



REVIEW PAPER

Soil compaction and the architectural plasticity of root systems

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Abstract

Soil compaction is a serious global problem, and is a major cause of inadequate rooting and poor yield in crops around the world. Root system architecture (RSA) describes the spatial arrangement of root components within the soil and determines the plant's exploration of the soil. Soil strength restricts root growth and may slow down root system development. RSA plasticity may have an adaptive value, providing environmental tolerance to soil compaction. However, it is challenging to distinguish developmental retardation (apparent plasticity) or responses to severe stress from those root architectural changes that may provide an actual environmental tolerance (adaptive plasticity). In this review, we outline the consequences of soil compaction on the rooting environment and extensively review the various root responses reported in the literature. Finally, we discuss which responses enhance root exploration capabilities in tolerant genotypes, and to what extent these responses might be useful for breeding. We conclude that RSA plasticity in response to soil compaction is complex and can be targeted in breeding to increase the performance of crops under specific agronomical conditions.

Keywords: Adaptive plasticity, genotype×environment interaction, phenotypic variation, root responses, root traits, soil bulk density, soil strength.

Introduction

Plant root functions are: soil water and nutrient uptake, anchorage, reserve storage, vegetative propagation (e.g. Weaver, 1926; Fitter, 1987), and root to shoot signaling (Shabala *et al.*, 2015). Root system architecture (RSA) describes the spatial arrangement of root components within the soil [i.e. the spatial arrangement of nodal, lateral (first-, second-, *ith*-order), primary roots, etc.]. RSA determines the plant's exploration of the soil to forage for water and nutrients (e.g. Lynch, 1995, 2007b). RSA results from three processes: extending root tips, formation of lateral roots, and tropisms or curvatures (e.g. Lynch, 1995; Smith and De Smet, 2012; Rogers and Benfey, 2015). These processes respond dynamically to soil bio-physico-chemical properties that vary in time and space, and therefore

the resulting RSA phenotype arises from both the plant genetics and the soil conditions. This responsiveness of RSA to soil conditions can be termed 'RSA plasticity'.

An individual organism cannot be considered outside the context of its environment (Bradshaw, 1965), and the actual phenotype of a particular genotype depends on the particular environment that it experiences (Via *et al.*, 1995). In a broad sense, phenotypic plasticity is the property of a given genotype to express different phenotypes under different environmental conditions (Bradshaw, 1965; Sultan, 1987; Via *et al.*, 1995; Pigliucci, 2001; Palmer *et al.*, 2012). Phenotypic plasticity is thought to enable plants to cope with or even take advantage of environmental heterogeneity (Crossett *et al.*, 1975; Via *et al.*,

1995; Forde, 2002; El-Soda *et al.*, 2014). Although plasticity can provide an increased environmental tolerance in many circumstances (Bradshaw, 1965; Via *et al.*, 1995; Palmer *et al.*, 2012; Des Marais *et al.*, 2013), this is not always the case. If plasticity is expressed, it may not have any appreciable, beneficial effect, and it may even be counterproductive (see below).

Here we review the literature to establish the importance of RSA plasticity in the context of soil strength. Soil strength is a major cause of inadequate rooting. It affects nearly all soil bio-physico-chemical properties (Håkansson *et al.*, 1988) such as soil porosity, water conductivity, and nutrient availability, and millions of hectares of agricultural lands are affected globally (Oldeman *et al.*, 1991). While the majority of affected lands are located in Europe, Africa, and Asia, some areas of the Americas are also prone to compaction (Soane and van Ouwerkerk, 1994). Yield losses by compaction have been estimated to be ~20% (Arvidsson, 1999) and 25% (Barken *et al.*, 1987). Higher estimates (~50–75%) occur when the soil is affected by another constraint such as drought (Hoque and Kobata, 2000). In Fig. 1, we compiled an overview of the negative effect of soil compaction on yield in several crops, soils, and countries. The lower yields result from reduced uptake of water and nutrients, and lower biomass, which in turn are consequences of soil mechanical impedance on root growth and development (Håkansson *et al.*, 1988; Lipiec and Stępniewski, 1995; Stirzaker *et al.*, 1996; Passioura, 2002). In this review, we do not discuss the effect of soil compaction on the soil microbiota and their interactions with the roots and surrounding rhizosphere because it is a complex topic. Nevertheless, mechanical impedance can increase the accumulation of microorganisms on roots, making the plant more prone to infection and disease (Watt *et al.*, 2003).

As far as we know, the role of RSA plasticity in providing tolerance to soil compaction is poorly understood. Few studies have addressed RSA plasticity directly and, additionally, it is challenging to distinguish adaptive mechanisms from ontological processes. To investigate the possible role of RSA plasticity in responses to soil compaction, we first discuss plasticity, and how phenotypic plasticity may confer tolerance to diverse environments. Secondly, we describe the consequences of soil compaction on the rooting environment and extensively review the various root responses to soil compaction reported in the literature, such as shortened root length, increased root diameter, and fewer lateral roots. Thirdly, we propose some of those responses as plastic adaptations. Finally, we discuss to what extent these plasticity responses might have utility in agricultural production and breeding.

This review expands the focus of previous reviews, conducted by Unger and Kaspar (1994), Bengough *et al.* (2011), Jin *et al.* (2013), Gao *et al.* (2016a), and others, by examining specifically different aspects of the RSA and highlighting the link between soil compaction and RSA plasticity not only from a theoretical point of view but also discussing their practical consequences in breeding. Our goal was not to focus on the mechanical aspects of soil compaction, which have been extensively reviewed by Unger and Kaspar (1994), Jin *et al.* (2013), and Gao *et al.* (2016a). Additionally, we did not cover those soil management practices to alleviate the problems

associated with soil compaction (for reviews, see Unger and Kaspar, 1994; Batey, 2009). Instead, we describe the consequences of soil compaction on the rooting environment and review the various root responses reported in the literature. Finally, we discuss to what extent these responses might be useful for breeding, and which one of them enhances the root exploration capabilities in tolerant genotypes. With this review, we demonstrate that RSA plasticity is key to understanding the effects of soil compaction on plant performance.

Defining phenotypic plasticity of root system architecture

Our detailed definition of RSA plasticity is the reorganization of the RSA in response to one or several exogenous disturbances that affect the RSA by influencing the extension of root tips, the formation of lateral roots, or root tropisms. The evolutionary concept of fitness is complex and its definition is outside the scope of this review (see Orr, 2009). However, in plant breeding, yield integrates the ‘agricultural fitness’ indicators (Nicotra and Davidson, 2010). We define ‘soil compaction tolerance’ as the ability of a genotype to have stable yield or biomass production across locations varying in soil compaction.

A plastic response would be labeled as adaptive as long as it is positively correlated with some fitness components, such as the number of seeds and fruits per plant, germination and fruit set rate, and offspring survival (for more fitness components, see Primack and Kang 1989; Younginger *et al.*, 2017). For example, plant size has been used as an estimator for plant fitness. In general, within a species, larger plants have greater fitness since they produce more seeds, leading to a greater likelihood of leaving viable offspring (Younginger *et al.*, 2017). Below we will discuss several specific examples of adaptive plasticity in the context of soil compaction. Figure 2 shows that the phenotype of a trait can be divided into two main components: the constitutive and the facultative phenotype (apparent plasticity). These two components can also be divided in turn into other subcomponents, such as genotypic and environmental effects. We expressed the relationships among those subcomponents as a linear model for reasons of simplicity. Note that many possible models may exist, such as second- and third-order non-linear relationships, models with only one subcomponent; and/or with no constitutive phenotype at all. Accordingly, if a plastic response has a genetic component, then it is a manifestation of the genotype×environment interaction. When this plastic response is positively associated with fitness (the plant has a higher fitness when it has such a response), it should be labeled as adaptive.

Tolerance and adaptive plasticity

Theoretically, plasticity may provide environmental tolerance especially in heterogeneous environments. If we define tolerance as the ability to maintain fitness while facing environmental stress, we need to define ‘plant stresses’ as well. Lichtenthaler (1996) defines plant stress as any unfavorable condition, or substance, that affects the plant metabolism, growth, or development. In crop production, the stress is any

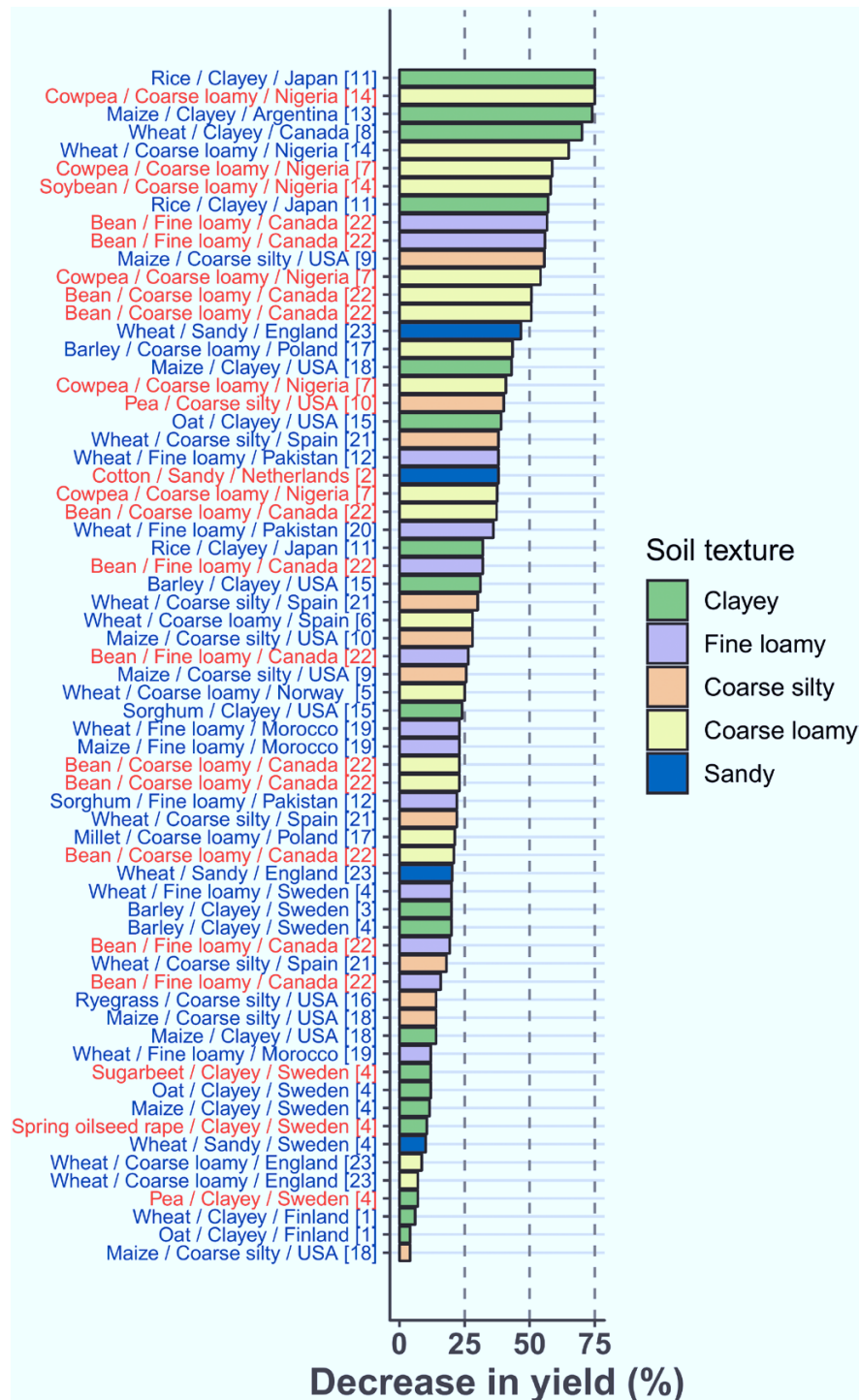


Fig. 1. Yield penalties caused by compaction in crops, soils, and countries. Labels on the y-axis are different studies on soil compaction where yield was registered. If the crop is a dicot or a monocot plant, the label is red or blue, respectively. The labels are indicated as follows: Crop/Soil textural class/Country [reference]. The specific reference list for this plot can be found in Supplementary Table S1 at JXB online.

