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Quo vadis, breeding for an efficient root system, in the era of climate change?

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Abstract: Despite all the complications that arise with root research, such as slow, laborious, and unclear genetics, roots are a promising object of interest for breeders because many root traits are compatible with high yield potential. It is a great challenge for further research that there is a wide demand for information on the "hidden half of plant metabolism" from many research fields. We have summarized the main obstacles in root system research and sketched a solution for breeding in field conditions so that the result was more meaningful to the farmer. (*i*) The most important challenge in root research is linking the functional identification of root system properties with the aboveground parts. (*ii*) Field breeding is irreplaceable, and methods allowing the evaluation of roots under field conditions are indispensable. (*iii*) Low heritability of root system trait discourages breeders. However, root properties show broad genotypic variability, allowing the efficient use of these traits as selection criteria. (*iv*) The root traits are variable, and many fluctuate under the influence of environmental factors, which complicates efforts to define ideotypes and explains the different conclusions obtained by researchers from different environments. The breeding programs targeting the root system are sporadic even in a global context. This is a great reserve for breeding progress in the era of climate change, water scarcity, a possible shift to extensive farming systems, and in the era of environmental programs.

Keywords: adaptive measures; carbon sequestration; drought; ideotype; phenotyping; regenerative agriculture

Drought or water limitation is major plant stress, where the plant response differs depending on multiple factors, including the duration, severity and last but not least the timing of occurrence of dry conditions (Jatayev et al. 2020). As water resources for agricultural purposes become more limiting, the development of drought-tolerant varieties also becomes increasingly important. Varieties with reduced water requirements could contribute to food security while improving the sustainability of agriculture.

The success of the Green Revolution in the 1960s and 1970s was mainly due to the incorporation of dwarf genes, which increased plant resistance to lodging and increased the harvest index by a substantial reduction in height, thereby increasing the production of grain rather than straw (Hedden 2003).

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For wheat and barley, the harvest index increased from 30 to 55% without a significant increase in biomass production, which would be accompanied by an increase in water demand (Cattivelli et al. 1994). Nevertheless, for the crops described above, two of the world's four most important cereals (maize, wheat), grain yield is expected to decrease 15–30% as a result of 2 °C warming forecast for 2040 (Zhao et al. 2017). Thus, it is not possible to quantify in advance the effects of new varieties on yield increase due to genotype-by-environment interactions, as plant responses to environmental conditions are often very complex (Chuchma et al. 2016; Lukasová et al. 2020). Because, when breeding for drought tolerance, which is manifested by yield, we are not able to clearly define which specific properties and processes cause such tolerance. This is called the "black box" system (Fischer 1981). Thus, the probability that a single property of a plant will have a sufficient effect to cause a statistically significant difference in grain yield is not very high. Besides, the benefits of new varieties could be limited unless their development is followed by the optimization of farming practices with respect to varietal specificity (Kirkegaard & Hunt 2010; Manschadi et al. 2013; Thorup-Kristensen & Kirkegaard 2016).

Together with water shortages, problems associated with a lack of efficiency in the use of nutrients exist. Dissolution and uptake, as well as the long-distance xylem transport of nutrients are restricted by water shortage (Cramer et al. 2009). In agricultural intensive regions, human activities have accelerated the rate and extent of eutrophication through both point-source discharges and non-point loadings of limiting nutrients, such as nitrogen (N) and phosphorus (P), with dramatic consequences for water sources (Chislock et al. 2013; Středová et al. 2024). On the other hand, in developing countries, there is a shortage of fertilizers, which limits production. The average global water efficiency (expressed as grain yield per unit of evapotranspiration over the growing season) of wheat is only 32–44% of the achievable efficiency and the great part of this problem due to a deficiency in nutrients and the non-optimal agricultural practices (Sadras & Angus 2006). The efficiency of nitrogen and phosphorus utilization does not exceed 50% of the applied amount in a certain crop (Raun & Johnson 1999; Tilman et al. 2002; Manschadi et al. 2013). Bingham et al. (2012) raised barley varieties bred from 1931 to 2005 and found that the potential yield for this period increased by 72% at a nitrogen dose of 110 kg N/ha but increased only by 40% if nitrogen was not used. It can therefore be assumed that the new varieties are able to use the supplied N more efficiently. The potential yield of major crops (maize, wheat, and rice) increased at 1.6%, 1.0% and 0.9% per year, respectively, which is less than the 2.4% per year rate required to double global production by 2050 (Ray et al. 2013). Even the yield slowed down during the last years in some parts of the world due to further increases in global temperature which continues to suppress yields, despite crops' adaptation efforts to extreme drought climates (Lukasová et al. 2014; Zhao et al. 2017). There is evidence that in the case of cereals, such growth begins to stagnate. Fischer and Edmeades (2010) also note that in the United Kingdom, the difference between the potential and actual yield of wheat is only 30%, which in their opinion offers little opportunity for further breeding progress. Besides, Lobell et al. (2009) reported much higher differences of approximately 20–80%, with the largest decrease observed in dry areas.

The lack of resources, issues with their effective use, yield fluctuations, yield insecurity, low crop yield increases despite breeders' efforts, and the increased risk of abiotic stress have all motivated a search for alternative ways to continue improving plant productivity. One possibility in this respect, which has been known for decades but still neglected due to the absence of appropriate methods, is breeding for properties related to plant root systems. The root system is an important part of a plant affecting its adaptation to different environmental conditions (Lynch 2007; Lynch et al. 2014), especially drought (Lopes & Reynolds 2010; Vadez 2014), and its resource efficiency (Kell 2011). However, there is still no consensus in the scientific community regarding whether the bigger root system always has beneficial impact (Palta et al. 2011). For example, if drought does not occur, then the development of a larger root system was an unnecessary investment for the plant at the expense of other photosynthetic products. Root is a sink organ, and thus high resource allocation to the root system may become disadvantageous under optimal growing conditions.

Plant roots fulfil a wide range of functions – water and nutrient uptake, synthesis of hormonal substances, facilitation of interaction with soil microorganisms, the ability to detect stress and adapt to it, the storage of compounds, etc. All functions performed by the root system interact with the aboveground part of the plant. Therefore, the root system should always be viewed in the context of plant integrity (Comas et al. 2013) and the environment in which it grows, a factor often overlooked. Furthermore, different combinations of root system characteristics can be successful in diverse environments (Schroth 1995; Ryser 2006; Comas et al. 2012).

Plant production is dependent on maintaining transpiration during water shortages. All other criteria are always secondary in terms of production (Blum 2011; Chaves et al. 2011). As the soil dries or transpiration demand increases, transpiration is increasingly determined by the capacity of root systems (Ober et al. 2021). Under the climate conditions of Central Europe (supply driven), water intake can be optimized in three ways: (*i*) rapid root penetration, which is particularly important when early spring droughts occur, (*ii*) high maximum root system depth if water is available, or (*iii*) increased root density (Bodner et al. 2015). In the future, we can expect a more frequent onset of terminal drought at the end of the cereal vegetative period in the temperate zone, especially in soils with low water retention capacity (Středa et al. 2019; Mrekaj et al. 2024). Therefore, the moisture in deeper layers of soil and the roots that are able to use it will gain more importance (Gregory et al. 1978; Kirkegaard et al. 2007; Lynch & Wojciechowski 2015). Thus, the adverse effects of drought can also be mitigated by building a deep root system before drought occurs (Blum & Jordan 1985; O´Toole & Bland 1987; Manschadi et al. 2006). The locations where such drought occurs depend upon the earliness of genotypes. Their productivity can be supported by a higher vitality of the root system in the early stages of vegetative growth (Palta & Fillery 1995).

The varied range of interactions of the root system with the environment makes it impossible to easily describe its traits. The results of studies depend on the soil conditions, climatic conditions of the area, meteorological conditions during the growing season, severity of stress and used variety. Pot experiments are a special case, as their results cannot always be successfully verified under field conditions. The key root traits that contribute to yield under adverse conditions are still being studied.

VOSviewer software (van Eck & Waltman 2010) was used to perform the bibliometric analysis of the research field. This helps to identify the main directions of research in the scientific field. We set the following search strings via the advanced search method of Web of Science Core Collection: "root traits" AND breeding (Title) OR "root traits" AND breeding (Author Keywords) OR "root traits" AND breeding (Abstract). The search was conducted in May 2024. Based on these criteria, 549 records were obtained. The 549 publications were imported into the VOSviewer, and the results are shown in Figure 1. The most frequent words from the titles and abstract

