

Matching roots to their environment

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Overview Article

Matching Roots to Their Environment

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ABSTRACT

● *Background* Plants form the base of the terrestrial 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 to play in soil sustainability, carbon sequestration, reducing emissions of greenhouse gasses, and in preventing the eutrophication of water bodies associated with the application of mineral fertilisers.

● *Scope* This article provides the context for a Special Issue of *Annals of Botany* on ‘Matching Roots to Their Environment’. It 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 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 phenotypes that improve the acquisition of mineral elements and water, and discusses high-throughput methods to screen for these traits in the laboratory, glasshouse and field. Finally, it considers whether knowledge of adaptations improving the acquisition of resources in natural environments can be used to develop root systems for sustainable agriculture in the future.

Key words: Anatomy, arabidopsis, cereal, evergreen revolution, fertiliser use efficiency, legume, morphology, nitrogen, phosphorus, physiology, potassium, water.

INTRODUCTION

Land plants support most terrestrial life. They form the base of the food chain and also provide medicines, fuel, fibre and industrial materials for humans. Cultivated plants provide about 83% of the dietary energy for the world's population directly and 16% indirectly through animal products (Figure 1). Less than 1.2% of the dietary energy for the world's population comes from aquatic products, fish and seafood. Similarly, edible crops deliver between 83-94% of the minerals and 70-99% of the vitamins (with the exception of vitamins A and B12, which mostly come from animal products) to human diets (Figure 1). Meyer *et al.* (2012) estimated that just over 100 terrestrial plant species contribute more than 90% of the world's food supply. Plants must acquire the water and mineral elements, essential for their survival in nature or their yield and nutritional quality in agriculture, through their roots (White and Brown, 2010).

Major fluxes of all elements occur through land plants and, in particular, their root systems (Figure 2). Interactions between plant roots and their surroundings during evolutionary time have led to many fundamental changes in the Earth's environment, including a decrease in atmospheric carbon dioxide (CO₂), a lowering of the temperature of the Earth's surface, and the formation of complex soil environments (Kenrick and Crane, 1997; Raven and Edwards, 2001; Pires and Dolan, 2012). The interactions between plant roots and their surroundings 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 (Figure 2; Rockström *et al.*, 2009; Canfield *et al.*, 2010). The roots of agricultural crops, both annual and perennial, have a significant role to play in sequestering C belowground (Norby and Jackson, 2000; Kell, 2011), in decreasing

the emissions of greenhouse gasses (GHG; CO₂, NO, N₂O) from agriculture (Smith *et al.*, 1997, 2008; Hofstra and Bouwman, 2005; Galloway *et al.*, 2008; 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 fertilisers (Conley *et al.*, 2009; Rockström *et al.*, 2009; Vitousek *et al.*, 2009; Good and Beatty, 2011). Plant roots also have a role to play in sustaining the productivity of agricultural soils, by stabilising them physically, by improving their structure, and by driving microbial processes, through substrate inputs, that maintain soil fertility (Feeney *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 wellbeing 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 colonised 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, 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 colonisation 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 specialised 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 root hairs, had evolved at least 400 million years ago (Raven and Edwards, 2001).

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 Ziegler, 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, 2012*ab*). 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 (Figure 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 colonisation of the land, plants evolved strategies to acquire water and essential mineral elements from the soil. These included 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 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 solubilising 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).