condition that decreases yield (Wallace, 1986). Thus, when yield reductions are minimal, the genotype might be considered tolerant or resistant (Negin and Moshelion, 2016). Plants respond phenotypically to stress. The initial result of stress is strain and has been defined as the phenotypic expression of stress before damage occurs (Lichtenthaler, 1996; Blum, 2016). Therefore, by definition, strain includes both morphological (structural) changes and physiological responses (Blum,

2016). The term 'strain' is rarely used and is usually replaced by stress responses (Lichtenthaler, 1996). Thus, strain, unlike stress, can be phenotyped (Blum, 2016). For instance, the primary strain under drought stress is water loss from cells (Blum, 2016). Biological systems have developed adaptive mechanisms to cope with stress (Kranner *et al.*, 2010; Blum, 2016). It may be difficult to distinguish between adaptive responses and damage, especially as adaptive responses have costs and

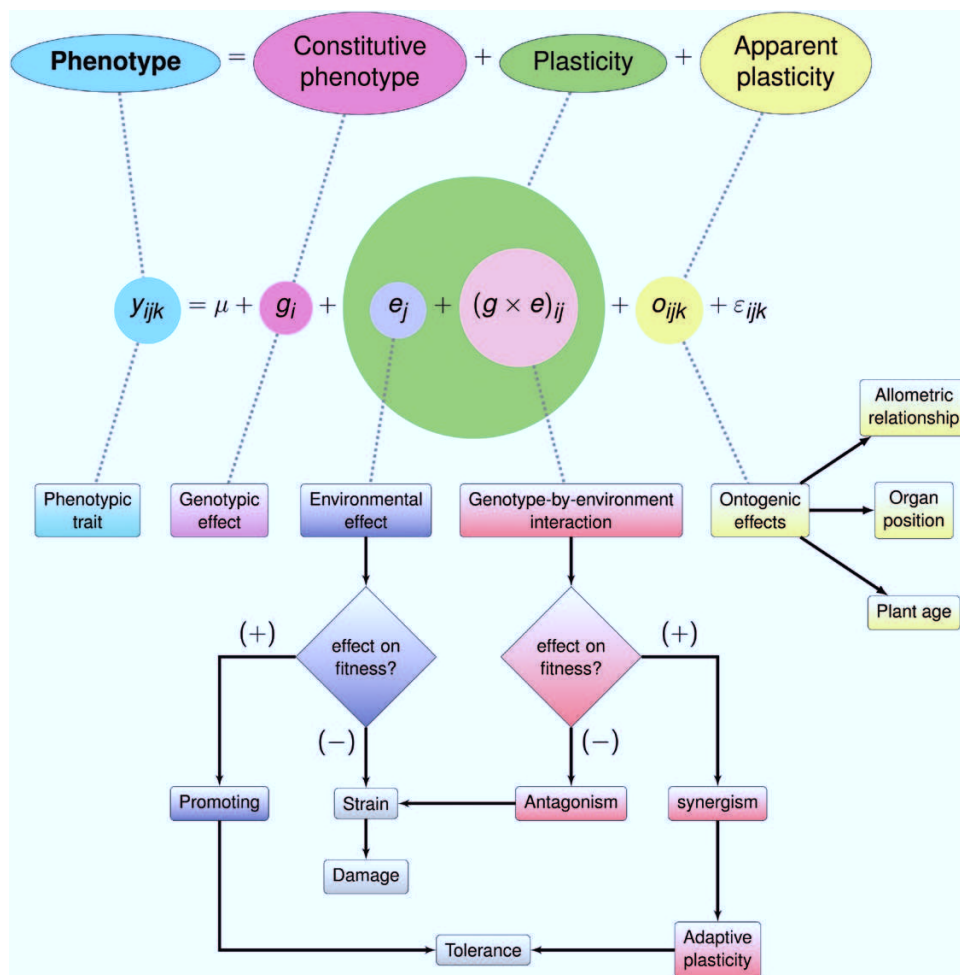


Fig. 2. Model for plant phenotypic plasticity. At the population level, we can split a phenotypic trait into three components: (i) the constitutive phenotype; (ii) plasticity; and (iii) apparent plasticity. The relationships among those components for simplicity may be expressed as a basic linear model: where y_{ijk} is the phenotype measured for the trait y on the plant k of the genotype i under the environment j ; μ corresponds to the overall mean; g_i is the effect of genotype i representing the effect of each genotype or genotypic effect on trait y (constitutive phenotype); e_j is the effect of environment j (i.e. not all genotypes have the same degree of response to e_j); $(g \times e)_{ij}$ is the interaction between genotype i and environment j (i.e. not all genotypes have the same degree of response to e_j); and ε_{ijk} is the residual error. We also assume an additive ontogenic effect, o_{ijk} , as a covariable. For instance, the phenotype of a flower may depend on the position and developmental stage of its node along the shoot. Thus, the plasticity is given by e_j and $(g \times e)_{ij}$. In addition, the effects of plasticity on performance can be both negative and positive, leading to damage or tolerance, respectively.

limits (see below). In some cases, however, plants may recover from stress and reverse the damage. Such recovery may be considered adaptive and is sometimes referred to as an ‘elastic response’ (Kranner *et al.*, 2010; Blum, 2016). When elastic responses allow the plant to return to a reference or pre-stress state, we may call the genotype ‘resilient’ (Grimm and Wissel, 1997; Negin and Moshelion, 2016). For example, a resilient plant decreases its stomatal conductance (g_s) as a response to drought stress, but it is able to return to its previous g_s levels after the stress ceases (Negin and Moshelion, 2016). Thus, we can conclude that plasticity encompasses strain, damage, and adaptive responses (Fig. 2), and that these adaptive responses can cause a genotype to be tolerant, resistant, or resilient.

Costs and trade-offs of phenotypic plasticity

As mentioned above, phenotypic plasticity may have positive or negative consequences on plant performance. Additionally there may be negative interactions among root traits, such as

trade-offs within a single environment, or across different environments. A plastic response may be adaptive in one environment, but detrimental in another (Lynch, 2007a). This is particularly evident when resources are stratified in the soil profile (Ho *et al.*, 2005; Lynch and Ho, 2005).

The type of RSA expressed is controlled by the genetic background of a particular plant and the available resources and environmental condition (Fitz Gerald *et al.*, 2006). Since the resource costs associated with production or maintenance associated with soil exploration (metabolic costs) by root systems have been shown to be relatively high, sometimes exceeding 50% of daily photosynthesis (Nielsen *et al.*, 1998, 2001; Lambers *et al.*, 2002), breeding for genotypes having an increased allocation of resources to roots may carry negative consequences for yield, especially in resource-poor environments. The metabolic costs of enhanced root growth should be subsidized by resources which might be used for yield instead (Ho *et al.*, 2005; Lynch and Ho, 2005; Lynch, 2007b; Mi *et al.*, 2010; Lynch, 2013). Thus, traits that enhance the effectiveness

or efficiency of roots in acquiring soil resources would be better selection targets than root size *per se* (Lynch, 2007b).

The carbon costs associated with any plastic root response are assumed as long as there are greater returns in terms of soil resources for the carbon investment (Eissenstat, 1992). For instance, fine root proliferation may be costly in terms of carbon, oxygen, and nitrogen since those roots have high respiration rates, a relatively short life span, rapid turnover, and quick decomposition (Eissenstat and Yanai, 1997; Jackson *et al.*, 1997; Pregitzer *et al.*, 1998). The low availability of nitrogen and oxygen in compacted soil (Håkansson *et al.*, 1988; Passioura, 2002; Tubeileh *et al.*, 2003; Bengough *et al.*, 2011) would hinder the production of fine roots. To test these, specific studies on the carbon economy under soil compaction conditions are needed.

True adaptive versus apparent plasticity

As we previously discussed, plasticity responses encompass strain, damage, and adaptive responses. The distinction between these types of plasticity from stress and/or ontological effects may be challenging. Changes in biomass allocation may also result from 'ontogenetic drift' (Evans, 1972) since biomass allocation usually changes as a function of plant size or total biomass during growth and development.

In general, edaphic stress causes whole-plant growth to be reduced while growth of roots is favored over that of shoots (e.g. increased resource allocation to the root system). For example, increased root to shoot ratios (R/S) have been found to be associated with nutrient deficiencies (Poorter and Nagel, 2000; Lynch and Ho, 2005; Walk *et al.*, 2006) and drought (Huang and Fry, 1998; Verslues *et al.*, 2006). In the case of compaction, both increases and decreases in R/S have been observed, and we will discuss the various explanations.

These changes are often explained using theories such as the 'functional equilibrium theory' (Poorter and Nagel, 2000), which states that plants shift their allocation of biomass towards shoots or roots, depending on the availability of above- or below-ground resources, respectively. This is an important limiting factor for plant growth, prioritizing and optimizing the acquisition of resources in a manner that maximizes plant growth (Poorter and Nagel, 2000; Reich, 2002). For example, an increase in the R/S in response to a reduced availability of nutrients, such as nitrogen, occurs as long as the availability of assimilates is not limiting (Ericsson, 1995). Under these conditions, carbon may have little value relative to the value of the most limiting resource, and large amounts of carbon may be allocated to acquire the most limiting resource (Eissenstat, 1992). Thus, these plastic responses could be clearly indicated as adaptive (Poorter and Nagel, 2000). However, smaller or younger plants generally have a greater R/S, and thus at least part of the observed plasticity might be explained by ontogeny if we assume that the stressed plants are simply 'behind schedule'. For instance, under stressful conditions, plant size may be reduced and show changes in R/S. However, for each plant size there seems to be a 'pre-defined' R/S independent of the environmental conditions, and the observed R/S may merely be a result of the reduction in plant size and not an active

response to cope with this stress. Thus, the changes in biomass allocation may also result from 'ontogenetic drift' (Evans, 1972) since biomass allocation usually changes as a function of plant size or biomass during growth and development. In general, during the vegetative growth phase of most herbaceous plants, seedlings have the highest R/S values, which decline over time as plants grow and develop (McConnaughay and Coleman, 1999). These changes in allocation may result from environmental gradients (true plasticity), ontogenetic drift (apparent plasticity), or both (McConnaughay and Coleman, 1999; Poorter and Nagel, 2000; Reich, 2002; Geng *et al.*, 2007; Xie *et al.*, 2012). Therefore, to understand plasticity in biomass allocation, it is necessary to distinguish these sources of variation (Xie *et al.*, 2012). For that, the log-log relationship (e.g. log-log plots to describe the growth of one plant component or organ in relation to the growth of another component) during different developmental stages has been used (Poorter and Nagel, 2000; Reich, 2002). This growth covariation among plant components may be referred to as allometric trajectory (Alfoncillo *et al.*, 2016). According to that, two treatments have a different allometric trajectory between root and shoot if they have different slopes in the log-log model of root versus shoot biomass (Reich, 2002). Otherwise, the differences in terms of R/S are given by differences in size or age (apparent plasticity). This allows the experimental distinction between true plasticity and apparent plasticity. The latter not only is key for the theoretical interpretation of the data but also has practical consequences (Fig. 2). Without this distinction, an involuntary selection could be made in favor of genotypes that present juvenile traits such as a low rate of development and/or growth if genotypes with a greater allocation to the roots are selected in a breeding program.

We summarize that plasticity might encompass strain, damage, and adaptive responses (Fig. 2). As long as an adaptive response has a clear genetic basis, it will be useful for breeding. However, it is not always possible to differentiate between adaptive and non-adaptive responses. Additionally, these responses may be restricted by costs and limits. In this review, we will focus on RSA plasticity in response to an agronomically important stress—soil compaction—and ask to what extent the observed responses might be termed as strain, damage, or ontological (apparent) or true adaptive responses (Fig. 2). Before reviewing the various reported phenotypic responses to soil strength, we will discuss in what ways soil strength may cause strain in plants.

