Annals of Botany **112**: 207–222, 2013
doi:10.1093/aob/mct123, available online at www.aob.oxfordjournals.org

ANNALS OF BOTANY Founded 1887

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

Matching roots to their environment

Philip J. White[1,*], Timothy S. George[1], Peter J. Gregory[2,3], A. Glyn Bengough[1,4], Paul D. Hallett[1,†] and Blair M. McKenzie[1]

[1]*The James Hutton Institute, Invergowrie, Dundee, DD2 5DA, UK,* [2]*East Malling Research, East Malling, Kent ME19 6BJ, UK,* [3]*Centre for Food Security, School of Agriculture, Policy and Development, University of Reading, Reading RG6 6AR, UK and* [4]*Division of Civil Engineering, University of Dundee, Dundee DD1 4HN, UK*
[†]*Present address: Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen AB24 3UU, UK.*
* *For correspondence. E-mail philip.white@hutton.ac.uk*

Received: 7 February 2013 Revision requested: 13 February 2013 Accepted: 28 February 2013

• *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 fertilizers.
• *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, fertilizer use efficiency, legume, morphology, nitrogen, phosphorus, physiology, potassium, roots, 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 (Fig. 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 (Fig. 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 for 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 (Fig. 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 (CO_2) concentration, 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 (Fig. 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 below ground (Norby and Jackson, 2000; Kell, 2011), in decreasing the emissions of greenhouse gasses (GHG; CO_2, NO, N_2O) 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 fertilizers (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 stabilizing 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 well-being of the planet itself. This article, which provides the context for a

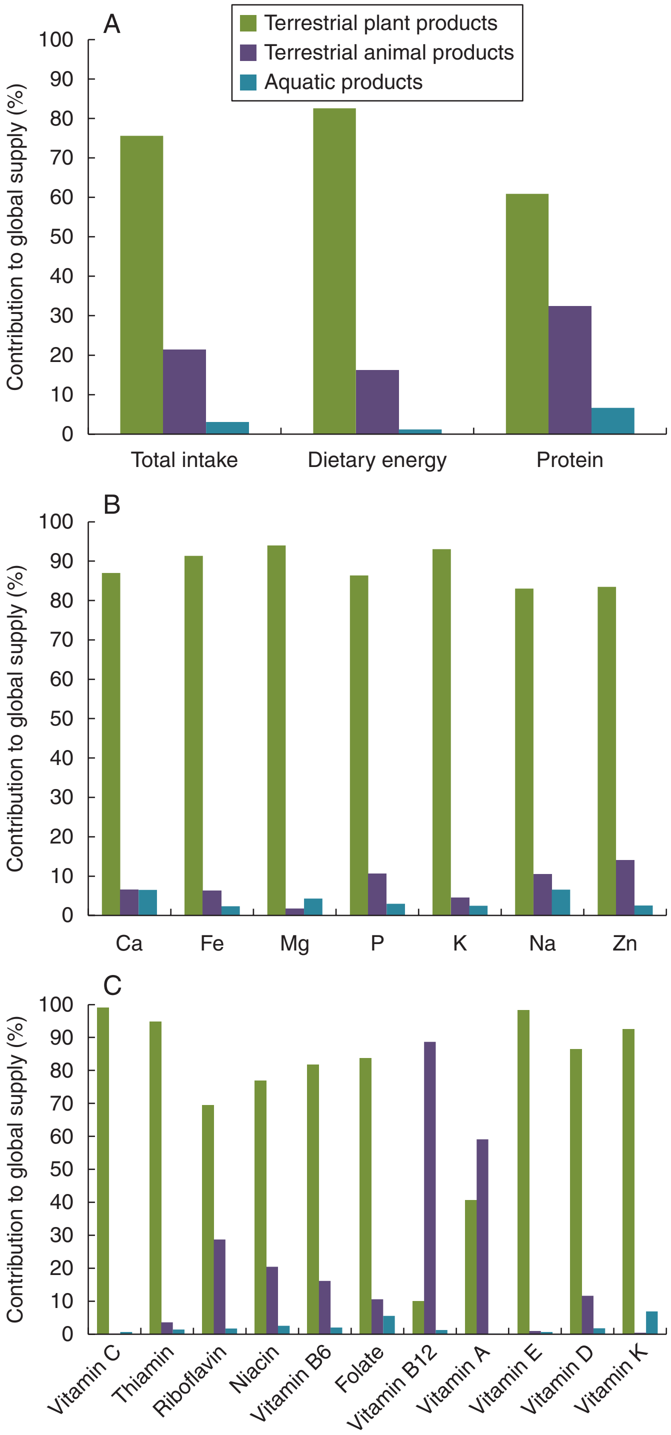


FIG. 1. Contribution of terrestrial plant products, terrestrial animal products and aquatic products to the global supply of foodstuffs in terms of (A) the total quantity, its dietary energy and protein, (B) mineral elements, and (C) vitamins. Data are estimated from the global supplies of foodstuffs (*FAOSTAT*, http://faostat.fao.org/site/345/default.aspx) and the composition of individual food items (USDA-ARS *Nutrient Data Laboratory*, http://www.ars.usda.gov/ba/bhnrc/ndl).

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 CO_2 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 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*a*, *b*). Seago and Fernando (2013) observe that Nympheales 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 Nympheales 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 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

