VIEWPOINT: PART OF A SPECIAL ISSUE ON MATCHING ROOTS TO THEIR ENVIRONMENT

Matching roots to their environment

Philip J. White1,*, Timothy S. George1, Peter J. Gregory23, A. Glyn Bengough14, Paul D. Hallett1† and Blair M. McKenzie1

1The James Hutton Institute, Invergowrie, Dundee, DD2 5DA, UK, 2East Malling Research, East Malling, Kent ME19 6BJ, UK, 3Centre for Food Security, School of Agriculture, Policy and Development, University of Reading, Reading RG6 6AR, UK and 4Division of Civil Engineering, University of Dundee, Dundee DD1 4HN, UK

* For correspondence. E-mail philip.white@hutton.ac.uk

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INTRODUCTION

Land plants support most terrestrial life. They form the base of the food chain and provide medicines, fuel, fibre and industrial materials to humans. Vascular land plants rely on their roots to acquire the water and mineral elements necessary for their survival in nature or their yield and nutritional quality in agriculture. Major biogeochemical fluxes of all elements occur through plant roots, and the roots of agricultural crops have a significant role in soil sustainability, carbon sequestration, reducing emissions of greenhouse gasses, and in preventing the eutrophication of water bodies associated with the application of mineral fertilizers.

The interactions between plant roots and their environments continue to influence the planet’s carbon (C) cycle, which has been distorted recently through the burning of fossil fuels, and the cycles of other mineral elements including nitrogen (N), phosphorus (P) and sulphur (S), which have been influenced significantly by their use in intensive agriculture (Smith et al., 1997, 2008; Hofstra and Bouwman, 2005; Galloway et al., 2008; Rockström et al., 2009; Canfield et al., 2010). The roots of agricultural crops, both annual and perennial, have a significant role in sequestering C below ground (Norby and Jackson, 2000; Kell, 2011), in decreasing the emissions of greenhouse gases (GHG; CO2, NO, N2O) from agriculture (Smith et al., 1997, 2008; Hofstra and Bouwman, 2005; Galloway et al., 2008; Rockström et al., 2009; Rockström et al., 2009; Canfield et al., 2010; Good and Beatty, 2011), and in preventing the eutrophication of water bodies associated with the application of mineral fertilizers (Conley et al., 2009; Rockström et al., 2009; Vitousek et al., 2009; Good and Beatty, 2011). Plant roots also have a role in maintaining the productivity of agricultural soils, by stabilizing them physically, by improving their structure, and by driving microbial processes, through substrate inputs, that maintain soil fertility (Feeley et al., 2006; Hinsinger et al., 2009; Hallett and Bengough, 2013).

Thus, an understanding of the root/soil interface is essential to address the immediate issues facing humankind, from food security and human nutrition to the climate and well-being of the planet itself. This article, which provides the context for a
Special Issue of *Annals of Botany* on ‘Matching Roots to Their Environment’, first examines how land plants and their roots evolved, describes how the ecology of roots and their rhizospheres contributes to the acquisition of soil resources, and discusses the continued influence of plant roots on biogeochemical cycles. It then describes the role of roots in overcoming the constraints to crop production imposed by hostile or infertile soils, illustrates root ideotypes (ideal attributes of a plant root system) for improving the acquisition of mineral elements and water, and discusses high-throughput methods to screen for these traits in the laboratory, glasshouse and field. Finally, the article considers whether knowledge of root adaptations that improve the acquisition of resources in natural environments can be used to develop root systems for sustainable agricultural intensification.

**MATCHING ROOTS TO THEIR ENVIRONMENT: PHYSIOLOGICAL ECOLOGY**

The evolution of land plants and their roots

Life originated about 3.5 billion years ago in the oceans of the Earth (Hodson and Bryant, 2012). At that time, the planet’s atmosphere contained no oxygen gas. The evolution of photosynthetic organisms, and the oxygenation process that led to the evolution of aerobic organisms, occurred 2.20–2.45 billion years ago. The first photosynthetic eukaryotes evolved about 1.6 billion years ago, but it was not until 450–490 million years ago that plants successfully colonized the land (Dolan, 2009). It is possible that mycorrhizal symbioses between plants and fungi enabled this (Brundrett, 2002; Taylor et al., 2004; Karandashov and Bucher, 2005). Mycorrhizal symbioses can protect plants from a variety of abiotic and biotic challenges and assist in their acquisition of essential mineral elements (Morgan et al., 2005; Smith and Read, 2008). The proliferation of land plants led to a decrease in atmospheric CO2 concentration, both through photosynthesis and by the weathering of calcium (Ca) and magnesium (Mg) silicate minerals, a lowering of the planet’s surface temperature, and global alterations in the fluxes of energy, carbon, water and mineral elements (Kenrick and Crane, 1997; Raven and Edwards, 2001; Pires and Dolan, 2012). This resulted in the formation of complex soils and the bioengineering of new terrestrial and freshwater ecosystems. The flowering plants (angiosperms) evolved during the Jurassic period (208–144 million years ago) and their rapid diversification to occupy diverse ecological niches on land occurred during the Cretaceous period, 100–65 million years ago (Kenrick and Crane, 1997; Raven and Edwards, 2001; Pires and Dolan, 2012).

