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Significance of root hairs in developing stress-resilient plants for sustainable crop production

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Abstract

Root hairs represent a beneficial agronomic trait to potentially reduce fertiliser and irrigation inputs. Over the past decades, research in the plant model *Arabidopsis thaliana* has provided insights about root hair development, the underlying genetic framework, and the integration of environmental cues within this framework. Recent years have seen a paradigm shift, where studies are now highlighting conservation and diversification of root hair developmental programs in other plant species and the agronomic relevance of root hairs in a wider ecological context. In this review, we specifically discuss the molecular evolution of RSL (RHD Six-Like) pathway that controls root hair development and growth in land plants. We also discuss how root hairs contribute to plant performance as an active physiological rooting structure by performing resource acquisition, providing anchorage, and constructing the rhizosphere with desirable physical, chemical, and biological properties. Finally, we outline future research directions that can help achieve the potential of root hairs in developing sustainable agroecosystems.

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Introduction

Land plants evolved with vital rooting structures that contributed to their diversification and adaptation to the new habitats, especially in low fertility soils. Among them, rhizoids are the most primitive and sole rooting organ in early land plants and bryophytes (Goffinet, Buck & Shaw 2008; Renzaglia, Villarreal & Duff 2008). Like rhizoids, root hairs are present as unicellular epidermal appendages on the roots of vascular plants (Leavitt 1904; Brown, George, Neugebauer & White 2017). Both emerge as the first line of root contact with the soil and assist in anchorage and resource (water and nutrients) acquisition (Keyes *et al.* 2013; Carminati *et al.* 2017). Beyond these fundamental functions, root hairs shape the soil structure, enhance soil health, and promote beneficial microbial diversity (Robertson-Albertyn *et al.* 2017; Koebernick *et al.* 2017). Collectively, these functions enable root hair contribution to maintaining vegetation, particularly in harsh environments (Shane, McCully, Canny, Pate & Lambers 2011).

Over the past decades, intensive research in the plant model *Arabidopsis thaliana* has led to a significantly improved understanding of root hair development and underlying genetic and molecular programs (Datta *et al.* 2011; Salazar-Henao, Vélez-Bermúdez & Schmidt 2016). This vital understanding further aided the evaluation of how phytohormone signaling feeds into this genetic framework to integrate biotic and abiotic signals from the rhizosphere and fine-tune root hair growth, density and morphology (Vissenberg, Claeijs, Balcerowicz & Schoenaers 2020). Such wealth of knowledge provided an opportunity to probe the similarities of root hair developmental programs in other plant species (Nestler *et al.* 2014; Kim, Han & Dolan 2017), and to investigate the agronomic relevance of root hairs (Horn, Wingen, Snape & Dolan 2016; Marin *et al.* 2021). As a result, in recent years, large scale genetic mutant screens and transcriptomics studies have provided key insights into the conservation and diversification of root hair developmental programs in land plants (Huang, Shi, Wang, Ryu & Schiefelbein 2017; Bonnot *et al.* 2019). Furthermore, an increasing number of mutant and genetic diversity studies in various crops under different environmental conditions are showing key roles of root hairs in maintaining plant fitness in a wider ecological context including sustainable agroecosystems (Zhang *et al.* 2021a; Marin *et al.* 2021).

In this review, we particularly focus on the molecular evolution of root hair development in comparison to similar rooting structure called rhizoid, especially the RSL (RHD Six-Like) pathway and epidermal cells patterning. We highlight the essential properties of root hairs that helped land plants establish on earth and shaped such diversity. We also sketch a holistic viewpoint on how root hairs' widespread contributions can synergistically act with edaphic factors in improving plant survival and play an important role in achieving yield protection in suboptimal conditions (Marin *et al.* 2021). Lastly, we discuss recent studies that explored genetic diversity in root hair traits and their agronomic relevance as an important resource for breeders for developing future climate-resilient agroecosystems.