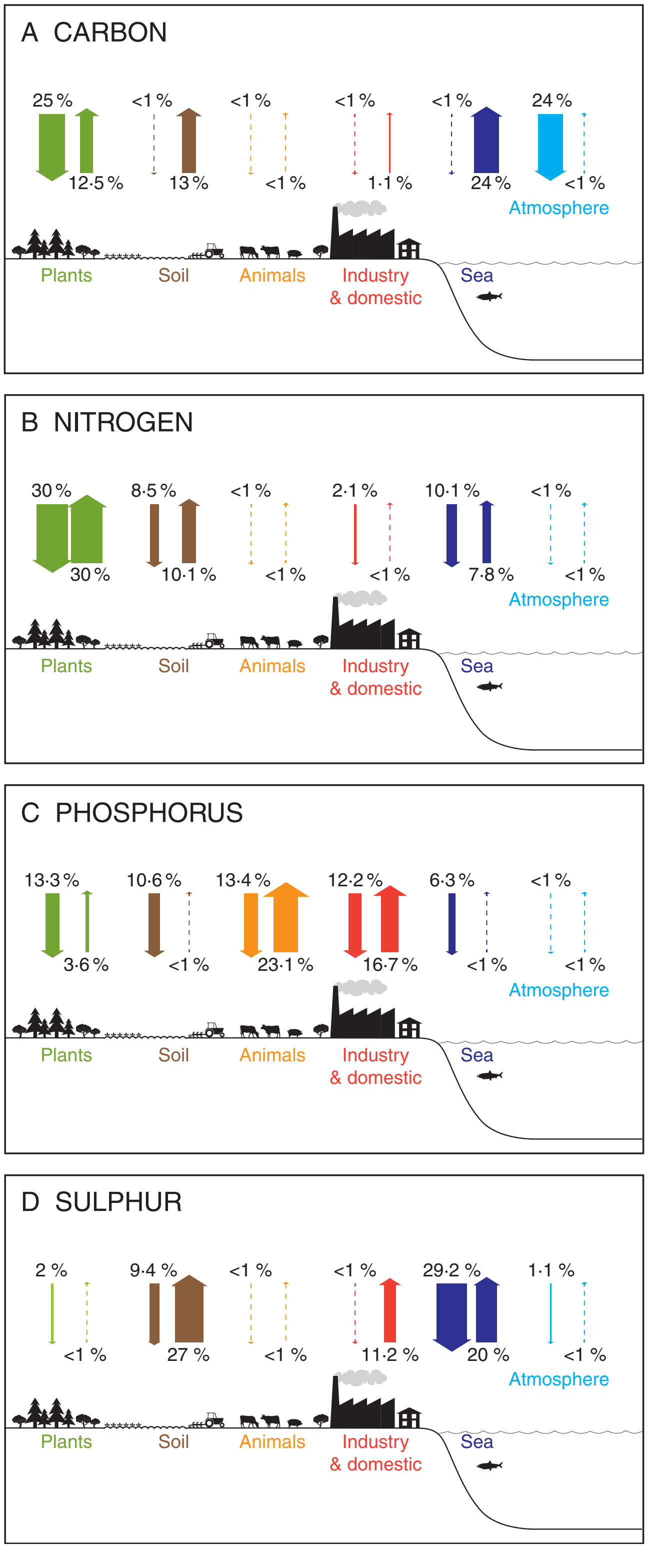


FIG. 2. Global fluxes of (A) carbon, (B) nitrogen, (C) phosphorus and (D) sulphur through different compartments of the environment. Arrows represent fluxes into and out of each compartment. When fluxes into and out of a compartment are unequal the stock of an element in that compartment increases or 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, 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.

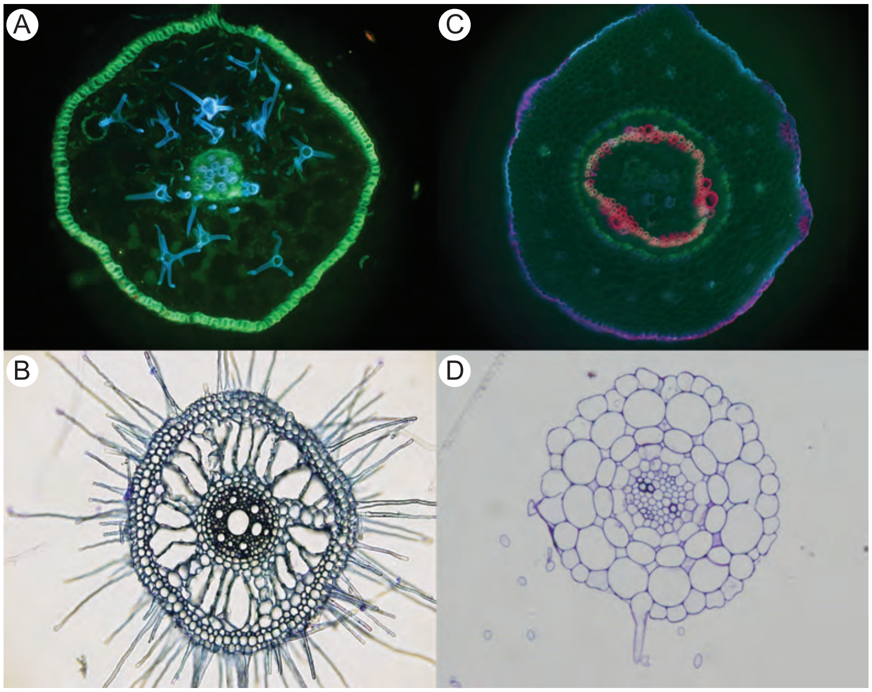


FIG. 3. (A) Cross-section of a root of *Nymphaea* sp. with a polyarch stele surrounded by a broad cortex with aerenchyma and astrosclereids. (B) Cross-section of a young rice (*Oryza sativa*) root with a polyarch stele and aerenchyma cavities in the mid cortex. (C) Cross-section of a young root of *Magnolia 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 caerulescens* root with a diarch stele. All photographs courtesy of Professor Alexander Lux, Comenius University, Bratislava. Section in (D) courtesy of Dr Ivan Zelko.

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 N_2-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 $^{11}CO_2$-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.*, 2010*b*; 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 (Dunbabin, 2007; Dupuy *et al.*, 2010*a*; 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 rhizoboxes 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 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 (Fig. 1). Today, forests are responsible for most of the CO_2 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 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

(~5 Tg N year^{-1}), biological N_2-fixation (100–300 Tg N year^{-1}, of which 20–50 Tg N year^{-1} occurs in agricultural systems), burning of fossil fuels (~25 Tg N year^{-1}) and the application of N-fertilizers (>125 Tg N, of which about 106 Tg N was applied in the form of chemical fertilizers 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-fertilizers, problematic leaching of nitrate to watercourses, and large emissions of greenhouse gasses. 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 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-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 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).

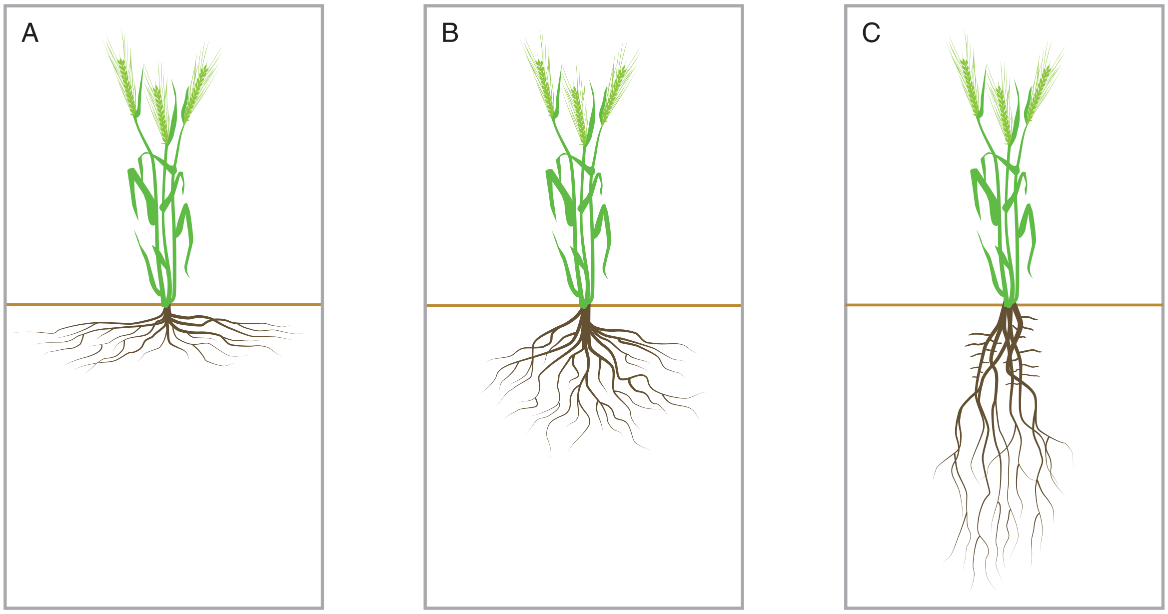
The success of the 'Green Revolution', which increased crop production dramatically during the last half-century, was founded on the development of semi-dwarf crops resistant to pests and pathogens, whose yields are maintained through applications of herbicides, fungicides and pesticides, chemical fertilizers, 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 (NUtE; 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 (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 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 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 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; 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, 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