1 Many interactions between neighbouring plants occur belowground. Competitive
 2 interactions often dominate in environments with ample supplies of mineral elements
 3 (Schenk, 2006; Brooker *et al.*, 2008; Trinder *et al.*, 2012). The root systems of fast-growing,
 4 competitive species appear to be adapted for rapid exploration of the soil volume, especially
 5 the topsoil, by having low tissue densities and highly branched architectures, both of which
 6 contribute to high specific root lengths (Wright and Westoby, 1999; Wahl and Ryser, 2000;
 7 Craine *et al.*, 2001; Comas and Eissenstat, 2004; Holdaway *et al.*, 2011). This phenotype is
 8 also observed in many invasive species and is typical of most crops (Craine *et al.*, 2001;
 9 White *et al.*, 2005; Lynch, 2007). Greater seed reserves and efficient root foraging also
 10 improve the establishment and growth of seedlings in resource-poor soils (White and
 11 Veneklaas, 2012), but the roots of adapted species tend to be thinner and tissues denser than
 12 those of other species, especially in P-limited environments (Wright and Westoby, 1999;
 13 Holdaway *et al.*, 2011). In resource-poor environments, more facilitative interactions appear
 14 to occur between plants (Brooker *et al.*, 2008). One well-studied example is the improved N-
 15 nutrition and growth of beneficiary plants in the presence of legumes. Beneficiary plants are
 16 able to acquire more N in the presence of legumes either because competition for soil N from
 17 legumes is not as intense as that from other species or because they obtain additional N
 18 indirectly from legumes either because they release more N into the soil or because resources
 19 are exchanged between plants through mycorrhizae (Temperton *et al.*, 2007; Fornara and
 20 Tilman, 2009; Bessler *et al.*, 2012). Similarly it has been observed that neighbouring
 21 mycorrhizal plants can benefit the mineral nutrition of non-mycorrhizal plants (Schenk,
 22 2006). It has been speculated that increased secretion of protons, organic acids or enzymes
 23 into the soil by benefactor plants can facilitate the mineral nutrition of neighbouring plants
 24 directly, and that interactions between roots of benefactor plants and soil organisms, whether
 25 beneficial or pathogenic, can improve the growth of beneficiary plants (Schenk, 2006; Li *et*

1 *al.*, 2007; de Kroon *et al.*, 2012). However, detailed studies reporting the interactions between
 2 roots of neighbouring plants and the rhizosphere changes effected by roots are scarce.

3 In this Special Issue, **Faget *et al.* (2013)** and **Blossfeld *et al.* (2013)** describe a variety
 4 of novel, non-invasive methods to study spatial and temporal aspects of root development and
 5 rhizosphere processes *in vivo*. Faget *et al.* (2013) review methods that will allow researchers
 6 to identify the roots of individual plants (or particular species) within the soil including
 7 genotype-marking using the expression of fluorescent proteins (Faget *et al.*, 2009, 2012) or
 8 $^{11}\text{CO}_2$ -labelling combined with positron emission tomography (Jahnke *et al.*, 2009). Formerly,
 9 dyes might have been injected into the phloem to identify the roots of individual plants or
 10 species-specific infrared or fluorescence characteristics might have been used (Rewald *et al.*,
 11 2012). Faget *et al.* (2013) also discuss methods for tracking individual roots in sequential
 12 images from rhizotron tubes or high-throughput phenotyping systems (Dupuy *et al.*, 2010b;
 13 Iyer-Pascuzzi *et al.*, 2010; Galkovsky *et al.*, 2012; Nagel *et al.*, 2012) and from the sequential
 14 3D images obtained using magnetic resonance imaging (Rascher *et al.*, 2011), X-ray
 15 computed tomography (Gregory *et al.*, 2003; Perret *et al.*, 2007; Flavel *et al.*, 2012; Mairhofer
 16 *et al.*, 2012) or optical computed tomography (Clark *et al.*, 2011; Downie *et al.*, 2012). These
 17 methods will complement and parameterise architectural and continuum root system models
 18 to facilitate studies of the interactions between roots, rhizospheres and soils (Dunbabin, 2007;
 19 Dupuy *et al.*, 2010a; Postma and Lynch, 2012). Blossfeld *et al.* (2013) describe the use of
 20 commercially available planar optodes and fluorescence microscopy to quantify the spatial
 21 and temporal dynamics of changes in pH and CO_2 concentrations in the rhizospheres of
 22 durum wheat (*Triticum durum*), chickpea (*Cicer arietinum*) and the native Australian legume
 23 *Viminaria juncea* whilst growing in rhizoboxes either separately or together.