Soil compaction and strength

Soil compaction is a process by which the soil particles are pressed together, decreasing the space between them when external forces are applied (Soil Science Society of America, 2008). Almost all soil properties are affected by compaction (Fig. 3) which interact with each other producing complex temporal and spatial patterns of resistance to penetration (Håkansson *et al.*, 1988; Zobel, 1992). Compaction results in an increase in bulk density, a decrease in soil porosity or a change in the proportion of pores with water and air (mainly

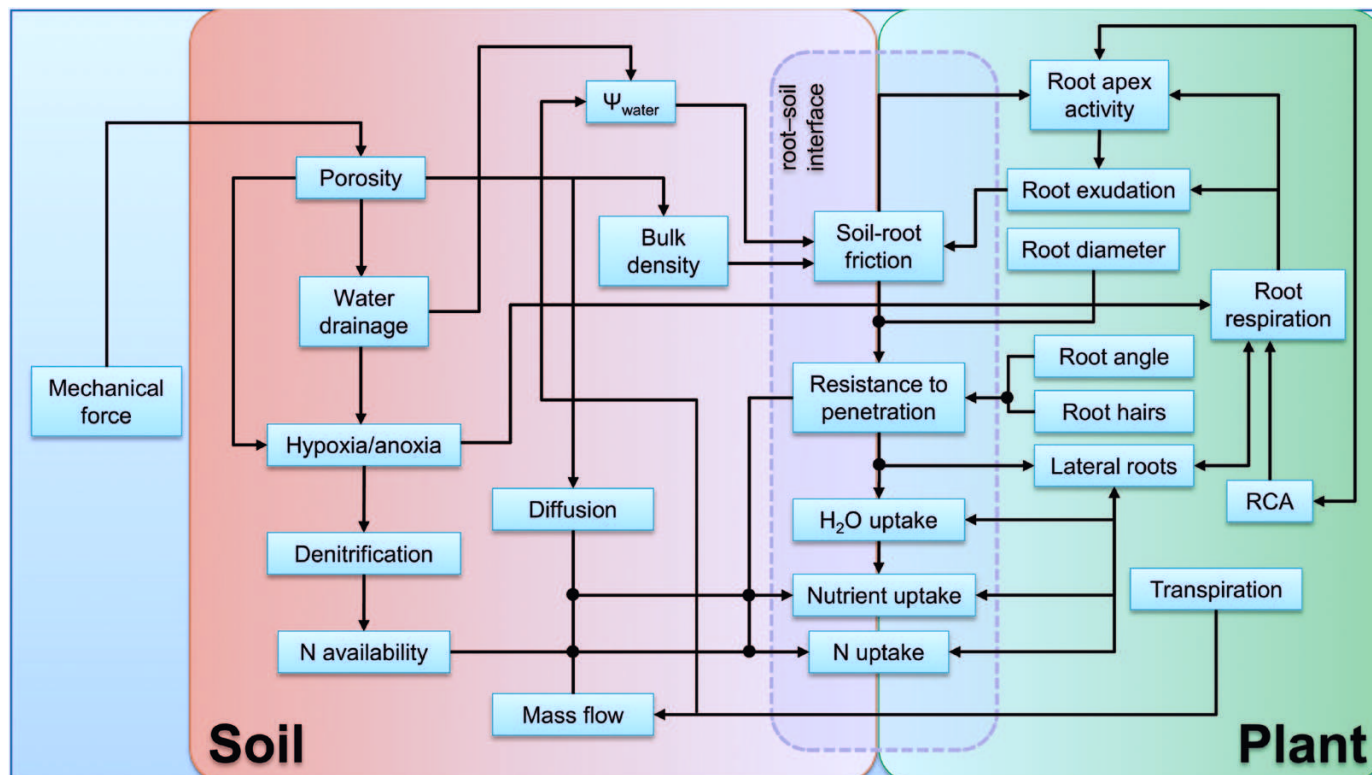


Fig. 3. Relational diagram of the main interactions among soil physicochemical properties and root function and structure observed under conditions of soil compaction. Ψ_{water} , water potential; RCA, root cortical aerenchyma. The arrow (\rightarrow) indicates the influence of one property on another whose interaction can be of synergistic or antagonistic nature (explained in the main text); a two-way arrow (\leftrightarrow) indicates a reciprocal influence between two properties; a black bullet (\bullet) indicates converging influence between two or more properties on the following property; if two or more arrows have a point of intersection without a bullet, no direct interaction between them is indicated.

loss of large pores), and an increase in mechanical resistance or strength. The resulting low levels of oxygen (hypoxia or anoxia), reduced water and nutrient supply, and mechanical impedance cause reductions in root growth and development (Håkansson et al., 1988; Lal, 1997; Bengough et al., 2011; Hoad et al., 2001; Casanova et al., 2013).

Soil compaction can occur in both top and subsoil. At the top, it may cause the formation of a crust which seals the soil surface. More often subsurface compaction, namely the formation of a dense soil layer some distance below the soil surface, is intended when authors write about 'soil compaction' (Nortjé et al., 2012). In agricultural soils, the main factors responsible for compaction are excessive traffic, the use of farm equipment that exceeds the bearing capacity of soil, and tillage at unsuitable soil water contents, in particular wet soils (Barken et al., 1987; Håkansson et al., 1988; Lipiec and Stępniewski, 1995; Bengough et al., 2011; Casanova et al., 2013).

Soil compaction is often described by measurements such as bulk density and penetrometer resistance (Passioura, 2002). Bulk density is the weight of dry soil divided by the total soil volume, and its commonly used units are g cm^{-3} . Penetrometer (or penetration) resistance has been used to provide a relative measure of the resistance offered by soil to the penetration of roots or soil strength (van Huysteen, 1983; Nortjé et al., 2012; Gao et al., 2016a, b; Kolb et al., 2017). It has been shown to be a good predictor of the ability of roots to penetrate soil (Bengough and Mullins, 1990; Jin et al., 2013; Gao et al., 2016b).

Soil properties affecting compaction

Many soil properties affect how easily the soil gets compacted and how resistive the soil is to root penetration. For instance, the soil density level at which root growth and penetration begin to be reduced depends on the soil texture (Jones, 1983; Pierce et al., 1983; Unger and Kaspar, 1994). For example, soils with high clay content are thought to be most inhibitory when compacted (Atwell, 1993). Even though there is a strong negative correlation between percentage clay and soil bulk density (Jones, 1983), clayey soils have higher soil strength than soils with a lower clay proportion at the same density values. For instance, root growth ceases in clayey and sandy soils at 1.47 g cm^{-3} and 1.85 g cm^{-3} , respectively (Jones, 1983; Pierce et al., 1983; Jin et al., 2017). At the same bulk density, clayey soils have a larger contact area between soil particles per soil volume than sandy soils, which in turn would increase the soil strength (Mathers et al., 1966).

A decrease of soil organic matter leads to a loss of structural stability, causing soils to be more susceptible to compaction (Casanova et al., 2013) and to increase the soil mechanical resistance under different ranges of water potentials (To and Kay, 2005). This is because increasing levels of soil organic matter has been associated with an improved aggregation, decreased dispersible clay content, decreased soil bulk density, increased number of failure zones, reduced strength, and increased ease of formation of micro-cracks (Kay, 1990). Soil organic matter is thereby a key contributor to the formation of the soil pore

structure, and it greatly affects the diffusion behavior of soil gases such as O_2 (Hamamoto *et al.*, 2012). However, when soil bulk density is held constant, soil mechanical resistance increases as the organic matter content increases, especially when soil is dryer. Under these conditions, increased cementation within substrate micro-aggregates may occur (for a graphical illustration, see To and Kay, 2005).

Physically, soil strength increases with decreasing soil water content (Gerard, 1965; Mathers *et al.*, 1966; Whalley *et al.*, 2005; Bengough *et al.*, 2011). Thus, root growth in drying soil is generally limited by a combination of increased resistance to root penetration and water shortage (Bengough *et al.*, 2011; Kolb *et al.*, 2017). It should be noted that this is not always the case. For example, vermiculite shows a very small decrease in mechanical strength as it dries (Sharp *et al.*, 1988).

High levels of exchangeable cations, such as K^+ or Na^+ , can cause an increase in soil strength, especially when the soil dries out (Mathers *et al.*, 1966; Dexter and Chan, 1991; Unger and Kaspar, 1994). Cations cause small clay particles to repulse each other, which facilitates the dispersion of the particles and eventually results in a denser packing arrangement (Dexter and Chan, 1991).

Soil properties affected by compaction

Increasing bulk density occurs at the cost of soil porosity, especially larger air-filled pores (Kolb *et al.*, 2017). Evaluating a sandy loam soil mix at 15% moisture content, Tubeileh *et al.* (2003) found that air-filled porosity occupied 29% and 35% of

the total volume under a soil density of 1.45 g cm^{-3} and 1.3 g cm^{-3} respectively. Such a loss in pore space decreases the water conductivity and holding capacity substantially (Douglas and Crawford, 1993; Tubeileh *et al.*, 2003). Waterlogging may occur when a compacted layer interferes with the water drainage capacity of soil (Unger and Kaspar, 1994; Batey, 2009). Additionally, gas diffusion ($\text{m}^2 \text{ s}^{-1}$) in soil is reduced significantly in compacted soils which quickly may lead to (locally) anaerobic conditions (Fujikawa and Miyazaki, 2005; Hamamoto *et al.*, 2012). Consequently, soil microbial activity may switch from aerobic mineralization to anaerobic denitrification, and thereby the nitrogen availability to the plant might be reduced significantly (Smith and Tiedje, 1979; Barken *et al.*, 1987; Sitaula *et al.*, 2000).

Root system plasticity in response to soil compaction and strength

We summarize RSA and other trait responses to soil compaction and strength in Fig. 4. Additionally, Fig. 3 shows some relationships between some soil properties associated with soil compaction and plant responses. Here we describe the major plasticity responses and ask to what extent these responses might be adaptive.

Root length and number

The main influence of higher impedance by soil compaction is the decrease in total root length (Grzesiak *et al.*, 2002; Bingham

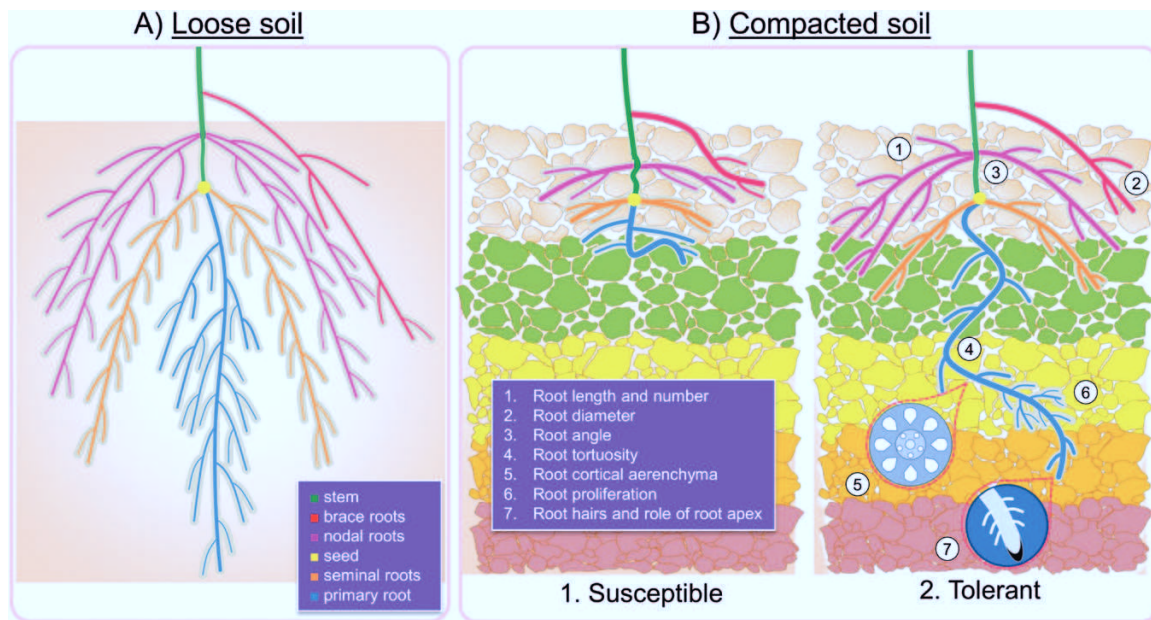


Fig. 4. Generalized cereal root phenotype for maize or sorghum in non-compacted and compacted conditions. (A) Root system expressing its full, potential suite of phenotypes under an ideal soil condition, which is neither too hard nor too loose, but has the optimum density homogeneously distributed thoroughly the soil profile. (B) Two root systems growing into several layers of soil with different degrees of compaction (highlighted in colors and indicated by the right arrow) that increases with depth. Root system 1: if the resistance to the penetration is too high and/or the genotype is susceptible to soil strength, measurable changes in the root system are as follows: (1) reduction in root length and number, which results in a smaller root system size; (2) increased root diameter; (3) less steep root angles; and (4) deflected root growth. These changes make the plant susceptible to compaction especially under rain-fed conditions when the crop depends on water from deeper soil layers. Root system 2: the contrasting, expected responses of a tolerant plant, which include an increased root diameter and higher tortuosity. This would allow an improved exploration of soil by increasing both their penetration rate and chances to grow into those paths of least resistance (see text for details).