The colonization of land by plants required a number of adaptations (Kenrick and Crane, 1997; Raven and Edwards, 2001; Pires and Dolan, 2012). These included adaptations for the uptake and movement of water and solutes within the plant, adaptations to prevent desiccation and overheating, adaptations to regulate gas exchange, adaptations enabling an upright stature, and the development of specialized sexual organs. The evolution of roots served both to anchor plants to their substrate and to acquire water and mineral elements from the substrate. Roots probably evolved at least twice during the Devonian period (480–360 million years ago), first in lycophytes and then in euphyllophytes, from the ancestral generic meristems of dichotomizing rhizome axes (Kenrick and Crane, 1997; Raven and Edwards, 2001; Brundrett, 2002; Friedman et al., 2004; Dolan, 2009; Pires and Dolan, 2012). Further elaborations, such as
The article by Seago and Fernando (2013) in this Special Issue provides an insight to the evolution of the anatomy of angiosperm roots, illustrated by representative species from the basal angiosperms, magnoliids, monocots and eudicots. The authors begin by noting that the primary root system derived from the radicle is dominant in eudicots and gives rise to lateral roots with various degrees of branching, whereas in monocots the primary root system is often ephemeral and their root system is composed mainly of seminal (derived from the mesocotyl) and adventitious (derived from stems and leaves) roots and the lateral roots arising from these (Taiz and Zieglter, 2002; Osmont et al., 2007). They then note that the key anatomical features of roots of all angiosperms include the rootcap, root apical meristem (RAM), epidermis, endodermis, pericycle, xylem and phloem. The rootcap protects the RAM from damage and assists in penetrating the soil, the RAM ensures apical elongation, the root hairs of the epidermis acquire water and mineral elements to sustain plant growth, the endodermis ensures the selectivity of solute transport to the shoot and protects the vasculature from ingress of alien organisms, the pericycle is the site of lateral root initiation, and the xylem and phloem are the pathways for long-distance transport of solutes and signals between root and shoot (White, 2012a, b). Seago and Fernando (2013) observe that Nymphaeales resemble monocots in their root-system architecture and root anatomy, whereas the Amborellales, Austrobaileyales and magnoliids resemble eudicots. Specifically, they observe that (1) the same group of initials give rise to the protoderm and the ground meristem in Nymphaeales and monocots, whereas the protoderm and the lateral rootcap are derived from the same group of initials in other basal angiosperms, magnoliids and eudicots; (2) the root systems of most Nymphaeales and monocots are dominated by adventitious roots, but primary roots that give rise to a taproot system dominate the root systems of other basal angiosperms, magnoliids and eudicots; and (3) the Nymphaeales and monocots often have polyarch (heptarch or more) steles, whereas other basal angiosperms, magnoliids and eudicots usually have diarch to hexarch steles (Fig. 3). Shishkova et al. (2013) test the hypothesis that early exhaustion of the RAM and determinate primary root growth, as observed for some Cactaceae for example, is an evolutionary adaptation to arid environments and provide some insight to the genetic basis of this trait.

During the colonization of the land, plants evolved strategies to acquire water and essential mineral elements from the soil. These include the development of appropriate root architectures and the manipulation of rhizosphere physical, chemical and biological properties to improve the acquisition of resources. During the Devonian period, the depth of roots of vascular plants increased and their access to mineral elements in the soil improved (Raven and Edwards, 2001). This increased terrestrial processes include photosynthesis, respiration, plant uptake, nitrogen fixation, fertilizer application, cultivation, decay of plant material, erosion losses, denitrification, methanogenesis, biogenic sulphur production, volcanic eruptions, sewage production, animal feed production, animal manure production, mining, fossil fuel use, fertilizer production, food production, non-food industrial production, waste, dry deposition, lightening, wet deposition, sea–atmosphere exchange and ocean uptake. Data are presented as a percentage of the total global annual fluxes, which approximate to 479 Tg year\(^{-1}\) for carbon, 3848 Tg year\(^{-1}\) for nitrogen, 3809 Tg year\(^{-1}\) for phosphorus and 890 Tg year\(^{-1}\) for sulphur.

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<table>
<thead>
<tr>
<th>Compartment</th>
<th>FS-Carbon</th>
<th>FS-Nitrogen</th>
<th>FS-Phosphorus</th>
<th>FS-Sulphur</th>
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<tr>
<td><strong>Plants</strong></td>
<td>25%</td>
<td>30%</td>
<td>13.3%</td>
<td>2%</td>
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<tr>
<td><strong>Soil</strong></td>
<td>&lt;1%</td>
<td>8.5%</td>
<td>10.6%</td>
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<td><strong>Animals</strong></td>
<td>&lt;1%</td>
<td>&lt;1%</td>
<td>23.1%</td>
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<td><strong>Industry &amp; domestic</strong></td>
<td>&lt;1%</td>
<td>1.1%</td>
<td>11.2%</td>
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<td><strong>Sea</strong></td>
<td>24%</td>
<td>&lt;1%</td>
<td>&lt;1%</td>
<td>1.1%</td>
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**Fig. 2.** Global fluxes of (A) carbon, (B) nitrogen, (C) phosphorus and (D) sulphur through different compartments of the environment. Arrows represent fluxes into and out of each compartment. When fluxes into and out of a compartment are unequal the stock of an element in that compartment increases or decreases. Compartments represent: (1) plants in natural and agricultural ecosystems (green), (2) soils (brown), (3) wild and domesticated animals (orange), (4) industrial and domestic activities (red), (5) marine ecosystems (dark blue), and (6) the atmosphere (light blue). Fluxes are the average of a range of processes. Key root hairs, had evolved at least 400 million years ago (Raven and Edwards, 2001).
biomass production and the cycling of mineral elements. The acquisition of essential mineral elements with limited mobility in the soil, but required in high amounts by plants, benefitted from associations with arbuscular mycorrhizal fungi (Brundrett, 2002; Karandashov and Bucher, 2005) and the evolution of long, thin, branching roots with abundant root hairs (Raven and Edwards, 2001). The release of organic compounds capable of solubilizing mineral elements contained in rocks and the secretion of enzymes capable of releasing mineral elements from organic compounds further benefitted the mineral nutrition of angiosperms. The translocation of photoassimilates via the phloem (or analogous tissues) to the roots, and the redistribution of carbon and mineral elements from mature or senescent tissues to juvenile and perennial plant tissues through the vasculature, facilitated the growth of the root system and improved mineral economies of evolving plants (Raven and Edwards, 2001). Associations between N₂-fixing bacteria (Rhizobiales, Burkholderiales, Frankia) and roots of the ancestral Rosid I clade evolved on multiple occasions from about 65–55 million years ago, improving their nitrogen nutrition and fitness (Gualtieri and Bisseling, 2000; Karandashov and Bucher, 2005; Sprent and James, 2007, Gyaneshwar et al., 2011). Possession of traits improving the acquisition of scarce mineral resources provided an advantage for successful plant species.

