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CHAPTER FOUR

THE ROLE OF MINERAL NUTRITION ON ROOT GROWTH OF CROP PLANTS

N. K. Fageria* and A. Moreira†

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Abstract

Agriculture is going through a profound revolution worldwide due to increasing world demand for food, higher costs of energy and other inputs, environmental pollution problems, and instability of cropping systems. In this context,
knowledge of factors that affect root development is fundamental to improving nutrient cycling and uptake in soil–plant systems. Roots are important organs that supply water, nutrients, hormones, and mechanical support (anchorage) to crop plants and consequently affect economic yields. In addition, roots improve soil organic matter (OM) by contributing to soil pools of organic carbon (C), nitrogen (N), and microbial biomass. Root-derived soil C is retained and forms more stable soil aggregates than shoot-derived soil C. Although roots normally contribute only 10–20% of the total plant weight, a well-developed root system is essential for healthy plant growth and development. Root growth of plants is controlled genetically, but it is also influenced by environmental factors. Mineral nutrition is an important factor influencing the growth of plant roots, but detailed information on nutritional effects is limited, primarily because roots are half-hidden organs that are very difficult to separate from soil. As a result, it is difficult to measure the effect of biotic and abiotic factors on root growth under field conditions. Root growth is mainly measured in terms of root density, length, and weight. Root dry weight is often better related to crop yields than is root length or density. The response of root growth to chemical fertilization is similar to that of shoot growth; however, the magnitude of the response may differ. In nutrient-deficient soils, root weight often increases in a quadratic manner with the addition of chemical fertilizers. Increasing nutrient supplies in the soil may also decrease root length but increase root weight in a quadratic fashion. Roots with adequate nutrient supplies may also have more root hairs than nutrient-deficient roots. This may result in greater uptake of water and nutrients by roots well supplied with essential plant nutrients, compared with roots grown in nutrient-deficient soils. Under favorable conditions, a major part of the root system is usually found in the top 20 cm of soil. Maximum root growth is generally achieved at flowering in cereals and at pod-setting in legumes. Genotypic variations are often found in the response of root growth to nutrient applications, and the possibility of modifying root system response to soil properties offers exciting prospects for future improvements in crop yields. Rooting pattern in crop plants is under multi- or polygenic control, and breeding programs can be used to improve root system properties for environments where drought is a problem. The use of crop species and cultivars tolerant to biotic and abiotic stresses, as well as the use of appropriate cultural practices, can improve plant root system function under favorable and unfavorable environmental conditions.

1. Introduction

Roots are important plant organs. They absorb water and nutrients from the soil and translocate them to plant tops (Merrill et al., 1996, 2002; Sainju et al., 2005a; Stone et al., 2001). Roots also give mechanical support to plants and supply hormones that affect many physiological and biochemical processes associated with growth and development. Roots exert control
over whole-plant growth and development by controlling the uptake of mineral nutrients (Zobel, 1986). Cytokinins produced in roots are translocated to shoots and participate in the control of leaf protein biosynthesis (Oritani, 1995). In addition, cytokinins may control nitrogen assimilation in the root itself. Oritani (1995) also reported that rice roots synthesize zeatin glucoside, a bound cytokinin, in addition to isopentenyladenine (IP), isopentenyl-adenosine (IPA), trans-zeatin riboside (tZR), and trans-zeatin (tZ), which are free cytokinins in zeatin-related compounds. Zobel (2005a) reported that root system dynamics are instrumental in the maintenance of biological and chemical equilibrium within the soil and modulate changes to soil quality. In addition, genotypes with inherently large root systems have been associated with reduced lodging in cereals and legumes (Stoffella and Kahn, 1986). Soil is knitted together by plant roots, which form complex and structurally diverse reinforcing structures. Near the soil surfaces, fibrous plant roots hold soil aggregates together against the stresses of water and wind.

Vigorous root systems are needed for the development of healthy plants and consequently, higher yields. Roots that are left in the soil after crop harvest improve soil organic matter (OM) content and contribute to the nitrogen cycle and microbial activity (Sainju et al., 2005a). All these activities improve soil structure, soil water holding capacity, water infiltration into the soil, as well as reduce soil bulk density and soil erosion, ultimately leading to greater soil productivity.

Processes that are largely controlled or directly influenced by roots and often occur in the vicinity of the root surface are often referred to as rhizosphere processes (Cheng and Kuzyakov, 2005). These processes may include root turnover, rhizodeposition, root respiration, and rhizosphere microbial respiration that are a result of microbial utilization of rhizodeposits. Rhizosphere processes play an important role in the global C cycle. Terrestrial ecosystems are intimately connected to atmospheric carbon dioxide levels through photosynthetic fixation of CO₂, sequestration of CO₂ in plant and soil biomass, and the subsequent release of C through respiration and decomposition of organic matter (Cheng and Kuzyakov, 2005). Carbon cycling belowground is increasingly being recognized as one of the most significant components of the ecosystem C fluxes and pools (Cheng and Kuzyakov, 2005; Jackson et al., 1997; Zak and Pregitzer, 1998).

Roots improve soil aggregation, which controls biological and hydrologic properties of the soil. A soil aggregate is a group of primary soil particles that adhere to one another more strongly than to surrounding soil particles (Follett et al., 2009). Root materials remain mixed within the soil as they decompose, providing a gum-like material that cements soil particles into aggregates (Melillo and Gosz, 1983; Tresder et al., 2005). Root exudation occurs when organic acids either are leaked from the root or are released as a means of interacting with microbes in the rhizosphere. These
exudates can influence microbial activity and the subsequent metabolism of root detritus. Mucilages released by the root cap and epidermis link particulate organic residues with mineral fragments. Microbes in the rhizosphere use plant mucilage as a substrate for growth and secrete their own mucilage, thereby producing mucigel, a mucilaginous material of mixed origin which stabilizes finer aggregates. In addition, in many soils, fungal hyphae are important for stabilizing larger structural units (Goss and Kay, 2005). Finally, allocation of carbohydrates and other C-containing molecules directly to mycorrhizal fungi forms another conduit of C into the soil as these microbes secrete their own exudates and as their tissues senesce (Tresder et al., 2005).

The amount of C and N supplied by roots can be significant for maintaining or improving soil organic matter (Sainju et al., 2005b). The organic input from plant roots to the surrounding soil is the principal support of the biological activity and abundance of organisms in the rhizosphere (Cheng et al., 1994; Kirchner et al., 1993). As much as 7–43% of the total aboveground and belowground plant biomass can be contributed by roots (Kuo et al., 1997a,b). Roots can supply from 400 to 1460 kg C ha⁻¹ during a growing season (Kuo et al., 1997a; Qian and Doran, 1996). Liang et al. (2002) reported that roots contributed as much as 12% of soil organic C, 31% of water soluble C, and 52% of microbial biomass C within a growing season. Roots may play a dominant role in soil C and N cycles (Gale et al., 2000a; Puget and Drinkwater, 2001; Wedin and Tilman, 1990). Roots may have relatively greater influence on soil organic C and N levels than the aboveground plant biomass (Boone, 1994; Haider et al., 1993; Milchumas et al., 1985; Norby and Corrufolo, 1998; Sanchez et al., 2002). Balesdent and Balabane (1996) reported that corn roots contributed 1.6 times more C to soil organic C than did stover. Root-derived C is retained and forms more stable aggregates than does shoot-derived C (Gale et al., 2000a,b).

Rhizodeposition, such as root exudates, mucilages, and sloughed cells, may be a significant source of soil organic C (Balesdent and Balabane, 1996; Buyanovsky et al., 1986; Sainju et al., 2005a). Helal and Sauerbeck (1987) estimated that the amount of C released from roots as rhizodeposit could be more than 580 kg C ha⁻¹. This rhizodeposition increases microbial activity and influences N mineralization in the soil (Bakken, 1990; Texier and Biles, 1990). Carbon contribution from corn root biomass and rhizodeposition to soil organic C can be as much as 1.7–3.5 times greater than from stover (Allmaras et al., 2004; Wilts et al., 2004).

The environment is seldom optimum for extensive and effective root growth. Canopy conditions that limit photosynthesis reduce shoot growth and limit assimilate translocation to the roots, thus reducing root growth (Miller, 1986). Root growth is under multi- or polygenic control and is also influenced by environmental factors, including soil temperature, soil moisture content, solar radiation and soil physical, chemical, and biological
properties (Fageria, 2002c, 2009; Klepper, 1992; Merrill et al., 1996; Russell, 1977; Sainju et al., 2005b; Zobel, 1991). Most of the root biomass of annual crops is located in the 0–20 cm soil depth. This may be associated with greater organic matter, nutrients, aeration, and water availability in the top soil layer compared to lower soil depths (Merrill et al., 1996, 2002; Qin et al., 2004; Sainju et al., 2005a; Stone et al., 2001).

Increased knowledge of root architecture and root development dynamics could help improve crop productivity in agroecosystems. Better understanding of root architecture and growth dynamics of annual crops may lead to a more efficient use of applied nutrients and water. The study of plant roots is one of the most promising, but least explored, areas of research related to plant growth. The aerial portions of plant species have received greater attention and study, probably because of their conspicuousness and easy access, while the subterranean portions have been neglected because of the difficulty of observing and sampling them and the disruption of root systems when they are removed from soil. Many crop root studies have relied on soil cores and more recently on minirhizotron observations (Box and Ramseur, 1993; Zobel, 2005b). The data collected using these methods may not be representative of the crop as a whole (Andren et al., 1991; Hansson et al., 1992; Hoad et al., 2001; Parker et al., 1991). In addition, information about annual field crop root growth dynamics as a function of environmental factors is scattered and often not readily accessible.

The primary objectives of this chapter are to review the latest advances in relation to the role of mineral nutrition in the growth and development of roots of annual crops. To make the subject matter as practical as possible, most of the discussion is supported by experimental results. Our approach should enhance understanding on the contribution of roots to total dry matter of crops, to assess the effects of root system size and form on overall crop growth, and to relate the effects of root growth on the environment. This information may be useful for agricultural scientists in the fields of plant nutrition, water use, breeding, and plant physiology who are interested in conducting research to manipulate plant root systems in favor of higher yields.

2. Root-Induced Changes in the Rhizosphere

Pinton and Varannini (2001) suggested that the soil layer surrounding roots should be termed the ectorhizosphere and the root inside the layer colonized by microorganisms should be designated as endorhizosphere. The two areas are separated by the root surface known as rhizoplane (Fig. 1). Growing roots release an appreciable amount of organic components into the rhizosphere. Marschner (1995) reported that three major components released by roots are low-molecular weight organic compounds (free
exudates), high-molecular weight gelatinous materials (mucilage), and sloughed-off cells and tissues and their lysates (Fig. 1). The rhizosphere is the soil zone adjacent to plant roots which is physically, chemically, and biologically different than bulk or nonrhizosphere soil. Plants influence the physical (temperature, water availability, and structure), chemical (pH, redox potential, nutrient concentration, root exudates, Al detoxification, and allelopathy), and biological properties (microbial association) in the rhizosphere. Their effects include changes in nutrient solubility, transport, and uptake of mineral nutrient, and ultimately plant growth. Major rhizosphere changes are synthesized in Fig. 2 and their influence on nutrient availability is discussed in details by Fageria and Stone (2006).

3. Root Systems of Cereals and Legumes

Cereals as well as legume seeds contain relatively large reserves of storage carbohydrates and nutrients which allow the initial root system to grow rapidly to considerable depth (Marschner, 1998). Branching often
begins before the leaves have unfolded, with the result that the plant establishes early contact with moist soil (Hoad et al., 2001). Generally, roots are classified into four groups. These groups are the taproot, basal roots, lateral roots, and shootborn or adventitious roots (Zobel, 2005a). When plants produce secondary shoots (tillers) or shoot branches which develop roots, these roots are commonly called adventitious roots. To indicate the true origin of these adventitious roots, the term shootborn is sometimes used (Zobel, 2005a). The primary function of the taproot, basal roots, and adventitious roots is to establish the most optimum framework from which to initiate small lateral roots to effect water and nutrient uptake (Zobel, 2005b). The taproot penetrates relatively deeply to ensure an

**Figure 2** Major physical, chemical, and biological changes in the rhizosphere (Fageria and Stone, 2006).
adequate supply of soil water, the basal roots spread out laterally to ensure a structure for lateral roots that take up P and other nutrients that are less abundant in the lower levels of the soil profile (Zobel, 2005b), and to provide a degree of lodging resistance to the plant as it matures and produces seed (Barlow, 1986; Stoffella et al., 1979). For many grasses and other species in which root secondary thickening is not important, the shootborn roots take over the role of the basal roots. The shootborn roots continue to build the framework with larger and larger conducting roots as the plant increases in size (Zobel, 2005b). The basal and shootborn roots probably provide little direct uptake of nutrients and water (St. Aubin et al., 1986).

Besides length and weight, surface area is an important parameter of the root system in crop plants. The form of root systems and their development conditions greatly affect the surface area of roots. The surface area of roots has a high positive correlation with the amount of nutrient absorption (Takenaga, 1995). Various studies show that 90–95% or more of the root length of an intact plant is made up of roots < 0.6 mm in diameter (Zobel, 2003, 2005b).

Monocots and dicots typically have different root system structures. Root systems of monocots are fibrous, whereas dicots often have taproots. The fibrous root systems of monocots consist of seminal, nodal, and lateral roots. Seminal roots develop from primordia within seeds and nodal roots develop adventitiously from lower stem nodes. All adventitious roots of stem origin are called nodal roots to distinguish them from other adventitious roots that emerge from the mesocotyl or elsewhere on the plant. Nodal roots are identified by the node number from which they originate. Nodal roots may be functional or nonfunctional (Thomas and Kaspar, 1997). Functional nodal roots are defined as roots that have emerged from stem nodes, entered the soil, and developed lateral roots and/or root hairs. Nonfunctional nodal roots are defined as roots that have emerged from aboveground stem nodes and have not entered the soil or produced lateral roots (Thomas and Kaspar, 1997).