et al., 2010; Pfeifer *et al.*, 2014) with a coincident increase in root diameter (Eavis, 1972; Goss, 1977; Rich and Watt, 2013; Popova *et al.*, 2016). Roots begin to undergo a reduction of their growth with bulk density values of 1.39–1.49 g cm⁻³ and 1.69 g cm⁻³ in clay and in sandy texture soils, respectively (Pierce *et al.*, 1983). The limiting values of soil bulk density at which root growth and penetration cease range from ~1.47–1.58 g cm⁻³ in clay texture soils (depending on the percentage of clay) to 1.85 g cm⁻³ in sandy texture soils (Pierce *et al.*, 1983). In terms of penetrometer resistance, root elongation is typically affected in soils with values >0.8–2 MPa and may arrest root growth completely at a resistance of ~5 MPa (Passioura, 2002; Bengough *et al.*, 2011).

Grzesiak *et al.* (2002), comparing the effect of bulk densities (1.33 g cm⁻³ versus 1.50 g cm⁻³ in a 1:1:3 mixture of garden soil, peat, and sand) on triticale root systems, found a decrease of seminal root length, number and length of lateral roots, and number and length of nodal roots with higher soil densities. In 14 winter wheat, decreased axial and lateral root numbers in response to soil compaction (soil column, 1.6 g cm⁻³, 1.06 MPa) were found (Colombi and Walter, 2017). In addition, lateral root initiation is delayed under compacted soil in tomato (Tracy *et al.*, 2012), wheat (Colombi and Walter, 2017), and triticale and soybean (Colombi and Walter, 2016).

If a plant keeps a relatively greater number of roots under compacted soil, it would supposedly have a better soil exploration than a plant with a severely affected root system with few roots. However, the root penetration and consequent growth into a compacted soil layer may also depend on how plastic the root diameter and angle are (see below).

Root diameter

Several studies have shown that root diameter is increased in compacted soil (Eavis, 1972; Materechera *et al.*, 1992; Hanbury and Atwell, 2005; Tracy *et al.*, 2012; Pfeifer *et al.*, 2014; Popova *et al.*, 2016). Increased diameter of the main roots is thought to lead to favorable mechanical properties, such as greater axial root growth pressure, radial expansion, and potential growth rate (Eavis, 1972; Crossett *et al.*, 1975; Materechera *et al.*, 1992; Atwell, 1993; Whalley *et al.*, 1995; Pagès *et al.*, 2010; Kolb *et al.*, 2017; Potocka and Szymanowska-Pulka, 2018). Consequently, thicker roots have a greater ability to explore hard soil (Bengough *et al.*, 2011). Concordantly, Materechera *et al.* (1992), studying several dicot and monocot species (barley, fava bean, lupine, oats, pea, ryegrass, safflower, and wheat), found that a greater proportion of thicker roots is associated with a higher penetration ratio under compacted soil.

Roots must exert a growth pressure in order to displace soil particles, overcome friction, and elongate through the soil. Differences between species in their ability to penetrate compacted soil layers are not only related to differences in growth pressure, but are also due to differences in root diameter and in the tendency of roots to deflect or buckle (Clark *et al.*, 2003). The increased diameter would allow the root to penetrate substrates with higher penetration resistance at the same root penetration pressure (Popova *et al.*, 2016). The observed increase in the diameter of root tips and roots in compacted soil may reduce

buckling and deflecting of roots as they attempt to displace soil particles during extension growth (Clark *et al.*, 2003; Tracy *et al.*, 2012). Otherwise, a greater tortuosity level will be found in the root system (see: 'Root tortuosity'). Thus, we expect a genotype that is tolerant to soil compaction to have increased root diameter which would allow it to penetrate compacted layers, and explore more soil with a greater root length.

Root angle

The angle of incidence of a root at a soil layer, or simply 'root growth angle' (RGA, i.e. degrees from the horizontal), determines the direction of root elongation, and the volume of soil in which roots can forage for water and nutrients. Thereby, RGA defines whether a plant will develop a shallow or deep RSA (Uga *et al.*, 2015). The empirical model proposed by Dexter and Hewitt (1978) shows that the proportion of roots penetrating into a denser soil layer decreases as the soil strength increases; however, this relationship varies as a function of RGA. Thus, at a given level of soil strength, as RGA increases (i.e. steeper root angles and an interface perpendicular to the gradient of the gravity), the proportion of roots that can penetrate the interface also increases. For example, Ramalingam *et al.* (2017) found in rice genotypes that the proportion of roots with steeper angles (45°–90° from the horizontal) is highly and positively correlated with root length density (cm cm⁻³) at a depth from 30 cm to 60 cm at both maximum tillering and maturity stages under both loose (0–0.5 MPa, on average) and compacted soil (with a maximum strength of ~1.8 MPa at 10 cm depth), and this proportion is lower under compacted soil. Additionally, the proportion of roots with steeper angles in response to compaction was genotype dependent, which suggests that this may be an adaptive trait.

When roots suddenly hit a compacted soil layer, such as a plough pan, they have three options: (i) circumvent it by deflecting themselves sideways; (ii) penetrate it in order to grow downwards through the strong soil; or (iii) stop growing (Dexter and Hewitt, 1978; Clark *et al.*, 2003). Thus, if the root diameter and angle are not thick and steep enough to penetrate a strong soil layer, roots may be horizontally deflected when growth continues. Less steep angles in compacted soil have been found in triticale (Colombi and Walter, 2016) and lupine plants (Chen *et al.*, 2014). This may be a strategy to compensate the limited function of an impeded taproot, due to subsoil compaction, by horizontal exploration of the top soil as long as lateral roots become stronger and longer as they grow (Chen *et al.*, 2014), but this also may be a purely mechanical effect.

Even though these antecedents show an existing link between angles and soil strength, it is not clear yet whether those responses are an example of adaptive plasticity or passive consequences of the effect of compaction on root growth. In the case of having adaptive plasticity for RGA, a plant would produce much steeper root angles as a response to soil strength to explore deeper soils. This would be beneficial as long as the compact soil layers were thin enough to be penetrated and if deeper layers were looser and richer in soil resources. However, this response would be counterproductive in soils that at depth are even more compacted, anoxic, or cold.

Root tortuosity

Even though roots often grow through cracks, biopores, and holes in the soil, they have the tendency to nutate as they are flexible organs that follow tortuous paths through the soil, apparently seeking out the path of least resistance. Following planes of weakness between soil particles, they may reduce soil frictional resistance to root tip penetration (Bengough and Mullins, 1990). Roots may be buckled as a result of physical impedance imposed by the soil as the roots are forced to follow more convoluted pathways (Dexter and Hewitt, 1978; Clark *et al.*, 2003). Root tortuosity can be described as the waviness of the growth pattern (Popova *et al.*, 2016). The degree of tortuosity of a root system is dependent on both soil bulk density and soil type, as Tracy *et al.* (2012) and Popova *et al.* (2016) have demonstrated for tomato and maize plants, respectively. Both works found greater values of tortuosity for plants grown in compacted soil, with greater values in coarser textured soils. An active increased tortuosity, as an adaptive plastic response, may improve the chances to explore a larger volume of soil which in turn potentially increases acquisition of soil resources (Popova *et al.*, 2016). However, as commented on previously for root angles, questions are still open regarding whether roots respond passively by bending physically as they face a strong layer, or whether they are able to actively guide a new orientation of growth (Clark *et al.*, 2003; Popova *et al.*, 2016). Furthermore, there must be a compromise between an increase in soil exploration that requires more allocation of resources and energy to the roots, and the limited availability of resources that are often found in compacted soils (Popova *et al.*, 2016).

Root to shoot ratio

Occasionally the carbon allocation to below-ground organs is decreased, which is associated with a lower R/S. This phenomenon has also been observed as a response to soil compaction. Thus, in maize cultivated in cylindrical pots (40 cm height × 15.5 cm diameter) with a soil mix as substrate but with two bulk densities (1.3 g cm⁻³ and 1.45 g cm⁻³), the biomass-based R/S decreased under the denser substrate condition at 42 d after planting. Also, in sugar beet, the R/S (cm mg⁻¹) decreases as bulk density increases (silt loam soil, 1.3–1.65 g cm⁻³) (Hoffmann and Jungk, 1995). For example, Masle (1992) found that most genotypes of wheat or barley with enhanced R/S at high soil resistance (5.3–5.5 MPa) were modern lines, whereas landraces showed a decreased R/S under these soil conditions. Thus, R/S may be reduced or increased in impeded plants depending on the plant's genetic background.

As mentioned, smaller or younger plants generally are more 'rooty' (high R/S); therefore, those plants with enhanced R/S may simply lag in their development and this response may be just evidence for apparent plasticity or allometry. On the other hand, we can speculate that a lower R/S may help plants to reallocate more carbon to seed production, maximizing the chances for reproduction, as long as carbon fixation is not affected (Masle, 1992). It is also possible that although less carbon is spent on construction of roots, more is spent on the increased reliance on alternative nutrient acquisition strategies such as

mycorrhizae or root exudation. Root exudation may not only enhance nutrient acquisition but may also play a beneficial role in penetrating compacted layers (Tubieleh *et al.*, 2003) (see: 'Rhizosphere'). As discussed above, changes in R/S may be a function of the plant size (or development) or be truly plastic. This is also true for R/S responses to soil compaction. Thus, a correct interpretation of any change in R/S should be based on allometric analysis, which, in the best case, should be carried out in plants of different ages.

Compensatory growth

For soil compaction, Goss (1977) demonstrated that if only the apical parts of the main root axes of barley plants are exposed to compaction, the laterals freely penetrating into looser soil express a much greater length than root laterals of plants growing completely unimpeded root systems. This increased growth of laterals could mask the effect of compacted soil on the root main axis, when the total dry mass of the root system is found to be similar between unaffected and the impeded root main axes (Goss, 1977). A compensatory behavior of the whole RSA of barley plants was observed in a compaction experiment by Pfeifer *et al.* (2014) using vertically split rhizoboxes. These authors observed that rooting depth of roots under loose soil in a split rhizobox (compacted and loose soil) was significantly greater than rooting depth under uniform loose conditions (loose substrate in both compartments of the split system) and in all compacted compartments. This phenomenon is accompanied by several changes in other RSA parameters in the loose compartment such as longer root length, earlier occurrence of laterals, and larger root area (the smallest polygonal area that encloses the portion of the root system observed in a rhizotron plate). Thus, the compensatory growth of laterals is analogous to that observed when the growth of part of a root system is restricted by other stresses. Compensatory growth may be a strategy of adaptive plasticity to counterbalance the limited function of an impeded portion of a root system, by growing less in those soil zones where the strength is high and growing more in looser zones.