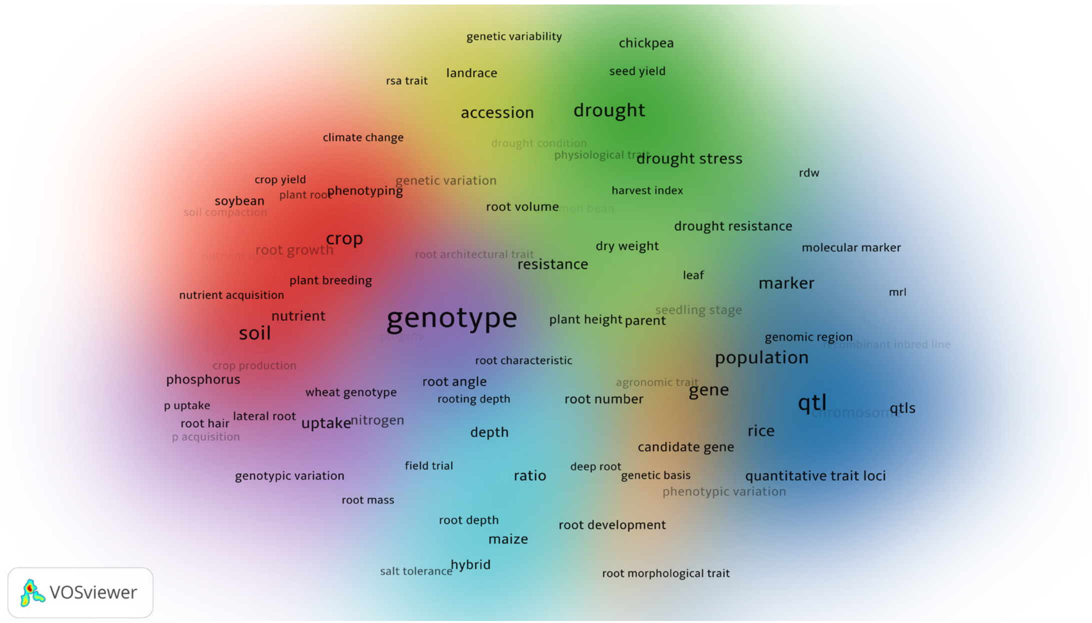

Figure 1. Bibliometric map generated by VOSViewer based on Web of Science Core Collection; seven clusters with the essential areas of the problem have been identified on the base of used titles and abstracts of articles

were mainly: root trait, genotype, quantitative trait locus (QTL), population, yield, root system, drought, environment, root length, marker, uptake, drought tolerance, root system architecture, and others. These findings contributed to the direction of this review.

ROOT SYSTEM TRAITS USEFUL IN BREEDING

It is important to begin by defining key root system traits which are then related to functional significance and to methods of determination. These traits and methods of determination (e.g. root system branching, root production, root growth rate, mycorrhizal infection, vertical distribution – rooting depth, horizontal distribution, root activity etc.) as well as physiological parameters associated with root systems and their significance and estimation are described by Atkinson (2000).

The anatomical characteristics of the root system are mainly related to the properties of tissues, dimensions of conductive elements, and presence of specialized structures. Morphological characteristics include root length, area, volume, weight, diameter, and root system depth. These values are often reported as indexes and related to a unit of soil volume where they are located or to a unit of root weight: root length density (RLD; cm/cm^3), root weight density (RWD; g/cm^3), specific root length (SRL; cm/g), specific root area (SRA; cm^2/g), root surface density (RSD; cm^2/cm^3).

The characteristics of root system architecture include a complex of traits (branching angle, number of primary roots, the distance between lateral roots, etc.) that form a qualitative description of the root system. Soil properties and availability of resources significantly influence the architecture of the plant root system. Besides, root system architecture plays an important role in exploiting unevenly distributed soil resources such as water and nutrients, which in turn determines plant productivity (Paez-Garcia et al. 2015). This can be significant in the case of competition for resources in natural, the same as agricultural canopies (Hodge et al. 1999).

Growth rate characteristics mainly relate to the root elongation rate in response to resources (reaction to the presence of water, phosphorus or nitrogen) or abiotic environmental stressors (drought, soil compaction, soil temperature, exposure to toxic elements, pH, etc.) (McMichael & Burke 1998). Water and nutrient uptake characteristics are the least explored properties of root systems, especially under field conditions (ion uptake rate, radial and axial hydraulic conductivity).

To identify relevant traits of the root system regarding the effective use of depth water and increased yield in critical drought conditions, it is necessary to delimit and define the target ecosystem or environment where the variety will be grown. In addition to climatic conditions, as described above, the soil retention ability and depth of the soil profile also play important roles, although they mainly affect the intensity of root penetration, root system architecture and maximum root depth. Javaux et al. (2008) proposed considering soil conductivity and the water retention capacity of the soil when defining desirable root system properties (hydraulic conductivity, architecture).

Root length density (RLD)

The RLD is an important parameter in explaining crop growth and in evaluating advantages of root strength in water and nutrient uptake and consequently, define a plant's ability to withstand water stress (Faye et al. 2019). In this sense, the high RLD values increase the number of root-soil contact points. Thus, the importance of increasing root and soil contact through greater root length density is that it allows plants to access greater quantity of soil in water-limited environments (Mateva et al. 2020). Under sufficient soil moisture, plant transpiration demands are already met at low RLD levels of 0.5 to 1.0 cm/cm^3 of soil (Willigen et al. 2000). Zhang et al. (2020) confirmed that a root length density of at least 1 cm/cm^3 is needed to drain all the available water in the soil. For example, in surface layers where the RLD was far greater than 1 cm/cm^3 water uptake was independent of rooting density due to competition for water. However, in deeper layers where RLD was less than 1 cm/cm^3, water uptake by roots was proportional to root density. Besides, Barraclough (1989) considers this density to be sufficient even under desiccating soil conditions. Nevertheless, Bodner et al. (2015) suggested that in desiccated soil, a high RLD is required to overcome soil resistance to water conduction. For field crops, the values of RLD are significantly higher, especially for the upper part of the soil (0–40 cm). Dal Cortivo et al. (2018) in their study reported values of approximately 7–10 cm/cm^3 in a field trial with common wheat. This was confirmed in previous multi-year experiments from agroecologically different conditions

(Figure 2). RLD values corresponding to 2–10 cm/cm^3 at 0–30 cm soil depth (depending on conditions) for spring barley and maize. RLD varies not only with depth below the soil surface, but is significantly influenced by genotype, meteorological conditions of the year and soil conditions, and their interactions. The amount of root biomass was significantly affected by year (by up to 43.5%), locality (by up to 19.5%) and their mutual interaction. The influence of the genotype increased with the increasing depth of the measurement and amounted to a maximum of 10.2% (Klimešová & Středa 2013; Hajzler et al. 2018; Němec et al. 2019). In spring barley, the highest percentage of the total observed variation of root system size was explained by the location (42–88%), followed by the variety (3–16%) and by unexplained variation (2–8%) in experiment of Chloupek et al. (2010).

In the field studies, RLD decreases exponentially with depth (Fan et al. 2016; Xu et al. 2016), which contrasts to many laboratory experiments with repacked soils (Jin et al. 2015; Gao et al. 2016), where there is relatively high root density at depth and a less noticeable exponential decrease of root length density with depth. Besides a high RLD in the upper soil layer often reflects the presence of mineral nutrients, precipitation or irrigation water (Sánchez-Blanco et al. 2014). However, in the case of heterogeneous soil conditions or a non-standard soil moisture regime, the RLD may be higher in a deeper soil layer than in a shallower layer. For instance, the root length density may change substantially, especially if a compacted layer limits the maximum depth in the profile through which roots can penetrate. Shallower roots may limit crop yield if sufficient water and nutrients are not available within the smaller volume of soil explored by the roots (Freschet et al. 2021). Shallow roots are beneficial for capturing small but rapid rainfalls in the upper soil layer (see below for details). The benefit of a higher RLD depends also on the depth of the soil. For example, the statisti-

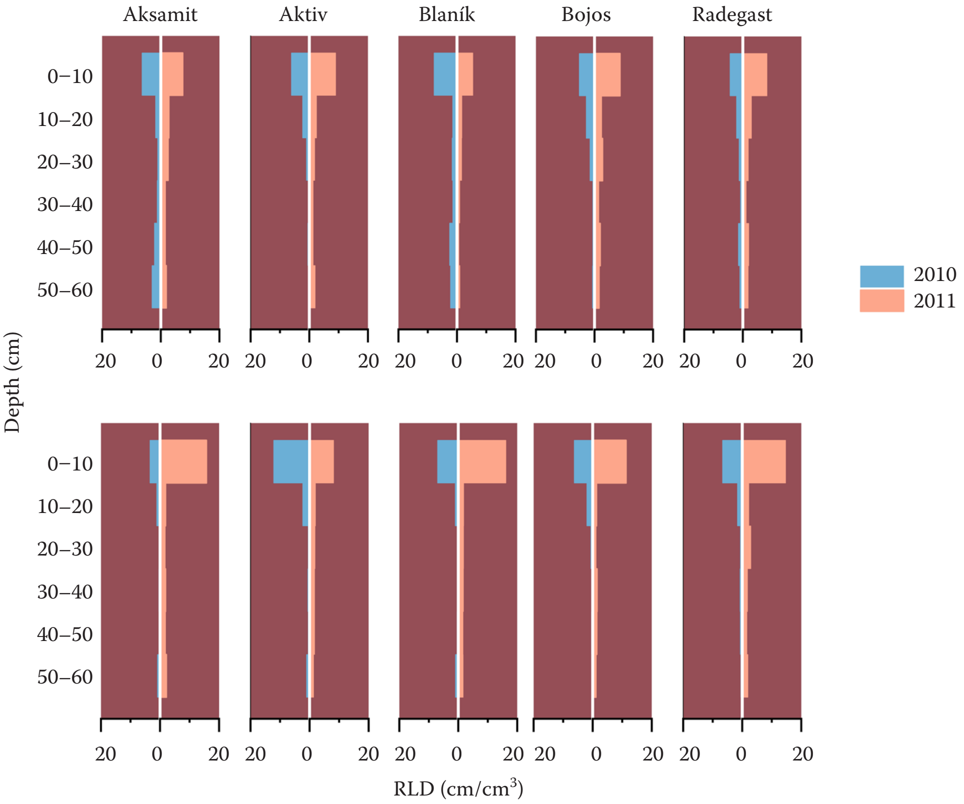

Figure 2. Root length density (RLD; cm/cm^3) of five varieties of spring barley at different depths below the soil surface; experimental site Hrubčice (upper part of the figure) with optimal soil conditions for spring barley growing (average value of RLD 2.50, 3.63 cm/cm^3 at 0–30 cm soil depth); experimental site Želešice (lower part of the figure) with reduced tillage and less favourable physical soil properties (average value of RLD 2.74, 4.36 cm/cm^3 at 0–30 cm soil depth); year 2010 (average value of RLD 2.02, 3.11 cm/cm^3 at 0–30 cm soil depth) with very wet growing season, year 2011 (average value of RLD 3.22, 4.88 cm/cm^3 at 0–30 cm soil depth) with normal precipitation totals during the growing season

