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Root System Architecture in Wheat: Implications for the Breeding Program

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ABSTRACT

The current climate change is expected to affect crop geography and particularly alter the Brazilian agricultural landscape. In this scenario, in addition to crop management alternatives, it is imperative to introduce morphological traits for adaptation to these abiotic stresses into genetic breeding programs. Wheat root system architecture (RSA) describes the spatial organization of roots and is a fundamental factor in plant development. Improving this architecture can lead to plants that are more efficient in taking up water and nutrients, resulting in greater productivity and tolerance to adverse environmental conditions, such as drought and nutrient deficiencies. One of the breeding challenges is performing adequate, rapid, and affordable phenotyping and selecting the desired root trait, given the difficulty of evaluating roots underground. This work addresses theoretical aspects of the genetic components, environmental factors, and phenotyping methodologies associated with RSA, which are considered important and could play a relevant role in the selection of wheat genotypes adapted to Brazilian conditions. It is a contribution to researchers and students committed to promoting wheat production. We discuss a small subset of recent discoveries impacting RSA, believing that manipulating RSA will help develop better-performing crops. Different types of RSA offer growth advantages under different environmental conditions. In wheat, the seminal root angle is representative of the root architecture of the adult plant, thus providing a useful tool for phenotyping at early stages of plant development. RSA with a narrower, vertically oriented seminal root angle is typically more drought-tolerant. Therefore, RSA is a promising field that can be incorporated into existing breeding programs and has great potential to influence future wheat production.

Keywords: *Triticum aestivum, adaptation, drought, root angle*

INTRODUCTION

Climate change is expected to affect crop geography and particularly alter the Brazilian agricultural landscape. The area planted with wheat (*Triticum aestivum* L.) in Brazil in 2024 was 3.0 million hectares (CONAB, 2025), producing 7.9 million tons of grain, representing 66% of domestic consumption, which is 12 million tons. The demand for imported wheat for domestic supply, which is around 4 million tons, impacts the trade balance (CONAB, 2025). Traditional wheat genetic improvement relies heavily on selection for grain yield. Grain yield is a quantitative trait characterized by low heritability and high genotype-by-environment (G × E) interactions, especially under stress conditions. In this scenario, in addition to crop management alternatives, the introduction of morphological traits for adaptation to these abiotic stresses into genetic improvement programs becomes imperative as an innovative solution. The root system architecture (RSA) is responsible for anchoring plants, efficient absorption of water and nutrients, and is also a point of interaction with the soil microbiota.

RSA can provide a growth advantage in different environments and directly influences the aerial parts of the plant, which impacts yield (Manschadi et al., 2008). Low soil fertility and environmental stress reduce crop productivity in many parts of the world; therefore, genetic improvement programs based on RSA, aiming to develop crops with better performance, are of great importance for agriculture and food security. This review aims to present some of the recently identified genetic components and environmental factors that influence RSA and have direct application in wheat, with the hope that these factors can be exploited to promote crop production.

Root system architecture (RSA) impacts plant productivity and fitness

Root system architecture (RSA) describes the organization of roots under a given condition and is a fundamental factor in efficient water and nutrient absorption. RSA considers two important concepts: root system shape and structure. Shape defines the location of roots in space and how the root system occupies the soil. Its quantification is typically done by measuring variables such as primary root depth, angle, length, total surface area, or total volume (Maqbool et al., 2022; Abdullah, 2024).

The root system is generally divided into embryonic and post-embryonic roots, which are classified according to their time of emergence. Primary and seminal roots originate in the embryonic phase, while nodal (or crown) and adventitious roots are post-embryonic (Roger and Benfey, 2015) (Figure 1).

