

# Developing strategies to recover crop productivity after soil compaction—A plant eco-physiological perspective



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## ABSTRACT

Soil compaction constitutes a major threat to the fertility of arable soils and food security. The aim of this paper is to highlight the need and opportunities for plant eco-physiological approaches to identify strategies to recover crop yields after soil compaction. Reduced productivity on compacted soil primarily results from decreased root elongation rates and thus limited accessibility to water and nutrients. Hence, strategies to recover productivity after compaction must address plant eco-physiological phenomena that underlie low root system expansion rates. In compacted soil, root growth is decreased due to high soil penetration resistance and due to low oxygen concentration in soil air caused by reduced fluid transport capability. Thus, plant roots are exposed to a multi-stress environment, which needs to be addressed directly when aiming to recover productivity after compaction in the long-term. Here, we discuss possibilities to increase root growth in order to enhance resource accessibility and recover crop productivity on compacted soil. Yield recovery can be achieved through breeding of novel cultivars and targeted soil management approaches. On the one hand, the tolerance of plants to the different soil physical stresses can be enhanced by selecting for specific root traits that facilitate root growth in compacted soil. Soil management approaches that improve specific physical properties of compacted soil on the other hand can facilitate root growth in compacted soil. Since plant roots are major drivers of soil structure dynamics, increasing root growth in compacted soil may not only mitigate crop productivity losses but also recover soil structure.

## 1. Introduction: compacted soil constitutes a multi stress environment for plants

The use of heavy agricultural machinery in modern agriculture has resulted in an estimated 68 million hectares of compacted arable land (Hamza and Anderson, 2005). This area has increased in the last decade and will likely increase even more in the future due to ever rising weights of agricultural machinery (Schjønning et al., 2015; Stolte et al., 2016). These projections show that the problem of compacted soil in arable systems persists despite strategies to avoid compaction, such as conservation tillage and controlled traffic farming (e.g. Batey, 2009; Hamza and Anderson, 2005). Compacted soils typically show a degraded structure with low (macro-) porosity, and low pore continuity and connectivity (Horn et al., 1995). The structural degradation, which can last for decades (Berisso et al., 2013; Besson et al., 2013; Hakansson and Reeder, 1994), adversely affects ecosystem services of arable soil including crop productivity (Batey, 2009; Hamza and Anderson, 2005; Tracy et al., 2011). Graves et al. (2015) estimated the compaction costs

to be higher than 500 million Euros per year in England and Wales, of which productivity losses account for more than 40% (Graves et al., 2015). In order to mitigate these costs and to ensure food security in the long-term, strategies to recover crop yields on compacted soils are urgently needed.

Low crop productivity on compacted soil results primarily from impeded root system expansion and thus limited access to soil water and nutrients pools (Araki and Iijima, 2005; Bengough et al., 2011; Colombi et al., 2018; Nosalewicz and Lipiec, 2014; Valentine et al., 2012). Plants acquire different resources from the topsoil and the subsoil due to uneven resource distribution. Immobile nutrients such as phosphorus and potassium are mainly taken up from the topsoil, while mobile resources such as water and nitrogen are acquired from the topsoil and the subsoil. Whether root growth is slowed down in the topsoil or the subsoil, the consequence for plant is limited access to resources. Water and nutrient availability may also decrease as a result of compaction but results are inconsistent (Archer and Smith, 1972; Colombi et al., 2018; George et al., 2011; Kristoffersen and Riley, 2005;

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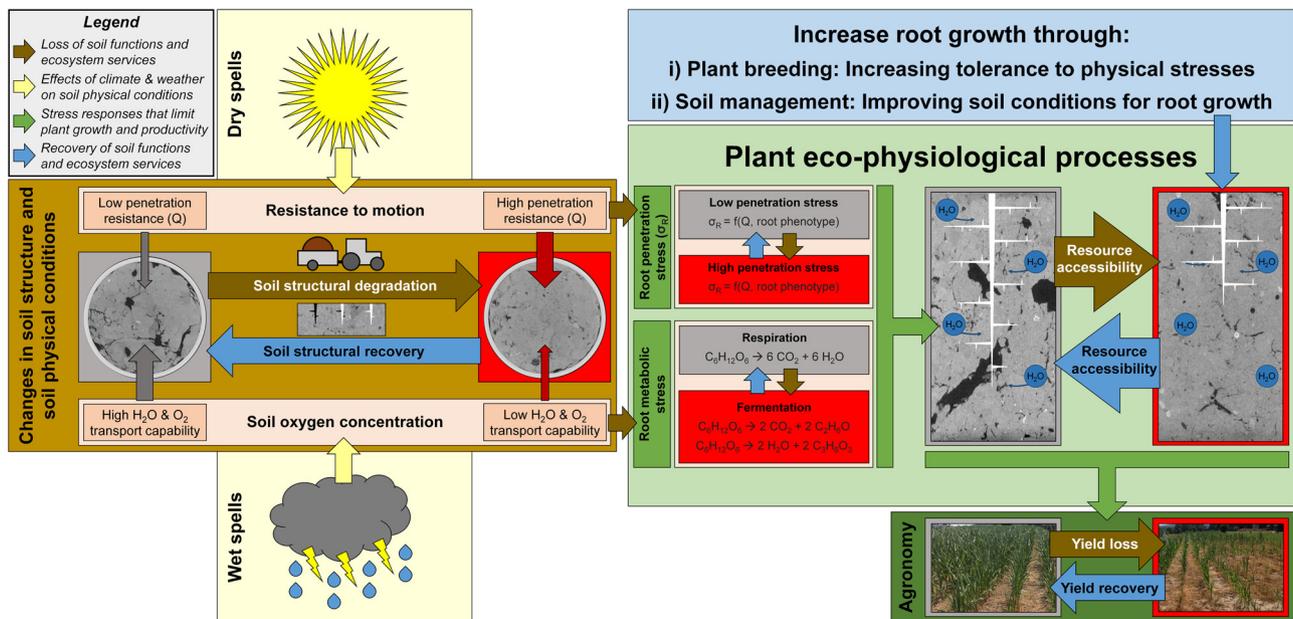


Fig. 1. Conceptual framework illustrating the need for a plant eco-physiological perspective to understand yield formation on compacted soil and the development of recovery strategies (light green box and arrows). Soil structural degradation upon compaction leads to unfavourable conditions for root growth, which imposes stress on plants and reduces access to soil resources and crop productivity (brown arrows). Increasing root growth by enhancing the tolerance of plants to stress through breeding and by improving the physical conditions for root growth through management contributes to the recovery of crop yields and soil structure (blue arrows).