24 It is evident that plant roots influence the physical, chemical and biological properties
 25 of the rhizosphere profoundly (Hinsinger *et al.*, 2009; Marschner, 2012; Neumann and

Römheld, 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; Dunbabin *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 (Figure 1). Today, forests are responsible for most of the CO₂ fixed by terrestrial ecosystems (Luyssaert *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 (Luyssaert *et al.*, 2007; Kattge *et al.*, 2011; Kempes *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 two 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 belowground 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 (Figure 2; Galloway, 2008; Schlesinger, 2009). These occur primarily through lightning ($\sim 5 \text{ Tg N y}^{-1}$), biological N_2 -fixation ($100\text{-}300 \text{ Tg N y}^{-1}$, of which $20\text{-}50 \text{ Tg N y}^{-1}$ occurs in agricultural systems), burning of fossil fuels ($\sim 25 \text{ Tg N y}^{-1}$) and the application of N-fertilisers ($>125 \text{ Tg N}$, of which about 106 Tg N was applied in the form of chemical fertilisers in 2010; FAO, 2011). Subbarao *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-fertilisers, problematic leaching of nitrate to

watercourses, and high emissions of greenhouse gasses. The land accumulates about 9 Tg N y^{-1} , whilst about 77 Tg N y^{-1} is accumulated in rivers and groundwater, about 54 Tg N y^{-1} is accumulated in the oceans via the atmosphere, and about 109 Tg N y^{-1} is returned to the atmosphere through denitrification processes (Schlesinger, 2009). About 25 Tg N y^{-1} is emitted into the atmosphere as N_2O 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-fertilisers 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 2,500 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 fertiliser 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 phytoavailabilities 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 fertilisers, and irrigation (Evans, 1997; Godfray *et al.*, 2010; Fageria *et al.*, 2011). The amounts of mineral fertilisers 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 fertilisers (Erisman *et al.*, 2008; Dawson and Hilton, 2011). The environmental consequences of using mineral fertilisers 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 fertilisers 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 fertilisers (Fageria, 2009; Wissuwa *et al.*, 2009; White *et al.*, 2012). Agronomic strategies to improve fertiliser 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 runoff, and optimising the placement, timing, chemistry and quantity of any fertiliser applications (Fageria *et al.*, 2011; Good and Beatty, 2011; McLaughlin *et al.*, 2011; Richardson *et al.*, 2011; Simpson *et al.*, 2011; James and Baldini, 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 utilised 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 utilisation efficiency (NUE; yield / N acquired) contributes more than N

acquisition efficiency (NUpE; N acquired / N available) to agronomic N use efficiency (NUE, yield / 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; Beaty *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 utilisation efficiency (KUtE) within crop species, agronomic K use efficiency (KUE) is often correlated with KUpE rather than KUtE (Rengel and Damon, 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 optimising 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 (Figure 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

1 and concentrated in the topsoil (Barber, 1995). Breeding for this root ideotype has proven
 2 successful for the development of crops for the low P soils of Africa, Asia and Latin America
 3 (Lynch, 2007, 2011, 2013). This ideotype should also suit the acquisition of other immobile
 4 mineral elements concentrated in the topsoil, such as manganese, copper and nickel (White
 5 and Greenwood, 2013). It is complemented by proliferation of lateral roots locally in regions
 6 of high P availability, the production of long root hairs, associations with mycorrhizal fungi,
 7 development of cortical aerenchyma, increasing P uptake capacity of root cells, and the
 8 secretion of organic acids and phosphatases into the rhizosphere (White *et al.*, 2005; Lambers
 9 *et al.*, 2006; Lynch, 2007, 2011, 2013; White and Hammond, 2008; Richardson *et al.*, 2011).
 10 Cost-benefit analyses of root traits for improving the P nutrition of crops generally suggest
 11 that root hairs have the greatest potential for P acquisition relative to their cost of production,
 12 and that the greatest gains are likely to be made by increasing the length and longevity of root
 13 hairs rather than by increasing their density (Junk, 2001; Lynch and Ho, 2005; Brown *et al.*,
 14 2013). **Brown *et al.* (2013)** suggest that breeding for a combination of appropriate
 15 architectural, anatomical and biochemical traits, such that more root hairs are located in the
 16 topsoil, on roots that are metabolically cheap to construct and maintain, that release sufficient
 17 organic acids and enzymes to exploit soil P reserves, will improve PUE in systems with low P
 18 input. **Rose *et al.* (2013)** describe root traits that increase the acquisition of P and Zn by rice.
 19 These include traits that (1) increase the phytoavailability of P and Zn in soils, such as the
 20 efflux of protons, organic acids, chelating agents (e.g. siderophores for Zn) and hydrolytic
 21 enzymes (e.g. phosphatases), or the release of carbon compounds that foster a beneficial
 22 microbial community that increase soil P and Zn turnover, (2) increase the volume of soil
 23 explored by roots, such as the traits discussed above, and (3) enhance the affinity or capacity
 24 for P and Zn uptake by root cells. They discuss the prospects of exploiting these traits in
 25 conventional plant breeding using a 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 Zn^{2+} into the xylem by Heavy Metal ATPases (HMA4) results in symplastic Zn concentrations increasing from the epidermis to the pericycle, (2) Zn^{2+} 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 double haploid mapping population developed from a cross between a European winter OSR (cv. Tapidor) and a Chinese semi-winter OSR (cv. 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 Pi 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 (cv. Eyou Changjia) and P-inefficient (cv. 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; Osmont *et al.*, 2007; Chiou and Lin, 2011; Hammond and White, 2011; Péret *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, emphasising 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 in 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 (Figure 4B; 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 whorl of relatively unbranched brace roots of high occupancy, that are shallower than the crown roots, (4) lateral branching that is unresponsive to local N availability, (5) an abundance of cortical aerenchyma, and (6) a high affinity and high capacity for nitrate uptake by root epidermal cells. Lynch (2013) suggests that many features of this ideotype are relevant to other cereals and also to dicotyledonous crops. Furthermore, breeding crops with deep, extensive root systems, is not only a strategy to capture water and nitrate, but should also be effective in capturing other mineral elements subject to leaching, such as sulphate (Eriksen, 2009; Chien *et al.*, 2011), minimising soil erosion (Loades *et al.*, 2010), and sequestering C in the soil (Kell, 2011).

