Soil conditions and cereal root system architecture: review and considerations for linking Darwin and Weaver

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Abstract

Charles Darwin founded root system architecture research in 1880 when he described a root bending with gravity. Curving, elongating, and branching are the three cellular processes in roots that underlie root architecture. Together they determine the distribution of roots through soil and time, and hence the plants’ access to water and nutrients, and anchorage. Most knowledge of these cellular processes comes from seedlings of the model dicotyledon, Arabidopsis, grown in soil-less conditions with single treatments. Root systems in the field, however, face multiple stimuli that interact with the plant genetics to result in the root system architecture. Here we review how soil conditions influence root system architecture; focusing on cereals. Cereals provide half of human calories, and their root systems differ from those of dicotyledons. We find that few controlled-environment studies combine more than one soil stimulus and, those that do, highlight the complexity of responses. Most studies are conducted on seedling roots; those on adult roots generally show low correlations to seedling studies. Few field studies report root and soil conditions. Until technologies are available to track root architecture in the field, soil analyses combined with knowledge of the effects of factors on elongation and gravitropism could be ranked to better predict the interaction between genetics and environment (G×E) for a given crop. Understanding how soil conditions regulate root architecture can be effectively used to design soil management and plant genetics that best exploit synergies from G×E of roots.

Key words: Cereals, crop productivity, gravitropism, root architecture, root elongation, root branching, tropisms.

Darwin and root architecture research

In 1880, Darwin elegantly described how a single root tip bends towards gravity. A century and a half later, the molecular processes underlying the events in the root tip during gravitropism are documented. Gravitropism is one of the most studied root processes, and has been elucidated primarily through studies in soil-free conditions that impose a gravitational treatment on young plants. In the 1920s, Weaver’s meticulous drawings of root systems down soil profiles illustrated clearly that the sensing of gravity is a key determinant of architecture (Weaver et al., 1922; Weaver, 1925). Weaver’s drawings highlight that adult root system architecture depends on species, soil conditions, and root type. Recent reviews (Jovanovic et al., 2007; Osmont et al., 2007; Hodge et al., 2009; Ingram and Malamy, 2010) address the influence of factors on processes underlying root architecture. However, most data come from experiments where treatments are applied singly in controlled conditions, with an emphasis on molecular studies with the model dicotyledonous plant Arabidopsis. Root systems start as a single root formed during embryogenesis and expand exponentially as the plant grows. By grain development and plant maturity, a root system can have millions of roots. Few studies manipulate more than one stress factor, and few molecular mechanisms have been determined from field-grown roots which continuously encounter multiple soil conditions through space and time. Today the gap between Darwin’s carefully controlled experiment and Weaver’s field observations remains.
Here we review effects of soil conditions on cereal root architecture. We place particular emphasis on studies on the monocots because cereal species belong to this family and provide >50% of human calories.

Plant root systems

Cereals are members of the grass family, with a monocotyledonous root system comprised of primary axile root(s) from the embryo in the seed, and axile nodal roots from nodes along the stem (Fig. 1). Depending on the cereal, the number of primary roots varies (e.g. from one in the warm climate cereals maize, rice, and sorghum, to six or seven in the cool climate cereals, triticale and wheat). The number and position of emergence of the earliest axile nodal roots also vary, depending on whether the cereal forms a mesocotyl, planting depth, and genotype. Nodal axile roots from the scutellum node from within the seed, and nodal axile roots from the coleoptile node above the seed, may appear as primary roots and collectively be termed ‘seminal’ roots. Anatomical observations show that primary roots from the embryo have a central, large metaxylem vessel surrounded by small metaxylem vessels, while the basal region of nodal axile roots have a central pith of parenchyma cells surrounded by large and small metaxylem vessels (Watt et al., 2008). Both axile types develop branch roots, which in turn can develop successively higher order branched roots from their pericycle, up to third order. See table 2 in Fitter (1994) showing the different growth rate, length, and longevity of cereal roots of different branching order. Cereal roots, as with all grasses, do not have a vascular cambium, and must develop more root length to generate new xylem and phloem tissues for water and sugar transport, respectively (Fig. 1A). The embryonic and nodal root systems that develop over time offer some flexibility over the lack of cambia because they emerge over time to re-colonize the soil profile and differ in their responses to soil stimuli.

The dicotyledonous root system, such as that of Arabidopsis, Medicago, and bean, has a single primary axile root (tap root) that emerges from the base of the embryo. This tap root develops successive orders of branch roots (Fig. 1B). Thus the dicotyledonous root system is simpler than the cereal root systems, with only one type of axile root. ‘Adventitious’ roots can emerge directly from the stems in dicotyledons, but their contribution to the root system depends on genotype, age, and soil conditions, and they may not be as predictable and substantial as the cereal node axile roots. In contrast to the monocotyledons, dicotyledons have vascular cambia. Vascular cambia divide to differentiate into xylem and phloem tissues, continually thickening the root and providing additional transport capacity.

Despite obvious developmental differences between the monocotyledonous and dicotyledonous root systems, functional differences have not been studied intensively. Hamblin and Tennant (1987) showed in field crops that wheat had longer root length than lupin per unit time, but that water uptake per unit length of lupin was higher than that of wheat. Bramley and colleagues (2009) suggested that this was in part due to anatomical differences, whereby the vascular thickening from the cambium of lupin roots increased water uptake per unit length, while wheat without a cambium needed additional length to add vascular capacity. Nagel et al. (2012) compared the two-dimensional distribution of Arabidopsis roots with the grass model Brachypodium in 60 cm deep root observation boxes. This careful study showed that Brachypodium had greater root length in the middle and deep layers, suggesting that nodal root growth enables denser roots at depth when compared with basal branch roots from the Arabidopsis tap root. Brachypodium provides an opportunity to understand the extent to which processes discovered in Arabidopsis can be applied to cereals because it is a small, easy to grow monocotyledonous root system. Despite obvious developmental differences between the monocotyledonous and dicotyledonous root systems, functional differences have not been studied intensively. Hamblin and Tennant (1987) showed in field crops that wheat had longer root length than lupin per unit time, but that water uptake per unit length of lupin was higher than that of wheat. Bramley and colleagues (2009) suggested that this was in part due to anatomical differences, whereby the vascular thickening from the cambium of lupin roots increased water uptake per unit length, while wheat without a cambium needed additional length to add vascular capacity. Nagel et al. (2012) compared the two-dimensional distribution of Arabidopsis roots with the grass model Brachypodium in 60 cm deep root observation boxes. This careful study showed that Brachypodium had greater root length in the middle and deep layers, suggesting that nodal root growth enables denser roots at depth when compared with basal branch roots from the Arabidopsis tap root. Brachypodium provides an opportunity to understand the extent to which processes discovered in Arabidopsis can be applied to cereals because it is a small, easy to grow monocotyledonous root system.

Processes underlying root architecture: tropism, root elongation, and branching

Root architecture is a term that describes the pattern of distribution of roots within the soil profile through space and time (Lynch, 1995). Root processes affecting individual roots are what underlie root system architecture, and can be termed ‘component traits’. These are (i) branching rates; (ii) tropism; and (iii) elongation rates. Together, over time, these component traits determine the architecture of the entire root system. These are also the underlying processes attributed to shoot architecture where they can be explained largely by auxin movements determined in laboratory condition experiments (Prusinkiewicz and Runions, 2012). However, resultant
shoot and root architecture in the field are a combination of internal and external signals. Soil conditions are much more complex than aerial conditions experienced by shoots. For simplicity and length, this review deals with abiotic soil conditions and root architecture. Biotic factors are not considered here, although it is recognized that soil organisms such as root-infecting disease, symbiotic organisms, and other rhizosphere organisms have a large effect on root architecture.

**Soil conditions and root system architecture: a review of single factors imposed in controlled-environment experiments**

A root system is predisposed to a shape due to its underlying genetics; however, as soon as roots emerge, soil conditions exert an influence (Fig. 2). A root constantly experiences gravity (Fig. 2A). Layered over this are soil characteristics (Fig. 2B), water content (Fig. 2C), oxygen availability (Fig. 2D), patches of nutrients (Fig. 2E), and temperature changes (Fig. 2F). Gravity is static over a plant’s lifespan, but the other stimuli are heterogeneous both spatially and temporally, and are subject to local depletion or replenishment. In this section, we provide an overview of how root systems respond to these stimuli, resulting in changes to root architecture.