cal analysis of root length distribution presented by Zhang et al. (2020) indicated limited genotypic differences between the wheat lines. The numerical analysis of water uptake showed that in the surface densely rooted layer (RLD > 1 cm/cm^3) there was only a weak relationship between water uptake and root length density while at deeper layer (RLD < 1 cm/cm^3) the water uptake was proportional to root length density. Ramamoorthy et al. (2017) suggested that increased RLD and rooting depth are often considered to be primal drivers of the effective adaptation to drought. A functional adaptation to drought is then an increase in RLD especially in deeper soil layers, while maintaining the same weight of the whole root system (Blum 2011). However, Leitner et al. (2014) found that independently evaluated maize RLD is not sufficient to model water uptake from the soil. Significant positive effects of RLD on wheat yield (Wang et al. 2014; Peng et al. 2019) and rice yield (Manickavelu et al. 2006) have been found. In experiments with various rice lines under arid conditions, the RLD positively correlated with biomass yield in some genotypes (Kijoji et al. 2014). Nevertheless, the effect of RLD on yield is not always positive. Selection for higher yields contributed to the generation of genotypes with smaller roots in some regions. The yield of 44 wheat genotypes cultivated by the International Maize and Wheat Improvement Center (CIMMYT) over 45 years increased by 50.4 kg/ha/year, whereas the RLD values did not significantly change (Manske 1997). Tardieu et al. (1992) note that higher RLD values in the upper soil layers can lead to the unnecessary investment of assimilates without a proportional increase in yield. A higher RLD could also mean a faster depletion of water resources if precipitation is not expected during the growing season (Palta et al. 2011). Yu et al. (2007) found in experiments with maize that the highest water consumption occurred in the layer of soil with the highest root density. If this layer became desiccated, the roots at deeper levels would not be able to fully compensate this deficiency. Thus, the significance of a large root system lies more in its precise distribution in soil layers where water is available than in the total weight or volume of root biomass (Barraclough 1984; Manske & Vlek 2002; Lopes & Reynolds 2011).

The effect of the RLD on nutrient uptake depends on the mobility of ions in the soil (Atkinson 1990). Hence, root length density is important, especially for the uptake of relatively immobile ions of elements such as phosphorus (Slafer et al. 2021). Effective P uptake requires RLD values of 2–5 cm/cm^3 (Barker et al. 2005). Although the specific properties of each nutrient in the soil impose different RLD requirements for effective uptake. For example, due to the low mobility of phosphorus in the soil, a higher RLD of ca. 10 cm/cm^3 is required for effective P uptake compared to water and/or nitrogen (López-Bucio et al. 2002). Besides in previous experiments conducted by Manske et al. (1995, 2000), they showed that wheat had a positive relationship between RLD and P uptake in phosphorus-poor soils. Genotypic variability in P uptake for rice was also found to be dependent on the overall size (weight) of the root system and its absorption mechanisms (Wissuwa & Ae 2001).

The importance of the properties of the root system in terms of nitrogen uptake increases with a lack of water, as even relatively mobile ions are dependent on the presence of water in the soil, as described above. For typical nitrate concentrations, any RLD value is usually more than sufficient to allow maximum uptake rates (Robinson & Rorison 1983), but specific values become more important regarding the uptake of the less mobile ammonium ion (Hoad et al. 2001). In this sense, several studies indicated that greater root length densities are generally more effective in N acquisition (Svoboda & Haberle 2006; Carvalho & Foulkes 2018). Moreover, a previous study conducted by Aziz et al. (2017) showed the results of a comparison of N uptake among nine Australian wheat varieties bred between 1958 and 2007 where they observed an increase in the capacity for N uptake per unit of root length as well as a decrease in the RLD and total root system length. Besides genotypic differences in N uptake per unit of root length have been found (Greef & Kullmann 1992). As well as evidence of genotypic differences in the activity of phosphatase, which breaks down poorly accessible organic P and is bound to the surface of wheat roots (McLachlan 1980).

In addition, Manske and Vlek (2002) demonstrated the complexity of the RLD issue. Drought tolerant semi-dwarf wheat varieties formed more roots in deeper layers than in more shallow layers, and the higher RLD in the upper layers was negatively correlated with grain yield ($r = -0.7$). However, grain yield was not significantly associated with the RLD in deeper layers, as some varieties, along with high RLD values, showed low yield potential. Therefore, breeding for improved drought tolerance should consider both a high yield potential and a more efficient root system.

Rooting depth

With increasing rooting depth, the potentially available water volume increases (Gregory 2006). A deep root system with few lateral roots in the upper layer is most effective in receiving water from relatively deep soil layers (Hund et al. 2009). Campos et al. (2004) assessed water acquisition through the root systems of old and modern varieties of corn. The old varieties showed high water consumption mainly from the upper parts of the soil profile. In particular, the depletion of water reserves in the soil before the beginning of flowering was the reason for the significant decrease in the yield of older varieties in comparison to that observed in modern hybrids. The growth phase during which water scarcity occurs is also important for yield formation. Grieder et al. (2014) found no correlation between corn root system properties in the vegetative stage of growth and grain yield. In general, the periods of flowering and grain filling at the end of the growing season are considered to be critical (Palta & Yang 2014). Using a crop model, it was found that a deep root system at this stage was correlated with a high yield (Hammer et al. 2009).

Rooting depth can be directly related to drought adaptation (Friedli et al. 2019) only in soils of sufficient depth. Hund et al. (2009) showed that a drought-tolerant maize inbred line rooted deeper and took up more water from deeper soil layers compared to an old inbred line with shallow rooting. Besides deeper rooting of spring wheat was related to improved stay green effect due to the acquisition of deep soil water in Australia (Christopher et al. 2008). Thus, a deeper root system and the use of water in the subsoil can only be successful in areas where soil properties do not limit the expression of these traits. In moist soil, water is first removed from shallow layers by the roots. Doussan et al. (2006) found that water intake begins in the basal part of the plant and extends to its distal parts. Thus, the root system is not constantly involved in water intake as a whole. As the soil dries in the upper layers, the water potential of the roots becomes more negative, and the main water intake shifts to the deeper layers (Li et al. 2002). Thus, a deeper root system is often associated with drought tolerance (Passioura 1983; Manschadi et al. 2006; Kirkegaard et al. 2007). There is also a correlation between the depth of the root system and the availability of nutrients. A shallow root system is believed to be a positive adaptation to the low availability of phosphorus. Miguel et al. (2015) evaluated the importance of a shallow root system and dense root hairs in P uptake by beans. They found a positive synergistic effect of both those traits on P uptake, in contrast to what was observed in deep-rooted, short-root-hair genotypes.

It should be noted that the rooting depth is a function of both genotype (G) and environment (E), however, the interaction among them makes it difficult to separate genotypic differences from the environmental factors in the root architecture, due to high G × E interactions and plasticity of roots (Ehdaie et al. 2012). Phenotypic plasticity is the ability of an organism to alter its phenotype in response to the environment and may involve changes in physiology, morphology, anatomy, development, or resource allocation, as, for example, in the case of phosphorus stress – plants with many nodal roots with a steep angle, many short lateral branches, root exudation, root cortical aerenchyma formation, and long, dense root hairs (Sultan 2000; Schneider & Lynch 2020).

The influence of G × E interactions on the morphological traits of plant roots is confirmed by Figure 3. In different agroecological conditions of two environments and in two meteorologically different years, the root system of five varieties of spring barley was evaluated (for a detailed description of the experiment see Figure 2 and Klimešová and Středa (2013), for a detail description of agroecological conditions see Středa et al. (2012); Svačina et al. (2014); Vintrlíková and Středa (2014)). The environment (year, locality) significantly influenced the root surface, and the influence of the genotype was thus significantly reduced.

Blum (2005) considers genotypes with deep roots as unusable if the roots are not produced before the onset of drought due to a significant reduction of new roots during prolonged drought (Gregory et al. 1978; Gavloski et al. 1992; Muller et al. 2011). Babé et al. (2012) reported that lateral roots are more affected by drought than primary roots. Thus, the root system reduces carbon investment in the side roots and accumulates it in the primary roots in order to create a "steep, cheap and deep" root system (Lynch 2013). Maize plants reduce metabolic and carbon costs when creating a deeper root system. Drought-tolerant hybrids are characterized by a deep root system with a high proportion of aerenchyma (Chimungu et al. 2014; de Souza et al. 2016). However, the benefits of this strategy are not universal. The final root depth depends not only on the elongation rate but also on the duration of growth. For example, in cereals, root growth typically ceases after flowering (Lucas et al. 2000). The aboveground part of the plant also affects the depth of the root system by determining the time available for roots grow (Gregory 1989). Manipulation with the sowing term and photoperiod sensitivity in order to increase root depth in Australia was described by Richards (2006).

