation of second- and third-order lateral roots, while growth of the taproots and first-order laterals (seminar/basal) is suppressed (Breckle, 1991).

Table 4. Effects of heavy metal toxicity on root morphology and growth.¹

Metal	Crops	Effect on Roots	Known phytotoxic levels ($\mu\text{g}\cdot\text{g}^{-1}$ soil)	Leaf concn	
				Sufficient	Toxic
				($\mu\text{g}\cdot\text{g}^{-1}$)	
		<i>Nonessential</i>			
Cd	Oats, barley, wheat, bean, soybean, radish, carrots	Brown and stunted roots. Compact branched root system.	3–8	0.05–0.2	5–30
Ni	Cereals, ryegrass, maize, white clover	Brown and stunted roots. Reduced root mass, length, and root : shoot ratio.	100	0.1–5.0	10–100
Pb	Onion, bushbeans, beech	Brown, short roots. Reduced root extension and root hair density. No effect on radicle and seminal root emergence. Increase in 2nd and 3rd order lateral length. Compact root architecture and branched.	100–400	5–10	30–300
		<i>Essential</i>			
Cu	Cereals, legumes, spinach, citrus, gladiolus	Increase or decrease of lateral roots. Short or barbed wire roots. Denser and compact root system.	60–125	5–30	20–100
Mn	Cereals, legumes, potato, cabbage	Stunted main roots. Increased laterals. Denser and compact root system.	150–3000	30–300	400–1000
Zn	Cereals, spinach, legumes	Injured roots resembling barbed wire. Increased lateral roots. Denser and compact root system.	70–300	27–150	100–400

¹From Adriano (1986); Alloway (1995a); Breckle (1991); Kabata-Pendias and Pendias (1992).Table 5. Effect of essential macro- and micro-element deficiencies on root morphology and growth.¹

Elements	Crops	Effects on roots	Concn in plant		
			Critical	Sufficient	Toxic
				$\text{g}\cdot\text{kg}^{-1}$	
		<i>Macronutrients</i>			
N (NO_3)	Cereals, legume, spinach, tomato	Increase root hair length. Increase, decrease, or no change in root hair density. Less branching.	20	20–50	Nontoxic
P	Cereals, legumes, spinach, rape, lupin, tomato	Longer roots and root hairs. Increased 2nd order laterals. Increased or no change in root hair density. Decreased shoot/root. Induce proteoid roots.	2	2–5	Nontoxic (>10)
K	Maize, cowpea, common bean, rice, barley	Reduced root mass, length. Reduced volume of root axes and 1st order laterals. Complete prevention of 2nd order lateral development.	10	10–50	Nontoxic (>30)
Ca	Cereals, legume, peas, watermelons	Shorter and denser root system. Translucent extensions of main root tips. Growth severely affected. Required for root formation.	1	1–10	Nontoxic
Mg	Rice, common bean, cowpea	Reduced dry mass, increased shoot/root.	1	1–4	Nontoxic
		<i>Micronutrients</i>		$\text{mg}\cdot\text{kg}^{-1}$	
B	Rice, common bean, soybean, wheat, squash	Inhibition or cessation of root elongation. Stubby and bushy appearance.	<10	10–100	>100
Mn	Tomato	Reduction in length of main axis. Complete absence of lateral roots.	10–20	20–300	>300
Fe	Dicots and monocots, lupines	Inhibition of root elongation, increased diameter of apical root zones, and abundant root hair formation. Formation of proteoid roots.	<50	50–250	Nontoxic

¹From Bennett (1993), Fageria et al. (1997), Marschner (1995).

ELEMENTAL DEFICIENCY CONSTRAINTS

Macronutrients (N, P, K, Ca, Mg)

Effects of macronutrient deficiencies on root growth and morphology are summarized in Table 5. Nitrogen stimulated root length in corn in the area of application without affecting total root length (Durieux et al., 1994). Root mass was less affected by N than root

length, and the effect may depend on the stage of maturity of the crop. High rates of application of N reduced root growth and depth of rooting in wheat (Comfort et al., 1988) and reduced root : shoot ratio in rye (Brouwer, 1965).