**Gravity**

Gravity exerts itself constantly and uniformly on all plant organs over the life cycle of the plant, unlike most environmental stimuli. The cell biology of root gravitropism has received a large amount of research attention in controlled conditions. As Darwin and Darwin (1880) hypothesized, the tip is considered the part of the root which senses gravity. The prevailing hypothesis is that dense starch-filled amyloplasts (statoliths) sediment to the lower side of specialized polar cells (statocytes) which are located in the columella of the root cap, and this is sensed by the root (Chen et al., 1999; Boonsirichai et al., 2002). Other mechanisms of gravitational sensing have been proposed: differential pressures within cells are caused by the settling of the protoplast within the extracellular matrix (e.g. in rice, Staves et al., 1997); gravitropic signals move apoplastically within the root cap mucilage from the root cap to the main root (e.g. in maize, Moore and McClen, 1989); and a signal within the elongation zone contributes to the root gravimetric response (e.g. in maize, Wolverton et al., 2003). Further evidence for these alternative theories is needed, as current evidence generally supports the starch–statolith hypothesis (Boonsirichai et al., 2002; Blancaflor and Masson, 2003).

The signalling cascade that transduces gravimetric information to altered growth once the position of the statoliths is perceived is not completely resolved (Sack, 1991). However, the Cholodny–Went model is widely accepted. It proposes that auxin is redistributed across the elongation zone in gravistimulated roots. Auxin accumulates on the lower side, resulting in differential growth inhibition, leading to downward curvature (Chen et al., 1999; Blancaflor and Masson, 2003; Swarup et al., 2005). Detailed biophysical measurements of cells in the elongation zone of graviresponding roots are lacking in cereals; therefore, it is unknown if the difference in growth rates from changes in turgor pressure or from asymmetric changes in cell wall properties (Pritchard, 1994). In maize roots, the acceleration of growth on the upper side of the root is accompanied by enhanced acid efflux along the upper surface of the root, and a reduction in acid efflux on the lower surface. Therefore, acid-induced wall loosening on the upper surface may account for the downward curvature of the root (Mulkey and Evans, 1981; Versel and Pilet, 1986). Maize has also been used to examine the role of calcium in the root gravitropic response. The upper and lower surfaces of a maize root showed significantly different concentrations of apoplastic calcium, potentially resulting in proton exchange with the stele on the lower side, giving reduced cell wall acidification and, therefore, tighter cell walls and reduced cell elongation on the lower side (Björkman and Cleland, 1991). Calcium is also an essential element in polar auxin transport and has been demonstrated in maize to form gradients in maize root tips when gravistimulated (Lee et al., 1983a, b), potentially resulting in auxin asymmetry (Young et al., 1990) in the elongation zone, resulting in gravitropic curvature. Although little recent work has been conducted on the mechanism of monocot gravitropism, in Arabidopsis, it has been elucidated that root gravitropism is regulated by a transient lateral auxin gradient (Band et al., 2012b).

The angle at which roots emerge (Fig. 2A) is known as the ‘gravitropic set-point angle’ (Digby and Fins, 1995). It has a genetic component (Uga et al., 2011; Mace et al., 2012) and has been used as an early screen for root traits in cereal breeding programmes (Wasson et al., 2012). The root angle at which primary roots emerge has been linked to the depth of the mature roots system in the field for several cereal species (e.g. in rice, Kato et al., 2006; sorghum, Mace et al., 2012; wheat, Oyanagi et al., 1993b; Manschadi et al., 2008). The association between deeper rooting and root angle has been exploited in rice, leading to the discovery of quantitative trait loci (QTLs) which appear to correlate strongly with a narrower and potentially deeper rooting phenotype (Uga et al., 2011). Nodal root angle QTLs have also been identified in maize (Omori and Mano, 2007) and sorghum (Mace et al., 2012), where three QTLs show homology to the previously identified root angle QTLs in rice and maize.

Although gravity is distributed uniformly across roots in soil, and hence gravitropism is relatively straightforward to target for crop improvement, the actual directions of growth of roots in soil are variable. They depend on root type, soil condition, and genotype. For example, primary, leaf node, and branch roots of cereals behave plagiogravitropically. They do not grow directly downwards, but, after emergence, can elongate horizontally for some time before curving vertically downwards (Nakamoto et al., 1991; Oyanagi et al., 1993a). Root angle can be influenced by temperature and water availability (Oyanagi et al., 1993a). Oryanagi et al. (1992) found that the angle from the horizontal of wheat primary roots...
Fig. 2. Examples of the effects of soil conditions on roots. In each case, a single condition is imposed. (A) Gravity: soil-grown seedlings of hybrid bread wheat with an acute gravitropic set-point angle (left) and a rye with a wider seminal root angle (right). (B) Hardness: wheat cv. Janz seminal axile root growing through a pore (left) and in hard soil (right). (C) Water: nodal roots of a well-watered wheat cv. Seri (left) and in dry soil (insert). (D) Oxygen: maize grown in drained soil (left) or in waterlogged soil for 21 d (right). (E) Nutrients: wheat cv. Gregory with even supply of phosphate (left) compared with a patch of phosphate applied at 8 μM between the blue beads (right). (F) Temperature: MRI of maize roots grown with a root zone temperature of 14 °C (left) or 24 °C (right). Images courtesy of
increased with water stress in 50 of 133 genotypes tested. The remaining 63 lines did not show significant change from the angle of well-watered plants, indicating a genetic by environment interaction. The use of the root angle in response to gravity as an early screening proxy for deeper root systems may need to include additional screens for responses in nodal and branch roots, and responses in the presence of water and other soil conditions, for improved correlation to the field. The mechanisms by which root tips perceive multiple stimuli such as gravity, water, and temperature, and integrate those for a resultant curvature, are not known, but could be critical for field crop improvement.

**Soil structure**

Soils are triphasic, consisting of solid particles, liquid water, and air. The solid phase constitutes ~50% of the total soil volume, and the texture of the soil is determined by the size of these particles. Soils will often contain numerous different particle sizes, with this composition having a significant effect on the soil structure (i.e. the size of particle aggregates and the resultant soil porosity). Both soil texture and structure impact on bulk density and on how easily a soil will be compacted, in turn contributing to soil strength. Moisture content also influences soil strength, which increases with decreasing soil water, due to the matric potential becoming more negative as a result of capillary forces (Whalley et al., 2005). These soil conditions are highly influential for root architecture, impacting the mechanical impedance (physical stress) to root elongation through the soil, as well as affecting the availabilities of water, oxygen, and nutrients (Gliński and Lipiec, 1990; Gregory, 2006) (Fig. 2B).

Roots encounter some amount of mechanical impedance to elongation as they grow through the soil. The main influence of higher impedance is a slowing in the rate of root elongation, with a coinciding increase in root diameter (Bengough and Mullins, 1990; Gliński and Lipiec, 1990; Gregory, 2006). Root elongation decreases in an approximately linear fashion until very high resistance is encountered (Whittlemore and Whalley, 2009). For example, Merotto and Mundstock (1999) grew wheat at 1.0, 2.0, 3.5, and 5.5 MPa and found that as soil resistance increased, from as early as 16 d after emergence there was a significant difference in root growth between the four soil treatments, with roots in stronger soils showing a heavily reduced length, surface area, and dry matter, but having a higher root diameter. This has also been shown in numerous other cereals (e.g. oats, Ehlers et al., 1983; maize, Goodman and Ennos, 1999). The effect of soil mechanical impedance on lateral root growth in cereals has received less attention, and there is not agreement about how lateral roots are affected. Bingham and Bengough (2003) found that variation in soil strength had no effect on the density of lateral roots (number per unit main axis length) in either barley or wheat, although in stronger soils elongation was repressed in lateral roots and similar results have been found in oats (Schuurman, 1965). Primary wheat roots in dense soil had decreased elongation but accelerated initiation of branch roots compared with those in loose soil (Watt et al., 2003). Other authors, however, uphold that branching density is also affected by soil strength (Goss, 1977; Iijima and Kono, 1991). Variation in responses in branch roots may be due to interactions with aspects of soil texture such as soil pore size (discussed further below) and clod density (Konôpka et al., 2008), which can strongly affect lateral branching density. Shorter total root length in strong soil results in less effective soil exploration, resulting in lower water and nutrient interception, consequentially diminishing supply to the shoot, which can result in reduced total plant growth on compacted soils.

Soil strength and mechanical impedance are rarely uniform. Soils can have subsoil hardpans, cracks, and macro pores due to drying and areas of higher compaction. Hardpans can decrease root elongation, although this does not necessarily correlate with a lower overall root mass as plants may respond with increased root exploration above the hardpan (Barraclough and Weir, 1988). In areas of uneven compaction, such as under tractor wheel tracks, roots will tend to be significantly less dense where compaction is highest (Tardieu, 1988). The previous two examples demonstrate that roots systems will favour areas of least mechanical resistance, and this is especially highlighted in soils containing cracks or pores (Fig. 2B). Roots will favour the low impedance pathway formed by root channels from previous crops or cracks. For example, in a maize crop planted in rotation after alfalfa, 41% of the maize roots were found in alfalfa root channels (Rasse and Smucker, 1998). White and Kirkegaard (2010) found >90% of wheat roots deeper than 40 cm clustered in cracks and pores in red brown clay field soil. The exploration of soil cracks and pores may allow roots to penetrate hardpans, or to explore deeper areas or soil, thereby gaining access to larger pools of water and nutrients (Passioura, 1991).

