Planta (2014) 240:667–678
DOI 10.1007/s00425-014-2150-y

REVIEW

Phenotypic plasticity of the maize root system in response to heterogeneous nitrogen availability

Peng Yu · Philip J. White · Frank Hochholdinger · Chunjian Li

Received: 31 July 2014 / Accepted: 8 August 2014 / Published online: 21 August 2014

Abstract Mineral nutrients are distributed in a non-uniform manner in the soil. Plasticity in root responses to the availability of mineral nutrients is believed to be important for optimizing nutrient acquisition. The response of root architecture to heterogeneous nutrient availability has been documented in various plant species, and the molecular mechanisms coordinating these responses have been investigated particularly in *Arabidopsis*, a model dicotyledonous plant. Recently, progress has been made in describing the phenotypic plasticity of root architecture in maize, a monocotyledonous crop. This article reviews aspects of phenotypic plasticity of maize root system architecture, with special emphasis on describing (1) the development of its complex root system; (2) phenotypic responses in root system architecture to heterogeneous N availability; (3) the importance of phenotypic plasticity for N acquisition; (4) different regulation of root growth and nutrients uptake by shoot; and (5) root traits in maize breeding. This knowledge will inform breeding strategies for root traits enabling more efficient acquisition of soil resources and synchronizing crop growth demand, root resource acquisition and fertilizer application during crop growing season, thereby maximizing crop yields and nutrient-use efficiency and minimizing environmental pollution.

Keywords Maize · Root growth and development · Nitrogen · Phenotypic plasticity

Abbreviations

AR	Axial root
BR	Brace root
CR	Crown root
LR	Lateral root
N	Nitrogen
TRL	Total root length

Introduction

Plant root architecture displays a considerable degree of plasticity in response to the heterogeneous distribution of soil resources (Hodge 2004; Malamy 2005; Nibau et al. 2008). In particular, the availability and distribution of nitrate, the main source of nitrogen (N) for plants growing in aerobic soils, influences both the carbon investment in, and the architecture of, plant root systems (Lynch et al. 2012). In recent decades, researchers have developed various laboratory-based technologies for studying the root systems of seedlings grown in non-soil or soil media (Armengaud et al. 2009; Iyer-Pascuzzi et al. 2010; Clark et al. 2011, 2013; Downie et al. 2012; Gruber et al. 2013; Shi et al. 2013; Adu et al. 2014). These techniques have revealed how root architectures of different plants respond to the heterogeneous distribution of nutrients in the rooting medium (Drew 1975; Robinson 1994; Hodge 2004, 2006;

P. Yu · C. Li (✉)
Department of Plant Nutrition, China Agricultural University, Yuanmingyuan West Road 2, Beijing 100193, People's Republic of China
e-mail: lichj@cau.edu.cn

P. J. White
Ecological Sciences, The James Hutton Institute, Invergowrie, Dundee DD2 5DA, UK

F. Hochholdinger
Institute of Crop Science and Resource Conservation, Crop Functional Genomics, University of Bonn, 53113 Bonn, Germany

Hodge et al. 2009; Li et al. 2014) and provided some knowledge of the molecular mechanisms coordinating these processes (Zhang and Forde 1998, 2000; Forde and Walch-Liu 2009; Ruzicka et al. 2010; Ruffel et al. 2011; Giehl et al. 2013; Kellermeier et al. 2013; Mounier et al. 2014). However, although breeding for root traits could play an unprecedented role in improving crop establishment and increasing yield (Lynch 2007, 2013; Hammer et al. 2009; Gewin 2010; White et al. 2013a, b; York et al. 2013), limited attention has been paid to genotypic responses of root architecture to the heterogeneous availability of soil resources in crop breeding programs. One reason for this might be that roots are entangled belowground and studying the architectures of root systems is very time consuming, which limit both the accuracy and speed of measuring root traits in the field (Waines and Ehdaie 2007; Gewin 2010; Herder et al. 2010). Irrespective of the great progress in documenting and understanding the phenotypic plasticity of plant roots in the laboratory, there are still various aspects of root growth and nutrient acquisition, especially of cereal crops, that must be addressed in the field.

An understanding of genotypic variation in the responses of root system architecture to the heterogeneous distribution of nutrients in the field will determine the potential for the exploitation of such traits to increase crop yields and maximize nutrient-use efficiency. Maize, which is a classic model cereal plant and a staple crop in many areas of the world, forms a complex root system composed of several different root types (Hochholdinger et al. 2004; Hochholdinger and Tuberosa 2009). This paper reviews the aspects of phenotypic plasticity of maize root system architecture with emphasis on describing (1) the development of its complex root system; (2) phenotypic responses in its root system architecture to heterogeneous N availability; (3) the importance of phenotypic plasticity in root system architecture for N acquisition; (4) different regulation of root growth and nutrient uptake by shoot; and (5) root traits in maize breeding.

Development of the maize root system

Maize plants possess an embryonic root system consisting of a single primary root and a variable number of seminal roots and a post-embryonic root system consisting of several whorls of shoot-borne roots (Hochholdinger et al. 2004). The root axes of all seminal roots and shoot-borne roots are called axial roots (ARs), and the roots initiated from these ARs are called lateral roots (LRs). There are also higher-order LRs initialed from lower-order LRs. The maize root system develops in an orderly manner that is coordinated with the development of the shoot, starting with the emergence of the primary root, then seminal and shoot-borne roots that subsequently branch to form different orders of LRs (Foth 1962; Hanway 1963; Hoppe et al. 1986; Feldman 1994; Fig. 1). The LRs are initiated from pericycle and endodermal cells close to the phloem poles in the differentiation zone of roots (Bell and McCully 1970; Esau 1977; Fahn 1990; Casero et al. 1995; Jansen et al. 2012). In most cases, some of the first-order LRs and ARs become leaders that elongate rapidly, persist for a long time, and thicken with time (Varney et al. 1991). These roots comprise most of the biomass of the root system and form the long-distance transport pathways and branch-root junctions (McCully and Canny 1988; Varney et al. 1991; Shane et al. 2000). The higher-order LRs are usually finer roots that make up most of the length and surface area of the root system, and are essential for water and nutrient uptake (Varney et al. 1991; McCully 1995, 1999; Sullivan et al. 2000). The diameter of individual roots varies widely. The ARs are thicker roots, which are able to exert greater force to penetrate compacted soil (McCully and Canny 1988; McCully 1995; Waisel and Eshel 2002; Hund et al. 2009a) and determine both the direction of growth of the root system and its spatial distribution in the soil (Eissenstat 1997).

Embryonic roots of maize are functionally important during early growth, but their function is soon replaced by post-embryonic shoot-borne roots (Varney and McCully 1991; Feldman 1994; Feix et al. 2002; Fig. 1). Nevertheless, if the development and growth of the shoot-borne roots of maize plants is restricted, then the remaining seminal roots will show compensatory growth and increased nutrient uptake compared to those of control plants (Jeschke et al. 1997; Xu et al. 2009; Yan et al. 2011a), suggesting that the longevity and importance of different root classes can alter depending on the integrated functioning of the entire root system.

Post-embryonic shoot-borne roots include crown roots (CRs; Fig. 1a, b, c; Hochholdinger et al. 2004) and brace roots (BRs; Fig. 1d, e; Feldman 1994). The CRs start to emerge from below-ground stem nodes 5–10 days after germination and BRs emerge from above-ground stem nodes approximately 6 weeks after germination (Hochholdinger et al. 2004). The number and diameter of CRs are greater on higher shoot nodes (Fig. 1b, c). The growth of the BRs results in dramatic increases in both the total length of the root system (TRL) and its dry weight (DW), and is contemporaneous with a rapid increase of shoot growth and demand for nutrients (Hoppe et al. 1986; Niu et al. 2010; Peng et al. 2012a). Although 35–55 % of the N in maize plants at harvest is taken up by the root during the reproductive stage (Hirel et al. 2007), the TRL of the maize root system reaches its highest value at silking (Durieux et al. 1994; Peng et al. 2012a). This is consistent with