Subbarao *et al.* (2013) discuss the possibilities of manipulating the release of inhibitors of nitrification from roots to limit the amount of N cycling through the soil nitrification pathway and, thereby improve NUE and minimise N pollution from agricultural systems. Substances effecting ‘biological nitrification inhibition’ (BNI) include the unsaturated fatty acids linoleic acid and linolenic acid and their esters, the phenyl propanoids methyl-p-coumarate and methyl ferulate, the di-terpenoid brachialactone, various isothiocyanates, methyl 3-(4-hydroxyphenyl) propionate and sorgoleone (Subbarao *et al.*, 2013). The release of these substances appears to occur in regions of the root exposed directly to NH_4^+ under mildly-acidic conditions. The authors report extensive genetic variation in BNI both between and within plant species. In general, forage grasses adapted to low N-input systems have higher BNI than those adapted to high N-input systems, cereals often have low BNI, and many legumes have negative BNI (Subbarao *et al.*, 2007, 2013). However, there is considerable variation in BNI between genotypes of, for example, the forage grass *Brachiaria humidicola*, small-grained cereals, and soybean (Subbarao *et al.*, 2007, 2013), which allows

the possibility of breeding crops with increased BNI. Subbarao *et al.* (2013) provide evidence that crops with high BNI capacity can improve NUE whilst reducing the rate of ammonium oxidation, nitrate leaching and N₂O emissions from agricultural soils.

Water scarcity limits food production in many regions of the world (Boutraa, 2010; de Fraiture and Wichelns, 2010). The ‘*steep, cheap, and deep*’ root architectural ideotype allows greater acquisition of water during progressive drought as the water table drops (Lynch, 2013). Genotypes with deeper roots generally have greater yields than shallow-rooted genotypes under drought conditions (Ho *et al.*, 2005; Hund *et al.*, 2009; Lopes and Reynolds, 2010; Henry *et al.*, 2011) and deeper rooting is more prevalent among species found in dry environments (Schenk and Jackson, 2005). Reducing the metabolic cost of roots, either by producing thinner roots or roots with more aerenchyma, allows longer root systems to be produced and maintained (Zhu *et al.*, 2010; Lynch, 2013). In this Special Issue, **Jaramillo *et al.* (2013)** observe that root respiration among six maize genotypes growing in soil columns was positively correlated with living cortical area (LCA), and that increasing the area of root cortical aerenchyma decreased root respiration. They report that a 3.5 fold reduction in LCA is associated with a 2.5 fold improvement in growth under drought, which supports the hypothesis that drought tolerance can be improved by decreasing the metabolic costs of root exploration of the soil.