Topsoil foraging for P
- Early root vigour
- Large root biomass or root/shoot ratio
- More cortical aerenchyma
- Large root surface area (lateral rooting, root hairs) in topsoil
- High root length density
- Proliferation in patches of high P phytoavailability
- Mycorrhizal associations
- Greater exudation of H^+ and organic compounds
- Greater exudation of phosphatases
- Greater phosphate uptake capacity of root cells

Intermediate response for K
- Early root vigour
- Large root biomass or root/shoot ratio
- More cortical aerenchyma
- Large root surface area (lateral rooting, root hairs)
- High root length density
- Proliferation in patches of high K phytoavailability
- Greater exudation of H^+ and organic compounds
- Greater K^+ uptake capacity of root cells
- Greater water uptake through transpiration

Steep, cheap and deep for N
- Early root vigour
- Large root biomass or root/shoot ratio
- More cortical aerenchyma
- Initial roots with shallow growth angles
- Later roots with steep root growth angles
- Large root surface area (lateral rooting, root hairs)
- High root length density
- Greater N-uptake capacity of root cells
- Greater water uptake through transpiration
- Greater exudation of Biological Nitrification Inhibitors
- Greater association with organisms fixing N_2

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

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;

(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), minimizing 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 minimize 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 N_2O 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 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 barriers in the laboratory, which is often, but not always, correlated with rooting depth and crop performance under field conditions (Clark *et al.*, 2002; Samson *et al.*, 2002; Cairns *et al.*, 2004; Botwright Acuña *et al.*, 2007; Kubo *et al.*, 2008). In the field, significant G × E interactions occur for this trait, which has major implications for breeding strategies (Botwright Acuña *et al.*, 2007; Botwright Acuña and Wade, 2012). For broad selection, the root system of ideal genotypes will have a long mean depth irrespective of environment, whereas genotypes that will perform best in particular environments will have long mean rooting depth but this trait will vary between environments (Botwright Acuña and Wade, 2012). In this Special Issue, Botwright Acuña and Wade (2013) explore the reasons for G × E interactions for rooting depth observed in the field trials of 24 wheat genotypes performed in six environments in Australia. They 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 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 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 (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 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 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; Stoate *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 believed that crops grown with legumes benefit greatly from the extra nitrogen that N_2-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 N_2-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.

ACKNOWLEDGEMENTS

This work was supported by the Rural and Environment Science and Analytical Services Division (RESAS) of the Scottish Government through Work Package 3·3, ‘The soil, water and air interface and its response to climate and land use change’ (2011–2016). We thank Professor Alexander Lux of The Comenius University, Bratislava, for the photographs presented in Fig. 3 and Professor Rob Brooker, Dr Lionel Dupuy and Dr Euan James of The James Hutton Institute for comments on an early version of the manuscript.

LITERATURE CITED

Ainsworth EA, Yendrek CR, Skoneczka JA, Long SP. 2012. Accelerating yield potential in soybean: potential targets for biotechnological improvement. *Plant, Cell and Environment* **35**: 38–52.

Altieri MA. 2004. Linking ecologists and traditional farmers in the search for sustainable agriculture. *Frontiers in Ecology and the Environment* **2**: 35–42.

Altieri MA, Funes-Monzote FR, Petersen P. 2012. Agroecologically efficient agricultural systems for smallholder farmers: contributions to food sovereignty. *Agronomy for Sustainable Development* **32**: 1–13.

Amanullah MM, Somasundaram E, Vaiyapuri K, Sathyamoorthi K. 2007. Intercropping in cassava – a review. *Agricultural Reviews* **28**: 179–187.

Barber SA. 1995. *Soil nutrient bioavailability: a mechanistic approach*, 2nd edn. New York: Wiley.

Barker G. 2006. *The agricultural revolution in prehistory: why did foragers become farmers?* Oxford: Oxford University Press.

Barraclough PB, Howarth JR, Jones J, *et al.* 2010. Nitrogen efficiency of wheat: genotypic and environmental variation and prospects for improvement. *European Journal of Agronomy* **33**: 1–11.

Beatty PH, Anbessa Y, Juskiw P, Carroll RT, Wang J, Good AG. 2010. Nitrogen use efficiencies of spring barley grown under varying nitrogen conditions in the field and growth chamber. *Annals of Botany* **105**: 1171–1182.

Beebe SE, Rojas-Pierce M, Yan X, *et al.* 2006. Quantitative trait loci for root architecture traits correlated with phosphorus acquisition in common bean. *Crop Science* **46**: 413–423.

Bengough AG. 2012. Water dynamics of the root zone: rhizosphere biophysics and its control on soil hydrology. *Vadose Zone Journal* **11**(2). doi:10.2136/vzj2011.0111.

Bengough AG, McKenzie BM, Hallett PD, Valentine TA. 2011. Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. *Journal of Experimental Botany* **62**: 59–68.

Berry PM, Spink J, Foulkes MJ, White PJ. 2010. The physiological basis of genotypic differences in nitrogen use efficiency in oilseed rape (*Brassica napus* L.). *Field Crops Research* **119**: 365–373.

Bessler H, Oelmann Y, Roscher C. 2012. Nitrogen uptake by grassland communities: contribution of N_2 fixation, facilitation, complementarity, and species dominance. *Plant and Soil* **358**: 301–322.

Bingham IJ, Karley AJ, White PJ, Thomas WTB, Russell JR. 2012. Analysis of improvements in nitrogen use efficiency associated with 75 years of barley breeding. *European Journal of Agronomy* **42**: 49–58.

Blossfeld S, Schreiber CM, Liebsch G, Kuhn AJ, Hinsinger P. 2013. Quantitative imaging of rhizosphere pH and CO_2 dynamics with planar optodes. *Annals of Botany* **112**: 267–276.

Botwright Acuña TL, Wade LJ. 2012. Genotype × environment interactions for root depth of wheat. *Field Crops Research* **137**: 117–125.

Botwright Acuña TL, Wade LJ. 2013. Use of genotype × environment interactions to understand rooting depth and the ability of wheat to penetrate hard soils. *Annals of Botany* **112**: 359–368.

Botwright Acuña TL, Pasuquin E, Wade LJ. 2007. Genotypic differences in root penetration ability of wheat through thin wax layers in contrasting water regimes and in the field. *Plant and Soil* **301**: 135–149.

Boutraa T. 2010. Improvement of water use efficiency in irrigated agriculture: a review. *Journal of Agronomy* **9**: 1–8.

Broadley MR, White PJ, Hammond JP, Zelko I, Lux A. 2007. Zinc in plants. *New Phytologist* **173**: 677–702.

Brooker RW, Callaghan TV. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* **81**: 196–207.

Brooker RW, Maestre FT, Callaway RM, *et al*. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* **96**: 18–34.

Brown LK, George TS, Dupuy L, White PJ. 2013. A conceptual model of root hair ideotypes for future agricultural environments: what combination of traits should be targeted to cope with limited P availability? *Annals of Botany* **112**: 317–330.

Brundrett MC. 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytologist* **154**: 275–304.

Cai H, Chen F, Mi G, *et al*. 2012. Mapping QTLs for root system architecture of maize (*Zea mays* L.) in the field at different developmental stages. *Theoretical and Applied Genetics* **125**: 1313–1324.

Cairns JE, Audebert A, Townend J, Price AH, Mullins CE. 2004. Effect of soil mechanical impedance on root growth of two rice varieties under field drought stress. *Plant and Soil* **267**: 309–318.