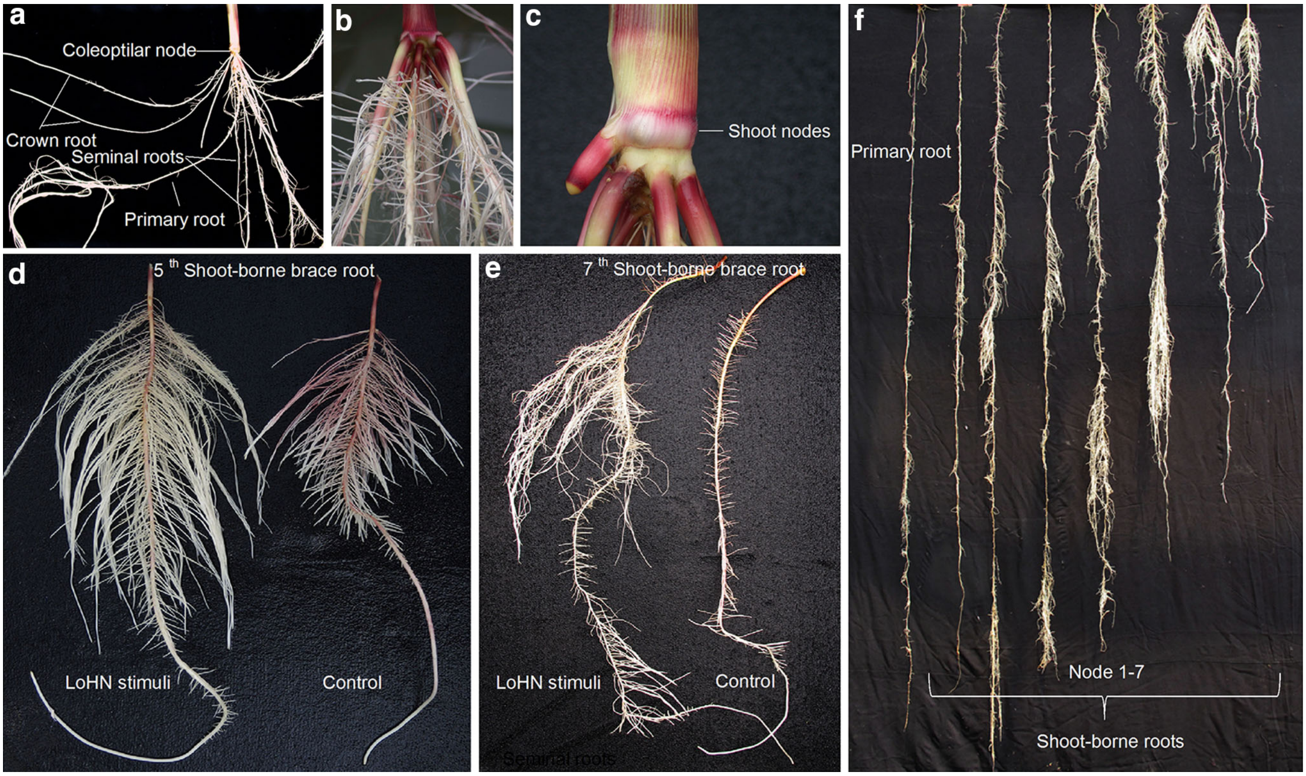

Fig. 1 Development of the maize root system from embryonic roots in seedlings to crown and brace roots initiated from shoot nodes in adult plants. **a** The root system of a 35-day-old maize plant with the major root types indicated. **b** The root system of a 49-day-old maize plant with its shoot-borne roots from the fifth node. **c** Roots emerging from shoot nodes on a 49-day-old maize plant. **d** Phenotypic responses of the shoot-borne roots from the fifth node of a 49-day-old maize plant to a non-uniform N environment (LoHN, local high nitrate supply: HN 4 mM, Control 0.5 mM). **e** Phenotypic responses of the shoot-borne roots from the seventh node of a 70-day-old maize plant in response to non-uniform N environments. **f** All root types of a 70-day-old maize plant grown with a sufficient N supply

studies on many cereals in which it has been observed that the DW of the whole root system does not increase after flowering and in some studies a substantial decrease has been observed during grain filling (reviewed by Gregory 2006). Although the TRL of the maize root system decreases markedly after silking, there is only a small change in the DW of the root system (Peng et al. 2012a). This is because LRs comprise only a small portion of the total root DW, but constitute the majority of the TRL (Walk et al. 2005; Hund et al. 2009b; Peng et al. 2010).

The decline in total length of LRs after silking is primarily due to root mortality. Root mortality during the reproductive stage has been associated with the translocation of N and carbon from roots to the developing ear of plants grown in the field (Wiesler and Horst 1993). The rapid reduction in TRL of maize plants grown in the field might be explained by the influence of soil biota. The presence of microorganisms, decomposers, herbivores and parasites in the rhizosphere could accelerate root mortality, especially when roots receive less carbon from the shoot during the reproductive stage (Eissenstat and Yanai 1997; Eissenstat et al. 2000; Watt et al. 2006a, b). Interestingly, when maize plants are grown in quartz sand or nutrient solution their root DW and TRL increase continuously until maturity (Warncke and Barber 1974) even when they suffer from N deficiency, which indicates that their roots do not exhibit ontogenetically programmed mortality during the reproductive stage (Niu et al. 2010; Yu et al. 2014). Overall, the developmental and environmental signaling that co-regulates root growth and development allows plants to optimize the placement of roots within root system adapted to complex and flexibly changing soil environments (Malamy 2005).

Phenotypic plasticity of maize root responses to nitrogen supply

Root architecture is controlled both by intrinsic developmental programs and by complex interactions between the plant physiological status and exogenous biotic and abiotic stimuli in the rhizosphere (McCully 1995, 1999; Rich and Watt 2013). The phenotypic plasticity of plant root systems is manifest in the ability of plants to optimize root system architecture for resource acquisition under diverse environmental conditions in response to the identity, availability and distribution of soil resources (Fitter 1994;

Robinson 1994; Hodge et al. 1999; Fitter 2002; Hodge 2004, 2006; Shemesh et al. 2010; Croft et al. 2012; Gruber et al. 2013). The stimulation of LR development by nitrate-rich patches is a classic example of a nutrient-induced alteration in root system architecture (Drew et al. 1973; Drew and Saker 1975; Granato and Raper 1989; Schortemeyer et al. 1993; Forde and Lorenzo 2001; López-Bucio et al. 2003; Forde and Walch-Liu 2009; Giehl et al. 2013). In the short-term, systemic N deficiency in maize seedlings increases carbon partitioning to roots, accelerates root growth, and results in fewer, longer ARs with longer LRs (Pan et al. 1985; Feil et al. 1990; Eghball and Maranville 1993; Barber 1995; Gaudin et al. 2011) as is also observed in other plant species (Hermans et al. 2006; Giehl et al. 2013; Gruber et al. 2013). However, the lengths of ARs of the 60-day-old (adult) maize plants respond less dramatically than those of seedlings to systemic N deficiency (Gaudin et al. 2011; Orman-Ligeza et al. 2013; Yu et al. 2014). By contrast, although nitrate-rich patches only increase the length of LRs from the treated roots of maize seedlings, they increase both the length and density of LRs from shoot-borne roots of adult maize plants (Peng et al. 2012a; Yu et al. 2014). Thus, the mechanisms controlling the responses of embryonic roots and shoot-borne roots to nitrate-rich patches appear to differ (Hochholdinger and Tuberosa 2009; Zhu et al. 2011) and merit further investigation. In seedlings, a transient IAA increase in root tips of nitrate-fed root segments is observed 2 days after the treatment (Sattelmacher and Thoms 1995). Auxin and auxin transport inhibitor application revealed the pivotal roles of auxin transported from shoot to roots in response of LR growth to localized supply of nitrate in maize (Wang et al. 2004; Guo et al. 2005; Liu et al. 2008, 2010).

Another general response of roots of maize to systemic N deficiency is to increase rooting depth (Gastal and Lemaire 2002; Dunbabin et al. 2003, 2004). Root growth angles of maize plants become steeper when they are grown with a reduced N supply (Gaudin et al. 2011; Lynch 2013; Trachsel et al. 2013). Conversely, excessive N supply inhibits root growth and produces a shallower root system (Durieux et al. 1994; Walch-Liu et al. 2006; Gaudin et al. 2011). The N concentration in shoot tissues affects the root responses to the availability and distribution of nitrate in the soil, implicating long-distance signals from the shoot to the root in these responses (Zhang and Forde 1998, 2000; Zhang et al. 1999; Hermans et al. 2006; Desnos 2008; Ruffel et al. 2008; Alvarez et al. 2012).