Root extension occurs when the turgor pressure within cells of the elongation zone becomes sufficiently large so as to overcome the constraints imposed by cell wall resistance and resistance of the surrounding medium (Pritchard, 1994). Roots easily elongate through the air and liquid phases of the soil. Where the solid phase dominates, roots must exert enough pressure to displace soil particles and overcome friction, allowing elongation (Clark et al., 2003). It has been demonstrated in maize that mechanical impedance results in increased ethylene biosynthesis (Moss et al., 1988; Sarquis et al., 1991); however, the action of ethylene in root sensing and response to soil impedance is not yet understood.

The genetic basis of the ability of roots to penetrate soil is not completely elucidated for any species, and in the cereals has received limited attention. Studies of rice and maize have shown strong genotypic differences in root penetration capacity (Yu et al., 1995; Bushamuka and Zobel, 1998),

Marga Garcia-Vila (B), Mina Rostamza (C), Richard Favel (E). (D) Reproduced with permission from Plant, Cell and Environment 35, 1618–1630 (Abiko et al., 2012), Wiley. (F) Reproduced with permission from Functional Plant Biology 36, 947–59 (Nagel et al., 2012). Copyright © CSIRO 2009. Published by CSIRO Publishing, Collingwood, Victoria Australia.
indicating a genetic basis to this ability. In rice, several QTLs have been identified using a wax penetration screening system (Ray et al., 1996; Zheng et al., 2000). Root penetration is a complex trait and it is possible that differences in root thickness, allowing roots of different genotypes to resist buckling, could be a major contributor to better root penetration; this is supported by evidence that QTLs for the ability of roots to penetrate a wax layer are associated with QTLs which make the roots either thicker or longer in other studies (Price et al., 2000).

Given the propensity for roots to grow in cracks and spaces rather than push through hard soil, it may be beneficial to select for inherent rapid elongation rates of root systems, to increase colonization of dense soils in the field (Watt et al., 2005; Palta and Watt, 2009). This approach should, however, take into careful consideration the size of the pores into which the roots will grow. Plants with roots in large pores can have poorer shoot growth compared with plants with roots in compacted soil (Stirzaker et al., 1996; shoots of roots shown in Fig. 2B; Garcia, Watt, and Passioura, unpublished). The mechanisms by which shoot growth is inhibited by roots growing in large pores are unknown, but may include inhibitory signals from the root tips that accumulate because of lack of soil contact, or inhibitory biotic factors in pores (Passioura and Stirzaker, 1993).

**Soil water content**

Water deficit is the most prevalent limitation to plant growth. Severe water stress, when the water potential is significantly lower within the soil than in the plant, will result in dehydration and loss of cell turgor, usually resulting in severe restriction of root elongation (Fig. 2C, inset). However, the often heterogeneous nature of water within the soil profile and the plastic nature of root systems means that while prolonged periods of water stress are generally detrimental to overall plant health and crop yields, many species can withstand extended periods without water inputs.

Under limited water conditions, tolerant plants tend to grow a deeper root system, prioritizing assimilates from shoot growth to root growth so roots can extend into still moist deeper zones (Gregory, 2006). A deeper root system is achieved by the ability in many species for root systems to continue to grow, even at extremely low water availabilities (Sharp et al., 2004). Maintenance of root elongation when water stressed allows for continued soil exploration and, therefore, increased chances of maintaining adequate water supply to the shoots (Ingram and Malamy, 2010). In primary roots, this feature could be vital in seedling establishment when topsoils are dry (Sharp et al., 1988), and in nodal roots this may be important for penetration of dry surface soils. Westgate and Boyer (1985) demonstrated this ability in the nodal roots of maize which continued to elongate several days after water was withheld; root elongation was still occurring at water potentials of −1.4 MPa, whereas leaf elongation ceased at −1.00 MPa. Although root elongation can be maintained during periods of water stress, and new nodal root production may continue (Pardales and Kono, 1990), roots developed while under water stress will usually be thinner (Sharp et al., 1988) and the rates of elongation and branching are usually lower than those in well-watered soils (Salim et al., 1965; Stasovski and Peterson, 1991). However, in some cases, elongation rates in water-stressed roots have exceeded that of plants with sufficient water (e.g. maize, Sharp and Davies, 1979). Although roots can maintain growth at matric potentials which inhibit shoot growth, under extremely low water potentials (i.e. less than −1.5 MPa) root growth will be inhibited. This is demonstrated in a pot experiment where water availability was stratified down the pot, and for wheat, oats, and barley most root growth stopped as soon as roots reached the dry (2.3% moisture content) soil layer (Salim et al., 1965). Continued elongation under water stress probably relates to the hydrotropic nature of roots which may allow them to bend towards areas of higher water potential (Takahashi, 1997; Eapen et al., 2005). Although it is likely that all roots show hydrotropism, it has received little attention in the cereals; however, Takahashi and Scott (1991) showed root hydrotropism in maize and concluded that the hydrosensory site was located within the root cap.

Our understanding of the physiological mechanisms involved in the maintenance of root elongation under water stress is based primarily on studies of short-term water stress on the primary root of maize seedlings (reviewed by Sharp et al., 2004). These experiments reveal that the root growth zone behind the tip is shortened by water stress, from 12 mm in a well-watered root to 7 mm under water stress, but the time over which growth occurs is independent of water stress (Sharp et al., 1988). Maize roots undergo substantial osmotic adjustment during water stress (Sharp and Davies, 1979; Sharp et al., 1990); however, this is insufficient to maintain enough turgor for growth. Therefore, it appears that cell wall-loosening proteins such as expansins are involved in the maintenance of elongation in the root apices of water-stressed roots (Wu et al., 1996). Hormonal involvement in root elongation during water deficit is not well understood. The roles of abscisic acid (ABA) and ethylene have received some attention, although their roles are yet to be fully elucidated. ABA has been shown to accumulate in the root growth zone at low matric potentials, leading to restricted ethylene production, and this interaction may function to maintain root growth (Sharp, 2002).

When one part of the root system receives water, other parts in dry environments can elongate (Boyer et al., 2010). Working with wheat primary roots, these authors showed that roots extend into extreme dry conditions (in air) provided another part of the root system has water. These experiments were used to suggest that ~50% of the water used for wheat primary axis extension came from the phloem; and the remaining 50% came from the soil. In maize, the proportion of water for root growth from the phloem was estimated to be 80% (Brett-Harte and Silk, 1994). Anatomical or transporter processes associated with the phloem could be manipulated to increase the efficiency of water phloem transport to roots to maintain root extension as the surrounding soil dries.
Drought tolerance is a primary aim in breeding, and this has resulted in the genetics of cereal root growth in response to water stress receiving attention. In rice, for example, numerous QTLs have been identified under water stress for root traits such as seminal root length, root diameter, total root length, or mass (Champoux et al., 1995; Yadav et al., 1997; Zhang et al., 2001; Price et al., 2002).

Anoxia and hypoxia

Excess soil water is a common problem at transient or seasonal time scales (Kozlowski, 1984). Waterlogging results in soil hypoxia (low oxygen) or anoxia (no oxygen) of the rhizosphere within hours (Ponnamperuma, 1984). Even short-term (hours or days) transient root exposure to hypoxic soils can have considerable negative effects on growth and yield of dryland crops (e.g. wheat, Davies and Hillman, 1988; barley, Leyslon and Sheard, 1974; Sharma and Swamp, 1988; millet, Sharma and Swamp, 1989). Although the responses of root systems to excess water are highly variable, a combination of reduced primary root growth in anoxic sediments and root decay generally reduces the root to shoot ratio (R:S). Even flood-tolerant paddy rice has a low R:S of 0.13–0.23 depending on variety and age (Teo et al., 1995), compared with 0.4–0.55 in dry-land cereals such as wheat when in drained soil (Siddique et al., 1990).

Excess anoxic water around roots is generally detrimental to primary cereal roots, inhibiting elongation and lateral root initiation. When wheat seedlings were returned to aerated conditions after 10–14 d waterlogging, seminal roots of wheat did not recover or resume elongating, indicating either death or serious injury (Barrett-Lennard et al., 1988; Malik et al., 2002). With shorter periods of waterlogging, seminal apices appear to have died but lateral emergence from the basal zones of seminal roots did occur once roots were returned to aerated conditions (Barrett-Lennard et al., 1988).