The root system of cereals comprises at least two distinct root types: primary roots, which originate from the embryo, and nodal roots, which emerge subsequently from stem nodes. The relative contribution of each type of root to resource acquisition and crop 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 three 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

1 lack of correlation to environmental factors that might change during the season or through
 2 the soil profile that affect wheat genotypes differently.

3 Many agricultural soils have compacted subsoils that can occur naturally but are often
 4 the result of the passage of heavy machinery. The dense soil, together with the absence of
 5 continuous macropores, limits the depth of root systems, their access to water and mineral
 6 elements and, ultimately, crop yields (Hamza and Anderson, 2005; Whalley *et al.*, 2006;
 7 Valentine *et al.*, 2012). To penetrate soil the root requires pressure both to expand a cavity
 8 and to overcome the root-soil friction associated with elongating into the cavity (McKenzie *et*
 9 *al.*, 2013). The friction component can be a substantial part of the total penetration resistance.

10 Root traits improving penetration of strong soils include greater root diameter, increased
 11 release of border cells and secretion of mucilage at the root tip, stiffening of cell walls, and
 12 the proliferation of longer root hairs closer to the root tip for anchorage (Clark *et al.*, 2008;
 13 Bengough *et al.*, 2011; McKenzie *et al.*, 2013). Several researchers have reported genotypic
 14 variation in the ability of cereal roots to penetrate wax barriers in the laboratory, which is
 15 often, but not always, correlated with rooting depth and crop performance under field
 16 conditions (Clark *et al.*, 2002; Samson *et al.*, 2002; Cairns *et al.*, 2004; Botwright Acuña *et*
 17 *al.*, 2007; Kubo *et al.*, 2008). In the field, significant G×E interactions occur for this trait,
 18 which has major implications for breeding strategies (Botwright Acuña *et al.*, 2007;
 19 Botwright Acuña and Wade, 2012). For broad selection, the root system of ideal genotypes
 20 will have a high mean depth irrespective of environment, whereas genotypes that will perform
 21 best in particular environments will have high mean rooting depth but this trait will vary
 22 between environments (Botwright Acuña and Wade, 2012). In this Special Issue, **Botwright**
 23 **Acuña and Wade (2013)** explore the reasons for G×E interactions for rooting depth observed
 24 in the field trials of 24 wheat genotypes performed in six environments in Australia. They
 25 observe that G×E interactions accounted for 40 % of the variation in this trait, which was

more than three times greater than that attributed to genotype alone. Clustering of the experimental data using Principal Component Analysis and using genotype plus G×E interaction (GGE) biplots allowed them to explore (1) the characteristics driving separation into different environments and (2) the attributes of the root system partitioning genotypes into these environments. They conclude that this approach is applicable to many crop phenotypes and not only allows the interpretation of complex interactions between plants and their environment but can also inform the selection of appropriate traits for target environments in a crop breeding programme.

In addition to assaying root system architecture in controlled environments, there is a need for simple, cost-effective methods to estimate the size of root systems in the field. Measurement of the electrical capacitance between an electrode in the rooting substrate and an electrode inserted at the base of a stem has been proposed as a suitable technique for screening large plant populations (Chloupek, 1977; Chloupek *et al.*, 2006, 2010; Středa *et al.*, 2012). Many studies have reported good linear correlations between the measured capacitance and root mass (Dietrich *et al.*, 2012; Ellis *et al.*, 2013), and these relationships have generally been interpreted using an electrical model in which roots are considered to behave as cylindrical capacitors wired in parallel (Dalton, 1995). Recently, however, this model has been re-evaluated (Dietrich *et al.*, 2012; Ellis *et al.*, 2013). In this Special Issue, **Dietrich *et al.* (2013)** have tested and validated, for plants growing in soil, an alternative electrical model in which plant tissues and the rooting substrate behave as capacitors wired in series. These results imply that, whilst the measured capacitance might often be correlated with root mass, capacitance is not a direct measure of root mass, and previous capacitance measurements should be reinterpreted.