While many studies have focused on the morphological responses of roots within nitrate-rich patches, less attention has been paid to morphological responses of roots outside these patches. However, recent studies have demonstrated that, whilst the root length density (RLD; cm cm^{-3}) and specific root length (SRL; m g^{-1}) of the root system within nitrate-rich patches are increased, the development and growth of LRs outside the nitrate-rich patches is reduced, which suggests a systemic carbon partitioning strategy within a whole root system both in *Arabidopsis* and maize plants (Mounier et al. 2014; Yu et al. 2014). It is known that *CHL1* functions upstream of *ANR1* in regulating the proliferation of LRs in response to a locally high nitrate supply; there are also some additional components involved in *ANR1* function regulated by high nitrate supply (Zhang and Forde 1998; Remans et al. 2006). It is hypothesized that, at low-nitrate concentrations, *CHL1* represses the growth of LRs by promoting basipetal auxin transport (Krouk et al. 2010) and acts locally to modulate auxin levels and meristematic activity in *Arabidopsis* plants (Mounier et al. 2014). Alternatively, or additionally, the increased N concentration in shoots resulting from a localized high N supply might initiate a 'systematic inhibitory effect' on the development and growth of LRs outside nitrate-rich patches (Mounier et al. 2014; Yu et al. 2014). The NO-signaling pathway also plays a role in the responses of maize roots to nitrate availability (Trevisan et al. 2011; Manoli et al. 2014), and it is thought that peroxisomal NO modulates auxin-induced lateral root formation both in *Arabidopsis* and maize (Schlicht et al. 2013). Microarray analyses revealed that early-responsive genes related to cell division and expansion such as α-expansin, cellulose synthase, kinesin, plasma membrane and tonoplast aquaporins are possibly involved in localized nitrate stimulation of lateral root development in maize (Liu et al. 2008). But so far, it remains unclear what triggers LR elongation and initiation to deploy nitrogen in the heterogeneous nutrients medium in maize.

The importance of root phenotypic plasticity in N capture

Our knowledge of both the physiology and molecular biology of root N acquisition has improved greatly over the past few decades (Crawford 1995; Crawford and Glass 1998; Miller et al. 2007; Gojon et al. 2009; Gojon 2013; Nacry et al. 2013). The role of root architecture in N acquisition has also been studied widely. The development of a plant root system continuously extends the rhizosphere periphery into the soil, and the resulting root architecture largely determines the efficiency of nutrient acquisition (Lynch 1995; Linkohr et al. 2002; Zhu et al. 2005). Root length per unit of soil volume (RLD) is an important factor for nutrient acquisition (Robinson and Rorison 1983; Wiesler and Horst 1994; Garnett et al. 2009; White et al. 2013a). Increasing the total length of LRs results in greater N acquisition (Linkohr et al. 2002; Wang et al. 2004, 2006) and fine roots take up more N than thicker roots on a dry weight (DW) basis (Sullivan et al. 2000). As mentioned in the previous section, LRs proliferate in regions of the soil with higher N availability.

In addition to root architecture, the characteristics of nitrate uptake by root cells (i.e., their uptake capacity $V_{\max}$ and affinity for nitrate K_{m}) also play an important role in N acquisition. When roots encounter a local region of high nitrate supply, their N uptake capacity increases transiently by up to 75 % compared to regions of the root outside the nitrate-rich patch (Jackson et al. 1990; Robinson 1994; van Vuuren et al. 1996; Hodge 2004). In maize, three nitrate transporters have been characterized: *ZmNrt1.1* encodes a low-affinity nitrate transporter expressed in both root and shoot tissues (Quaggiotti et al. 2004), *ZmNrt2.1* encodes a high-affinity nitrate transporter that is predominantly expressed in the epidermis and cortex of roots and is implicated in high-affinity NO_3^- uptake, and *ZmNrt2.2* encodes a constitutive and inducible high-affinity nitrate transporter that is expressed in the cortex and central cylinder of the root (Santi et al. 2003; Trevisan et al. 2008). Transcription of *ZmNrt2.1* and *ZmNrt2.2* is 1000-fold higher than that of *ZmNrt1.1A, ZmNrt1.1B* and *ZmNrt1.2*; even when plants are grown with an optimal N supply, and basal transcription of *ZmNRT2.1* and *ZmNRT2.2* is much higher than other *ZmNRT2* and *ZmNRT1* genes over a plant's life cycle (Garnett et al. 2013). Curiously, however, the expression of *ZmNRT2.1* and *ZmNRT2.2* in roots of maize plants within nitrate-rich patches is suppressed, and the nitrate uptake capacity of roots within these patches is lower than in those outside the patches (Quaggiotti et al. 2003). Increased N uptake by maize roots in nitrate-rich patches is achieved mainly by changes in root system architecture, which is observed not only in seedlings, but also in adult plants (Yu et al. 2014). Because nitrate is highly mobile in the soil profile, due to its high water solubility, morphological plasticity of high-order laterals of adult maize plants is beneficial for taking up nitrate leached to deeper soil layers and, thereby, improving crop N use efficiency and preventing environmental pollution (Lynch and Brown 2001; Peng et al. 2012a; White et al. 2013a, b). Further studies demonstrated that deep root genotypes are important for deep soil exploration and that low crown root numbers in maize tend to deserve consideration as a potential trait for genetic improvement in low N soil (Lynch et al. 2012; York et al. 2013; Saengwilai et al. 2014).

The investigation on temporal and spatial dynamics of root distribution and nutrient depletion in the soil is imperative (Kuchenbuch et al. 2009; Buczko and Kuchenbuch 2013). Roots are generally more abundant in the topsoil than in deeper soil horizons, and this distribution corresponds primarily to the availability of phosphorus and other immobile soil nutrients (Lynch and Brown 2001; Fitter 2002; Zhu et al. 2005; White et al. 2013a). The relationship between root distribution and soil depth can be described by a simple asymptotic function in most cases (Jackson et al. 1996) and the length and mass of roots decreases exponentially with depth for many crops (Gerwitz and Page 1974; Robertson et al. 1993; Oikeh et al. 1999; Zhuang et al. 2001). A close correlation of RLD of catch crops in the sub-soil layer with nitrate depletion is reported in the field (Thorup-Kristensen 2001, 2006; Kristensen and Thorup-Kristensen 2004) and similar trends with soil residual mineral nitrogen ($N_{\min}$) in the whole soil profile in maize (Wiesler and Horst 1994; Peng et al. 2010). In the upper 0.1 m of soil, typical values of RLD are about 20 cm cm^{-3} in grasses, 5–10 cm cm^{-3} in temperate cereal crops, and 1–2 cm cm^{-3} in other crops (reviewed by Jackson et al. 1996). It is clear that root systems with greater RLD in the topsoil horizon can acquire more of the N fertilizer applied and reduce the movement of water and nitrate toward deeper soil layers (Dunbabin et al. 2002; Lynch 2013; White et al. 2013b).

Different regulation of root growth and nutrients uptake by shoot

The balance between root growth and shoot photosynthesis accumulation should be coordinated in crop production and vary in relation to factors such as genotypic differences and resource supply. In annual crops, the allocation of dry matter to roots changes during their life cycle. Typically, proportionally more assimilates are allocated to roots during early stages of plant growth. After flowering, a large proportion of recent assimilates are translocated to the growing reproductive structures and the proportion of assimilates translocated to roots decreases (Brown and Biscoe 1985; Snapp and Shennan 1992; Wells and Eissenstat 2003). Data from many studies indicate that the root: shoot DW ratio (R/S) of maize decreases from about 0.68 at emergence (9 days after planting) to 0.16 at physiological maturity (137 days after planting) (Amos and Walters 2006). During the vegetative growth period, the increase in RLD is synchronized with shoot growth and demand for nutrients, and is correlated with fluctuations in carbon flux from shoot to roots (Rajcan and Tollenaar 1999; Gallais and Coque 2005; Hirel et al. 2007). During reproductive growth, reduced carbon flux from shoot to roots, and accelerated root mortality, results in a rapid decrease in R/S DW ratio (Wiesler and Horst 1993; Wells and Eissenstat 2003; Ogawa et al. 2005).

The amounts of mineral nutrients taken up by the root system are coordinated with shoot growth and demand for nutrients. Although covering or removing ears of maize leads to greater allocation of carbon and nutrients to the root, and results in a larger root system and a higher R/S ratio, less nutrients are taken up after these treatments compared with control plants (Christensen et al. 1981; Ceppi et al. 1987; Yan et al. 2011b; Ning et al. 2012). These results demonstrate that the growth and absolute size of the maize root system is not necessarily correlated with the amount of nutrients it acquires. Root growth is often determined by the amount of carbon translocated from the shoot, whilst the amounts of mineral nutrients taken up is often determined by shoot demand or shoot growth potential (Ma and Dwyer 1998; Wang et al. 2006; Coque et al. 2008; Yan et al. 2011b; Ning et al. 2012).