Lipiec and Hatano, 2003; Pfeifer et al., 2014; Richard et al., 2001; Romero et al., 2011). Even though low resource availability may contribute to yield losses on compacted soil, reduced resource accessibility resulting from impeded root growth is considered the main cause for decreased crop productivity (Bengough et al., 2011; Valentine et al., 2012). There are different soil physical properties that cause root growth rates in compacted soil to decrease (Fig. 1). On the one hand, compaction increases soil penetration resistance due to the decreased void space available for displacement of soil particles (Batey, 2009; Hamza and Anderson, 2005). On the other hand, compaction results in low connectivity and continuity of the pore space, reduced water and air transport capability of soil (Keller et al., 2017; Kuncoro et al., 2014), which may lead to critically low concentrations of oxygen in soil air (Horn and Smucker, 2005; Tracy et al., 2011). Therefore, reduced crop productivity on compacted soils results from adversely changed soil physical conditions, which are a consequence of soil structural degradation.

Soil penetration resistance and oxygen concentration in soil air are strongly influenced by soil moisture and thus local pedo-climatic conditions, and short-term precipitation and temperature events. Penetration resistance increases as soils dry, while the risk for low oxygen concentration in soil air is particularly high after heavy rainfall (Batey, 2009; Bengough et al., 2011; Colombi et al., 2018; Gziesiak et al., 2014; Tracy et al., 2011). Hence, soil penetration resistance is likely to be the dominant stress for growing roots under dry conditions. Under wet conditions, root growth in compacted soil is likely to be limited by low concentration of oxygen in soil air (Fig. 1). Since both dry and wet periods typically occur during the same season, an individual plant is exposed to different physical stresses, which fluctuate over time. Finally, plants themselves affect their soil physical environment by root water uptake and consumption of oxygen in soil air due to root respiration (Fig. 2). Therefore, crops growing on compacted soil experience critical levels of soil penetration resistance (Colombi et al., 2018) and oxygen concentrations in soil air (Buyanovsky and Wagner, 1983) multiple times during a single season. Due to the projected increase in extreme weather events with climate change (IPCC, 2014), the severity of dry and wet spells and thus periods of high penetration resistance and low concentration of oxygen in soil air will

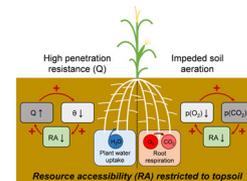


Fig. 2. Illustration of feedbacks between soil physical properties, i.e., soil penetration resistance and aeration, and root physiological processes in compacted soil. Root growth and thus resource accessibility is limited to shallow soil layers leading to increased water uptake (left) and root respiration (right) in the topsoil. In turn, soil penetration resistance increases while oxygen concentration in soil air decreases, leading to even more unfavourable conditions for root growth.

increase in the future. Hence, reductions of crop yields resulting from compaction are likely to increase in the course of global change.

This paper discusses the need for the integration of a plant eco-physiological perspective into the development of strategies to recover crop productivity on compacted soil. Plant eco-physiological research aims to understand relationships and interactions between environmental parameters and plant physiological processes. We argue that accounting for plant eco-physiological processes is crucial in order to understand why crop yields decrease with soil compaction. Such an understanding is pivotal to identify measures that increase root growth and resource accessibility on compacted soil, and ultimately allow to regain crop productivity. Because plant roots significantly contribute to soil structure dynamics through bioturbation, carbon input, and water uptake (Dexter, 1991; Vogel et al., 2018), increased root growth will not only contribute to yield recovery but also to structural and functional recovery of compacted soil.

## 2. Plant eco-physiological responses to soil compaction underlying low crop productivity

Root and shoot growth respond within hours to days to changes in soil penetration resistance (Bengough et al., 2011; Young et al., 1997) and reduced oxygen concentration in soil air (Dresbøll et al., 2013;

Thomson et al., 1992; Watkin et al., 1998). Both high penetration resistance and low concentration of oxygen in soil air result in reduced root elongation rates, shallow root growth and in delayed initiation of lateral roots (Barraclough and Weir, 1988; Blackwell and Wells, 1983; Botta et al., 2010; Colombi et al., 2018; Colombi and Walter, 2016; Dresbøll et al., 2013; Fukao and Bailey-Serres, 2004; Grzesiak et al., 2014; Materechera et al., 1992). However, the underlying plant physiological mechanisms and the functional implications of stress responses differ distinctly between high penetration resistance and low concentration of oxygen in soil air (Fig. 1).

Increased soil penetration resistance imposes greater mechanical stresses on the root tip in the form of higher frictional resistance and higher cavity expansion pressure (Bengough et al., 2011). Hence, high penetration resistance mainly affects the apical zone of roots. Plants acclimate to increased penetration resistance by various adjustments of the root phenotype. Mucilage excretion and sloughing of root cap cells increases under high penetration resistance, which lubricates the root-soil interface and decreases frictional resistance (Bengough and McKenzie, 1997; Iijima et al., 2000, 2003a). To reduce the resistance to cavity expansion and to stabilize roots against buckling, plants increase the diameter of their roots upon greater penetration resistance (Chimungu et al., 2015; Kirby and Bengough, 2002; Materechera et al., 1992). Low oxygen concentration in soil air affects not only the root tip but the entire root system (Fukao and Bailey-Serres, 2004). Sufficient oxygen in root tissues is required to maintain aerobic cell respiration. Upon decreasing cellular oxygen concentration, respiration is replaced by anaerobic fermentation, resulting in reduced metabolic efficiency (Bailey-Serres et al., 2012; Drew, 1997; Fukao and Bailey-Serres, 2004). As with high soil penetration resistance, plants modify their roots in order to withstand low concentration of oxygen in soil air. Many plant species develop an internal aeration system to counteract reduced oxygen in soil air (Colmer, 2003a; Sauter, 2013; Yamauchi et al., 2018). The formation of cortical aerenchyma, which are continuous air-filled structures in roots, connects the root system to the aboveground (Marashi and Mojaddam, 2014; Shimamura et al., 2003; Striker et al., 2007; Thomas et al., 2005; Xu et al., 2013; Yamauchi et al., 2014). Furthermore, the development of oxygen barriers in the outer root cortex prevent radial oxygen loss (Colmer, 2003b; Manzur et al., 2015; Nishiuchi et al., 2012; Sauter, 2013).