The ecology of roots and their rhizospheres

The evolution and survival of a species depends on the success of its interactions with its neighbours and its environment. Plants can interact with each other both negatively and positively, either directly or indirectly (Tilman, 1990; Brooker and Callaghan, 1998; Grime, 2001; Brooker et al., 2008). Competition between plants for limiting resources is an example of a negative interaction. It is thought to drive the evolution of traits allowing species to occupy different niches, and therefore to access separate resources, either in space or time (Tilman, 1990; Grime, 2001). An example of a positive interaction is facilitation, whereby benefactor plants provide the environment or resources for beneficiary plants to establish themselves (Brooker et al., 2008). Thus, both negative and positive interactions can promote the coexistence of species and, through their complementarity, increase the productivity of an ecosystem (Temperton et al., 2007; Brooker et al., 2008; Marquard et al., 2009; Bessler et al., 2012).

Many interactions between neighbouring plants occur below ground. Competitive interactions often dominate in environments with ample supplies of mineral elements (Schenk, 2006; Brooker et al., 2008; Trinder et al., 2012). The root systems of fast-growing, competitive species appear to be adapted for rapid exploration of the soil volume, especially the topsoil, by having low tissue densities and highly branched architectures, both of which contribute to high specific root lengths (Wright and Westoby, 1999; Wahl and Ryser, 2000; Craine et al., 2001; Comas and Eissenstat, 2004; Holdaway et al., 2011). This phenotype is also observed in many invasive species and is typical of most crops (Craine et al., 2001; White et al., 2005; Lynch, 2007). Greater seed reserves and efficient root foraging also improve the establishment and growth of seedlings in resource-poor soils (White and Veneklaas, 2012), but the roots of
adapted species tend to be thinner and tissues denser than those of other species, especially in P-limited environments (Wright and Westoby, 1999; Holdaway et al., 2011). In resource-poor environments, more facilitative interactions appear to occur between plants (Brooker et al., 2008). One well-studied example is the improved N-nutrition and growth of beneficiary plants in the presence of legumes. Beneficiary plants are able to acquire more N in the presence of legumes either because competition for soil N from legumes is not as intense as that from other species or because they obtain additional N indirectly from legumes either because they release more N into the soil or because resources are exchanged between plants through mycorrhizae (Temperton et al., 2007; Fornara and Tilman, 2009; Bessler et al., 2012). Similarly it has been observed that neighbouring mycorrhizal plants can benefit the mineral nutrition of non-mycorrhizal plants (Schenk, 2006). It has been speculated that increased secretion of protons, organic acids or enzymes into the soil by benefactor plants can facilitate the mineral nutrition of neighbouring plants directly, and that interactions between roots of benefactor plants and soil organisms, whether beneficial or pathogenic, can improve the growth of beneficiary plants (Schenk, 2006; Li et al., 2007; de Kroon et al., 2012). However, detailed studies reporting the interactions between roots of neighbouring plants and the rhizosphere changes effected by roots are scarce.

In this Special Issue, Faget et al. (2013) and Blossfeld et al. (2013) describe a variety of novel, non-invasive methods to study spatial and temporal aspects of root development and rhizosphere processes in vivo. Faget et al. (2013) review methods that will allow researchers to identify the roots of individual plants (or particular species) within the soil including genotype-marking using the expression of fluorescent proteins (Faget et al., 2009, 2012) or \(^{13}\)CO\(_2\)-labelling combined with positron emission tomography (Jahnke et al., 2009). Formerly, dyes might have been injected into the phloem to identify the roots of individual plants or species-specific infrared or fluorescence characteristics might have been used (Rewald et al., 2012). Faget et al. (2013) also discuss methods for tracking individual roots in sequential images from rhizotron tubes or high-throughput phenotyping systems (Dupuy et al., 2010b; Iyer-Pascuzzi et al., 2010; Galkovsky et al., 2012; Nagel et al., 2012) and from the sequential 3-D images obtained using magnetic resonance imaging (Rascher et al., 2011), X-ray computed tomography (Gregory et al., 2003; Perret et al., 2007; Flavel et al., 2012; Mairhofer et al., 2012) or optical computed tomography (Clark et al., 2011; Downie et al., 2012). These methods will complement and parameterize architectural and continuum root system models to facilitate studies of the interactions between roots, rhizospheres and soils (Dunabin, 2007; Dupuy et al., 2010a; Postma and Lynch, 2012). Blossfeld et al. (2013) describe the use of commercially available planar optodes and fluorescence microscopy to quantify the spatial and temporal dynamics of changes in pH and CO\(_2\) concentrations in the rhizospheres of durum wheat (Triticum durum), chickpea (Cicer arietinum) and the native Australian legume Viminaria juncea whilst growing in rhizobases either separately or together. It is evident that plant roots influence the physical, chemical and biological properties of the rhizosphere profoundly (Hinsinger et al., 2009; Marschner, 2012; Neumann and Römhild, 2012). In this Special Issue, Carminati and Vetterlein (2013) discuss whether the manipulation of the hydraulic properties of the rhizosphere by roots could be a strategy by which plants control the part of the root system that will have greatest access to water and solutes. They propose two classes of rhizosphere, the first (Class A) dominated by hydrated mucilage that connects root and soil hydraulically, which would facilitate the uptake of water from drying soils, and the second (Class B) dominated by air-filled pores and/or hydrophobic compounds that isolate roots from the soil hydraulically. They present evidence (1) for the occurrence of Class A and Class B rhizospheres; (2) that the hydraulic properties of the rhizosphere change with both root development and soil water status; and (3) that the chemical properties of mucilage secreted at the root tip could be a major determinant of rhizosphere hydraulic properties. They then explore hypotheses (1) that the secretion of hydrated mucilage facilitates water and solute uptake by younger root tissues at the root apex (Read et al., 2003; Dunabin et al., 2006), and (2) that the degradation and drying of mucilage restricts the loss of water from older root tissues and facilitates long-distance transport of water. Such changes in hydraulic properties of the rhizosphere might complement the hydraulic architecture of the root system (Garrigues et al., 2006) and also influence preferential flow pathways for water and solute transport through the bulk soil (Ghestem et al., 2011; Bengough, 2012).