It is interesting to observe that post-silking uptake accounts for 16–43 % of the total N and 16–55 % of the total P in maize plants at maturity, whilst there is little accumulation of potassium (K) post-silking. The ratio of grain K content to whole plant K content was the lowest compared with the other two macro-elements N and P at maturity. Indeed, there can even be a net loss of K in the post-silking period (Peng et al. 2012b; Ciampitti et al. 2013; Ning et al. 2013). It is believed that the asynchronous uptake of N, P and K is closely related to their functions in plants. A requirement for K to maintain enzyme activities and cell turgor underlies vigorous vegetative growth (Hawkesford et al. 2012), which might explain the preferential accumulation of K pre-silking, whereas N and P are required in large amounts for the formation of new tissues and the accumulation of seed reserves during post-silking grain development. Also K is important for the loading of sucrose and the rate of the mass flow-driven solute transport in the sieve tubes of the phloem (Hawkesford et al. 2012). There is a net remobilization of N and P from vegetative to reproductive tissues post-silking (Ning et al. 2012, 2013).

Plasticity in the partitioning of carbon between shoot and roots also depends upon external environmental factors. In the short-term, plants experiencing nutrient deficiency can increase resource acquisition by increasing their R/S DW ratio (Ågren and Ingestad 1987; Aikio and Markkola 2002; Hermans et al. 2006). This plasticity of carbon allocation to compensate for limitations in nutrient uptake is modulated by species-specific developmental patterns (Siddique et al. 1990; Gedroc et al. 1996), and is negatively correlated with the concentrations of mineral nutrients in leaves (Scheible et al. 1997; de Groot et al. 2003; Hermans et al. 2006). However, greater carbon allocation to roots will restrict shoot growth, which can ultimately result in reduced grain yield. Optimized nutrient supply in crop production is therefore important for maximizing grain yield and, since agronomic nutrient-use efficiency is the quotient of grain yield and nutrient supply, improving nutrient-use efficiency.

Root traits in maize breeding

Although roots play a significant role in increasing nutrient acquisition, limited attention has been paid to root traits in crop breeding during the past decades, possibly because roots grow belowground and are difficult to study (Gewin 2010; White et al. 2013b). Plant breeders usually make considerable gains on ‘aboveground’ traits and tremendous genetic variations trapped in roots have been neglected (Duvick 2005). The development of new crop varieties with enhanced soil resource acquisition is an important strategy for global grain security (Lynch 1998, 2007; Vance et al. 2003; White et al. 2013b). Improvement in the ability of plants to tolerate stress conditions, rather than increases in primary productivity perse, has been the primary driving force for increasing grain yield in maize breeding in recent decades (Duvick 2005; Fischer and Edmeades 2010). The ‘Green Revolution’ succeeded in increasing maize yields using conventional germplasm to develop disease-resistant F1-hybrid varieties, whose yields responded positively to irrigation and fertilizer applications without lodging (Evenson and Gollen 2003; Godfray et al. 2010). Increased root DW in new maize varieties plays an important role in providing resistance to lodging at high plant densities (Duvick and Cassman 1999; Duvick 2005; Echarte et al. 2008). In addition, the deeper roots of the new varieties enable maize plants to access more water and soluble nutrients, such as nitrate, in deep soil horizons (Dunbabin et al. 2003; Hammer et al. 2009; Lynch 2013). Hammer et al. (2009) modeled the relationship between root architecture and grain yield for maize varieties released in the US over the last century and concluded that improvements in root system architectures and, in particular, water capture through breeding have increased both biomass accumulation and crop yields. Study on the three-dimensional distributions of roots from maize varieties released in different eras have demonstrated that new maize varieties have larger root DW, but similar TRLs and vertical root distributions, to older varieties at silking, when the root system of maize attains its largest size, but new maize varieties have greater TRL and deeper roots than older varieties at maturity. The latter phenomenon was the result of more growth of new roots and/or less root mortality after silking in the new varieties, especially of roots in the topsoil (Ning et al. 2014). Irrespective of similar TRLs in both new and older maize varieties at silking, new varieties accumulate more mineral nutrients than older varieties. This is likely to be partly a consequence of greater shoot demand, rather than simply an effect of root size per se, as discussed in the preceding section (Clarkson et al. 1988; Imsande and Touraine 1994; Peng et al. 2010; Yan et al. 2011b). Fortunately, some ongoing breeding and genetic improvement programs have been implemented gradually by the geneticists and agronomists in characterizing promising root traits for enhancing nutrient acquisition and increasing the ability of stresses tolerance (Tuberosa et al. 2003; Hund et al. 2004, 2011; Zhu et al. 2005, Trachsel et al. 2009; Ruta et al. 2010; Lynch 2013; Rose et al. 2013; White et al. 2013a, b; Postma et al. 2014; Saengwilai et al. 2014).

Concluding remarks and future perspectives

Much is known about how root architecture responds to heterogeneous nutrient availabilities in plants of different species and of contrasting nutritional status under controlled environmental conditions, and the molecular mechanisms coordinating these responses are beginning to be elucidated in model plants, such as *Arabidopsis* (reviewed by Casimiro et al. 2003; López-Bucio et al. 2003; Hardtke 2006; Desnos 2008; Benková and Bielach 2010; De Smet 2012; Ubeda-Tomás et al. 2012). However, little is known about the responses' root architecture to heterogeneous nutrient availability under field conditions (reviewed by Hochholdinger et al. 2004; Hochholdinger and Tuberosa 2009; Smith and De Smet 2012; Orman-Ligeza et al. 2013).

While nitrate-rich patches increase the length of LRs from the treated roots of maize seedlings, they increase both the length and density of LRs of shoot-borne roots that form adult maize plants at reproductive growth stage, when TRL begins to decrease dramatically under field conditions (Peng et al. 2012a; Yu et al. 2014). The possible regulatory mechanism underlying the markedly increase in both the length and density of LRs initiated from shoot-borne roots is unknown. In *Arabidopsis,* systemic LP supply also causes an increase in length and density of LRs. Expressional induction of the auxin receptor TRANSPORT INHIBITOR RESPONSE1 (TIR1) in pericycle cells promotes LRs initiation and emergence; as a result, root density is significantly enhanced in P-deficient roots (Pérez-Torres et al. 2008). Since modern maize varieties take up more post-silking nutrients than old ones, more attention should be paid to the genetic improvements and novel adaptive mechanism of maize shoot-borne roots, especially the later initiated ones to resource deployment (Gaudin et al. 2011; Saengwilai et al. 2014; Yu et al. 2014).

Although the amount of nutrients taken up is decided by shoot demand, a larger and deeper root system is apparently beneficial for increasing the contact with the soil and thus nutrients uptake; and intercept/take up the nitrate leached to deeper soil layers. Knowledge of root development and the phenotypic plasticity of root system architecture to nutrient availability will help harnessing the potential for manipulating root growth in the field to exploit the biological potential of root system on one hand, and breeding roots with more efficient acquisition of soil resources on the other hand, and thereby maximizing the nutrient-use efficiency and reducing N losses in maize production.

Approaches toward the understanding of the changing demands of crops for nutrients over the growing season, and the temporal and spatial heterogeneities in the availability of mineral nutrients in the field, enable us optimizing root zone management to synchronize crop growth demand, root resource acquisition and fertilizer application throughout the crop growing season (Peng et al. 2012a; Shen et al. 2013).

Acknowledgments We thank the National Natural Science Foundation of China (No. 31272232), the State Key Basic Research and Development Plan of China (No. 2013CB127402), the Innovative Group Grant of National Natural Science Foundation of China (No. 31121062), Chinese Universities Scientific Fund (No. 2012YJ039), Post-graduate Study Abroad Program of China Scholarship Council, and the Rural and Environment Science and Analytical Services Division (RESAS) of the Scottish Government for financial support.