Canfield DE, Glazer AN, Falkowski PG. 2010. The evolution and future of Earth's nitrogen cycle. *Science* **330**: 192–196.

Carminati A, Vetterlein D. 2013. Plasticity of rhizosphere hydraulic properties as a key for efficient utilization of scarce resource. *Annals of Botany* **112**: 277–290.

Chien SH, Mercedes Gearhart M, Villagarcía S. 2011. Comparison of ammonium sulfate with other nitrogen and sulfur fertilizers in increasing crop production and minimizing environmental impact: a review. *Soil Science* **176**: 327–335.

Chin JH, Gamuyao R, Dalid C, *et al*. 2011. Developing rice with high yield under phosphorus deficiency: Pup1 sequence to application. *Plant Physiology* **156**: 1202–1216.

Chiou T-J, Lin S-I. 2011. Signaling network in sensing phosphate availability in plants. *Annual Review of Plant Biology* **62**: 185–206.

Chloupek O. 1977. Evaluation of the size of a plant's root system using its electrical capacitance. *Plant and Soil* **48**: 525–532.

Chloupek O, Forster BP, Thomas WTB. 2006. The effect of semi-dwarf genes on root system size in field-grown barley. *Theoretical and Applied Genetics* **112**: 779–786.

Chloupek O, Dostál V, Středa T, Psota V, Dvořáčková O. 2010. Drought tolerance of barley varieties in relation to their root system size. *Plant Breeding* **129**: 630–636.

Cichy KA, Blair MW, Galeano Mendoza CH, Snapp SS, Kelly JD. 2009. QTL analysis of root architecture traits and low phosphorus tolerance in an Andean bean population. *Crop Science* **49**: 59–68.

Clark LJ, Cope RE, Whalley WR, Barraclough PB, Wade LJ. 2002. Root penetration of strong soil in rainfed lowland rice: comparison of laboratory screens with field performance. *Field Crops Research* **76**: 189–198.

Clark LJ, Price AH, Steele KA, Whalley WR. 2008. Evidence from near-isogenic lines that root penetration increases with root diameter and bending stiffness in rice. *Functional Plant Biology* **35**: 1163–1171.

Clark RT, MacCurdy RB, Jung JK, *et al*. 2011. Three-dimensional root phenotyping with a novel imaging and software platform. *Plant Physiology* **156**: 455–465.

Clark RT, Famoso AN, Zhao K, *et al*. 2013. High-throughput two-dimensional root system phenotyping platform facilitates genetic analysis of root growth and development. *Plant, Cell and Environment* **36**: 454–456.

Claus J, Bohmann A, Chavarría-Krauser A. 2013. Zinc uptake and radial transport in roots of *Arabidopsis thaliana*: a modelling approach to understand accumulation. *Annals of Botany* **112**: 369–380.

Comas LH, Eissenstat DM. 2004. Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology* **8**: 388–397.

Conley DJ, Paerl HW, Howarth RW, *et al*. 2009. Controlling eutrophication: nitrogen and phosphorus. *Science* **323**: 1014–1015.

Cordell D, Drangert JO, White S. 2009. The story of phosphorus: global food security and food for thought. *Global Environmental Change* **19**: 292–305.

Craine JM, Froehle J, Tilman DG, Wedin DA, Chapin FS. 2001. The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. *Oikos* **93**: 274–285.

Dalton FN. 1995. *In-situ* root extent measurements by electrical capacitance methods. *Plant and Soil* **173**: 157–165.

Dawson CJ, Hilton J. 2011. Fertiliser availability in a resource-limited world: production and recycling of nitrogen and phosphorus. *Food Policy* **36**: S14–S22.

Dietrich RC, Bengough AG, Jones HG, White PJ. 2012. A new physical interpretation of plant root capacitance. *Journal of Experimental Botany* **63:** 6149–6159.

Dietrich RC, Bengough AG, Jones HG, White PJ. 2013. Can root electrical capacitance be used to predict root mass in soil? *Annals of Botany* **112**: 457–464.

Ding G, Zhao Z, Liao Y, *et al*. 2012. Quantitative trait loci for seed yield and yield-related traits, and their responses to reduced phosphorus supply in *Brassica napus*. *Annals of Botany* **109**: 747–759.

Dolan L. 2009. Body building on land – morphological evolution of land plants. *Current Opinion in Plant Biology* **12**: 4–8.

Downie H, Holden N, Otten W, Spiers AJ, Valentine TA, Dupuy LX. 2012. Transparent soil for imaging the rhizosphere. *PLoS ONE* **7**: pe44276.

Dunbabin V. 2007. Simulating the role of rooting traits in crop–weed competition. *Field Crops Research* **104**: 44–51.

Dunbabin V, Diggle A, Rengel Z. 2003. Is there an optimal root architecture for nitrate capture in leaching environments? *Plant Cell and Environment* **26**: 835–844.

Dunbabin VM, McDermott S, Bengough AG. 2006. Upscaling from rhizosphere to whole root system: modelling the effects of phospholipid surfactants on water and nutrient uptake. *Plant and Soil* **283**: 57–72.

Dupuy L, Gregory PJ, Bengough AG. 2010*a*. Root growth models: towards a new generation of continuous approaches. *Journal of Experimental Botany* **61**: 2131–2143.

Dupuy L, Vignes M, McKenzie B, White PJ. 2010*b*. The dynamics of root meristem distribution in the soil. *Plant, Cell and Environment* **33**: 358–369.

Eichhorn MP, Paris P, Herzog F, *et al*. 2006. Silvoarable systems in Europe – past, present and future prospects. *Agroforestry Systems* **67**: 29–50.

Ellis T, Murray W, Kavalieris L. 2013. Electrical capacitance of bean (*Vicia faba*) root systems was related to tissue density – a test for the Dalton Model. *Plant and Soil* **366**: 575–584.

Eriksen J. 2009. Soil sulfur cycling in temperate agricultural systems. *Advances in Agronomy* **102**: 55–89.

Erisman JW, Sutton MA, Galloway J, Klimont Z, Winiwarter W. 2008. How a century of ammonia synthesis changed the world. *Nature Geoscience* **1**: 636–639.

Eshel A, Grünzweig JM. 2013. Root–shoot allometry of tropical forest trees determined in a large-scale aeroponic system. *Annals of Botany* **112**: 291–296.

Evans LT. 1997. Adapting and improving crops: the endless task. *Philosophical Transactions of the Royal Society B* **352**: 901–906.

Fageria NK. 2009. *The use of nutrients in crop plants*. Boca Raton, FL: CRC Press.

Fageria NK, Baligar VC, Jones CA. 2011. *Growth and mineral nutrition of field crops*. Boca Raton, FL: CRC Press.

Faget M, Herrera JM, Stamp P, Aulinger-Leipner I, Frossard E, Liedgens M. 2009. The use of green fluorescent protein as a tool to identify roots in mixed plant stands. *Functional Plant Biology* **36**: 930–937.

Faget M, Liedgens M, Feil B, Stamp P, Herrera JM. 2012. Root growth of maize in an Italian ryegrass living mulch studied with a non-destructive method. *European Journal of Agronomy* **36**: 1–8.

Faget M, Nagel KA, Walter A, *et al.* 2013. Root–root interactions: extending our perspective to be more inclusive of the range of theories in ecology and agriculture using *in-vivo* analyses. *Annals of Botany* **112**: 253–266.