Initial seminal or nodal roots develop laterals that are classed as roots of the first order, roots that develop from first-order roots are classed as second-order roots, and additional roots that develop from these laterals are classed as third-order roots, fourth-order roots, etc. (Yamauchi et al., 1987a,b). Nodal roots are also known as adventitious, coronal, and/or crown roots. Roots of cereals such as rice include mesocotyl, radical (seminal), and nodal or adventitious roots (Yoshida, 1981). Mesocotyl roots emerge from the axis between the coleoptile node and the base of the radical, and they typically develop only when seeds are planted very deep or are treated with chemicals (Yoshida, 1981). Until adventitious roots develop, seedlings must rely on roots which initiate on the subcoleoptile internodes above the seed or seminal roots below the seed. Adventitious roots are important to seedling establishment because they can conduct
more water than smaller diameter seminal roots. Adventitious roots may develop as early as 2 weeks after sowing. Seedling survival may increase when seeds are sown at greater soil depths, where greater soil water availability may increase adventitious root development (Fageria et al., 2006).

Tiller roots do not form in cereals until tillers have two to three leaves (Kleeper et al., 1984), and until these roots have developed, parent culms must provide nutrients and water. Parent culms may also have to provide hormonal control so essential for tiller survival. Delayed root production by tillers may explain why late tillers often do not survive (Kleeper et al., 1984).

Figure 3 shows the radical and adventitious root system of upland rice (*Oryza sativa* L.) (cereal) and Fig. 4 shows the tap root system of dry bean (*Phaseolus vulgaris* L.) (legume).

In addition to their morphological differences, roots of cereals and legumes have different physiochemical properties. The surface of plant roots has a negative electric charge, mainly due to carboxyl groups in the pectin of the root cell walls. The density of this negative charge is defined as a cation exchange capacity (CEC; Takenaga, 1995). The CEC of cereals...
such as rice, barley, and corn is typically lower than the CEC of legumes like dry bean and broad bean. Roots with high CEC absorb more divalent cations like \( \text{Ca}^{2+} \) and \( \text{Mg}^{2+} \) than monovalent cations such as \( \text{K}^{+} \) and \( \text{NH}_{4}^{+} \). On the other hand, roots with lower CEC absorb more monovalent than divalent cations. Hence, in grass–legume mixtures, legumes generally suffer with \( \text{K}^{+} \) deficiency due to large uptake of this element by grasses. Essau (1977), Fageria et al. (2006), Klepper (1992), Leskovarant and Stofella (1995), O’Toole and Bland (1987), and Zobel (1991, 2005a,b) have dealt extensively with various types of monocotyledonous and dicotyledonous roots and root hairs, and their growth and morphology.

4. **CONTRIBUTION OF ROOT SYSTEMS TO TOTAL PLANT WEIGHT**

Crops can accumulate photosynthetic products in their stems, leaves, grains, and roots, and the development of robust root systems is necessary to produce good crop yields. A well-developed root system is needed to absorb adequate amounts of water and nutrients, especially when plants...
are under abiotic or biotic stress. The traditional view is that a large vigorous root system, through avoidance of plant water deficits, is required for high yields in water-limited environments (Ludlow and Muchow, 1990). In addition, large root systems add more organic matter to the soil, creating better environmental conditions for the growth and development of crops. The distribution of photosynthetic products in the root, shoot, and grain is determined genetically, but it also varies with environmental conditions (Fageria, 1992, 2009; Sainju et al., 2005a). Because roots are so difficult to separate from soils, little is known about the effects of soil and crop management practices on their growth and development (Sainju et al., 2005b).

In most annual plant species, only 10–20% of mature plant biomass consists of root tissue (Zobel, 1986). Similarly, Fageria (1989a) also reported that the contribution of roots of food crops to the total plant weight varies from 10–20%, depending on species and cultivars within species. However, Sainju et al. (2005b) reported that C accumulation in cotton and sorghum roots ranged from 1% to 14%. Data in Table 1 show the contribution of the root system of 20 upland rice genotypes grown at two N rates in a Brazilian Oxisol. In this study, the nitrogen × genotype interaction was significant because some genotypes were highly responsive to the N application while others were not. Thus, genotype selection is an important strategy for upland rice production in Brazilian Oxisols. In the control treatment, the contribution of the root system to total plant weight varied from 12% to 30%, with an average value of 22%. At the 300 mg N kg\(^{-1}\) soil treatment, the contribution of root weight to total plant weight varied from 3% to 21%, with an average value of 14%. The proportionally lower root dry weight at the higher N rate was associated with a significant increase in the grain and shoot weight of rice genotypes with the addition of N fertilizer (Fageria and Baligar, 2005).

The contribution of root systems to total plant weights of tropical legume cover crops under three P levels is shown in Table 2. There was a significant influence of P rate, cover crop species and P × species interaction was significant, indicating different responses of cover crops at different P rates. At 0 mg P kg\(^{-1}\) level, the contribution of roots to total plant weight varied from 4.91% to 21.50%, with an average value of 12.98%. With 100 mg P kg\(^{-1}\), the root contribution to the total plant weight varied from 11.30% to 25.16%, with an average value of 18.93%. At the 200 mg P kg\(^{-1}\) P rate, the contribution of roots to the total plant weight varied from 6.36% to 25.91%, with an average value of 14.79%. Overall, increase in root contribution to the total plant weight with the increase in P rate may be associated with the response of legumes to P fertilization. Significant differences have been reported among the crop species and genotypes of the same species in the absorption and utilization of P (Epstein and Bloom, 2005; Fageria, 2009; Marschner, 1995). Tian et al. (1998) reported significant responses of legume cover crops grown on
Alfisols in Africa. Similarly, *Ae et al. (1990)* reported that pigeon pea as a cover crop was more efficient in utilizing iron-bound P than several other cover crops. These authors also reported that this ability of pigeon pea was attributed to root exudates, in particular, piscidic acid and its $p$-O-methyl derivative, which release P from Fe–P by chelating Fe$^{3+}$. These results also show that P fertilization also improves the root weight of cover crops, which may be beneficial in improving soil organic matter content and soil microbial activities.

Table 1  Contribution of upland rice roots in the total plant dry weight (%) as influenced by N rates

<table>
<thead>
<tr>
<th>Genotype</th>
<th>0 mg N kg$^{-1}$ soil</th>
<th>300 mg N kg$^{-1}$ soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>BRA01506</td>
<td>18abcd</td>
<td>3g</td>
</tr>
<tr>
<td>BRA01596</td>
<td>18abcd</td>
<td>3g</td>
</tr>
<tr>
<td>BRA01600</td>
<td>23abcd</td>
<td>6fg</td>
</tr>
<tr>
<td>BRA02535</td>
<td>25abcd</td>
<td>14cde</td>
</tr>
<tr>
<td>BRA02601</td>
<td>23abcd</td>
<td>19abcd</td>
</tr>
<tr>
<td>BRA032033</td>
<td>20abcd</td>
<td>15bcde</td>
</tr>
<tr>
<td>BRA032039</td>
<td>14cd</td>
<td>21ab</td>
</tr>
<tr>
<td>BRA032048</td>
<td>12d</td>
<td>19abc</td>
</tr>
<tr>
<td>BRA032051</td>
<td>23abcd</td>
<td>14cde</td>
</tr>
<tr>
<td>BRA042094</td>
<td>25abcd</td>
<td>12e</td>
</tr>
<tr>
<td>BRA042156</td>
<td>24abcd</td>
<td>15cde</td>
</tr>
<tr>
<td>BRA042160</td>
<td>28abc</td>
<td>15cde</td>
</tr>
<tr>
<td>BRA052015</td>
<td>17abcd</td>
<td>13de</td>
</tr>
<tr>
<td>BRA052023</td>
<td>16bcd</td>
<td>21a</td>
</tr>
<tr>
<td>BRA052033</td>
<td>22abcd</td>
<td>15bcde</td>
</tr>
<tr>
<td>BRA052034</td>
<td>30a</td>
<td>12e</td>
</tr>
<tr>
<td>BRA052045</td>
<td>27abc</td>
<td>17abcde</td>
</tr>
<tr>
<td>BRA052053</td>
<td>29ab</td>
<td>11ef</td>
</tr>
<tr>
<td>BRS Primavera</td>
<td>28abc</td>
<td>12e</td>
</tr>
<tr>
<td>BRS Sertaneja</td>
<td>26abc</td>
<td>14de</td>
</tr>
<tr>
<td>Average</td>
<td>22</td>
<td>14</td>
</tr>
</tbody>
</table>

$F$-test

N rate (N)  $*$

Genotype (G)  $**$

N × G  $**$

CV(%)  17

Contribute of roots in total plant dry weight(%) = \( \frac{\text{Root dry weight}}{\text{Dry weight of root, shoot, and grain}} \times 100 \).

*** Significant at the 5% and 1% probability levels, respectively. Means followed by the same letter in the same column are not significant at the 5% probability level by Tukey’s test.
5. Rooting Depth and Root Distribution

Rooting depth and distribution are important traits for absorption of water and nutrients from the soil profile. Rooting depth, that is, the maximum depth that roots reach, is difficult to ascertain in the field (Hoad et al., 2001). Hsiao et al. (2009) reported that roots typically reach maximum depth about the time when the canopy begins to senesce under nonstress conditions. Gregory (1994) reported that rooting depth in cereals increases until anthesis. Hoad et al. (2001) reviewed the rooting depth literature for cereals and concluded that individual roots of cereal crops can reach a depth of over 2.0 m under favorable conditions. Soil compaction reduces rooting depth (Lipiec et al., 1991; Unger and Kaspar, 1994).

### Table 2

Contribution of tropical legume cover crops root dry weight (%) in the total plant weight as influenced by phosphorus rates

<table>
<thead>
<tr>
<th>Cover crop</th>
<th>0 mg P kg⁻¹</th>
<th>100 mg P kg⁻¹</th>
<th>200 mg P kg⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crotalaria breviflora</td>
<td>20.77a</td>
<td>11.39ef</td>
<td>21.22ab</td>
</tr>
<tr>
<td>Crotalaria juncea L.</td>
<td>12.28abc</td>
<td>19.77abcdef</td>
<td>12.49bcd</td>
</tr>
<tr>
<td>Crotalaria mucronata</td>
<td>4.91c</td>
<td>19.29abcdef</td>
<td>21.96ab</td>
</tr>
<tr>
<td>Crotalaria spectabilis Roth</td>
<td>11.66abc</td>
<td>24.72ab</td>
<td>9.26cd</td>
</tr>
<tr>
<td>Crotalaria ochroleuca G. Don</td>
<td>5.18c</td>
<td>22.76abc</td>
<td>17.38abc</td>
</tr>
<tr>
<td>Calopogonium mucunoides</td>
<td>11.66abc</td>
<td>12.16def</td>
<td>25.91a</td>
</tr>
<tr>
<td>Pueraria phaseoloides Roxb.</td>
<td>7.22bc</td>
<td>17.17abcdef</td>
<td>8.15cd</td>
</tr>
<tr>
<td>Cajanus cajan L. Millspaugh</td>
<td>21.50a</td>
<td>21.12abcde</td>
<td>6.36d</td>
</tr>
<tr>
<td>Cajanus cajan L. Millspaugh</td>
<td>16.90abc</td>
<td>21.80abcd</td>
<td>13.77bcd</td>
</tr>
<tr>
<td>Dolichos lablab L.</td>
<td>12.81abc</td>
<td>22.22abc</td>
<td>14.71bcd</td>
</tr>
<tr>
<td>Mucuna deeringiana (Bort) Merr.</td>
<td>19.70ab</td>
<td>15.08bcdef</td>
<td>13.36bcd</td>
</tr>
<tr>
<td>Mucuna aterrima (Piper &amp; Tracy) Holland</td>
<td>14.17abc</td>
<td>25.16a</td>
<td>16.43abc</td>
</tr>
<tr>
<td>Mucuna cinereum L.</td>
<td>11.09abc</td>
<td>13.44cdef</td>
<td>16.94abc</td>
</tr>
<tr>
<td>Canavalia ensiformis L. DC.</td>
<td>11.83abc</td>
<td>11.30f</td>
<td>9.12cd</td>
</tr>
<tr>
<td>Average</td>
<td>12.98</td>
<td>18.93</td>
<td>14.79</td>
</tr>
</tbody>
</table>

**F-test**

| P rate (P) | **
| Cover crops (C) | **
| P × C | **

Contribute of roots in total plant dry weight(%) = \( \frac{\text{Root dry weight}}{\text{Dry weight of root and shoot}} \) \times 100.

** Significant at the 1% probability level. Means followed by the same letter in the same column are not significant at the 5% probability level by Tukey’s test.
Martino and Shaykewich (1994) reported that the proportion of roots penetrating the soil is inversely related to the soil penetration resistance.

Ueda (1936) observed that wheat cultivars with relatively great cold resistance had roots that penetrated rapidly into deeper soil layer at early stages of growth. Similarly, Sanders and Brown (1978) reported that differences in the yields of indeterminate and determinate soybean varieties mirrored the distribution of their root systems, although the dry weights of their root systems were almost the same. Yamauchi et al. (1987b) compared the root system distributions of 13 species of cereals and reported that there was a significant difference among cereals in the distribution and depth of penetration of root systems. Some of the cereals had “concentrated” root systems and others had “scattered” type root systems.

Large amounts of organic matter and immobile nutrients are generally found in the upper soil layers. Hence, a major part of the roots of the most crops is concentrated in the upper 0–20 cm soil depth (Gregory, 1994). Application of nitrogen fertilizer to barley caused an accumulation of 90–97% of the root mass in the top 30 cm soil layer (Hansson and Andren, 1987). Similarly, Haberle et al. (1996) reported only a few unbranched primary roots below a depth of 25 cm in fertilized wheat. Differences in root lengths, dry weights of roots at different soil depths, and the extent of rooting at the seedling stage were related to differences in yield and the ability of wheat cultivars to escape drought (Hurd, 1974). Upland rice cultivars, which are more drought tolerant than lowland cultivars, have deeper and more prolific rooting systems (Steponkus et al., 1980). When soil types did not restrict the rooting potential, deep rooting of bean cultivars was positively associated with seed yield, crop growth, cooler canopy temperature, and soil water extraction (Sponchiado et al., 1989).

Because about 90% of the total NH₄, P, and K uptake and root length of flooded rice cultivars occur within the surface 20 cm of soil, samples collected for routine soil tests should be taken from the top 20 cm (Teo et al., 1995). Lowland rice plants develop a surface mat of roots in the oxygenated zone near the soil surface soon after application of flood waters (University of Arkansas Cooperative Extension Service Rice Committee, 1990).