Root hairs

Root hairs are unicellular and unbranched extensions of root epidermal cells whose principal function is to extend the root absorbing surface for water and nutrients (Evert, 2006). Various root hair traits have been shown to be important in nutrient uptake, with length and density (number of root hairs per millimeter of root length) being particularly important (Peterson and Farquhar, 1996; Bates and Lynch, 2001; Ma *et al.*, 2001a, b). Additionally, root hairs have been associated with an improved anchoring of root to the substrate (Atwell, 1993; Müller and Schmidt, 2004; Bengough *et al.*, 2016). Root hairs may provide anchorage due to their tensile strength (Bengough *et al.*, 2011, 2016) and by greatly increasing the surface area in contact with the surrounding substrate (Müller and Schmidt, 2004). According to Bengough and Mullins (1990) and Bengough *et al.* (2011, 2016), the anchorage of the root axis may facilitate the root penetration from a looser to a denser layer. Root hairs

close to the root tip may contribute to friction between the surrounding substrate and maturing tissues behind the elongation zone. They might, thereby, enable growing root axes to attach themselves firmly to the soil pore walls and penetrate further into the surrounding soil layers (Bengough *et al.*, 2011, 2016). This may be supported by the fact that a hairless maize mutant (*rth3-3*) has been shown to have a lower penetration rate than its wild-type counterpart under soil densities between 1.0 g cm⁻³ and 1.2 g cm⁻³ (Bengough *et al.*, 2016). Similarly, Haling *et al.* (2013) found that barley root hair-bearing genotypes have a better root penetration into high-strength layers (1.6–1.7 g cm⁻³ versus 1.2 g cm⁻³) than root hairless mutants. The presence of root hairs increased the proportion of roots that penetrated high-strength layers, rather than the rate of elongation through the high-strength layers. When the two genotypes (root hair-bearing versus root hairless) were grown in soils with a high and uniform compaction level, there were no significant differences in terms of total root length. Comparing the plant pulling resistance of an *Arabidopsis thaliana* root hair-deficient mutant (*rhd 2-1*) with a wild type, Bailey *et al.* (2002) found, in contrast, that root hairs, unlike lateral roots, do not contribute to whole-plant anchorage. Furthermore, average root hair length has been shown to decrease under higher bulk densities [i.e. 1.65 g cm⁻³ (silt loam soil)] in sugar beet (Hoffmann and Jungk, 1995). Based on these various observations, we propose that the possible benefits of an increased root hair proliferation on root penetration may be observed as long as roots are growing in loose soil conditions or when they are transitioning from looser into denser soil layers.

Rhizosphere

In addition to the tensile strength to help the anchoring of root axes by root hairs, there are also a number of chemical, physical, and biological factors in the rhizosphere such as the release of mucilages by roots and the presence of microorganism activity (associated or not with the development of the rhizosphere) that may allow the adhesion of the soil to roots and therefore the root exploration into a compacted layer of soil (Haling *et al.*, 2013). Under compacted soil, plants may have lower R/S (see: 'Root to shoot ratio'); one consequence of this is that a hampered root system tends to accumulate much more carbon that they can use to grow which may be released into the soil (Tubieleh *et al.*, 2003). This may help to face the soil resistance to root penetrations by facultative or modulated secretion of mucilage to reduce the friction between the root surface and soil particles (see: 'Role of the root apex').

Nutrient uptake

Lower nutrient concentrations in plants growing under compacted soil conditions have been observed. This may result not only from effects on physico-chemical soil properties which reduces their availability (e.g. anaerobic denitrification; see: 'Soil properties affected by compaction') but also from direct effects of compaction on roots. Since the total extension of the root system is reduced in compacted soil (see: 'Root length and number'), and possibly the root hair surface area as well, both

the absorbing root surface and the radial access to soil resources are reduced, probably affecting nutrient uptake (Atwell, 1993; Hoffmann and Jungk, 1995; Rich and Watt, 2013).

Low yields under severely compacted soils are linked to low concentrations of nitrogen, phosphorus, and potassium in plants (Lipiec and Stępniewski, 1995; Arvidsson, 1999). For example, in a field experiment, growing wheat on a loamy soil with a compacted soil layer (1.76 g cm⁻³) between 10 cm and 55 cm depth and deep-tilled profile (loosened soil), Atwell (1993) found that the concentrations of N and K of shoots were reduced in plants grown in compacted soil conditions. Douglas and Crawford (1993) studied in the field (Scotland, clay loam soil) the effect of soil compaction due to wheel traffic on the biomass response of perennial ryegrass plants to the application of nitrogen. They found that there is an interaction between the N concentration applied and the degree of compaction which finally affects the plant growth: the plant biomass increases (1–5 t ha⁻¹) as the N application rate increases (0, 50, 100, and 150 kg ha⁻¹), but the degree of this increase is reduced as the soil compaction levels increase. Kuht and Reintam (2004) carried out an experiment compacting soil by riding over a field with a 17.4 t tractor. They achieved the compaction of both the plough layer and the subsoil (1.6–1.9 g cm⁻³ at the soil plough layer). They found that compaction decreased the N, P, K, and Ca contents in shoot dry matter of spring barley and spring wheat plants by almost 30% and 50% in the case of heavy soil compaction (1.9 g cm⁻³). However, on other occasions, plants did not show any reduction in nutrient content. For instance, Masle and Passioura (1987) found that both shoot N and P concentrations are independent of soil strength (from 1.5 MPa to 5.5 MPa), a reason why the negative effect observed on shoot mass may not be mainly due to nutrient deficiencies (Masle and Passioura, 1987). Accordingly, Hoffmann and Jungk (1995) found that [P] of sugar beet shoots which were grown in pots under growth chamber conditions was not affected by bulk density (silt loam soil, 1.3–1.65 g cm⁻³) in spite of decreased shoot dry mass, R/S (cm mg⁻¹), root hair length, and total root length. Thus, this evident loss of the absorbing surface of roots may be compensated by other mechanisms associated with increased nutrient uptake efficiency (g m⁻¹ root) such as differential expression of high-affinity nutrient transporters or a higher rate of root exudation. Alternatively the nutrient demand of the plant was reduced by adapting the shoot size to the reduced root system size. We conclude that the reduced root length and soil exploration in compacted soils may limit the nutrient uptake, causing plants to have reduced nutrient concentrations in shoots. However, this has not been observed consistently, and we propose that plants, beside pre-emptively reducing shoot growth to avoid nutrient limitations, may also have compensatory mechanisms which increase the nutrient uptake per unit root length.

Root cortical aerenchyma (RCA)

RCAs are intercellular gas-filled spaces in the root cortex that form either by cell death or by cell separation (He *et al.*, 1996; Lynch and Brown, 2008; Postma and Lynch, 2011a, b; York *et al.*, 2013; Lynch and Wojciechowski, 2015). Formation of

aerenchyma is essential to the survival and functioning of plants subjected to waterlogging (Nishiuchi *et al.*, 2012; Cardoso *et al.*, 2013) because RCA contributes to the ability of plants to tolerate low-oxygen soil environments, by providing an internal aeration system for the transfer of oxygen (O_2) from the shoot to the root apical meristem (Drew *et al.*, 2000; Nishiuchi *et al.*, 2012; Yamauchi *et al.*, 2013; Iijima *et al.*, 2016). It has been proposed that the formation of RCA reduces the root metabolic cost of soil exploration by transforming living cortical tissue to air space through programmed cell death, permitting greater root growth and nutrient acquisition for a given metabolic investment (Lynch, 2007a; Lynch and Brown, 2008; Lynch and Wojciechowski, 2015). Even though soil strength stimulates the ethylene-dependent RCA formation in maize roots, its role in response to mechanical impedance stress is not clear (He *et al.*, 1996). Also, the RCA induction by soil compaction, found at 5, 10, and 15 cm from the root base, has been observed in triticale and to a smaller extent also in soybean (Colombi and Walter, 2016). In the first crop, the proportion of RCA depended on the root type, being higher in seminal roots than in primary and nodal roots. Due to the low levels of oxygen found in compacted soils, the mechanical induction of RCA under mechanical impedance could be potentially adaptive for root growth. However, RCA would not affect root penetration ability since it forms in mature root tissue behind the zone of active root elongation and root hair formation (Chimungu *et al.*, 2015; Lynch and Wojciechowski, 2015).

Role of the root apex

The root apex with the root cap is thought to be an important sensory organ, sensitive to soil compaction. Goss and Russell (1980) observed the elongation rate of intact and decapped maize root apices when they faced a high density layer (made of 'ballotini'). Intact apices had an abrupt reduction in elongation rate when touching the layer, whereas decapped apices did not. In contrast to this finding, Iijima *et al.* (2003) found that the decapped roots of maize seedlings are significantly more sensitive than intact roots to the effect of mechanical impedance. Growing in compacted soil (sandy loam soil, 1.4 g cm^{-3} , 1.06 MPa), decapped roots had a 71% lower elongation rate and 52% thicker root diameters than those growing in loose soil (0.8 g cm^{-3} , 0.06 MPa). Intact roots had a 44% reduced elongation rate and 17% increased root diameter. Growing tomato plants in a vertically split-pot with 1.1 g cm^{-3} and 1.5 g cm^{-3} of soil in each half for 30 d, Hussain *et al.* (1999) found that excising roots in the compacted half increased shoot dry mass and leaf area above that of plants with intact roots located in both soil compartments. On the other hand, Rao *et al.* (1989) found that plants of sorghum growing in soil densities of 1.4 g cm^{-3} and 1.5 g cm^{-3} have slight differences in terms of root dry mass and root length, but shoot and plant dry mass were not affected appreciably. At a soil density of 1.7 g cm^{-3} , however, both root and shoot dry mass were severely decreased. Apparently, the root system of sorghum is more sensitive to soil compaction than the shoot. Based on these observations, we may conclude that the shoot response to soil compaction is controlled by the root, which first senses the strength. Th

is mediated specifically by signals produced in the root apex such as ethylene or abscisic acid (ABA) (Goss and Russell, 1980; Masle and Passioura, 1987; Atwell, 1993; Mullholland *et al.*, 1996; Hussain *et al.*, 1999). ABA has been indicated to have a positive role in maintaining leaf expansion under compaction ($1.6\text{--}1.7 \text{ g cm}^{-3}$) because an ABA-deficient mutant (Az34) genotype of barley produces much smaller leaves and has a higher leaf conductance than a wild-type genotype (Steptoe) under compacted soil. These responses were correlated with lower ABA concentrations in the xylem sap in Az34 (Mullholland *et al.*, 1996). Furthermore, tomato ABA-deficient mutants had a more reduced root volume, surface area, and lateral roots than a wild-type tomato genotype at high bulk densities (Tracy *et al.*, 2015). This suggests that ABA mediates the impact of soil compaction not only on stomatal conductance, leaf expansion, and shoot growth, but also on RSA by improving the root capabilities to explore the soil.

The root cap is located at the apex of the root and protects the root apical meristem as the root is penetrating the surrounding soil (Fig. 4; Bengough *et al.*, 2006; Iijima *et al.*, 2008). The root cap may protect the apex by reducing the mechanical resistance imposed by soil. This is achieved by both sloughing of root cap cells and secretion of mucilage (Atwell, 1993; Bengough and McKenzie, 1997; Iijima *et al.*, 2003, 2004, 2008; Bengough *et al.*, 2006; McKenzie *et al.*, 2013; Potocka and Szymanowska-Pulka, 2018). The lubrication is thought to occur in the zone immediately behind the root apex and in the zone of extension (Bengough and McKenzie, 1997; McKenzie *et al.*, 2013). This results in a decrease of the coefficient of friction between the root surface and soil particles (Bengough and McKenzie, 1997; Potocka and Szymanowska-Pulka, 2018). Facultative (or plastic) cell sloughing and mucilage secretion as the root penetrates harder soil layers may be adaptive strategies to face the soil strength. However, adaptive strategies should limit the carbon costs and maximize the returns in terms of soil resources such as carbon, nitrogen, or oxygen. In other words, the amount of carbon earned, or fixed, after the response is expressed must be, at least, greater than or equal to the amount of carbon spent on the investment of such a response (see: 'Costs, limits, and trade-offs of phenotypic plasticity' and 'Root to shoot ratio').