The continued influence of roots on biogeochemical cycles

Terrestrial vegetation has a large effect on the cycling of carbon, water and mineral elements (Fig. 1). Today, forests are responsible for most of the CO\(_2\) fixed by terrestrial ecosystems (Luysaert et al., 2007; Pan et al., 2011). This is enabled by canopy photosynthesis, but is counteracted by plant respiration. A large proportion of plant respiration is attributed to roots. Information on the root systems of trees is scarce, principally because of their large size and their depth. Biomass partitioning between canopy and root is an important parameter for estimating the balance of photosynthesis and respiration and, therefore, the modelling of regional and global carbon cycles (Luysaert et al., 2007; Katge et al., 2011; Kempe et al., 2011; Makita et al., 2012). In this Special Issue, Eshel and Grünzweig (2013) describe a large-scale aeroponics system in which the roots of saplings of tropical trees can be studied. They report the allometric relationships between the relative biomass of stem, branch and leaves of two tropical forest species, the rapid-growing kapok (Ceiba pentandra) and the slow-growing African mahogany (Khaya anthotheca), grown aeroponically or in containers filled with soil. They observe identical allometric relationships between stem, branch and leaves for saplings grown in both systems and conclude that aeroponics can be used to determine the partitioning of biomass. For saplings growing in aeroponics the shoot/root biomass quotients approximated 2 for both species and 92–95 % of the length of the root systems of both species had a diameter <2 mm. This information is important for assessing the role of fine roots as C stores, the rates of root turnover, and the chemistry of below-ground organic inputs to soil.

The role of terrestrial ecosystems in global N cycles is discussed by Subbarao et al. (2013). Various authors have estimated N inputs to terrestrial ecosystems (Fig. 2; Galloway et al., 2008; Schlesinger, 2009). These occur primarily through lightning
et al. (2013) observe that N availability is generally low in natural ecosystems and N cycling efficient, but excess N is often applied in agricultural systems, which results in inefficient use of N-fertilizers, problematic leaching of nitrate to watercourses, and large emissions of greenhouse gases. The land accumulates about 9 Tg N year\(^{-1}\), whilst about 77 Tg N year\(^{-1}\) is accumulated in rivers and groundwater, about 54 Tg N year\(^{-1}\) is accumulated in the oceans via the atmosphere, and about 109 Tg N year\(^{-1}\) is returned to the atmosphere through denitrification processes (Schlesinger, 2009). About 25 Tg N year\(^{-1}\) is emitted into the atmosphere as \(\text{N}_2\text{O}\) from terrestrial ecosystems (Galloway et al., 2008; Schlesinger, 2009). There can be no doubt that anthropogenic activities are altering global nitrogen cycles. Hence, improving the efficiency by which N-fertilizers are used in agriculture, and the efficiency by which N is acquired by roots of crops, is an imperative for humankind.

MATCHING ROOTS TO THEIR ENVIRONMENT: AGRICULTURE

Since agriculture began 13,000 years ago, humans have domesticated about 2500 plant species (Barker, 2006; Pickersgill, 2007; Meyer et al., 2012). These species were selected for a greater yield of harvested product, effective competition with other plants, resistance to pests and diseases, and, initially, a low resource requirement for growth. Thus, it is likely that they were selected indirectly for root vigour and the ability to acquire water and mineral elements in hostile and infertile environments. However, modern crops have been selected for greater yields in high input / high output monoculture agricultural systems, especially following the advent of the chemical fertilizer industry 200 years ago. It is possible, therefore, that modern crops have lost beneficial root traits for low input agricultural systems because there has been no requirement for these adaptations (Wissuwa et al., 2009). Indeed, modern crops often have reduced fitness in the natural environment (Meyer et al., 2012). In addition, current breeding programmes generally use ploughed soils that might not present the mechanical constraints found in the reduced tillage systems that are gaining prominence in modern agriculture (Newton et al., 2012).