In corn, the primary root system was 16% thicker when $\text{NH}_4\text{-N}$ was applied rather than $\text{NO}_3\text{-N}$. The $\text{NH}_4\text{-N}$ treatment also increased the diameters of lateral, first- and second-order nodal roots (Anderson et al., 1991).

Teyker and Hobbs (1992) reported that fresh mass of maize roots were similar with $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ treatment, but elongation of the primary root axis and its longest first-order lateral was less with $\text{NH}_4\text{-N}$. In $\text{NH}_4\text{-N}$ treatment, the primary root was 54% thicker than in the $\text{NO}_3\text{-N}$ treatment. We observed (unpublished data) that relative dry masses of roots of rice, common bean, corn, and soybean were reduced by 38%, 56%, 35%, and 11% when N was omitted from a complete fertilizer (Fig.

2). Nitrogen deficiency increases root hair length, increases or has no effect on root hair density, and reduces branching (Table 5).

Phosphorus deficiency increases overall growth of roots and root hair length, increases the number of second-order laterals, and either increases or does not affect root hair density (Table 5). Hackett (1968) showed that shoot and root mass of barley receiving $0.24 \text{ mg}\cdot\text{L}^{-1}$ of P was 50% to 60% less than those of plants receiving $4.6 \text{ mg}\cdot\text{L}^{-1}$, and P deficiency reduced the volume of the root axes and first-order laterals per plant. Romer et al. (1989) observed that a low P supply increased wheat root length. In our study (unpublished data) in an Inceptisol, root dry mass was reduced by 62%, 74%, 50%, and 21% in lowland rice, common bean, corn and soybean, respectively, when P was omitted from a complete fertilizer (Fig. 2); P was the most growth-limiting nutrient for all four crops. In another study under greenhouse conditions, wheat, common bean, and cowpea were grown at varying levels of P (0–200 $\text{mg}\cdot\text{kg}^{-1}$) in an Oxisol (Fig. 3, Fageria et al., 1997). Maximal root dry mass for wheat was achieved at a P level of $152 \text{ mg}\cdot\text{kg}^{-1}$ of soil, whereas maxima for common bean and cowpea were achieved at 130 and $159 \text{ mg}\cdot\text{kg}^{-1}$, respectively. These results show that increasing levels of P generally increased root growth, but excessive levels can inhibit growth, and that crop species differ in their requirements for P to achieve maximal growth.

Proteoid root formation in Proteaceae and Fabaceae is enhanced by P deficiency (Dinkelaker et al., 1995). Exudation of citrate and, to some extent, malate by proteoid roots increases P availability to plants by mobilizing the sparingly soluble mineral P and possibly organic P (Marschner, 1995). Root exudates containing citric, tartaric, and malic acids may also chelate and detoxify Al in the root zone (Marschner, 1995).

A strictly localized proliferation of lateral roots can occur if part of the root system is provided with adequate supplies of P or N (Drew and Shaker, 1975). Scott-Russell (1977) predicted that increased nutrient uptake by the treated portion of the root system would enhance the fraction of metabolites that it received from the shoot. This is evidenced by increased dry matter content before laterals begin to proliferate. Scott-Russell (1977) also speculated that hormones increased transport of metabolites from shoot to the zone of the roots where nutrients are absorbed more rapidly.

Potassium deficiency symptoms have recently increased throughout the U.S. cotton-producing region (Pettigrew et al., 1996). Inadequate levels of K reduced root growth, and consequently yields. A deficiency of K in an Inceptisol reduced root growth by 23%, 30%, 12%, and 11% relative to the controls (adequate N, P, K) in lowland rice, common bean, corn, and soybean, respectively (Fig. 2). On an Oxisol, a 35% lower root dry mass was observed in 13 maize genotypes when K levels were $0 \text{ mg}\cdot\text{kg}^{-1}$ vs. $200 \text{ mg}\cdot\text{kg}^{-1}$ of soil (data not shown). Maize genotypes differed signifi-

Fig. 3. Root dry mass of wheat, common bean, and cowpea at varying P levels in an Oxisol (Fageria et al., 1997).

cantly in root dry mass and length at both low and adequate K levels.