Similar root responses have been observed in waterlogged maize roots. After waterlogging for 12–13 d, seminal root elongation either ceased or slowed significantly and there was also significant root senescence (Wenkert et al., 1981; Przywara and Stepniowski, 1999). New nodal root growth, however, can also be promoted by waterlogging (Fig. 2D) (Trought and Drew, 1980; Wenkert et al., 1981; Erdmann and Wiedenroth, 1986; Lizaso et al., 2001; Malik et al., 2002; Abiko et al., 2012). These new nodal roots can be thicker (due to aerenchyma formation) and shorter than pre-existing roots (Malik et al., 2001; Abiko et al., 2012), and branching patterns can also be different. The survival of these nodal roots after waterlogging varies between species but, if maintained, can influence future root system architecture.

In dicotyledons, auxin and ethylene are accepted to be the hormones associated with initiation of new adventitious roots after soil waterlogging (Visser and Voessenek, 2004). They are thought to interact; ethylene modulating auxin transport and biosynthesis, and sensitizing plant perception of auxin (Visser et al., 1996). However, for monocotyledons, the hormones involved in adventitious root initiation are less clear, as data are limited and somewhat contradictory. Zhou et al. (2003) found polar auxin transport essential for adventitious root initiation and elongation in rice, while Lorbiecke and Sauter (1999) found no effect of applied auxin on adventitious root formation in rice. Little experimental evidence exists for the role of ethylene in cereals; however, in rice, it has been demonstrated to induce adventitious root growth (Lorbiecke and Sauter, 1999) where it may be involved in facilitating penetration of the epidermis and thus emergence of adventitious roots from stem nodes. High concentrations of ethylene resulted in programmed cell death of epidermal cells of the node, just external to the tip of adventitious root primordium (Mergemann and Sauter, 2000). Several studies have looked at a possible role for gibberellins in adventitious root formation in rice, but results are contradictory (Suge, 1985; Lorbiecke and Sauter, 1999).

The genetic basis of adventitious root formation as a response to excess water is still not completely understood, and in the cereals little has been elucidated. In teosinte (Zea maysssp. hutenangensis) a QTL on chromosome 8 has a strong association with adventitious root formation (Mano et al., 2005), and in rice cdc2Os-1 has been shown to be expressed exclusively in developing adventitious roots, and may, therefore, be part of a root-specific signal transduction pathway triggered by ethylene (Lorbiecke and Sauter, 1999).

Nutrients

Root architecture determines access to nutrients in soil, and the underlying processes—curving, elongating, and branching—can all be influenced by internal and external nutrient availability. For example, limited plant-available phosphorus is associated with a more horizontal root angle in bean, placing roots in surface soil where phosphorus can accumulate because it is highly immobile (Bonser et al., 1996). Root elongating and branching can be triggered by local nutrient abundance (Robinson, 1994). The most well known of the numerous studies examining root responses to nutrient heterogeneity are those by Drew (1975). Via destructive harvests, Drew (1975) demonstrated that in barley, grown for 21 d in pots stratified with different concentrations of phosphate, nitrate, or ammonium, seminal roots initiated many new first- and second-order laterals in zones supplied with high nutrient concentration. Micro-computed tomography now allows non-destructive illustration of lateral root proliferation in nutrient patches (Fig. 2E). Root proliferation within patches of high nutrient availability can result from changes to branching or elongation. The angle at which lateral branches emerge will affect the area over which the roots spread, so narrower branching angles will create a denser patch, especially if the root also changes its branching pattern (Fitter, 1994). Higher root proliferation can also be reflected in high nutrient soils; however, for some nutrients such as nitrate, high concentrations can inhibit root elongation in some genotypes (e.g. maize, Tian et al., 2005; Wang et al., 2005). ‘Plasticity’, that is, the extent of root architecture response to local or general nutrient changes in the soil or plant, due to plant genetics, may be an advantage where nutrient distribution is heterogeneous through the season and with depth.
Extreme nutrient deficiency will hinder root system growth, but under less severe nutrient deficiency carbon is allocated away from shoots and towards roots, leading to root elongation (e.g. rice, Kirk and Du, 1997; barley, Steingrobe et al., 2001). Nutrient uptake, particularly for immobile nutrients such as phosphorus, is restricted by the root surface area available for uptake, and elongation increases soil exploration (Manske and Vlek, 2002). In a pot experiment with nine genotypes of wheat, low phosphorus supply significantly increased the total root length by 56% (Römer et al., 1988). Maize had a similar response when exposed to nitrogen deficiency, increasing total root length and lateral root growth (Chun et al., 2005).

Knowledge of the signalling and genetics of root architecture responses to nutrient availability is limited largely to Arabidopsis, with a focus on lateral root development and inhibition (Osmont et al., 2007; Nibau et al., 2008; Ingram and Malamy, 2010). In the cereals, QTLs for root responses to phosphorus or nitrate levels have been identified in maize (Zhu et al., 2005; Liu et al., 2008) and rice (Shimizu et al., 2004).

Temperature

Soil temperature is highly dynamic, and can differ from the temperature experienced by shoots. It fluctuates daily, seasonally, and with depth. Deeper soils are insulated and fluctuate much less than the surface, and the temperature range around the root system depends on location (Fullner et al., 2012).

Soil temperature directly affects root elongation, metabolism, and transporters, and indirectly affects shoot processes. Studies in controlled environments show that roots generally elongate more rapidly as temperature warms (Fig. 2F), reaching a peak after which rates decrease (Gregory, 2006). Abbas Al-Ani and Hay (1983) reported that barley, rye, oat, and wheat seminal root elongation increases linearly from 5 °C to 25 °C, and suggested that the fastest rates for these cereals lie at or above 25 °C. However peak rates may depend on other experimental conditions. For example, wheat grew most rapidly at 16 ± 3.7 °C (Porter and Gawith, 1999). Among cereals, the temperature at which roots grow the quickest is wide; maize radicals were quickest at 30 °C (Blacklow, 1972), and oat radicals at 5 °C (Nielsen et al., 1960). However, temperatures in older studies may not have been well controlled and peak rates may depend on root age (Gliński and Lipiec, 1990). As well as elongation, branching can also be affected. Nagel et al. (2009) showed in maize that at 14 °C (as opposed to 24 °C) root biomass was reduced, particularly in the laterals. Interestingly Burström (1956) found in wheat that while individual root elongation rates increased with temperature, the overall root length actually decreased. Although root elongation rates increase with increasing temperatures, an increased development rate within individual roots can result in smaller cells, due to a decreased cell elongation phase. Further, correlations between temperature and root diameter have been shown to be both positive and negative (Nielsen et al., 1960; Macduff et al., 1986; Pahlavanian and Silk, 1988), or unaffected (Abbas Al-Ani and Hay, 1983). Inconsistency in thickness responses to temperature may be due to methodology, age measurements, branch order, or types of roots used in different studies.

Changes in root growth are intrinsically linked to temperature mediation of other root processes (Gliński and Lipiec, 1990). Water and nutrient uptake by roots increases with temperature (up to a point). Warm soils may correspond to warmer shoots and, therefore, higher photosynthetic rates, providing more substrate for growth (Takeshima, 1964; Chapin, 1974; Frossard, 1985; Borisova, 1991); alternatively, soils may be cooler than the shoot atmosphere, resulting in negative feedback to the shoots. Root to shoot communication regulating soil temperature effects on roots and shoots is poorly understood, yet has wide implications for crop productivity.

Soil conditions on root system architecture: review of multiple factors imposed in controlled-environment experiments

In contrast to a root in laboratory experiments where most often one stimulus is manipulated (Fig. 2 examples), a root in the field is exposed to multiple stimuli at one point in time (Fig 3). Over the life of a field root system, stimuli such as...
gravity are static, but most others such as temperature, nutrients, and water fluctuate diurnally and seasonally around each root as it elongates, and its rhizosphere is depleted and replenished over time and space. How do roots sense and respond to multiple soil conditions of the field? Are resultant root architecture and function a net, sum, or compound response? While there are some controlled-environment studies testing interacting effects of two soil conditions on roots, studies beyond a single interaction are scarce, even of dicotyledons.

Studies of interactions between temperature and other soil conditions are relatively common, possibly because it is relatively straightforward to impose a uniform temperature difference in an experiment. These studies tend to show warmer soil reducing growth restrictions by other stimuli. For example, Abbas Al-Ani and Hay (1983) demonstrated that higher temperatures compensated for detrimental effects of mechanical impedance in four cereals growing in four media of different temperatures. However, when waterlogging was added to impedance experienced by maize roots, warmer temperatures did not increase penetration depth; rather they increased waterlogging-induced senescence compared with roots in cooler soils (Przywara and Stepniewski, 1999). In drier conditions, a 15 °C temperature increase doubled water absorption by rice roots (Takeshima, 1964). Higher temperatures also increased water uptake in maize roots (Frossard, 1985; Borisova, 1991). Nutrient uptake also tends to be higher at warmer temperatures (e.g. barley, MacDuff and Hopper, 1986; rice, Takeshima, 1964). Hussain and Maqsood (2011) recently found that a 4.2 °C increase around maize roots increased uptake of P, Cu, and Zn per root dry matter. Temperature has also been implicated in the gravimetric response of roots in several species. For example, maize nodal root angle was most shallow at 17 °C, becoming more vertical in warmer or cooler soil. Interestingly, Onderdonk and Ketcheson (1973) imposed fluctuating temperatures, as would be found in the field, and these resulted in a similar root angle to the warmest point in the temperature cycle.