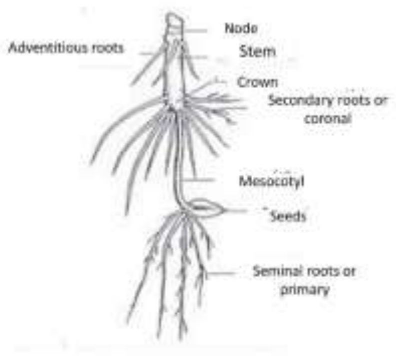

Figura 1. Wheat root system. Fonte: Arf (2025)

Wheat has two main root systems: seminal (embryonic) roots and nodal (crown or adventitious) roots. Seminal roots in cultivated wheat include a primary root, two pairs of symmetrical roots, and sometimes a sixth central root. Nodal roots usually become visible when the fourth leaf emerges at the tillering stage (Shereen et al., 2011). Seminal roots penetrate the soil earlier and deeper than nodal roots and remain functional throughout the plant's life cycle, thus contributing to moisture extraction from deeper soil layers (Manschadi et al., 2008). Due to their ability to develop earlier and deeper in the soil, seminal roots can be as important, or even more important, than nodal roots in maintaining yield (Araki and Iijima, 2001). Furthermore, under conditions of insufficient soil moisture, wheat plants reach maturity mainly through their seminal roots, since nodal roots have restricted development (Maccaferri et al., 2016; Sanguineti et al. 2007).

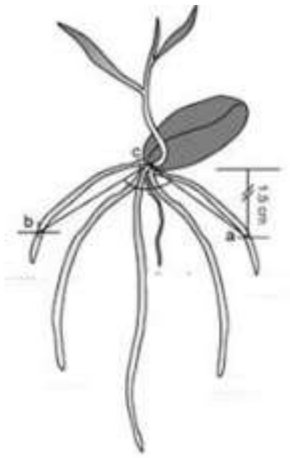

Figure 2. Schematic representation of the wheat seminal root system.

In addition to the six seminal roots, the angle (a, b, c) between the first two seminal roots is represented. Adapted from Sanguineti et al. (2007). In wheat, genotypic diversity has been found in root traits (Pais et al. 2022). Considering the difficulties in accessing mature root systems in the soil, it is possible to select genotypes based on traits expressed in the early stages of development. Indeed, at the seedling stage, seminal root growth, specifically the root growth angle, is closely linked to the architecture of adult plant root systems (Manschadi et al. 2006; Hohn and Bektas, 2020). The morphology and/or anatomical characteristics of the wheat root help the plant sustain higher grain yields with low resource availability, such as a deeper root distribution, which allows water consumption during droughts (Manschadi et al. 2006).

Genetic Components Influencing RSA

Several genes that influence RSA and root growth have been characterized at the molecular level. Specifically, in wheat, due to the complexity of its genome, their effects on yield remain to be tested (Table 1). These studies suggest that RSA is influenced by interactions between genes, signaling molecules, and nutrient and water availability. These studies report a biological trade-off in the allocation of root growth during root establishment, which directly impacts nutrient acquisition and yield. A deeper understanding of these interactions could allow RSA to be modified to achieve higher performance in a specific environment (Rogers and Benfey, 2015).

With the advancement of technology, many approaches have been adopted to study the quantitative aspects of various root types. Because RSA encompasses many root types with distinct functions, individual roots of soil-grown wheat seedlings were analyzed, and several QTLs specific to each root type were identified. These QTLs can be used in marker-assisted breeding for desirable root traits for efficient soil nutrient acquisition and may offer a sustainable solution for nutrient management in wheat production (Laperche et al., 2006; Sanguineti et al., 2007; Canè et al., 2014; Maccaferri et al., 2016; Alahmad et al., 2019). The quantitative nature of root traits, their complex control, and the strong environmental effect on the traits make this study difficult. In wheat, there are indeed few examples of quantitative trait loci (QTL) that can individually explain above 50% of the phenotypic variation (Ren et al., 2017), while in most cases root traits are regulated by a set of small-effect loci that interact with the environment (Sanguineti et al., 2007; Maccaferri et al., 2008; Zhang et al., 2008; Alahmad et al. 2019).