References

Adu MO, Chatot A, Wiesel L, Bennett MJ, Broadley MR, White PJ, Dupuy LX (2014) A scanner system for high resolution quantification of variation in root growth dynamics of *Brassica rapa* genotypes. J Exp Bot. doi:10.1093/jxb/eru048

Ågren GI, Ingestad T (1987) Root: shoot ratio as a balance between nitrogen productivity and photosynthesis. Plant Cell Environ 10:579–586

Aikio S, Markkola AM (2002) Optimality and phenotypic plasticity of shoot-to-root ratio under variable light and nutrient availabilities. Funct Ecol 16:67–76

Alvarez JM, Vidal EA, Gutiérrez RA (2012) Integration of local and systemic signaling pathways for plant N responses. Curr Opin Plant Biol 15:185–191

Amos B, Walters DT (2006) Maize root biomass and net rhizodeposited carbon: an analysis of the literature. Soil Sci Soc Am J 70:1489–1503

Armengaud P, Zambaux K, Hills A, Sulpice R, Pattison RJ, Blatt MR, Amtmann A (2009) EZ-Rhizo: integrated software for the fast and accurate measurement of root system architecture. Plant J 57:945–956

Baluška F, Barlow PW, Baskin TI, Chen R, Feldman L, Forde BG, Geisler M, Jernstedt J, Menzel D, Muday GK, Murphy A, Šamaj J, Volkmann D (2005) What is apical and what is basal in plant root development? Trends Plant Sci 10:409–411

Barber SA (1995) Soil nutrient bioavailability: a mechanistic approach, 3rd edn. Wiley, New York

Bell JK, McCully ME (1970) A histological study of lateral root initiation and development in *Zea mays*. Protoplasma 70:179–205

Benková E, Bielach A (2010) Lateral root organogenesis-from cell to organ. Curr Opin Plant Biol 13:677–683

Böhm W (1979) Methods of Studying Root Systems. Springer/Berlin/Heidelberg, New York

Brown KF, Biscoe PV (1985) Fibrous root growth and water use of sugar beet. J Agric Sci 105:679–691

Buczko U, Kuchenbuch RO (2013) Spatial distribution assessment of maize roots by 3D monolith sampling. Communi Soil Sci Plan 44:2127–2151

Casero PJ, Casimiro I, Lloret PG (1995) Lateral root initiation by asymmetrical transverse divisions of pericycle cells in four plant species: *Raphanus sativus*, *Helianthus annuus*, *Zea mays*, and *Daucus carota*. Protoplasma 188:49–58

Casimiro I, Beeckman T, Graham N, Bhalerao R, Zhang H, Casero P, Sandberg G, Bennett MJ (2003) Dissecting *Arabidopsis* lateral root development. Trends Plant Sci 8:165–171

Ceppi D, Sala M, Gentinetta E, Verderio A, Motto M (1987) Genotype-dependent leaf senescence in maize: inheritance and effects of pollination-prevention. Plant Physiol 85:720–725

Christensen LE, Below FE, Hageman RH (1981) The effects of ear removal on senescence and metabolism of maize. Plant Physiol 68:1180–1185

Ciampitti IA, Camberato JJ, Murrell ST, Vyn TJ (2013) Maize nutrient accumulation and partitioning in response to plant density and nitrogen rate: I. macronutrients. Agron J 105:783–795

Clark RT, MacCurdy RB, Jung JK, Shaff JE, McCouch SR, Aneshansley DJ, Kochian LV (2011) Three-dimensional root phenotyping with a novel imaging and software platform. Plant Physiol 156:455–465

Clark RT, Famoso AN, Zhao K, Shaff JE, Craft EJ, Bustamante CD, Mccouch SR, Aneshansley DJ, Kochian LV (2013) High-throughput two-dimensional root system phenotyping platform facilitates genetic analysis of root growth and development. Plant Cell Environ 36:454–466

Clarkson DT, Earnshaw MJ, White PJ, Cooper HD (1988) Temperature dependent factors influencing nutrient uptake: an analysis of responses at different levels of organization. Symp Soc Exp Biol 42:281–309

Coque M, Martin A, Veyrieras JB, Hirel B, Gallais A (2008) Genetic variation for N-remobilization and post silking N-uptake in a set of maize recombinant inbred lines. 3 QTL detection and coincidences. Theor Appl Genet 117:729–747

Crawford NM (1995) Nitrate: nutrient and signal for plant growth. Plant Cell 7:859–868

Crawford NM, Glass ADM (1998) Molecular and physiological aspects of nitrate uptake in plants. Trends Plant Sci 3:389–395

Croft SA, Hodge A, Pitchford JW (2012) Optimal root proliferation strategies: the roles of nutrient heterogeneity, competition and mycorrhizal networks. Plant Soil 351:191–206

de Groot CC, Marcelis LF, van den Boogaard R, Kaiser WM, Lambers H (2003) Interaction of nitrogen and phosphorus nutrition in determining growth. Plant Soil 248:257–268

De Smet I (2012) Lateral root initiation: one step at a time. New Phytol 193:867–873

Desnos T (2008) Root branching responses to phosphate and nitrate. Curr Opin Plant Biol 11:82–87

Downie H, Holden N, Otten W, Spiers AJ, Valentine TA, Dupuy LX (2012) Transparent soil for imaging the rhizosphere. PLoS One 7:e44276

Drew MC (1975) Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system and the shoot in barley. New Phytol 75:479–490

Drew MC, Saker LR (1975) Nutrient supply and the growth of the seminal root system in barley: II Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. J Exp Bot 26:79–90

Drew MC, Saker LR, Ashley TW (1973) Nutrient supply and the growth of the seminal root system in barley. I. The effect of nitrate concentration on the growth of axes and laterals. J Exp Bot 83:1189–1202

Dunbabin VM, Diggle AJ, Rengel Z (2002) Simulation of field data by a basic three-dimensional model of interactive root growth. Plant Soil 239:39–54

Dunbabin VM, Diggle AJ, Rengel Z (2003) Is there an optimal root architecture for nitrate capture in leaching environments? Plant Cell Environ 26:835–844

Dunbabin VM, Rengel Z, Diggle AJ (2004) Simulating form and function of root systems: efficiency of nitrate uptake is dependent on root system architecture and the spatial and temporal variability of nitrate supply. Funct Ecol 18:204–211

Durieux RP, Kamprath EJ, Jackson WA, Moll RH (1994) Root distribution of corn: the effect of nitrogen fertilization. Agron J 86:958–962

Duvick DN (2005) The contribution of breeding to yield advances in maize (*Zea mays*). Adv Agron 86:83–145

Duvick DN, Cassman KG (1999) Post-green revolution trends in yield potential of temperate maize in the north-central United States. Crop Sci 39:1622–1630

Echarte L, Rothstein S, Tollenaar M (2008) The response of leaf photosynthesis and dry matter accumulation to nitrogen supply in an older and a newer maize hybrid. Crop Sci 48:656–665

Eghball B, Maranville JW (1993) Root development and nitrogen influx of corn genotypes grown under combined drought and nitrogen stresses. Agron J 85:147–152

Eissenstat DM (1997) Trade-offs in root form and function. In: Jackson LE (ed) Ecology in agriculture. Academic Press, San Diego, pp 173–199

Eissenstat DM, Yanai R (1997) The ecology of root life-span. Adv Ecol Res 27:1–60

Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Building roots in a changing environment: implications for root longevity. New Phytol 147:33–42

Esau K (1977) Plant anatomy, 2nd edn. Wiley, New York

Evenson RE, Gollen D (2003) Assessing the impact of the Green Revolution, 1960–2000. Science 300:758–762

Fahn A (1990) Plant anatomy, 4th edn. Pergamon Press, Oxford

Feil B, Thiraporn R, Geisler G, Stamp P (1990) Root traits of maize seedlings-indicators of nitrogen efficiency? Plant Soil 123:155–159

Feix G, Hochholdinger F, Park WJ (2002) Maize root system and genetic analysis of its formation. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: The hidden half, 4th edn. Marcel Dekker, New York, pp 239–248

Feldman L (1994) The maize root. In: Freeling M, Walbot V (eds) The maize handbook. Springer, New York, pp 29–37

Fischer RA, Edmeades GO (2010) Breeding and cereal yield progress. Crop Sci 50:85–98

Fitter AH (1994) Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In: Caldwell MM, Pearcy RW (eds) Exploitation of environmental heterogeneity by plants. Academic, San Diego, pp 305–323

Fitter AH (2002) Characteristics and functions of root systems. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half, 3rd edn. CRC Press, Boca Raton, pp 15–32

Forde BG, Lorenzo H (2001) The nutritional control of root development. Plant Soil 232:51–68

Forde BG, Walch-Liu P (2009) Nitrate and glutamate as environmental cues for behavioural responses in plant roots. Plant Cell Environ 32:682–693