Root hair development

Root hairs are long tubular extensions of the specialised root epidermal cells called trichoblasts (Leavitt 1904; Grierson, Nielsen, Ketelaarc & Schiefelbein 2014). The development of root hairs occurs in three main stages, i.e., cell fate specification, initiation of outgrowth and elongation via tip growth (Figure 1) (Dolan *et al.* 1994; Carol & Dolan 2002). In Arabidopsis, root hair forming trichoblasts are specified by a complex transcriptional regulatory network operated by a set of early acting patterning genes that create a cell position-dependant distribution of hair and nonhair cells (Berger, Haseloff, Schiefelbein & Dolan 1998a; Berger, Hung, Dolan & Schiefelbein 1998b; Dolan 2006). Subsequently, specified root hair cells initiate the outgrowth of root hair through a cascade action of *RHD6 (Root Hair Defective 6)* and *RSL (RHD Six-Like)* family regulatory genes encoding basic helix-loop-helix (bHLH) transcription factors. This further activates the downstream root hair morphogenesis genes including cell wall synthesis, ion transport and reactive oxygen species regulation, generating the unidirectional tip growth of root hair (Menand *et al.* 2007; Won *et al.* 2009; Vijayakumar, Datta & Dolan 2016).

Root hairs are found on sporophytic roots of nearly all vascular plants. Similar rooting structure rhizoids are also observed in the gametophyte of early land plants (liverworts, mosses, hornworts, lycophytes and monilophytes), suggesting a common evolutionary origin (Supplementary Figure 1) (Menand *et al.* 2007; Jones & Dolan 2012; Proust *et al.* 2016). Studies in different plant species have shown distinct root hair distribution patterns (Figure 2), morphology and expression of genes controlling these processes, suggesting diversification of root hair development genes in vascular plants (Datta *et al.* 2011; Huang *et al.* 2017).

Evolution of RSL family genes and regulation in controlling tip growth and epidermal cell differentiation

RSL family genes are required for both rhizoid and root hair development (Menand *et al.* 2007; Honkanen *et al.* 2016); however, their negative regulatory mechanism controlling epidermal cell differentiation shows independent evolution among land plants (Honkanen, Thamm, Arteaga-Vazquez & Dolan 2018).

Land plants carry many members of a subgroup of the bHLH transcription factor gene family, bHLHVIIIc, which as a result of multiple duplications, form two major clades (RSL class I and II) (Menand *et al.* 2007). On the contrary, in streptophyte algae (*Chara brauni* and *Cholechete nautrilla*), bHLHVIIIc are comprised of a single member with no involvement in rhizoid development; indicating neo-functionalization of VIIIc proteins in land plants and an ancient duplication event in the common ancestor of bryophytes and vascular plants that resulted in two major classes of RSLs (Bonnot *et al.* 2019). Apart from sequence conservation in land plant lineages, RSLs regulate initiation and elongation of similar tip-growing rooting structures; hence, they also exhibit functional conservation, i.e., RSL1, and 2 of bryophytes (RSL class I) can recover Arabidopsis *atrhd6* root hair mutants (Menand *et al.* 2007). In vascular plants, RSLs are specific to root hair development, but bryophytes employ the RSL toolbox (in addition to rhizoids) in the development of epidermal (gemma cup and mucilage papillae in liverworts) and other tip growing (caulonema in mosses) structures (Menand *et al.* 2007; Jang, Yi, Pires, Menand & Dolan 2011; Proust *et al.* 2016).

Even though RSLs regulate tip-growing rooting structures in both seed plants and bryophytes, the gene regulation and the network topology vary. In seed plants, RSL class I generally induces RSL class II genes (but can be inhibitory for some) (Pires *et al.* 2013). In contrast, class II induction by class I is absent in *Physcomitrella patens*; only *PpRSL6* gets inhibited by RSL class I members. Further, auxin regulation of the RSL network differs. In *P. patens,* auxin regulates both classes I and II genes; but in Arabidopsis, auxin can only regulate RSL class II genes (Jang *et al.* 2011; Pires *et al.* 2013). The network's topology becomes highly complex in seed plants with the addition of multi-phytohormonal control, protein interactions, and transcriptional regulations (Datta, Prescott & Dolan 2015; Feng *et al.* 2017; Marzol, Borassi, Denita Juárez, Mangano & Estevez 2017; Bhosale *et al.* 2018; Han, Zhang, Yang & Hu 2020).

