



Root2Res

Root phenotyping and genetic improvement for rotational crops resilient to environmental change

Define target ideotypes

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INDEX

Executive Summary	5
1. Introduction	6
1.1. The ideotype concept	6
1.2. Selection Indices and plasticity indices	8
2. Defining the ideotype	9
2.1. The defined environments	9
2.2. Identifying the priority traits.....	9
3. The ideotypes	11
3.1. Cereal Ideotypes.....	12
3.2. Faba bean ideotypes	15
3.3. Potato ideotypes	19
4. Conclusion	22
5. References	23
6. Appendix I	26
7. Appendix II	27
8. Appendix III	28
8.1. Water stress.....	28
8.1.1. Root traits	28
8.1.2. Rhizosphere traits	29
8.2. Phosphate trait responses	30
8.2.1. Root traits	30
8.2.2. Rhizosphere Traits.....	30

FIGURES

Figure 1. A. Steep cheap and deep root ideotype proposed by Lynch (2013) for rainfed environments: B. Root ideotypes for rainfed and irrigated environments (Schmidt & Gaudin, 2017)	7
Figure 2. Dimensions of a lodging proof ideotype for wheat, extracted from Reynolds et al 2009, based on Berry et al. (2007). Which outlines the combined quantitative plant characteristics for height, root plate spread and bottom internode wall width and diameter/material strength	8
Figure 3. Agroclimatic zones: ACZ1 The Oceanic climate (cfb), ACZ2 humid continental climate (Dfa) and ACZ3 for the Mediterranean climate (Cs) according to the agroclimatic classification of Köppen-Geiger (Peel et al. 2007).	9
Figure 4. Diagram of a current typical cereal (barley and wheat) plant root system and rhizosphere.....	12
Figure 5. Diagram of a cereal root and rhizosphere ideotype for a water-logged environment	12

Figure 6. Diagram of a cereal root and rhizosphere ideotype for **early water deficit environments**. 13

Figure 7. Diagram of a cereal root and rhizosphere ideotype for **late water deficit environments**. 13

Figure 8. Diagram of a cereal root and rhizosphere ideotype **for a low phosphorus availability environment**. 14

Figure 9. Diagram of a cereal root and rhizosphere ideotype for **a water stressed environment**, including traits for both early and late water deficit. 14

Figure 10. Diagram of a cereal root and rhizosphere ideotype **for a water stressed and low phosphorus available environment**, including traits for both early and late water deficit. 15

Figure 11. Diagram of a current typical faba bean root system and rhizosphere. 15

Figure 12. Diagram of a faba bean root and rhizosphere ideotype **for a water-logged environment**. 16

Figure 13. Diagram of a faba bean root and rhizosphere ideotype **for early water deficit environments**. 16

Figure 14. Diagram of a faba bean root and rhizosphere ideotype **for late water deficit environments**. 17

Figure 15. Diagram of a faba bean root and rhizosphere ideotype **for a low phosphorus availability environment**. 17

Figure 16. Diagram of a faba bean root and rhizosphere ideotype **for a water stressed environment**, including traits for both early and late water deficit. 18

Figure 17. Diagram of a faba bean root and rhizosphere ideotype **for a water stressed and low phosphorus environment**, including traits for both early and late water deficit. 18

Figure 18. Diagram of a current typical potato root system and rhizosphere. With the different root types labelled. 19

Figure 19. Diagram of a potato root and rhizosphere ideotype for a **water-logged environment**. 19

Figure 20. Diagram of a potato root and rhizosphere ideotype for **an early water deficit environment**. 20

Figure 21. Diagram of a potato root and rhizosphere ideotype for **a late water deficit environment**. 20

Figure 22. Diagram of a potato root and rhizosphere ideotype **for a low phosphorus environment**. 21

Figure 23. Diagram of a potato root and rhizosphere ideotype **for a water stressed environment, including traits for both early and late water deficit**. 21

Figure 24. Diagram of a potato root and rhizosphere ideotype for a water stressed environment and low phosphorus environment, including traits for both early and late water deficit. 22

TABLES

Table 1. Environmental factors (abiotic stresses) in the targeted agroclimatic zones ...9

Table 2. Root and rhizosphere traits associated with superior crop performance in different environments. These were taken from the Root2Res deliverable 1.1 report and adapted with insight form the consortia. Traits in bold have the strongest association (identified more frequently in deliverable 1.1 report) 11

Table 3 Target root and rhizosphere traits divided into architectural/developmental root traits, anatomical root traits and rhizosphere traits. 26

Executive Summary

The deliverable describes the ideotypes for the different crops, agroclimatic zones and stresses. To do this, the concept of an ideotype is defined as a biological model which is expected to perform or behave in a particular manner within a defined environment. The concepts of selection indices and plasticity indices are explored, but it is concluded that the development of a selection index follows the description of an ideotype. The environments for the ideotypes are defined and the ideotypes are defined based on the selected priority traits outlined in [Deliverable D1.1 List of root rhizosphere ideotype traits](#).

1. Introduction

The aim of this document is to define the target root/rhizosphere ideotypes for each of the core crop species and agroclimatic zones studied in Root2Res to mitigate against water and nutrient (phosphorus) stress and therefore which ideotypes are more likely to be resilient to environmental change. These ideotypes were designed using the list of ideotype traits identified in [Deliverable D1.1](#).

1.1. The ideotype concept

The concept of ideotype in plant breeding was introduced by Donald in 1968 to describe the idealized appearance of a plant variety. It literally means 'a form denoting an idea'. According to Donald, an ideotype is a biological model which is expected to perform or behave in a particular manner within a defined environment. Ideotypes are usually defined qualitatively in terms of which traits should be maximized, minimized or optimised, e.g. the Steep, cheap, and deep root ideotype to have access to deep water in environments with limited water advocated by Lynch (2013) or Schmidt and Gaudin (2017) description of root ideotypes in rainfed (deep rooted) and irrigated (shallow rooted) environments (Figure 1), compacted and uncompacted soil (Correa et al. (2019), potatoes in hot/dry environments (George et al., 2017), and the influence of moderate drought on the rooting ideotype (Vadez et al. (2014). Occasionally, ideotypes can be quantitative, e.g. Berry et al (2007) which defines the dimensions of the plant characters required for a lodging-proof wheat plant (Figure 2), but this requires a precise definition of the target environment.

Most root ideotypes are defined for an environment with a single primary constraining factor (e.g. lack of water or lack of a nutrient). In practice, however, this is probably too simplistic as crops are frequently exposed to more than one constraining factor and these can change through time and space, e.g. in dryland soils under no-till management, topsoil nutrient stratification is an emergent profile characteristic, leading to spatial separation of water and nutrients as the soil profile dries. Van der Bom et al. (2020) argue that identifying root traits that enable efficient capture of multiple soil resources under fluctuating environmental constraints is a key step towards meeting the challenges experienced by many crops. This could be achieved by either i) producing a single root ideotype that is optimized to achieve the best performance in a range of environments or ii) assuming that the root system is plastic, and its growth will adapt to different environments, during the lifecycle of the plant, to achieve the ideotype trait combination needed for each environment.

It is also important to account for any synergistic effects or antagonistic effects between traits. For example, Miguel et al. (2015) demonstrated a positive synergistic effect between shallow basal root growth angle with root hair length and density for phosphorus acquisition efficiency in common field bean. An example of antagonism between traits is the complex relationship between stomatal opening, Water Use Efficiency (WUE), photosynthetic activity and yield.