Rapid resumption of root growth following soil rewetting may improve plant productivity under episodic drought (Comas et al. 2013). Consequently, another prerequisite for the advantage of a deep root system is that the water actually occurs at great depth. Ordóñez et al. (2018) found that the maximum rooting depth in soybean grown across 10 site-sowing date combinations varied from 88 to 154 cm and was closely related to the depth of the water table near the time when root growth ceased. Likewise, Kirkegaard et al. (2007) observed an increase in grain yield of 0.62 t/ha if wheat stands could receive 10.5 mm of soil moisture from the subsoil (1.35–1.85 m) at the time of grain filling.

Effectiveness of the assimilates spent on formation of deeper roots and the transpiration to create additional carbon is important (Bidinger & Witcombe 1989). For example, if the crop achieves higher yields and therefore needs more water, the additional intake of 30 mm from deeper layers at a predicted yield of 6 t/ha of wheat grain is only 10% of the total required. Therefore, deep rooting has value in those cases in which the extra water from depth represents a large portion of the entire crop water need (Vadez 2014). This means that a deeper root system will not have such a benefit for highly productive stands.

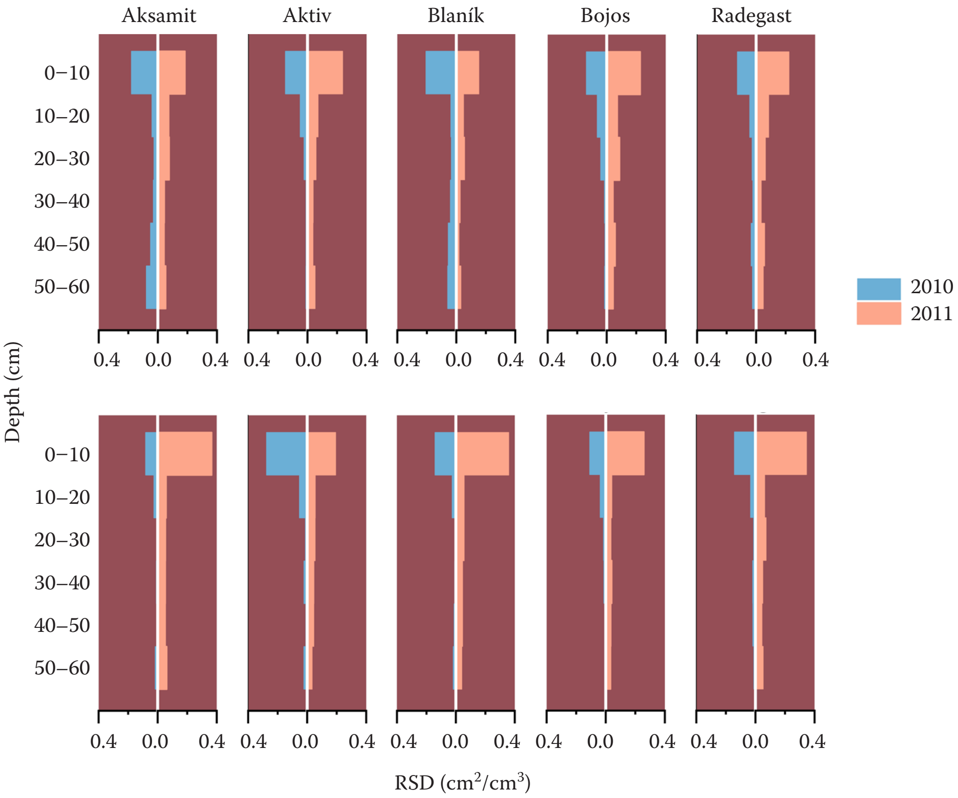

Figure 3. Root surface density (RSD; cm^2/cm^3) of five varieties of spring barley at different depths below the soil surface; experimental site Hrubčice (upper part of the figure) with optimal soil conditions for growing spring barley (average value of RSD 0.067, 0.097 cm^2/cm^3 at 0–30 cm soil depth); experimental site Želešice (lower part of the figure) with reduced tillage and less favourable physical properties of the soil (average value of RSD 0.066, 0.102 cm^2/cm^3 at 0–30 cm soil depth); year 2010 (average value of RSD 0.048, 0.073 cm^2/cm^3 at 0–30 cm soil depth) with very wet growing season; year 2011 (average value of RSD 0.085, 0.127 cm^2/cm^3 at 0–30 cm soil depth) with normal precipitation totals during the growing season

Likewise, a deep or large root system will not have an effect under moderate stress conditions or irrigation. Besides, El-Hassouni et al. (2018) observed the yield advantage of shallow root systems for 25 wheat genotypes in environments with irrigation. The results of Cope et al. (2024) show that modern Swedish cultivars of winter wheat pose root system architecture differences that could potentially increase yield stability in different environments and under different farm practices.

Hence, it can be concluded that selecting and breeding for root system architecture is a cost-effective strategy to increase crop productivity and adaptation.

Hydraulic conductivity

Plant hydraulic conductivity refers to the ratio of water flow (kg/s) per unit pressure drop (MPa), which drives flow through the plant or plant organ systems (Li et al. 2018). Thus, hydraulic conductivity reflects the water conveyance speed of plant organs having dependability on factors related to aquifer properties such as soil particle size, shape, degree of compaction, soil particles size distribution and fluid flow properties like viscosity and specific weight (Kango et al. 2019).

The availability of water at a great depth by itself may not be sufficient to satisfy plant requirements under hot and dry conditions (Sun et al. 2011). Consequently, other mechanisms could affect water management, especially under high temperatures and vapour pressure deficit (Yang et al. 2012), such as the hydraulic conductivity of the roots.

Vadez (2014) consider the hydraulic conductivity of roots to be a key mechanism controlling the water regime of a plant and related processes, such as leaf formation and stomata control mechanisms. Leaf hydraulic conductance (resistance) is decisive for plant hydraulics, especially under drought, when stomatal closure strongly restrict transpiration (Locke & Ort 2014). The hydraulic conductivity of the root system is affected by evapotranspiration demands, the properties of aboveground biomass, the soil moisture regime and root anatomical parameters.

The soil's ability to conduct and retain water defines the requirements for the hydraulic conductivity of roots (Javaux et al. 2008). The conductivity of wet soil is typically much greater than that of the roots (Draye et al. 2010). As the soil dries its conductivity rapidly declines. At the same time, soil drying causes a reduction in the radial conductivity of roots for water due to lignification and suberization (North & Nobel 1991; Kramer & Boyer 1995; Hose et al. 2001) as a defence against the negative effects of drought (Cruz et al. 1992). In this situation, the root-soil boundary layer is increasingly important for water flow (Blum 2011). The properties of the boundary layer can be modified by the root exudates and mucus, facilitating root contact with the soil and water uptake (White & Kirkegaard 2010).

The conductivity of the root system is influenced by the state of the aboveground part of the plant in relation to the microclimate and time of day (Thomas et al. 2020). Conductivity is highest during the night and early morning when plant water demand is low (Tardieu et al. 2017). In contrast, root resistance to water flow is highest during the afternoon, when plants have the highest water requirements, and thus limits evapotranspiration (Tardieu & Parent 2017) and stabilizes the transpiration level if evapotranspiration demands of the environment fluctuate (Vandeleur et al. 2014). In addition, it should be noted that soil hydraulic conductivity is large in a wet soil, and most of the belowground resistance comes from roots. As the soil becomes drier, hydraulic conductivity decreases and the soil contributes more to the total resistance (Bonan 2019). The short-term effects of stress stimulate the plant to reduce the conductivity of roots, which is also ascribed to water channels (aquaporins) (Maurel et al. 2010; Verdoucq & Maurel 2018). Aquaporins are known as significant contributors and regulators of transcellular water transport in roots (Javot & Maurel 2002). If water flow through the apoplast is prevented by suberization of cell walls, aquaporins facilitate the fine regulation of water flow (Steudle 1997; Parent et al. 2009). Thus, the plant can direct the hydraulic conductivity during acclimatization to adverse environmental conditions (Lipiec et al. 2013).

Leitner et al. (2014) modelled the growth of three maize phenotypes in the soil environment. An increase in the radial conductivity of lateral roots had a greater impact on overall transpiration than different architectures of the root systems. For plants with comparable root system depths, the overall conductivity of the root system is a key parameter affecting the dynamics of transpiration. Hydraulic conductivity is also influenced by the size and number of xylem vessels, which is described as hydraulic acclimation (Liu et al. 2020). Hamblin and Tennant (1987) found that a greater number of metaxylem vessels cause greater uptake of water by lupine than by cereals. Plants with a large xylem diameter may show better conductivity but greater water consump-

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tion and risk of cavitation than plants with narrow vessels (Richards & Passioura 1989; Tyree et al. 1994). The small xylem vessel size of wheat seminal roots increases hydraulic resistance and results in low water consumption from the soil by plants. Due to the lower intensity of water consumption, water keep maintained in the soil until the end of growing season, when plants use is for grain formation. This trait of the root system was used in the 1980s as a selection criterion for breeding drought-tolerant wheat varieties in the arid climate of Australia (Richards & Passioura 1989).

Too high values of root system conductivity can be counterproductive if crop productivity is fully dependent on the amount of water retained in the soil. Such a root system rapidly absorbs water, so water is soon depleted, and severe stress afflicts, for example the reproductive phase (Tardieu & Parent 2017). Waines and Ehdaie (2007) report that modern wheat varieties have a smaller root system, representing approximately two-thirds of the biomass, compared to regional varieties from which they originated. This is a result of breeding for high yield and growth under optimal water and nutrient conditions. An experiment with old and modern semi-dwarf wheat varieties revealed that however they had a higher RLD, they did not show higher water consumption, indicating increased root hydraulic conductivity in modern varieties (Siddique et al. 1990).