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 fertilisers 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 utilisation 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 fertiliser inputs, emissions of greenhouse gasses 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 (Figure 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 (Figure 4B). 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 fertilisers, proponents of sustainable agricultural practices often advocate a reduction in the use of herbicides. It is 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 belowground 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; Stoate *et al.*, 2001; Ndakidemi, 2006; Eichorn *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

1 maize, beans (*Phaseolus vulgaris*) and squash (*Cucurbita* sp.), intercropping with cassava
2 (*Manihot esculenta*), silvoagricultural systems, home-gardens, and the rice / fish systems
3 prevalent in the paddies of Asia and elsewhere (Gliessman, 1992; Altieri, 2004; Ndakidemi,
4 2006; Amanullah *et al.*, 2007; Knörzer *et al.*, 2009; Koohafkan and Altieri, 2010; Seran and
5 Brintha, 2010; Lansing and Kremer, 2011; Altieri *et al.*, 2012; Feike *et al.*, 2012; Nerlich *et*
6 *al.*, 2013). It has been hypothesised that both niche complementarity and facilitation enable
7 polyculture systems to yield more than their corresponding monocultures (Gliessman, 1992;
8 Altieri, 2004; Li *et al.*, 2007; Seran and Brintha, 2010; Lithourgidis *et al.*, 2011; Altieri *et al.*,
9 2012; Postma and Lynch, 2012). In particular, it is believed that crops grown with legumes
10 benefit greatly from the extra nitrogen that N₂-fixation brings into the system (Ndakidemi,
11 2006; Temperton *et al.*, 2007; Bessler *et al.*, 2012), and that roots of benefactor species might
12 secrete organic acids and enzymes that increase the phytoavailability of, for example, P in the
13 soil (Ndakidemi, 2006; Li *et al.*, 2007). Postma and Lynch (2012) have investigated niche
14 complementarity of rooting in the maize, bean, squash (*Cucurbita pepo*) polyculture using the
15 functional-structural plant model *SimRoot*. These crops differ in both root architectures and
16 foraging strategies. It was observed that, although polycultures acquired more N than the
17 corresponding monocultures in soils with low fertility, this was a consequence of
18 complementary root architectures and was independent of N₂-fixation by the legume. They
19 also observed that complementary root architectures had negligible effect on the acquisition
20 of phosphorus and potassium, and suggested that few roots of neighbouring plants are close
21 enough to benefit from the root exudates of their neighbours or for roots of neighbouring
22 plants to compete for immobile mineral elements (Postma and Lynch, 2012). Considering
23 these intriguing results, it would seem that the implementation of novel polycultures might
24 benefit from an improved understanding of how roots of different plant species complement
25 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 belowground 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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FIGURE LEGENDS

FIG. 1. Contribution of terrestrial plant products (green), terrestrial animal products (purple), and aquatic products (blue) to (A) the quantity (kg) of, and dietary energy, protein, (B) mineral elements and (C) vitamins in, the global food supply. Data were estimated from the global supplies of foodstuffs (FAO, 2009) and the composition of individual food items (USDA-ARS, 2012).

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 processes include photosynthesis, respiration, plant uptake, nitrogen fixation, fertiliser 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, fertiliser 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 479 Tg yr⁻¹ for carbon, 3848 Tg yr⁻¹ for nitrogen, 3809 Tg yr⁻¹ for phosphorus and 890 Tg yr⁻¹ for sulphur.

FIG. 3. (A) Cross section of a root of *Nymphaea* sp. with a polyarch stele surrounded by a broad cortex with aerenchyma and astrosclereids. (B) Cross section of a young rice (*Oryza sativa*) root with a polyarch stele and aerenchyma cavities in the mid cortex. (C) Cross section of a young root of *Magnolia x soulangeana* at an early stage of secondary thickening. Cambium activity results in the formation of a few secondary xylem elements in a circle (yellow and red) in addition to the originally triarch vascular cylinder (red xylem elements), whilst the pericycle produces a limited number of suberized cells at an early stage of periderm formation (yellow-green circle). (D) Cross section close to the root tip of a young *Noccaea caerulea* root with a diarch stele. All photographs courtesy of Professor Alexander Lux, Comenius University, Bratislava. Section D courtesy of Dr Ivan Zelko.

FIG. 4. Root ideotypes for efficient acquisition of (A) nitrogen, (B) phosphorus and (C) potassium.