Despite these adjustments, root system expansion and thus resource accessibility declines substantially under high soil penetration resistance and low oxygen concentration in soil air (Bengough et al., 2011; Colombi and Walter, 2017; Dresbøll et al., 2013; Grzesiak et al., 2014; Thomson et al., 1992; Watkin et al., 1998). Reduced root elongation rates and delayed initiation of lateral roots limit soil exploration to the topsoil. In turn, water uptake and root respiration in the upper soil layers increase, resulting in even higher soil penetration resistance and further depletion of oxygen in soil air (Araki and Iijima, 2005; Colombi et al., 2018; Dresbøll et al., 2013; Grzesiak et al., 2014; Nosalewicz and Lipiec, 2014). This feedback between soil physical conditions, root growth and resource accessibility, eventually leads to decreased shoot growth and low crop productivity (Fig. 2) (Colombi et al., 2018; Grzesiak et al., 2013; Pang et al., 2004; Tubeileh et al., 2003). In order to enhance root growth and resource accessibility in compacted soil, and thus to regain productivity, these feedback cycles need to be broken (Fig. 1).

### 3. Increasing root growth to recover crop productivity after compaction

Since limited crop productivity on compacted soil results primarily from impeded access to soil resources, root growth must be increased to recover yields. The abiotic stresses occurring on compacted soil – high penetration resistance and low oxygen concentration in soil air – need to be addressed directly in the development of recovery strategies (Fig. 1). It is known that the tolerance to high soil penetration

resistance and low soil oxygen differs between plant species (Azam et al., 2014; Bailey-Serres et al., 2012; Bushamuka and Zobel, 1998; Busscher et al., 2000; Fukao and Bailey-Serres, 2004; Grzesiak et al., 2014). Therefore, adapting crop rotations may contribute to yield recovery on compacted soil. Furthermore, perennial and deep rooting plants that tolerate high soil penetration resistance and low concentrations of oxygen in soil air can help recover soil structure, resulting in better soil penetrability and aeration (Chen et al., 2014; Lesturgez et al., 2004; Stewart et al., 2014; Young et al., 1998). By improving soil physical conditions, the introduction of such species into crop rotations may contribute to higher productivity of succeeding crops on compacted soils. However, climatic conditions as well as socio-economic preferences and constraints may prevent the inclusion of such tolerant species into rotations. Given these limitations, we suggest alternative approaches for the recovery of crop productivity on compacted soils. In principle, root growth can either be increased by breeding novel crop varieties with improved root growth in compacted soil or by improving the soil conditions for root growth through soil management and amelioration.

#### 3.1. Selection of physiological traits to increase root growth

Genotypic diversity of root traits within single crop species may be harnessed to adapt crop germplasm to unfavourable soil conditions (Bishopp and Lynch, 2015). The concept of ‘physiological breeding’, which refers to the selection of basic traits with direct physiological implications, is thereby of crucial importance (Ghanem et al., 2015; Reynolds and Langridge, 2016). Previous research showed that it is possible to identify such basic root traits, which lead to improved root growth under high soil penetration resistance and low oxygen concentration in soil air. Such fundamental information is needed to define selection targets for crop breeding programs.

Acute root tip angles reduce the penetration stress exerted by roots, which facilitates root elongation under high penetration resistance (Colombi et al., 2017b; Iijima et al., 2003b; Vollsnes et al., 2010). Anchoring roots to the soil with root hairs promotes the penetration of hard soil layers (Bengough et al., 2016; Haling et al., 2013) and small cells in the outer root cortex reduce the risk of root buckling (Chimungu et al., 2015). Moreover, mucilage excretion and sloughing of root cap cells differs among genotypes (Somasundaram et al., 2008). Hence, friction at the root-soil interface can be reduced by selecting for increased lubrication around the growing root tip. Efficient internal aeration of the root system is crucial for plants to maintain aerobic root respiration and thus to withstand low oxygen concentration in soil air. Increased abundance of root cortical aerenchyma promotes air diffusion from the soil surface to the root elongation zone and facilitates root growth under low soil oxygen concentrations (Broughton et al., 2015; Thomson et al., 1992; Watkin et al., 1998). Prevention of radial oxygen loss from roots by increased suberization and lignification of the outer root cortex is typical for wetland species such as paddy rice (Colmer, 2003a; Sauter, 2013; Yamauchi et al., 2018). However, genotypic differences in the development of barriers preventing radial oxygen loss were reported for upland rice, i.e., a dryland crop. The same study showed that the genotypic ability of upland rice to develop oxygen barriers promotes root growth under low oxygen concentrations in soil air (Colmer, 2003b). Wild relatives of maize and barley are also known to develop such barriers and this ability may be introduced into crop genomes through hybridization (Sauter, 2013; Yamauchi et al., 2018). Furthermore, a high number of lateral and adventitious roots increases the soil volume that plants can explore and contributes to improved shoot growth under low soil oxygen concentration and high penetration resistance (Colombi and Walter, 2017; Fukao and Bailey-Serres, 2004).

In summary, there is a plethora of root traits that improve root growth and resource accessibility and these traits may be selected for to develop new varieties with improved performance on compacted soil. Methods allowing for high throughput quantification, which are

required to screen large populations in order to link phenotypic information to the plant genome, are available for certain traits of interest. Root number (Bucksch et al., 2014; Lobet et al., 2011), root cortical aerenchyma and cortical cell size (Burton et al., 2012), root tip shape (Colombi et al., 2017b), and root hair area (Vincent et al., 2017) can be quantified from images using automated and semi-automated approaches. Furthermore, quantitative trait loci, i.e., regions in the genome associated with particular traits, have been reported for cortical aerenchyma (Broughton et al., 2015), root hair length (Zhu et al., 2005a), and root number in major crop species (Cai et al., 2012; Zhu et al., 2005b). However, effects of the above mentioned root traits on yield on compacted soil as well as possible tradeoffs between target traits and productivity remain to be investigated. Hence, further research is needed before varieties with improved tolerance to soil compaction can be developed.

### 3.2. Recovery of specific soil properties to improve physical conditions for root growth

Yield mitigation after compaction may also be achieved through soil management. Deep tillage can improve crop productivity on compacted soil in the short-term but beneficial effects may disappear rapidly due to severe recompaction (Botta et al., 2006; Hamza and Anderson, 2005; Tessier et al., 1997). Therefore, alternative management approaches are required. To improve physical conditions for root growth in the long-term, soil management needs to focus on the recovery of specific soil properties that were adversely affected by compaction and that are crucial for root growth and crop development.