Canè et al. (2014) evaluated 183 elite durum wheat accessions to identify QTLs for RSA. Forty-eight QTLs for RSA were identified, of which 15 overlapped with grain yield traits. Among the RSA traits evaluated, seminal root angle and root number appear to be the most promising for future studies on the adaptive role of RSA plasticity in wheat performance in field environments. Maccaferri et al. (2016) evaluated the RSA of wheat accessions on polycarbonate plates. They identified QTL for length, root number, and seminal root angle. Genotypes with divergent root angles were validated by root phenotyping of adult plants grown in the field. In the wheat consensus map, the identified RSA QTLs overlapped with six QTLs for grain yield located on chromosomes 2A, 2B, 4B, 6A, 7A, and 7B, which appear to be the most important for marker-assisted breeding.

Table 1. Genes associated with characteristics of root system architecture

Gene	*Chromosome*	*characteristics*	*References*
MOR	4A, 4B ,4D	Influences on RSA and grain yield	Li et al. (2016)
ARF4	3A, 3B, 3D	Influences root growth	Wang et al. (2019)
RSL4	2A, 2B, 2D	Influences the growth of root hairs	Han et al. (2016 b)
LBD16	4A, 4B, 4D	Influences the number and development of lateral roots	Wang et al. (2018a, b)
SERK1	2A, 2B, 2D	Influences the root growth and the secondary root length	Sing e Khurana (2017); Abdullah, 2024
BRi1	3A, 3B,3D	Influences root growth	Sing et al. (2016)
NAC69	5A, 5B, 5D	Influences on root cell activity and root development	Xue et al. (2006)
EXPA2	3A, 3B, 3D	Promotes root system extension, leaf water retention capacity and drought tolerance	Chen et al. (2016)
VP1	3A, 3B, 3D	Promotes root growth under drought stress conditions	Wang et al. (2009)
VRN1	5A, 5B, 5D	*VRN1* (vernalization) affects root length and volume	Voss-Fels et al. (2018)
Rht		Reduces sensitivity to gibberellin and reduces plant height. Has a negative effect on root biomass.	Bai (2013), Subira et al., (2016), Wang et al., (2014), Haque et al. (2011)
TAZFP34		Overexpression promotes root growth under drought stress conditions	Chang et al., (2016)

RSA= root system architecture

Phenotyping for Wheat Root Architecture

RSA has been used as an early screening tool in cereal breeding programs, as it can serve as an indicator of the gravitropic tendency of the root system (Wasson et al. 2012). Investigating root architectural characteristics in a large number of plants under field conditions is extremely challenging, as it is a technically difficult and resource-intensive task, particularly in species with very fine roots, such as wheat. For this reason, most field studies carried out with wheat have evaluated only a very limited number of genotypes (Richards & Passioura, 1981; Manschadi et al., 2006; Wasson et al., 2012; Alahmad et al., 2019). Labor-intensive and destructive field methods have more recently shifted to image-based methodologies. A variety of image-based phenotyping platforms and many programs have been developed for phenotypic characterization of the root system, such as Growscreen-Rhizo, Winrhizo, Smart Root, Giaroots, and Rhizo Vision Explorer (Nagel et al 2012).

RSA has been used as an early screening tool in cereal breeding programs, as it can serve as an indicator of the gravitropic tendency of the root system (Wasson et al. 2012). The vast diversity and complexity of soils with strong modulation of root systems make it difficult to obtain accurate information on the genetic components of root development in the field. As an alternative to field experiments, root analyses of plants grown under controlled conditions have been performed using various hydroponic cultivation techniques, agarose gel-filled chambers, and other rhizotron methods, paper rolls, pots, soil columns, etc., primarily for root characterization in seedlings, providing a much less costly means of investigating the genetic variability of root traits.

Such systems allow visualization of natural root growth and are ideal for low-noise imaging. Germination paper-based techniques, such as germination rolls and germination bags, have been used in many cereals, including wheat, because they are simple and rapid (Adeleke et al. 2020). In this regard, it is worth noting that several important characteristics of wheat seminal roots, which will determine the architecture of the root system in mature plants, can be more conveniently investigated at an early stage of growth (Laperche et al., 2006; Ren et al., 2012)