Calcium deficiency affects cell division, elongation, and cell membrane integrity (Foy, 1974), and leads to short roots, a dense root system, translucent extension of main root tips, and severe reduction of overall growth (Table 5). Yan et al. (1992) reported that increased root growth of maize and broad bean was obtained by increasing Ca from 0.1 to 5.0 mM at pH 4.1.

Mg deficiency is rarely observed in the field, mainly because need is low, and most soils have enough to meet plant demands. Fageria and Souza (1991) evaluated effects of Mg levels on root mass of upland rice, common bean, and cowpea in an Oxisol of central Brazil (Fig. 4). Root mass of upland rice was significantly higher at low rather than at higher soil Mg levels, but increase in soil Mg increased root dry mass in common bean and cowpea. Maximal dry mass of roots was achieved at 3.0 and $2.5 \text{ cmol Mg}\cdot\text{kg}^{-1}$ soil in common bean and cowpea, respectively. Higher Mg levels reduced dry mass of roots in all species.

Mineral element deficiency induces considerable variations in growth and morphology of roots (Fageria et al., 1997; Marschner, 1995; Scott-Russell, 1977; Zobel, 1995). Such variations are strongly influenced by plant species and genotypes. Overall the growth of the main root axis is little affected by nutrient deficiency, but that of lateral branches and their elongation rates may be substantially reduced (Drew, 1975). Many plant species produce finer roots when grown at low nutrient supply.

Fig. 4. Root dry mass of upland rice, common bean, and cowpea under varying Mg levels in an Oxisol (Fageria and Souza, 1991).

Fig. 5. Root dry mass of upland rice, corn, common bean, soybean, and wheat under varying B levels in an Oxisol (N.K. Fageria, unpublished).

Micronutrients (B, Cu, Zn, Mn, Fe, Mo)

In highly weathered Oxisols and Ultisols, deficiencies of Zn, B, Mo, and Fe have been reported by Fageria (1992), who also showed that growth of upland rice roots in nutrient culture was reduced at low levels of Zn, Fe, Mo, Cu, B, and Mn. Chairidchai and Ritchie (1993) reported that the response of wheat roots to Zn supply appeared to be pH-dependent. At pH 4.0 to 4.6, roots did not respond to increasing concentrations of Zn; however, at

pH 5.2 root growth increased with increasing Zn concentration. In a Brazilian Oxisol, increasing Zn from 0 to 80 mg·kg⁻¹ increased root mass and length of common bean, soybean, and wheat; however, no such improvements were observed for maize or rice (data not shown). On an Oxisol (Fig. 5), increasing soil B (0–12 mg·kg⁻¹) significantly reduced root mass of upland rice and corn. Root mass of common bean, soybean, and wheat increased at low levels of soil B, but a further increase in soil B reduced root mass.

Clark (1970) did an extensive study on the effect of various degrees of essential nutrient levels (from none to adequate) in root media on root : shoot ratio of maize. Reducing the supply of essential nutrients from full strength to none increased root : shoot ratio in P, Ca, S, and Zn treatments; however, root : shoot ratio decreased in NO₃-N, Mg, Mn, and Ca treatments. Levels of NH₄⁺-N, K, and Fe had no effect on root : shoot ratios.