Durieux et al. (1994) reported that more than half of the root length of maize was located in the surface 0–20 cm depth at all sampling times during a season. Roots of the peanut (Arachis hypogaea L.) cultivar Florunner penetrated to depths up to 280 cm when grown in a sandy soil, and the most extensive root growth occurred in the top 30 cm (Boote et al., 1982). Sharratt and Cochran (1993) reported that 85% and 95% of the root mass of barley was located in interrows of the top 20 and 40 cm of soil, respectively. Welbank and Williams (1968) also found that nearly 80% of barley roots occupied the uppermost 15 cm of soil. A study conducted by Stone and Pereira (1994a,b) of four common bean cultivars and three upland rice
cultivars to evaluate rooting depths in an Oxisol showed that 70% of the roots were concentrated in the top 20 cm layer and about 90% were concentrated in the top 40 cm soil depth of both crops.

The presence of these roots in surface soil layers may contribute to large amounts of nutrients measured in the upper 20 cm of the soil. Using the Claassen–Barber model to predict nutrient uptake by maize grown in silt loam soil, >90% of K and P uptake occurred in the top 20 cm soil depth (Schenk and Barber, 1980). Silberbush and Barber (1984) reported that about 80% of P and 54% of K uptake by soybean was from 0 to 15 cm depths.

Soybean cultivars differ in their rate of downward growth during specific shoot development stages and in their maximum rooting depth on specific. Cultivars selected for rapid taproot elongation rates in a greenhouse trial were found to have greater rooting depths in rhizotron and field trials than cultivars selected for slow taproot elongation (Kaspar et al., 1978, 1984).

6. Root Growth as a Function of Plant Age

Root development varies with stages of plant growth and development. The most rapid development of corn (Zea mays L.) roots occurs during the first 8 weeks after planting (Anderson, 1987). As corn plants age, growth of roots generally increases at slower rates than shoots (Baligar, 1986). After silking, corn root length declines (Mengel and Barber, 1974). This decline in root length after silking presumably is due to the high C demand of grain resulting in enhanced translocation of C and N to grain, including some C and N that roots would normally obtain (Wiesler and Horst, 1993).

Peanut (Arachis hypogaea L.) root length density and root weight density increased at each soil depth increment from planting to 80 days after planting (Ketring and Reid, 1993). These authors reported that roots had penetrated to depths of 120 cm 40–45 days after planting and spread laterally to 46 cm in mid-furrow. The 0–15 cm depth increment had the highest mean root length density, which increased to a maximum of 2.1 cm cm\(^{-3}\) at 80 days after planting (Ketring and Reid, 1993). This meant that peanut roots were established both deeply and laterally in the soil profile early in the growing season. This would be advantageous in drought environments and helpful for water management.

Sunflower (Helianthus annuus L.) rooting depth reached 1.88 m at the beginning of disk flowering and 2.02 m at the completion of disk flowering (Jaffar et al., 1993). In a review of depth development of roots with time for 55 crop species (Borg and Grimes, 1986), it was shown that maximum rooting depth for most crop species was generally achieved at physiological
maturity. Kaspar et al. (1984) noted that the rate of soybean (Glycine max L. Merr.) root depth penetration reached a maximum during early flowering and declined during seed fill. However, some root growth was observed throughout the reproductive stage until physiological maturity (Klepper and Kaspar, 1994).

Slaton et al. (1990) studied root growth dynamics of lowland rice and found that maximum root growth rates were reached between active tillering and panicle initiation, and maximum root length was reached by early booting. Beyrouty et al. (1987) noted that the most rapid rate of root and shoot growth in flooded rice occurred before panicle initiation, which corresponds to the plant transition between vegetative and reproductive growth. Approximately 77% and 81% of total shoot and root biomass, respectively, was achieved before panicle initiation. Following panicle initiation, the length of roots and shoots increased only slightly until harvest (physiological maturity). Beyrouty et al. (1988) also reported that lowland rice root growth was most rapid during vegetative growth, with maximum root length occurring at panicle initiation. Root length either plateaued or declined during reproductive growth.

Fageria and Santos (2011) studied the root and shoot growth of lowland rice during its growth cycle (Fig. 5). Root dry weight increased in a quadratic fashion with the advancement of plant age from 19 to 120 days, but shoot dry weight increased linearly during the growth cycle. Development of the root system was slow during the first 40 days after sowing and then it increased almost linearly until physiological maturity. The slow

![Figure 5](image_url) Root and shoot dry weight of lowland rice as a function of plant age (Fageria and Santos, 2011).
increase in root dry weight early in the growth cycle may be associated with low translocation of photosynthetic materials due to low leaf area (Fageria, 2007). When there is a low amount of photosynthetic product, a major part goes to the shoot, and very little is translocated to the roots (Fageria, 1992).

Root growth generally parallels shoot growth in crop plants. When a large amount of nutrients, especially N, is supplied to leaves from roots, photosynthesis remains high during maturation, which secures the supply of carbohydrates to roots. Hence, the activities of roots and shoots are mutually dependent (Osaki et al., 1997). Figure 6 shows maximum root length and root dry weight of dry bean during the growth cycle of a Brazilian cultivar BRS Valente under greenhouse conditions. Maximum root length was

![Graph showing the relationship between plant age and dry bean growth parameters.](chart)

**Figure 6** Relationship between plant age and dry bean growth parameters (Fageria and Santos, 2008).
achieved at 80 days after sowing. However, root dry weight increased quadratically with plant age, much like shoot growth. The youngest growing portions of the roots are most active in water and mineral nutrient uptake; therefore, the root system must continually grow to provide adequate nutrition for the plant (Brown, 1984).

7. Root–Shoot Ratio

The partitioning of photoassimilate between roots and shoots has frequently been analyzed as a balance between root and shoot activity (Brouwer, 1966; Davidson, 1969a; Werf, 1996). Different plant species may have different patterns for photosynthate transportation and allocation to shoot and root (Dyer et al., 1991; Freckman et al., 1991). There is an interdependence of shoot and root for growth and development. The shoot relies on the root for water and nutrients, while the roots depend on the shoot for carbohydrates (Hoad et al., 2001). The terms “shoot” and “root” are used here in a botanical sense and refer, respectively, to the entire aerial and subterranean portions of higher seed plants (Aung, 1974). In the early part of the twentieth century, shoot–root ratios were used rather extensively to characterize plant response to imposed nutritional changes. Root growth is closely related to the whole plant growth. This relationship is called “allometry” or relative growth. Root dry weight is related to the total dry weight of a plant using the following equation (Yoshida, 1981):

\[ W_R = HW_T^h, \]

where \( W_R \) is the root dry weight, \( W_T \) is the total dry weight (shoot dry weight + root dry weight), and \( H \) and \( h \) are constants. The above relationship has been tested for different rice cultivars grown under various environmental conditions, and can be expressed by the following equation (Yoshida, 1981):

\[ W_R = 0.212W_T^{0.936}. \]

When plants are small (substitute 1 for \( W_T \)), \( W_R/W_T \) is \( \sim 0.2 \); \( W_R/W_T \) values approach 0.1 as plants grow larger (substitute 10\(^5\) for \( W_T \)). In other words, ratio of root dry weight to total dry weight ranges from \( \sim 0.2 \) at the seedling stage to \( \sim 0.1 \) at the reproductive stage (heading) for rice (Yoshida, 1981).

The above relationship between root and total dry weights gives an estimate of root mass that remains in soil if shoot weight is known. For example, when plants produce shoot dry weights of 3 Mg ha\(^{-1}\) at heading,
root dry weights remaining in soil should be $\sim 330$ kg ha$^{-1}$. Partitioning of dry matter in roots relative to shoots is high during the seedling stages of growth and steadily declines throughout development (Evans and Wardlaw, 1976). The shoot:root biomass ratio changes during ontogeny, generally becoming high as the plant approaches flowering, and stabilizing after flowering (Zobel, 1986). Shoot-to-root ratios of common bean, rice, wheat, and cowpea increased as plants advanced in age (Fageria, 1992). Increases in shoot-to-root ratios indicate that shoots have a higher priority for photosynthate accumulation than roots. If shoot–root ratios decrease with time, roots have preferential utilization of photosynthates under the existing plant growth conditions. A relatively high conservation of photosynthate in shoots may increase the plant’s photosynthetic leaf area while decreasing root biomass and the plant’s capacity for water and nutrient uptake (Werf, 1996).

Environmental stresses increase the relative weights of roots compared to shoots (Eghball and Maranville, 1993). Decrease in the availability of N, P, or water increased root–shoot ratios of perennial ryegrass (Lolium perenne L.) (Davidson, 1969b). Although deficiencies of many mineral elements influence plant growth and root–shoot relationships, invariably water and N deficiency limit shoot growth the most. Root–shoot ratios of 28-day-old maize plants were 0.27, 0.15, and 0.18 at volumetric soil moisture contents of 0.22, 0.27, and 0.32 m$^3$ m$^{-3}$, respectively (Mackay and Barber, 1985). When plants are N-deficient, relatively more photosynthate is used by roots as they develop greater length to aid the plant in obtaining more N. In general, when low nutrient levels do not reduce maize grain yield by more than 20%, addition of N will reduce total root weights even though shoot weights increase (Barber, 1995). Champigny and Talouizte (1981) reported that under N deprivation, translocation of photoassimilates from shoots to roots increased because of increased sink strength of roots compared to shoot sinks. In an experiment with 18-day-old wheat seedlings deprived of N for 7 days, soluble sugar contents in roots were higher than in the corresponding roots of seedlings grown continuously with complete nutrient solutions (Talouizte et al., 1984). Similarly, root–shoot ratios of maize plants were higher when grown with low soil N compared to adequate N (Eghball and Maranville, 1993).

Soil salinity is another important soil chemical property that influences shoot–root ratios. The depressing effect of salinity on root growth is generally less severe than its effect on shoot growth. Shalhevet et al. (1995) summarized the results of 10 experiments relating shoot and root growth to salinity. In all the experiments, the root and shoot responses were evaluated by measuring fresh or dry weights at the end of the experimental periods. All the 10 experiments produced either the same or stronger growth responses of shoots than roots because of the imposed osmotic potential. However, Slaton and Beyrouty (1992) observed shoot–root ratios
Partitioning of photosynthates and their effects on dry matter distribution is influenced by several environmental factors such as low temperature, drought, and mineral nutrient deficiency (Wardlaw, 1990). The mineral nutrients P and N exerted pronounced influences on photosynthate and dry matter partitioning between shoots and roots (Costa et al., 2002). Phosphorus and N-deficient plants usually produce proportionately more dry matter to roots than shoots, compared with unstressed plants. This probably results from higher export rates of photosynthate to roots in deficient plants. Leaf expansion is highly sensitive to low tissue P concentrations, producing higher concentrations of sucrose and starch in P-deficient leaves because of reduced demand (Fredeen et al., 1989). Thus, roots become more competitive for photosynthates than shoots, which leads to higher export of carbohydrates to roots with correspondingly lower shoot-root ratios (Rufty et al., 1993). Cakmak et al. (1994) reported that dry matter partitioning between shoots and roots of common bean was affected differently by low supplies of P, K, and Mg. Although total dry matter production was somewhat similar in P-, K-, and Mg-deficient plants, K- and especially Mg-deficient plants had greater than normal shoot-root ratios, while P-deficient plants had smaller than normal shoot-root ratios (Cakmak et al., 1994). Shoot-root dry weight ratios were 1.8 in P-deficient, 4.9 in control, 6.9 in K-deficient, and 10.2 in Mg-deficient plants. Upland rice usually has high root/shoot weight ratios than lowland rice, an adaptation improving access to soil water (Dingkuhn and Kropff, 1996).

8. Root Growth Versus Crop Yield

Roots are responsible for absorption of water and nutrients which are important resources affecting crop yields. In addition, roots improve soil organic matter content and biological activity in the rhizosphere. Root length and root dry weight are standard root parameters that are measured in many studies, largely because they are more easily determined than other root system properties (Gregory, 1994). Barber and Silberbush (1984) studied the relationship between root length and soybean yield and concluded that yield was significantly related to total root length at the R6 (full seed) stage. These authors concluded that root growth is important in determining the nutrient supply to the shoot which, in turn, affects crop yield. Similarly, Thangaraj et al. (1990) reported that root length density of lowland rice at flowering was directly proportional to grain yield. Leon and Schwang (1992) used the grid intercept method (Newman, 1966) to evaluate differences in total root length between cultivars of oats and barley and
found that yield stability was correlated with root system length. The first author studied the relationship between maximum root length and root dry weight and grain yield of upland rice (Figs. 7 and 8). Grain yield increased in a quadratic fashion with increasing root length or root dry weight, and root dry weight was a better predictor than root length of yield. Similarly, the author studied the relationships between root length and root dry weight and shoot dry weight of tropical legume cover crops (Figs. 9 and 10). There was a significant increase in shoot dry weight of legume cover crops with increasing root length and dry weight, and as with upland rice, root dry weight was a better predictor than root length of shoot dry weight.

9. Genotypic Variation in Root Growth

Variability in root growth among crop species and among genotypes of the same species is widely reported in the literature (Fageria, 2009; Gregory, 1994; Kujira et al., 1994; Marschner, 1998; O’Toole and Bland, 1987). This variability can be used in improving the yield of annual crops by
incorporating vigorous root growth into desirable cultivars. Vigorous root growth is especially important when nutrient and water stress are significant (Gregory, 1994). Ludlow and Muchow (1990), in their review of traits likely to improve yields in water-limited environments, place a vigorous rooting system high in their list of properties to be sought.

O’Toole and Bland (1987) reviewed genotypic variation in root growth of annual crops and reported significant differences in rooting depths, maximum root length, and distribution pattern in the soil profile. Hurd (1974) and Yoshida and Hasegawa (1982) reported rooting depth differences among genotypes of wheat (*Triticum aestivum* L.) and rice,

**Figure 9** Relationship between maximum root length and shoot dry weight of tropical legume cover crops. Values are averages of 14 tropical legume cover crops.