Table 2. Phenotyping methods for wheat root traits

	Method	Characteristic	Specie	References
Laboratory-based methods	Gemination paper	Seminal root length, lateral and nodal roots. Root number, angle type and root diameter, área	*Triticum. aestivum*	Adeleke et al. (2020); Shorinola et al. (2019)
	Petri dishes	Seminal root length, Root number and angle type	*Triticum.. aestivum*	Pais et al. (2022)
Laboratory and greenhouse-based methods	clear pot	Seminal root length, Root number and root angle	*Triticum. aestivum*	El Hassouni et al. (2018); Richard et al. (2015); Alahmad et al., 2019
	hydroponics	length, area, root volume	*Triticum. durum* Desf.	Petrarulo et al. (2015)
	Rhizotron on polycarbonate plates	Root lenght, area, number, root angle	*Triticum. aestivum*	Nagel et al. 2012); Laperche et al., 2006
	Rhizotron in tubos	Root length, root intensity at depth, root aspect at depth	*Triticum. durum* Desf. *Triticum. aestivum*	El Hassouni et al. (2018) Chen et al. (2019)
Field based methods	Plastic basket or pasta drainer	Root angle	*Triticum. durum* Desf.	El hassouni et al. (2018)
	Soil core-break	Depth of root system, rate of penetration, temperature at flowering, root density at depth	*Triticum. aestivum*	Wasson et al. (2014)
	Shovelomics	Branches number and root angle	*Triticum. durum* Desf.	Alahmad, et al. (2019); Traschsel et al. 2011

RSA determines drought tolerance

Among cereals, wheat is predominantly grown under rainfed conditions in regions where water stress is the main environmental factor limiting productivity. Drought can affect wheat at all vegetative stages, particularly from flowering to grain filling. Breeding for greater water and nutrient uptake would therefore result in increased and stable productivity, particularly in water-limited environments (Wasson et al., 2012).

Optimizing root anatomy and growth characteristics can significantly increase water use efficiency (Wasson et al., 2012) and/or moisture extraction from deep soil layers.

The RSA determines the distribution and direction of root elongation, i.e., whether a plant has a shallow or deep root system. Narrow seminal root angles have been associated with deeper root systems, which can be advantageous in drought conditions. Conversely, wide angles have been associated with shallow root systems that promote lateral root growth, resulting in some benefits under wetter conditions and artificial irrigation (Uga et al., 2015). Some authors have observed significant genetic variation in wheat RSA, which is related to the genetic background and geographic adaptation of varieties, and is a valuable breeding resource for increasing crop productivity (Manschadi et al. 2008; Hohn and Bektas, 2020; Pais et al. 2022). In wheat, the seminal root angle is representative of the root architecture of the adult plant, therefore, it is a useful tool because it is a trait that can be easily phenotyped in the early stages of plant development. For example, a narrow seminal root angle is associated with high proportions of deep-rooting in more advanced stages of mature wheat (El Hassouni et al. 2018). A narrow seminal root angle can increase access to residual moisture at depth, particularly in terminal drought conditions (Manschadi et al. 2008), and can prolong grain filling and increase yield. Conversely, an wide seminal root angle is associated with a shallow root system that can benefit the superficial exploration of soil layers and the absorption of seasonal rainfall.

Therefore, identifying the optimal root architecture angle in each target environment is critical to guiding breeding efforts (El Hassouni et al. 2018). Smaller differences in root distribution in the soil can lead to greater impacts on yield. For example, results from modeling studies have suggested that in wheat, yield increases of 55 kg ha^{-1} can be achieved for each additional millimeter of water extracted from the soil during the critical grain-filling phase (Manschadi et al., 2008). Furthermore, recent studies examining root architecture in wheat have suggested that genotypes with deep root systems can increase grain yield by up to 35% and 1000-grain weight by about 9% in moisture-limited environments, compared to genotypes with shallow root systems (El Hassouni et al., 2018).

Root growth rate and root angle are key factors contributing to water and nutrient uptake. Narrower, vertically oriented RSAs are typically more drought-tolerant. Incorporating additional RSA genes that confer drought tolerance will provide more potential genetic targets for improving crop productivity. Breeding for a more efficient root system has been neglected due to difficulties in phenotyping and finding an association between root system shape and crop productivity. Improving the root system requires significant genetic variation, as well as reliable tools to determine genetic control and its variation (Pais et al., 2022).