A few studies have examined the interaction between moisture stress and other soil conditions. For example, nodal roots of maize grow more verticallv in drier conditions (Nakamoto, 1993). In an elegant study using a miniature tension table with Arabidopsis lines reported to have differences in nitrogen responses, Chapman et al. (2011) found that small changes in water-filled porosity of sand (e.g. water around the roots) stimulated tap root growth, and removed induction of branch root growth by nitrate previously characterized on agar.

Some soil conditions are intrinsically related, and root responses cannot be attributed to a single stimulus in controlled or field experimental conditions. Water and oxygen are an example. Both are essential for healthy root growth. In soil, they are negatively correlated; as soil dries, water in pores decreases and oxygen diffusion and availability increase. However, lower water increases soil strength due to capillary forces, increasing mechanical impedance to roots (reviewed in Bengough et al., 2011). For optimal root growth, a balance must be achieved between water availability, oxygen diffusion, and mechanical impedance. The effect of water content on aeration and impedance is strongly affected by bulk density and soil texture.

In controlled-environment studies, interactions between the growth media and the characteristics of interest need to be considered. This is especially relevant for studies using the model Arabidopsis, often on agar. In investigating the interaction between water supply and nitrate on Arabidopsis root growth, Chapman et al. (2011) found that, with the exception of lateral root number, root architectural characteristics varied significantly for seedlings grown on sand as opposed to agar. Root growth responses to changes in nitrate supply were also different depending on growth media. As well as differences in mechanical impedance and root gas exchange, the hydraulic properties of sand and agar are very different, as are those of different concentrations of agar (a 0.1% change in agar concentration can significantly alter the water matric potential; Spomer and Smith, 1996). Given that this determines delivery of water and nutrients to the root, it is likely that properties of the agar would create a significant interaction in water or nutrient use studies (Chapman et al., 2011).

### Root architecture in the field

Although the controlled environment has limitations for root studies, the field is not without its restrictions due to field-sown trials experiencing all soil parameters simultaneously and all possible interactions between these parameters. While some manipulation of the soil condition is possible (fertilizers, rainout shelters, soil preparation), much of the soil environment is beyond the researcher’s control. For example, Fig. 4 shows two field sites, situated on the same farm, <1 km apart, which were sown with various cereals in 2011. Site preparation and treatment were the same; however, plant roots respond to the sites very differently. The sites were cored to 2 m at maturity and core break counts were used to assess root depth and distribution. Rapid measurement of root architecture in relation to depth in the field is most commonly undertaken using soil cores of 4–10 cm diameter taken below the crop with the core break method (e.g. Fig. 4A, B). In this method, the number of roots observed on the broken faces of a core are counted and then a selection of samples are washed out to calculate a calibration of the method from the correlation of root length density or root dry mass to core face root counts at different depths. At best, destructive root counts are then correlated to multiple soil conditions taken at the time of root coring (Fig. 4C–F); however, root and soil cores are often taken at different times: soil analyses at the beginning of crop growth; roots at the end.

In the example in Fig. 4, significant genotype×soil condition variation is observed. Wheat cv. Westonia root systems are deeper and more dense at depth than those of cv. Beaufort at soil Site 1 (Fig. 4A, B), but of a similar depth but less dense at soil Site 2. Soil analyses confirm that Site 1 is less dense (Fig. 4C), and with higher water (Fig. 4D) and nitrate (Fig. 4B) holding capacity than Site 2, possibly suggesting that the Westonia is more sensitive to the impedance...
of Site 2. Westonia is a vigorous variety, and may have exhausted water through excessive transpiration, increasing soil strength around the roots in Site 2. However, this is purely speculation as both soil and root measures are at a single and separate point in time. The soil analyses, however, do not explain Beaufort’s relatively poor root growth in Site 1. This illustrates the challenge faced by root scientists working in the field; it is currently impossible to quantify all factors that could potentially be affecting root growth, and the interactions between them are even more difficult to characterize. Although these root and soil analyses are crude, they are the first step towards understanding root architecture responses to soil conditions. They are rare in the literature.

Some ideas for linking Darwin and Weaver

From the time of Darwin, our understanding of root architecture in the field has relied on the results of reductionist studies in the laboratory, as illustrated in Fig. 5. However, laboratory conditions are much simplified compared with pots and soil conditions in the field. Compounding this are differences in the roots themselves, with older plants containing...
different root types and ages, and varying in density with depth (Fig. 5A–C).

Fig. 5. Examples of the increasing complexity of root systems in different growth environments from germination paper studies or seedlings (A) through to pot studies (B) to field studies (C). With increasing plant size and age comes increasing complexity of time, conditions, and root types and density. (B) Adapted by permission from Macmillan Publishers Ltd on behalf of Nature News, copyright (2010).

different root types and ages, and varying in density with depth (Fig. 5A–C).

Three research disciplines allow two-way scaling in root research, between controlled and field environments. First, models could be parameterized with ranked effects of soil factors on root architecture. Letey (1985) suggests the concept of the ‘non-limiting water range’ as a way of discussing the relationship between soil water content and other soil factors which constrain plant growth. Letey (1985) defines the ‘non-limiting water range’ as being within the range of water availabilities at which the plant will grow and then the lower end of this range is increased to a point where mechanical resistance is not limiting and the upper end of the range reduced to a point where aeration is not limiting. Depending on the soil type, this range can be similar to that given by plant-available soil water, or could be far smaller. As well as interacting with oxygen availability and soil strength, water availability will also interact with the uptake of most nutrients. For example, in wheat, low water availability decreases the R:S, whereas low N availability results in an increased R:S; the interaction of low water availability and low N results in the increased root exploration response to low N being repressed and the root mass being lower than in controls (Barraclough et al., 1989). In Table 1, we hypothesize the importance of various environmental stimuli on root architecture processes. While our assessment is primarily drawn from controlled-environment and glasshouse studies, we believe rankings such as these could be used in combining traditional soil measurements with controlled-environment knowledge of effects on root architecture cellular processes (curving, elongation, and branching) to estimate root architecture for a given soil and management practice. Mechanistic models of root growth have primarily described the regulatory processes involved in root development, often at a single root scale, and usually on dicot model species (Dupuy et al., 2010). These models therefore, while providing a good foundation, are of somewhat limited usefulness due to the significance of environmental stimuli to root growth and architecture. Recent models are making forays into incorporating environmental factors (Roose and Schnepf, 2008; Draye et al., 2010). The inclusion of rhizosphere and environmental data into mechanistic models and the production of environmental data able to be incorporated into multiscale models (Band et al., 2012a) will result in both a greater understanding of the genotype to phenotype gap and as a guiding framework for new experimental work.

Secondly, our understanding of the biology of sensory and signalling pathways at the root–soil interface could be greatly expanded. Plants with reporter systems can be studied in non-invasive measurement systems for roots in intact soil methods, such as X-ray tomography (e.g. Flavel et al., 2012; Fig. 2E) and magnetic resonance imaging (MRI) (e.g. Jahnke et al., 2009). Real-time, high-resolution root–soil methods are the beginning of understanding root architecture in the field; however, as yet, most of these technologies are restricted to pot-based studies. Small model plants growing to maturity in intact soil [such as the model grass Brachypodium where adult stages can be studied and selected in soil columns to 50 cm (Chochois et al., 2012)] can increase our understanding not only of root architectural phenotypes but also of the sensory and signalling pathways which determine root growth response to soil conditions. These systems have also yet to be exploited to understand sensory and signalling processes, which are likely to be the key to genetic improvement by gene marker-based breeding. Crop plants with disruptions known to be in signalling pathways (tilling, mutagenized, sequenced) can also be studied in these non-invasive systems that allow 4D root measurements.

The third, and most important, discipline to link Darwin and Weaver is agronomy: the science of soil management and crop production (Oxford English Dictionary). This sounds like an old-fashioned science, but it is the only to cover the linking of soil and root architecture for crop production gains.
Underlying agromony today are technology developments in plant genetics, computing power for models, and engineering technologies. Better real-time imaging technologies will enable better understanding of root responses to multiple soil conditions and genotypic root architectural phenotypes, and allow researchers to work readily from the field to the lab and back.