**Figure 10** Relationship between root dry weight and shoot dry weight of tropical legume cover crops. Values are averages of 14 tropical legume cover crops.
respectively. Similarly, Brown et al. (1987) and Pan et al. (1985) also reported differences in rooting depths of corn and barley (Hordeum vulgare L.), respectively. Similar variability exists in dicotyledonous species where most work has been undertaken on legumes, including dry bean (Fageria, 2002a; White and Castillo, 1989), soybean (Taylor et al., 1978; Zobel, 2005a), chickpea (Cicer arietinum L.; Vincent and Gregory, 1986), peanut (Mathews et al., 1988), and white clover (Trifolium repens L.; Caradus, 1990). Hamblin and Tennant (1987) compared root growth and water uptake of wheat and lupin (Lupinus albus L.) and Gregory and Brown (1989) did similar work with barley and chick pea. These authors concluded that there were differences between the species in the root length necessary to extract water, and the rate of water extraction was greater in legumes than in cereals. Fageria (1991) studied root dry weight of the Brazilian upland rice cultivars IAC 47 and the International Rice Research Institute (IRRI) cultivar IR 43 and concluded that root dry weight of Brazilian cultivars was almost double that of the IRRI cultivar during the entire growth cycle. Xiaoe et al. (1997) reported that hybrid rice has a more vigorous root system, larger panicle, and more grains per panicle than traditional rice cultivars.

The genotypic variability in the root growth of annual crops has been used to identify superior genotypes for drought-prone environments (Gregory, 1994; Hurd et al., 1972). Gregory and Brown (1989) reviewed the role of root characters in moderating the effects of drought and concluded that roots may have a direct effect, by increasing the supply of water available to the crop, or an indirect effect by changing the rate at which the supply becomes available. Where crops are grown on deep soils and water is stored throughout the whole soil profile, the depth of rooting has a major influence on the potential supply of water (Gregory, 1994). Rain may replenish the upper soil during the season, but later growth and grain filling in many crops are accomplished during periods of low rainfall when soil moisture stored deep in the profile must be utilized. Sponchiado et al. (1989) reported that in dry bean, drought avoidance results from root growth and soil water extraction deep in the profile.

Atkinson (1990) reported significant variation in the speed of root penetration, specific root length, branching pattern, root density, total root mass, and root hair development of 25 spring barley cultivars. Information reported in the literature on old and new cereal cultivars indicates that more modern cultivars are more responsive than older cultivars to high nutrient availability (Haberle, 1993; Haberle et al., 1995), although they tend to have a lower root fraction (Wahbi and Gregory, 1995). Root physiological characteristics also differ among cultivars and can affect processes like nutrient acquisition (Hoad et al., 2001; Marschner, 1998). The rate of uptake of nutrient per unit root length depends on the nutrient availability but also varies considerably among cultivars (Hoad et al., 2001; Romer, 1985).
Roots require O$_2$ for respiration, water and mineral absorption, and other metabolic activities. Brailsford et al. (1993) reported that roots asphyxiate within a few hours or days at normal growing temperatures unless at least a small amount of oxygen (0.1 kPa in a flowing gas phase) is available. The O$_2$ used by roots is replaced largely by molecular diffusion between soil air and the aboveground atmosphere (Miller, 1986). Waterlogging, defined as the soil saturated or nearly saturated with water, significantly reduces oxygen availability to roots, causes the soil to become “reduced,” results in the production of toxic compounds, and generally reduces root growth (Ellis, 1979; Hoad et al., 2001). Cereals are generally more tolerant to waterlogging than legumes. Hoad et al. (2001) reported that cereal roots can survive short periods of waterlogging without adverse effects because they can use the small quantities of oxygen dissolved in the soil water and are capable of anaerobic metabolism when oxygen demand exceeds supply. Oxygen requirements are higher for growing root tips than for the older parts of the root system. The effect of waterlogging is least at low temperatures when more oxygen can be dissolved in the water and biological activity is depressed (Hoad et al., 2001). The effect of waterlogging is reduced with the application of chemical fertilizers, especially K, which can improve the respiration capacity of roots (Fageria, 2009).

Most agricultural crops are mesophytes, which, for maximum growth, require an environment that is neither too wet nor too dry (Fageria, 1992). However, some plant species grow well under anaerobic conditions. It has long been known that marsh plants or hydrophytes, such as rice, are genetically adapted to grow in reduced soil environments (Horiguchi, 1995). Adaptation to waterlogging in hydrophytes is the result of their unique ability to translocate O$_2$ from the shoot to the root system. Ando et al. (1983) reported that in rice oxygen absorbed from the atmosphere by the shoots can be translocated to the root system and released into the rhizosphere within 5 min. Generally, flooded rice roots have a reddish brown color due to oxidation of the Fe ions by oxygen release from the roots and their deposition on the root surface (Fageria et al., 2008a,b). Flooding induces many changes in plant roots, of which formation of aerenchyma (large interconnected intercellular spaces) is an important adaptive mechanism (Laan et al., 1989). Some species like corn (Z. mays L.) develop aerenchyma as a response to flooding or anoxia (Armstrong and Drew, 2002), a facultative development, while others develop them routinely regardless of the environmental conditions (constitutive development; Barlow, 2002; Zobel, 2005a). The development of aerenchyma in
rice (*O. sativa* L.), and other species and crops growing in wet soils, allows the roots to grow into saturated soils and still extract nutrients (Zobel, 2005b). In corn, the leaf bases also form aerenchyma when submerged, while the enclosed stem bearing aerenchymatous nodal (adventitious) roots may elongate more rapidly (Jackson, 1994). Aerenchyma formation in corn roots appears to be triggered by the loss of tonoplast integrity (Campbell and Drew, 1983), although cell wall disintegration is also involved at an early stage, at least in rice (Jackson, 1994; Webb and Jackson, 1986). Aerenchymatous roots are formed either by some cell wall separation and cell collapse (lysigeny) or by cell separation without collapse (schizogeny). Figure 11 shows cross sections of rice and wheat roots, and lysigenous and schizogenous intercellular space. Both forms result in large longitudinal channels in root cortices, and such structures enhance diffusion of atmospheric or photosynthetic oxygen from shoots to roots so that aerobic respiration and growth can be maintained (Armstrong, 1979). Changes in root morphology occur after flooding for both wetland and nonwetland plant species. Flooding may also increase branching of roots, development of new adventitious roots, and superficial rooting (Laan et al., 1989).

Cellular spaces that exist in roots facilitate oxygen diffusion; however, the amount of aeration varies greatly among plant species. In the case of certain marsh plants like rice, root cortical cells are arranged in columns, and when channels form, the spaces become large and continuous, facilitating diffusion. However, in the case of certain terrestrial plants, the cellular arrangement is oblique and the spaces formed are small (Horiguchi, 1995). There are marsh plants, however, that do not display columnar forms, while some terrestrial plants do (Horiguchi, 1995). In the case of rice, large cortical aerenchyma spaces develop schizogenously and lysigenously even in well-aerated soils. Horiguchi (1995) reported that in rice and other graminaceous plants, aerenchymatous cells are well developed in both the nodes and the internodes. The oxidizing capacity of roots of crop plants also depends on the soil fertility level. Higher soil fertility improves the oxidation activity of rice roots (Horiguchi, 1995). Application of silicon to rice

![Figure 11](image_url)  
**Figure 11** Cross section of a rice (A) and wheat (B) root showing lysigenous and schizogenous intercellular spaces (from Horiguchi, 1995).
crops increases the diffusion of oxygen from the tops to the roots, strengthening oxidation activity and the deposition of ferrous iron on root surfaces, and restricting the transport of excess iron to the top (Horiguchi, 1995).

Development of adventitious roots in some crops is related to plant tolerance of soil waterlogging. Such roots developed by corn after one day of flooding were short and porous enough to allow significant O$_2$ movement from the shoots to the root meristems (Miller, 1986; Wenkert et al., 1981). Despite this adventitious root formation and increased root porosity, corn and most other crop plants soon perish under such conditions (Miller, 1986).

11. Root Growth in Conservation Tillage Systems

Conservation tillage is defined as any tillage sequence, the object of which is to minimize or reduce loss of soil and water; operationally, a tillage or tillage and planting combination that leaves a 30% or greater cover of crop residue on the surface (Soil Science Society of America, 2008). The benefits of conservation tillage are reducing soil erosion, conserving soil moisture, avoiding fluctuations of soil temperature in the arable soil depth, and reducing the costs of soil preparation. In addition, the use of conservation tillage is being encouraged as part of a strategy to reduce C loss from agricultural soils (Kern and Johnson, 1993). Decomposition rates are generally slower in no-till than conventional tillage in which the decomposition of soil organic matter is promoted by the stirring of the soil and alterations in the soil microclimate (Parton et al., 1996). Holland and Coleman (1987) suggested that C retention is increased in no-till because the surface residue is primarily decomposed by fungi, which have higher assimilation efficiency than the bacteria, which dominate the decomposition processes of residue mixed into the soil. Gale and Cambardella (2000) reported that there was a clear difference in the partitioning of surface residue and root-derived C during decomposition and imply that the beneficial effects on no-till on soil organic C accrual are primarily due to the increased retention of root-derived C in the soil. Knowledge of how plant root systems grow under conservation tillage is important because this practice is widely adopted in many countries around the world, most notably, in countries such as United States, Brazil, Argentina, Canada, and Australia (Bolliger et al., 2006). Forty-five percent of the total cultivated land in Brazil is now estimated to be managed with conservation tillage, although in southern Brazil, this figure is reported to exceed 80% (Bolliger et al., 2006).

Conservation tillage reduces soil erosion, conserves soil moisture, conserves energy, increases soil organic matter content, and consequently, soil
quality. However, conservation tillage may compact surface soil horizons and may lead to poor root growth. Adverse effects of soil compaction on crop production have been recognized for many years. Cato the Elder (234–149 B.C.) wrote that the first principle of good crop husbandry is to plow well and the second principle is to plow again, presumably to provide a “mellow” (well-aerated) seedbed (Unger and Kaspar, 1994). Conservation tillage increases soil bulk density (Martino and Shaykewich, 1994) which may inhibit root growth in the upper part of the soil profile (Cannell, 1985; Lampurlanes et al., 2001), reducing nutrient uptake and plant growth (Peterson et al., 1984). Qin et al. (2004) reported that wheat root length density, mean root diameter, and percentage of small-diameter roots were lower in no-till than conventional tillage. Root diameter may be indicative of the effects of soil strength on root growth and affects the utilization of nutrients in the soil. Sidiras et al. (2001) reported thicker barley roots under conventional tillage than under no-till. In general, bulk densities that impede root growth are 1.55 Mg m$^{-3}$ for clay loams, 1.65 Mg m$^{-3}$ for silt loams, 1.80 Mg m$^{-3}$ for sandy loams, and 1.85 Mg m$^{-3}$ for loamy fine sands (Miller, 1986).

Tillage-induced differences in the soil nutrient status may also have a significant impact on root growth (Qin et al., 2004). Conservation tillage often results in the stratification of soil nutrients, especially of immobile nutrients like P (Crozier et al., 1999; Holanda et al., 1998; Logan et al., 1991). This produces greater soil fertility near the soil surface which, in contrast to the effects of compaction described above, causes an increase in root length density near the soil surface under conservation tillage (Cannell and Hawes, 1994; Gregory, 1994). Frequently, root growth is greater from 0 to 5 cm in conservation and no-tillage systems than in conventional tillage systems (Chan and Mead, 1992; Rasmussen, 1991; Wulfsohn et al., 1996).

Radial root swelling has been reported for lupins (Lupinus angustifolius L.) grown in compacted soil (Atwell, 1989), for barley (H. vulgare L.) under mechanical impedance (Wilson et al., 1977), and for mustard (Brassica sp.) in drying soil (Vartanian, 1981). Studies on root elongation of cotton as a function of soil strength and soil water content showed that root elongation is more sensitive to soil strength than water content (Taylor and Radiff, 1969). Root volumes were less affected than length, indicating an increase in root diameter (Ball et al., 1994). Chassot et al. (2001) reported that conservation tillage decreases soil temperature, and this may be the main reason for the poor growth of the roots and shoots of corn seedlings compared with conventional tillage under temperate humid conditions.

Considering the many advantages of conservation tillage compared to conventional tillage, the effects of soil compaction produced by conservation tillage can be minimized. Unger and Kaspar (1994) reported that growing deep-rooted crops in rotation will help avoid or alleviate compaction, improving root distribution and increasing rooting depth. These authors also reported that weather conditions and soil moisture can enhance
or diminish the effects of compaction on root growth. Even if compaction limits root growth, subsequent weather events may either enhance or diminish the effect of the root limitation on crop growth. The first author has conducted field experiments on an upland rice-dry bean rotation using conservation tillage on Brazilian Oxisols. The upland rice root system was adversely affected, and rice yields were low (around 2000 kg ha\(^{-1}\)), about half that expected in a field experiment with conventional soil preparation and favorable environmental conditions. However, dry bean yields were greater than 3000 kg ha\(^{-1}\) (Fageria, 2008; Fageria and Stone, 2004). Hence, selecting the appropriate crop is important.

### 12. Mineral Nutrition Versus Root Growth

There are 17 nutrients essential for plant growth and development and these are carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), zinc (Zn), copper (Cu), manganese (Mn), iron (Fe), boron (B), molybdenum (Mo), chlorine (Cl), and nickel (Ni). Among these nutrients, plants take C, H, and O from air and soil water and the remaining from the soil solution. About 95% of the plant weight is C, H, and O, and the remaining 5% is the other 14 nutrients. The C, H, O, N, P, K, Ca, Mg, and S are required by plants in large amounts and for this reason are known as major or macronutrients. The remaining nutrients, Zn, Cu, Mn, Fe, B, Mo, Cl, and Ni, are classified as micronutrients because they are required in small amounts by plants (Fageria et al., 2002). Among the micronutrients, Cl is also absorbed by plants in large amounts, but it is needed in only small amounts, and Cl deficiency is rarely observed in crop plants.

All the 17 nutrients are equally important for plant growth. If any of these nutrients is limiting in the growth medium, plant growth will be reduced. An example is given in Fig. 12, where at an adequate fertility level, the relative dry weight of dry bean was 100%. When essential nutrients were omitted from the soil or were not applied, growth was reduced, but the amount of reduction depended on the nutrient. The impacts of deficiencies on growth were in the order of P > Ca > Mg > N = K > S among macronutrients and B > Zn > Cu > Fe > Mn > Mo among micronutrients. Similarly, the influence of N, P, and K on shoot and root growth of dry bean is shown in Fig. 13. Both shoot and root growth were significantly reduced when N, P, or K were omitted from the growth medium. Figures 14 and 15 show root growth of wheat, upland rice, and corn with the addition of N + P + K and with the omission of these nutrients from the growth medium. Root growth of these three crop species was decreased in the absence of N, P, and K in the soil. A significant amount of variation
exists, both within and among crop species, in nutrient acquisition and use. This variability reflects differences in root morphology and mechanisms that either aid or prevent ion movement into the root (Gabelman et al., 1986).