Negative regulation of RSL class I narrates a different story from the conserved nature of the RSL proteins. Inhibitory action on RSL class I exhibits independent evolution among land plants species and divergence for molecular action and stage of inhibition (Thamm, Saunders & Dolan 2020). Among bryophytes, *Marchantia polymorpha* inhibits RSL1 through a microRNA *FEW RHIZOIDS1 (MpFRH1)* by binding to the *MpRSL1* transcript. MpRSL1 positively regulates *MpFRH1* expression in rhizoid cells, from where *MpFRH1* travels to adjacent cells to inhibit *MpRSL1* mRNA (Figure 3). The extent of *MpRSL1* expression is randomly distributed among early differentiating epidermal cells, i.e., the ones with more RSL1 expression form rhizoid cells and vice-versa for non-rhizoidal cells (Figure 2b; Figure 3). Further, MpFRH1 target sites are conserved among liverworts only and are absent in mosses or any other land plant lineage (Honkanen *et al.* 2018), suggesting independent and early evolution in liverworts after they diverged from the rest of the land plants. Also, mosses and hornworts lack GL2 like proteins that inhibit RSL class I in Arabidopsis (Lin *et al.* 2015a); thereby, there could be probable unknown RSL inhibition mechanisms in these lineages.

Being the focal regulator, the negative regulation of RSL class I is the ultimate checkpoint for cell fate decisions. Due to its independent evolution among different lineages and species, epidermal patterning displays immense diversity among angiosperms. Random patterning (Type 1) is prevalent, although many of the lineages show asymmetric division (Type 2) or stripped patterning (Type 3) (Figure 2a) (Datta *et al.* 2011). Arabidopsis belongs to Type 3 (stripped patterning), and being the model plant, most molecular and genetic studies are done on Arabidopsis for understanding cell patterning. Arabidopsis genes controlling cell fate have homologs in various vascular plants; though, it is not valid for many of the major cell fate-determining genes (Huang *et al.* 2017). Some are Arabidopsis specific, like *MYB23/WER*, which can be an essential player for stripe patterning. Similarly, *TTG2* and *GL3/EGL3* are specific to eudicots. The variation in the genetic tool kit indicates independent evolution in different lineages of land plants, thus, generating considerable diversity in cell patterning (Huang *et al.* 2017).

Root hair development has also been studied in monocots, especially in cultivated species. Monocots display internal diversity for epidermal patterning and their mechanisms differ from Arabidopsis (Kim & Dolan 2011; Marzec, Melzer & Szarejko 2014). However, fundamental players like RSL genes work in a similar way. Both RSL class I and class II genes are known in rice and other species that positively regulate root hair development (Han *et al.* 2016; Kim *et al.* 2017; Moon *et al.* 2019). Further, various mutant screens have identified many root hair developmental genes. These mutants display retarded root hair growth and can be of varied types (root hairless mutant, bud root hair mutant and mutant with short root hairs) depending on the stage of development in which the mutant gene is involved (Table 1). For the last two decades, these mutants have helped significantly to understand root hair physiology and identify diverse root hair functions (Table 1).

Conquering the planet: role of root hairs in root anchorage, penetration, and soil adhesion

Rooting microstructures such as root hairs and rhizoids assist in effective attachment to the substratum. This section focuses on the biophysical and biochemical properties of root hairs that allow roots to anchor and penetrate the ground.

Roots penetrate the ground via turgor-mediated axial extension and anchors itself behind the elongation zone. Here, root hairs assist in penetration of the root by resisting the backward push from the ground (Bengough, McKenzie, Hallett & Valentine 2011; Bengough, Loades & McKenzie 2016). To counter the backward thrust, root hairs dispense the required tensile strength and provide superior anchorage by firmly adhering to soil pore walls (Bengough *et al.* 2011; Bengough *et al.* 2016), making roots with root hairs penetrate deeper. However, this advantage of root hairs in penetration is selectively present for low strength soil and absent for denser soil. As root hair length is dependent on the soil strength (Haling *et al.* 2014), shorter root hairs in high strength soil may result in poor anchorage to the pore walls, thus losing the advantage of superior anchorage and deeper penetration that is present in low strength soil (Bengough *et al.* 2016).

Superiorly anchored roots with longer root hairs can resist soil disruption (Choi & Cho 2019) and can also aid in adhering to some of the difficult substrates (Huang *et al.* 2019; Zenone *et al.* 2020). One of the challenges that many species, e.g., climber, English Ivy (*Hedera helix*) and seagrass, *Posidonia oceanica* (L.), face is adhering to non-soil hard surfaces against forces like gravity and sea currents. *H. helix* climbs the vertical walls using its adventitious root system, where root hairs secrete a yellow adhesive from small protrusions on its tip. This adhesive comprises arabinogalactan protein-rich nanoparticles that can enter the substrate's micro aberrations and tether base and root hairs (Zhang, Liu, Prest & Fischer 2008; Melzer *et al.* 2010; Lenaghan & Zhang 2012; Huang *et al.* 2019). Attachment further strengthens after desiccation of root hairs due to a hardening of adhesive and change in root hairs' shape (Melzer *et al.* 2010).