FAO [Food and Agriculture Organization of the United Nations]. 2011. *Current world fertilizer trends and outlook to 2015*. Rome, Italy: FAO.

Feeney D, Crawford JW, Daniell TJ, *et al.* 2006. 3D micro-organisation of the soil–root–microbe system. *Microbial Ecology* **52**: 151–158.

Feike T, Doluschitz R, Chen Q, Graeff-Hönninger S, Claupein W. 2012. How to overcome the slow death of intercropping in the North China Plain. *Sustainability* **4**: 2550–2565.

Flavel RJ, Guppy CN, Tighe M, Watt M, McNeill A, Young IM. 2012. Non-destructive quantification of cereal roots in soil using high-resolution X-ray tomography. *Journal of Experimental Botany* **63**: 2503–2511.

Fornara DA, Tilman D. 2009. Ecological mechanisms associated with the positive diversity–productivity relationship in an N-limited grassland. *Ecology* **90**: 408–418.

de Fraiture C, Wichelns D. 2010. Satisfying future water demands for agriculture. *Agricultural Water Management* **97**: 502–511.

Friedman WE, Moore RC, Purugganan MD. 2004. The evolution of plant development. *American Journal of Botany* **91**: 1726–1741.

Galkovskyi T, Mileyko Y, Bucksch A, *et al.* 2012. GiA Roots: software for the high throughput analysis of plant root system architecture. *BMC Plant Biology* **12**: 116.

Galloway JN, Townsend AR, Erisman JW, *et al.* 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* **320**: 889–892.

Gamuyao R, Chin JH, Pariasca-Tanaka J, *et al.* 2012. The protein kinase Pstol1 from traditional rice confers tolerance of phosphorus deficiency. *Nature* **488**: 535–539.

Garrigues E, Doussan C, Pierret A. 2006. Water uptake by plant roots: I – Formation and propagation of a water extraction front in mature root systems as evidenced by 2D light transmission imaging. *Plant and Soil* **283**: 83–98.

Ghestem M, Sidle RC, Stokes A. 2011. The influence of plant root systems on subsurface flow: implications for slope stability. *Bioscience* **61**: 869–879.

Gliessman SR. 1992. Agroecology in the tropics: achieving a balance between land use and preservation. *Environmental Management* **16**: 681–689.

Godfray HCJ, Beddington JR, Crute IR, *et al.* 2010. Food security: the challenge of feeding 9 billion people. *Science* **327**: 812–818.

Good AG, Beatty PH. 2011. Fertilizing nature: a tragedy of excess in the commons. *PLoS Biology* **9**: pe1001124.

Gregory PJ, Hutchison DJ, Read DB, Jenneson PM, Gilboy WB, Morton EJ. 2003. Non-invasive imaging of roots with high resolution X-ray microtomography. *Plant and Soil* **255**: 351–359.

Gregory PJ, Bengough AG, Grinev D, *et al.* 2009. Root phenomics of crops: opportunities and challenges. *Functional Plant Biology* **36**: 922–929.

Grime JP. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. London: Wiley.

Gualtieri G, Bisseling T. 2000. The evolution of nodulation. *Plant Molecular Biology* **42**: 181–194.

Gyaneshwar P, Hirsch AM, Moulin L, *et al.* 2011. Legume-nodulating betaproteobacteria: Diversity, host range, and future prospects. *Molecular Plant–Microbe Interactions* **24**: 1276–1288.

Hallett PD, Bengough AG. 2013. Managing the soil physical environment for plants. In: Gregory PJ, Nortcliff S**.** eds. *Soil conditions and plant growth*. Oxford: Blackwell Publishing, 238–268.

Hammond JP, White PJ. 2011. Sugar signalling in root responses to low phosphorus availability. *Plant Physiology* **156**: 1033–1040.

Hammond JP, Broadley MR, White PJ, *et al.* 2009. Shoot yield drives phosphorus use efficiency in *Brassica oleracea* and correlates with root architecture traits. *Journal of Experimental Botany* **60**: 1953–1968.

Hamza MA, Anderson WK. 2005. Soil compaction in cropping systems: a review of the nature, causes and possible solutions. *Soil and Tillage Research* **82**: 121–145.

Henry A, Gowda VRP, Torres RO, McNally KL, Serraj R. 2011. Variation in root system architecture and drought response in rice (*Oryza sativa*): phenotyping of the OryzaSNP panel in rainfed lowland fields. *Field Crops Research* **120**: 205–214.

Hermans C, Hammond JP, White PJ, Verbruggen N. 2006. How do plants respond to nutrient shortage by biomass allocation? *Trends in Plant Science* **11**: 610–617.

Hinsinger P, Bengough AG, Vetterlein D, Young I. 2009. Rhizosphere: biophysics, biogeochemistry and ecological relevance. *Plant and Soil* **321**: 117–152.

Hirel B, Le Gouis J, Ney B, Gallais A. 2007. The challenge of improving nitrogen use efficiency in crop plants: towards a more central role for genetic variability and quantitative genetics within integrated approaches. *Journal of Experimental Botany* **58**: 2369–2387.

Ho MD, Rosas JC, Brown KM, Lynch JP. 2005. Root architectural tradeoffs for water and phosphorus acquisition. *Functional Plant Biology* **32**: 737–748.

Hodson MJ, Bryant JA. 2012. *Functional biology of plants*. Chichester, UK: Wiley-Blackwell.

Hofstra N, Bouwman AF. 2005. Denitrification in agricultural soils: summarizing published data and estimating global annual rates. *Nutrient Cycling in Agroecosystems* **72**: 267–278.

Holdaway RJ, Richardson SJ, Dickie IA, Peltzer DA, Coomes DA. 2011. Species- and community-level patterns in fine root traits along a 120 000-year soil chronosequence in temperate rain forest. *Journal of Ecology* **99**: 954–963.

Hund A, Ruta N, Liedgens M. 2009. Rooting depth and water use efficiency of tropical maize inbred lines, differing in drought tolerance. *Plant and Soil* **318**: 311–325.

Hund A, Reimer R, Messmer R. 2011. A consensus map of QTLs controlling the root length of maize. *Plant and Soil* **344**: 143–158.

Husáková E, Hochholdinger F, Soukup A. 2013. Lateral root development in the maize (*Zea mays* L.) *lateral rootless1* mutant. *Annals of Botany* **112**: 417–428.

Ismail AM, Heuer S, Thomson JT, Wissuwa M. 2007. Genetic and genomic approaches to develop rice germplasm for problem soils. *Plant Molecular Biology* **65**: 547–570.

Iyer-Pascuzzi AS, Symonova O, Mileyko Y, *et al.* 2010. Imaging and analysis platform for automatic phenotyping and trait ranking of plant root systems. *Plant Physiology* **152**: 1148–1157.

Jahnke S, Menzel MI, van Dusschoten D, *et al.* 2009. Combined MRI–PET dissects dynamic changes in plant structures and functions. *Plant Journal* **59**: 634–644.

James EK, Baldani JI. 2012. The role of biological nitrogen fixation by non-legumes in the sustainable production of food and biofuels. *Plant and Soil* **356**: 1–3.

Jaramillo RE, Nord EA, Chimungu JG, Brown KM, Lynch JP. 2013. Root cortical burden influences drought tolerance in maize. *Annals of Botany* **112**: 429–437.

Jungk A. 2001. Root hairs and the acquisition of plant nutrients from soil. *Journal of Plant Nutrition and Soil Science* **164**: 121–129.