Continuous vertical macropores and cracks offer pathways of least resistance for growing roots and reduce the risk of low soil oxygen concentration due to improved water infiltration and soil aeration (Colombi et al., 2017a; Dexter, 1991; Mori et al., 2014; Stirzaker et al., 1996). It has been observed that roots grow preferentially towards macropores to use them as a path of least resistance as well as a source of oxygen (Colombi et al., 2017a; Dexter, 1986; Stirzaker et al., 1996; White and Kirkegaard, 2010). In addition, increased water infiltration through macropores may also decrease soil penetration resistance, and increase water replenishment, and thus water retention in the subsoil. Pot and field plot experiments showed that artificial macropores inserted into compacted soil foster root growth, resource accessibility and shoot development (Colombi et al., 2017a; Mori et al., 2014; Stirzaker et al., 1996). Similar to such artificial pores, vertical biopores created by roots of preceding crops can be exploited by plants to reach resources in deeper soil layers (Athmann et al., 2013; Kautz et al., 2013; White and Kirkegaard, 2010). Vertical macropores are rather stable under uniaxial compression (Schäffer et al., 2008) and may therefore resist tractor passes. Hence, it is likely that such macropores can persist over several seasons, similar to vertical burrows from anecic earthworms (Edwards et al., 1990; Lighthart and Peek, 1997). While soil perforation is so far limited to small experimental plots (Colombi et al., 2017a; Mori et al., 2014), soil slotting can be carried out at much large scales (Blackwell et al., 1990, 1991; Kirchhof et al., 1991). Through slotting, only parts of the soil are loosened whereas other parts of the soil remain undisturbed, which decreases the risk of recompaction compared to deep tillage. Similar to soil perforation, slotting opens pathways for growing roots and improves water infiltration and soil aeration, which facilitates root growth and crop productivity (Hartmann et al., 2008a, 2008b). These vertical slots can additionally be stabilized by applying gypsum in order to maintain their beneficial effects on soil physical conditions in the longer term (Blackwell et al., 1991; Jayawardana and Chan, 1994).

Hence, restoring specific soil properties, rather than entirely breaking up compacted soil may improve soil physical conditions for root growth and plant productivity in the long-term. The effects of such targeted soil management approaches and the resulting increase in root growth on properties of the bulk soil remain to be investigated. Such

knowledge is ultimately needed to assess the potential of these measures to recover not only crop productivity but also soil structure.

## 4. Conclusion: plant eco-physiology needs to be included in the development of recovery strategies

Low yields on compacted soil result from interactions and feedbacks between soil penetration resistance, oxygen concentration in soil air, soil moisture, root growth and the accessibility of plants to water and nutrients. Addressing high root penetration stress and low cellular oxygen concentration, and thus plant physiological processes that ultimately underlie low root growth, allows to develop efficient and sustainable mitigation strategies. The root penetrability of hard soil and the internal aeration of root systems can be improved through breeding, resulting in increased root growth in compacted soil. Root growth may also be enhanced by creating vertical soil macropores or opening thin slots in soil, which enhance water infiltration and soil aeration, and create root pathways of least resistance. Hence, increased tolerance to abiotic stresses occurring in compacted soil and improved soil physical conditions for root growth enhance the accessibility of plants to resources in compacted soil. Ultimately, greater access to water and nutrients fosters whole plant development and therefore crop productivity. In addition, increased root growth also accelerates structural and functional recovery of compacted soils through bioturbation and macropore formation, carbon input, as well as crack formation caused by water uptake. Taking plant eco-physiological processes into account is crucial to understand crop responses and crop productivity decrease caused by soil compaction and to develop sustainable recovery strategies for compacted soils.

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### References

- Araki, H., Iijima, M., 2005. Stable isotope analysis of water extraction from subsoil in upland rice (*Oryza sativa* L.) as affected by drought and soil compaction. *Plant Soil* 270, 147–157. <https://doi.org/10.1007/s11104-004-1304-2>.
- Archer, J.R., Smith, P.D., 1972. The relation between bulk density, available water capacity and air capacity of soils. *J. Soil Sci.* 23, 475–480. <https://doi.org/10.1111/j.1365-2389.1972.tb01678.x>.
- Athmann, M., Kautz, T., Pude, R., Köpke, U., 2013. Root growth in biopores—evaluation with in situ endoscopy. *Plant Soil* 371, 179–190. <https://doi.org/10.1007/s11104-013-1673-5>.
- Azam, G., Murray, R.S., Grant, C.D., Nuberg, I.K., 2014. Tolerance of young seedlings of different tree species and a cereal to poor soil aeration. *Soil Res.* 52, 751–759. <https://doi.org/10.1071/SR13219>.
- Bailey-Serres, J., Lee, S.C., Brinton, E., 2012. Waterproofing crops: effective flooding survival strategies. *Plant Physiol.* 160, 1698–1709. <https://doi.org/10.1104/pp.112.208173>.
- Barraclough, P.B., Weir, A.H., 1988. Effects of a compacted subsoil layer on root and shoot growth, water use and nutrient uptake of winter wheat. *J. Agric. Sci.* 110, 207–216. <https://doi.org/10.1017/S0021859600081235>.
- Batey, T., 2009. Soil compaction and soil management – a review. *Soil Use Manag.* 25, 335–345. <https://doi.org/10.1111/j.1475-2743.2009.00236.x>.
- Bengough, A.G., McKenzie, B.M., 1997. Sloughing of root cap cells decreases the frictional resistance to maize (*Zea mays* L.) root growth. *J. Exp. Bot.* 48, 885–893. <https://doi.org/10.1093/jxb/48.4.885>.
- Bengough, A.G., McKenzie, B.M., Hallett, P.D., Valentine, T.A., 2011. Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. *J. Exp. Bot.* 62, 59–68. <https://doi.org/10.1093/jxb/erq350>.
- Bengough, G.A., Loades, K., McKenzie, B.M., 2016. Root hairs aid soil penetration by anchoring the root surface to pore walls. *J. Exp. Bot.* 67, 1071–1078. <https://doi.org/10.1093/jxb/erv560>.
- Berisso, F.E., Schjønning, P., Keller, T., Lamandé, M., Simojoki, A., Iversen, B.V., Alakukku, L., Forkman, J., 2013. Gas transport and subsoil pore characteristics: anisotropy and long-term effects of compaction. *Geoderma* 195–196, 184–191. <https://doi.org/10.1016/j.geoderma.2012.12.002>.
- Besson, A., Séger, M., Giot, G., Cousin, I., 2013. Identifying the characteristic scales of soil structural recovery after compaction from three in-field methods of monitoring. *Geoderma* 204–205, 130–139. <https://doi.org/10.1016/j.geoderma.2013.04.010>.