Previous studies of root architecture at the seedling stage can predict root architecture in plants in the field at the adult stage (Richard et al., 2015; Uga et al., 2015). In cereals, the seminal root angle (also called gravitropic angle) has been presented as an excellent characteristic to predict root depth in the field (Manshadi et al., 2008; Mace et al., 2012; El Haussoni et al., 2018). From a methodological point of view, seminal root phenotyping using non-destructive techniques provides accurate and cost-effective evaluation of a large number of genotypes, as required in genome-wide association studies and in prospecting studies in germplasm banks (Sanguineti et al., 2007; Cané et al., 2014).

A study is underway at the Brazilian Agricultural Research Corporation (Embrapa wheat) to select germoplasm used in the wheat breeding program, and genotypes conserved in the germplasm bank for drought stress tolerance adapted to Brazilian Cerrado conditions. This study preliminarily evaluated 537 wheat (*Triticum aestivum* L.) genotypes (cultivars and breeding lines) for root architecture traits. The set included 100 accessions used in the Embrapa Trigo breeding program's cross-breeding block, 85 accessions from the collection of new lines selected in Uberaba, Minas Gerais, under the Cerrado conditions, and 352 accessions from the Embrapa wheat genebank collection previously selected under Cerrado conditions in

Uberaba (MG), for blast resistance. Wheat seedlings were evaluated for root architecture in a hanging file system (Hund et al., 2009). The inside of the folders was covered on both sides with sheets of germination paper. The seeds were disinfected with 0.5% sodium hypochlorite for 5 minutes, washed with distilled water, and glued with water-based white glue to the top of the folders, on top of the germination paper sheets. The folders were suspended vertically in plastic boxes containing water.

Water was placed in the boxes in sufficient quantity to moisten the bottom of the folders. The boxes were placed in a greenhouse at 23°C. The experiment was conducted in a randomized block design with three replicates, and the cultivars BRS 404 and BRS 394, adapted for cultivation in the Cerrado, were used as controls, these cultivars are recommended for dryland and irrigated cultivation, respectively. After 10 days, the folders were opened, and images were taken using a camera. For each plant, measurements were taken of root architecture characteristics, the angle between the first pair of seminal roots, and the length and number of seminal roots. For each plant, the angle between the first two seminal roots was measured approximately 3 cm from the seed using the ImageJ program (NIH National Institutes of Health, USA).

The controls cultivars BRS 404 and BRS 394 had average root angles of 54.73° and 84.00°, respectively. Based on the controls cultivars, the selection criteria were standardized: roots with an angle less than 60º were classified as narrow angle, between 61º and 80º were classified as intermediate, and above 80º were classified as wide angle (Table 3). Wheat genotypes with a narrower lateral root distribution can access more moisture deeper in the soil profile (Manschadi et al., 2008). A more vertical seminal root angle and a greater number of seminal roots are associated with a more compact root system with a greater number of roots at depth (Manschadi et al., 2008). A narrow seminal root angle and a greater number of seminal roots are considered fundamental traits for early selection for root architecture in wheat breeding programs (Manschadi et al., 2008, 2010; Wasson et al., 2012).

The method allowed cultivar differentiation based on the angle between the first pair of seminal roots, root length, and root number. The general collection of 537 evaluated accessions presented 17.24% of roots with a narrow angle less than 60º, 25.51% of roots with an intermediate angle and 57.16% with a wide angle. The average seminal root angle was 82.00º with a variation of 29.63º to 134.25º (Table 3). For root length, the average was 16.54 cm, with a variation from 6.58 cm to 32.60 cm. For the number of seminal roots, the average was 4.0, with a variation from 2.67 to 6.0.

Table 3. Seminal root angle, number of genotypes, percentage and angle classification of wheat genotypes evaluated for 10 days in a hanging file system.