Foth HD (1962) Root and top growth of corn. Agron J 54:49–52

Gallais A, Coque M (2005) Genetic variation and selection for nitrogen use efficiency in maize: a synthesis. Maydica 50:531–547

Garnett T, Conn V, Kaiser BN (2009) Root based approaches to improving nitrogen use efficiency in plants. Plant Cell Environ 32:1272–1283

Garnett T, Conn V, Plett D, Conn S, Zanghellini J, Mackenzie N, Enju A, Francis K, Holtham L, Roessner U, Boughton B, Bacic A, Shirley N, Rafalski A, Dhugga K, Tester M, Kaiser BN (2013) The response of the maize nitrate transport system to nitrogen demand and supply across the lifecycle. New Phytol 198:82–94

Gastal F, Lemaire G (2002) N uptake and distribution in crops: an agronomical and ecophysiological perspective. J Exp Bot 53:789–799

Gaudin ACM, Mcclymont SA, Holmes BM, Lyons E, Raizada MN (2011) Novel temporal, fine-scale and growth variation phenotypes in roots of adult-stage maize (*Zea mays* L.) in response to low nitrogen stress. Plant Cell Environ 34:2122–2137

Gedroc JJ, McConnaughay KDM, Coleman JS (1996) Plasticity in root/shoot partitioning: optimal, ontogenetic, or both? Funct Ecol 10:44–50

Gerwitz A, Page ER (1974) An empirical mathematical model to describe plant root systems. J Appl Ecol 11:773–782

Gewin V (2010) An underground revolution. Nature 466:552–553

Giehl RF, Gruber BD, von Wirén N (2013) It's time to make changes: modulation of root system architecture by nutrient signals. J Exp Bot. doi:10.1093/jxb/ert421

Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C (2010) Food security: the challenge of feeding 9 billion people. Science 327:812–818

Gojon A (2013) Inorganic nitrogen acquisition and signaling: physiological and molecular aspects. In: Eshel A, Beeckman T (eds) Plant roots: the hidden half, 4th edn. CRC Press, Boca Raton, pp 25:15–32

Gojon A, Nacry P, Davidian JC (2009) Root uptake regulation: a central process for NPS homeostasis in plants. Curr Opin Plant Biol 12:328–338

Granato TC, Raper CD (1989) Proliferation of maize (*Zea mays* L.) roots in response to localized supply of nitrate. J Exp Bot 40:263–275

Gregory PJ (2006) Plant roots: growth, activity and interaction with soils. Blackwell Publishing, Oxford

Gruber BD, Giehl RF, Friedel S, von Wirén N (2013) Plasticity of the *Arabidopsis* root system under nutrient deficiencies. Plant Physiol 109:161–179

Guo Y, Chen F, Zhang F, Mi G (2005) Auxin transport from shoot to root is involved in the response of lateral root growth to localized supply of nitrate in maize. Plant Sci 169:894–900

Hammer GL, Dong ZS, McLean G, Doherty A, Messina C (2009) Can changes in canopy and/or root system architecture explain historical maize yield trends in the US corn belt? Crop Sci 49:299–312

Hanway JJ (1963) Growth stages of corn (*Zea mays*, L.). Agron J 55:487–492

Hardtke CS (2006) Root development-branching into novel spheres. Curr Opin Plant Biol 9:66–71

Hawkesford M, Horst W, Kichey T, Lambers H, Schjoerring J, Skrumsager M, White P (2012) Functions of macronutrients. In: Marschner P (ed) Marschner's mineral nutrition of higher plants, 3rd edn. Academic Press, London, pp 178–189

Herder GD, Isterdael GV, Beeckman T, De Smet I (2010) The roots of a new green revolution. Trends Plant Sci 15:600–607

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

Hetz W, Hochholdinger F, Schwall M, Feix G (1996) Isolation and characterization of *rtcs*, a maize mutant deficient in the formation of nodal roots. Plant J 10:845–857

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. J Exp Bot 58:2369–2387

Hochholdinger F, Tuberosa R (2009) Genetic and genomic dissection of maize root development and architecture. Curr Opin Plant Biol 12:172–177

Hochholdinger F, Park WJ, Sauer M, Woll K (2004) From weeds to crops: genetic analysis of root development in cereals. Trends Plant Sci 9:42–48

Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytol 162:9–24

Hodge A (2006) Plastic plants and patchy soils. J Exp Bot 57:401–411

Hodge A, Stewart J, Robinson D, Griffiths BS, Fitter AH (1999) Plant, soil fauna and microbial responses to N-rich organic patches of contrasting temporal availability. Soil Biol Biochem 31:1517–1530

Hodge A, Berta G, Doussan C, Merchan F, Crespi M (2009) Plant root growth, architecture and function. Plant Soil 321:153–187

Hoppe DC, McCully ME, Wenzel CL (1986) The nodal roots of *Zea*: their development in relation to structural features of the stem. Can J Bot 64:2524–2537

Hund A, Fracheboud Y, Soldati A, Frascaroli E, Salvi S, Stamp P (2004) QTL controlling root and shoot traits of maize seedlings under cold stress. Theor Appl Genet 109:618–629

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

Hund A, Trachsel S, Stamp P (2009b) Growth of axile and lateral roots of maize: I development of a phenotying platform. Plant Soil 325:335–349

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

Imsande J, Touraine B (1994) N demand and the regulation of nitrate uptake. Plant Physiol 105:3–7

Iyer-Pascuzzi AS, Symonova O, Mileyko Y, Hao Y, Belcher H, Harer J, Weitz JS, Benfey PN (2010) Imaging and analysis platform for automatic phenotyping and trait ranking of plant root systems. Plant Physiol 152:1148–1157

Jackson RB, Manwarning JH, Caldwell MM (1990) Rapid physiological adjustment of roots to localized soil enrichment. Nature 344:58–59

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411

Jansen L, Roberts I, De Rycke R, Beeckman T (2012) Phloem-associated auxin response maxima determine radial positioning of lateral roots in maize. Phil Trans R Soc B 367:1525–1533

Jeschke WD, Holobrada M, Hartung W (1997) Growth of *Zea mays* L. plants with their seminal roots only. Effects on plant development, xylem transport, mineral nutrition and the flow and distribution of abscisic acid (ABA) as a possible shoot to root signal. J Exp Bot 48:1229–1239

Kellermeier F, Chardon F, Amtmann A (2013) Natural variation of *Arabidopsis* root architecture reveals complementing adaptive strategies to potassium starvation. Plant Physiol 161:1421–1432

Kristensen HL, Thorup-Kristensen K (2004) Root growth and nitrate uptake of three different catch crops in deep soil layers. Soil Sci Soc Am J 68:529–537

Krouk G, Lacombe B, Bielach A, Perrine-Walker F, Malinska K, Mounier E, Hoyerova K, Tillard P, Leon S, Ljung K, Zazimalova E, Benkova E, Nacry P, Gojon A (2010) Nitrate-regulated auxin transport by *NRT1.1* defines a mechanism for nutrient sensing in plants. Dev Cell 18:927–937

Kuchenbuch RO, Gerke HH, Buczko U (2009) Spatial distribution of maize roots by complete 3D soil monolith sampling. Plant Soil 315:297–314

Li H, Ma Q, Li H, Zhang F, Rengel Z, Shen J (2014) Root morphological responses to localized nutrient supply differ among crop species with contrasting root traits. Plant Soil 376:151–163

Linkohr BI, Williamson LC, Fitter AH, Leyser HMO (2002) Nitrate and phosphate availability and distribution have different effects on root system architecture of *Arabidopsis*. Plant J 29:751–760

Liu J, Han L, Chen F, Bao J, Zhang F, Mi G (2008) Microarray analysis reveals early responsive genes possibly involved in localized nitrate stimulation of lateral root development in maize (*Zea mays* L.). Plant Sci 175:272–282

Liu J, An X, Cheng L, Chen F, Bao J, Yuan L, Zhang F, Mi G (2010) Auxin transport in maize roots in response to localized nitrate supply. Ann Bot 106:1019–1026

López-Bucio J, Cruz-Ramírez A, Herrera-Estrella L (2003) The role of nutrient availability in regulating root architecture. Curr Opin Plant Biol 6:280–287

Lynch J (1995) Root architecture and plant productivity. Plant Physiol 109:7–13

Lynch JP (1998) The role of nutrient efficient crops in modern agriculture. J Crop Prod 1:241–264

Lynch JP (2007) Roots of the second green revolution. Aust J Bot 55:1–20

Lynch JP (2013) Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. Ann Bot 112:347–357