- Bishopp, A., Lynch, J.P., 2015. The hidden half of crop yields. *Nat. Plants* 1, 1–2. <https://doi.org/10.1038/nplants.2015.117>.
- Blackwell, P.S., Wells, E.A., 1983. Limiting oxygen flux densities for oat root extension. *Plant Soil* 73, 129–139. <https://doi.org/10.1007/BF02197762>.
- Blackwell, J., Jayawardane, N.S., Butler, R.K., 1990. Design, construction and preliminary testing of a slotting. *J. Agric. Eng. Res.* 46, 81–92.
- Blackwell, P.S., Jayawardane, N.S., Green, T.W., Wood, J.T., Blackwell, J., Beatty, H.J., 1991. Subsoil macropore space of a transitional red-brown earth after either deep tillage, gypsum or both. I. Physical effects and long-term changes. *Aust. J. Soil Res.* 29, 141–154. <https://doi.org/10.1071/SR9910141>.
- Botta, G.F., Jorajuria, D., Balbuena, R., Ressia, M., Ferrero, C., Rosatto, H., Tourn, M., 2006. Deep tillage and traffic effects on subsoil compaction and sunflower (*Helianthus annuus* L.) yields. *Soil Tillage Res.* 91, 164–172. <https://doi.org/10.1016/j.still.2005.12.011>.
- Botta, G.F., Tolon-Becerra, a., Lastra-Bravo, X., Tourn, M., 2010. Tillage and traffic effects (planters and tractors) on soil compaction and soybean (*Glycine max* L.) yields in Argentinean pampas. *Soil Tillage Res.* 110, 167–174. <https://doi.org/10.1016/j.still.2010.07.001>.
- Broughton, S., Zhou, G., Teakle, N.L., Matsuda, R., Zhou, M., O'Leary, R.A., Colmer, T.D., Li, C., 2015. Waterlogging tolerance is associated with root porosity in barley (*Hordeum vulgare* L.). *Mol. Breed.* 35 <https://doi.org/10.1007/s11032-015-0243-3>. 27–27.
- Bucksch, A., Burridge, J., York, L.M., Das, A., Nord, E., Weitz, J.S., Lynch, J.P., 2014. Image-based high-throughput field phenotyping of crop roots. *Plant Physiol.* 166, 470–486. <https://doi.org/10.1104/pp.114.243519>.
- Burton, A.L., Williams, M., Lynch, J.P., Brown, K.M., 2012. RootScan: Software for high-throughput analysis of root anatomical traits. *Plant Soil* 357, 189–203.
- Bushamuka, V.N., Zobel, R.W., 1998. Differential genotypic and root type penetration of compacted soil layers. *Crop Sci.* 38, 776–781.
- Busscher, W.J., Lipiec, J., Bauer, P.J., Carter, T.E.J., 2000. Improved root penetration of soil hard layers by a selected genotype. *Commun. Soil Sci. Plant Anal.* 31, 3089–3101. <https://doi.org/10.1080/00103620009370652>.
- Buyanovsky, G.A., Wagner, G.H., 1983. Annual cycles of carbon dioxide level in soil air. *Soil Sci. Soc. Am. J.* 47, 1139–1145. <https://doi.org/10.2136/sssaj1983.03615995004700060016x>.
- Cai, H., Chen, F., Mi, G., Zhang, F., Maurer, H.P., Liu, W., Reif, J.C., Yuan, L., 2012. Mapping QTLs for root system architecture of maize (*Zea mays* L.) in the field at different developmental stages. *Theor. Appl. Genet.* 125, 1313–1324. <https://doi.org/10.1007/s00122-012-1915-6>.
- Chen, G., Weil, R.R., Hill, R.L., 2014. Effects of compaction and cover crops on soil least limiting water range and air permeability. *Soil Tillage Res.* 136, 61–69. <https://doi.org/10.1016/j.still.2013.09.004>.
- Chimungu, J.G., Loades, K.W., Lynch, J.P., 2015. Root anatomical phenes predict root penetration ability and biomechanical properties in maize (*Zea Mays*). *J. Exp. Bot.* 66, 3151–3162. <https://doi.org/10.1093/jxb/erv121>.
- Colmer, T.D., 2003a. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant Cell Environ.* 26, 17–36. <https://doi.org/10.1046/j.1365-3040.2003.00846.x>.
- Colmer, T.D., 2003b. Aerenchyma and an inducible barrier to radial oxygen loss facilitate root aeration in upland, paddy and deep-water rice (*Oryza sativa* L.). *Ann. Bot.* 91, 301–309. <https://doi.org/10.1093/aob/mcf114>.
- Colombi, T., Walter, A., 2016. Root responses of triticale and soybean to soil compaction in the field are reproducible under controlled conditions. *Funct. Plant Biol.* 43, 114–128. <https://doi.org/10.1071/FP15194>.
- Colombi, T., Walter, A., 2017. Genetic diversity under soil compaction in wheat: root number as a promising trait for early plant vigor. *Front. Plant Sci.* 8, 1–14. <https://doi.org/10.3389/fpls.2017.00420>.
- Colombi, T., Braun, S., Keller, T., Walter, A., 2017a. Artificial macropores attract crop roots and enhance plant productivity on compacted soils. *Sci. Total Environ.* 574, 1283–1293. <https://doi.org/10.1016/j.scitotenv.2016.07.194>.
- Colombi, T., Kirchgessner, N., Walter, A., Keller, T., 2017b. Root tip shape governs root elongation rate under increased soil strength. *Plant Physiol.* 174, 2289–2301. <https://doi.org/10.1104/pp.17.00357>.
- Colombi, T., Torres, L.C., Walter, A., Keller, T., 2018. Feedbacks between soil penetration resistance, root architecture and water uptake limit water accessibility and crop growth – a vicious circle. *Sci. Total Environ.* 626, 1026–1035. <https://doi.org/10.1016/j.scitotenv.2018.01.129>.
- Dexter, A.R., 1986. Model experiments on the behaviour of roots at the interface between a tilled seed-bed and a compacted sub-soil III. Entry of pea and wheat roots into cylindrical biopores. *Plant Soil* 95, 149–161.
- Dexter, A.R., 1991. Amelioration of soil by natural processes. *Soil Tillage Res.* 20, 87–100.
- Dresbøll, D.B., Thorup-Kristensen, K., McKenzie, B.M., Dupuy, L.X., Bengough, A.G., 2013. Timelapse scanning reveals spatial variation in tomato (*Solanum lycopersicum* L.) root elongation rates during partial waterlogging. *Plant Soil* 369, 467–477. <https://doi.org/10.1007/s11104-013-1592-5>.
- Drew, M.C., 1997. Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 48, 223–250. <https://doi.org/10.1146/annurev.arplant.48.1.223>.
- Edwards, W.M., Shipitalo, M.J., Owens, L.B., Norton, L.D., 1990. Effect of *Lumbricus terrestris* L. burrows on hydrology of continuous no-till corn fields. *Geoderma* 46, 73–84. [https://doi.org/10.1016/0016-7061\(90\)90008-W](https://doi.org/10.1016/0016-7061(90)90008-W).
- Fukao, T., Bailey-Serres, J., 2004. Plant responses to hypoxia - Is survival a balancing act? *Trends Plant Sci.* 9, 449–456. <https://doi.org/10.1016/j.tplants.2004.07.005>.
- George, T.S., Brown, L.K., Newton, A.C., Hallett, P.D., Sun, B.H., Thomas, W.T.B., White, P.J., 2011. Impact of soil tillage on the robustness of the genetic component of variation in phosphorus (P) use efficiency in barley (*Hordeum vulgare* L.). *Plant Soil* 339, 113–123. <https://doi.org/10.1007/s11104-009-0209-5>.