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References

Abbas Al-Ani MK, Hay RKM. 1983. The influence of growing temperature on the growth and morphology of cereal seedling root systems. Journal of Experimental Botany 34, 1720–1730.

Abiko T, Kotula L, Shiono K, Malik AI, Colmer TD, Nakazono M. 2012. Enhanced formation of aerenchyma and induction of a barrier to radial oxygen loss in adventitious roots of Zea nicaraguensis contribute to its waterlogging tolerance as compared with maize (Zea mays ssp. Mays). Plant, Cell and Environment 35, 1618–1630.

Arihara J, Crosbie TM. 1982. Relationships among seedling and mature root system traits of maize. Crop Science 22, 1197–1202.

Band LR, Fozard JA, Godin C, Jensen OE, Pridmore T, Bennett MJ, King JR. 2012a. Multiscale systems analysis of root growth and development: modeling beyond the network and cellular scales. The Plant Cell 24, 3892–3906.

Band LR, Wells DM, Larrieu A, et al. 2012b. Root gravitropism is regulated by a transient lateral auxin gradient controlled by a tipping-point mechanism. Proceedings of the National Academy of Sciences, USA 109, 4668–4673.

Barraclough PB, Kuhlmann H, Weir AH. 1989. The effects of prolonged drought and nitrogen fertilizer on root and shoot growth and water uptake by winter wheat. Journal of Agronomy and Crop Science 163, 352–360.

Barraclough PB, Weir AH. 1988. Effects of a compacted subsoil layer on root and shoot growth, water use and nutrient uptake of winter wheat. Journal of Agricultural Science 110, 207–216.

Barrett-Lennard E, Leighton P, Buwalda F, Gibbs J, Armstrong W, Thomson C, Greenway H. 1988. Effects of growing wheat in hypoxic nutrient solutions and of subsequent transfer to aerated solutions. I. Growth and carbohydrate status of shoots and roots. Functional Plant Biology 15, 585–598.

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.

Bengough AG, Mullins CE. 1990. Mechanical impedance to root growth: a review of experimental techniques and root growth responses. Journal of Soil Science 41, 341–358.

Bingham IJ, Bengough AG. 2003. Morphological plasticity of wheat and barley roots in response to spatial variation in soil strength. Plant and Soil 250, 273–282.

Björkman T, Cleland RE. 1991. The role of extracellular free-calcium gradients in gravitropic signalling in maize roots. Planta 185, 379–384.

Blacklow WM. 1972. Influence of temperature on germination and elongation of the radicle and shoot of corn (Zea mays L.). Crop Science 12, 647–650.

Blancaflor EB, Masson PH. 2003. Plant gravitropism. Unraveling the ups and downs of a complex process. Plant Physiology 133, 1677–1690.

Bonser A, Lynch J, Snapp S. 1996. Effect of phosphorus deficiency on growth angle of basal roots in Phaseolus vulgaris. New Phytologist 132, 281–288.

Boonsirichai K, Guan C, Chen R, Masson PH. 2002. Root gravitropism: an experimental tool to investigate basic cellular and molecular processes underlying mechanosensing and signal transmission in plants. Annual Review of Plant Biology 53, 421–447.

Borisova T. 1991. Effect of exogenous factors on water relations in maize roots. Developments in Agricultural and Managed-forest Ecology 24, 9–16.

Boyer JS, Silk WK, Watt M. 2010. Path of water for root growth. Functional Plant Biology 37, 1105–1116.

Bramley H, Turner NC, Turner DW, Tyerman SD. 2009. Roles of morphology, anatomy, and aquaporins in determining contrasting hydraulic behaviour of roots. Plant Physiology 150, 348–364.

Brett-Harte MS, Silk WK. 1994. Nonvascular, symplasmic diffusion of sucrose cannot satisfy the carbon demands of growth in the primary root tip of Zea mays L.. Plant Physiology 105, 19–33.

Burström H. 1956. Temperature and root cell elongation. Physiologia Plantarum 9, 682–692.
Bushamuka VN, Zobel RW. 1998. Differential genotypic and root type penetration of compacted soil layers. Crop Science 38, 776–781.

Champoux MC, Wang G, Sarkarung S, Mackill DJ, O’Toole JC, Huang N, McCouch SR. 1995. Locating genes associated with root morphology and drought avoidance in rice via linkage to molecular markers. Theoretical and Applied Genetics 90, 969–981.

Chapin FS. 1974. Morphological and physiological mechanisms of temperature compensation in phosphate absorption along a latitudinal gradient. Ecology 55, 1180–1198.

Chapman N, Whalley WR, Lindsey K, Miller AJ. 2011. Water supply and nitrate concentration determines primary root growth in Arabidopsis. Plant, Cell and Environment 34, 1630–1638.

Chen R, Rosen E, Masson PH. 1999. Gravitropism in higher plants. Plant Physiology 120, 343–350.

Chocois V, Vogel JP, Watt M. 2012. Application of Brachypodium to the genetic improvement of wheat roots. Journal of Experimental Botany 63, 3467–3474.

Chun L, Mi G, Li J, Chen F, Zhang F. 2005. Genetic analysis of maize root characteristics in response to low nitrogen stress. Plant and Soil 276, 369–382.

Clark LJ, Whalley WR, Barraclough PB. 2003. How do roots penetrate strong soil? Plant and Soil 255, 93–104.

Darwin C, Darwin F. 1880. The power of movement in plants. London: John Murray.

Davies MS, Hillman GC. 1988. Effects of soil flooding on growth and grain yield of populations of tetraploid and hexaploid species of wheat. Annals of Botany 62, 597–604.

Digby J, Firn RD. 1995. The gravitropic set-point angle (GSA): the identification of an important developmentally controlled variable governing plant architecture. Plant, Cell and Environment 18, 1434–1440.

Draye X, Kim Y, Lobet G, Javaux M. 2010. Model-assisted integration of physiological and environmental constraints affecting the dynamic and spatial patterns of root water uptake from soils. Journal of Experimental Botany 61, 2145–2155.

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

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

Eapen D, Barroso ML, Ponce G, Campos ME, Cassab GL. 2005. Hydrotropism: root growth responses to water. Trends in Plant Science 10, 44–50.

Ehlers W, Kopke U, Hesse F, Böhm W. 1983. Penetration resistance and root growth of oats in tilled and untilled loess soil. Soil and Tillage Research 3, 261–275.

Erdmann B, Wiedenroth EM. 1986. Changes in the root system of wheat seedlings following root anaerobiosis II. Morphology and anatomy of evolution forms. Annals of Botany 55, 607–616.

Fitter AH. 1994. Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In: Caldwell M, Pearce RW, ed. Exploitation of environmental heterogeneity by plants. San Diego: Academic Press, 305–323.

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.

Frossard J. 1985. Root temperature effect on root respiration and growth in maize seedlings of two grain types. Agronomic 5, 719–726 (in French with English abstract).

Fuller N, Temperton VM, Rascher U, Jahnke S, Rist R, Schurr U, Kuhn AJ. 2012. Vertical gradient in soil temperature stimulates development and increases biomass accumulation in barley. Plant, Cell and Environment 35, 884–892.

Gliński J, Lipiec J. 1990. Soil physical conditions and plant roots. Boca Raton, FL: CRC Press.

Goodman AM, Ennos AR. 1999. The effects of soil bulk density on the morphology and anchorage mechanics of the root systems of sunflower and maize. Annals of Botany 83, 293–302.

Goss MJ. 1977. Effects of mechanical impedance on root growth in barley (Hordeum vulgare L.) 1. Effects on the elongation and branching of seminal root axis. Journal of Experimental Botany 28, 96–111.

Gregory P. 2006. Plant roots. Oxford: Blackwell Publishing Ltd.

Hamblin A, Tannant. D. 1987. Root length density and water uptake in cereals and grain legumes: how well are they correlated? Australian Journal of Agricultural Research 38, 513–527.

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

Hussain S, Maqsood MA. 2011. Root zone temperature influences nutrient accumulation and use in maize. Pakistan Journal of Botany 43, 1551–1559.

Iijima M, Kono Y. 1991. Interspecific differences of the root system structures of four cereal species as affected by soil compaction. Japanese Journal of Crop Science 60, 130–138.

Ingram PA, Malamy JE. 2010. Root system architecture. Advances in Botanical Research 55, 75–117.

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

Jovanovic M, Lefebvre V, Laporte P, Gonzalez-Rizzo S, Lelandais-Brière C, Frugier F, Hartmann C, Crespi M. 2007. How the environment regulates root architecture in dicots. Advances in Botanical Research 46, 35–74.

Kato Y, Abe J, Kamoshita A, Yamagishi J. 2006. Genotypic variation in root growth angle in rice (Oryza sativa L.) and its association with deep root development in upland fields with different water regimes. Plant and Soil 287, 117–129.