Fineness of the root system

The optimal resources distribution strategy is limited by appropriate biomass allocation and growth control of various plant parts and also by morphological properties. Among the list of root system properties, specific root length (SRL; understood as the ratio of root length to dry mass of fine roots) is a key element of plant plasticity (Fitter & Hay 2002) and determines water and nutrient uptake as a large root-absorptive area allows more rapid resource uptake (Weemstra et al. 2020).

Plants can compensate a water shortage by increasing contact between roots and the soil by creating a dense network of fine roots (Ewers et al. 2000) or by increasing their conductivity (McElrone et al. 2007). Tight contact between root and soil is mediated by root hairs (Figure 4). Their purpose is to increase the effective diameter of the roots, thereby increasing the volume of soil occupied by the roots with relatively low assimilation requirements. Given by this fine structures, the isolation of intact living root systems from the soil in the field has not yet been performed and appears to be impossible. This fact complicates research progress in this field. Currently developed non-destructive root phenotyping techniques under field conditions (Gu et al. 2024) are needed in this regard.

Root hairs can grow into very small pores smaller than 5 µm and, due to mucilage secretion, form connections between the roots and soil (Driouich et al. 2013). Without this connection, the intake of water and nutrients would be reduced (Banerjee et al. 2019). Nobel et al. (2009) reported that roots without hairs receive only 1–5% of the volume of water compared to roots with hairs. Likewise, Wasson et al. (2012), Carminati et al. (2017), and Ahmed et al. (2018)

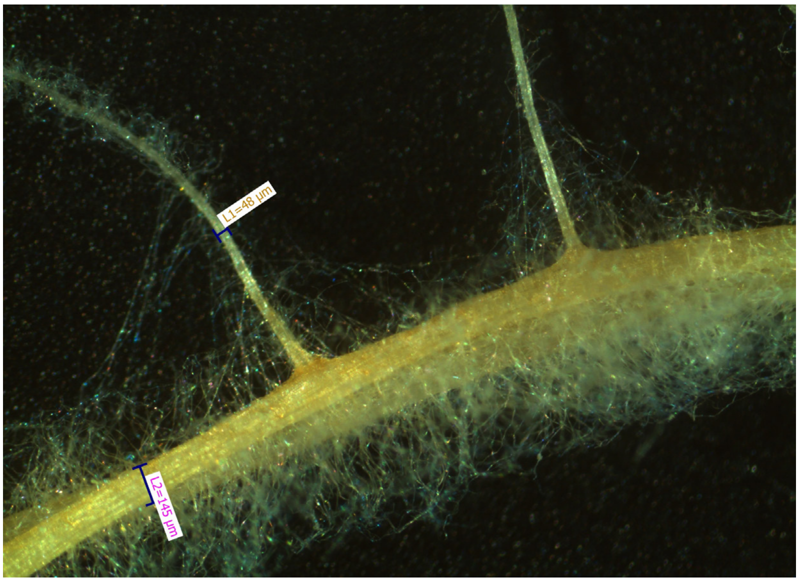

Figure 4. Dense root hairs increase the root absorption surface and improve root contact with the soil (primary root of wheat); the isolation of root hairs from the soil appears to be impossible

confirmed the important role of root hairs in water uptake in desiccating soil.

On the other hand, fine roots with high values of length per unit of root weight (SRL), together with high RLD values in layers with available moisture, increase productivity under drought (Comas et al. 2013). While a higher SRL increases the biomass of roots and makes resources available at no extra cost to build larger structures (Corneo et al. 2017).

High SRL values may also be associated with nutrient intake. Thinner and shallower roots are associated with increased N uptake efficiency in wheat (Liu et al. 2022). Root hairs significantly contribute to the uptake of nutrients that move slowly through the soil (e.g., phosphates), and plants obtain them by diffusion (Sehgal et al. 2021). For instance, phosphorus mainly enters the roots as $H_2PO_4^-$ through the soil solution (Sehgal et al. 2021) and impacts root length and root hairs (Singh & Singh 2016). In addition, it has been documented that the plants also induce more root hairs under low P soils, and the trait is directly related to the increased P uptake (Vandamme et al. 2013). Moreover, low P stress-induced modifications of SRL, such as inhibition of primary root growth, proliferation lateral roots, and root hairs, were seen in many plants (Lambers et al. 2011; Jin et al. 2012). Thus, these modifications are helpful for topsoil foraging under low P-stress condition (Ceasar et al. 2020). Fine roots are particularly beneficial in nutrient-poor environments (Bonifas & Lindquist 2009) because they allow rapid root extension and provide the maximal root surface area for nutrient uptake (Bowsher et al. 2016). The length of root hairs significantly correlated with P uptake by barley in phosphorus-poor soils (Gahoonia & Nielsen 2004) and also by soybean (Vandamme et al. 2013). In terms of competition, plants with fast root proliferation obtain the most nutrients (Craine & Dybzinski 2013). This morphological adaptation, in response to the local availability of water or competition between plants, is a process that can take days but also several months (Doussan et al. 2003).

In contrast, some cruciferous plants form short, thick roots without root hairs under dry conditions (Farooq et al. 2009). In a field trial with mustard (Brassicaceae), the lowest SRL values were found in the upper soil layer (0–10 cm) in a dry environment compared to wet environment (Hajzler et al. 2018). However, a large root diameter in a dry soil layer does not conflict with the presence of fine roots in a wetter soil layer. A large root diameter is also related to the ability to penetrate compacted soil and overcome the mechanical resistance of the soil during desiccation. For rice, these traits have been associated with the ability to avoid drought (Gregory 2006; Hazman & Brown 2018). Moreover, Elazab et al. (2016) in durum wheat observed increased SRL in the upper soil layer under good moisture conditions.

Branching angle

Root architecture is a crucial part of plant adaptation to heterogeneous soil conditions and is mainly controlled by root branching (Orosa-Puente et al. 2018). Fitter (2002) denoted that the architecture of the plant root system shows regularity and predictability. However, it is highly variable in response to environmental conditions (de Moraes et al. 2018). Moreover, Fitter et al. (1991) defined two basic topological models – the dichotomous model and the fish skeleton model – but the root architecture of most plants is intermediate between these two extremes.

Uneven distribution and local exhaustibility, or plant competition, causes asymmetry in the root system, including a change in branching angle. Root systems with narrow branching angles and a high number of seminal roots may be more effective than other root systems in terms of the uptake of water from the subsoil (Leitner et al. 2014). Leitner et al. (2014), using a model, simulated root growth in three maize phenotypes that differed in their root system branching angle. The highest transpiration was found in plants with a root axe orientation corresponding to available water in the soil. Furthermore, some authors affirmed that root angle is important in determining the vertical distribution of roots, as demonstrated by Kato et al. (2006) and further by Ramalingam et al. (2017). Thus, the proportion of roots with a steep angle (i.e., 45–90 degrees from the horizontal) was associated with deep roots (> 30 cm soil layer).

Recent studies with rice have shown genotypic variation in root angle or deep-root ratio under aerobic conditions (Kato et al. 2013) or upland conditions (Kitomi et al. 2015); thus, it is feasible to develop rice varieties with deeper root systems for aerobic conditions with reduced irrigation requirements. Thus, the importance of steep-angle roots with larger deep root ratio has been found by in water limiting conditions. Consequently, the root angle regulators, such as genes DRO1 in rice and TaVRN1 in wheat, may adjust root system architecture and yield under drought stress (Uga et al. 2013; Voss-Fels et al. 2018). In addition, Manschadi et al. (2008) evaluated 26 Australian wheat genotypes and identified narrow branching angles of root system in genotypes from dry environments with available water at great depths, while genotypes from conditions with frequent precipitation had root system with wide branching angles. Vieira et al. (2008) demonstrated the genotypic variability of beans in the depth of basal root penetration, the angle of growth that the basal root forms with the vertical and the number of formed lateral roots.

Root system vitality

The ability to assess the vitality of roots, with its extremes "life" and "dead," is of utmost importance to identify the active (fine) root biomass available for water and nutrient uptake and to determine root longevity (Rewald & Meinen 2013).

Previous results confirm the possibility of using this property as a selection criterion in plant breeding (Ullmannová et al. 2013). With the development of digital image analysis, more accurate, detailed and automated vitality assessment is being developed and successfully implemented. Precise phenotyping based on root biomass growth rate of is thus possible.

Early, rapid root growth ("early vigour" (Palta & Watt 2009)) is one of the attributes used to increase grain yield in Mediterranean climate where terminal drought is a problem (Acevedo 1987). Under Central European climate, this trait could be suitable in areas with a risk of rainfall deficit at the time of sowing. Plants with rapid development can escape drought and use the moisture accumulated during the winter. It is likely that young plants from seeds with higher vigour will more easily escape drought in the early stages of vegetation. These plants will develop a larger root system and thus be more tolerant to stresses (Březinová Belcredi et al. 2022). However, in areas with low rainfall during the growing season, the available water may be depleted rapidly, due to the larger root systems. Consequently, this water may absent at the end of growing season during grain filling (Richards 1989; Campos et al. 2004).

Tardieu and Parent (2017) simulated the growth of corn roots in depth using a crop model. The growth rate had a slightly negative to positive effect on yield (–400 to + 1 300 kg/ha). In shallow soils up to 0.5 m, no effect was observed; in soils with a depth of approximately 1 m, the yields were variable. The growth rate in soils deeper than 1.5 m had a positive effect on yield. The benefits of a rapidly growing root system that had previously reached a greater depth were evident in the case of early flowering at high temperatures. In the case of colder weather and later flowering, this benefit was not observed because all monitored genotypes had more time to create a sufficiently deep root system.