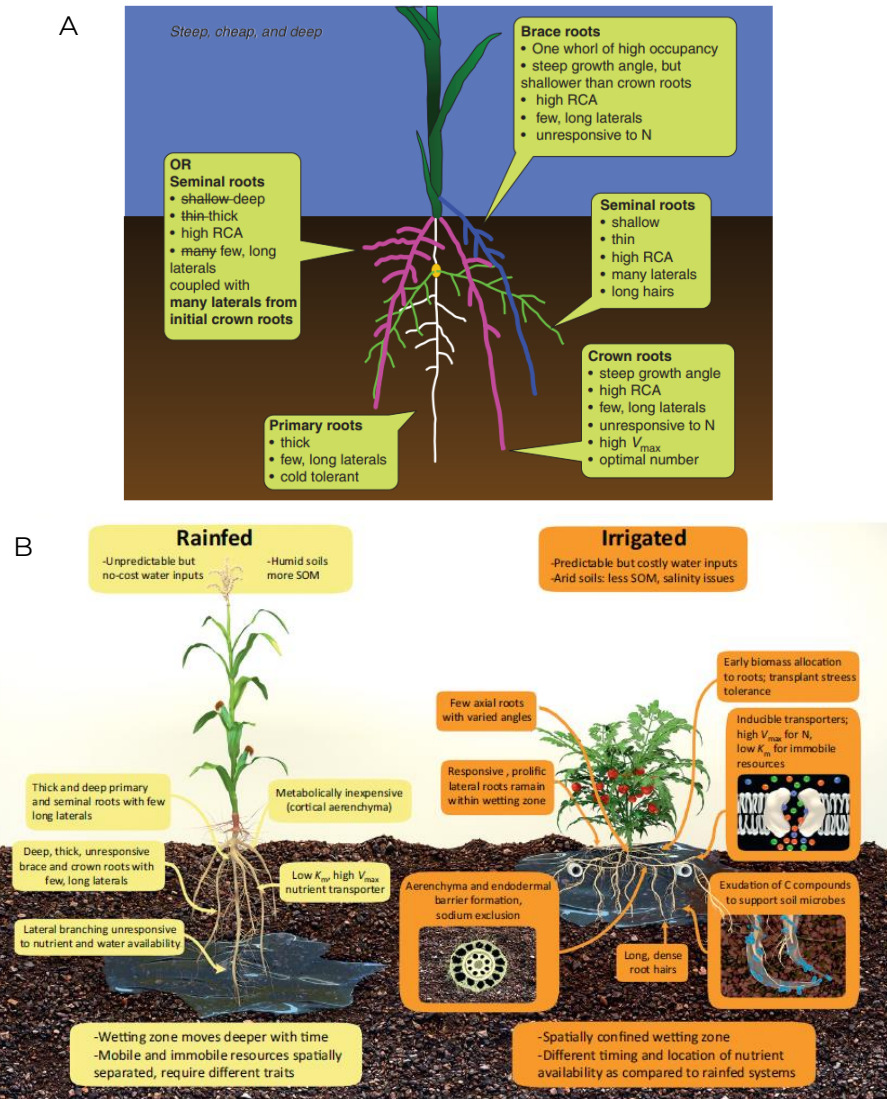


Figure 1. A. Steep cheap and deep root ideotype proposed by Lynch (2013) for rainfed environments: B. Root ideotypes for rainfed and irrigated environments (Schmidt & Gaudin, 2017)

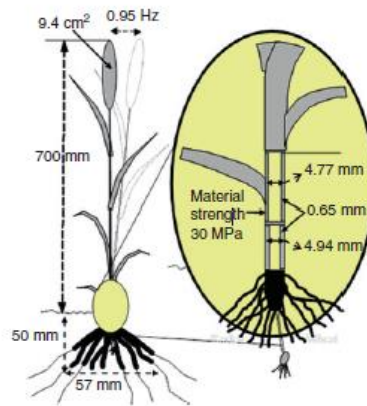


Figure 2. Dimensions of a lodging proof ideotype for wheat, extracted from Reynolds et al 2009, based on Berry et al. (2007). Which outlines the combined quantitative plant characteristics for height, root plate spread and bottom internode wall width and diameter/material strength

1.2. Selection Indices and plasticity indices

Plant breeders often try to combine various suitable agronomic features in one superior genotype that finally leads to achieving high performance. In this regard, several selection indices have been suggested to aid the selection of superior genotypes, e.g. the Smith-Hazel index and the multi-trait index based on factorial analysis and genotype-ideotype distance index (MGIDI) (Olivoto and Nardino, 2020). These indices are usually weighted in such a way that an expected gain in aggregate genotypic value would be maximized. They should also account for any synergistic or antagonistic effects. The weights are calculated using information on 1) the economic value of each trait, and 2) the phenotypic and genotypic variances of each trait and the respective covariances among traits. See Appendix II for more information on selection indices.

An ideotype is usually optimized for a specific environment. Plasticity is optimized for its potential to adapt to fluctuating environments. Phenotypic plasticity is the ability of an organism to alter its phenotype in response to the environment. There is a clear distinction between ideotype and plasticity, with ideotype being a combination of traits adapted for a specific environment and plasticity being the capacity for a plant to change its traits to achieve different ideotypes when it experiences different environments. Plasticity indices have been developed to evaluate genotypes for their level of plasticity, e.g. Relative Distances Plasticity Index (RDPI) developed by Valladares et al. (2006) (see also [Deliverable D5.1](#)). The value of plasticity as a breeding target is discussed in Schneifer and Lynch (2020). See Appendix II for more information on plasticity indices.

It is concluded that selection indices are useful tool for plant breeders to screen large populations of genotypes to identify the most well adapted genotypes for a specific environment. The development of a selection index follows the description of an ideotype.

2. Defining the ideotype

2.1. The defined environments

The Root2Res project works in three agroclimatic zones (ACZ, Figure 3) and has identified 4 key environmental factors (abiotic stresses) in the targeted agroclimatic zones (ACZ) to define root ideotypes for (Table 1).

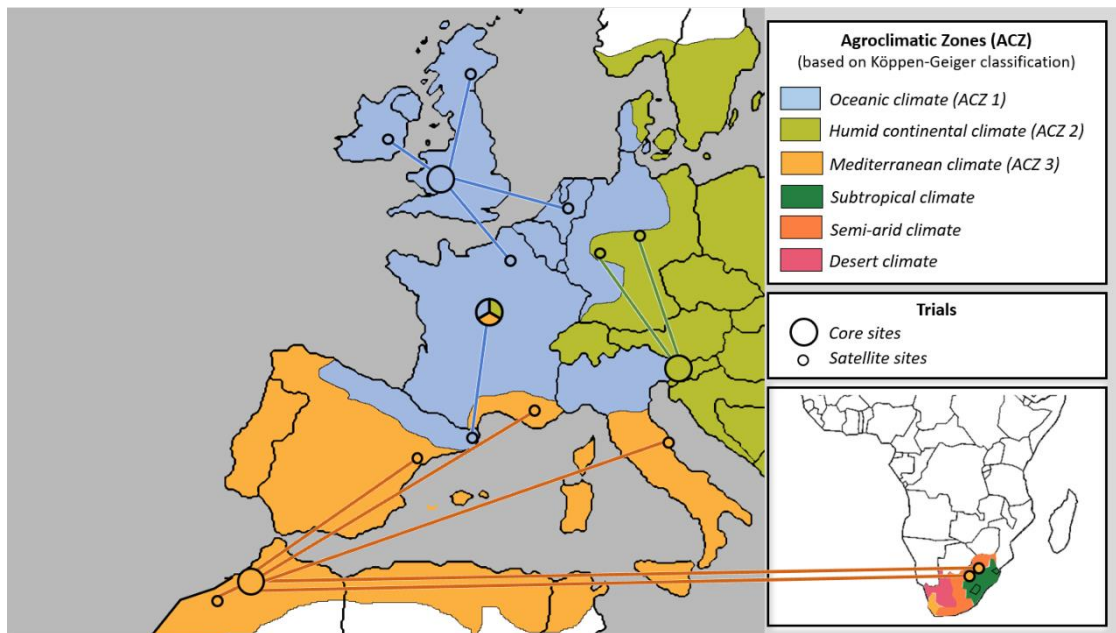


Figure 3. Agroclimatic zones: ACZ1 The Oceanic climate (cfb), ACZ2 humid continental climate (Dfa) and ACZ3 for the Mediterranean climate (Cs) according to the agroclimatic classification of Köppen-Geiger (Peel et al. 2007).

Table 1. Environmental factors (abiotic stresses) in the targeted agroclimatic zones

	ACZ1	ACZ2	ACZ3
Early water deficit (pre flower)			Y
Late water deficit (post flower)	Y	Y	Y
Water logging	Y		
P availability deficit	Y	Y	Y

2.2. Identifying the priority traits

To ascertain which below ground traits confer tolerance against water and phosphorus stress, the scientific literature was assessed and stakeholders were consulted. The literature was reviewed via two methods; firstly, a quick scoping review (QSR) was undertaken to provide a 'balanced assessment' of the literature, including project reports. Secondly, a review of published reviews of belowground crop traits was undertaken ([Deliverable D1.1 List of root rhizosphere ideotype traits](#)).

Deliverable 1.1 identified a priority list of target belowground crop traits that confer tolerance to water and phosphorus stress, which was divided into architectural/developmental root traits, anatomical root traits and rhizosphere traits (Appendix I, Table 3).

The deliverable report did not indicate whether different traits are more suited to a particular ACZ. The traits identified are specific to the different stresses specified and these are more or less prevalent in each ACZ and therefore root and rhizosphere traits which are helpful in elevating these stresses will be more appropriate for these environments.

The deliverable report identified deeper rooting, the density and length of root hairs as important for resilience to both water and phosphorus stress for a wide range of crop species. Deeper roots with greater hydraulic conductance and wide xylem diameter have been identified as important for resilience to water stress and more roots in surface soil horizons with wider spread and more lateral roots as important for resilience to phosphorus stress since most phosphorus resides in the soil surface. More aerenchymatous roots have been identified as important for resilience to water logging as this aids gas exchange in anaerobic conditions, as well as improving resilience to water and phosphorus stress by being less expensive for the plant to produce. Greater adventitious root porosity can also be considered advantageous to increased root growth and exploration because it is less metabolically expensive to grow. A pulse ideotype of 'wide, shallow & fine' was suggested for low rainfall temperate regions with little water in deep soil, such as the South-eastern cropping system of Australia (Rao, et al., 2021). This ideotype may also be appropriate for irrigated environments (Figure 1). This ideotype contrasts with the 'steep, cheap and deep' ideotype which proposed in cereal crops with access to deep water.