- Ghanem, M.E., Marrou, H., Sinclair, T.R., 2015. Physiological phenotyping of plants for crop improvement. *Trends Plant Sci.* 20, 139–144. <https://doi.org/10.1016/j.tplants.2014.11.006>.
- Graves, A.R.R., Morris, J., Deeks, L.K.K., Rickson, R.J.J., Kibblewhite, M.G.G., Harris, J.A.A., Farewell, T.S.S., Truckle, I., 2015. The total costs of soil degradation in England and Wales. *Ecol. Econ.* 119, 399–413. <https://doi.org/10.1016/j.ecolecon.2015.07.026>.
- Grzesiak, S., Grzesiak, M.T., Hura, T., Marcińska, I., Rzepka, A., 2013. Changes in root system structure, leaf water potential and gas exchange of maize and triticale seedlings affected by soil compaction. *Environ. Exp. Bot.* 88, 2–10. <https://doi.org/10.1016/j.envexpbot.2012.01.010>.
- Grzesiak, M.T., Ostrowska, A., Hura, K., Rut, G., Janowiak, F., Rzepka, A., Hura, T., Grzesiak, S., 2014. Interspecific differences in root architecture among maize and triticale genotypes grown under drought, waterlogging and soil compaction. *Acta Physiol. Plant.* 36, 3249–3261. <https://doi.org/10.1007/s11738-014-1691-9>.
- Hakansson, I., Reeder, R.C., 1994. Subsoil compaction by vehicles with high axle load extent, persistence and crop response. *Soil Tillage Res.* 29, 277–304.
- Haling, R.E., Brown, L.K., Bengough, A.G., Young, I.M., Hallett, P.D., White, P.J., George, T.S., 2013. Root hairs improve root penetration, root-soil contact, and phosphorus acquisition in soils of different strength. *J. Exp. Bot.* 64, 3711–3721. <https://doi.org/10.1093/jxb/ert200>.
- Hamza, M.A., Anderson, W.K., 2005. Soil compaction in cropping systems. *Soil Tillage Res.* 82, 121–145. <https://doi.org/10.1016/j.still.2004.08.009>.
- Hartmann, C., Lesturgez, G., Sindhusen, P., Ratana-Anupap, S., Hallaire, V., Bruand, A., Poss, R., 2008a. Consequences of slotting on the pore characteristics of a sandy soil in northeast Thailand. *Soil Use Manag.* 24, 100–107. <https://doi.org/10.1111/j.1475-2743.2007.00138.x>.
- Hartmann, C., Poss, R., Noble, A.D., Jongskul, A., Bourdon, E., Brunet, D., Lesturgez, G., 2008b. Subsoil improvement in a tropical coarse textured soil: effect of deep-ripping and slotting. *Soil Tillage Res.* 99, 245–253. <https://doi.org/10.1016/j.still.2008.02.009>.
- Horn, R., Smucker, A., 2005. Structure formation and its consequences for gas and water transport in unsaturated arable and forest soils. *Soil Tillage Res.* 82, 5–14. <https://doi.org/10.1016/j.still.2005.01.002>.
- Horn, R., Domzal, H., Slowikha-Jurkiewicz, A., Van Ouwerkerk, C., 1995. Soil compaction processes and their effects on the structure of arable soils and the environment. *Soil Tillage Res.* 35, 23–36.
- Iijima, M., Griffith, B., Bengough, A.G., 2000. Sloughing of cap cells and carbon exudation from maize seedling roots in compacted sand. *New Phytol.* 145, 477–482. <https://doi.org/10.1046/j.1469-8137.2000.00595.x>.
- Iijima, M., Barlow, P.W., Bengough, A.G., 2003a. Root cap structure and cell production rates of maize (*Zea mays*) roots in compacted sand. *New Phytol.* 160, 127–134. <https://doi.org/10.1046/j.1469-8137.2003.00860.x>.
- Iijima, M., Higuchi, T., Barlow, P.W., Bengough, A.G., 2003b. Root cap removal increases root penetration resistance in maize (*Zea mays* L.). *J. Exp. Bot.* 54, 2105–2109. <https://doi.org/10.1093/jxb/erg226>.
- IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva. <https://doi.org/10.1017/CBO9781107415324>.
- Jayawardane, N.S., Chan, K.Y., 1994. The management of soil physical properties limiting crop production in Australian sodic soils—a review. *Aust. J. Soil Res.* 32, 13–44. <https://doi.org/10.1071/SR9940013>.
- Kautz, T., Perkons, U., Athmann, M., Pude, R., Köpke, U., 2013. Barley roots are not constrained to large-sized biopores in the subsoil of a deep Haplic Luvisol. *Biol. Fertil. Soils* 49, 959–963. <https://doi.org/10.1007/s00374-013-0783-9>.
- Keller, T., Colombi, T., Ruiz, S., Manalili, M.P., Rek, J., Stadelmann, V., Wunderli, H., Breitenstein, D., Reiser, R., Oberholzer, H., Schymanski, S., Romero-Ruiz, A., Linde, N., Weisskopf, P., Walter, A., Or, D., 2017. Long-term soil structure observatory for monitoring post-compaction evolution of soil structure. *Vadose Zone J.* 16. <https://doi.org/10.2136/vzj2016.11.0118>.
- Kirby, J.M., Bengough, A.G., 2002. Influence of soil strength on root growth: experiments and analysis using a critical-state model. *Eur. J. Soil Sci.* 53, 119–127. <https://doi.org/10.1046/j.1365-2389.2002.00429.x>.
- Kirchhof, G., Blackwell, J., Smart, R.E., 1991. Growth of vineyard roots into segmentally ameliorated acidic subsoils. *Plant Soil* 134, 121–126. <https://doi.org/10.1007/BF00010724>.
- Kristoffersen, A.Ø., Riley, H., 2005. Effects of soil compaction and moisture regime on the root and shoot growth and phosphorus uptake of barley plants growing on soils with varying phosphorus status. *Nutr. Cycl. Agroecosyst.* 72, 135–146. <https://doi.org/10.1007/s10705-005-0240-8>.
- Kuncoro, P.H., Koga, K., Satta, N., Muto, Y., 2014. A study on the effect of compaction on transport properties of soil gas and water I: relative gas diffusivity, air permeability, and saturated hydraulic conductivity. *Soil Tillage Res.* 143, 172–179. <https://doi.org/10.1016/j.still.2014.02.006>.
- Lesturgez, G., Poss, R., Hartmann, C., Bourdon, E., Noble, A., Development, L., 2004. Roots of *Stylosanthes hamata* create macropores in the compact layer of a sandy soil. *Plant Soil* 260, 101–109.
- Ligthart, T.N., Peek, G.J.C.W., 1997. Evolution of earthworm burrow systems after inoculation of lumbricid earthworms in a pasture in the Netherlands. *Soil Biol. Biochem.* 29, 453–462. [https://doi.org/10.1016/S0038-0717\(96\)00041-7](https://doi.org/10.1016/S0038-0717(96)00041-7).
- Lipiec, J., Hatano, R., 2003. Quantification of compaction effects on soil physical properties and crop growth. *Geoderma* 116, 107–136. [https://doi.org/10.1016/S0016-7061\(03\)00097-1](https://doi.org/10.1016/S0016-7061(03)00097-1).
- Lobet, G., Pagès, L., Draye, X., 2011. A novel image-analysis toolbox enabling quantitative analysis of root system architecture. *Plant Physiol.* 157, 29–39. <https://doi.org/10.1093/plphys/157.1.29>.