Literature Cited

- Adriano, D.C. 1986. Trace elements in the terrestrial environment. Springer-Verlag, New York.
- Alloway, B.J. (ed.). 1995a. Heavy metals in soils. 2nd ed. Wiley, New York.
- Alloway, B.J. 1995b. Soil processes and the behaviour of metals, p. 11–38. In: B.J. Alloway (ed.). Heavy metals in soils. Wiley, New York.
- Alloway, B.J. 1995c. The origins of heavy metals in soils, p. 38–57. In: B.J. Alloway (ed.). Heavy metals in soils. Wiley, New York.
- Alva, A.K., D.G. Edwards, C.J. Asher, and F.P.C. Blamey. 1986. Relationship between root length of soybean and calculated activities of aluminum monomers in nutrient solution. Soil Sci. Soc. Amer. J. 50:959–962.
- Anderson, D.S., R.H. Teyker, and A.L. Rayburn. 1991. Nitrogen form effects on early corn root morphological and anatomical development. J. Plant Nutr. 14:1255–1266.
- Baligar, V.C. and R.R. Duncan (eds.). 1990. Crops as enhancers of nutrient use. Academic, San Diego, Calif.
- Barcelo, J., M.D. Vazquez, and C. Poschenrieder. 1988. Cadmium-induced structural and ultrastructural changes in the vascular system of bush bean stems. Bot. Acta. 101:205–282.
- Bennett, W.F. 1993. Plant nutrient utilization and diagnostic plant symptoms, p. 1–7. In: W.F. Bennett (ed.). Nutrient deficiencies and toxicities in crop plants. APS Press, St. Paul, Minn.
- Breckle, S.W. 1991. Growth under stress—Heavy metals, p. 351–373. In: Y. Waisel, A. Eshel, and U. Kafkafi (eds.). Plant roots—The hidden half. Marcel Dekker, New York.
- Brendel, G.F., A.M. DiGiola, Jr., and S.S. Tyson. 1997. Developing an effective CCB marketing program, p. 94–194–23. In: Intl. Symp. on management and use of coal combustion by-products (CCBs): Innovation for a sustainable future. vol. 3. Amer. Coal Ash Assn., Alexandria, Va.
- Brouwer, R. 1965. Root growth of cereals and grasses, p. 153–166. In: F.L. Milthorpe and J.D. Ivins (eds.). The growth of cereals and grasses. Butterworths, London.
- Brune, A. and K.J. Dietz. 1995. A comparative analysis of element composition of roots and leaves of barley seedlings grown in the presence of toxic Cd, Mo, Ni, and Zn concentrations. J. Plant Nutr. 18:853–868.
- Chairidchai, P. and G.S.P. Ritchie. 1993. The effect of citrate and pH on zinc uptake by wheat. Agron. J. 85:322–328.
- Clark, R.B. 1970. Mineral deficiencies of corn. Agrichem. Age 13:4, 8.
- Clark, R.B. 1982. Plant response to mineral element toxicity and deficiency, p. 71–73. In: M.N. Christiansen and C.F. Lewis (eds.). Breeding plants for less favorable environments. Wiley, New York.
- Comfort, S.D., G.L. Malzer, and R.H. Busch. 1988. Nitrogen fertilization of spring wheat genotypes: Influence on root growth and soil water depletion. Agron. J. 80:114–120.
- Dinkelaker, B., C. Hengeler, and H. Marschner. 1995. Distribution and function of proteoid roots. Bot. Acta 108:183–200.
- Drew, M.C. 1975. Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system and the shoot in barley. New Phytol. 75:479–490.
- Drew, M.C. and L.R. Saker. 1975. Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increase in lateral root growth and nitrate uptake when nitrate supply is restricted to only part of the root system. J. Expt. Bot. 26:79–90.
- Durieax, R.P., E.J. Kamprath, W.A. Jackson, and R.H. Moll. 1994. Root distribution of corn: The effect of nitrogen fertilization. Agron. J. 86:958–962.
- Esau, K. 1977. Anatomy of seed plants. 2nd ed. Wiley, New York.
- Fageria, N.K. 1992. Maximizing crop yields. Marcel Dekker, New York.