High vitality of the root system is related to high vitality and properties of the aboveground part of the plant (Watt et al. 2005). Furthermore, root growth is related to the intensity of tillering. A great root depth is likely associated with a low number of adventitious roots that are positively correlated with the number of tillers (Blum 2005). For this reason, when the yield is primarily influenced by a high number of tillers, a large root system may reduce the yield (Blum 2005). Wheat genotypes with large root systems that grow rapidly have a rapid leaf growth (van den Boogaard et al. 1996), which may reduce an unproductive evaporation (Gregory 1989).

Vigorous root systems are promising for nutrient utilization. Wheat genotypes with fast and early root growth show high N uptake in sandy soils (Liao et al. 2006; Palta & Yang 2014). These genotypes had a 50–70% larger root system and received 42–60% more nitrogen than other genotypes, despite the equal depth of penetration. However, in some cases, few non-vigorous wheat genotypes with small root system can capture as much nitrogen per plant as those with large root system (Pang et al. 2015). This indicates that nitrogen uptake and, likely, water uptake, are not always directly or entirely associated with a large root system (Figueroa-Bustos et al. 2018). The question remains, to what extent does the size of the root system influence nitrogen and water uptake efficiency.

The phenomenon of "root turnover" is also often mentioned in connection with the vitality of roots, i.e. the frequency at which plants replace their root biomass (McCormack et al. 2015). "Root turnover rate" is defined as the number of times when fine root biomass is replaced each year and constitutes the inverse of root longevity. Turnover of fine roots of field-grown crops during a whole growing season, as observed in minirhizotrons in the field reported by Willigen and Noordwijk (1987), was for wheat on average 13%, for sugar beet about 50% and for grassland 40%. The half-life of individual roots of five groundnut cultivars was calculated by Krauss and Deacon (1994) as 3.7–4.4 weeks based on assessments of the roots that died up to plant maturity (14–20 weeks, depending on cultivar). Progressive root turnover is considered to be a normal feature of groundnut, perhaps representing an energy-economy strategy in this case.

PERSPECTIVES, POSSIBILITIES AND STRATEGIES OF BREEDING FOR AN IMPROVED ROOT SYSTEM

Initial status

Roots have been addressed for a long time in connection with strategies of plant adaptation to unfavourable conditions. Scientific studies from the late 1980s suggested the incorporation of root system properties as secondary traits in breeding strategies (e.g., O'Toole & Bland 1987; Bidinger & Witcombe 1989; Gregory 1989; Richards & Passioura 1989; Clarke & McCaig 1993). Despite the growing interest in the root system for breeding and agricultural practices, limited scientific knowledge has been obtained under field conditions. However, molecular biology and phenotyping techniques are rapidly improving. There are several issues related to the application of knowledge in breeding practices:

- A lack of knowledge regarding the functional characteristics of the root system.
- Insufficient definition of ideotypes for specific environmental conditions.
- Unclear genetic characterization, i.e., the inability to use marker-assisted selection procedures.
- Low heritability of most root system traits i.e., significant interaction between genotypes and the environment.
- Unstable positive correlation with yield depending on the meteorological conditions of the year.
- A lack of methods for the rapid, cheap and simple screening of parental genotypes and selection in offspring.
- Inevitable selection in the target genotype/variety application environment.

It is frequently reported, that breeding on root system in order to cope with stress contradicts high yield potential as for instance drought tolerance is sometimes considered to be limiting in this regard (Blum 2005).

In summary, the relationships between root system characteristics and yield are not always demonstrable. Root properties are influenced not only by soil conditions and nutrient availability but also by climate and precipitation distribution during the growing season. Other factors that significantly influence the relationship between the root system and yield are farming practices (Lilley & Kirkegaard 2011; Wasson et al. 2012; Comas et al. 2013; Lynch & Wojciechowski 2015) and the occurrence of biotic stressors including roots' pests (Středa et al. 2013). For example, the contribution of a genotype to grain yield and the prevention of nitrogen leaching is often influenced by sowing term, pre-crop or intercrop. This is described by Thorup-Kristensen and Kirkegaard (2016) for wheat genotypes with deep root system in the contrasting moisture conditions of Australia and Denmark.

Environment location strategies for plant breeding

It is essential for breeders to choose an environment for selection that allows the identification of a suitable genotype through the phenotype. Shakhatreh et al. (2001) emphasize the importance of target conditions. Selection is the simplest and the most effective in environments where the maximum expression of genotypes can be achieved. This most commonly occurs in favourable environments, where genotypes can fully demonstrate their yield potential (Mohammadi 2017; Slafer et al. 2021). Direct selection under stress conditions is recommended in cases of severe stress where yields reach 30–40% of the yield potential (Bänziger & Lafitte 1997). Ceccarelli and Grando (1989) emphasised pros of direct selection of locally adapted germplasm which, compared to indirect selection with conventional germplasms, showed multiple increased selection efficiency. However, Edmeades et al. (1989), Pardo et al. (2015) and Cai et al. (2020) for breeding on drought tolerance recommend screening under controlled conditions rather than in the field. Venuprasad et al. (2007) noted that selection response in the target population must correspond to the response from field conditions.

In areas with mild to moderate drought stress with average wheat and barley yields of 2–5 t/ha, breeding for higher yields also contributed to higher yields also in optimum environments (Araus et al. 2002). Breeding for high yield potential and yield stability results in the production of varieties with above-standard yields that are able to maintain satisfactory yield even under drought stress (Slafer et al. 2005). However, opinions on the positive relationship between high yield potential under optimal conditions and that under stress vary as some authors dismiss this relationship (Arraudeau 1989; Ceccarelli & Grando 1991; Sadras & Calderini 2009; Ndiaye et al. 2019).

Gregory (1989), Lopes and Reynolds (2010), Bodner et al. (2015), and Ober et al. (2021) consider many traits of the root system to be compatible with high yield potential. In particular, the architecture of the root system may be an important determinant of yield (Lopes et al. 2011; Morris et al. 2017). A negative correlation between yield and the quantity of roots is probable rather in well-irrigated environments, while the reversed relationship can be expected in drought-prone environments. In fact, Palta and Turner (2019) reported that there was a positive correlation between water use in the vegetative phase and grain yield under mild drought conditions, indicating that vigorous plants and higher transpiration in the vegetative phase, supported by a vigorous root system, could be adaptive for mild drought. Consequently, these facts can complicate comparisons of these relationships among sites or years in the same locality (Clarke & McCaig 1993).

The success of genotypes with improved root system depends on whether the nature of the root system is in accordance with the onset and duration of stress. Different characteristics may be appropriate for better drought tolerance, and it is necessary to design a proper drought process scenario (Tardieu 2011). For breeding, it is therefore necessary to define a target environment for the application of the variety of interest and a dominant scenario of drought stress onset before assessing an appropriate morphology of the root system (Palta et al. 2011). Furthermore, properties that are beneficial in one environment do not necessarily have a positive effect in another (Harrison et al. 2014).

The significant interaction between genotypes and the environment is mainly due to a great diversity of soil conditions (Gregory 2006). Besides, the expression of the root system traits increasing drought tolerance depends on a number of factors and their interactions making the relationship between the root system and drought tolerance so complex (Palta & Turner 2019). The plasticity of the root system allows plant to face temporal and spatial variability in the soil environment. Through the lens of the breeder the interaction between genotypes and the environment complicates breeding progress.

Phenotyping and ideotype identification strategies

Phenotyping aims at the characterization of root system traits because of its functional role in resource acquisition, as well as at the identification of suitable, sufficiently genetically variable properties of roots (Bodner et al. 2018). These properties must be stable under strictly defined conditions and should be correlated with agronomically important crop characteristics. To identify an ideotype, it is necessary to know which property of the root system is significant in the target environment (Clarke & McCaig 1993; Takahashi & Pradal 2021). However, the target trait of the root system is not always clearly defined. It should be noted that identifying the root system ideotype is a complex process (Singh et al. 2021). For example, it is clear that a well-developed root system will not ensure the full utilization of water supplies in the case of closing stomata (McGowan et al. 1984; Tron et al. 2015). Closer cooperation between research and practical breeding is needed to obtain practical results (Herrera et al. 2020; Ober et al. 2021). Such an approach can complement conventional breeding programmes and accelerate an increase in potential yield (Cattivelli et al. 2008).

In the United States, breeding for a higher soybean yield was associated with a change in the size of the root system (Boyer et al. 1980). Higher yields were achieved by genotypes that were able to maintain the water potential of leaves below the critical level in the afternoon due to a higher root density. Paradoxically, this effect was achieved unintentionally only by selecting productive individuals. In contrast, after the long-term breeding of maize for higher grain yield and drought tolerance at flowering, a 33% reduction of roots in the topsoil was observed (Bolaños et al. 1993). Hammer et al. (2009) consider the untargeted selection of maize root system architecture as a response to the higher crop density that has been used in the United States since the 20th century. Further evidence that selection for higher yields has mostly unintentionally altered the characteristics of the root system is provided by studies and comparisons of characteristics of modern and old or regional varieties. Research addressing roots in relation to yield formation under target crop conditions provides first discussions and suggestions of ideotypes (Wasson et al. 2012; Lynch 2013; Bodner et al. 2015; Singh et al. 2021). Regional water scarcity and yield growth requirements are likely to increase the importance of properly designed root system characteristics.

The breeding goals may significantly contradict in terms of specific requirements related to carbon sequestration and regenerative agriculture as changed the root:shoot ratio in order to maximize the amount of carbon in the belowground biomass is the primal. Long-term results of root system research provide objective, comprehensive and valuable answers to many questions. There are many studies dealing with the assessment of root biomass in wide soil environments (e.g. Figure 5). These experiments are currently highly valued in terms of new trends in environmentally friendly measures.