Kaiser J. 2004. Wounding Earth's fragile skin. *Science* **304**: 1616–1618.

Karandashov V, Bucher M. 2005. Symbiotic phosphate transport in arbuscular mycorrhizas. *Trends in Plant Science* **10**: 22–29

Kattge J, Díaz S, Lavorel S, *et al.* 2011. TRY – a global database of plant traits. *Global Change Biology* **17**: 2905–2935.

Kell DB. 2011. Breeding crop plants with deep roots: their role in sustainable carbon, nutrient and water sequestration. *Annals of Botany* **108**: 407–418.

Kempes CP, West GB, Crowell K, Girvan M. 2011. Predicting maximum tree heights and other traits from allometric scaling and resource limitations. *PLoS One* **6**: e20551.

Kenrick P, Crane PR. 1997. The origin and early evolution of plants on land. *Nature* **389**: 33–39.

Kesler SE. 2007. Mineral supply and demand into the 21st century. In: Briskey JA, Schulz KJ. eds. *US Geological Survey circular 1294: proceedings for a workshop on deposit modeling, mineral resource assessment, and their role in sustainable development*. Reston, VA: US Geological Survey, 55–62.

Knörzer H, Graeff-Hönninger S, Guo B, Wang P, Claupein W. 2009. The rediscovery of intercropping in China: a traditional cropping system for future Chinese agriculture – a review. *Sustainable Agriculture Reviews* **2**: 13–44.

Koltai H. 2013. Strigolactones activate different hormonal pathways for regulation of root development in response to phosphate growth conditions. *Annals of Botany* **112**: 409–415.

Koohafkan P, Altieri MA. 2010. *Globally important agricultural heritage systems: a legacy for the future*. Rome, Italy: UN-FAO.

de Kroon H, Hendriks M, van Ruijven J, *et al*. 2012. Root responses to nutrients and soil biota: drivers of species coexistence and ecosystem productivity. *Journal of Ecology* **100**: 6–15.

Kubo K, Uchino H, Jitsuyama Y, Iwama K. 2008. Relationship between deep root distribution and root penetration capacity estimated by pot experiments with a paraffin and vaseline layer for landraces and recent cultivars of wheat. *Plant Production Science* **11**: 487–497.

Kumar J, Pratap A, Solanki RK, *et al*. 2012. Genomic resources for improving food legume crops. *Journal of Agricultural Science* **150**: 289–318.

Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ. 2006. Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Annals of Botany* **98**: 693–713.

Lansing JS, Kremer JN. 2011. Rice, fish, and the planet. *Proceedings of the National Academy of Sciences of the USA* **108**: 19841–19842.

Li J, Xie Y, Dai A, Liu L, Li Z. 2009. Root and shoot traits responses to phosphorus deficiency and QTL analysis at seedling stage using introgression lines of rice. *Journal of Genetics and Genomics* **36**: 173–183.

Li L, Li S-M, Sun J-H, *et al*. 2007. Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Proceedings of the National Academy of Sciences of the USA* **104**: 11192–11196.

Liang Q, Cheng X, Mei M, Yan X, Liao H. 2010. QTL analysis of root traits as related to phosphorus efficiency in soybean. *Annals of Botany* **106**: 223–234.

Lithourgidis AS, Dordas CA, Damalas CA, Vlachostergios DN. 2011. Annual intercrops: an alternative pathway for sustainable agriculture. *Australian Journal of Crop Science* **5**: 396–410.

Loades KW, Bengough AG, Bransby MF, Hallett PD. 2010. Planting density influence on fibrous root reinforcement of soils. *Ecological Engineering* **36**: 276–284.

Lobell DB, Cassman KG, Field CB. 2009. Crop yield gaps: their importance, magnitudes, and causes. *Annual Review of Environment and Resources* **34**: 179–204.

Lopes MS, Reynolds MP. 2010. Partitioning of assimilates to deeper roots is associated with cooler canopies and increased yield under drought in wheat. *Functional Plant Biology* **37**: 147–156.

Loudet O, Gaudon V, Trubuil A, Daniel-Vedele F. 2005. Quantitative trait loci controlling root growth and architecture in *Arabidopsis thaliana* confirmed by heterogeneous inbred family. *Theoretical and Applied Genetics* **110**: 742–753.

Luyssaert S, Inglima I, Jung M, *et al*. 2007. CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology* **13**: 2509–2537.

Lynch JP. 2007. Roots of the second green revolution. *Australian Journal of Botany* **55**: 493–512.

Lynch JP. 2011. Root phenes for enhanced soil exploration and phosphorus acquisition: tools for future crops. *Plant Physiology* **156**: 1041–1049.

Lynch JP. 2013. Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany* **112**: 347–357.

Lynch JP, Brown KM. 2001. Topsoil foraging – an architectural adaptation of plants to low phosphorus availability. *Plant and Soil* **237**: 225–237.

Lynch JP, Ho MD. 2005. Rhizoeconomics: carbon costs of phosphorus acquisition. *Plant and Soil* **269**: 45–56.

Mairhofer S, Zappala S, Tracy SR, *et al*. 2012. RooTrak: automated recovery of three-dimensional plant root architecture in soil from X-ray microcomputed tomography images using visual tracking. *Plant Physiology* **158**: 561–569.

Makita N, Kosugi Y, Dannoura M, *et al*. 2012. Patterns of root respiration rates and morphological traits in 13 tree species in a tropical forest. *Tree Physiology* **32**: 303–312.

Marquard E, Weigelt A, Temperton VM, *et al*. 2009. Plant species richness and functional composition drive overyielding in a six-year grassland experiment. *Ecology* **90**: 3290–3302.

Marschner P. 2012. Rhizosphere biology. In: Marschner P. ed. *Marschner's mineral nutrition of higher plants*, 3rd edn. London: Academic Press, 369–388.

Mayzlish-Gati E, De-Cuyper C, Goormachtig S, *et al*. 2012. Strigolactones are involved in root response to low phosphate conditions in *Arabidopsis*. *Plant Physiology* **160**: 1329–1341.

McKenzie BM, Mullins CE, Tisdall JM, Bengough AG. 2013. Root–soil friction: quantification provides evidence for measurable benefits for manipulation of root tip traits. *Plant, Cell and Environment* **36**: 1085–1092.

McLaughlin MJ, McBeath TM, Smernik R, Stacey SP, Ajiboye S, Guppy C. 2011. The chemical nature of P-accumulation in agricultural soils – implications for fertiliser management and design: an Australian perspective. *Plant and Soil* **349**: 69–87.

Meyer RS, DuVal AE, Jensen HR. 2012. Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytologist* **196**: 29–48.

Morgan JAW, Bending GD, White PJ. 2005. Biological costs and benefits to plant–microbe interactions in the rhizosphere. *Journal of Experimental Botany* **56**: 1729–1739.

Mueller ND, Gerber JS, Johnston M, Ray DK, Ramankutty N, Foley JA. 2012. Closing yield gaps through nutrient and water management. *Nature* **490**: 254–257.

Munns R, Tester M. 2008. Mechanisms of salinity tolerance. *Annual Review of Plant Biology* **59**: 651–681.

Nagel KA, Putz A, Gilmer F, *et al*. 2012. GROWSCREEN-Rhizo is a novel phenotyping robot enabling simultaneous measurements of root and shoot growth for plants grown in soil-filled rhizotrons. *Functional Plant Biology* **39**: 891–904.