### 12.1. Nitrogen

Nitrogen is one of the most yield-limiting nutrients in crop production in most agroecosystems. Nitrogen plays numerous key roles in plant biochemistry, including being an essential constituent of enzymes, chlorophyll,
nucleic acids, storage proteins, cell walls, and a vast array of other cellular components (Harper, 1994). Consequently, a deficiency of N in crop plants profoundly influences plant growth, development, and yield. The recovery

**Figure 14** Root growth of wheat at the top and upland rice at the bottom grown at N + P + K and −N, −P, and −K levels.

**Figure 15** Corn root growth at N + P + K and −N, −P, and −K levels.
of applied N with chemical fertilizers is lower than 50% for most annual crops. The low recovery of N is associated with loss of this element by leaching, denitrification, volatilization, incorporation into soil microorganisms, and soil erosion (Fageria and Baligar, 2005). To improve the efficiency of N uptake and use by crop plants, root systems play an important role.

Root morphology is influenced by the amount of N fertilizer applied (Eghball et al., 1993) and factors such as temperature (Feil et al., 1991) and soil mechanical impedance (Bengough and Mullins, 1990). Eghball et al. (1993) showed that N stress in corn reduced root branching. Similarly, Maizlish et al. (1980) showed greater root branching in corn with increasing levels of applied fertilizer N. Costa et al. (2002) reported that greater root length and root surface area were obtained at an N fertilizer rate of 128 kg N ha\(^{-1}\) compared with either the absence of fertilizer N or the higher rate of 255 kg N ha\(^{-1}\). Nitrogen fertilizer improves root growth in soils having low-OM content (Gregory, 1994; Robinson et al., 1994). Nitrogen fertilization may increase crop root growth by increasing soil N availability (Garton and Widders, 1990; Weston and Zandstra, 1989). Sainju et al. (2001) observed that tomato (Lycopersicon esculentum Mill.) root growth was greater with hairy vetch and crimson clover cover crops and 90 kg N ha\(^{-1}\) than with no cover crops or N fertilization. Nitrogen also improves production of lateral roots and root hairs, as well as increasing rooting depth and root length density deep in the profile (Hansson and Andren, 1987). Hoad et al. (2001) reported that surface application of nitrogen fertilizer increases root densities in the surface layers of the soil.

Nitrogen fertilization can increase root length and root surface area and decrease root mass per unit area of corn (Anderson, 1987; Costa et al., 2002). It is well known that roots tend to proliferate in nutrient-enriched soil zones (Drew et al., 1973; Qin et al., 2005). Russell (1977) refers to this as a compensatory response. The results of pot experiments showed that corn roots were longer and thinner in zones that were rich in N (Durieux et al., 1994; Zhang and Barber, 1992, 1993).

Root mass was less affected by N than root length, but the effect may depend on the stage of maturity of the crop (Baligar et al., 1998). Higher 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, 1966). In corn, the primary root system was 16% thicker when NH\(_4^+\)-N was applied rather than NO\(_3^-\)N. The NH\(_4^+\)-N treatment also increased the diameters of lateral and first- and second-order nodal roots (Anderson et al., 1991). Baligar et al. (1998) reported that relative dry weights of roots of rice, dry bean, corn, and soybean were reduced by 38%, 56%, 35%, and 11%, respectively, when N was omitted from a complete fertilizer. Nitrogen deficiency also reduces branching and root hairs in cereals and legumes (Baligar et al., 1998).
Figure 16 shows that increasing the N fertilizer rate from 0 to 400 mg kg\textsuperscript{-1} increased root dry weight of upland rice in a linear fashion in Brazilian Oxisol, with the rate of N fertilizer explaining 59\% of the variation in root weight. Nitrogen fertilization increases production of thinner roots with fine root hairs (personal visual observation).

Data in Table 3 show root length and root dry weight of 20 upland rice genotypes grown on a Brazilian Oxisol. These two traits were significantly influenced by N rate and genotype treatments. A significant interaction between genotypes and N rates was found for root growth because some genotypes were highly responsive to the N application while others were not. Figures 17–20 show root growth of upland rice cultivars/genotypes at two N rates. Root growth of all the cultivars/genotypes improved with the addition of N; however, there were differences among genotypes for root development. Thus, selecting genotypes for N use efficiency may be an important aspect of improving root growth and consequently, the yield of upland rice in Brazilian Oxisols.

Nitrogen sources also affect root growth in upland rice (Fig. 21). Root dry weight increased in a quadratic exponential fashion with the application of N in the range of 0–400 mg kg\textsuperscript{-1} of soil. In the case of urea, maximum root dry weight was obtained with 281 mg N kg\textsuperscript{-1} of soil. Figures 22 and 23 show how the root growth of upland rice is affected by application of urea and ammonium sulfate in the Brazilian Oxisol. Ammonium sulfate produced more vigorous root systems, especially at higher N rates, than urea, perhaps because upland rice is highly tolerant to soil acidity and ammonium sulfate reduces soil pH more than urea. Fageria (2009) reported that upland rice can tolerate up to 70\% Al saturation in the soil. Fageria

![Figure 16](image_url)

**Figure 16**  Influence of nitrogen on root dry weight of upland rice. Values are averages of 20 upland rice genotypes.
(2009) also reported that rice growth was better in 10 mg L\(^{-1}\) Al than with 0 mg Al L\(^{-1}\) in nutrient solution. Brazilian rice cultivars (lowland as well as upland) are highly tolerant to soil acidity (Fageria et al., 2004). Another possible explanation is that ammonium sulfate has about 24% S, which may improve root growth if the extractable soil S level is lower than 10 mg kg\(^{-1}\).

The timing of nitrogen application can also influence the root growth of crop plants (Table 4). The treatment \(T_3\), which produced maximum grain yield, also produced minimum root length; treatment \(T_2\) which produced minimum grain yield produced maximum root length. There was a

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Root length (cm)</th>
<th>Root dry weight (g plant(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 mg N kg(^{-1})</td>
<td>300 mg N kg(^{-1})</td>
</tr>
<tr>
<td>BRA01506</td>
<td>34.67ab</td>
<td>21.00cd</td>
</tr>
<tr>
<td>BRA01596</td>
<td>30.00b</td>
<td>15.67d</td>
</tr>
<tr>
<td>BRA01600</td>
<td>27.00ab</td>
<td>25.33bcd</td>
</tr>
<tr>
<td>BRA02535</td>
<td>31.67ab</td>
<td>30.00abcd</td>
</tr>
<tr>
<td>BRA02601</td>
<td>28.00b</td>
<td>32.67abc</td>
</tr>
<tr>
<td>BRA032033</td>
<td>30.00a</td>
<td>28.00abcd</td>
</tr>
<tr>
<td>BRA032039</td>
<td>43.00a</td>
<td>34.67abc</td>
</tr>
<tr>
<td>BRA032048</td>
<td>28.50b</td>
<td>32.00abc</td>
</tr>
<tr>
<td>BRA032051</td>
<td>30.67ab</td>
<td>35.67ab</td>
</tr>
<tr>
<td>BRA042094</td>
<td>30.33b</td>
<td>38.00ab</td>
</tr>
<tr>
<td>BRA042156</td>
<td>29.33b</td>
<td>33.00abc</td>
</tr>
<tr>
<td>BRA042160</td>
<td>29.67b</td>
<td>32.50abc</td>
</tr>
<tr>
<td>BRA052015</td>
<td>31.00ab</td>
<td>35.00abc</td>
</tr>
<tr>
<td>BRA052023</td>
<td>29.67b</td>
<td>26.50abcd</td>
</tr>
<tr>
<td>BRA052033</td>
<td>30.33b</td>
<td>31.33abc</td>
</tr>
<tr>
<td>BRA052034</td>
<td>29.00b</td>
<td>37.67ab</td>
</tr>
<tr>
<td>BRA052045</td>
<td>28.67b</td>
<td>37.67ab</td>
</tr>
<tr>
<td>BRA052053</td>
<td>29.00b</td>
<td>36.50ab</td>
</tr>
<tr>
<td>BRS Primavera</td>
<td>29.33b</td>
<td>36.33ab</td>
</tr>
<tr>
<td>BRS Sertaneja</td>
<td>30.00b</td>
<td>40.33a</td>
</tr>
<tr>
<td>Average</td>
<td>30.49</td>
<td>31.99</td>
</tr>
</tbody>
</table>


**Significant at the 5% and 1% probability levels, respectively. Means followed by the same letter in the same column are not significant at the 5% probability level by Tukey’s test.

Table 3 Root length and root dry weight of 20 upland rice genotypes as influenced by nitrogen fertilization

F-test

<table>
<thead>
<tr>
<th>N rate (N)</th>
<th>NS</th>
<th>*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genotype (G)</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>N × G</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>CV(%)</td>
<td>14.25</td>
<td>15.86</td>
</tr>
</tbody>
</table>
**Figure 17** Root growth of cultivar BRS Sertaneja at 0 and 300 mg N kg$^{-1}$ soil (Fageria, 2011).

**Figure 18** Root growth of cultivar BRS Primavera at 0 and 300 mg N kg$^{-1}$ soil (Fageria, 2011).
negative association between root length and grain yield ($Y = 31.2041 - 0.2718X, R^2 = 0.7396**$). Root dry weight was significantly related to grain yield ($Y = -7.6345 + 5.8030X - 0.4081X^2, R^2 = 0.8747**$; Fageria, 2011). Figure 24 shows root growth of upland rice under different N timing treatments. Root dry weight was least (treatment $T_2$) when all N fertilizer was applied at planting. Root and shoot yields were better in treatments $T_3$ and $T_4$, when N was applied later in the growth cycle (Fageria, 2011). Better root growth may be responsible for higher absorption of nutrients and water in the $T_3$ and $T_4$ treatments which resulted in higher grain and straw yields.

The depth of N placement can influence NO$_3$–N distribution in the soil and root growth of wheat (Sharma and Chaudhary, 1984). Root length density decreased abruptly below the 15 cm depth when N was surface applied, whereas root length density decreased more gradually below 15 cm when N was placed at the 10 cm depth. Drew (1975) reported that barley root weight increased in the zone of nutrient localization and decreased in the deficient zone. Murphy and Zaurov (1994) reported that N fertilization at the 5, 10, and 15 cm soil depths produced greater root mass than N fertilization at 0 cm soil depth or surface fertilization.

Figure 19 Root growth of genotype BRA052053 at 0 and 300 mg N kg$^{-1}$ soil (Fageria, 2011).
Figure 20  Root growth of genotype BRA0522045 at 0 and 300 mg N kg\(^{-1}\) soil (Fageria, 2011).

Figure 21  Relationship between nitrogen application rate by ammonium sulfate and urea and root dry weight of upland rice (Fageria et al. 2011).
The effects of two N rates on root length and root dry weight of six tropical legume cover crops are showed in Table 5. Root length as well as root dry weight were significantly increased with the addition of N fertilizer. Similarly, root length as well as root dry weight were significantly different among cover crop species. Root growth of four legume cover crops is shown in Figs. 25–28. In all cases, root growth was better at the higher N rate compared to low N rate.

12.2. Phosphorus

Phosphorus is one of the most yield-limiting nutrients in tropical highly weathered soils (Fageria, 2009; Fageria and Baligar, 2003, 2008). The deficiency of P in these soils may be related to the low natural level of this element in these soils as well as to the immobilization of P in these soils (Fageria and Baligar, 2008). Phosphate plays many roles in the physiology and biochemistry of plants. It is a component of important compounds like

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**Figure 22**  Root growth of upland rice at 0 (left), 50 (center), and 300 (right) mg N kg$^{-1}$ soil supplied with urea.
Figure 23  Root growth of upland rice at 0 (left), 300 (center), and 400 (right) mg N kg$^{-1}$ soil with ammonium sulfate.

Table 4  Root length and root dry weight of upland rice as influenced by nitrogen timing treatments

<table>
<thead>
<tr>
<th>Nitrogen timing treatment$^a$</th>
<th>Root length (cm)</th>
<th>Root dry weight (g plant$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_1$</td>
<td>28.75b</td>
<td>4.21bc</td>
</tr>
<tr>
<td>$T_2$</td>
<td>35.00a</td>
<td>2.56c</td>
</tr>
<tr>
<td>$T_3$</td>
<td>25.75b</td>
<td>5.74ab</td>
</tr>
<tr>
<td>$T_4$</td>
<td>27.00b</td>
<td>7.70a</td>
</tr>
<tr>
<td>$T_5$</td>
<td>28.25b</td>
<td>4.98b</td>
</tr>
<tr>
<td>Average</td>
<td>28.95</td>
<td>5.04</td>
</tr>
<tr>
<td>$F$-test</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>CV(%)</td>
<td>8.7</td>
<td>20.9</td>
</tr>
</tbody>
</table>


$^a$ Significant at the 1% probability level. Means followed by the same letter in the same column are not significant at the 5% probability level by the Tukey’s test.

$T_1$ (1/2 N applied at sowing + 1/2 applied at panicle initiation), $T_2$ (total N applied at sowing), $T_3$ (1/3 N applied at sowing + 1/3 N applied at active tillering + 1/3 N applied at the panicle initiation), $T_4$ (1/2 N applied at initiation of tillering + 1/2 N applied panicle initiation), and $T_5$ (2/3 N applied at sowing + 1/3 N applied at panicle initiation).
Figure 24  Root growth of upland rice at harvest under N timing treatments. $T_1$ (1/2 N applied at sowing + 1/2 applied at panicle initiation), $T_2$ (total N applied at sowing), $T_3$ (1/3 N applied at sowing + 1/3 N applied at active tillering + 1/3 N applied at the panicle initiation), $T_4$ (1/2 N applied at initiation of tillering + 1/2 N applied panicle initiation), and $T_5$ (2/3 N applied at sowing + 1/3 N applied at panicle initiation). Source: Fageria (2011).