- Fageria, N.K., V.C. Baligar, and R.J. Wright. 1997. Soil environment and root growth dynamics of field crops. Recent Res. Dev. in Agron. 1:15–58.
- Fageria, N.K. and C.M.R. Souza. 1991. Upland rice, common bean, and cowpea response to magnesium application on an Oxisol. Comm. Soil Sci. Plant Anal. 22:1805–1816.
- Foy, C.D. 1974. Effect of soil calcium availability on plant growth, p. 565–600. In: E. W. Carson (ed.). The plant root and its environment. Univ. Press., Charlottesville, Va.
- Foy, C.D. 1992. Soil chemical factors limiting plant root growth. Adv. Soil Sci. 19:97–149.
- Foy, C.D., A.L. Fleming, and W.H. Armiger. 1969. Aluminum tolerance of soybean varieties in relation to calcium nutrition. Agron. J. 61:505–511.
- Galvez, L. and R.B. Clark. 1991. Effect of silicon on growth and mineral composition of sorghum (*Sorghum bicolor*) grown with toxic levels of aluminum, p. 815–823. In: R.J. Wright, V.C. Baligar, and R.P. Murrmann (eds.). Plant-soil interactions at low pH. Kluwer Academic, The Netherlands.
- Gupta, R.K. and I.P. Abrol. 1990. Salt-affected soils: Their reclamation and management for crop production. Adv. Soil Sci. 11:223–288.
- Hackett, C. 1968. A study of the root system of barley. I. Effects of nutrition on two varieties. New Phytol. 67:287–300.
- Henry, C.L. and R.B. Harrison. 1992. Fate of trace metals in sewage sludge compost, p. 195–216. In: D.C. Adriano (ed.). Biochemistry of trace elements. Lewis Publishers, Boca Raton, Fla.
- Himelrick, D.G. 1991. Growth and nutritional response of nine grape cultivars to low soil pH. HortSci. 26:269–271.
- Huang, J.W. and D.L. Grunes. 1992. Potassium/magnesium ratio effects on aluminum tolerance and mineral composition of wheat forage. Agron. J. 84:643–650.
- Jalil, A., F. Selles, and J.M. Clarke. 1994. Effect of cadmium on growth and the uptake of cadmium and other elements by durum wheat. J. Plant Nutr. 17:1839–1858.
- Juste, C. and M. Mench. 1992. Long-term application of sewage sludge and its effects on metal uptake by crops, p. 159–193. In: D.C. Adriano (ed.). Biogeochemistry of trace metals. Lewis Publishers, Boca Raton, Fla.
- Kabata-Pendias, A. and H. Pendias. 1992. Trace elements in soils and plants. 2nd ed. CRC Press, Boca Raton, Fla.
- Kafkafi, U. 1991. Root growth under stress—Salinity, p. 375–391. In: Y. Waisel, A. Eshel, and U. Kafkafi (eds.). Plant roots—The hidden half. Marcel Dekker, New York.
- Klepper, B. 1992. Development and growth of crop root systems. Adv. Soil Sci. 19:1–25.
- Leskovar, D.I. and P.J. Stofella. 1995. Vegetable seedling root systems: Morphology, development, and importance. HortScience 30:1153–1159.
- Lin, Z. and D.L. Myhre. 1990. Citrus root growth as affected by soil aluminum level under field conditions. Soil Sci. Soc. Amer. J. 54:1340–1344.
- Lin, Z. and D.L. Myhre. 1991. Differential response of citrus rootstocks to aluminum levels in nutrient solutions: I. Plant growth. J. Plant Nutr. 14:1223–1238.
- Liu, A., J.G. Latimer, and R.E. Wilkinson. 1994. Effect of pH on seedling growth of six cultivars of watermelon. J. Plant Nutr. 17:537–548.
- Maas, E.V. and R.H. Nieman. 1977. Physiology of plant tolerance to salinity, p. 227–299. In: Crop tolerance to suboptimal land conditions. Amer. Soc. Agron., Madison, Wis.
- Marschner, H. 1995. Mineral nutrition of higher plants. 2nd ed. Academic Press, New York.
- O'Toole, J.C. and W.L. Bland. 1987. Genotypic variation in crop plant root systems. Adv. Agron. 41:91–145.