Breeding for plasticity?

As previously stated, soil resistance to root penetration is positively associated with soil dryness (Whalley *et al.*, 2005). The effects of soil compaction are thereby greater in warmer and dryer climates, especially when dense layers, such as a plough pan, impede access to deeper soil water (Batey, 2009). Soil strength varies not only spatially but also temporally because of changing soil water content, which in turn is very variable (Passioura, 2002), and also due to the fact that nearly all soil physico-chemical properties, which interact and are affected by compaction, are rarely uniformly distributed. Thus, each soil may have its own spatial and temporal patterns of strength, which cannot be accurately foreseen. Therefore, the ability of plant root systems to make short-term adaptations in response to those changing environmental factors altering

resource allocation to the root system (i.e. plasticity) might be of great value for breeding an 'adaptive' cultivar (O'Toole and Bland, 1987). In addition, the future impact of climate change on agriculture is known to be caused not only by changes in long-term mean climate but also by changes in both inter- and intraseasonal variability such as changes in both frequency and intensity of rainfall events per year as well as the occurrence of extreme weather events such as heatwaves, drought, and heavy rainfall (Olesen and Bindi, 2002; Porporato *et al.*, 2004; Gornall *et al.*, 2010; Fishman, 2016; Gray and Brady, 2016). This is likely to have negative effects on yields especially in mid- to low-latitude areas where an increased number of water shortages and extreme weather events are expected (MacDonald *et al.*, 1994; Olesen and Bindi, 2002). As phenotypic plasticity has been proposed to have a positive adaptive value in many circumstances (Bradshaw, 1965; Via *et al.*, 1995; Palmer *et al.*, 2012; Des Marais *et al.*, 2013), providing an increased environmental tolerance (Via *et al.*, 1995), especially in heterogeneous environments (Sultan and Spencer, 2002), phenotypic plasticity in response to climate change may be critical in maintaining the agricultural productivity in the future (Gray and Brady, 2016).

Since phenotypic plasticity has been historically recognized as a heritable feature (Bradshaw, 1965; O'Toole and Bland, 1987; Via *et al.*, 1995) and some studies have started to reveal the genetic basis of RSA traits such as root length, thickness, volume, distribution, and allometric ratios (Fitz Gerald *et al.*, 2006; Uga *et al.*, 2011, 2013, 2015), study of the genetics of RSA plasticity seems like an important next research step (e.g. Fitz Gerald *et al.*, 2006; Sandhu *et al.*, 2016). New phenotyping methods have been developed for root traits, such as 2D image analysis, anatomy of cross-sections, shovelomics, 3D-MRI, X-ray, tomography technology, etc., which have a great potential for breeding (for an in-depth review, see Kuijken *et al.*, 2015; Atkinson *et al.*, 2019). Whatever the case, for an efficient root trait-based breeding, the target trait, such as yield, should be highly correlated with some root traits with high heritability (Kuijken *et al.*, 2015). As we mentioned, root phenotype is very plastic and influenced by numerous interactions between genes and between genes and the environment (Kuijken *et al.*, 2015). All in all, this makes the breeding for root traits quite difficult (Kuijken *et al.*, 2015).

We propose that selection in favor of RSA plasticity may be more useful under low-input farming systems or rain-fed agricultural systems. Under those conditions, the edaphic environment is often suboptimal for root growth and development, and the root system must be able to cope with temporal and spatial variability in soil properties associated with uncertain soil water status such as the amount and frequency of precipitation during the growing season, soil temperature regime, and level of native soil fertility (O'Toole and Bland, 1987).

Accordingly, we expected from a putative tolerant genotype the following plastic responses for soil compaction under rain-fed agricultural systems (Fig. 4): an increased root diameter would allow improvement in the penetration and, consequently, the exploration of the soil profile (Bengough *et al.*, 2011). A genotype which is able to produce and keep a relatively greater number of root axes with steeper root angles as the penetration resistance increases would have a better chance

to explore due to the increased root length (Dexter and Hewitt, 1978; Ramalingam *et al.*, 2017). A high degree of tortuosity could be an indicator of a greater and active reorientation of root axis growth, which would help to find paths, if they exist, with lower mechanical impedance to penetration (Clark *et al.*, 2003; Popova *et al.*, 2016). In those soil patches, the resources, such as oxygen and nitrogen, may be more available than in their surroundings (see 'Soil properties affected by compaction'). Proliferation of roots into patches with more favorable soil conditions may be advantageous and a way to compensate for lost root length (Jin *et al.*, 2017). The increased presence of root cortical aerenchyma under compaction would facilitate the oxygen transport to those zones where its supply is in high demand to support the root proliferation (Colombi and Walter, 2016). Finally, both root hairs and the apex may have an important role to improve the penetration into compacted layers by improving the root anchoring to the soil and secreting mucilage to reduce the frictional resistance of soil (Bengough and McKenzie, 1997; McKenzie *et al.*, 2013). It is important to emphasize that not all environments might benefit from a better penetration into deeper layers since root exploration and depth might be largely restricted by harsh conditions at depth such as waterlogged soils or high and toxic concentrations of some chemical elements. In contrast, a rapid root extension rate and deep final rooting depth may be desirable features to exploit water stored in deeper soil layers under rain-fed agricultural systems (Hamblin and Tennant, 1987; Siddique *et al.*, 1990; Colombi *et al.*, 2018). Therefore, tolerance (see definition above) is an environment-dependent characteristic, and the list of features that makes a plant tolerant to a specific constraint may be different for different agricultural conditions.

Concluding remarks

Soil compaction is a serious global problem and it is a major cause of inadequate rooting and poor yield in different crops around the world (Fig. 1). Soil physico-chemical and biological properties vary in both time and space, and they interact with each other. The plant root system must adjust and compensate its growth and development to such changing and interacting constraints through RSA phenotypic plasticity. Roots increase their diameter along that axis to penetrate into the strong soil as long as the soil strength is not too high to bend or deflect the root. At this point, the roots can find the paths of least soil resistance. On the other hand, the root can grow less in areas where the strength is high, and the oxygen and nutrient availability is scarce. Thus, plants may compensate the lower growth in compacted layers by growing more into the looser zones of the soil (Fig. 4).

We conclude that the understanding of the underlying mechanisms behind RSA plasticity provides a theoretical framework for future cropping techniques or breeding programs focused on minimizing yield penalties where the root plasticity is exploited, which might be of great value for breeding an 'adaptive' cultivar in specific low-input farming systems. The study of phenotypic plasticity of RSA requires careful formulation of hypotheses, a clear definition of the plant material (genotypes)

and environments used, and a suitable experimental design that takes into account possible nuisance variables such as environmental and developmental factors. All these requirements are needed to determine not only the presence but also the actual role of plasticity in plant tolerance to soil constraints. Furthermore, these requirements need knowledge of different disciplines such as quantitative genetics, plant physiology, soil science, and statistics to understand this phenomenon; and they must be integrated as a whole in the context of plant breeding and agronomic practice.

Supplementary data

Supplementary data are available at *JXB* online.

Table S1. References of Fig. 1.

References

- Atkinson JA, Pound MP, Bennett MJ, Wells DM. 2019. Uncovering the hidden half of plants using new advances in root phenotyping. *Current Opinion in Biotechnology* **55**, 1–8.
- Arvidsson J. 1999. Nutrient uptake and growth of barley as affected by soil compaction. *Plant and Soil* **208**, 9–19.
- Atwell BJ. 1993. Response of roots to mechanical impedance. *Environmental and Experimental Botany* **33**, 27–40.
- Bailey PH, Currey JD, Fitter AH. 2002. The role of root system architecture and root hairs in promoting anchorage against uprooting forces in *Allium cepa* and root mutants of *Arabidopsis thaliana*. *Journal of Experimental Botany* **53**, 333–340.
- Barken LR, Børresen T, Njøss A. 1987. Effect of soil compaction by tractor traffic on soil structure, denitrification, and yield of wheat (*Triticum aestivum* L.). *Journal of Soil Science* **38**, 541–552.
- Bates TR, Lynch JP. 2001. Root hairs confer a competitive advantage under low phosphorus availability. *Plant and Soil* **236**, 243–250.
- Batey T. 2009. Soil compaction and soil management—a review. *Soil Use and Management* **25**, 335–345.
- Bengough AG, Bransby MF, Hans J, McKenna SJ, Roberts TJ, Valentine TA. 2006. Root responses to soil physical conditions; growth dynamics from field to cell. *Journal of Experimental Botany* **57**, 437–447.
- Bengough AG, Loades K, McKenzie BM. 2016. Root hairs aid soil penetration by anchoring the root surface to pore walls. *Journal of Experimental Botany* **67**, 1071–1078.
- Bengough AG, McKenzie BM. 1997. Sloughing of root cap cells decreases the frictional resistance to maize (*Zea mays* L.) root growth. *Journal of Experimental Botany* **48**, 885–893.
- 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.
- Bingham IJ, Bengough AG, Rees RM. 2010. Soil compaction–N interactions in barley: root growth and tissue composition. *Soil and Tillage Research* **106**, 241–246.
- Blum A. 2016. Stress, strain, signaling, and adaptation—not just a matter of definition. *Journal of Experimental Botany* **67**, 562–565.
- Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**, 115–155.
- Cardoso JA, Rincón J, Jiménez JC, Noguera D, Rao IM. 2013. Morpho-anatomical adaptations to waterlogging by germplasm accessions in a tropical forage grass. *AoB Plants* **pl047**. doi: 10.1093/aobpla/pl047.
- Casanova M, Salazar O, Seguel O, Luzio W. 2013. The soils of Chile. Cham: Springer.
- Chen YL, Palta J, Clements J, Buirchell B, Siddique KHM, Rengel Z. 2014. Root architecture alteration of narrow-leaved lupin and wheat in response to soil compaction. *Field Crops Research* **165**, 61–70.
- Chimungu JG, Loades KW, Lynch JP. 2015. Root anatomical phenes predict root penetration ability and biomechanical properties in maize (*Zea mays*). *Journal of Experimental Botany* **66**, 3151–3162.
- Clark LJ, Whalley WR, Barraclough PB. 2003. How do roots penetrate strong soil? *Plant and Soil* **255**, 93–104.
- Colombi T, Kirchgessner N, Walter A, Keller T. 2017. Root tip shape governs root elongation rate under increased soil strength. *Plant Physiology* **174**, 2289–2301.
- Colombi T, Torres LC, Walter A, Keller T. 2018. Feedbacks between soil penetration resistance, root architecture and water uptake limit water accessibility and crop growth—a vicious circle. *The Science of the Total Environment* **626**, 1026–1035.
- Colombi T, Walter A. 2016. Root responses of triticale and soybean to soil compaction in the field are reproducible under controlled conditions. *Functional Plant Biology* **43**, 114–128.
- Colombi T, Walter A. 2017. Genetic diversity under soil compaction in wheat: root number as a promising trait for early plant vigor. *Frontiers in Plant Science* **8**, 420.
- Crossett RN, Campbell DJ, Stewart HE. 1975. Compensatory growth in cereal root systems. *Plant and Soil* **42**, 673–683.
- Des Marais DL, Hernandez KM, Juenger TE. 2013. Genotype-by-environment interaction and plasticity: exploring genomic responses of plants to the abiotic environment. *Annual Review of Ecology, Evolution, and Systematics* **44**, 5–29.
- Dexter AR, Chan KY. 1991. Soil mechanical properties as influenced by exchangeable cations. *European Journal of Soil Science* **42**, 219–226.
- Dexter AR, Hewitt JS. 1978. The deflection of plant roots. *Journal of Agricultural Engineering Research* **23**, 17–22.
- Douglas JT, Crawford CE. 1993. The response of a ryegrass sward to wheel traffic and applied nitrogen. *Grass Forage Science* **48**, 91–100.
- Drew MC, He CJ, Morgan PW. 2000. Programmed cell death and aerenchyma formation in roots. *Trends in Plant Science* **5**, 123–127.
- Eavis BW. 1972. Soil physical conditions affecting seedling growth I. Mechanical impedance, aeration and moisture availability as influenced by bulk density and moisture levels in a sandy loam soil. *Plant and Soil* **36**, 613–622.
- Eissenstat DM. 1992. Costs and benefits of constructing roots of small diameter. *Journal of Plant Nutrition* **15**, 763–782.
- Eissenstat DM, Yanai RD. 1997. The ecology of root lifespan. *Advances in Ecological Research* **27**, 1–60.
- El-Soda M, Malosetti M, Zwaan BJ, Koornneef M, Aarts MG. 2014. Genotype×environment interaction QTL mapping in plants: lessons from Arabidopsis. *Trends in Plant Science* **19**, 390–398.
- Ericsson T. 1995. Growth and shoot:root ratio of seedlings in relation to nutrient availability. *Plant and Soil* **168**, 205–214.
- Evans GC. 1972. The quantitative analysis of plant growth. Berkeley, CA: University of California Press.
- Evert RF. 2006. Esau's plant anatomy, meristems, cells, and tissues of the plant body: their structure, function, and development. Chichester, UK: John Wiley and Sons.
- Fishman R. 2016. More uneven distributions overturn benefits of higher precipitation for crop yields. *Environmental Research Letters* **11**, 024004.
- Fitter AH. 1987. An architectural approach to the comparative ecology of plant root systems. *New Phytologist* **106**, 61–77.
- Fitz Gerald JN, Lehti-Shiu MD, Ingram PA, Deak KI, Biesiada T, Malamy JE. 2006. Identification of quantitative trait loci that regulate Arabidopsis root system size and plasticity. *Genetics* **172**, 485–498.
- Forde BG. 2002. Local and long-range signaling pathways regulating plant responses to nitrate. *Annual Review of Plant Biology* **53**, 203–224.