Angle º	Nº Genotypes	%	Root angle classification
< 50 º	53	9,80	
51-60	40	7,44	Narrow
61-70	63	11,73	
71-80	74	13,78	Intermediate
81-90	102	18,99	
91-100	82	15,27	Wide
>100	123	22,90	
Total	537		

The collection of new lines presented the highest number of selected accessions, with 33% of the genotypes having a narrow angle of the first pair of seminal roots, an average of 73.00º, and a variation of 34.00º to 115.00º. The collection of the crossing block presented 31% of the genotypes with a narrow angle (less than 60º), an average of 75.10º and a variation of 32.65º to 134.97º, followed by the collection of the germplasm bank, which presented 23% of the accessions with a narrow angle, an average of 87.01º and a variation of 56.00º to 156.00º.

Information regarding the values of the root architecture traits of the 537 genotypes was made available in the System of Allele Vegetal, which manages data and information on Embrapa's plant genetic resources (Embrapa, 2025). The values obtained for root architecture traits—the angle between the first pair of seminal roots, root length, and number of seminal roots—as well as the variation in values among genotypes, are similar to those found in the literature. Richard et al. (2015), evaluating a panel of wheat seedlings from different drought-tolerant regions using germination paper bags, observed a variation in the angle of the first pair of seminal roots from 108.10° to 84.00° after 10 days, with an average of 109.70°. Macaferri et al. (2016), evaluating a population of recombinant lines of durum wheat seedlings derived from the Colosseo cultivar, not adapted to the arid conditions of the Mediterranean, and the Loyd cultivar, adapted to drought conditions, on polycarbonate plates lined with germination paper, observed a variation in the angle of the first pair of seminal roots from 48° to 147° after 9 days. The Colosseo cultivar had a 42.0% wider angle of the first pair of seminal roots than the adapted Loyd cultivar.

Cané et al. (2014) evaluated a panel of 183 elite durum wheat cultivars on polycarbonate plates covered with germination paper after 10 days and observed a variation in the angle of the first pair of seminal roots from 48º to 147º, with an average of 100º and seminal root length with a variation of 13.8 cm to 32.9 cm, with an average of 21.10 cm. For the number of seminal roots, an average of 5.18 was obtained with a variation of 4.01 to 6.00. Recently, several QTLs mapped to seminal root angle in wheat have been shown to have important impacts on deep rooting and root growth angle (Table 4). In some cases, these studies have suggested possible roles for these QTL in determining plant productivity. Due to the overlap of QTL for root traits with those for yield-related traits (Kulkarni et al. 2017; Alahmad et al. 2019), these results are fundamental for marker-assisted breeding for root traits.

Table 4. QTLs associated with wheat root architecture under drought stress conditions

Characteristic	Location of QTL on the chromosome	Wheat Specie	Reference
Root development	7A	Emmer	Merchuk-Ovnat et al., 2017
Root angle, diameter and área	2B, 5B, 7B, 6D	*Triticum aestivum*	Ahmad et al., 2017
Root lenght	1B, 2D, 5A 6A, 7B, 3A	Sintético e *Triticum aestivum*	Ayalew et al., 2017
Root and seedlings characteristcs	4B	*Triticum durum*	Iannucci et al., 2017
Yield and root morphology	1A, 1B, 4B, 6B	*Triticum durum*	Lucas et al., 2017
Root lenght, number and root angle	4B, 7A, 7B	*Triticum aestivum*	Ma et al., 2017
root morphology	1A, 1B, 2A, 3A, 6A e 6B	*Triticum durum*	Petrarulo et al., 2015
Root angle and root number	2A 2B,4B,6A,7A, 7B,	*Triticum durum*	Maccaferri et al.,2016; Alahmad et al., 2019

RSA Responds to Nutrient Heterogeneity

Roots are modular structures, making them highly capable of sensing environmental changes and responding to seasonal and climatic changes, toxic compounds, and nutrient fluctuations, which can have a significant impact on fertilizer use and crop productivity (Lynch, 2019). The relationship between RSA and productivity is complicated by soil heterogeneity. There is no ideal RSA that provides high productivity in all environments. Phosphorus has low mobility and is primarily located near the soil surface, while nitrogen and water are often found deeper in the soil, especially late in the growing season (Rogers and

Benfey, 2015). Because soil heterogeneity occurs in space and time, plants have adapted mechanisms to cope with limitations during root establishment and in the final stages of development. Nitrogen (N) and phosphorus (P) are vital for plant survival, and therefore, the dynamics of the RSA response to these nutrients have been studied in detail using experimental data and computational modeling (Rogers and Benfey, 2015; Niu et al., 2013; Postma et al., 2014).