- Patterson, W.A. and J.J. Olson. 1983. Effect of heavy metals on radicle growth of selected woody species germinated on filter paper, mineral and organic soil substrates. Can. J. For. Res. 13:233–238.
- Pettigrew, W.T., J.J. Heitholt, and W.R. Meredith, Jr. 1996. Genotypic interactions with potassium and nitrogen in cotton of varied maturity. Agron. J. 88:89–93.
- Romer, W., J. Augustin, and G. Schilling. 1989. The relationship between phosphate absorption and root length in nine wheat cultivars, p. 123–125. In: B.C. Loughman, O. Gasporikova, and J. Kolek (eds.). Structural and functional aspects of transport in roots. Kluwer Academic, The Netherlands.
- Scott-Russell, R. 1977. Plant root systems. McGraw-Hill, London.
- Seaward, M.R.D. and D.H.S. Richardson. 1990. Atmospheric sources of metal pollution and effects on vegetation, p. 75–92. In: A. J. Shaw (ed.). Heavy metal tolerance in plants: evolutionary aspects. CRC Press, Boca Raton, Fla.
- Snapp, S.S. and C. Shennan. 1992. Effect of salinity on root growth and death dynamics of tomato (*Lycopersicon esculentum* Mill.). New Phytol. 121:71–79.
- Stofella, P.J., M.L. DiPaola, A. Pordossi, and F. Tognoni. 1991. Rhizosphere pH influences early root morphology and development of bell pepper. HortScience 26:112–114.
- Suresh, R., C.D. Foy, and J.R. Weidner. 1989. Effects of water deficit and manganese toxicity on two cultivars of soybeans: Possible applications in remote sensing. J. Plant Nutr. 12:995–1003.
- Szabolcs, L. 1979. Review of research on salt-affected soils. Natural Resources Res. 15:137. UNESCO, Paris.
- Teyker, R.H. and D.C. Hobbs. 1992. Growth and root morphology of corn as influenced by nitrogen forms. Agron. J. 84:694–700.
- von Uexkull, H.R. and E. Mutert. 1995. Global extent, development and economic impact of acid soils, p. 5–19. In: R.A. Date, N.J. Grundon, G.E. Rayment, and M.E. Probert (eds.). Plant-soil interactions at low pH: Principles and management. Kluwer Academic, The Netherlands.
- Yan, F., S. Schubert, and K. Mengal. 1992. Effect of low root medium pH on net proton release, root respiration, and root growth of corn (*Zea mays* L.) and broad bean (*Vicia faba* L.). Plant Physiol. 9:415–421.
- Yang, X., V.C. Baligar, D.C. Martens, and R.B. Clark. 1996a. Plant tolerance to nickel toxicity. II. Nickel effects on influx and transport of mineral nutrients in four plant species. J. Plant Nutr. 19:265–279.
- Yang, X., V.C. Baligar, D.C. Martens, and R.B. Clark. 1996b. Cadmium effects on influx and transport of mineral nutrients in plant species. J. Plant Nutr. 19:643–656.
- Yeo, A.R. and T.J. Flowers. 1992. Selection for physiological characters—Examples from breeding for salt tolerance, p. 217–234. In: H.G. Jones, T.J. Flowers, and M.B. Jones (eds.). Plant under stress. Cambridge Univ. Press, Cambridge, U.K.
- Zobel, R.W. 1975. The genetics of root development, p. 261–275. In: J.G. Torrey and D.F. Clarkson (eds.). The development and function of roots. Academic, London.
- Zobel, R.W. 1991a. Root growth and development, p. 61–71. In: D.L. Keister and P.B. Cregan (eds.). The rhizosphere and plant growth. Kluwer Academic, The Netherlands.
- Zobel, R.W. 1991b. Genetic control of root systems, p. 25–38. In: Y. Waisel, A. Eshel, and U. Kafkafi (eds.). Plant roots—The hidden half. Marcel Dekker, New York.
- Zobel, R.W. 1995. Genetic and environmental aspects of roots and seedling stress. HortScience 30:1189–1192.