- Fujikawa T, Miyazaki T. 2005. Effects of bulk density on the gas diffusion coefficient in repacked and undisturbed soils. *Soil Science* **170**, 892–901.
- Gao W, Hodgkinson L, Jin K, *et al.* 2016a. Deep roots and soil structure. *Plant, Cell & Environment* **39**, 1662–1668.
- Gao W, Whalley WR, Tian Z, Liu J, Ren T. 2016b. A simple model to predict soil penetrometer resistance as a function of density, drying and depth in the field. *Soil and Tillage Research* **155**, 190–198.
- Geng YP, Pan XY, Xu CY, Zhang WJ, Li B, Chen JK. 2007. Plasticity and ontogenetic drift of biomass allocation in response to above- and below-ground resource availabilities in perennial herbs: a case study of *Alternanthera philoxeroides*. *Ecological Research* **2**, 255–260.
- Gerard CJ. 1965. The influence of soil moisture, soil texture, drying conditions, and exchangeable cations on soil strength. *Soil Science Society of America, Proceedings* **29**, 641–645.
- Gornall J, Betts R, Burke E, Clark R, Camp J, Willett K, Wiltshire A. 2010. Implications of climate change for agricultural productivity in the early twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2973–2989.
- Goss MJ. 1977. Effects of mechanical impedance on root growth in barley (*Hordeum vulgare* L.): I. Effects on the elongation and branching of seminal root axes. *Journal of Experimental Botany* **28**, 96–111.
- Goss MJ, Russell RS. 1980. Effects of mechanical impedance on root growth in barley (*Hordeum vulgare* L.): III. Observations on the mechanism of response. *Journal of Experimental Botany* **31**, 577–588.
- Gray SB, Brady SM. 2016. Plant developmental responses to climate change. *Developmental Biology* **419**, 64–77.
- Grimm V, Wissel C. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* **109**, 323–334.
- Grzesiak S, Grzesiak MT, Filek W, Hura T, Stabryła J. 2002. The impact of different soil moisture and soil compaction on the growth of triticale root system. *Acta Physiologiae Plantarum* **24**, 331–342.
- Håkansson I, Voorhees WB, Riley H. 1988. Vehicle and wheel factors influencing soil compaction and crop response in different traffic regimes. *Soil and Tillage Research* **35**, 239–282.
- Haling RE, Brown LK, Bengough AG, Young IM, Hallett PD, White PJ, George TS. 2013. Root hairs improve root penetration, root–soil contact, and phosphorus acquisition in soils of different strength. *Journal of Experimental Botany* **64**, 3711–3721.
- Hamamoto S, Moldrup P, Kawamoto K, Komatsu T. 2012. Organic matter fraction dependent model for predicting the gas diffusion coefficient in variably saturated soils. *Vadose Zone Journal* **11**, vzj2011.0065.
- Hamblin AP, Tennant 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.
- Hanbury CD, Atwell BJ. 2005. Growth dynamics of mechanically impeded lupin roots: does altered morphology induce hypoxia? *Annals of Botany* **96**, 913–924.
- He C, Finlayson SA, Drew MC, Jordan WR, Morgan PW. 1996. Ethylene biosynthesis during aerenchyma formation in roots of maize subjected to mechanical impedance and hypoxia. *Plant Physiology* **112**, 1679–1685.
- Ho M, Rosas J, Brown K, Lynch J. 2005. Root architectural tradeoffs for water and phosphorus acquisition. *Functional Plant Biology* **32**, 737–748.
- Hoad SP, Russell G, Lucas ME, Bingham IJ. 2001. The management of wheat, barley, and oat root systems. *Advances in Agronomy* **74**, 193–246.
- Hodge A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* **162**, 9–24.
- Hoffmann C, Jungk J. 1995. Growth and phosphorus supply of sugar beet as affected by soil compaction and water tension. *Plant and Soil* **176**, 15–25.
- Hoque M, Kobata T. 2000. Effect of soil compaction on the grain yield of rice (*Oryza sativa* L.) under water-deficit stress during the reproductive stage. *Plant Production Science* **3**, 316–322.
- Huang B, Fry JD. 1998. Root anatomical, morphological, and physiological responses to drought stress for tall fescue cultivars. *Crop Science* **38**, 1017–1022.
- Hussain A, Black CR, Taylor IB, Roberts JA. 1999. Soil compaction. A role for ethylene in regulating leaf expansion and shoot growth in tomato? *Plant Physiology* **121**, 1227–1238.
- Iijima M, Awala SK, Watanabe Y, Kawato Y, Fujioka Y, Yamane K, Wada KC. 2016. Mixed cropping has the potential to enhance flood tolerance of drought-adapted grain crops. *Journal of Plant Physiology* **192**, 21–25.
- Iijima M, Higuchi T, Barlow PW. 2004. Contribution of root cap mucilage and presence of an intact root cap in maize (*Zea mays*) to the reduction of soil mechanical impedance. *Annals of Botany* **94**, 473–477.
- Iijima M, Higuchi T, Barlow PW, Bengough AG. 2003. Root cap removal increases root penetration resistance in maize (*Zea mays* L.). *Journal of Experimental Botany* **54**, 2105–2109.
- Iijima M, Morita S, Barlow PW. 2008. Structure and function of the root cap. *Plant Production Science* **11**, 17–27.
- Jackson RB, Mooney HA, Schulze ED. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences, USA* **94**, 7362–7366.
- Jin K, Shen J, Ashton RW, Dodd IC, Parry MA, Whalley WR. 2013. How do roots elongate in a structured soil? *Journal of Experimental Botany* **64**, 4761–4777.
- Jin K, White PJ, Whalley WR, Shen J, Shi L. 2017. Shaping an optimal soil by root–soil interaction. *Trends in Plant Science* **22**, 823–829.
- Jones AC. 1983. Effect of soil texture on critical bulk densities for root growth. *Soil Science Society of America Journal* **47**, 1208–1211.
- Kay BD. 1990. Rates of change of soil structure under different cropping systems. In: Stewart BA, ed. *Advances in soil science* 12. New York: Springer, 1–52.
- Kolb E, Legué V, Bogeat-Triboulot MB. 2017. Physical root–soil interactions. *Physical Biology* **14**, 065004.
- Kranner I, Minibayeva FV, Beckett RP, Seal CE. 2010. What is stress? Concepts, definitions and applications in seed science. *New Phytologist* **188**, 655–673.
- Kuht EJ, Reintam ER. 2004. Soil compaction effect on soil physical properties and the content of nutrients in spring barley (*Hordeum vulgare* L.) and spring wheat (*Triticum aestivum* L.). *Agronomy Research* **2**, 187–194.
- Kuijken RC, van Eeuwijk FA, Marcelis LF, Bouwmeester HJ. 2015. Root phenotyping: from component trait in the lab to breeding. *Journal of Experimental Botany* **66**, 5389–5401.
- Lal R. 1997. Degradation and resilience of soils. *Philosophical Transactions of the Royal Society B: Biological Sciences* **352**, 997–1010.
- Lambers H, Atkin O, Millenaar FF. 2002. Respiratory patterns in roots in relation to their functioning. In: Waisel Y, Eshel A, Kafkaki K, eds. *Plant roots: the hidden half*. New York: Marcel Dekker, 521–552.
- Lichtenthaler HK. 1996. Vegetation stress: an introduction to the stress concept in plants. *Journal of Plant Physiology* **148**, 4–14.
- Lipiec J, Stępniewski W. 1995. Effects of soil compaction and tillage systems on uptake and losses of nutrients. *Soil and Tillage Research* **35**, 37–52.
- Lynch JP. 1995. Root architecture and plant productivity. *Plant Physiology* **109**, 7–13.
- Lynch JP. 2007a. Rhizoeconomics: the roots of shoot growth limitations. *Horticultural Science* **42**, 1107–1109.
- Lynch JP. 2007b. Roots of the second green revolution. *Australian Journal of Botany* **55**, 493–512.
- Lynch JP. 2013. Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. *Annals of Botany* **112**, 347–357.
- Lynch JP, Brown KM. 2008. Root strategies for phosphorus acquisition. In: White P, Hammond J, eds. *The ecophysiology of plant–phosphorus interactions*. Dordrecht: Springer, 83–116.
- Lynch JP, Ho MD. 2005. Rhizoeconomics: carbon costs of phosphorus acquisition. *Plant and Soil* **269**, 45–56.
- Lynch JP, Wojciechowski T. 2015. Opportunities and challenges in the subsoil: pathways to deeper rooted crops. *Journal of Experimental Botany* **66**, 2199–2210.
- Ma Z, Bielenberg DG, Brown KM, Lynch JP. 2001a. Regulation of root hair density by phosphorus availability in *Arabidopsis thaliana*. *Plant, Cell & Environment* **24**, 459–467.
- Ma Z, Walk TC, Marcus A, Lynch JP. 2001b. Morphological synergism in root hair length, density, initiation, and geometry for phosphorus acquisition in *Arabidopsis thaliana*: a modeling approach. *Plant and Soil* **236**, 221–235.