- 10.1104/pp.111.179895.
- Manzur, M.E., Grimoldi, A.A., Insausti, P., Striker, G.G., 2015. Radial oxygen loss and physical barriers in relation to root tissue age in species with different types of aerenchyma. *Funct. Plant Biol.* 42, 9–17. <https://doi.org/10.1071/FP14078>.
- Marashi, S.K., Mojjaddam, M., 2014. Adventitious root and aerenchyma development in wheat (*Triticum aestivum* L.) subjected to waterlogging. *Int. J. Biosci.* 6655, 168–173.
- Matechera, S.A., Alston, A.M., Kirby, J.M., Dexter, A.R., 1992. Influence of root diameter on the penetration of seminal roots into a compacted subsoil. *Plant Soil* 144, 297–303.
- Mori, Y., Fujihara, A., Yamagishi, K., 2014. Installing artificial macropores in degraded soils to enhance vertical infiltration and increase soil carbon content. *Prog. Earth Planet. Sci.* 1, 1–10. <https://doi.org/10.1186/s40645-014-0030-5>.
- Nishiuchi, S., Yamauchi, T., Takahashi, H., Kotula, L., Nakazono, M., 2012. Mechanisms for coping with submergence and waterlogging in rice. *Rice* 5, 1–14. <https://doi.org/10.1186/1939-8433-5-2>.
- Nosalewicz, A., Lipiec, J., 2014. The effect of compacted soil layers on vertical root distribution and water uptake by wheat. *Plant Soil* 375, 229–240. <https://doi.org/10.1007/s11104-013-1961-0>.
- Pang, J., Zhou, M., Mendham, N., Shabala, S., 2004. Growth and physiological responses of six barley genotypes to waterlogging and subsequent recovery. *Aust. J. Agric. Res.* 55, 895. <https://doi.org/10.1071/AR03097>.
- Pfeifer, J., Kirchgessner, N., Walter, A., 2014. Artificial pores attract barley roots and can reduce artifacts of pot experiments. *J. Plant Nutr. Soil Sci.* 177, 903–913. <https://doi.org/10.1002/jpln.201400142>.
- Reynolds, M., Langridge, P., 2016. Physiological breeding. *Curr. Opin. Plant Biol.* 31, 162–171. <https://doi.org/10.1016/j.pbi.2016.04.005>.
- Richard, G., Cousin, I., Sillon, J.F., Bruand, A., Guérif, J., 2001. Effect of compaction on soil porosity: consequences on hydraulic properties. *Eur. J. Soil Sci.* 52, 49–58. <https://doi.org/10.1046/j.1365-2389.2001.00357.x>.
- Romero, E., Della Vecchia, G., Jommi, C., 2011. An insight into the water retention properties of compacted clayey soils. *Geotechnique* 61, 313–328. <https://doi.org/10.1680/geot.2011.61.4.313>.
- Sauter, M., 2013. Root responses to flooding. *Curr. Opin. Plant Biol.* 16, 282–286. <https://doi.org/10.1016/j.pbi.2013.03.013>.
- Schäffer, B., Stauber, M., Mueller, T.L., Müller, R., Schulin, R., 2008. Soil and macro-pores under uniaxial compression. I. Mechanical stability of repacked soil and deformation of different types of macro-pores. *Geoderma* 146, 183–191. <https://doi.org/10.1016/j.geoderma.2008.05.019>.
- Schjøning, P., Akker, J., Keller, T., Greve, M., Lamandé, M., Simojoki, A., Stettler, M., Arvidsson, J., Breuning-Madsen, H., 2015. Driver-Pressure-State-Impact-Response (DPSIR) analysis and risk assessment for soil compaction – a European perspective. *Adv. Agron.* 133, 183–237.
- Shimamura, S., Mochizuki, T., Nada, Y., Fukuyama, M., 2003. Formation and function of secondary aerenchyma in hypocotyl, roots and nodules of soybean (*Glycine max*) under flooded conditions. *Plant Soil* 251, 351–359.
- Somasundaram, S., Bonkowski, M., Iijima, M., 2008. Functional role of mucilage - border cells: a complex facilitating protozoan effects on plant growth. *Plant Prod. Sci.* 11, 344–351. <https://doi.org/10.1626/pp.11.344>.
- Stewart, C.E., Follett, R.F., Pruessner, E.G., Varvel, G.E., Vogel, K.P., Mitchell, R.B., 2014. Nitrogen and harvest effects on soil properties under rainfed switchgrass and no-till corn over 9 years: implications for soil quality. *Gcb Bioenergy* 7, 288–301. <https://doi.org/10.1111/gcbb.12142>.
- Stirzaker, R.J., Passioura, J.B., Wilms, Y., 1996. Soil structure and plant growth: Impact of bulk density and biopores. *Plant Soil* 185, 151–162. <https://doi.org/10.1007/BF02257571>.
- Stolte, J., Tesfai, M., Keizer, J., 2016. Soil threats in Europe: status, methods, drivers and effects on ecosystem services. *JRC Tech. Rep. Soil Threat. Eur.* 206. <https://doi.org/10.2788/828742>.
- Striker, G.G., Insausti, P., Grimoldi, A.A., Vega, A.S., 2007. Trade-off between root porosity and mechanical strength in species with different types of aerenchyma. *Plant Cell Environ.* 30, 580–589. <https://doi.org/10.1111/j.1365-3040.2007.01639.x>.