Kirk GJD, Du LV. 2003. How do roots penetrate strong soil? Plant and Soil 255, 93–104.

Kozlowski TT, ed. 1984. Extent, causes, and impacts of flooding. In: Kozlowski TT, ed. Flooding and plant growth. London: Academic Press Inc., 1–8.
Dekker, Inc., 249–259.
In: Waisel Y, Eshel A, Kafaki U, eds.
Manschadi A, Hammer G, Christopher J, deVoil P.
2008.
Euphytica
33–42.

Malik AI, Colmer TD, Lambers H, Setter TL, Schortemeyer M.
2001. Variability for root and shoot traits in a maize population grown in hydroponics and in the field and their relationships with vertical root pulling resistance. Maydica 46, 177–182.

Lee JS, Mulkey TJ, Evans ML. 1983a. Gravity-induced polar transport of calcium across root tips of maize. Plant Physiology 73, 874–876.

Lee JS, Mulkey TJ, Evans ML. 1983b. Reversible loss of gravitropic sensitivity in maize roots after tip application of calcium chelators. Science 220, 1375–1376.

Leyshon A, Sheard R. 1974. Influence of short-term flooding on the growth and plant nutrient composition of barley. Canadian Journal of Soil Science 54, 463–473.

Liu J, Li J, Chen F, Zhang F, Ren T, Zhuang Z, Mi G. 2008. Mapping QTLs for root traits under different nitrate levels at the seedling stage in maize (Zea mays L.). Plant and Soil 305, 253–265.

Lizaso JI, Melendez LM, Ramirez R. 2001. Early flooding of two cultivars of tropical maize. I. Shoot and root growth. Journal of Plant Nutrition 24, 979–995.

Lorbiecke R, Sauter M. 1999. Adventitious root growth and cell-cycle induction in deepwater rice. Plant Physiology 119, 21–30.

Lynch J. 1995. Root architecture and plant productivity. Plant Physiology 109, 7–13.

MacDuff J, Hopper M. 1986. Effects of root temperature on uptake of nitrate and ammonium ions by barley grown in flowing-solution culture. Plant and Soil 91, 303–306.

Macduff J, Wild A, Hopper M, Dhanoa M. 1986. Effects of temperature on parameters of root growth relevant to nutrient uptake: measurements on oilseed rape and barley grown in flowing nutrient solution. Plant and Soil 94, 321–332.

Mace E, Singh V, Van Oosterom E, Hammer G, Hunt C, Jordan D. 2012. QTL for nodal root angle in sorghum (Sorghum bicolor L. Moench) co-locate with QTL for traits associated with drought adaptation. Theoretical and Applied Genetics 124, 97–109.

Malik AI, Colmer TD, Lambers H, Schortemeyer M. 2001. Changes in physiological and morphological traits of roots and shoots of wheat in response to different depths of waterlogging. Functional Plant Biology 28, 1121–1131.

Malik AI, Colmer TD, Lambers H, Setter TL, Schortemeyer M. 2002. Short-term waterlogging has long-term effects on the growth and physiology of wheat. New Phytologist 153, 225–236.

Mano Y, Muraki M, Fujimori M, Takamizo T, Kindiger B. 2005. Identification of QTL controlling adventitious root formation during flooding conditions in teosinte (Zea mays ssp. Huetenangensis) seedlings. Euphytica 142, 33–42.

Manschadi A, Hammer G, Christopher J, deVoil P. 2008. Genotypic variation in seedling root architectural traits and implications for drought adaptation in wheat (Triticum aestivum L.). Plant and Soil 303, 115–129.

Manske G, Vlek P. 2002. Root architecture—wheat as a model plant. In: Waisel Y, Estel A, Kafaki U, eds. Plant roots. New York: Marcel Dekker, Inc., 249–259.

Mergemann H, Sauter M. 2000. Ethylene induces epidermal cell death at the site of adventitious root emergence in rice. Plant Physiology 124, 609–614.

Merotto A Jr, Mundstock CM. 1999. Wheat root growth as affected by soil strength. Revista Brasileira de Ciência do Solo 23, 197–202.

Moore R, McClelen CE. 1989. Characterizing pathways by which gravitropic effectors could move from the root cap to the root of primary roots of Zea mays. Annals of Botany 64, 415–423.

Moss GI, Hall KC, Jackson MB. 1988. Ethylene and the responses of roots of maize (Zea mays L.) to physical impedance. New Phytologist 109, 303–311.

Mulkey TJ, Evans ML. 1981. Geotropism in corn roots: evidence for its mediation by differential acid efflux. Science 212, 70–71.

Nagel KA, Kastenholz B, Jahnke S, et al. 2009. Temperature responses of roots: impact on growth, root system architecture and implications for phenotyping. Functional Plant Biology 36, 947–959.

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.

Nakamoto T. 1993. Effect of soil water content on the gravitropic behavior of nodal roots in maize. Plant and Soil 152, 261–267.

Nakamoto T, Shimoda K, Matsuzaki A. 1991. Elongation angle of nodal roots and its possible relation to spatial root distribution in maize and foxtail millet. Japanese Journal of Crop Science 60, 543–549.

Nass HG, Zuber MS. 1971. Correlation of corn (Zea mays L.) roots early in development to mature root development. Crop Science 11, 655–658.

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

Nielsen KF, Halstead RL, MacLean AJ, Holmes RM, Bourget SJ. 1960. The influence of soil temperature on the growth and mineral composition of oats. Canadian Journal of Soil Science 40, 255–263.

Omori F, Mano Y. 2007. QTL mapping of root angle in F2 populations from maize ‘b73’×teosinte ‘Zea luxurians’. Plant Root 1, 57–65.

Onderdonk JJ, Ketcheson JW. 1973. Effect of soil temperature on direction of corn root growth. Plant and Soil 39, 177–186.

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

Oyanagi A, Nakamoto T, Morita S. 1993a. The gravitropic effectors could move from the root cap to the root of primary roots of Zea mays. Annals of Botany 64, 415–423.

Oyanagi A, Nakamoto T, Wada M. 1993b. Relationship between root growth angle of seedlings and vertical distribution of roots in the field in wheat cultivars. Japanese Journal of Crop Science 62, 565–570.

Oyanagi A, Sato A, Wada M. 1992. Effect of water potential of culture medium on geotropic response of primary seminal root in Japanese wheat cultivars. Japanese Journal of Crop Science 61, 119–123.
Pahlavian AM, Silk WH. 1988. Effect of temperature on spatial and temporal aspects of growth in the primary maize root. Plant Physiology 87, 529–532.

Paltal J, Watt M. 2009. Crop roots systems form and function: improving the capture of water and nutrients with vigorous root systems. In: Sadras V, Calderini D, eds. Crop physiology: applications for genetic improvement and agronomy. San Diego: Academic Press, 309–325.

Pardales JR, Kono Y. 1990. Development of sorghum root system under increasing drought stress. Japanese Journal of Crop Science 59, 752–761.

Passioura JB. 1991. Soil structure and plant growth. Australian Journal of Soil Research 29, 717–728.

Passioura JB, Stirzaker RJ. 1993. Feedforward responses of plants to physically inhospitable soil. International Crop Science 1, 715–719.

Ponnamperuma FN. 1984. Effects of flooding on soils. In: Kozlowski TT, ed. Flooding and plant growth. London: Academic Press, 9–45.

Porter JR, Gawith M. 1999. Temperatures and the growth and development of wheat: a review. European Journal of Agronomy 10, 23–36.

Price AH, Steele KA, Moore BJ, Barracough PP, Clark LJ. 2000. A combined RFLP and AFLP linkage map of upland rice (Oryza sativa L.) used to identify QTLs for root-penetration ability. Theoretical and Applied Genetics 100, 49–56.

Price AH, Steele KA, Moore BJ, Jones RGW. 2002. Upland rice grown in soil-filled chambers and exposed to contrasting water-deficit regimes: II. Mapping quantitative trait loci for root morphology and distribution. Field Crops Research 76, 25–43.

Pritchard J. 1994. The control of cell expansion in roots. New Phytologist 127, 3–26.

Prusinkiewicz P, Runions A. 2012. Computational models of plant development and form. New Phytologist 193, 549–569.

Przylawa G, Stepniewski W. 1994. The influence of waterlogging and root mortality of winter barley and its implication with regard to mechanical impedance. Plant Physiology 96, 1171–1177.

Rasse DP, Swarup A. 1988. Effects of short-term flooding on growth, yield and mineral composition of wheat on sodic soil under field conditions. Plant and Soil 107, 137–143.

Rasse DP, Swarup A. 1989. Response of pearl millet (Pennisetum americanum) to short-term flooding in a moderately sodic soil under field conditions. Journal of Agricultural Science, Cambridge 113, 331–337.