- MacDonald AM, Matthews KB, Paterson E, Aspinall RJ.** 1994. The impact of climate change on the soil/moisture regime of Scottish mineral soils. *Environmental Pollution* **83**, 245–250.
- Masle J.** 1992. Genetic variation in the effects of root impedance on growth and transpiration rates of wheat and barley. *Australian Journal of Plant Physiology* **19**, 109–125.
- Masle J, Passioura JB.** 1987. The effect of soil strength on the growth of young wheat plants. *Australian Journal of Plant Physiology* **14**, 643–656.
- Materechera SA, Alston AM, Kirby JM, Dexter AR.** 1992. Influence of root diameter on the penetration of seminal roots into a compacted subsoil. *Plant and Soil* **144**, 297–303.
- Mathers AC, Lotspeich FB, Laase GR, Wilson GC.** 1966. Strength of compacted Amarillo fine sandy loam as influenced by moisture, clay content, and exchangeable cation. *Soil Science Society of America Journal* **30**, 788–791.
- McConaughay KDM, Coleman JS.** 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* **80**, 2581–2593.
- McKenzie BM, Mullins CE, Tisdall JM, Bengough AG.** 2013. Root–soil friction: quantification provides evidence for measurable benefits for manipulation of root-tip traits. *Plant, Cell & Environment* **36**, 1085–1092.
- Mi G, Chen F, Wu Q, Lai N, Yuan L, Zhang F.** 2010. Ideotype root architecture for efficient nitrogen acquisition by maize in intensive cropping systems. *Science China. Life Sciences* **53**, 1369–1373.
- Müller M, Schmidt W.** 2004. Environmentally induced plasticity of root hair development in *Arabidopsis*. *Plant Physiology* **134**, 409–419.
- Mullholland BJ, Black CR, Taylor IB, Roberts JA, Lenton JR.** 1996. Effect of soil compaction on barley (*Hordeum vulgare* L.) growth. I. Possible role for ABA as a root-sourced chemical signal. *Journal of Experimental Botany* **47**, 539–549.
- Negin B, Moshelion M.** 2016. The advantages of functional phenotyping in pre-field screening for drought-tolerant crops. *Functional Plant Biology* **44**, 107–118.
- Nicotra AB, Davidson A.** 2010. Adaptive phenotypic plasticity and plant water use. *Functional Plant Biology* **37**, 117–127.
- Nielsen KL, Bouma TJ, Lynch JP, Eissenstat DM.** 1998. Effects of phosphorus availability and vesicular-arbuscular mycorrhizas on the carbon budget of common bean (*Phaseolus vulgaris*). *New Phytologist* **139**, 647–656.
- Nielsen KL, Eshel A, Lynch JP.** 2001. The effect of phosphorus availability on the carbon economy of contrasting common bean (*Phaseolus vulgaris* L.) genotypes. *Journal of Experimental Botany* **52**, 329–339.
- Nishiuchi S, Yamauchi T, Takahashi H, Kotula L, Nakazono M.** 2012. Mechanisms for coping with submergence and waterlogging in rice. *Rice* **5**, 2.
- Nortjé GP, van Hoven W, Laker MC.** 2012. Factors affecting the impact of off-road driving on soils in an area in the Kruger National Park, South Africa. *Environmental Management* **50**, 1164–1176.
- O'Toole JC, Bland WL.** 1987. Genotypic variation in crop plant root systems. *Advances in Agronomy* **41**, 91–145.
- Oldeman LR, Hakkeling RTA, Sombroek WG.** 1991. World map of the status of human-induced soil degradation: an explanatory note. Wageningen: International Soil Reference and Information Centre.
- Olesen JE, Bindi M.** 2002. Consequences of climate change for European agricultural productivity, land use and policy. *European Journal of Agronomy* **16**, 239–262.
- Orr HA.** 2009. Fitness and its role in evolutionary genetics. *Nature Reviews. Genetics* **10**, 531–539.
- Pagès L, Serra V, Draye X, Doussan C, Pierret A.** 2010. Estimating root elongation rates from morphological measurements of the root tip. *Plant and Soil* **328**, 35–44.
- Palmer CM, Bush SM, Maloof JN.** 2012. Phenotypic and developmental plasticity in plants. eLS. doi: 10.1002/9780470015902.a0002092.pub2.
- Passioura JB.** 2002. Soil conditions and plant growth. *Plant, Cell & Environment* **25**, 311–318.
- Peterson RL, Farquhar ML.** 1996. Root hairs: specialized tubular cells extending root surfaces. *Botanical Review* **62**, 1–40.
- Pfeifer J, Faget M, Walter A, Blossfeld S, Fiorani F, Schurr U, Nagel KA.** 2014. Spring barley shows dynamic compensatory root and shoot growth responses when exposed to localised soil compaction and fertilisation. *Functional Plant Biology* **41**, 581–597.
- Pierce FJ, Larson WE, Dowdy RH, Graham WAP.** 1983. Productivity of soils: assessing long-term changes due to erosion. *Journal of Soil and Water Conservation* **38**, 39–44.
- Pigliucci M.** 2001. Phenotypic plasticity: beyond nature and nurture. Baltimore, MD: John Hopkins University Press.
- Poorter H, Nagel O.** 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Australian Journal of Plant Physiology* **27**, 595–607.
- Popova L, van Dusschoten D, Nagel KA, Fiorani F, Mazzolai B.** 2016. Plant root tortuosity: an indicator of root path formation in soil with different composition and density. *Annals of Botany* **118**, 685–698.
- Porporato A, Daly E, Rodriguez-Iturbe I.** 2004. Soil water balance and ecosystem response to climate change. *The American Naturalist* **164**, 625–632.
- Postma JA, Lynch JP.** 2011a. Root cortical aerenchyma enhances the growth of maize on soils with suboptimal availability of nitrogen, phosphorus, and potassium. *Plant Physiology* **156**, 1190–1201.
- Postma JA, Lynch JP.** 2011b. Theoretical evidence for the functional benefit of root cortical aerenchyma in soils with low phosphorus availability. *Annals of Botany* **107**, 829–841.
- Potocka I, Szymanowska-Pulka J.** 2018. Morphological responses of plant roots to mechanical stress. *Annals of Botany* **122**, 711–723.
- Pregitzer KS, Laskowski MJ, Burton AJ, Lessard VC, Zak DR.** 1998. Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* **18**, 665–670.
- Primack RB, Kang H.** 1989. Measuring fitness and natural selection in wild plant populations. *Annual Review of Ecology and Systematics* **20**, 367–396.
- Ramalingam P, Kamoshita A, Deshmukh V, Yaginuma, Uga Y.** 2017. Association between root growth angle and root length density of a near-isogenic line of IR64 rice with *DEEPER ROOTING 1* under different levels of soil compaction. *Plant Production Science* **20**, 162–175.
- Rao MS, Datta B, Rao VK.** 1989. Sorghum growth and dry matter yield as influenced by soil water, bulk density and temperature. *Soil Technology* **2**, 107–111.
- Reich PB.** 2002. Root–shoot relations: optimality in acclimation and adaptation or the ‘Emperor’s new clothes’? In: Waisel Y, Eshel A, Kafkafi U, eds. *Plant roots: the hidden half*. New York: Marcel Dekker, 205–220.
- Rich SM, Watt M.** 2013. Soil conditions and cereal root system architecture: review and considerations for linking Darwin and Weaver. *Journal of Experimental Botany* **64**, 1193–1208.
- Rogers ED, Benfey PN.** 2015. Regulation of plant root system architecture: implications for crop advancement. *Current Opinion in Biotechnology* **32**, 93–98.
- Sandhu N, Raman KA, Torres RO, Audebert A, Dardou A, Kumar A, Henry A.** 2016. Rice root architectural plasticity traits and genetic regions for adaptability to variable cultivation and stress conditions. *Plant Physiology* **171**, 2562–2576.
- Shabala S, White RG, Djordjevic MA, Ruan Y-L, Mathesius U.** 2015. Root-to-shoot signalling: integration of diverse molecules, pathways and functions. *Functional Plant Biology* **43**, 87–104.
- Sharp RE, Silk WK, Hsiao TC.** 1988. Growth of the maize primary root at low water potentials: I. Spatial distribution of expansive growth. *Plant Physiology* **87**, 50–57.
- 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.
- Sitaula BK, Hansen S, Sitaula JIB, Bakken LR.** 2000. Effects of soil compaction on N₂O emission in agricultural soil. *Chemosphere* **2**, 367–371.
- Smith MS, Tiedje JM.** 1979. Phases of denitrification following oxygen depletion in soil. *Soil Biology and Biochemistry* **11**, 261–267.
- Smith S, de Smet I.** 2012. Root system architecture: insights from *Arabidopsis* and cereal crops. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**, 1441–1452.
- Soane BD, van Ouwerkerk C.** 1994. Soil compaction problems in world agriculture. In: Soane BD, van Ouwerkerk C, eds. *Soil compaction in crop production*. Amsterdam: Elsevier, 1–21.

- Soil Science Society of America.** 2008. Glossary of soil science terms 2008. Madison, WI: Soil Science Society of America.
- Stirzaker RJ, Passioura JB, Wilms Y.** 1996. Soil structure and plant growth: impact of bulk density and biopores. *Plant and Soil* **185**, 151–162.
- Sultan SE.** 1987. Evolutionary implications of phenotypic plasticity in plants. In: Hecht MK, Wallace B, Prance GT, eds. *Evolutionary biology*. Boston, MA: Springer, 127–178.
- Sultan SE, Spencer HG.** 2002. Metapopulation structure favors plasticity over local adaptation. *The American Naturalist* **160**, 271–283.
- To J, Kay BD.** 2005. Variation in penetrometer resistance with soil properties: the contribution of effective stress and implications for pedotransfer functions. *Geoderma* **126**, 261–276.
- Tracy SR, Black CR, Roberts JA, Dodd IC, Mooney SJ.** 2015. Using X-ray computed tomography to explore the role of abscisic acid in moderating the impact of soil compaction on root system architecture. *Environmental and Experimental Botany* **110**, 11–18.
- Tracy SR, Black CR, Roberts JA, Sturrock C, Mairhofer S, Craigon J, Mooney SJ.** 2012. Quantifying the impact of soil compaction on root system architecture in tomato (*Solanum lycopersicum*) by X-ray micro-computed tomography. *Annals of Botany* **110**, 511–519.
- Tubeileh A, Groleau-Renaud V, Plantureux S, Guckert A.** 2003. Effect of soil compaction on photosynthesis and carbon partitioning within a maize–soil system. *Soil and Tillage Research* **71**, 151–161.
- Uga Y, Kitomi Y, Ishikawa S, Yano M.** 2015. Genetic improvement for root growth angle to enhance crop production. *Breeding science* **65**, 111–119.
- 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.
- Uga Y, Sugimoto K, Ogawa S, et al.** 2013. Control of root system architecture by *DEEPER ROOTING1* increases rice yield under drought conditions. *Nature Genetics* **45**, 1097–1102.
- Unger PW, Kaspar TC.** 1994. Soil compaction and root growth: a review. *Agronomy Journal* **86**, 759–766.
- vanHuysteen L.** 1983. Interpretation and use of penetrometer data to describe soil compaction in vineyards. *South African Journal for Enology and Viticulture* **4**, 59–65.
- Verslues PE, Agarwal M, Katiyar-Agarwal S, Zhu J, Zhu JK.** 2006. Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. *The Plant Journal* **45**, 523–539.
- Via S, Gomulkiewicz R, De Jong G, Scheiner SM, Schlichting CD, Van Tienderen PH.** 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology & Evolution* **10**, 212–217.
- Walk T, Jaramillo R, Lynch JP.** 2006. Architectural tradeoffs between adventitious and basal roots for phosphorus acquisition. *Plant and Soil* **279**, 347–366.
- Wallace A.** 1986. Definition of stresses in crop production—iron, plant nutrient, and non-nutrient stress interactions. *Journal of Plant Nutrition* **9**, 187–192.
- 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.** 1926. Root development of field crops. New York: McGraw-Hill.
- Whalley WR, Dumitru E, Dexter AR.** 1995. Biological effects of soil compaction. *Soil and Tillage Research* **35**, 53–68.
- 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.
- Xie J, Tang L, Wang Z, Xu G, Li Y.** 2012. Distinguishing the biomass allocation variance resulting from ontogenetic drift or acclimation to soil texture. *PLoS One* **7**, e41502.
- Yamauchi T, Shimamura S, Nakazono M, Mochizuki T.** 2013. Aerenchyma formation in crop species: a review. *Field Crops Research* **152**, 8–16.
- Younginger BS, Sirová D, Cruzan MB, Ballhorn DJ.** 2017. Is biomass a reliable estimate of plant fitness? Applications in Plant Sciences **5**: apps.1600094.
- York LM, Nord EA, Lynch JP.** 2013. Integration of root phenes for soil resource acquisition. *Frontiers in Plant Science* **4**, 355.
- Zobel RW.** 1992. Soil environment constraints to root growth. In: Hatfield JL, Stewart BA, eds. *Limitations to plant root growth*. New York: Springer, 27–51.