Genetic variation in root system

Natural genotypic variation for root traits is essential for adaptation to water deficit conditions. However, root traits have not been fully utilised as selection criteria to improve drought stress (Mateva et al. 2022).

The potential for breeding lies in acquiring unused genetic diversity that is available for almost every crop property, including those related to the root system (Fischer & Edmeades 2010). The results of many scientific studies confirm the genetic variability of root system traits. For example, the range of characteristic values depends on the number of genotypes that are compared (Fried et al. 2018). Thus, it is possible that by comparing current genotypes, we are not able to capture the whole genetic variability of a particular characteristic within a species (Palta et al. 2011). O'Toole and Bland (1987) described the extensive genetic variability of root system properties in many crop species. Various manifestations of root system architecture depending on the genotype of important legume species were described by Ye et al. (2018). However, the most studied crops are cereals. Genotypic variability has been found in the root length, RLD, rooting depth (Gregory 1989; Narayanan et al. 2014; El Hassouni et al. 2018), root growth rate (Hund et al. 2007), hydraulic conductivity and xylem vessel diameter of wheat (Richards & Passioura 1981). Using the established semi-hydroponic phenotyping platform, Chen et al. (2020) characterized the root properties of 184 common wheat genotypes and discovered large variation in several root traits and correlations between morphological and functional traits at the onset of tillering. For rice, differences in root segment diameter, depth and biomass were found by Gowda et al. (2011). Atkinson (1990) observed differences in root growth rate, SRL, root branching, root density, and total root biomass among 25 barley genotypes. Even though the genotypic differences in the root dry weight and root system area of sorghum were demonstrated, no differences in the dimensions of xylem vessels were found under controlled conditions or drought stress (Guha et al. 2018). Genotypic differences in root diameter, length and area per unit of root weight were described for nine cotton varieties by Singh et al. (2018).

There is a tendency to use relatively easily measurable root traits in target root system ideotypes (Xiong et al. 2021). Root size, length, and geometry are thus the main characteristics of ideotypes because they are the most easily measured (Freschet et al. 2021). However, a better understanding of root functional traits and their relation to whole plant strategies to increase crop productivity is needed (Comas et al. 2013). Thus, until today relatively few studies have been dealing with physiological uptake processes and genetic variability. This is due to the complexity of roots that are hidden in the soil and the absence of rapid field methods for their evaluation.

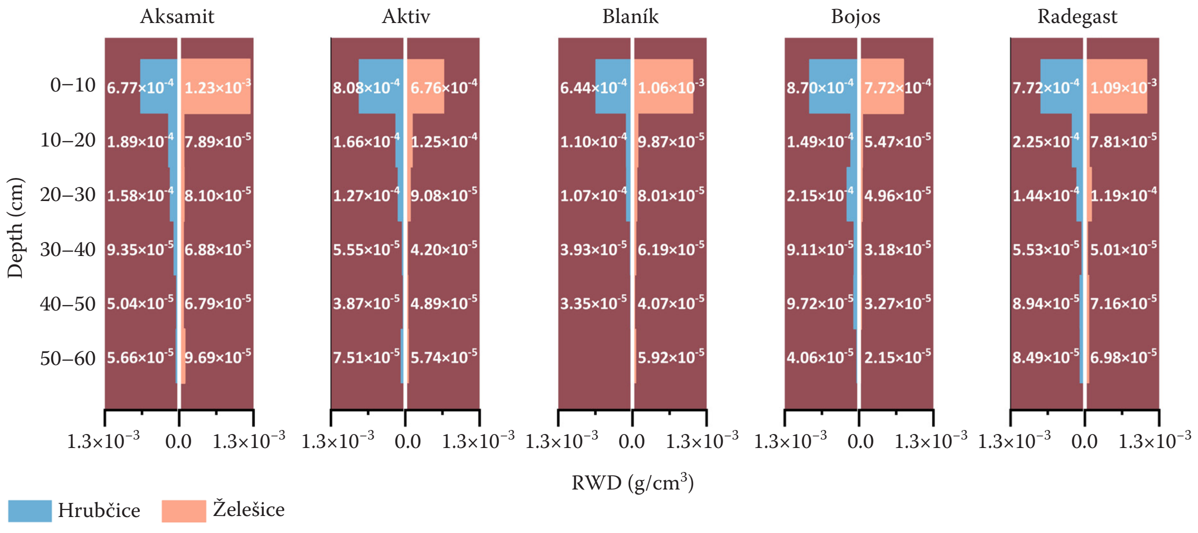

Figure 5. Root weight density (RWD; g/cm^3) of five varieties of spring barley at different depths below the soil surface in different environments (one year results)

BREEDING FOR EFFICIENT ROOT SYSTEMS

A plant's root is the most relevant organ for the plant adaptation to stress conditions. Thus, breeding new crop cultivars with efficient root systems poses a great potential to enhance resource use efficiency and plant adaptation to unstable climate (Jia et al. 2019).

The overall size of a root system is controlled by complex polygenic systems (Sertse et al. 2019). Therefore, a significant interaction between genotypes and the environment and low inheritance of root system traits are typical. Low inheritance strongly discourages breeders, but there is no reason to assume that the inheritance of root traits is lower than that of comparable shoot characteristics (Gregory 2006). Indeed, heterosis in wheat was shown for different root characteristics such as root length, root dry matter and root surface area (Wang et al. 2006) and root weight density in maize (Kamphorst et al. 2022). Besides, heterosis has been observed for maize, where hybrid progenies were found to produce more fine roots than their parents (Li et al. 2008). Wang et al. (2019) and Liu et al. (2021) reported that characteristics such as root hair length and root depth can be strongly influenced by the additive effect of genes, which allows selection on these traits. Nonetheless, the low inheritance of root formation in relatively deep soil layers may complicate changes in the vertical distribution of the root system without increasing the maximum penetration depth. Heritability values for total root length ($h^2 = 0.62$) and root branching ($h^2 = 0.42$) of wheat were described by Monyo and Whittington (1970), and that for xylem vessel diameter ($h^2 = 0.52$) was reported by Richards and Passioura (1981). A relatively high heritability ($h^2 = 0.56–0.62$) was found for the number of adventive roots and root diameter of corn (Guingo et al. 1998). Values of $h^2 = 0.42–0.43$ were found for the RLD of chickpea (Lalitha et al. 2015). Low heritability for shallow root mass ($h^2 = 0.26$), deep root mass ($h^2 = 0.14$) and total root system biomass ($h^2 = 0.22$) in wheat was observed during the tillering phase (Ehdaie et al. 2014), however, at maturity, the heritability was 0.81, 0.79 and 0.83, respectively. The authors, therefore, recommend phenotyping the properties of the root system at the time of wheat grain physiological maturity. However, it should be taken into consideration that the heritability determined this way estimates only the inheritance of the genotype used (Holland et al. 2003). Moreover, in quantitative genetics, heritability refers to the proportion of genetic variance in phenotypic variance, the latter being composed of genetic and environmental variances. Improving field management practices will minimize environmental impacts and reduce experimental errors, thereby enhancing the accuracy of heritability estimates and predictions (Xu et al. 2020).

The aim of Heřmanská et al. (2015) was to assess the relationship between the parents and progeny root system size (i.e., heritability) of winter wheat as a potential for breeding. After an initial screening of 39 parental lines, six lines with significantly different root system size were selected, and 30 parental combinations were created via diallel crossing. The seeds were then propagated to the F_3 generation and all obtained grains were sown in autumn 2016 at a dry locality in South Moravia, Czech Republic. The root system size of the plants was determined by measuring the electrical capacitance according to Chloupek (1977). The lack of precipitation, together with the high potential evapotranspiration, resulted in severe drought stress during the growing period. Plants from F_3 generation progeny were selected for large (Selection A) and small (Selection B) root system in 2017. The average root system size and root system size in the heading phase correlated with the root system size of the mother or the average root system size of both parents. A closer relationship was found for the plants selected for the smaller root system. Based on a regression analysis between the root system size of the progeny and parental genotypes, the root system size heritability was derived. Heritability in selection A were $h^2 = 0.219$ for the entire growing period (average root system size for two phenophases – heading and grain filling), while that in selection B was $h^2 = 0.548$. Consequently, the small root system was more dependent on the genetic system of the F_3 hybrids, and thus, the coefficient for this quantitative-based trait was relatively high. Heřmanská et al. (2015) demonstrated a similar heritability coefficient after the selection of wheat progeny in the F_3 generation for large root system size and small root system size ($h^2 = 0.262$ and $h^2 = 0.314$, respectively). The heritability of the small root system size was higher in both cases, and the size of the root system was found to be a genetically fixed characteristic. This knowledge is important for the effective use of this trait as a selection criterion.

Clarke and McCaig (1993) highlighted the importance of the precise definition of the parents characteristics involved in crossing. Initial screening and selection for root parameters should be performed under controlled conditions. Thus, eliminating the genotype-by-environment interaction. The use of non adapted parents, despite having desirable characteristics, is complicated, and they often have to be crossed back repeatedly to a locally adapted parent. To accelerate breeding for tolerance to abiotic stress, it is appropriate to evaluate variability using a large number of genotypes and locally adapted genotypes. Introgression of a target trait from non adapted materials can cause a significant decrease in yield (Hao et al. 2020). The use of a large number of genotypes eliminates the risk of differences in genetic variability among genotypes due to selection, accidental genetic drift, or mutation (Holland et al. 2003). Another principle is to evaluate several traits simultaneously under conditions with and without stress in order to select properties with sufficient genetic variability for further use (Dwivedi et al. 2017). It is not optimal to breed only for one property (Bidinger & Witcombe 1989). In near isogenic line (NIL) tests with variability limited only to a particular researched trait, the effect of that specific trait can be demonstrated, while in breeding nurseries, yield response to selection for one trait will not be demonstrable. This is due to the higher coefficient of variation under field conditions, which is rarely less than 10% (Hoad et al. 2001).