Once the root hair is desiccated, it loses its soft protoplasm, and as per the arrangement of cellulose microfibrils of the stiff cell wall, root hairs change their shape to short, spiralled, and flat-bodied with bent tips. These desiccated *H. helix* root hairs can easily stick inside the microcavities and perforations, and due to shortening during desiccation, root hairs reinforce the attachment by pulling roots closer to the substrate (Melzer *et al.* 2010). In a climber *Syngonium podophyllum*, the cell wall of desiccated root hairs cracks and leads to spiral and helical crack hairs (Yang & Deng 2017). Helically cracked root hairs could act as shock absorbers against growing plants and wind (Yang & Deng 2017). Both *H. helix* and *S. pdophyllum* root hairs resist breaking and remain attached to the substrate (along with the hardened mucilage/adhesive) by modulating their shape after desiccation.

However, in *P. oceanica* seedlings, adaptive change in the shape of living root hair tip generates the mechanical architecture for root hair adherence. The root hair tip self-replicates the substrate’s micro-texture and form mushroom-like branch structures depending on the substrate’s roughness and coarseness (Zenone *et al.* 2020). It ensures suction and interlocking to establish seedlings against the sea currents and massive storms. Thus, both biophysical and biochemical properties of root hairs assist the plant in attaching or penetrating the ground; however, these attributes vary as per the condition and the substrate.

Root hair maintains rhizosphere structure, chemical, and biological properties

Root hairs affect both abiotic and biotic units of the rhizosphere that shapes soil structure, influence the boundaries of resource depletion and accumulation zones, accrue soil carbon, and maintain soil microbiota (Figure 4) (Brown *et al.* 2017; Robertson-Albertyn *et al.* 2017; Holz, Zarebanadkouki, Kuzyakov, Pausch & Carminati 2018).

Role of root hair in rhizosheath formation

Mucigel promotes soil aggregation in the vicinity of roots, where these soil aggregates get enmeshed in a scaffold of root hairs to form rhizosheath (Burak *et al.* 2021). Consistently, *nrh (no root hair), brb (bald root barley),* and *brh (bud root hair)* mutants of barley form minimal rhizosheath (George *et al.* 2014; Haling *et al.* 2014; Burak *et al.* 2021) and root-hairless mutants of different plant species lack or have reduced rhizosheath (Brown *et al.* 2017). Rhizosheath forms a functional bridge between the bulk rhizosphere soil and the plant, assisting in water dynamics, alleviating nutrient deficiencies, and protecting against desiccation and heat stress (Shane *et al.* 2010; Brown *et al.* 2012; Haling *et al.* 2013; Zhang *et al.* 2021a). Therefore, dissecting the role of root hair traits in beneficial rhizosheath formation is imperative for crop research.

Root hair length is a promising candidate to consider as a proxy for rhizosheath size, while some studies show no correlation (Haling, Simpson, Delhaize, Hocking & Richardson 2010b; Haling *et al.* 2013; George *et al.* 2014; Delhaize, Rathjen & Cavanagh 2015; Brown *et al.* 2017; Ruiz *et al.* 2020). For example, Brown *et al.* (2017) reported that rhizosheath size positively correlates with root hair length up to 0.28 mm. After this length, other root hair traits such as density, persistence, and shape also become apparent in influencing rhizosheath size. Reports about the correlation between root hair density (Haling, Richardson, Culvenor, Lambers & Simpson 2010a) and persistence with rhizosheath size are limited, however, their importance cannot be neglected in some instances. Like in *Lyginia barbata* (perennial grass, native of western Australian sand plains), plants form sandsheath with particles of sand enmeshed in persistent and dense hairs (Shane *et al.* 2011). The persistence of dead root hairs is so effective that even after removing the plant, the structure of the sandsheath remained intact. Root hairs acquire persistence because of thick cell walls composed of ferulic acid, lignin, and probably layered with suberin (Shane *et al.* 2011). The property of persistence is also present in mesophytic grasses (Weaver 1925; Goossens 1935), though the biochemical attributes have not yet been explored (Knirel *et al.* 1989). Further, root hairs' shape before and after desiccation is an exciting and less explored attribute as shape enhances adherence of root hairs with the substrate (Melzer *et al.* 2010; Zenone *et al.* 2020). For instance, hooked or branched root hairs could adhere to the soil particles more efficiently and thus, root hair shape may contribute to the formation of rhizosheath (Brown *et al.* 2017). Overall, irrespective of the varied contribution of root hair traits to the rhizosheath size, these morphological traits work more or less similarly through increasing soil adhesion leading to better scaffolding of soil particles.