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

Lynch JP, Marschner P, Rengel Z (2012) Effect internal and external factors on root growth and development. In: Marschner P (ed) Marschner's mineral nutrition of higher plants, 3rd edn. Academic Press, London, pp 331–346

Ma BL, Dwyer LM (1998) Nitrogen uptake and use of two contrasting maize hybrids differing in leaf senescence. Plant Soil 199:283–291

Malamy JE (2005) Intrinsic and environmental response pathways that regulate root system architecture. Plant Cell Environ 28:67–77

Manoli A, Begheldo M, Genre A, Lanfranco L, Trevisan S, Quaggiotti S (2014) No homeostasis is a key regulator of early nitrate perception and root elongation in maize. J Exp Bot 65:185–200

McCully ME (1995) How do real roots work? Plant Physiol 109:1–6

McCully ME (1999) Roots in soil: unearthing the complexities of roots and their rhizospheres. Annu Rev Plant Physiol Plant Mol Biol 50:697–718

McCully ME, Canny MJ (1988) Pathways and processes of water and nutrient movements in roots. Plant Soil 111:159–170

Miller AJ, Fan X, Orsel M, Smith SJ, Wells DM (2007) Nitrate transport and signalling. J Exp Bot 58:2297–2306

Mounier E, Pervent M, Ljung K, Gojon A, Nacry P (2014) Auxin-mediated nitrate signalling by NRT1.1 participates in the adaptive response of *Arabidopsis* root architecture to the spatial heterogeneity of nitrate availability. Plant Cell Environ 37:162–174

Nacry P, Bouguyon E, Gojon A (2013) Nitrogen acquisition by roots: physiological and developmental mechanisms ensuring plant adaptation. Plant Soil 370:1–29

Nibau C, Gibbs DJ, Coates JC (2008) Branching out in new directions: the control of root architecture by lateral root formation. New Phytol 179:595–614

Ning P, Liao C, Li S, Yu P, Zhang Y, Li X, Li C (2012) Maize cob plus husks mimics the grain sink to simulate nutrient uptake by roots. Field Crops Res 130:38–45

Ning P, Li S, Yu P, Zhang Y, Li C (2013) Post-silking accumulation and partitioning of dry matter, nitrogen, phosphorus and potassium in maize varieties differing in leaf longevity. Field Crops Res 144:19–27

Ning P, Li S, Li XX, Li CJ (2014) New maize hybrids had larger and deeper post-silking root than old ones. Field Crops Res. doi:10.1016/j.fcr.2014.06.009

Niu J, Peng Y, Li C, Zhang F (2010) Changes in root length at the reproductive stage of maize plants grown in the field and quartz sand. J Plant Nutr Soil Sci 173:306–314

Ogawa A, Kawashima C, Yamauchi A (2005) Sugar accumulation along the seminar root axis as affected by osmotic stress in maize: a possible physiological basis for plastic lateral root development. Plant Prod Sci 8:173–180

Oikeh SO, Kling JG, Horst WJ, Chude VO, Carsky RJ (1999) Growth and distribution of maize roots under nitrogen fertilization in plinthite soil. Field Crops Res 62:1–13

Orman-Ligeza B, Parizot B, Gantet PP, Beeckman T, Bennett MJ, Draye X (2013) Post-embryonic root organogenesis in cereals: branching out from model plants. Trends Plant Sci 18:459–467

Osmont KS, Sibout R, Hardtke CS (2007) Hidden branches: developments in root system architecture. Annu Rev Plant Biol 58:93–113

Pan WL, Jackson WA, Moll RH (1985) Nitrate uptake and partitioning by corn (*Zea mays* L.) root systems and associated morphological differences among genotypes and stages of root development. J Exp Bot 36:1341–1351

Passioura JB (1972) The effect of root geometry on the yield of wheat growing on stored water. Aust J Agric Res 23:745–752

Peng Y, Li X, Li C (2012a) Temporal and spatial profiling of root growth revealed novel response of maize roots under various nitrogen supplies in the field. PLoS One 7:e37726. doi:10.1371/journal.pone.0037726

Peng Y, Zhang Y, Sun G, Ning P, Li X, Li C (2012b) Temporal and spatial dynamics in root length density of field-grown maize and NPK in the soil profile. Field Crops Res 131:9–16

Pérez-Torres CA, López-Bucioa J, Cruz-Ramírezb A, Ibarra-Lacletteb E, Dharmasiric S, Estellec M, Herrera-Estrella L (2008) Phosphate availability alters lateral root development in *Arabidopsis* by modulating auxin sensitivity via a mechanism involving the TIR1 auxin receptor. Plant Cell 20:3258–3272

Postma J A, Dathe A, Lynch J (2014) The optimal lateral root branching density for maize depends on nitrogen and phosphorus availability. Plant Physiol 113.233916

Quaggiotti S, Ruperti B, Borsa P, Destro T, Malagoli M (2003) Expression of a putative high-affinity NO_3^- transporter and of an H^+-ATPase in relation to whole plant nitrate transport physiology in two maize genotypes differently responsive to low nitrogen availability. J Exp Bot 54:1023–1031

Quaggiotti S, Ruperti B, Pizzeghello D, Francioso O, Tugnoli V, Nardi S (2004) Effect of low molecular size humic substances on nitrate uptake and expression of genes involved in nitrate transport in maize (*Zea mays* L.). J Exp Bot 55:803–813

Rajcan I, Tollenaar M (1999) Source: sink ratio and leaf senescence in maize: II Nitrogen metabolism during grain filling. Field Crops Res 60:255–265

Remans T, Nacry P, Pervent M, Girin T, Tillard P, Lepetit M, Gojon A (2006) The *Arabidopsis* NRT1.1 transporter participates in the signaling pathway triggering root colonization of nitrate-rich patches. Proc Natl Acad Sci USA 103:19206–19211

Rich SM, Watt M (2013) Soil conditions and cereal root system architecture: review and considerations for linking Darwin and Weaver. J Exp Bot 4:1193–1208

Robertson MJ, Fukai S, Hammer GL, Ludlow MM (1993) Modelling root growth of grain sorghum using the CERES approach. Field Crops Res 33:113–130

Robinson D (1994) The responses of plants to nonuniform supplies of nutrients. New Phytol 127:635–674

Robinson D, Rorison IH (1983) Relationship between root morphology and nitrogen availability in a recent theoretical model describing nitrogen uptake from soil. Plant Cell Environ 6:641–647

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. Ann Bot 112:331–345

Rubio G, Lynch JP (2007) Compensation among root classes in *Phaseolus vulgaris* L. Plant Soil 290:307–321

Ruffel S, Freixes S, Balzergue S, Tillard P, Jeudy C, Martin-Magniette ML, van der Merwe MJ, Kakar K, Gouzy J, Fernie AR, Udvardi M, Salon C, Gojon A, Lepetit M (2008) Systemic signaling of the plant nitrogen status triggers specific transcriptome responses depending on the nitrogen source in *Medicago truncatula*. Plant Physiol 146:2020–2035

Ruffel S, Krouk G, Ristova D, Shasha D, Birnbaum KD, Coruzzi GM (2011) Nitrogen economics of root foraging: transitive closure of the nitrate–cytokinin relay and distinct systemic signaling for N supply vs. demand. Proc Natl Acad Sci USA 108:18524–18529

Ruta N, Liedgens M, Fracheboud Y, Stamp P, Hund A (2010) QTLs for the elongation of axile and lateral roots of maize in response to low water potential. Theor Appl Genet 120:621–631

Ruzicka DR, Barrios-Masias FH, Hausmann NT, Jackson LE, Schachtman DP (2010) Tomato root transcriptome response to a nitrogen-enriched soil patch. BMC Plant Biol 10:75

Saengwilai P, Tian X, Lynch J (2014) Low crown root number enhances nitrogen acquisition from low nitrogen soils in maize (*Zea mays* L.) Plant Physiol 113.232603

Santi S, Locci G, Monte R, Pinton R, Varanini Z (2003) Induction of nitrate uptake in maize roots: expression of a putative high-affinity nitrate transporter and plasma membrane H^+-ATPase isoforms. J Exp Bot 54:1851–1864

Sattelmacher B, Thoms K (1995) Morphology and physiology of the seminal root system of young maize (*Zea mays* L.) plants as influenced by a locally restricted nitrate supply. Zeitschrift für Pflanzenernährung und Bodenkunde 158:493–497

Scheible WR, Lauerer M, Schulze ED, Caboche M, Stitt M (1997) Accumulation of nitrate in the shoot acts as a signal to regulate shoot-root allocation in tobacco. Plant J 11:671–691