Soil properties restrict crop production worldwide (Broadley et al., 2007; Ismail et al., 2007; Lynch, 2007; White and Brown, 2010; White et al., 2012). It is estimated that >40 % of agricultural soils are acidic (Von Uexküll and Mutert, 1995; Sumner and Noble, 2003), 25–30 % are alkaline or calcareous (White and Broadley, 2009), and 5–15 % are saline or sodic (Munns and Tester, 2008). These soils are compromised not only by high phytoavailability of toxic mineral elements, for example aluminium (Al) and manganese (Mn) in acidic soils and sodium (Na), chlorine (Cl) or boron (B) in saline and sodic soils, but also by low phytoavailability of essential mineral elements (Ismail et al., 2007; White and Brown, 2010; White et al., 2012; White and Greenwood, 2013). The phytoavailability of N, P and potassium (K) limit crop production in most agricultural soils (Lynch, 2007, 2011; Fageria et al., 2011; Mueller et al., 2012).

The success of the ‘Green Revolution’, which increased crop production dramatically during the last half-century, was founded on the development of semi-dwarf crops resistant to pests and pathogens, whose yields are maintained through applications of herbicides, fungicides and pesticides, chemical fertilizers, and irrigation (Evans, 1997; Godfray et al., 2010; Fageria et al., 2011). The amounts of mineral fertilizers applied to crops during this period also increased dramatically (Erisman et al., 2008; Galloway et al., 2008; Cordell et al., 2009; Vitousek et al., 2009; Good and Beatty, 2011) and it is estimated that almost half the world’s food production now depends upon manufactured N fertilizers (Erisman et al., 2008; Dawson and Hilton, 2011). The environmental consequences of using mineral fertilizers in agriculture include the emissions of GHG from their production, transport and application, and the eutrophication of natural environments (Galloway et al., 2008; Smith et al., 2008; Conley et al., 2009; Vitousek et al., 2009; Good and Beatty, 2011). Furthermore, commercially viable geological reserves required for the production of mineral fertilizers are depleting rapidly (Kesler, 2007; Dawson and Hilton, 2011) and fluctuating prices of energy and raw materials cause uncertainty in the supplies of mineral fertilizers, with detrimental impacts on food security (Cordell et al., 2009).

Nevertheless, crop production must increase if the projected future human population is to be supplied with sufficient food (Cordell et al., 2009; Godfray et al., 2010; White et al., 2012).

It has been argued that sustainable intensification of crop production will require an ‘Evergreen Revolution’ that must continually focus on reducing inputs without compromising yield or quality (Lynch, 2007; Wissuwa et al., 2009; Godfray et al., 2010; Fageria et al., 2011; Good and Beatty, 2011; White et al., 2012). It is envisaged that a judicious combination of agronomy and breeding might be employed to decrease inputs of mineral fertilizers (Fageria, 2009; Wissuwa et al., 2009; White et al., 2012). Agronomic strategies to improve fertilizer use efficiency seek to address (1) soil pH through amendments; (2) soil physical characteristics through composts and amendments, tillage and restricted traffic; (3) water availability through irrigation and drainage management; and (4) soil biology through inoculants or manure and compost inputs, intercropping or rotations, in addition to reducing losses from leaching and run-off, and optimizing the placement, timing, chemistry and quantity of any fertilizer applications (Fageria et al., 2011; Good and Beatty, 2011; McLaughlin et al., 2011; Richardson et al., 2011; Simpson et al., 2011; James and Baldani, 2012; Mueller et al., 2012; White et al., 2012). Approaches to breed crops for greater yields in environments with limited phytoavailability of mineral nutrients focus on improving the efficiency by which mineral elements are acquired from the soil and the efficiency by which nutrients are utilized physiologically to produce yield (Hirel et al., 2007; Lynch, 2007, 2013; White et al., 2012; Veneklaas et al., 2012; White, 2013). It is generally observed that physiological N utilization efficiency (NUE; yield per N acquired) contributes more than N acquisition efficiency (NUpE; N acquired per N available) to agronomic N use efficiency (NUE, yield per N available), although greater NUpE and, in particular, continued N uptake after anthesis, often improves NUE when crops are grown with a restricted N.
supply (Hirel et al., 2007; Fageria, 2009; Sylvester-Bradley and Kindred, 2009; Barraclough et al., 2010; Beatty et al., 2010; Berry et al., 2010; Bingham et al., 2012) and genotypes of both legumes and non-legumes that foster greater biological nitrogen fixation often have higher yields in N-limited environments (Rengel, 2002; Ainsworth et al., 2012; James and Baldani, 2012; Kumar et al., 2012; Urquiaga et al., 2012). By contrast, differences between genotypes in agronomic P use efficiency (PUE) are generally correlated with P acquisition efficiency (PUpE), and with root architectural traits, rather than with physiological P utilization efficiency (PUtE; White et al., 2005; White and Hammond, 2008; Hammond et al., 2009; White et al., 2012). Similarly, although there is significant genetic variation in both K uptake efficiency (KUpE) and K utilization efficiency (KUE) within crop species, agronomic K use efficiency (KUE) is often correlated with KUpE rather than KUE (Rengel and Daman, 2008; Fageria, 2009; White et al., 2010; White, 2013). Thus, root traits affecting the acquisition of mineral elements will often determine yields in reduced-input agricultural systems. In this Special Issue Brown et al. (2013) suggest root ideotypes for improving P acquisition by barley (Hordeum vulgare), Rose et al. (2013) suggest root ideotypes for improving the acquisition of P and Zn by rice (Oryza sativa), Lynch (2013) describes a root ideotype for optimizing water and N acquisition by maize (Zea mays), and Botwright Acuña and Wade (2013) describe how exploration of the interactions between genotype and environment (G × E) can be used to identify root traits to overcome mechanical impedance in different soils.