Table 5  Influence of nitrogen rate on root length and root dry weight of six tropical legume cover crops

<table>
<thead>
<tr>
<th>Cover crops</th>
<th>Root length (cm)</th>
<th>Root dry weight (g plant$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 mg N kg$^{-1}$</td>
<td>100 mg N kg$^{-1}$</td>
</tr>
<tr>
<td></td>
<td>0 mg N kg$^{-1}$</td>
<td>100 mg N kg$^{-1}$</td>
</tr>
<tr>
<td>Showy crotalaria</td>
<td>22</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>0.48</td>
<td>0.77</td>
</tr>
<tr>
<td>Calopogonio</td>
<td>28</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>0.30</td>
<td>0.46</td>
</tr>
<tr>
<td>Pueraria</td>
<td>23</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>0.16</td>
<td>0.15</td>
</tr>
<tr>
<td>Pigeon pea</td>
<td>30</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>0.73</td>
<td>0.48</td>
</tr>
<tr>
<td>Lablab</td>
<td>27</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>0.74</td>
<td>1.72</td>
</tr>
<tr>
<td>Gray mucuna bean</td>
<td>28</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>2.01</td>
<td>1.84</td>
</tr>
<tr>
<td>Average</td>
<td>26b</td>
<td>31a</td>
</tr>
<tr>
<td></td>
<td>0.74b</td>
<td>0.90a</td>
</tr>
</tbody>
</table>

F-test
N rate (N) **  **
Cover crops **  **
N × C NS  **
CV(%) 6.47 16.27

** NS Significant at the 1% probability level and nonsignificant, respectively. Means in the same line for each growth parameter, followed by the same letter are not significantly different by Tukey’s test at the 5% probability level.
**Figure 25** Root growth of black mucuna bean tropical legume cover crop at 0 (left) and 100 (right) mg N kg\(^{-1}\) soil.

**Figure 26** Root growth of gray mucuna bean tropical legume cover crop at 0 (left) and 100 (right) mg N kg\(^{-1}\) soil.
phospholipids, phosphorylated sugars and proteins, DNA (deoxyribonucleic acid), and RNA (ribonucleic acid). It is also a component of ATP (adenosine 5-triphosphate), PEP (phosphoenolpyruvate), NADPH (nicotinamide adenine dinucleotide phosphate, reduced), and other biochemicals that use the phosphate bond in energy utilization and storage (Blevins, 1994).

Phosphorus is a key nutrient essential for root development in highly weathered tropical soils. Baligar et al. (1998) reported that P increased the root weight of wheat, dry bean, and cowpea in a quadratic fashion with increasing P rate from 0 to 200 mg kg$^{-1}$ of soil. The regression equations related to P rates versus root dry weight were

\[ Y = 0.4019 + 0.094X - 0.00031X^2, \quad R^2 = 0.74* \] for wheat,

\[ Y = 0.4813\exp(0.019X - 0.000071X^2), \quad R^2 = 0.63* \] for dry bean, and

\[ Y = 0.7351 + 0.0232X - 0.000073X^2, \quad R^2 = 0.80** \] for cowpea. Based on these regression equations, maximum root dry weight for wheat was achieved at 152 mg P kg$^{-1}$, whereas maximum root dry weight for common bean and cowpea was achieved at 134 and 159 mg P kg$^{-1}$ soil, respectively. These results indicate that increasing P levels increased root growth, but root growth was reduced at

\[ 0 \text{ N} \quad 100 \text{ N} \]

Figure 27  Root growth of Lablab tropical cover crops at two N levels: 0 (left) and 100 (right) mg N kg$^{-1}$ soil.
higher P levels, and the crops had different P requirements to achieve maximum growth. Overall, the root growth of cereals and legume crops was reduced if P was deficient. Most studies indicate that, within certain limits, both root and shoot growth vary similarly as P level increases. Above certain levels, further increases in P supply do not affect root or shoot growth (Troughton, 1962). Fageria et al. (2006) reported that root dry weight was reduced 62% in rice, 74% in common bean, 50% in corn, and 21% in soybean without added soil P, compared to adequate P in a Brazilian Oxisol.

Fageria et al. (2011) studied the influence of phosphorus on root dry weight and root length of 20 upland rice genotypes grown on a Brazilian Oxisol. Phosphorus level and genotype interactions for root dry weight and root length were significant, indicating different responses of genotypes to varying P levels (Table 6). Root dry weight of 20 upland rice genotypes at low P level varied from 2.00 to 5.68 g plant\(^{-1}\), with an average value of 3.41 g plant\(^{-1}\). At the high P level, root dry weight varied from 2.43 to 8.55 g plant\(^{-1}\), with an average value of 4.01 g plant\(^{-1}\). However, the effect
of P level on root system dry weight was not significant. Root length varied from 23.00 to 38.33 cm with an average value of 30.9 cm at low P level. At high P level, root length varied from 23.67 to 34.33 cm, with an average value of 28.20 cm. There was a significant 10% decrease in root length at the high P level compared to the low P level. However, higher P level roots had more fine hairs compared to lower P level (personal observations).

### Table 6  Root dry weight and root length of 20 upland rice genotypes as influenced by P levels

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Root dry weight (g plant$^{-1}$)</th>
<th>Root length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low P (25 mg kg$^{-1}$)</td>
<td>High P (200 mg kg$^{-1}$)</td>
</tr>
<tr>
<td>BRA01506</td>
<td>3.92ab</td>
<td>3.22c</td>
</tr>
<tr>
<td>BRA01596</td>
<td>2.78ab</td>
<td>2.73c</td>
</tr>
<tr>
<td>BRA01600</td>
<td>2.81ab</td>
<td>3.03c</td>
</tr>
<tr>
<td>BRA02535</td>
<td>3.12ab</td>
<td>4.30c</td>
</tr>
<tr>
<td>BRA02601</td>
<td>4.42ab</td>
<td>3.20c</td>
</tr>
<tr>
<td>BRA032033</td>
<td>3.70ab</td>
<td>3.62c</td>
</tr>
<tr>
<td>BRA032039</td>
<td>2.91ab</td>
<td>4.36c</td>
</tr>
<tr>
<td>BRA032048</td>
<td>3.96ab</td>
<td>3.91c</td>
</tr>
<tr>
<td>BRA032051</td>
<td>2.00b</td>
<td>2.58c</td>
</tr>
<tr>
<td>BRA042094</td>
<td>2.82ab</td>
<td>3.92c</td>
</tr>
<tr>
<td>BRA042156</td>
<td>2.50b</td>
<td>2.91c</td>
</tr>
<tr>
<td>BRA042160</td>
<td>5.68a</td>
<td>8.32ab</td>
</tr>
<tr>
<td>BRA052015</td>
<td>3.91ab</td>
<td>2.98c</td>
</tr>
<tr>
<td>BRA052023</td>
<td>4.69ab</td>
<td>8.55a</td>
</tr>
<tr>
<td>BRA052033</td>
<td>2.23b</td>
<td>2.43c</td>
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<td>BRA052034</td>
<td>3.18ab</td>
<td>3.99c</td>
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<td>3.08c</td>
</tr>
<tr>
<td>BRA052053</td>
<td>2.57ab</td>
<td>3.87c</td>
</tr>
<tr>
<td>BRS Primavera</td>
<td>3.56ab</td>
<td>5.21bc</td>
</tr>
<tr>
<td>BRS Sertaneja</td>
<td>4.36ab</td>
<td>3.92c</td>
</tr>
<tr>
<td>Average</td>
<td>3.41</td>
<td>4.01</td>
</tr>
<tr>
<td>F-test P level (P)</td>
<td>NS</td>
<td>*</td>
</tr>
<tr>
<td>Genotype (G)</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>P × G</td>
<td>*</td>
<td>**</td>
</tr>
</tbody>
</table>

Source: Fageria et al. (2011).

*** NS Significant at the 5% and 1% probability level and nonsignificant, respectively. Means in the same column followed by the same letter are not significantly different at the 5% probability level by the Tukey’s test.
Figures 29–31 show root growth of upland rice under different P rates. Unlike the data cited above, root growth of all the cultivars/genotypes increased with increasing P levels.

The first author studied the influence of P levels on the root growth of 14 tropical legume cover crops grown on a Brazilian Oxisol. Root dry weight was significantly influenced by P; crop species and P × crop species interactions were significant (Fig. 32). The significant P × crop species interaction indicates significant variation in shoot dry weight with the variation in P levels. At the lowest P level (0 mg kg⁻¹), maximum root dry weight of 0.77 g plant⁻¹ was produced by white jack bean (*Canavalia ensiformis*) and minimum root dry weight of 0.01 g plant⁻¹ was produced by crotalaria (*Crotalaria mucronata*) and pueraria (*Pueraria phaseoloides*). At the medium P level (100 mg P kg⁻¹), maximum root dry weight of 1.91 g plant⁻¹ was produced by black mucuna bean (*Mucuna cinereum*) and minimum root dry weight of 0.07 was produced by crotalaria (*Crotalaria*).

**Figure 29** Root growth of upland rice under 0 (left), 50 (center), and 175 (right) mg P kg⁻¹ soil (*Fageria and Stone, 1999*).

**Figure 30** Root growth of upland rice cultivar IAC 164 at different P levels.
breviflora), with an average value of 0.63 g plant$^{-1}$. At the highest P level (200 mg P), maximum root dry weight of 1.42 g plant$^{-1}$ was produced by gray mucuna bean (*Mucuna cinereum*) and minimum root dry weight of 0.09 g plant$^{-1}$ was produced by calopogonio (*Calopogonium mucunoides*) and pueraria (*Pueraria phaseoloides*). The variation in root dry weight is genetically controlled and also influenced by environmental variables, like the supply of mineral nutrition (Baligar *et al.*, 2001; Caradus, 1990; Fageria *et al.*, 2006).

Maximum root length of tropical legume cover crops varied from 15.5 to 36 cm at the low P level, from 20.5 to 50.33 cm at the medium P level and 18.33 to 52.33 cm at the high P level (Fig. 33). Overall, root length also increased with increasing P level. Figures 34–36 show root growth of tropical legume cover crops as influenced by P levels. The improvement in root length by improved P nutrition has been reported by Fageria (2009) in various crop species. Barber (1995), Fageria *et al.* (2006), Marschner (1995), and Mengel *et al.* (2001) reported that mineral nutrition has tremendous effects on root growth, development, and function and, subsequently, the ability of roots to absorb and translocate nutrients. These authors further reported that mineral deficiencies induce considerable variations in the growth and morphology of roots and such variations are strongly influenced by plant species and genotypes.

**Figure 31** Root growth of upland rice genotype BRA01596 at two P levels.
The influence of P fertilization on dry bean root dry weight was studied by Fageria (1989b). Root dry weight of three bean genotypes increased significantly in a quadratic fashion but differed from genotype to genotype (Table 7). The variability in root dry weight due to P fertilization was about 200 mg P kg$^{-1}$.
52% in genotype Carioca, 35% in genotype CNF10, and 70% in genotype CNF4856. Such information may contribute to the selection of cultivars specific to soil type and management systems, resulting in increasing yields on the soils of variable P fertility (Fageria, 1989b).

**Figure 33**  Maximum root length of 14 tropical legume cover crops at three P levels.
Figure 34  Root growth of tropical legume cover crop *Crotalaria mucronata* at 0 and 200 mg P kg$^{-1}$ of soil.

Figure 35  Root growth of tropical legume cover crop gray mucuna bean at 0 (left) and 200 (right) mg P kg$^{-1}$ of soil.
12.3. Potassium

Potassium plays an important role in the growth and development of plants, including the root system. Many enzymes are activated in plants by potassium, and it is also required for photosynthesis, transport of photosynthate, and protein synthesis (Blevins, 1994). Potassium plays a role in cell growth following cell division by serving as a major component in cell turgor. It also maintains ionic balance and electrical neutrality in plants. Crops that produce large quantities of protein per unit area of land require more K than those that produce less protein (Blevins, 1994). Potassium also plays an important role in opening and closing the stomata.

Tennant (1976) reported that potassium deficiency stops root growth completely within 10–12 days of planting in wheat. Inadequate K reduces root growth and consequently, crop yields (Baligar et al., 1998). A deficiency of K in an Inceptisol reduced root growth by 23% in lowland rice, by 30% in dry bean, by 12% in corn, and by 11% in soybean (Baligar et al., 1998).
Table 7  Influence of phosphorus fertilization on the root growth of three dry bean genotypes at harvest

<table>
<thead>
<tr>
<th>P rate (mg kg(^{-1}))</th>
<th>Root dry weight (g per 2 plants)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Carioca</td>
</tr>
<tr>
<td>0</td>
<td>0.29</td>
</tr>
<tr>
<td>25</td>
<td>1.13</td>
</tr>
<tr>
<td>50</td>
<td>1.66</td>
</tr>
<tr>
<td>75</td>
<td>1.31</td>
</tr>
<tr>
<td>100</td>
<td>1.34</td>
</tr>
<tr>
<td>125</td>
<td>1.62</td>
</tr>
<tr>
<td>150</td>
<td>1.31</td>
</tr>
<tr>
<td>175</td>
<td>1.18</td>
</tr>
<tr>
<td>200</td>
<td>1.79</td>
</tr>
</tbody>
</table>

Regression analysis

- P rate versus Carioca \((Y) = 0.6459 + 0.0128X - 0.000044X^2\), \(R^2 = 0.5179\)**
- P rate versus CNF10 \((Y) = 0.8704 + 0.0109X - 0.000042X^2\), \(R^2 = 0.3509\)*
- P rate versus CNF4856 \((Y) = 0.6145 + 0.0193X - 0.000075X^2\), \(R^2 = 0.6953\)**

Source: Adapted from Fageria (1989b).

* Significance at the 5% and 1% probability levels, respectively.

On an Oxisol, a 35% lower root dry mass was observed in 13 corn genotypes when K levels were 0 versus 200 mg kg\(^{-1}\) of soil (Baligar et al., 1998). Data in Table 8 show that at 0 mg K kg\(^{-1}\) of soil root dry weight of common bean \((P. vulgaris\ L.)\) genotypes varied from 1.54 to 3.14 g per 3 plants, a variation of twofold. At the 200 mg K kg\(^{-1}\) level, root dry weight varied from 1.50 to 2.30 g per 3 plants, a variation of 1.5-fold. Similarly, maximum root length varied from 42 to 46 cm at low K level and 32–44 cm at higher K level. At the higher K level, there was a slight decrease in the root length of all the genotypes, and the root weight of three genotypes also decreased at the higher K level. However, at the higher K level, there were more root hairs than at the low K level (visual observations).

There is widespread evidence for genotype diversity in the root characteristics of many crops in response to the environment and increasing interest in using this diversity to improve agricultural production and consequently, nutrient-use efficiency (Barber, 1994; Gregory, 1994).