Backcrossing as part of a breeding strategy is suggested by Wasson et al. (2012). Backcrossing is advantageous under conditions of high heritability of a trait. If heritability is low but the trait is easily measurable, it can also be used for the introgression of quantitative traits (Richards 1989). Genetic variability should be evaluated among the maximum possible number of genotypes, including inbred lines, isogenic lines and populations (Richards 1987). Hurd (1974) recommends careful evaluation of smaller amounts of target crossings between well-described parents than cursively assessing a huge amount of crossings between unknown parents.

O'Toole and Bland (1987) propose selection of parents, then in early generations of the progeny to selection for agronomic traits, and only in advanced lines selection for a desired trait of the root system. Clarke and McCaig (1993) suggest three selection strategies for root system properties: (*i*) using a correlated response (selecting for yield in a particular environment is likely to change the properties of the root system in the desired direction), (*ii*) indirect selection for root properties, and (*iii*) selection by means of a selection index for both traits. In CIMMYT, both the selection index and direct breeding for yield were used to select for drought tolerance traits (Edmeades et al. 1989). The advantages of each type of selection must be derived from the heritability of the traits and the genetic relationship between them, although this approach is complicated by the fact that predicted correlation responses may change significantly during selection (Falconer 1989), under the influence of fluctuating environmental conditions. Heritability should be calculated based on observations at multiple sites and over multiple years. The assessment of genotypes at different locations in different years in the target environment provides objective data even if the characteristics are quantitatively inherited (Nyquist & Baker 1991).

Another aspect that complicates breeding for root system properties is their role as secondary selection criteria. The expected genetic gain when applying such criteria must justify the increased cost of their evaluation (Bidinger & Witcombe 1989). Such criteria must be genetically associated with yield, highly hereditary (Austin 1989; Edmeades et al. 2001) and easier to measure than yield alone. As the field root system measurement are demanding and rapid non-invasive methods are not yet available or do not provide sufficient information, the lack of appropriate methods for root system research and the screening of multiple genotypes is a major obstacle for breeding progress (Gregory 2006; Wasson et al. 2012).

The solution may be to use some related parameters functionally associated with root system properties. One possibility is to use the ability of root cells to store electrical charge on membranes in order to characterize the activity and size of the root systems using the electrical capacitance measurement method (Chloupek 1977; Středa et al. 2020). It was demonstrated that the dielectric response mainly originated from root tissue polarization and current conduction and is influenced by the actual physiological activity of the root system (Cseresnyés et al. 2024).

This polarization of root membranes is provoked by an external energy and is not an active process in plants – the polarization generates a measurable impedance response (Ehosioke et al. 2020). The method was used in the breeding of alfalfa (Chloupek et al. 1999) and in selection for root system size in the offspring of clover (Chloupek et al. 2003), spring barley (Svačina et al. 2014) and winter wheat (Heřmanská et al. 2015). This technique is considered as an adequate tool to assess root system size in situ (Cseresnyés et al. 2020). Due to root:shoot allometry, and the influence of the plant stem base on the measured electrical properties, electrical capacitance method proved to be useful for a whole-plant phenotyping, including the characterization of nutritional status and prediction of grain yield (Cseresnyés et al. 2022).

A limitation of this method is the inability to display the architecture of the root system and some functional characteristics, such as hydraulic conductivity. In contrast to commonly available methods for root system research (Smit et al. 2000), this technique, applicable under field conditions, can be used to measure hundreds of plants in a day (Cseresnyés et al. 2018). This is very advantageous for use in breeding programs.

Another possibility is, for example, the use of remote sensing – sensing vegetation using drones (Jones 2014; Sadras & Calderini 2015). Lopes and Reynolds (2010) found that the temperature of a wheat stand at the time of grain filling and the root system weight in deep soil layers were negatively correlated. Relatively low stand temperatures indicate transpiring leaf area and thus more efficient acquisition of water by roots (Blum et al. 1982). Similarly, low leaf surface temperatures have been observed in modern profitable maize genotypes exposed to drought stress. Relatively cold vegetation can indicate a deep root system and better access to water (Barker et al. 2005). A low stand temperature can thus be the result of a better and more efficient root system.

The lack of suitable field methods could be approached by genetic markers selection (MAS). However, the complex genetic foundation of root system properties makes it difficult to identify QTLs and specific genes responsible for their expression. Precise phenotyping represent an obstacle to the use of MAS (Francia et al. 2005). Reducing the "gap" between one genotype and the other is considered to be a major challenge in current biological research (Bray & Topp 2018). At the same time, the number of traits that will be suitable for use in MAS depends on the target environment and the research objective. Many markers and QTLs have been inaccurately determined due to inconsistent root phenotyping, variable population-environment relationships, or too low of a contribution of QTLs to variability in the trait of interest (Collins et al. 2008; Blum 2011). If the goal is to identify QTLs and apply this information in practice (e.g., MAS), it is important to know specifically the level and type of genotype-by-environment interaction for traits analysed in the progeny of mapped populations (Tuberosa et al. 2002). It is also important that there is a genetic relationship between yield and root system trait(s). Some overlap of QTLs for root traits and plant yield was observed by Tuberosa et al. (2002). In maize, Trachsel et al. (2009) located QTLs for the elongation rate and number of roots and yield. A more detailed overview of QTLs for the characteristics of the maize root system is presented by Bray and Topp (2018) and Hund et al. (2011). The idea of the future use of genes and marker knowledge could be based on breeding by design. This is a system in which, instead of concentrating on one target property, optimal combinations of specific alleles could be transferred to a new variety (Fischer 2011).

Barker et al. (2005) observed that the genes expressed under drought stress in a pot experiment differed from those expressed under drought stress from field conditions. The mapping of genes and related markers should be carried out under field conditions to be effectively integrated into breeding programmes (Comas et al. 2013). Laboratory experiments under conditions that differ considerably from field conditions should therefore be performed for the development of new genotypes which may incorporate genes encoding promising traits in the breeding material that is adapted to the conditions of the target environment (Passioura 2012). Automated phenotyping platforms that are able to screen large populations quickly and in detail and model root system phenotypes (Postma et al. 2017; Schnepf et al. 2018) will play a key role in this regard.

In addition to breeding improving selected traits (mentioned above) of the plant root systems, there is another area where scientists can direct their attention. That is the ability of roots to enter symbiotic relationships with microorganisms living in the soil. That may lead to enhancing plant physiological functions and adaptation (Vandenkoornhuyse et al. 2015). This trait can be considered as another phenotypic characteristic of the root system that deserves attention (Pérez-Jaramillo et al. 2017). There also arises a question whether the root system architecture impacts the structure of rhizobiome (Brown et al. 1997; Szoboszlay et al. 2015). King et al. (2021) suggest that the composition of microorganisms varies in different root parts according to their properties, and their functions depend on the roots' order. The dependence of species occurring in the rhizobiome on root system characteristics was confirmed by Robertson-Albertyn et al. (2017), who found that mutant plants without root hairs had a different rhizobiom composition than plants with root hairs.

CONCLUSION

- The breeding of most field crops has focused on the aboveground part of plants. The improvement of root system is a promising strategy for adapting agriculture to a changing climate and increasing the efficiency of water and nutrient use.
- One of the main challenges in root system research is an accurate description of genotypes for phenotype estimation and vice versa and the functional identification of root system properties.
- It is not possible to breed a better root system without identifying its links with the aboveground part of plants.
- The root system and its traits evolve and change during plant growth. Thus, the traits of the root system should be evaluated several times during the growing season, including the generative phases of ontogenesis significantly affecting yield (e.g. at the flowering for cereals, as it is the physiologically most active).
- The traits of the roots are variable, and many fluctuate with the environment, which complicates efforts to define ideotypes. Success in research regarding the root system and related breeding efforts depends on the precise definition of the target environment. Genotype testing must be performed using farming practices typical of the target area. Alternatively, it is necessary to specify a change in technology to enhance the positive manifestation of new property. Field breeding is irreplaceable, and methods that allow the evaluation of the root system under field conditions are indispensable.
- A large SRL (the ratio of root length to dry mass of fine roots) makes resources available to build larger structures at no additional cost.
- Beyond traditional breeding efforts aimed at enhancing specific root traits, the symbiotic interactions between roots and soil microorganisms offer a promising avenue for optimizing plant resilience.
- Water intake from deep soil layers is beneficial only in the case of significant and long-term rainfall deficits and the absence of irrigation. Furthermore, the vertical growth of roots must be faster than the drying of the soil. In regions with regular rainfall during the growing season, a shallow and highly branched root system is an advantageous adaptation.
- Breeding for better drought tolerance should consider both a high yield potential and an efficient root system.
- Research regarding the root system for breeding applications addresses traits essential for adaptation to heterogeneous conditions and related to water and nutrient uptake and thus also to yield.
- The mapping of genes and related markers should be carried out primarily under control climate for effective integration into breeding programmes.
- Despite all the challenges mentioned above, the root system is a promising object for biologists and breeders because many properties of the root system are compatible with high yield potential, and considerable genetic diversity is present.

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