Sachs MH, Todd GW, Schlehuber AM. 1985. Root development of wheat, oats and barley under conditions of soil moisture stress. Agronomy Journal 57, 603–607.

Sarquis Ji, Jordan WR, Morgan PW. 1991. Ethylene evolution from maize (Zea mays L.) seedling roots and shoots in response to mechanical impedance. Plant Physiology 96, 1171–1177.

Schauman JJ. 1965. Influence of soil density on root development and growth of oats. Plant and Soil 22, 352–374.

Sharma D, Swarup A. 1988. Effects of short-term flooding on growth, yield and mineral composition of wheat on sodic soil under field conditions. Plant and Soil 107, 137–143.

Sharma DP, Swarup A. 1989. Response of pearl millet (Pennisetum americanum) to short-term flooding in a moderately sodic soil under field conditions. Journal of Agricultural Science, Cambridge 113, 331–337.

Sharp R, Silk W, Hsiao T. 1988. Growth of the maize primary root at low water potentials. I. Spatial distribution of expansiv growth. Plant Physiology 87, 50–57.

Sharp RE. 2002. Interaction with ethylene: changing views on the role of abscisic acid in root and shoot growth responses to water stress. Plant, Cell and Environment 25, 211–222.

Sharp RE, Davies WJ. 1979. Solute regulation and growth by roots and shoots of water-stressed maize plants. Planta 147, 43–49.

Sharp RE, Hsiao TC, Silk WK. 1990. Growth of the maize primary root at low water potentials: II. Role of growth and deposition of hexose and potassium in osmotic adjustment. Plant Physiology 93, 1337–1346.

Shimizu A, Yanagihara S, Kawasaki S, Ikehashi H. 2004. Phosphorus deficiency-induced root elongation and its QTL in rice (Oryza sativa L.). Theoretical and Applied Genetics 109, 1361–1368.

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

Sponer LA, Smith M. 1996. Direct measurement of water availability in gelled plant tissue culture media. In Vitro Cellular and Developmental Biology – Plant 32, 210–215.

Stasovski E, Peterson CA. 1991. The effects of drought and subsequent rehydration on the structure and vitality of Zea mays seedling roots. Canadian Journal of Botany 69, 1170–1178.

Staves MP, Wayne R, Leopold A. 1997. The effect of the external medium on the gravitropic curvature of rice (Oryza sativa, poaceae) roots. American Journal of Botany 84, 1522–1529.

Steingrobe B, Schmid H, Claassen N. 2001. Root production and root mortality of winter barley and its implication with regard to phosphate acquisition. Plant and Soil 237, 239–248.

Stirzaker RJ, Passioura JB, Wilms. Y. 1996. Soil structure and plant growth: impact of bulk density and biopores. Plant and Soil 185, 151–162.

Suge H. 1985. Ethylene and gibberellin: regulation of internodal elongation and nodal root development in floating rice. Plant and Cell Physiology 26, 607–614.
Swarup R, Kramer EM, Perry P, Knox K, Leyser HMO, Haseloff J, Beemster GTS, Bhalerao R, Bennett MJ. 2005. Root gravitropism requires lateral root cap and epidermal cells for transport and response to a mobile auxin signal. Nature Cell Biology 7, 1057–1065.

Takahashi H. 1997. Hydrotropism: the current state of our knowledge. Journal of Plant Research 110, 163–169.

Takahashi H, Scott TK. 1991. Hydrotropism and its interaction with gravitropism in maize roots. Plant Physiology 96, 558–564.

Takeshima H. 1964. Studies on the effects of soil temperature on rice plant growth: III. Effects of root temperature upon water and nutrients absorptions at different stages and in alternating temperature. Japanese Journal of Crop Science 32, 319–324. (in Japanese, English abstract).

Tardieu F. 1988. Analysis of the spatial variability of maize root density, III. Effect of a wheel compaction on water extraction. Plant and Soil 109, 257–262.

Teo YH, Beyrouty CA, Norman RJ, Gbur EE. 1995. Nutrient uptake relationship to root characteristics of rice. Plant and Soil 171, 297–302.

Tian Q, Chen F, Zhang F, Mi G. 2005. Possible involvement of cytokinin in nitrate-mediated root growth in maize. Plant and Soil 277, 185–196.

Trought M, Drew M. 1980. The development of waterlogging damage in wheat seedlings (Triticum aestivum L.). Plant and Soil 54, 77–94.

Uga Y, Okuno K, Yano M. 2011. Dro1, a major QTL involved in deep rooting of rice under upland field conditions. Journal of Experimental Botany 62, 2485–2494.

Versel JM, Pillet PE. 1986. Distribution of growth and proton efflux in graviactive roots of maize (Zea mays L.). Planta 167, 26–29.

Visser EJW, Cohen JD, Barendse GWM, Blom C, Voesenek L. 1996. An ethylene-mediated increase in sensitivity to auxin induces adventitious root formation in flooded Rumex palustris Sm. Plant Physiology 112, 1687–1692.

Visser EJW, Voesenek LACJ. 2004. Acclimation to soil flooding—sensing and signal-transduction. Plant and Soil 254, 197–214.

Wang Y, Mi G, Chen F, Zhang J, Zhang F. 2005. Response of root morphology to nitrate supply and its contribution to nitrogen accumulation in maize. Journal of Plant Nutrition 27, 2189–2202.

Wasson AP, Richards RA, Chatrath R, Misra SC, Prasad SVS, Rebetzke GJ, Kirkegaard JA, Christopher J, Watt M. 2012. Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. Journal of Experimental Botany 63, 3485–3498.

Watt M, Kirkegaard J, Rebetzke G. 2005. A wheat genotype developed for rapid leaf growth copes well with the physical and biological constraints of unploughed soil. Functional Plant Biology 32, 695–706.

Watt M, Magee LJ, McCully ME. 2008. Types, structure and potential for axial water flow in the deepest roots of field-grown cereals. New Phytologist 178, 135–146.

Watt M, McCully ME, Kirkegaard JA. 2003. Soil strength and rate of root elongation alter the accumulation of Pseudomonas spp. and other bacteria in the rhizosphere of wheat. Functional Plant Biology 30, 483–491.

Weaver JE. 1925. Investigations on the root habits of plants. American Journal of Botany 12, 502–509.

Weaver JE, Jean FC, Crist JW. 1922. Development and activities of roots of crop plants: a study in crop ecology. Agronomy – Faculty Publications Paper 511, 1–117.

Wenkert W, Fausey N, Watters H. 1981. Flooding responses in Zea mays L. Plant and Soil 62, 351–366.

Westgate ME, Boyer JS. 1985. Osmotic adjustment and the inhibition of leaf, root, stem and silk growth at low water potentials in maize. Planta 164, 540–549.

Whalley WR, Leeds-Harrison PB, Clark LJ, Gowing DJG. 2005. Use of effective stress to predict the penetrometer resistance of unsaturated agricultural soils. Soil and Tillage Research 84, 18–27.

White RG, Kirkegaard JA. 2010. The distribution and abundance of wheat roots in a dense, structured subsoil—implications for water uptake. Plant, Cell and Environment 33, 133–148.

Whitmore AP, Whalley WR. 2009. Physical effects of soil drying on roots and crop growth. Journal of Experimental Botany 60, 2845–2857.

Wolverton C, Mullen J, Ishikawa H, Evans M. 2002. Root gravitropism in response to a signal originating outside of the cap. Planta 215, 153–157.

Wu Y, Sharp RE, Durachko DM, Cosgrove DJ. 1996. Growth maintenance of the maize primary root at low water potentials involves increases in cell-wall extension properties, expansin activity, and wall susceptibility to expansins. Plant Physiology 111, 765–772.

Young LM, Evans ML, Hertel R. 1990. Correlations between gravitropic curvature and auxin movement across gravi stimulated roots of Zea mays. Plant Physiology 92, 792–796.

Yu L-X, Ray JD, O’Toole JC, Nguyen HT. 1995. Use of wax–petrolatum layers for screening rice root penetration. Crop Science 35, 684–687.

Zhang WP, Shen XY, Wu P, Hu B, Liao CY. 2001. QTLs and epistasis for seminal root length under a different water supply in rice (Oryza sativa L.). Theoretical and Applied Genetics 103, 118–123.

Zheng H-g, Babu MRC, Pathan MS, Ali L, Huang N, Courtois B, Nguyen HT. 2000. Quantitative trait loci for root-penetration ability and root thickness in rice: comparison of genetic backgrounds. Genome 43, 53–61.

Zhou D-X, Yin K, Xu Z-H, Xue H-W. 2005. Mapping of QTLs for lateral root branching and length in maize (Zea mays L.) under differential phosphorus supply. Theoretical and Applied Genetics 111, 688–695.