Mullins et al. (1994) studied K placement effects on the root growth of cotton grown on a fine sandy loam soil. Root density measurements taken in-row showed that root growth at depths >20 cm was improved with in-row subsoil additions of K. Tupper (1992) also observed increased cotton taproot length when K fertilizer was band-applied in the subsoils of
Mississippi soils with low soil-test K. On the other hand, Hallmark and Barber (1984) and Yibrin et al. (1993) reported that localized applications of K did not promote root growth. However, K has been shown to promote the root growth of some vegetable crops (Zhao et al., 1991). Fageria (1992) determined the root growth of rice grown in nutrient solution as well as in an Oxisols at the stress and nonstress levels of K. At the stress levels of K, rice root growth was reduced compared with nonstress levels. Alfalfa herbage yield, root weight, and root total nonstructural carbohydrates increased with increasing K fertilizer (Kitchen et al., 1990).

### 12.4. Calcium

Absolute Ca deficiency is difficult to identify on plants grown in acidic soils (Kamprath and Foy, 1985). Most acidic soils contain adequate total Ca for most plants, and Ca-deficiency symptoms are rarely observed in the field. Only in highly leached, acidic, low-cation exchange soils (Oxisols and Ultisols) would absolute deficiencies be likely to occur (Garrity et al., 1983). Levels of Ca required for essential growth functions are so low as to approach those of micronutrients. Hence, the major role of Ca in soils and in plants is to exclude or detoxify other elements such as Al, Mn, and heavy metals that might otherwise become toxic (Garrity et al., 1983).

Gonzalez-Erico et al. (1979) evaluated the maize response to deep incorporation of limestone on an Oxisol. They reported that incorporation

<table>
<thead>
<tr>
<th>Genotypes</th>
<th>0 mg K kg(^{-1})</th>
<th>200 mg K kg(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Root dry weight (g per 3 plants)</td>
<td>Maximum root length (cm)</td>
</tr>
<tr>
<td>Apore</td>
<td>1.54</td>
<td>45</td>
</tr>
<tr>
<td>Perola</td>
<td>1.97</td>
<td>42</td>
</tr>
<tr>
<td>Ruda</td>
<td>1.94</td>
<td>44</td>
</tr>
<tr>
<td>IAC</td>
<td>3.14</td>
<td>45</td>
</tr>
<tr>
<td>Carioca</td>
<td>2.24</td>
<td>42</td>
</tr>
<tr>
<td>Jalo</td>
<td>1.77</td>
<td>46</td>
</tr>
<tr>
<td>Precoce</td>
<td>2.10</td>
<td>44</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Source: Fageria et al. (2008a).

Values were determined at physiological maturity.
of limestone to depths of 30 cm improved root growth and increased water utilization and grain yield of maize. Similar results were obtained for maize and cotton when limestone was incorporated to depths up to 45 cm (Doss et al., 1979).

Suitable diagnostic indices for prediction of Ca limitations on root growth are either Ca saturation of the effective CEC or Ca activity ratio of the soil solution, which has been defined as the ratio of Ca activity to the sum of the activities of Ca, Mg, K, and Na (Bruce et al., 1988). Values corresponding to 90% relative root length (RRL) of soybean were 0.05 for the Ca activity ratio and 11% for Ca saturation. Calcium activity and Ca concentrations in soil solutions and exchangeable Ca were less useful for diagnostic indices (Bruce et al., 1988). The root growth of soybean was improved with the addition of 12 Mg lime per hectare compared to control treatment (Fig. 37).

12.5. Magnesium

Magnesium is an essential macronutrient for plant growth. The most well-known and important role of Mg is its occurrence in chlorophyll molecules. In addition to this, Mg is required for many essential physiological reactions, especially phosphorylation reactions (Mengel and Kirkby, 1978).

Fageria and Souza (1991) determined the effects of Mg levels on root weights of rice, common bean, and cowpea grown in an Oxisols of Central Brazil (Fig. 38). Dry weights of rice roots were higher at the lowest Mg concentration compared with the highest soil Mg concentration. Initial exchangeable Mg levels of surface soils were 0.1 cmol kg\(^{-1}\). They increased to 0.3 cmol kg\(^{-1}\) within 3 days after liming and to 0.75 cmol kg\(^{-1}\) at harvest time (33 days after sowing). The lack of growth responses to applications of Mg indicated that this level of exchangeable Mg was adequate to meet Mg

![Figure 37](image) Root growth of soybean at two lime rates.
requirements of upland rice grown in this limed soil. Dry weight of roots of common bean increased with Mg application up to 3 cmol kg\(^{-1}\) of soil. Similarly, significant responses of cowpea root growth to soil Mg levels were observed, and maximum root weight was achieved at 2.5 cmol Mg kg\(^{-1}\) of soil.

12.6. Sulfur

Sulfur has long been recognized as an essential element for plant growth and development and classified as a macronutrient. Crop responses to applied sulfur have been reported in a wide range of soils in many parts of the world (Fageria, 2009). Sulfur plays many important roles in the growth and development of plants. Fageria and Gheysi (1999) summarized important functions of the sulfur in the plant. It is an important component of two amino acids, cysteine and methionine, which are essential for protein formation. Since animals cannot reduce sulfate, plants play a vital role in

![Figure 38](image_url)  
**Figure 38** Root dry weights of upland rice, common bean, and cowpea grown with different Mg levels in an Oxisol (adapted from Fageria and Souza, 1991).
supplying essential S-containing amino acids to them. Sulfur plays an important role in enzyme activation. It promotes nodule formation in legumes. Sulfur is necessary in chlorophyll formation, although it is not a constituent of chlorophyll. Maturity of seeds and fruits is delayed in the absence of adequate sulfur. Sulfur is required by the plants in the formations of nitrogenase. It increases the crude protein content of forages and improves the quality of cereals for milling and baking. Sulfur increases the oil content of oilseed crops and increases winter hardiness in plants. It increases drought tolerance in plants, controls certain soil-borne diseases, and helps in the formation of glucosides that give characteristic odors and flavors to onion, garlic, and mustard. Sulfur is necessary for the formation of vitamins and synthesis of some hormones and glutathione, and it is involved in oxidation–reduction reactions. Sulfur improves tolerance to heavy metal toxicity in plants, and it is a component of sulfur contain sulfolipids. Organic sulfates may serve to enhance the water solubility of organic compounds, which may be important in dealing with salinity stress, and fertilization with sulfate decreases fungal diseases in many crops. Few studies have assessed the impacts of sulfur on root growth and function; however, the effects of sulfur on root growth may be similar to those of N. Zhao et al. (2008) reported that S application increased the root number and root dry weight of soybean compared to control treatment.

12.7. Micronutrients

Micronutrients have also been called minor or trace elements, indicating that their required concentrations in plant tissues are small compared to the macronutrients (Fageria et al., 2002; Mortvedt, 2000). Based on physico-chemical properties, except B and Cl, the essential micronutrients are metals. Even though micronutrients are required in small quantities by field crops, their influence can be as great as that of macronutrients in crop production. Micronutrients are normally constituents of prosthetic groups that catalyze redox processes by electron transfer (such as with the transition elements Cu, Fe, Mn, and Mo) and form enzyme–substrate complexes by coupling enzymes with substrates (Fe and Zn) or enhance enzyme reactions by influencing molecular configurations between enzyme and substrate (Zn) (Fageria et al., 2002).

Micronutrient deficiencies in crop plants are widespread because of (i) increased micronutrient demands from intensive cropping practices and adaptation of high-yielding cultivars which may have higher micronutrient demand, (ii) enhanced production of crops on marginal soils that contain low levels of essential micronutrients, (iii) increased use of high-analysis fertilizers with low amounts of micronutrients, (iv) decreased use of animal manures, composts, and crop residues, (v) use of many soils that are inherently low in micronutrient reserves, (vi) use of liming in acid soils, and (vi)
involvement of natural and anthropogenic factors that limit adequate supplies and create elemental imbalance (Fageria et al., 2002).

12.7.1. Zinc
Deficiency of Zn in crop production is spread worldwide (Alloway, 2008). Graham (2008) reported that half of the world’s soils are intrinsically deficient in Zn. Zinc deficiency in annual crops is reported in Brazil (Fageria and Stone, 2008), Australia (Graham, 2008), India (Singh, 2008), China (Zou et al., 2008), Turkey (Cakmak, 2008), Europe (Sinclair and Edwards, 2008), USA (Brown, 2008), and Africa (Waals and Laker, 2008). Micronutrient deficiencies are also a worldwide problem in human health (Welch, 2008). Zinc deficiency is the highest priority among micronutrients for agriculture to address (Graham, 2008).

In the Brazilian Cerrado region, Zn deficiency is very common in annual crops, especially upland rice and corn (Fageria, 2009). Figures 39 and 40 show Zn-deficiency symptoms in upland rice and corn grown on Brazilian Oxisols. Data in Table 9 show that Zn application of up to 120 mg kg⁻¹ improved the root growth of upland rice and wheat significantly. Similarly, Figs. 41 and 42 show improvement in the root growth of soybean and dry dean, respectively, with the addition of Zn in Brazilian Oxisols.

12.7.2. Boron
Boron deficiency is common for plants grown in arid, semiarid, and heavy rainfall areas in calcareous, sandy, light textured, acid, and low-OM soils (Gupta, 1993). Differences between B sufficiency and toxicity are narrow.

Figure 39  Zinc deficiency in upland rice grown on Brazilian Oxisol.
and soils supplied with high amounts of municipal compost, sludge, and biosolids tend to accumulate high amounts of B, which may result in B toxicity. Boron is essential for pollen germination and pollen tube growth in crop plants (Blevins, 1994). Boron requirements (Marschner, 1995), and soils supplied with high amounts of municipal compost, sludge, and biosolids tend to accumulate high amounts of B, which may result in B toxicity. Boron is essential for pollen germination and pollen tube growth in crop plants (Blevins, 1994). Boron requirements
of dicots are generally higher than monocots (Fageria, 2000). Fageria (2000) reported that maximum root growth of upland rice can be achieved with the application of 0.4 mg B kg\(^{-1}\) soil, whereas maximum root growth of dry bean required 1.9 mg B kg\(^{-1}\) of soil. Figure 43 shows that B requirements for root growth varied among the crop species. Application of 24 mg B kg\(^{-1}\) soil decreased the root dry weight of upland rice and corn in greenhouse studies. However, application of B at lower rates to the same soil increased the root dry weight in dry bean, soybean, and wheat (Fig. 43).
Figure 43  Root dry weights of upland rice, maize, common bean, soybean, and wheat grown with different B levels on an Oxisols of central Brazil (adapted from Fageria, 2000).
12.7.3. Copper
Copper deficiency is often observed on plants grown in soils inherently low in Cu (coarse-textured and calcareous soils) and in soils high in OM, where Cu complexes with organic substances (Fageria et al., 2002). Higher-than-normal Cu supplies usually inhibit root growth more than shoot growth (Lexmond and Vorm, 1981). Use of Cu-containing fungicides and anthelmintic compounds in agriculture has resulted in Cu toxicity in some plants, but naturally occurring Cu toxicity is relatively uncommon (Welch et al., 1991). Root dry weight of wheat and root length of dry bean were significantly increased by the application of copper fertilization (Table 10).

12.7.4. Iron
Iron deficiency is a worldwide problem and occurs in numerous crops (Fageria et al., 2002; Marschner, 1995). Iron deficiency occurs not because of Fe scarcity in soil or plants, but because various soil and plant factors affect Fe availability, inhibit its absorption, or impair its metabolic use (Marschner, 1995; Welch et al., 1991). Plant species that commonly become Fe-deficient are peanut (A. hypogaea L.), soybean (G. max L.), sorghum (Sorghum bicolor L. Moench), and upland rice (O. sativa L.). Iron deficiency reduces root growth (Table 11). Iron toxicity (indicated by leaf bronzing) can be serious for production of crops in waterlogged soils. For wetland rice, Fe toxicity is the second most severe yield-limiting nutrient disorder, and it has been reported in South America, Asia, and Africa (Fageria et al., 2008b). Iron toxicity decreases the root growth of lowland rice (Fageria et al., 2008b); however, genotypic differences exist (Fig. 44).

Table 10  Root dry weight of wheat and root length of dry bean as influenced by copper fertilization

<table>
<thead>
<tr>
<th>Cu rate (mg kg⁻¹)</th>
<th>Wheat (g per 4 plants)³</th>
<th>Dry bean (cm)³</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.53</td>
<td>25</td>
</tr>
<tr>
<td>2</td>
<td>0.60</td>
<td>30</td>
</tr>
<tr>
<td>4</td>
<td>0.50</td>
<td>27</td>
</tr>
<tr>
<td>8</td>
<td>0.48</td>
<td>28</td>
</tr>
<tr>
<td>16</td>
<td>0.47</td>
<td>28</td>
</tr>
<tr>
<td>32</td>
<td>0.47</td>
<td>24</td>
</tr>
<tr>
<td>64</td>
<td>0.43</td>
<td>30</td>
</tr>
<tr>
<td>96</td>
<td>0.17</td>
<td>14</td>
</tr>
<tr>
<td>R²</td>
<td>0.88**</td>
<td>0.42**</td>
</tr>
</tbody>
</table>

Source: Adapted from Fageria (2002a).
** Significant at the 1% probability levels.
³ Wheat and dry bean plants were harvested 5 weeks after sowing.
Table 11  Root dry weight of lowland rice as influenced by iron concentration in nutrient solution

<table>
<thead>
<tr>
<th>Fe concentration (mg L(^{-1}))</th>
<th>Root dry weight (g plant(^{-1}))</th>
<th>20 days age</th>
<th>60 days age</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>0.03</td>
<td>0.64</td>
<td></td>
</tr>
<tr>
<td>2.5</td>
<td>0.09</td>
<td>1.19</td>
<td></td>
</tr>
<tr>
<td>5.0</td>
<td>0.13</td>
<td>1.05</td>
<td></td>
</tr>
<tr>
<td>10.0</td>
<td>0.10</td>
<td>1.07</td>
<td></td>
</tr>
<tr>
<td>20.0</td>
<td>0.08</td>
<td>1.18</td>
<td></td>
</tr>
<tr>
<td>40.0</td>
<td>0.11</td>
<td>1.24</td>
<td></td>
</tr>
<tr>
<td>80.0</td>
<td>0.07</td>
<td>0.84</td>
<td></td>
</tr>
<tr>
<td>160.0</td>
<td>0.02</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>0.08</td>
<td>0.92</td>
<td></td>
</tr>
</tbody>
</table>

Source: Fageria et al. (1981).