- Tessier, S., Lachance, B., Laguë, C., Chen, Y., Chi, L., Bachand, D., 1997. Soil compaction reduction with a modified one-way disk. *Soil Tillage Res.* 42, 63–77. [https://doi.org/10.1016/S0167-1987\(96\)01090-2](https://doi.org/10.1016/S0167-1987(96)01090-2).
- Thomas, A., Guerreiro, S.M.C., Sodek, L., 2005. Aerenchyma formation and recovery from hypoxia of the flooded root system of nodulated soybean. *Ann. Bot.* 96, 1191–1198. <https://doi.org/10.1093/aob/mci272>.
- Thomson, C.J., Colmer, T.D., Watkin, E.L.J., Greenway, H., 1992. Tolerance of wheat (*Triticum aestivum* cvs. Gamanya and Kite) and triticale (*Triticosecale* cv. Muir) to waterlogging. *New Phytol.* 120, 335–344.
- Tracy, S.R., Black, C.R., Roberts, J.A., Mooney, S.J., 2011. Soil compaction: a review of past and present techniques for investigating effects on root growth. *J. Sci. Food Agric.* 91, 1528–1537. <https://doi.org/10.1002/jsfa.4424>.
- 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 Tillage Res.* 71, 151–161. [https://doi.org/10.1016/S0167-1987\(03\)00061-8](https://doi.org/10.1016/S0167-1987(03)00061-8).
- Valentine, T.A., Hallett, P.D., Binnie, K., Young, M.W., Squire, G.R., Hawes, C., Bengough, G.A., 2012. Soil strength and macropore volume limit root elongation rates in many UK agricultural soils. *Ann. Bot.* 110, 259–270. <https://doi.org/10.1093/aob/mcs118>.
- Vincent, C., Rowland, D., Na, C., Schaffer, B., 2017. A high-throughput method to quantify root hair area in digital images taken in situ. *Plant Soil* 412, 61–80. <https://doi.org/10.1007/s11104-016-3016-9>.
- Vogel, H.-J., Bartke, S., Daedlow, K., Helming, K., Kögel-Knabner, I., Lang, B., Rabot, E., Russell, D., Stöfel, B., Weller, U., Wiesmeier, M., Wollschläger, U., 2018. A systemic approach for modeling soil functions. *SOIL* 4, 83–92. <https://doi.org/10.5194/soil-4-83-2018>.
- Vollnes, A.V., Futsaether, C.M., Bengough, A.G., 2010. Quantifying rhizosphere particle movement around mutant maize roots using time-lapse imaging and particle image velocimetry. *Eur. J. Soil Sci.* 61, 926–939. <https://doi.org/10.1111/j.1365-2389.2010.01297.x>.
- Watkin, E.L., Thomson, C.J., Greenway, H., 1998. Root development and aerenchyma formation in two wheat cultivars and one triticale cultivar grown in stagnant agar and aerated nutrient solution. *Ann. Bot.* 81, 349–354.
- White, R., Kirkegaard, J., 2010. The distribution and abundance of wheat roots in a dense, structured subsoil: implications for water uptake. *Plant Cell Environ.* 33, 133–148. <https://doi.org/10.1111/j.1365-3040.2009.02059.x>.
- Xu, Q.T., Yang, L., Zhou, Z.Q., Mei, F.Z., Qu, L.H., Zhou, G.S., 2013. Process of aerenchyma formation and reactive oxygen species induced by waterlogging in wheat seminal roots. *Planta* 238, 969–982. <https://doi.org/10.1007/s00425-013-1947-4>.
- Yamauchi, T., Abe, F., Kawaguchi, K., Oyanagi, A., Nakazono, M., 2014. Adventitious roots of wheat seedlings that emerge in oxygen-deficient conditions have increased root diameters with highly developed lysigenous aerenchyma. *Plant Signal. Behav.* 9, e28506. <https://doi.org/10.4161/psb.28506>.
- Yamauchi, T., Colmer, T.D., Pedersen, O., Nakazono, M., 2018. Regulation of root traits for internal aeration and tolerance to soil waterlogging-flooding stress. *Plant Physiol.* 176, 1118–1130. <https://doi.org/10.1104/pp.17.01157>.
- Young, I.M., Montagu, K., Conroy, J., Bengough, A.G., 1997. Mechanical impedance of root growth directly reduces leaf elongation rates of cereals. *New Phytol.* 135, 613–619. <https://doi.org/10.1046/j.1469-8137.1997.00693.x>.
- Young, I.M., Blanchart, E., Chenu, C., Dangerfield, M., Fragosos, C., Grimaldi, M., Ingram, J., Monrozier, L.J., 1998. The interaction of soil biota and soil structure under global change. *Glob. Chang. Biol.* 4, 703–712. <https://doi.org/10.1046/j.1365-2486.1998.00194.x>.
- Zhu, J., Kaeppeler, S.M., Lynch, J.P., 2005a. Mapping of QTL controlling root hair length in maize (*Zea mays* L.) under phosphorus deficiency. *Plant Soil* 270, 299–310. <https://doi.org/10.1007/s11104-004-1697-y>.
- Zhu, J., Kaeppeler, S.M., Lynch, J.P., 2005b. Mapping of QTLs for lateral root branching and length in maize (*Zea mays* L.) under differential phosphorus supply. *Theor. Appl. Genet.* 111, 688–695. <https://doi.org/10.1007/s00122-005-2051-3>.