In terms of rhizosphere traits that can improve resilience to phosphorus stress, these include arbuscular mycorrhizal fungi and traits that increase the plant availability of phosphorus such as rhizospheric phytase, phosphatase, organic acids and exudates that alter the pH of the rhizosphere. In general, there was a lack of good evidence, from field experiments, that rhizosphere traits can improve resilience against water stress. However, there are laboratory scale experiments which indicates that mucilage production can influence the water dynamics at the root soil interface, maintaining the hydraulic continuity (Abdalla, et al. 2024; Naveed et al. 2019)

Combinations of root and rhizosphere traits that have been associated with greater crop performance in different environments are summarized in Table 2. It is not known whether combining multiple traits associated with superior crop performance in specific environments may be antagonistic. None of the papers reviewed identified any antagonisms for the traits identified for specific environments in Table 1 and the ideotype diagrams in section 3. Additional details on the mechanisms of the selected root traits can be found in Appendix III.

Table 2. Root and rhizosphere traits associated with superior crop performance in different environments. These were taken from the Root2Res deliverable 1.1 report and adapted with insight from the consortia. Traits in bold have the strongest association (identified more frequently in deliverable 1.1 report)

<u>Late water deficit (post flower)</u>	<u>Early water deficit (pre flower)</u>
<p>Deeper roots with greater root length density at depth Greater root dry weight Greater root hair density More aerenchyma Greater adventitious root porosity More mycorrhiza and Rhizobia</p>	<p>Deeper roots with greater root length density at depth Early root vigour <i>More laterals?</i> Greater root dry weight Greater root hair density More aerenchyma Greater adventitious root porosity More mycorrhiza and Rhizobia</p>
<u>Water logging</u>	<u>P availability deficit</u>
<p>More aerenchyma Greater adventitious root porosity</p>	<p>Increased root length density and surface area in top soil More laterals Early root vigour Greater root dry weight Greater root hair density & longer hairs Greater adventitious root porosity Phosphate solubilizing bacteria Rhizobia – elite strains with specific functionality Root exudates, inc. organic acids. Increased rhizospheric phosphatase activity More mycorrhiza</p>

3. The ideotypes

The ideotypes for the different target environments were designed using the traits described above and photos and diagrams of the root systems of the three core crop types addressed in the Root2Res project (cereal [barley & wheat], faba bean, potato). A baseline, current typical root system diagram was designed first and the different ideotypes were based on this. High priority traits are those which were identified in Deliverable 1.1 literature review more times and the low priority traits are those which were identified at least three times. The traits are presented in Table 2. Ideotypes were also developed for environments with a combination of the abiotic stresses.

3.1. Cereal Ideotypes

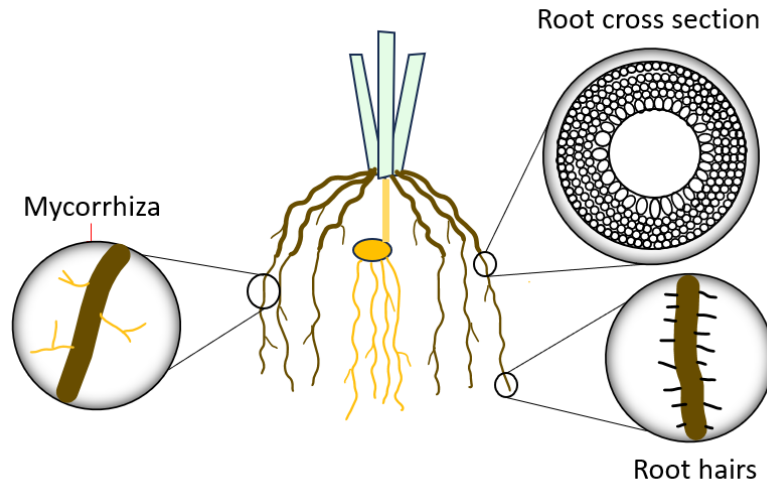


Figure 4. Diagram of a current typical cereal (barley and wheat) plant root system and rhizosphere.

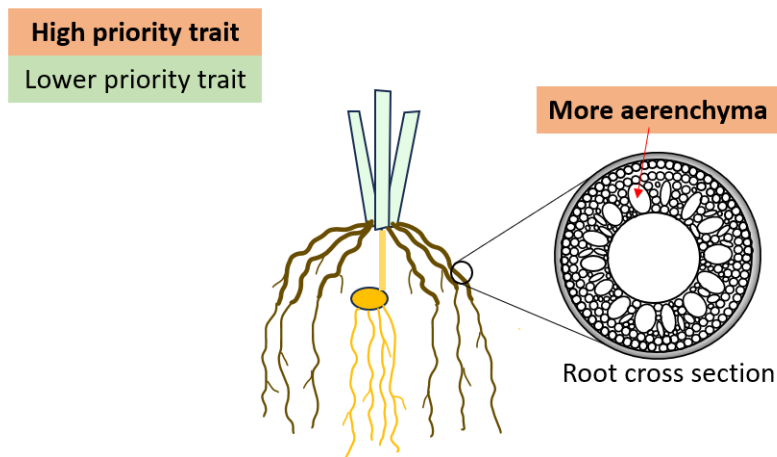


Figure 5. Diagram of a cereal root and rhizosphere ideotype for **a water-logged environment**.

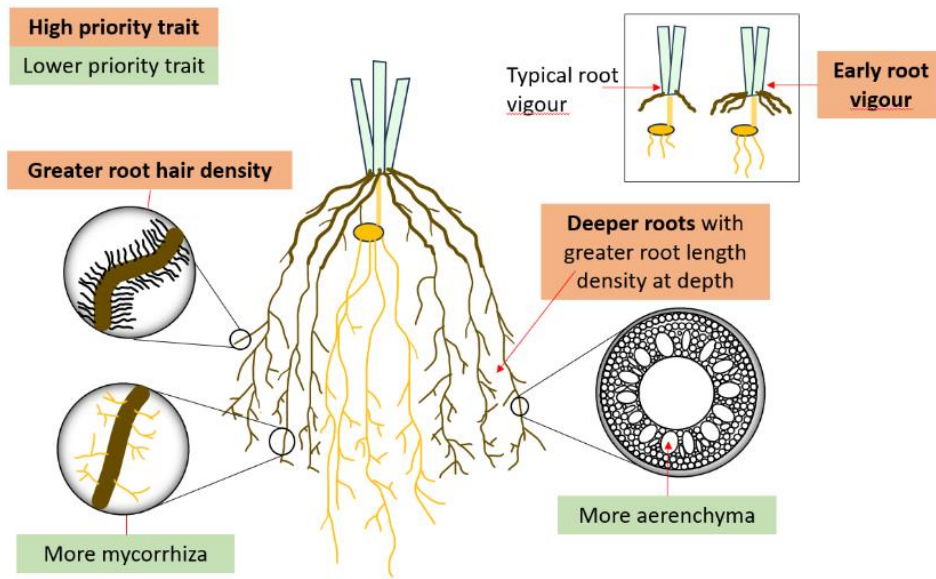


Figure 6. Diagram of a cereal root and rhizosphere ideotype for **early water deficit environments**.

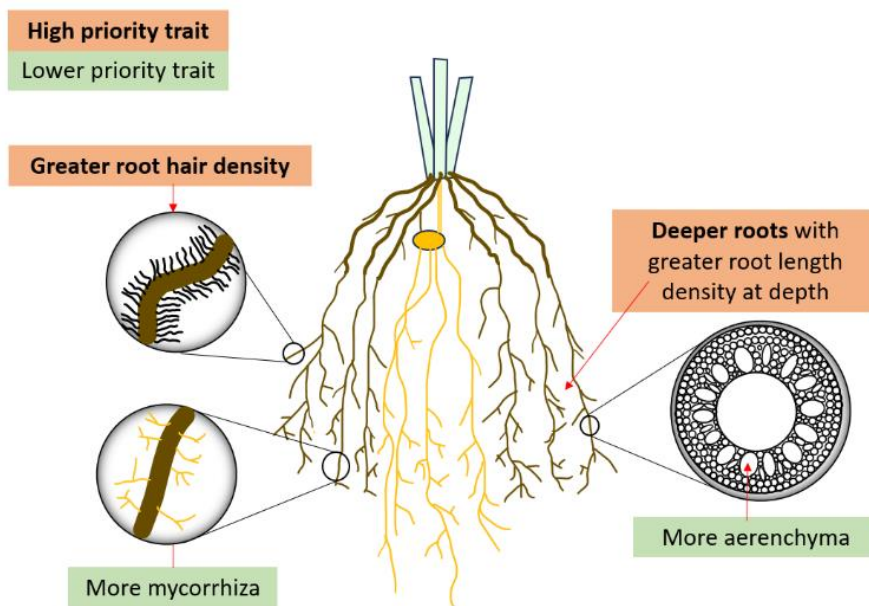


Figure 7. Diagram of a cereal root and rhizosphere ideotype for **late water deficit environments**.