Figure 44  Root growth development of two lowland rice genotypes at 100 mg Fe L\(^{-1}\) in nutrient solution. Source: Fageria et al. (2008a,b).
12.7.5. Other micronutrients

In addition to zinc, boron, copper, and iron, the other micronutrients that are essential for the growth of higher plants are manganese, molybdenum, chlorine, and nickel. Manganese deficiency has been reported for plants grown in the coarse-textured and poorly drained coastal plain soils of the United States (Reuter et al., 1988) and in the soils of Central America, Bolivia, and Brazil (Leon et al., 1985). In Europe, Mn deficiency has been reported on plants grown in peaty (England and Denmark), coarse-textured (Sweden and Denmark), coarse/fine textured (Netherlands), podzolic, and brown forest (Scotland) soils (Welch et al., 1991). Manganese deficiency has also been reported on plants grown in the semiarid regions of China, India, southeast and western Australia, Congo, Ivory Coast, Nigeria, and other western African countries (Fageria et al., 2002). Manganese toxicity on crop plants grown in many parts of the world has been reported to be more important than Mn deficiency (Foy, 1984; Welch et al., 1991).

Molybdenum is the least abundant of the micronutrients in the lithosphere (Mortvedt, 2000), and soil concentrations range from 0.2 to 5 mg kg\(^{-1}\) (mean of 2 mg kg\(^{-1}\)). Mo deficiency usually occurs on plants grown in the broad areas of well-drained acid soils and in soils formed from parent materials low in Mo. In Australia, Mo deficiency occurs on crops grown in soils derived from sedimentary rocks, basalts, and granites (Anderson, 1970). Peaty, alkaline, and poorly drained soils commonly have high Mo. Iron oxides adsorb more Mo than Al oxides (Fageria et al., 2002), and clay mineralogy can affect Mo adsorption, in the order montmorillonite > illite > kaolinite (Goldberg, 1993). Hydrous ferric oxides or ferric oxide molybdate complexes and insoluble ferric molybdates may form in well-aerated soils so that Mo solubility and availability to plants is low (Welch et al., 1991). In poorly drained soils, the formation of soluble ferrous molybdates or molybdites may lead to high Mo availability to plants. Plants grown in high Mo soils of the intermountain valleys of western United States have been reported to accumulate high Mo which has induced “molybdenosis” (Cu deficiency) in cattle (Welch et al., 1991).

Chloride is essential to higher plants and is required for the water-splitting reactions in photosystem II (Kelley and Izawa, 1978). Nickel has been shown to be essential for soybean (Eskew et al., 1983), and it is known to be a constituent of urease (Blevins, 1994; Klucas et al., 1983). Since urea is a widely used fertilizer in crop plants worldwide, Ni nutrition could be important (Blevins, 1994). Information on the influence of these micronutrients on the root growth of crop plants is not available, and this aspect is not discussed here.
13. **Management Strategies for Maximizing Root Systems**

Root growth of crop plants can be improved by adopting management practices that modify soils to fit crops, as well as to modify the plants to fit the soil. Both of these strategies can be combined to get maximum economic results.

13.1. **Soil management**

Soil management practices that can improve root growth of crop plants include liming acid soils, use of gypsum, maintenance of organic matter, use of adequate rates, sources and methods of fertilizer application, and deep plowing.

13.1.1. **Liming acid soils**

Liming is the most common and effective practice to reduce soil acidity. Lime requirements of crops grown on acid soils are determined by the quality of liming material, status of soil fertility, crop species and cultivar within species, crop management practices, and economic considerations. Soil pH, base saturation, and aluminum saturation are important acidity indices that are used to determine liming. Liming improves soil pH, Ca, and Mg contents and reduces Al concentrations in the soil solution. In addition, liming improves beneficial microbe populations in the soil. Furthermore, liming improves P concentration in the soil solution by reducing P immobilization by Fe and Al in acid soils (Fageria and Baligar, 2008). All these beneficial effects of liming improve the root growth of crop plants. Nurlaeny et al. (1996) found that liming increased shoot dry weight, total root length, and mycorrhizal colonization of roots in soybean and corn grown on tropical acid soils. Gonzalez (1976) reported that incorporation of lime to a 30 cm soil depth allowed the corn roots to penetrate and use stored water throughout the lime layer. Data in Table 12 show that liming increases soil pH and consequently, the root dry weight of dry bean grown on a Brazilian Oxisol. Similarly, Figs. 45 and 46 show how the root growth of dry bean and soybean is influenced by soil pH. The root growth of both the legumes was significantly influenced by increasing soil pH. Dry bean root growth was maximum at pH 5.9 and soybean produced vigorous root systems at pH 6.4.

13.1.2. **Use of gypsum**

Gypsum (CaSO₄·2H₂O) or phosphogypsum (e.g., byproducts of phosphoric acid manufacturing processes) applications are used to leach Ca deeper into soil profiles where Ca can replace Al on cation exchange complexes.
Much of the Al displaced by Ca can be leached from the root zones. This practice works well in sandy soils or Oxisols with clay loam aggregates which behave hydrologically like sands (Foy, 1992). Poor root growth of crop plants has been frequently observed in highly weathered acid soils in various countries (Alcordo and Rechcigl, 1993). The chemical factor identified as most responsible for poor root growth is excess soluble Al (Alcordo and Rechcigl, 1993; Foy, 1992). Excess Al$^{3+}$ has been reported to inhibit root growth by binding to the PO$_4$ portion of DNA in the root cell nuclei, reducing template activity and thus cell division (Matsumoto and Morimura, 1980). In legumes, it has been shown to impair the growth of root hairs and rhizobia, reducing root nodule initiation and function (Munns and Franco, 1982). Excess Al may also adversely affect the root and overall plant growth in nonphytotoxic ways by competing with Ca and

**Table 12**  Influence of soil pH on root growth of dry bean grown on a Brazilian Oxisol

<table>
<thead>
<tr>
<th>Soil pH in H$_2$O</th>
<th>Root dry weight (g per 4 plants)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.1</td>
<td>1.90</td>
</tr>
<tr>
<td>4.7</td>
<td>3.58</td>
</tr>
<tr>
<td>5.3</td>
<td>4.67</td>
</tr>
<tr>
<td>5.9</td>
<td>5.40</td>
</tr>
<tr>
<td>6.6</td>
<td>4.73</td>
</tr>
<tr>
<td>7.0</td>
<td>3.80</td>
</tr>
<tr>
<td>$R^2$</td>
<td>0.99**</td>
</tr>
</tbody>
</table>

Source: Adapted from Fageria (2002b).
** Significant at the 1% probability level.

**Figure 45**  Root growth of dry bean grown on a Brazilian lowland soil (Inceptisol; Fageria and Stone, 1999).
Mg for uptake by plants (Rengel and Robinson, 1989). The use of gypsum can neutralize subsoil acidity by leaching CaSO$_4$ and forming AlSO$_4^{+}$, which is not toxic for root growth (Alva and Sumner, 1989). Ritchey et al. (1980) reported that application of gypsum increased subsoil Ca and Mg while decreasing Al and improving the root growth of corn in Brazilian Oxisol.

### 13.1.3. Maintenance of adequate amounts of organic matter
The benefits of organic matter addition to soils include improving nutrient cycling and availability to plants through direct additions as well as through modification in soil physical and biological properties. The complementary use of organic manures and chemical fertilizers has proved to be the best soil fertility management strategy in the tropics (Fageria and Baligar, 2005). Enhanced soil organic matter increases soil aggregation and water-holding capacity, provides an additional source of nutrients, and reduces P fixation, toxicities of Al and Mn, and leaching of nutrients (Baligar and Fageria, 1999). Build-up of organic matter through additions of crop and animal residues increases the population and species diversity of microorganisms and their associated enzyme activities and respiration rates (Fageria, 2002c). The use of organic compost may result in a soil that has greater capacity to resist the spread of plant pathogenic organisms. The improvement in the overall soil quality may produce more vigorous root systems and higher crop yields (Fageria, 2002c).
13.1.4. Use of adequate nutrient rates, sources, and methods of application
Use of adequate rates and effective sources of nutrients are important management practices to improve crop yield and plant root systems. In addition, appropriate methods of fertilizer application are also important for the development of vigorous root systems. Immobile nutrients like P and K should be applied in bands to improve their uptake by plant roots.

13.1.5. Deep plowing
Deep plowing improves soil conditions for root growth by breaking compacted layers that roots cannot readily penetrate. If water tables are near the soil surfaces, drainage can also be useful. When depths to root-restricting hardpans are relatively shallow (<0.25 m), chisel plowing can be effective for disrupting compacted layers.

13.1.6. Mulching, greater sowing depth, and sowing larger seeds
Root growth may be manipulated through cultural practices like mulching, which can affect soil temperatures. Warmer soil temperatures generally produce larger root systems. In addition, crop residues on soil surfaces decrease soil evaporation and improve water-use efficiency. Greater sowing depths may decrease seedling emergence rate, but it can also increase the survival of emergent seedlings by increasing water availability. Larger seeds generally produce seedlings with more extensive root systems. Sowing good quality seeds could also improve root systems.

13.1.7. Leaching salts from soil profiles
Leaching may be required to prevent harmful accumulation of salts in the root zone. Steady-state leaching ($L_r$) requirements may be estimated (Reichman and Trooien, 1993) as

$$L_r = \frac{D_d}{D_a} = \frac{EC_a}{EC_d},$$

where $D_d$ and $D_a$ are depths of drainage water and applied water, respectively, and $EC_a$ and $EC_d$ are electrical conductivity of applied water and drainage water, respectively.

13.1.8. Integrated cropping systems and pest management
Reduced tillage, N side-dressing, and early planting can be included in integrated pest management programs with no risk of increasing potential for root damage from western maize rootworm (Roth et al., 1995). Miltner et al. (1991) reported that cyst nematodes suppressed soybean root growth on susceptible cultivars, whereas root growth of tolerant cultivars was
stimulated by the presence of soybean cyst nematodes. The use of tolerant or nutrient-use-efficient cultivars may be an important practice to improve root growth in stress environments. Stress-tolerant genotypes are being identified and bred worldwide to solve some of the most difficult problems of soil fertility such as subsoil acidity, salinity, low plant availability of Fe in calcareous soils, and low P availability in acidic soils (Foy, 1992). Rhizobial species/strains differ markedly in tolerance to low pH, and toxicities of Al and Mn in tropical soils have been identified. The use of improved strains can improve N2 fixation and the root growth of legumes grown in acidic soils.

13.2. Plant management

Plant management is another important strategy in improving root systems of crop plants. Adequate plant density and spacing can improve the root growth of crop plants.

13.2.1. Genetic variability

An important plant management strategy is to exploit root system genetic variability of crop species or cultivars within species. Plant genetic variability can be defined as the heritable characters of a particular crop species or cultivar that produce differences in the growth or production among species, or cultivars of the same species, under favorable or unfavorable growth conditions (Fageria, 1989a). Cultivar differences in root size are quite common and have been related to differences in nutrient uptake (Baligar et al., 1998; Caradus, 1990; Fageria et al., 2006). Differences between white clover (T. repens L) populations and cultivars in P uptake per plant at low levels of P have been related to differences in root size and absolute growth rate (Caradus and Snaydon, 1986). There is widespread evidence for genotype diversity in the root characteristics of many crops in response to environment and increasing interest in using this diversity to improve agricultural production and consequently, nutrient use efficiency (Barber, 1994; Gregory, 1994). Mineral deficiency and toxicity, mechanical impedance, moisture stress, oxygen stress, and temperature have tremendous effects on root growth, development, and function and, subsequently, the ability of roots to absorb and translocate nutrients (Arkin and Taylor, 1981; Baligar et al., 1998; Barber, 1995; Marschner, 1995; Mengel et al., 2001). Mineral deficiency induces considerable variations in growth and morphology of roots, and such variations are strongly influenced by plant species and genotypes. Overall, the growth of the main axis is little affected by nutrient deficiency, but growth of lateral branches and their elongation rates appear to be substantially reduced. Baligar et al. (1998) summarized the effects of various essential elements as follows: nitrogen deficiency increases root hair length, increases or has no effect on root hair density, and reduces
branching. Phosphorus deficiency increases the 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. K and Ca deficiencies reduce root growth; however, high Mg levels reduce the dry mass of roots. The effects of these nutrient stress factors on nutrient-use efficiency have not been well explored. Baligar et al. (1998) states that low pH reduces root mass, length, and root hair formation. In alkaline soils, ammonium toxicity causes severe root inhibition and in general, salinity leads to reduction in the mass and length of roots and dieback of laterals.

14. Conclusions

The study of plant roots is one of the most promising, but least explored, areas of research related to mineral nutrition. Roots are poorly studied primarily because of their physical location and growth habit. Understanding plant root growth is important for improving productivity of annual crops in agroecosystems. Root systems are important plant organs because they absorb water and nutrients and also provide mechanical support to the plant. In addition, roots synthesize growth substances and hormones such as cytokinins that are important in leaf function and possibly, grain development. In plant growth analysis, the role of roots is generally ignored due to the difficulty in getting accurate root growth data under field condition. The principal structure of the root system includes four developmentally distinct classes of roots. These are taproots, basal roots, lateral roots, and shootborn roots. Current evidence suggests that the four root classes that make up the primary and secondary root systems are physiologically distinct from each other. Rooting depth and spreading capacity are important traits for uptake of water and nutrients. Root growth varies among plant species and cultivars within species and can be modified by environmental factors. Genotypic differences in root growth among crop species and genotypes of the same species under similar and variable environmental conditions are now well demonstrated, and the possibility of developing genotypes of desirable root systems to soil properties offers exciting prospects for the future. Root number, maximum length, and root dry weight increase with increasing levels of macro- and micro-nutrients in the soil to a point beyond which root growth is suppressed. Plant roots together with their associated bacteria and fungi play an important role in the formation, maintenance, and turnover of soil aggregates. Currently, the techniques available to measure root systems are laborious and time consuming, and this limits their use in plant physiological research. Hence, it is necessary to develop root measurement techniques that are simple, cheap, and less time consuming.
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REFERENCES