The ideotype of ‘topsoil foraging’ has been proposed for improving P acquisition by roots (Fig. 4A; Lynch and Brown, 2001; White et al., 2005; Lynch, 2007, 2011, 2013; Richardson et al., 2011). The basic premise for this ideotype is that P is immobile in the soil and concentrated in the topsoil (Barber, 1995). Breeding for this root ideotype has proven successful for the development of crops for the low-P soils of Africa, Asia and Latin America (Lynch, 2007, 2011, 2013). This ideotype should also suit the acquisition of other immobile mineral elements concentrated in the topsoil, such as manganese, copper and nickel (White and Greenwood, 2013). It is complemented by proliferation of lateral roots locally in regions of high P availability, the production of long root hairs, associations with mycorrhizal fungi, development of cortical aerenchyma, increasing P uptake capacity of root cells, and the secretion of organic acids and phosphatases into the rhizosphere (White et al., 2005; Lambers et al., 2006; Lynch, 2007, 2011, 2013; White and Hammond, 2008; Richardson et al., 2011). Cost–benefit analyses of root traits for improving the P nutrition of crops generally suggest that root hairs have the greatest potential for P acquisition relative to their cost of production, and that the greatest gains are likely to be made by increasing the length and longevity of root hairs rather than by increasing their density (Jungk, 2001; Lynch and Ho, 2005; Brown et al., 2013). Brown et al. (2013) suggest that breeding for a combination of appropriate architectural, anatomical and biochemical traits, such that more root hairs are located in the topsoil, on roots that are metabolically cheap to construct and maintain, that release sufficient organic acids and enzymes to exploit soil P reserves, will improve PUE in systems with low P input. Rose et al. (2013) describe root traits that increase the acquisition of P and Zn by rice. These include traits that (1) increase the phytoavailability of P and Zn in soils, such as the efflux of protons, organic acids, chelating agents (e.g. siderophores for Zn) and hydrolytic enzymes (e.g. phosphatases), or the release of carbon compounds that foster a beneficial microbial community that increase soil P and Zn turnover; (2) increase the volume of soil explored by roots, such as the traits discussed above; and (3) enhance the affinity or capacity for P and Zn uptake by root cells. They discuss the prospects of exploiting these traits in conventional plant breeding using marker-assisted selection or through modern transgenic approaches. In a complementary paper, Claus et al. (2013) use a mathematical model to investigate how membrane transport processes and root anatomy interact to control the uptake and movement of Zn to the xylem in roots of Arabidopsis thaliana. Their model suggests that (1) restricted loading of Zn2+ into the xylem by Heavy Metal ATPases (HMA4) results in symplastic Zn concentrations increasing from the epidermis to the pericycle; (2) Zn2+ influx to root cells through ZIP (ZRT-, IRT-like protein) transporters is regulated on a timescale that provides sufficient Zn for plant nutrition without cytosolic Zn concentrations reaching toxicity; and (3) the rate of transpiration has a profound influence on the radial gradient in symplastic Zn concentration.

Shi et al. (2013) report QTLs associated with heritable root architectural traits of oilseed rape (OSR; Brassica napus) in a doubled-haploid mapping population developed from a cross between a European winter OSR (‘Tapidor’) and a Chinese semi-winter OSR (‘Ningyou 7’) using a high-throughput, agar-based, phenotyping system. They identified a cluster of highly significant QTLs for the number of lateral roots (LRN), the density of lateral roots (LRD), root dry weight (RDW) and shoot dry weight (SDW) at low P supply on chromosome A03, and QTLs for primary root length (PRL) on chromosomes A07 and C06. Interestingly, the QTLs associated with LRN, RDW and SDW on chromosome A03 between 36-8 and 46 cM co-locate with a QTL with pleiotropic effects on RDW, SDW, root volume, root surface area and plant height reported in a cross between P-efficient (‘Eyou Changjia’) and P-inefficient (‘B104-2’) OSR cultivars (Yang et al., 2010, 2011; Ding et al., 2012) and overlap with a QTL affecting shoot biomass and PUE traits on chromosome C03 of Brassica oleracea (Hammond et al., 2009). Similarly, the QTLs associated with PRL on chromosomes A07 and C06 are syntenous with a QTL for PRL in Arabidopsis thaliana (Loudet et al., 2005). These observations suggest that QTLs associated with root architectural traits are conserved within the Brassicaceae, which should facilitate breeding improved root phenotypes in crop brassicas.

It is becoming evident that root architecture is controlled by complex interactions between hormones and other signalling molecules, such as sugars and microRNAs (Hermans et al., 2006; Osmost et al., 2007; Chiou and Lin, 2011; Hammond and White, 2011; Pernet et al., 2011; Smith and De Smet, 2012). In this Special Issue, Niu et al. (2013) review progress in identifying the signalling cascades co-ordinating alterations in root architecture in response to low P availability, emphasizing the roles of the classical plant hormones, nitric oxide and reactive oxygen species, and Koltai (2013) reviews the involvement of strigalactone biosynthesis and signalling in the induction of lateral roots and the increase in root hair length and density in response to P starvation, noting that strigalactones appear to exert their effects by altering the balance between auxin and ethylene...
signalling pathways (Ruyter-Spira et al., 2011; Mayzlish-Gati et al., 2012). A particular response to P starvation is the initiation of lateral roots, and a detailed study of the maize lrt1 mutant by Husáková et al. (2013) in this Special Issue suggests that the Lrt1 gene affects the spatial distribution and morphology of lateral roots, but not their abundance. This gene is also required for correct cell division in the cortex and the development of the exodermis of primary roots.