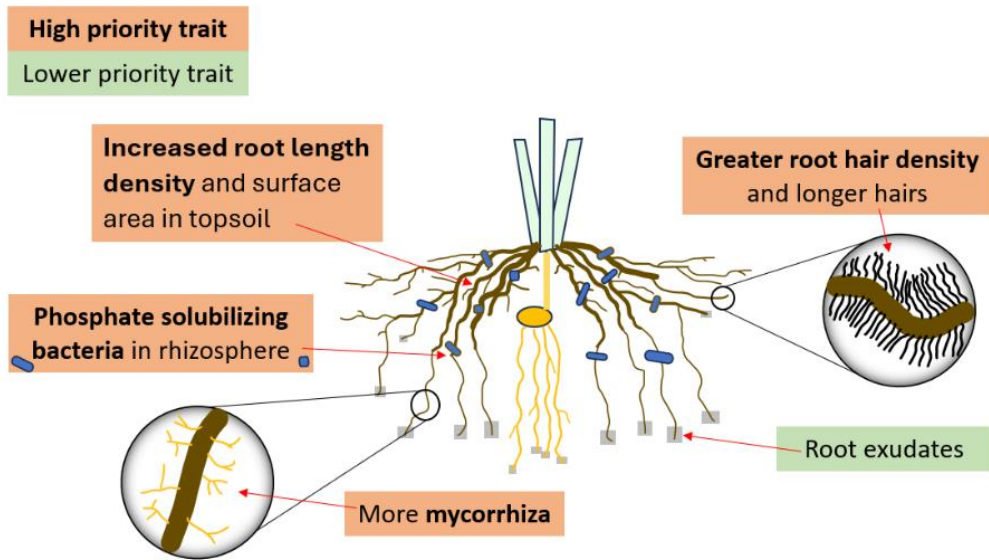


Figure 8. Diagram of a cereal root and rhizosphere ideotype **for a low phosphorus availability environment**.

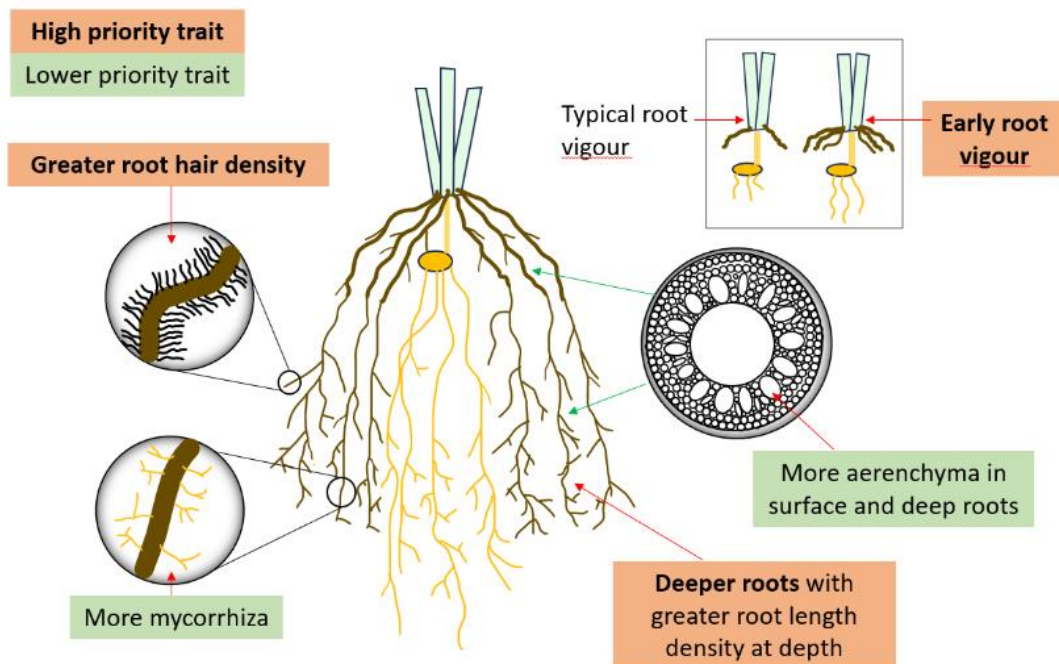


Figure 9. Diagram of a cereal root and rhizosphere ideotype **for a water stressed environment**, including traits for both early and late water deficit.

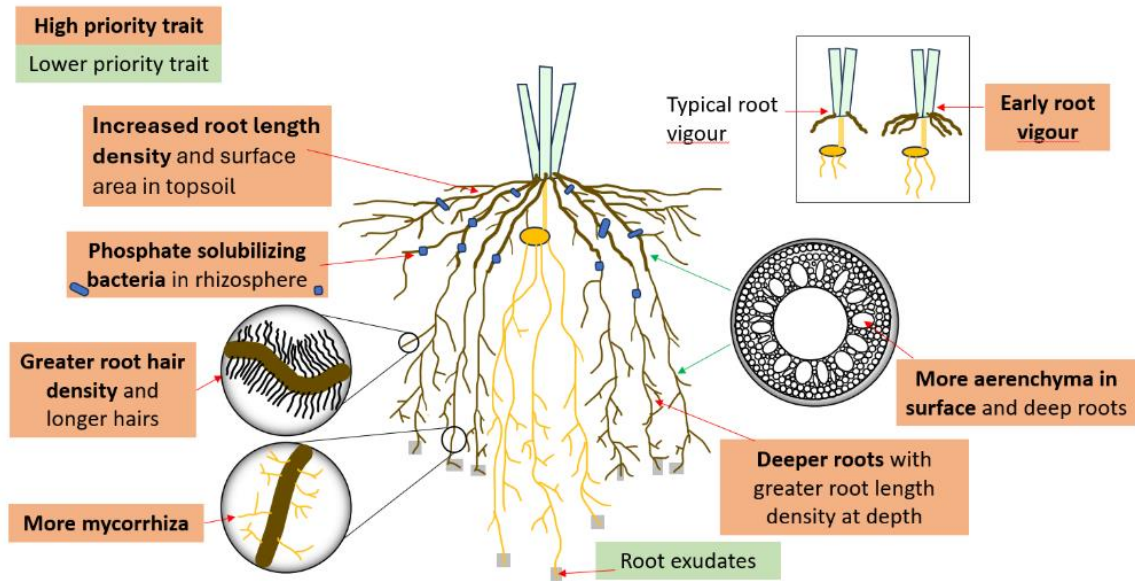


Figure 10. Diagram of a cereal root and rhizosphere ideotype **for a water stressed and low phosphorus available environment**, including traits for both early and late water deficit.

3.2. Faba bean ideotypes

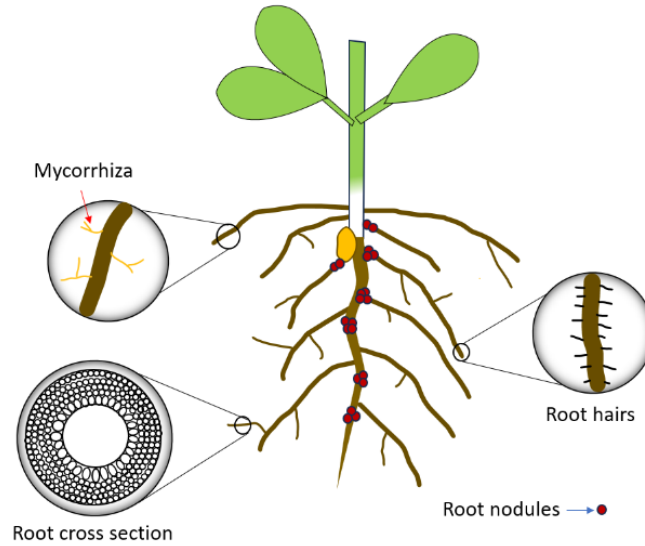


Figure 11. Diagram of a current typical faba bean root system and rhizosphere.

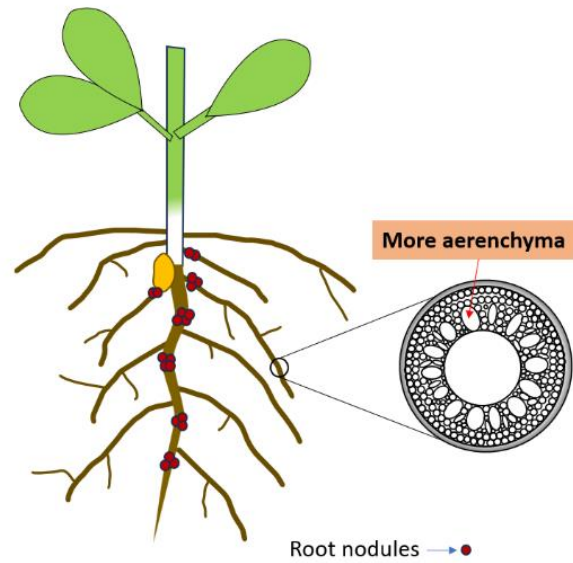


Figure 12. Diagram of a faba bean root and rhizosphere ideotype **for a water-logged environment.**