Apart from morphological attributes, root hairs could contribute to rhizosheath formation through mucilage exudation. Mucilage works as a cementing material for the soil particles and it can be of both plant and microbial origin (Watt, McCully & Jeffree 1993; Read *et al.* 2003). Root cap and root epidermis are the major contributors in mucilage secretion, while the involvement of root hairs is not yet concrete (Badri & Vivanco 2009). Nevertheless, some recent evidence suggests that rhizoids and root hairs exudate adhesive substances, including soil aggregation promoting polysaccharides (Sherrier & VandenBosch 1994; Galloway *et al.* 2018, 2020). Moreover, root hairs indirectly add to the mucilage pool by providing a colonizing surface to microbes (Buddrus-Schiemann *et al.* 2010). Mucilage from the bacteria growing near the root hair surface can directly contribute to soil aggregation, where root hairs provide an effective scaffold for rhizosheath formation.

Root hair-microbe interaction

Root hairs provide a micro-environment conducive to soil microbes and root endophytes for colonizing root hair surface or interior (Buddrus-Schiemann *et al.* 2010; Prieto *et al.* 2011). Largely Plant Growth Promoting Rhizobacteria (PGPR), nitrogen-fixing rhizobacteria, and pathogenic bacteria colonize root hairs, forming non-symbiotic, symbiotic, or pathogenic interactions (Ribaudo *et al.* 2006; Downie 2010; Pečenková *et al.* 2017). These interactions with root hairs are guided by microbial and plant originating chemical factors that act as adhesives, antimicrobial agents or growth modulators (Esseling, Lhuissier & Emons 2003; Ribaudo *et al.* 2006; Downie 2010) and their interplay with each other and with the molecular machinery is essential for the whole process (Poitout *et al.* 2017; Wheatley & Poole 2018).

For instance, in the case of rhizobia, which forms nitrogen-fixing nodules in leguminous plants, various chemical factors are involved in the critical events of the initial phase of infection, i.e., root hair curling and infection thread generation. Symbiotic rhizobia first bind to the root hair surface using lectin binding glucomannan/rhicadhesin proteins (Downie 2010; Wheatley & Poole 2018). Once attached, rhizobia then release Nod factors, causing reorientation of root hair tip growth towards the attachment site (Esseling *et al.* 2003). Steady release of nod factors by multiplying bacteria causes continuous tip growth resulting in curling of root hairs (Lhuissier, De Ruijter, Sieberer, Esseling & Emons 2001; Esseling *et al.* 2003). Here, root hair tip growth results from the nod factor-induced calcium spiking (Lhuissier *et al.* 2001) and RhoGTPases (Ke *et al.* 2016). Subsequently, nod factors initiate the infection thread inside the root hair, providing an entry for the bacteria from the curled root hair pocket to the cortical cells (Murray 2011).

Root hairs also interact with diverse PGPRs through chemical factors that affect root hair growth. Some non-symbiotic PGPRs and pathogenic strains modulate root hair growth by increasing root hair length and density in ethylene dependent manner (Ribaudo *et al.* 2006; Pečenková *et al.* 2017), while some induce auxin signaling (Zamioudis, Mastranesti, Dhonukshe, Blilou & Pieterse 2013) or utilize pathways independent of auxin (Ortíz-Castro, Martínez-Trujillo & López-Bucio 2008). Like bacterial quorum-sensing signals, N-acyl-L-homoserine lactones (AHLs) can induce root hair elongation independent of auxin (Ortíz-Castro *et al.* 2008). Such diversity in inducing systems involving different molecular pathways and chemical factors suggests that bacterial-induced root hair growth depends on the type of interaction and the interacting bacteria.

Microbes induce longer and denser root hairs that benefit bacteria by providing more colonizing space, attachment sites, and entry points. In addition, they also have multiple advantages for the plant, like in the presence of an endophyte 3F11, which is closest to *Enterobacter asburiae*, the root hair length of the plant increases and facilitates the uptake of solubilized phosphorus (Shehata, Dumigan, Watts & Raizada 2017). Root hairs of *Zea nicaraguensis* (wild corn, grows on the insoluble rock-P source) are a natural habitat for 3F11, where it acidifies the rhizosphere and solubilizes rock-P. Likewise, another *Enterobacter* sp. M6 induces root hair growth. Longer root hairs and M6 colonies form a physio-chemical barrier against the plant fungal pathogen *Fusarium graminearum* (Mousa *et al.* 2016). Here, root hairs elongate by M6 produced auxin and form root hair endophytic stacks (RHESt) along the rhizoplane. M6 in RHESts engulf the fungal pathogen acting as a biocontrol agent (Mousa *et al.* 2016). Thus, root hairs form mutualistic interactions with specified microbial species benefiting both plant and microbes.