The response to low P depends on the species, but general observations include inhibition of primary root growth, an increase in lateral roots and root hairs, and the formation of clustered roots (Niu et al. 2013). The general response to low N includes an increase in vertical and deep roots, with fewer roots near the soil surface. However, modeling of N uptake predicts a dynamic RSA in response to N and suggests that shallow roots are advantageous during root establishment, but deep roots are preferred later in crop development (McMurtrie et al., 2012). Tradeoffs exist between allocating root biomass near the soil surface and deep exploration. Rapid primary root growth plays an important role in nutrient uptake, so it has been hypothesized that genes for early root growth may facilitate selection for efficient nutrient use (Roger and Benfey, 2015).

Several QTLs in wheat have been identified with large effects on seminal and lateral root growth, which are also associated with yield and N and P acquisition (Ren et al., 2017). QTL analysis has observed overlap between QTLs for root traits and those for nutrient uptake and yield in many crop species, such as wheat (Sharma et al., 2011), suggesting the valuable potential of marker-assisted breeding for root traits in increasing nutrient use efficiency and yield. Ren et al. (2017) found three QTLs for root length and weight in wheat under low N and low P conditions on chromosomes 2A, 2D, and 3B. These studies show that the RSA response to nutritional conditions is largely controlled by genetic components and that there may be an optimal RSA for each nutrient deficiency. RSA exhibits a high level of plasticity due to environmental heterogeneity. Therefore, identifying the molecular mechanisms that control the root growth response will be valuable for future food production.

Soil Properties Influence RSA

Soil properties, such as density and particle size, vary greatly within a field and throughout a growing season, significantly impacting RSA and yield. Recent studies using wheat and tomato show that greater soil compaction produces short roots with a large diameter, resulting in a very shallow and narrow RSA, effectively decreasing the extent of soil exploration (Tracy et al. 2012). Furthermore, root elongation has been observed to be more influenced by mechanical and physical properties than by soil chemical properties (White and Kirkegaard et al. 2010; Gonçalves and Lynch, 2014). It has been hypothesized that the shape of root tips and the presence of root hairs aid in root penetration and anchoring in the soil. A complete understanding of how soil physical properties impact RSA will enable the development of crops that can be efficient and thrive in different soil types and could have a huge impact on food production worldwide.

Conclusions

We discuss a small subset of recent discoveries impacting RSA, believing that manipulating RSA will aid in the development of better-performing crops. Different types of RSA offer growth advantages under different environmental conditions, but RSA has been largely underutilized in wheat breeding. Breeding for a more efficient RSA has been neglected due to difficulties in phenotyping and finding an association between root system shape and crop productivity. Several genes that influence RSA and root growth have been characterized at the molecular level. Specifically, in wheat, due to the complexity of its genome, their effects on yield remain to be tested. The quantitative nature of root traits, their complex control, and the strong environmental effect on the traits make this study difficult. In wheat, the seminal root angle is representative of the root architecture of the adult plant; therefore, it is a useful tool because it is a trait that can be easily phenotyped in the early stages of plant development. Narrow seminal root angles have been associated with deeper root systems, which can be advantageous in drought conditions. Deeper rooting has a significant genetic component that can be easily integrated as a selection criterion in breeding programs. Conversely, wide angles have been associated with shallow root systems that promote lateral root growth, resulting in some benefits under wetter conditions and artificial irrigation. Therefore, identifying the optimal root architecture angle in each target environment is critical to guiding breeding efforts. There is no ideal RSA that provides high productivity in all environments. Therefore, RSA is a promising field that can be incorporated into existing breeding programs and has great potential to influence future wheat production.

ACKNOWLEDGMENTS
The author expresses gratitude to the National Council for Scientific and Technological Development (CNPq) for its financial support of the research under the project number 405115/2021-0.

CONFLICT OF INTEREST
The authors declare no conflict of interest

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