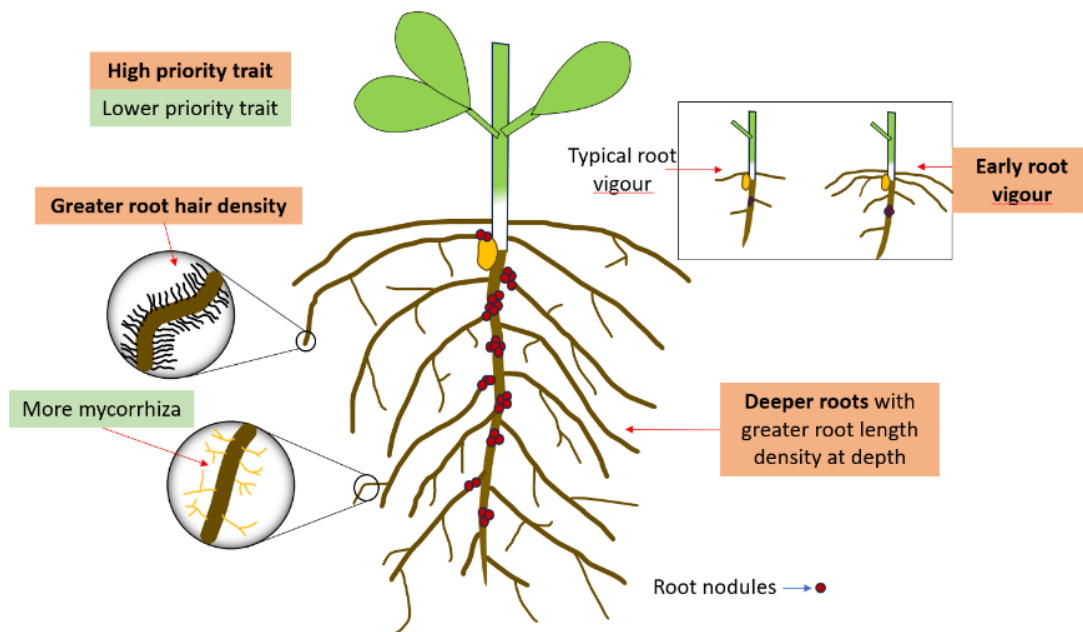


Figure 13. Diagram of a faba bean root and rhizosphere ideotype **for early water deficit environments.**

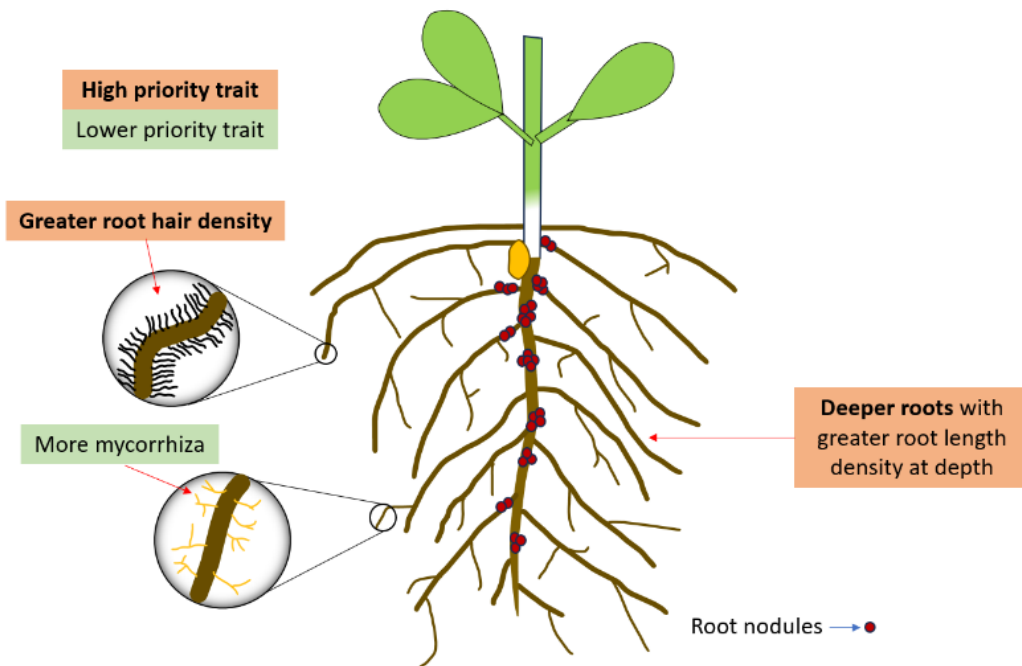


Figure 14. Diagram of a faba bean root and rhizosphere ideotype **for late water deficit environments.**

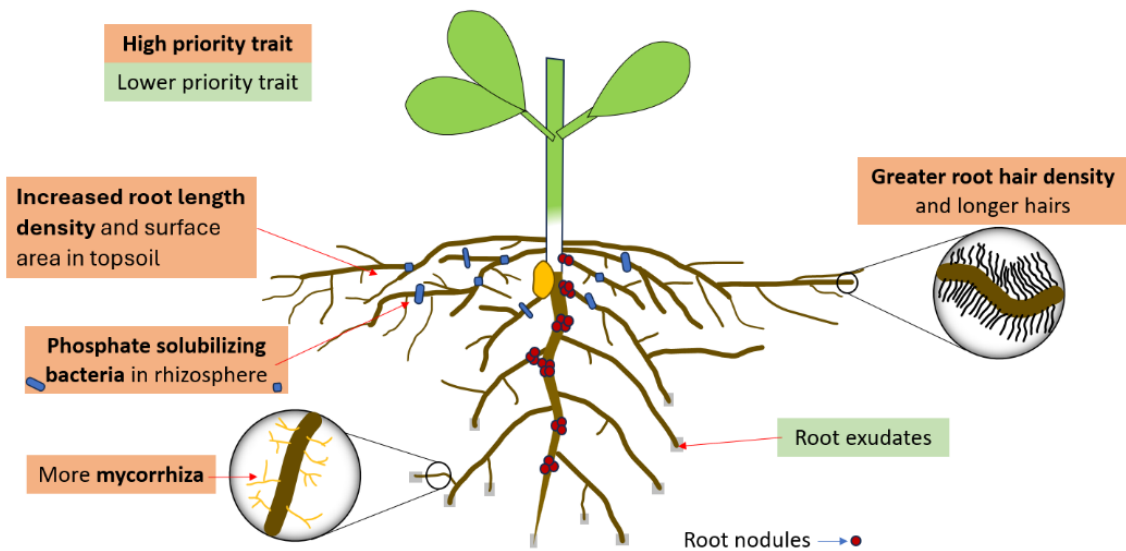


Figure 15. Diagram of a faba bean root and rhizosphere ideotype **for a low phosphorus availability environment.**

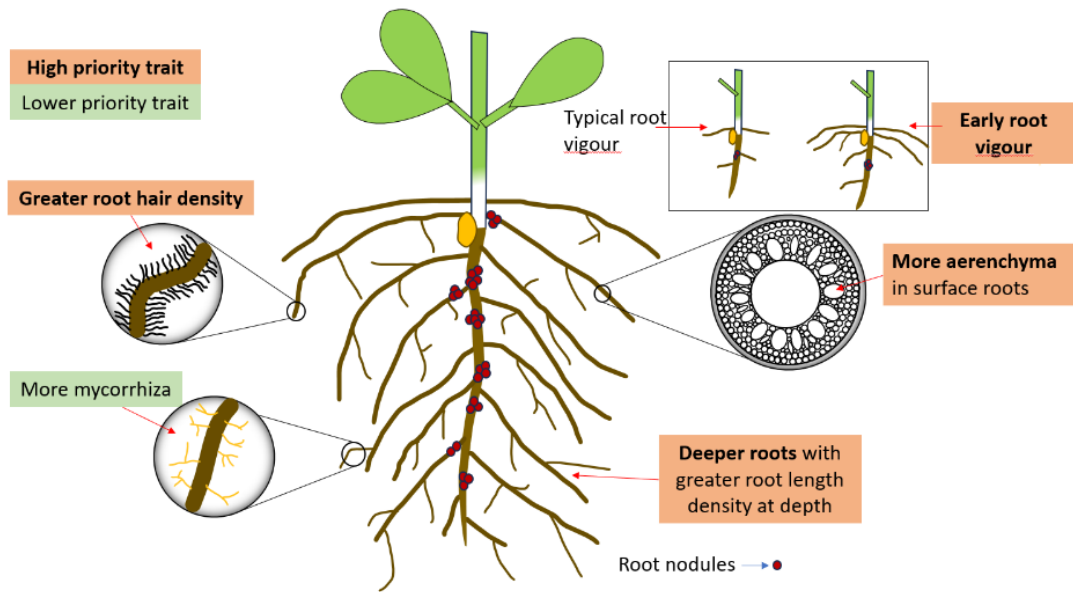


Figure 16. Diagram of a faba bean root and rhizosphere ideotype **for a water stressed environment**, including traits for both early and late water deficit.