Ndakidemi PA 2006. Manipulating legume/cereal mixtures to optimize the above and below ground interactions in the traditional African cropping systems. *African Journal of Biotechnology* **5**: 2526–2533.

Nerlich K, Graeff-Hönninger S, Claupein W. 2013. Agroforestry in Europe: a review of the disappearance of traditional systems and development of modern agroforestry practices, with emphasis on experiences in Germany. *Agroforestry Systems* **87**: 475–492.

Neumann G, Römheld V. 2012. Rhizosphere chemistry in relation to plant nutrition. In: Marschner P. ed. *Marschner's mineral nutrition of higher plants*, 3rd edn. London: Academic Press, 347–368.

Neumann K, Verburg PH, Stehfest E, Müller C. 2010. The yield gap of global grain production: a spatial analysis. *Agricultural Systems* **103**: 316–326.

Newton AC, Guy DC, Bengough AG, *et al*. 2012. Soil tillage effects on the efficacy of cultivars and their mixtures in winter barley. *Field Crops Research* **128**: 91–100.

Niu YF, Chai RS, Jin GL, Wang H, Tang CX, Zhang YS. 2013. Responses of root architecture development to low phosphorus availability: a review. *Annals of Botany* **112**: 391–408.

Norby RJ, Jackson RB. 2000. Root dynamics and global change: seeking an ecosystem perspective. *New Phytologist* **147**: 3–12.

Oerke E-C. 2006. Crop losses to pests. *Journal of Agricultural Science* **144**: 31–43.

Osmont KS, Sibout R, Hardtke CS. 2007. Hidden branches: developments in root system architecture. *Annual Review of Plant Biology* **58**: 93–113.

Pan Y, Birdsey RA, Fang J, *et al*. 2011. A large and persistent carbon sink in the world's forests. *Science* **333**: 988–993.

Péret B, Clément M, Nussaume L, Desnos T. 2011. Root developmental adaptation to phosphate starvation: better safe than sorry. *Trends in Plant Science* **16**: 442–450.

Perret JS, Al-Belushi ME, Deadman M. 2007. Non-destructive visualization and quantification of roots using computed tomography. *Soil Biology and Biochemistry* **39**: 391–399.

Pickersgill B. 2007. Domestication of plants in the Americas: insights from Mendelian and molecular genetics. *Annals of Botany* **100**: 925–940.

Pires ND, Dolan L. 2012. Morphological evolution in land plants: new designs with old genes. *Philosophical Transactions of the Royal Society B* **367**: 508–518.

Postma J, Lynch JP. 2012. Complementarity in root architecture for nutrient uptake in ancient maize/bean and maize/bean/squash polycultures. *Annals of Botany* **110**: 521–534.

Rascher U, Blossfeld S, Fiorani F, *et al*. 2011. Non-invasive approaches for phenotyping of enhanced performance traits in bean. *Functional Plant Biology* **38**: 968–983.

Raven JA, Edwards D. 2001. Roots: evolutionary origins and biogeochemical significance. *Journal of Experimental Botany* **52**: 381–401.

Read DB, Bengough AG, Gregory PJ, *et al*. 2003. Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. *New Phytologist* **157**: 315–326.

Ren Y, He X, Liu D, *et al*. 2012. Major quantitative trait loci for seminal root morphology of wheat seedlings. *Molecular Breeding* **30**: 139–148.

Rengel Z. 2002. Breeding for better symbiosis. *Plant and Soil* **245**: 147–162.

Rengel Z, Damon PM. 2008. Crops and genotypes differ in efficiency of potassium uptake and use. *Physiologia Plantarum* **133**: 624–636.

Rewald B, Meinen C, Trockenbrodt M, Ephrath JE, Rachmilevitch S. 2012. Root taxa identification in plant mixtures – current techniques and future challenges. *Plant and Soil* **359**: 165–182.

Richardson AE, Lynch JP, Ryan PR, *et al*. 2011. Plant and microbial strategies to improve the phosphorus efficiency of agriculture. *Plant and Soil* **349**: 121–156.

Rockström J, Steffen W, Noone K, *et al*. 2009. A safe operating space for humanity. *Nature* **461**: 472–475.

Rose TJ, Impa SM, Rose MT, Pariasca-Tanaka J, Mori A, Heuer S, Johnson-Beebout SE, Wissuwa M. 2013. Enhancing phosphorus and zinc acquisition efficiency in rice: a critical review of root traits and their potential utility in rice breeding. *Annals of Botany* **112**: 331–345.

Rostamza M, Richards RA, Watt M. 2013. Response of millet and sorghum to a varying water supply around the primary and nodal roots. *Annals of Botany* **112**: 439–446.

Ruyter-Spira C, Kohlen W, Charnikhova T, *et al*. 2011. Physiological effects of the synthetic strigolactone analog GR24 on root system architecture in Arabidopsis: another belowground role for strigolactones? *Plant Physiology* **155**: 721–734.

Samson BK, Hasan M, Wade LJ. 2002. Penetration of hardpans by rice lines in the rainfed lowlands. *Field Crops Research* **76**: 175–188.

Schenk HJ. 2006. Root competition: beyond resource depletion. *Journal of Ecology* **94**: 725–739.

Schenk HJ, Jackson RB. 2005. Mapping the global distribution of deep roots in relation to climate and soil characteristics. *Geoderma* **126**: 129–140.

Schlesinger WH. 2009. On the fate of anthropogenic nitrogen. *Proceedings of the National Academy of Sciences of the USA* **106**: 203–208.

Seago JL Jr, Fernando DD. 2013. Anatomical aspects of angiosperm root evolution. *Annals of Botany* **112**: 223–238.

Seran TH, Brintha I. 2010. Review on maize based intercropping. *Journal of Agronomy* **9**: 135–145.

Shi L, Shi T, Broadley MR, White PJ, Long Y, Meng J, Xu F, Hammond JP. 2013. High-throughput root phenotyping screens identify genetic loci associated with root architectural traits in *Brassica napus* under contrasting phosphate availabilities. *Annals of Botany* **112**: 381–389.

Shishkova S, Las Peñas ML, Napsucialy-Mendivil S, Matvienko M, Kozik A, Montiel J, Patiño A, Dubrovsky JG. 2013. Determinate primary root growth as an adaptation to aridity in Cactaceae: towards an understanding of the evolution and genetic control of the trait. *Annals of Botany* **112**: 239–252.

Simpson RJ, Oberson A, Culvenor RA, *et al*. 2011. Strategies and agronomic interventions to improve the phosphorus-use efficiency of farming systems. *Plant and Soil* **349**: 89–120.

Smith KA, McTaggart IP, Tsuruta H. 1997. Emissions of N_2O and NO associated with nitrogen fertilization in intensive agriculture, and the potential for mitigation. *Soil Use and Management* **13**: 296–304.

Smith P, Martino D, Cai Z, *et al*. 2008. Greenhouse gas mitigation in agriculture. *Philosophical Transactions of the Royal Society, B* **363**: 789–813.

Smith S, De Smet I. 2012. Root system architecture: insights from *Arabidopsis* and cereal crops. *Philosophical Transactions of the Royal Society, B* **367**: 1441–1452.

Smith SE, Read DJ. 2008. *Mycorrhizal symbiosis*, 3rd edn. New York: Academic Press.