An ideotype termed ‘steep, cheap and deep’ has been proposed for the acquisition of nitrogen from agricultural soils (Fig. 4C; Dunbabin et al., 2003; Lynch, 2013). The basic premise for this ideotype is that nitrate, which is the dominant form of nitrogen in agricultural soils, is highly soluble and its location moves deeper in the soil during the growing season as the water table drops (Lynch, 2013). The ideotype seeks to improve nitrate acquisition by accelerating the development of roots at depth and, thereby, reduce nitrate leaching and improve NUE. Lynch (2013) describes root traits contributing to this ideotype in maize. These include: (1) a thick, unbranched primary root; (2) the combination of a few deep, thick and relatively unbranched seminal or crown roots with many thin, shallow seminal or crown roots with prolific lateral branching and an abundance of root hairs; (3) a complete whorl of relatively unbranched brace roots, that are shallower than the crown roots;
yield depends greatly upon environmental conditions. In this Special Issue, Rostamza et al. (2013) report that the responses of primary and nodal roots to soil water availability differ both between root types and between plant species. They grew the drought-tolerant cereals sorghum (Sorghum bicolor) and pearl millet (Pennisetum glaucum) for 3 weeks in pots in which primary and nodal roots were contained in separate compartments. They observed that decreasing water availability to either the entire root system or just nodal roots decreased the length of the whole root system in both sorghum and pearl millet and that the nodal roots of both millet and sorghum grew more vertically in dry soil. Reducing water availability to either the entire root system or just nodal roots decreased the length of the primary root system but not that of the nodal root system in sorghum. By contrast, although decreasing water availability to the entire root system similarly decreased the length of the primary root system but not that of the nodal root system in pearl millet, reducing water availability to just nodal roots decreased the length of the nodal root system but not the primary root system in pearl millet.

Many techniques are available to assess root architectures of young seedlings grown in the laboratory or glasshouse (Gregory et al., 2009; Zhu et al., 2011), but these have rarely been compared with measurements obtained under field conditions. In this Special Issue, Watt et al. (2013) have assessed whether simple measurements of the length of the longest seminal roots of bread wheat (Triticum aestivum) seedlings grown for 15–20 days in rolls of moist germination paper are correlated with measurements of length and depth of root systems of plants grown in the field. They observe that the sum of the lengths of the two longest seminal roots was positively correlated with the total root length of seedlings grown in germination paper. They also observed positive correlations between the sum of the lengths of the two longest seminal roots of wheat seedlings grown in germination paper and the length and depth of root systems of plants with 2–5 leaves growing in the field. However, they did not observe any significant correlation between rooting depth at the reproductive stage and either the sum of the lengths of the two longest seminal roots of seedlings grown in germination paper or the rooting depth of young plants grown in the field. They attribute this lack of correlation to environmental factors, which might change during the season or through the soil profile, that affect wheat genotypes differently.

Many agricultural soils have compacted subsoils that can occur naturally but are often the result of the passage of heavy machinery. The dense soil, together with the absence of continuous macropores, limits the depth of root systems, their access to water and mineral elements and, ultimately, crop yields (Hamza and Anderson, 2005; Whalley et al., 2006; Valentine et al., 2012). To penetrate soil the root requires pressure both to expand a cavity and to overcome the root–soil friction associated with elongating into the cavity (McKenzie et al., 2013). The friction component can be a substantial part of the total penetration resistance. Root traits improving penetration of strong soils include greater root diameter, increased release of border cells and secretion of mucilage at the root tip, stiffening of cell walls, and the proliferation of longer root hairs closer to the root tip for anchorage (Clark et al., 2008; Bengough et al., 2011; McKenzie et al., 2013). Several researchers have reported genotypic variation in the ability of cereal roots to penetrate wax
CONCLUSIONS AND PERSPECTIVE

Cultivated plants provide most of the dietary energy, vitamins and minerals for the world’s human population. In the recent past, crop production has kept pace with the increasing human population. This was achieved primarily through irrigation and the application of pesticides, herbicides and chemical fertilizers to high-yielding crop genotypes adapted to specific climates and agronomic practices in monoculture systems (Evans, 1997; Godfray et al., 2010; Fageria et al., 2011). There is still the possibility of increasing crop yields, especially in rainfed and extensive agricultural systems (Mueller et al., 2012; White et al., 2012). Globally, yield gaps of 45–70% of the theoretically possible yield are observed for most crops (Lobell et al., 2009; Neumann et al., 2010; Mueller et al., 2012). However, there is now an imperative for sustainable intensification of crop production, which entails the reduction of inputs whilst increasing yield and quality (Lynch, 2007; Wissuwa et al., 2009; Godfray et al., 2010; Fageria et al., 2011; Good and Beatty, 2011; White et al., 2012). This will require greater efficiency in the utilization of natural resources, such as water, mineral elements and soils, for agricultural production. The efficient acquisition of water and mineral elements by plant roots is, therefore, a prerequisite for sustainable intensification of crop production. Improving resource capture by roots can help reduce irrigation and fertilizer inputs, emissions of greenhouse gases and the eutrophication of water bodies. This concluding section provides a brief summary of the strategies described in this Special Issue for developing crops with appropriate root systems for reduced-input monoculture systems, and examines whether knowledge of plant ecology could be used to increase resource use efficiency and yields using traditional or novel polyculture systems.