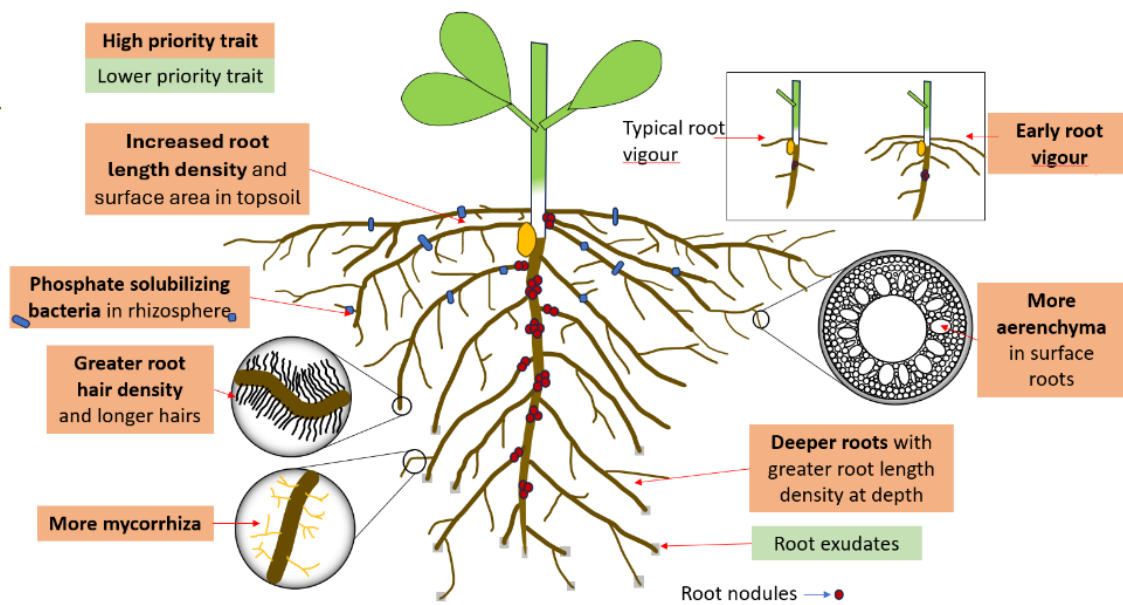


Figure 17. Diagram of a faba bean root and rhizosphere ideotype **for a water stressed and low phosphorus environment**, including traits for both early and late water deficit.

3.3. Potato ideotypes

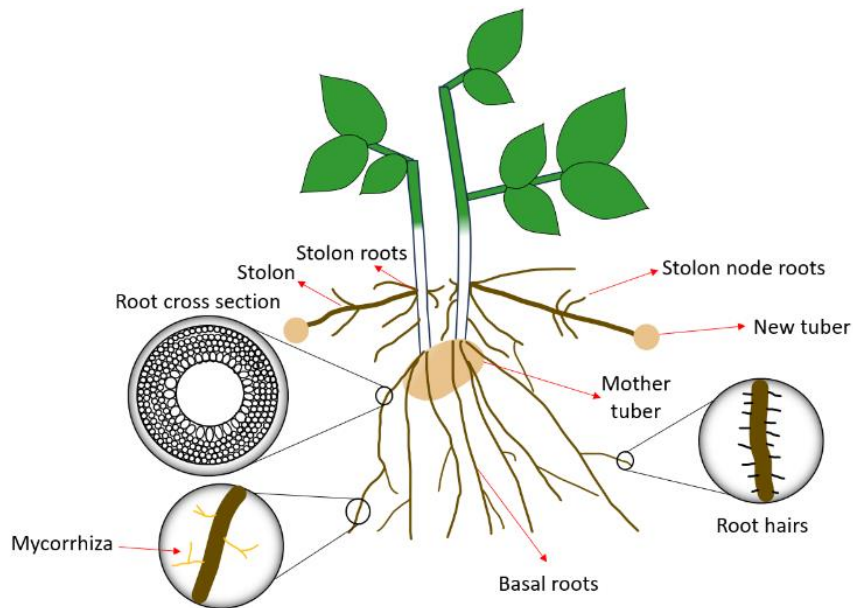


Figure 18. Diagram of a current typical potato root system and rhizosphere. With the different root types labelled.

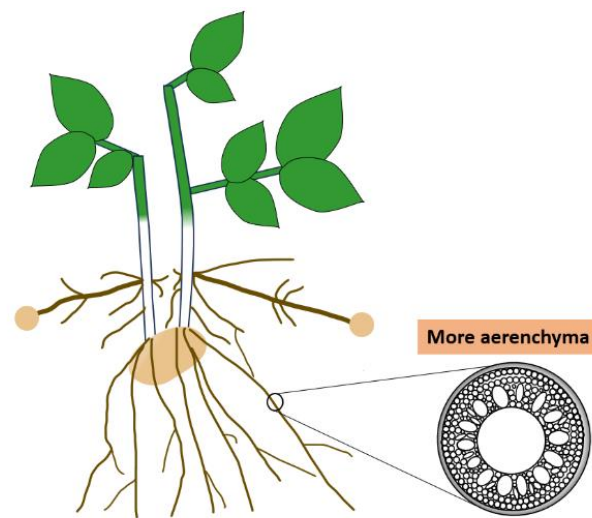


Figure 19. Diagram of a potato root and rhizosphere ideotype for a **water-logged environment**.

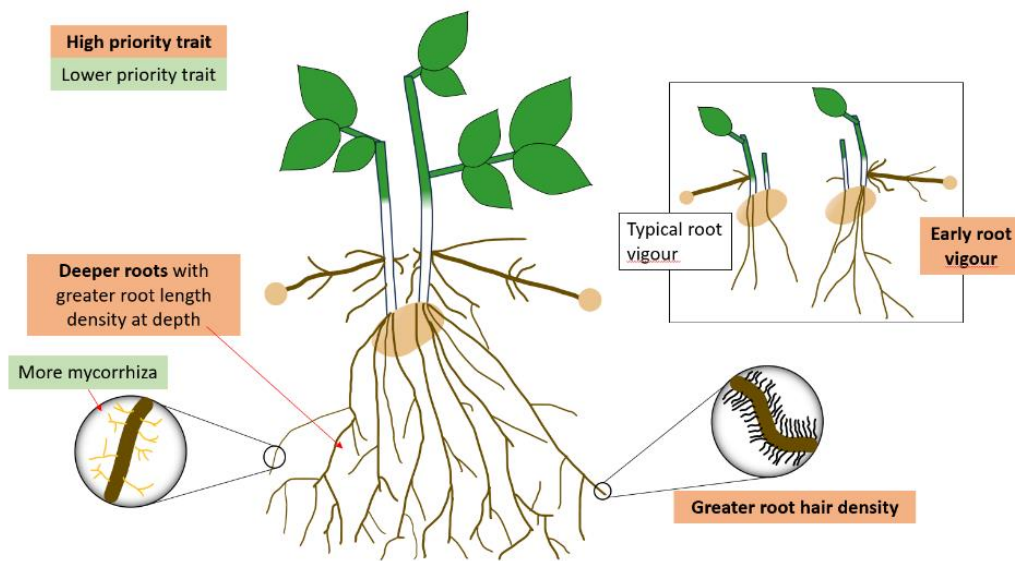


Figure 20. Diagram of a potato root and rhizosphere ideotype for **an early water deficit environment**.

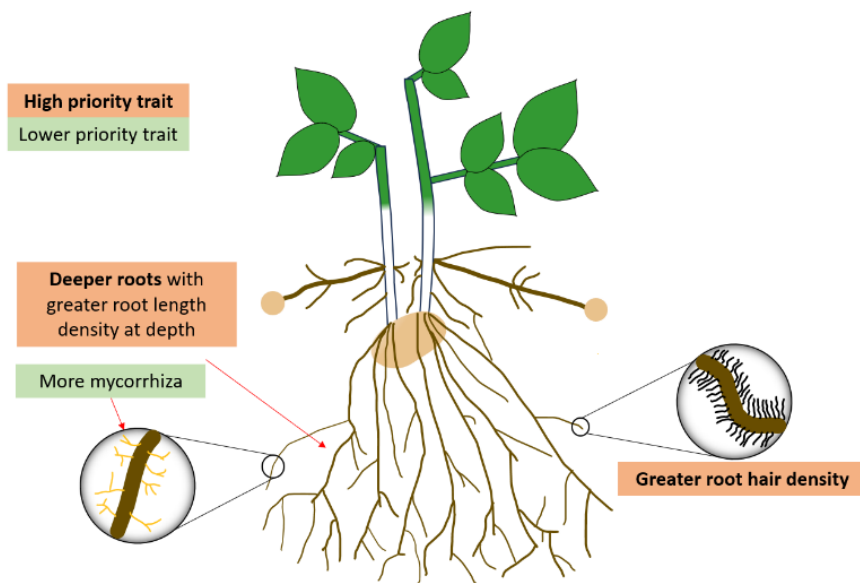


Figure 21. Diagram of a potato root and rhizosphere ideotype for **a late water deficit environment**.