Sprent JI, James EK. 2007. Legume evolution: Where do nodules and mycorrhizas fit in? *Plant Physiology* **144**: 575–581.

Stoate C, Boatman ND, Borralho RJ, Rio Carvalho CR, de Snoo GR, Eden P. 2001. Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* **63**: 337–365.

Středa T, Dostál V, Horáková V, Chloupek O. 2012. Effective use of water by wheat varieties with different root system sizes in rain-fed experiments in Central Europe. *Agricultural Water Management* **104**: 203–209

Subbarao GV, Rondon M, Ito O, *et al*. 2007. Biological nitrification inhibition (BNI) – is it a widespread phenomenon? *Plant and Soil* **294**: 5–18.

Subbarao GV, Sahrawat KL, Nakahara K, Rao IM, Ishitani M, Hash CT, Kishii M, Bonnett DG, Berry WL, Lata JC. 2013. A paradigm shift towards low-nitrifying production systems: the role of biological nitrification inhibition (BNI). *Annals of Botany* **112**: 297–316.

Sumner ME, Noble AD. 2003. Soil acidification: the world story. In: Rengel Z. ed. *Handbook of Soil Acidity*. New York: Marcel Dekker, 1–28.

Sylvester-Bradley R, Kindred DR. 2009. Analysing nitrogen responses of cereals to prioritize routes to the improvement of nitrogen use efficiency. *Journal of Experimental Botany* **60**: 1939–1951.

Taiz L, Zeiger E. 2002. *Plant Physiology*, 3rd edn. Sunderland, MA: Sinauer Associates.

Taylor TN, Klavins SD, Krings M, Taylor EL, Kerp H, Hass H. 2004. Fungi from the Rhynie chert: a view from the dark side. *Transactions of the Royal Society of Edinburgh – Earth Sciences* **94**: 457–473.

Temperton VM, Mwangi PN, Scherer-Lorenzen M, Schmid B, Buchmann N. 2007. Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. *Oecologia* **151**: 190–205.

Tilman D. 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. In: Grace JB, Tilman D. eds. *Perspectives on Plant Competition*. New York: Academic Press, 117–141.

Trachsel S, Kaeppler SM, Brown KM, Lynch JP. 2011. Shovelomics: high throughput phenotyping of maize (*Zea mays* L.) root architecture in the field. *Plant and Soil* **341**: 75–87.

Trinder CJ, Brooker RW, Davidson H, Robinson D. 2012. A new hammer to crack an old nut: interspecific competitive resource capture by plants is regulated by nutrient supply, not climate. *PLoS ONE* **7**: pe29413.

Urquiaga S, Xavier RP, de Morais RF, *et al*. 2012. Evidence from field nitrogen balance and ^{15}N natural abundance data for the contribution of biological N_2 fixation to Brazilian sugarcane varieties. *Plant and Soil* **356**: 5–21.

Valentine TA, Hallett PD, Binnie K, *et al*. 2012. Soil strength and macropore volume limit root elongation rates in many UK agricultural soils. *Annals of Botany* **110**: 259–270.

Veneklaas EJ, Lambers H, Bragg J, *et al*. 2012. Opportunities for improving phosphorus-use efficiency in crop plants. *New Phytologist* **195**: 306–320.

Vitousek PM, Naylor R, Crews T, *et al*. 2009. Nutrient imbalances in agricultural development. *Science* **324**: 1519–1520.

Von Uexküll HR, Mutert E. 1995. Global extent, development and economic impact of acid soils. *Plant and Soil* **171**: 1–15.

Wahl S, Ryser P. 2000. Root tissue structure is linked to ecological strategies of grasses. *New Phytologist* **148**: 459–471.

Watt M, Moosavi S, Cunningham SC, Kirkegaard JA, Rebetzke GJ, Richards RA. 2013. A rapid, controlled-environment root seedling screen for wheat correlates well with rooting depths at young vegetative, but not reproductive, stages in the field. *Annals of Botany* **112**: 447–455.

Whalley WR, Clark LJ, Gowing DJG, Cope RE, Lodge RJ, Leeds–Harrison PB. 2006. Does soil strength play a role in wheat yield losses caused by soil drying? *Plant and Soil* **280**: 279–290.

White PJ. 2012*a*. Ion uptake mechanisms of individual cells and roots: short-distance transport. In: Marschner P. ed. *Marschner's mineral nutrition of higher plants*, 3rd edn. London: Academic Press, 7–47.

White PJ. 2012*b*. Long-distance transport in the xylem and phloem. In: Marschner P. ed. *Marschner's mineral nutrition of higher plants*, 3rd edn. London: Academic Press, 49–70.

White PJ. 2013. Improving potassium acquisition and utilisation by crop plants. *Journal of Plant Nutrition and Soil Science* **176**: 305–316.

White PJ, Broadley MR. 2009. Biofortification of crops with seven mineral elements often lacking in human diets – iron, zinc, copper, calcium, magnesium, selenium and iodine. *New Phytologist* **182**: 49–84.

White PJ, Brown PH. 2010. Plant nutrition for sustainable development and global health. *Annals of Botany* **105**: 1073–1080.

White PJ, Greenwood DJ. 2013. Properties and management of cationic elements for crop growth. In: PJ Gregory PJ, Nortcliff S. eds. *Russell's soil conditions and plant growth*. Oxford: Blackwell Publishing, 160–194.

White PJ, Hammond JP. 2008. Phosphorus nutrition of terrestrial plants. In: White PJ, Hammond JP. eds. *The ecophysiology of plant–phosphorus interactions*. Dordrecht: Springer, 51–81.

White PJ, Veneklaas EJ. 2012. Nature and nurture: the importance of seed phosphorus. *Plant and Soil* **357**: 1–8.

White PJ, Broadley MR, Greenwood DJ, Hammond JP. 2005. *Proceedings 568. Genetic modifications to improve phosphorus acquisition by roots.* York, UK: International Fertiliser Society.

White PJ, Hammond JP, King GJ, *et al*. 2010. Genetic analysis of potassium use efficiency in *Brassica oleracea*. *Annals of Botany* **105**: 1199–1210.

White PJ, Broadley MR, Gregory PJ. 2012. Managing the nutrition of plants and people. *Applied and Environmental Soil Science* **2012**: article 104826.

Wissuwa M, Mazzola M, Picard C. 2009. Novel approaches in plant breeding for rhizosphere-related traits. *Plant and Soil* **321**: 409–430.

Wright IJ, Westoby M. 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology* **87**: 85–97.

Yang M, Ding G, Shi L, Feng J, Xu F, Meng J. 2010. Quantitative trait loci for root morphology in response to low phosphorus stress in *Brassica napus*. *Theoretical and Applied Genetics* **121**: 181–193.

Yang M, Ding G, Shi L, Xu F, Meng J. 2011. Detection of QTL for phosphorus efficiency at vegetative stage in *Brassica napus*. *Plant and Soil* **339**: 97–111.

Zegada-Lizarazu W, Monti A. 2011. Energy crops in rotation. A review. *Biomass and Bioenergy* **35**: 12–25.

Zhu JM, Brown KM, Lynch JP. 2010. Root cortical aerenchyma improves the drought tolerance of maize (*Zea mays* L.). *Plant, Cell and Environment* **33**: 740–749.

Zhu J, Ingram PA, Benfey PN, Elich T. 2011. From lab to field, new approaches to phenotyping root system architecture. *Current Opinion in Plant Biology* **14**: 310–317.