Schlicht M, Ludwig-Müller J, Burbach C, Volkmann D, Baluska F (2013) Indole-3-butyric acid induces lateral root formation via peroxisome-derived indole-3-acetic acid and nitric oxide. New Phytol 200:473–482

Schortemeyer M, Feil B, Stamp P (1993) Root morphology and nitrate uptake of maize simultaneously supplied with ammonium and nitrate in a split-root system. Ann Bot 72:107–115

Shane MW, McCully ME (1999) Root xylem embolisms: implications for water flow to the shoot in single-rooted maize plants. Aust J Plant Physiol 26:107–114

Shane MW, McCully ME, Canny MJ (2000) Architecture of branch-root junctions in maize: structure of the connecting xylem and the porosity of pit membranes. Ann Bot 85:613–624

Shemesh H, Arbiv A, Gersani M, Ovadia O, Novoplansky A (2010) The effects of nutrient dynamics on root patch choice. PLoS One 5:1–6

Shen J, Li C, Mi G, Li L, Yuan L, Jiang R, Zhang F (2013) Maximizing root/rhizosphere efficiency to improve crop productivity and nutrient use efficiency in intensive agriculture of China. J Exp Bot 64:1181–1192

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. Ann Bot 112:381–389

Siddique KHM, Belford RK, Tennant D (1990) Root: shoot ratios of old and modern, tall and semi-dwarf wheats in a mediterranean environment. Plant Soil 121:89–98

Smith S, De Smet I (2012) Root system architecture: insights from *Arabidopsis* and cereal crops. Phil Trans R Soc B 367:1441–1452

Snapp SS, Shennan C (1992) Effects of salinity on root growth and death dynamics of tomato. Lycopersicon esculentum mill. New Phytol 121:71–79

Sullivan WM, Jiang ZC, Hull RJ (2000) Root morphology and its relationship with nitrate uptake in Kentucky bluegrass. Crop Sci 40:765–772

Thorup-Kristensen K (2001) Are differences in root growth of nitrogen catch crops important for their ability to reduce soil nitrate-N content, and how can this be measured? Plant Soil 230:185–195

Thorup-Kristensen K (2006) Effect of deep and shallow root systems on the dynamics of soil inorganic N during 3-year crop rotations. Plant Soil 288:233–248

Trachsel S, Messmer R, Stamp P, Hund A (2009) Mapping of QTLs for lateral and axile root growth of tropical maize. Theor Appl Genet 119:1413–1424

Trachsel S, Kaeppler SM, Brown KM, Lynch JP (2013) Maize root growth angles become steeper under low N conditions. Field Crops Res 140:18–31

Trevisan S, Borsa P, Botton A, Varotto S, Malagoli M, Ruperti B, Quaggiotti S (2008) Expression of two maize putative nitrate transporters in response to nitrate and sugar availability. Plant Biol 10:462–475

Trevisan S, Manoli A, Begheldo M, Nonis A, Enna M, Vaccaro S, Caporale G, Ruperti B, Quaggiotti S (2011) Transcriptome analysis reveals coordinated spatiotemporal regulation of haemoglobin and nitrate reductase in response to nitrate in maize roots. New Phytol 192:338–352

Tuberosa R, Salvi S, Sanguineti MC, Maccaferri M, Giuliani S, Landi P (2003) Searching for quantitative trait loci controlling root traits in maize: a critical appraisal. In: Roots: the dynamic interface between plants and the earth. Springer Netherlands, pp 35–54

Ubeda-Tomás S, Beemster GTS, Bennett MJ (2012) Hormonal regulation of root growth: integrating local activities into global behaviour. Trends Plant Sci 17:326–331

Valladares F, Sanchez-Gomez D, Zavala MA (2006) Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. J Ecol 94:1103–1116

van Vuuren MMI, Robinson D, Griffiths BS (1996) Nutrient inflow and root proliferation during the exploitation of a temporally and spatially discrete source of nitrogen in soil. Plant Soil 178:185–192

Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol 157:423–447

Varney GT, McCully ME (1991) The branch roots of *Zea*. II Developmental loss of the apical meristem in field-grown roots. New Phytol 118:535–546

Varney GT, Canny MJ, Wang XL, McCully ME (1991) The branch roots of *Zea*. First order branches, their number, sizes and division into classes. Ann Bot 67:357–364

Waines JG, Ehdaie B (2007) Domestication and crop physiology: roots of green-revolution wheat. Ann Bot 100:991–998

Waisel Y, Eshel A (2002) Functional diversity of various constituents of a single root system. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant Roots: The Hidden Half, 3rd edn. CRC Press, Boca Raton, pp 243–268

Walch-Liu P, Ivanov II, Filleur S, Gan Y, Remans T, Forde BG (2006) Nitrogen regulation of root branching. Ann Bot 97:875–881

Walk T, Jaramillo R, Lynch JP (2005) Architectural tradeoffs between adventitious and basal roots for phosphorus acquisition. Plant Soil 279:347–366

Wang Y, Mi G, Chen F, Zhang J, Zhang F (2004) Response of root morphology to nitrate supply and its contribution to nitrogen accumulation in maize. J Plant Nutr 27:2189–2202

Wang H, Inukai Y, Yamauchi A (2006) Root development and nutrient uptake. Crit Rev Plant Sci 25:279–301

Warncke DD, Barber SA (1974) Root development and nutrient uptake by corn grown in solution culture. Agron J 66:514–516

Watt M, Kirkegaard JA, Passioura JP (2006a) Rhizosphere biology and crop productivity. Aust J Soil Res 44:299–317

Watt M, Hugenholtz P, White R, Vinall K (2006b) Numbers and locations of native bacteria on field grown wheat roots quantified by fluorescence in situ hybridization (FISH). Environ Microbiol 8:871–884

Wells CE, Eissenstat DM (2003) Beyond the roots of young seedlings: the influence of age and order on fine root physiology. J Plant Growth Regul 21:324–334

White PJ, George TS, Dupuy LX, Karley AJ, Valentine TA, Wiesel L, Wishart J (2013a) Root traits for infertile soils. Front Plant Sci 4:193

White PJ, George TS, Gregory PJ, Bengough AG, Hallett PD, McKenzie BM (2013b) Matching roots to their environment. Ann Bot 112:207–222

Wiesler F, Horst WJ (1993) Differences among maize cultivars in the utilization of soil nitrate and the related losses of nitrate through leaching. Plant Soil 151:193–203

Wiesler F, Horst WJ (1994) Root growth and nitrate utilization of maize cultivars under field conditions. Plant Soil 163:267–277

Xu L, Niu J, Li C, Zhang F (2009) Growth, nitrogen uptake and flow in maize plants affected by root growth restriction. J Integr Plant Biol 51:689–697

Yan H, Li K, Ding H, Liao C, Li X, Yuan L, Li C (2011a) Root morphological and proteomic responses to growth restriction in maize plants supplied with sufficient N. J Plant Physiol 168:1067–1075

Yan H, Shang A, Peng Y, Yu P, Li C (2011b) Covering middle leaves and ears reveals differential regulatory roles of vegetative and reproductive organs in root growth and nitrogen uptake in maize. Crop Sci 51:265–272

York LM, Nord EA, Lynch JP (2013) Integration of root phenes for soil resource acquisition. Front Plant Sci 4:355

Yu P, Li X, Yuan L, Li C (2014) A novel morphological response of maize (*Zea mays*) adult roots to heterogeneous nitrate supply revealed by a split-root experiment. Physiol Plant 150:133–144

Zhang H, Forde BG (1998) An *Arabidopsis* MADS box gene that controls nutrient-induced changes in root architecture. Science 279:407–409

Zhang H, Forde BG (2000) Regulation of *Arabidopsis* root development by nitrate availability. J Exp Bot 51:51–59

Zhang H, Jennings A, Barlow PW, Forde BG (1999) Dual pathways for regulation of root branching by nitrate. Proc Natl Acad Sci USA 96:6529–6534

Zhu JM, Kaeppler SM, Lynch JP (2005) Topsoil foraging and phosphorus acquisition efficiency in maize. Funct Plant Biol 32:749–762

Zhu JM, Ingram PA, Benfey PN, Elich T (2011) From lab to field, new approaches to phenotyping root system architecture. Curr Opin Plant Biol 14:310–317

Zhuang J, Yu GR, Nakayama K (2001) Scaling of root length density of maize in the field profile. Plant Soil 235:135–142