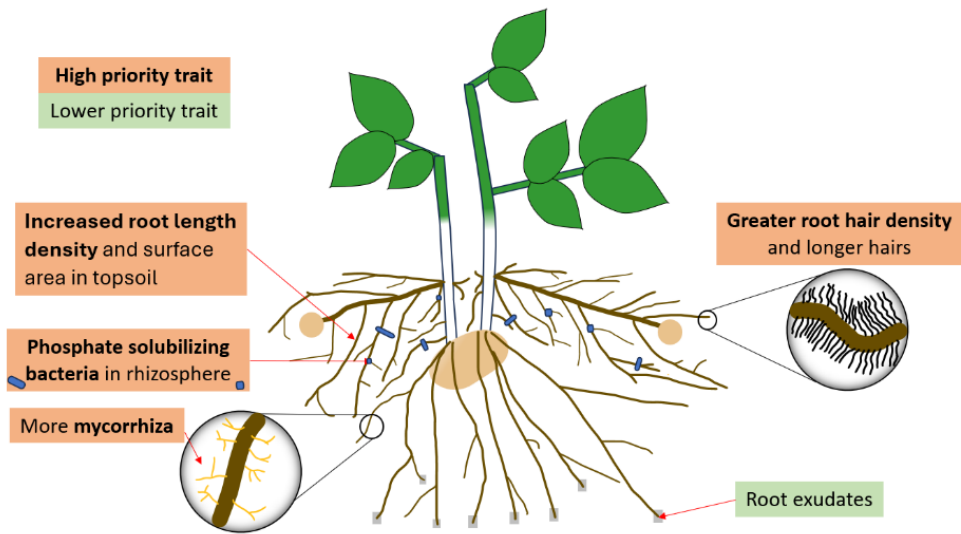


Figure 22. Diagram of a potato root and rhizosphere ideotype **for a low phosphorus environment**.

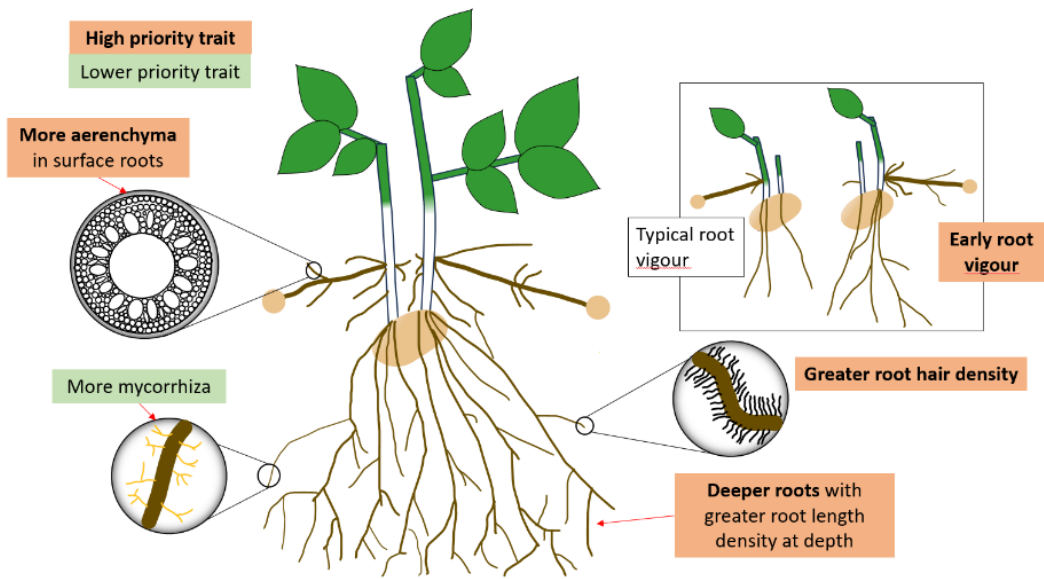


Figure 23. Diagram of a potato root and rhizosphere ideotype **for a water stressed environment, including traits for both early and late water deficit**.

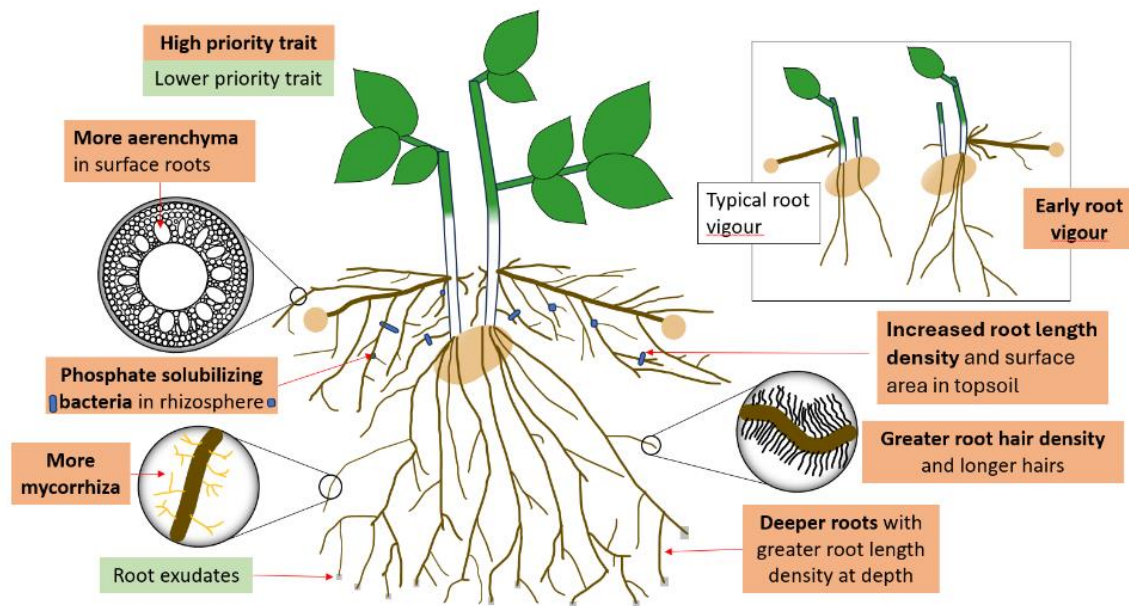


Figure 24. Diagram of a potato root and rhizosphere ideotype for a water stressed environment and low phosphorus environment, including traits for both early and late water deficit.

4. Conclusion

This deliverable describes the ideotypes for the three Root2Res core crops to mitigate against water and nutrient (phosphorus) stress in the different agroclimatic zones. An ideotype is a combination of traits adapted to a specific environment. The resulting defined crop ideotypes, and their associated traits, provide useful breeding targets for developing crops resilient to drought and phosphorus deficiency. These ideotypes highlight the priority root and rhizosphere traits on which to focus belowground breeding efforts. The traits identified were specific to the different stresses, rather than to the specific crop types, which means that the traits are generally transferable between the crop types. Therefore, the breeding targets for a specific environment (and its defined stresses) are similar between crop species.

Within the Root2Res project, the definition of the crop ideotypes will allow the selection of specific genotypes to be used in the WP1 validation field trials, which are designed to validate the crop ideotypes in the field. The ideotypes and the combination of selected traits will be used alongside analysis in WP4 (phenotyping the genotypic diversity) and with data from WP2 (the phenotyping toolbox), to select genotypes exhibiting the ideotype, or close to the target ideotype. These selected genotypes will then be used to validate the ideotypes in field trials at the Root2Res core field hub sites. The validation field trials will include treatments to provide water and nutrient stresses over two seasons and test the performance of the selected genotypes against current recommended genotypes, quantifying the effects of the ideotypes on crop performance.

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6. Appendix I

Table 3 Target root and rhizosphere traits divided into architectural/developmental root traits, anatomical root traits and rhizosphere traits.

	Traits	Water logging	Water deficit	Phosphorus deficit
Root Traits – Architectural/developmental	Greater root dry weight		✓	✓
	Deeper rooting		✓	
	Increased lateral root number		○	○
	Early root vigour		○	○
	Increased distribution of roots at depth		○	
	Root surface area			○
	Increased root length density			○
Root Traits - Anatomical	Aerenchyma formation	✓	✓	✓
	More root hairs (inc. density)		✓	✓
	Greater root hair length			✓
	Greater adventitious root porosity	○	○	○
Rhizosphere Traits	Arbuscular mycorrhizal fungi		✓	✓
	Rhizobia – elite strains with specific functionality		✓	✓
	Phosphate solubilizing bacteria			✓
	Root exudates		○	○
	Increased rhizospheric phosphatase activity			○

A symbol denotes if the trait contributes resilience towards one of the abiotic stresses addressed in the review (water logging, water deficit or phosphorus stress). Traits listed with ○ were identified at least three times and those traits with ✓ and in bold were identified at least 5 times.

7. Appendix II

Selection Indices

One way of selecting for more than one trait at a time in a breeding program is through a selection index. It is a procedure that provides a single criterion for selection among genotypes by including combinations of several traits. Selection indices composed of many major yield component traits are more efficient than the ones having one trait. The objective of a selection index is to find a linear combination of phenotypic values that maximizes the expected gain in aggregate genotype. Smith (1936) proposed a general method for handling more than one trait at a time in a plant breeding program. He developed a selection index based on a linear combination of phenotypic values weighted in such a way that expected gain in aggregate genotypic value would be maximized. The weights are calculated using information on 1) the economic value of each trait, and 2) the phenotypic and genotypic variances of each trait and the respective covariances among traits. The same index was also proposed by Hazel, but using estimated values for phenotypic and genotypic parameters. He presented the genetic basis for the construction of selection indices and outlined methods for estimating the required variances and covariances. They made use of the idea by Fisher (1936), who had suggested the concept of discrimination function and said that since genetic values cannot be determined, but it is possible to approximate its values using a linear function of observable phenotypic values.