Developing crops for reduced-input monoculture systems

The success of reduced-input monoculture systems will require greater efficiencies in the acquisition and utilization of water and mineral elements by crops. The development of crop genotypes with greater resource use efficiencies requires the identification of beneficial traits, the availability of genetic variation in these traits, and the ability to select either for the trait itself or for the alleles conferring this trait. Several articles in this Special Issue describe root ideotypes associated with efficient capture of water and mineral elements (Botwright Acuña and Wade, 2013; Brown et al., 2013; Jaramillo et al., 2013; Lynch, 2013; Rose et al., 2013). These include the ‘topsoil foraging’ root architectural ideotype for the efficient acquisition of phosphorus from agricultural soils (Fig. 4A) and the ‘steep, cheap and deep’ root architectural ideotype that allows greater acquisition of water during progressive drought and the efficient acquisition of nitrogen from agricultural soils (Fig. 4C). There is substantial variation among genotypes of many crops in the individual root traits that comprise these ideotypes, and chromosomal loci (QTL) affecting these traits have been identified (White et al., 2005, 2012; Beebe et al., 2006; Lynch, 2007, 2013; Cichy et al., 2009; Hammond et al., 2009; Li et al., 2009; Liang et al., 2010; Chin et al., 2011; Hund et al., 2011; Cai et al., 2012; Gamuyao et al., 2012; Ren et al., 2012; Shi et al., 2013). Indeed, selection and breeding for the ‘topsoil foraging’ root architectural ideotype has already proven successful for the development of crops for the low-P soils of Africa, Asia and Latin America (Lynch, 2007, 2011, 2013). The development of high-throughput techniques for assessing aspects of root architecture linked to greater yields in reduced-input agricultural systems will allow larger plant populations to be screened for the identification of appropriate genotypes and the mapping of further QTL affecting root architectural traits, accelerating crop improvement (Gregory et al., 2009; Trachsel et al., 2011; Zhu et al., 2011; Clark et al., 2013; Lynch, 2013).
Crops could also be developed to improve the sustainability of soil resources. The roots of such crops might deposit more, or more-recalcitrant, carbon into the soil (Kell, 2011), promote the presence of beneficial biological communities and processes (Subbarao et al., 2007), or exert a direct impact on the physical structure and stability of soils (Loades et al., 2010). Two of the greatest ecological disasters of the past century, the Great Dust Bowl in the USA and the erosion of the Loess Plateau in China, were caused by agricultural practices that resulted in a deficiency in root traits providing soil stability (Kaiser, 2004).

In addition to reducing the use of mineral fertilizers, proponents of sustainable agricultural practices often advocate a reduction in the use of herbicides. It was estimated that 20–40% of crop production is lost to competition with weeds when herbicides are not applied (Oerke, 2006). The roots of weeds compete with those of crops for below-ground resources. Dunbabin (2007) explored how root architecture affected crop productivity in the presence of weeds using the ROOTMAP model. She observed that crop yield was improved by rapid root growth and greater foraging intensity. These traits denied weeds access to soil resources and, thereby, maintained crop yields (Dunbabin, 2007). The development of crop genotypes for rapid establishment and exploitation of the soil volume might allow a reduction in the use of herbicide.

Translating ecological observations to improve the productivity of polyculture systems

Traditional low-input agricultural systems are often based on rotations or polycultures of different plant species (Gliessman, 1992; Staat et al., 2001; Ndakidemi, 2006; Eichhorn et al., 2006; Knörzer et al., 2009; Lithourgidis et al., 2011; Zegada-Lizarazu and Monti, 2011; Altieri et al., 2012; Feike et al., 2012). Traditional polycultures include pastoral systems, cereal/legume and cereal/vegetable polycultures, such as the ‘Three Sisters’ polyculture of maize, beans (Phaseolus vulgaris) and squash (Cucurbita sp.), intercropping with cassava (Manihot esculenta), silvoagricultural systems, home-gardens, and the rice/fish systems prevalent in the paddies of Asia and elsewhere (Gliessman, 1992; Altieri, 2004; Ndakidemi, 2006; Amanullah et al., 2007; Knörzer et al., 2009; Koohafkan and Altieri, 2010; Seran and Brintha, 2010; Lansing and Kremer, 2011; Altieri et al., 2012; Feike et al., 2012; Nerlich et al., 2013). It has been hypothesized that both niche complementarity and facilitation enable polyculture systems to yield more than their corresponding monocultures (Gliessman, 1992; Altieri, 2004; Li et al., 2007; Seran and Brintha, 2010; Lithourgidis et al., 2011; Altieri et al., 2012; Postma and Lynch, 2012). In particular, it is hypothesized that crops grown with legumes benefit greatly from the extra nitrogen that N₂-fixation brings into the system (Ndakidemi, 2006; Temperton et al., 2007; Bessler et al., 2012), and that roots of benefactor species might secrete organic acids and enzymes that increase the phytoavailability of, for example, P in the soil (Ndakidemi, 2006; Li et al., 2007). Postma and Lynch (2012) have investigated niche complementarity of rooting in the maize–bean–squash (Cucurbita pepo) polyculture using the functional–structural plant model SimRoot. These crops differ in both root architectures and foraging strategies. It was observed that, although polycultures acquired more N than the corresponding monocultures in soils with low fertility, this was a consequence of complementary root architectures and was independent of N₂-fixation by the legume. They also observed that complementary root architectures had negligible effects on the acquisition of phosphorus and potassium, and suggested that few roots of neighbouring plants are close enough to benefit from the root exudates of their neighbours or for roots of neighbouring plants to compete for immobile mineral elements (Postma and Lynch, 2012). Considering these intriguing results, it would seem that the implementation of novel polycultures might benefit from an improved understanding of how roots of different plant species complement each other to achieve greater overall productivity. Some of these interactions might be investigated using the methods reviewed in this Special Issue (Blossfeld et al., 2013; Faget et al., 2013). If the nature and consequences of below-ground interactions between plants can be predicted accurately, it might then be possible to design and manipulate the species composition of polycultures and the varietal composition of monocultures to achieve consistently greater productivity in a sustainable manner.

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LITERATURE CITED