Taking advantage of selection indices was first proposed by Smith in order to improve plants. Hazel (1943) extended the index procedure for the selection of individuals in animal populations. This method is now known as Smith-Hazel index (Williams, 1962) was afterwards developed by Baker (1986) and widely used in different breeding programs. Asghar and Mehdi (2010) used data on yield and quality traits among S1 families of *Zea mays* L. Saccharata to construct Smith-Hazel selection indices and reported it to be the most efficient selection index in improving the aggregate genotype of yield traits for most of the selection strategies. Ziyomo and Bernardo (2013) constructed a selection index used to combine information from several traits correlated with drought tolerance in maize. Selection was based on both grain yield under drought and ASI. Based on the estimates of genetic and phenotypic variances and covariances for these two traits, a Smith-Hazel index would be useful and this index has a predicted relative efficiency of 1.13. Al-Obaidy et al. (2015), reported that selection indices including grain yield were more important than others and the best selection index was composed of grain yield, ears plant⁻¹ and grain weight which led to the identification of superior genotypes.

The proposed indices such as Smith- Hazel (Hazel, 1936; Smith, 1943), and factor analysis and ideotype-design (Olivoto and Nardino 2020), restrict breeders in selection the best genotypes due to some limitations like expressing the economic values and converting them into realistic economic weightings (Pedroso, 2017). To overcome these limitations, recently the multi-trait index based on factorial analysis and genotype-ideotype distance index (MGIDI) was suggested by Olivoto and Nardino (2020). Indeed, MGIDI focuses on the selection of best genotypes where multiple traits have been measured. The use efficiency of this index in identifying the superior genotypes was also reported in several studies (Benakanahalli (2021), Pour-Aboughadareh and Poczai (2021), Pour-Aboughadareh et al. (2021).

8. Appendix III

Brief overview of the mechanisms of the root trait responses to alleviate environmental stresses

8.1. Water stress

8.1.1. Root traits

Aerenchyma formation

Aerenchyma is tissue containing a high proportion of gas-filled spaces and provides a low-resistance pathway for long-distance gas transport (Armstrong 1979). In water stressed conditions, large root cortical aerenchyma reduces respiration, nutrient content of root tissues, and the metabolic cost of soil exploration (Oyiga, Palczak, Wojciechowski, & al., 2020).

In waterlogged conditions, a major limitation is oxygen transportation from shoots to submerged tissues. Root aerenchyma formation can enable efficient gaseous exchange between the atmosphere and the root tip, greatly improving oxygen transportation from shoots to submerged tissue in the root cortex, to maintain normal aerobic metabolic activity. Root cortical aerenchyma also reduces root respiratory consumption, ensuring normal growth of new tissues (Manik et al., 2022).

Higher adventitious root porosity

Porosity is volume of gas-filled intercellular spaces (% gas volume per unit tissue volume). Porosity is an indicator of aerenchyma formation and as such the mechanisms to achieve resilience under waterlogging conditions are similar. Namely, increased oxygen movement into the roots benefits cellular energy status, in turn increasing root growth and tissue survival in anaerobic/hypoxic (low oxygen) conditions. Other benefits of increased oxygen movement in the roots are increased nutrient uptake and translocation to the shoots (Broughton et al., 2015).

More root hairs

Root hairs are the tubular-shaped outgrowths of root epidermis cells, which increase total soil exploration and the root-soil contact area.

An increased number of root hairs function to increase the interaction between the plant and the soil. Root hairs facilitate the uptake of water by substantially reducing the decline in water potential at the interface between root and soil in rapidly transpiring plants. This is achieved by the greater water carrying capacity of root hairs and the provision of a shorter path for osmosis. Root hairs also access smaller soil pores than the main root axis, allowing the roots to influence a greater soil volume. Root hairs also facilitate rhizosphere development and the formation of a rhizosheath, which protects roots from drought (Marin et al., 2021).

Deeper rooting

Deeper rooting allows plants to access water otherwise lost to deep drainage. This can improve productivity in water deficit conditions. Deep rooted crops benefit from accessing water stored deeper in the soil profile in times of drought.

Early root vigour

Early root vigour relates to the rapid development of roots in length and density. Under water deficit conditions, this trait is advantageous for rapidly accessing water stored in deeper soil layers (Puertolas et al., 2014). This can facilitate successful establishment and seedling survival under conditions where the soil surface dries up rapidly while sufficient soil moisture remains available in deeper zones. This trait also reduces the chance of water stress in situations of early drought.

Increased distribution of roots at depth

Greater root length density (RLD) at lower depths allows plants to obtain more water from deep soil horizons which is advantageous in water deficit environments. This is driven by the increased surface area caused by greater RLD which allows increased water extraction from lower layers of soil.

Greater root dry biomass

Greater root dry biomass is often associated with deeper rooting and greater RLD at depth and thus enhanced capacity of a plant to extract water from deeper soil strata and to take up nutrients (Kumar et al., 2012). The benefit of greater root dry weight assumes that it acts as a reliable proxy for RLD. If it is not related to RLD then greater root dry weight may be disadvantageous because of the metabolic cost of producing the roots.

8.1.2. Rhizosphere traits

Arbuscular Mycorrhizal fungi (AMF)

AMF form symbiotic relationships with plants involving the intake of carbon from the plant in exchange for nutrients. AMF usually provide an overall benefit for plants through the mechanisms described below.

AMF associations can improve plant acquisition of soil water. One mechanism for this is AMF produce external mycelium which allows the exploration of a higher soil volume and so a better contact with plant roots. AMF can also alleviate the negative effects of water stress on plants by indirectly increasing photosynthetic activity, soluble proteins contents and osmotic regulation and decreasing electrolyte leakage. Furthermore, AMF enhance plant production under drought conditions through the absorption of non-mobile nutrients such as phosphorus P, Zn and Cu (Jerbi et al., 2022). AMF also connect plants to fungal hyphal networks which provide water and nutrients to the plant in exchange for carbohydrates (Valdebenito et al., 2022). This improves water absorption of the plant and allows plants to maintain higher hydration. AMF help the plants maintain the turgor of their organs, which allows for the natural activity of the cells in general to be maintained, as they are primarily linked to the photosynthetic machinery. AMF symbiosis increased stomatal conductance, net photosynthesis, and related parameters, showing a higher photosynthetic capacity in these plants. AMF inoculation also regulates free proline accumulation which plays a critical role in maintaining relative water content in soybean and water potential (Tian et al., 2013)

8.2. Phosphate trait responses

8.2.1. Root traits

Greater root hair length and more root hairs

Root hairs are the tubular-shaped outgrowths of root epidermis cells which increase total soil exploration and the root-soil contact area. Therefore, more and longer root hairs can access a greater volume of soil which provides a greater source of phosphate. Root hairs can also acquire resources across air-filled voids and aid penetration through strong soils by acting as bracing structures (Haling et al., 2013). More and longer roots hairs provide greater competition for P near the root surface, in turn creating a P depletion zone near the root surface (Gahoonia & Nielsen, 2003). Given the limited diffusion of P, the depletion zone has to be overcome by continuous growth (of root hairs and/or roots) to reach to new soil volumes.

Increased root length density

Increased RLD provides increased root-soil contact which increases the efficiency of nutrient uptake by the plant, especially in resource limited and spatially heterogeneous environment (Flave et al., 2014). This is particularly important in P acquisition as P is highly immobile, so roots have time to respond to low concentrations via architectural changes in the topsoil.

Early root vigour

Early proliferation of the root system enhances the ability of a crop to acquire P to enable plant growth and canopy development by increasing the soil-root surface area. Which can increase P uptake efficiency in the core R2R crops. In potatoes, This associated increase in P uptake efficiency (PUPE) was strongly correlated with potato tuber yields (White et al., 2018). Therefore, improving juvenile root vigour should improve tuber yields of early varieties and short season crops, with greater effects in low P availability soils. As well potatoes, improving early root vigour in cereals and legumes should also increase PUE.

8.2.2. Rhizosphere Traits

Phosphate solubilizing bacteria

Phosphate Solubilizing Bacteria (PSB) can enhance P uptake through remobilization of recalcitrant forms of P in soil. PSB are a class of plant growth-promoting bacteria (PGPR). Remobilization mechanisms include local soil acidification through direct proton release, linkages to ammonium assimilation, or production of organic acids (e.g. gluconic acid, auxin, and citric acid) (Amy et al., 2022).. PSB facilitate the hydrolysis of a range of phosphorus compounds, increasing bioavailability for plant uptake (Malboobi et al., 2009). PSB produce phosphatases, which induce the release of phosphorus from organic compounds in soil or fertilizers by dephosphorylating (hydrolysing) phospho-ester or phosphoanhydride bonds. This process removes a phosphate ion and thus creates a free hydroxyl group and soluble phosphate (Ibáñez et al., 2021). Some other PGPR traits of PSB's include siderophore production, phytate utilization and HCN (Hydrogen cyanide) production (Ibáñez et al., 2021).

Rhizobia – elite strains with specific functionality

In addition to the main function of rhizobia to fix atmospheric N, they can also increase P availability by producing organic acids to decrease soil pH which triggers phosphate solubilization (Ouerghi et al., 2022).

Root exudates

Selected root exudates, such as organic acids, cause rhizosphere acidification, chelation and exchange reactions to improve phosphorous mobilisation of organic and inorganic P sources (Touhami et al., 2020).