Apart from specific interactions, root hairs can influence the entire microbial diversity in the endosphere and rhizosphere. The endosphere becomes more diverse with higher root hair density; however, conflicting reports exist for its impact on rhizosphere microbiota (Fitzpatrick *et al.* 2018). In a study with 30 angiosperms, rhizosphere microbial diversity had no dependence on root hair density (Fitzpatrick *et al.* 2018). On the contrary, the absence of root hairs promotes *Bacillus subtilis* growth on the rhizoplane, depicting root hairs' influence on the rhizosphere microbiome (Massalha, Korenblum, Malitsky, Shapiro & Aharoni 2017). Similarly, barley root hairless mutants (*rhl1.a* and *rhp1.b*) preferentially supported a microbial species growth that reduced the rhizosphere's microbial diversity (Robertson-Albertyn *et al.* 2017). However, in the presence of root hairs, the rhizosphere was more diverse with a higher percentage of PGPRs (Robertson-Albertyn *et al.* 2017). Thus, root hairs' role in microbe interactions is more than just providing a suitable colonizing environment; their influence goes further in the rhizosphere, where root hairs enhance microbial diversity, particularly for PGPRs, thus affecting the biological richness of the rhizosphere.

The emerging role of root hairs in soil organic carbon accrual

Root hairs could modulate soil organic carbon (SOC) dynamics by contributing to root exudation and influencing physio-chemical soil matrix and rhizosphere microbiota (Holz *et al.* 2018; Zhang *et al.* 2020a). Microbes metabolize root exudates from which a fraction is stabilized to mineral-associated SOC (MASOC) in the soil matrix, and the remaining fraction is channelled for microbial turnover (Dijkstra, Zhu & Cheng 2021). Microbes use this labile fraction for their growth and metabolic needs, from which a part goes into microbial respiration and is released as CO_2 (carbon-dioxide), and the remaining adds as microbial mucilage or litter to the SOC pool. This freshly added microbial necromass flows into the physio-chemical soil matrix to get stabilized. In the soil matrix, already present MASOC can get destabilized and goes back to the labile fraction for microbial use (Dijkstra *et al.* 2021). Here, root hairs could affect both microbial activity and physio-chemical soil matrix, thus influencing the gain or loss of the SOC pool (Figure 4).

Exudation from root hairs directly adds organic carbon to the soil. In a study comparing the *brb* root hair less mutant to the wild type, the wild type had three times higher rates of exudation (Holz *et al.* 2018). These exudates act as a substrate for microbes, though some, like organic acids, can directly interact with soil minerals to form mineral complexes on the soil matrix (Jones & Edwards 1998; van Hees, Vinogradoff, Edwards, Godbold & Jones 2003). However, in certain reports, organic acids in the soil matrix can promote the conversion of MASOC to labile carbon (Keiluweit *et al.* 2015). This disparity might be the cause of the efflux of carbon in certain reports (Pausch *et al.* 2016). Although, increased efflux could also be due to the higher input in the case of root hairs.

Despite higher exudation and carbon allocation to the rhizosheath in WT plants, Holz *et al.* (2018) observed a similar efflux of CO_2 from soil and root respiration in WT and *brb*, which suggests a role of root hairs in carbon stabilization and maintaining efflux. This will result in carbon accrual as more carbon is coming into the soil in the presence of root hairs. Thus, root hairs seem to stabilise carbon in the soil via several possible mechanisms.

Root hairs could affect carbon sequestration by controlling microbial growth in favour of carbon accrual. In the presence of root hairs, microbial metabolic quotient (MMQ, microbial respiration per unit of biomass) gets reduced, corresponding to efficient use of carbon for microbial biomass and lower carbon efflux compared to *brb* (Holz *et al.* 2018). Similarly, maize (WT) accumulates higher microbial biomass in the rhizosphere than *rth3 (roothairless 3)* (Zhang *et al.* 2020a). Microbial hotspots with WT carried less efficient and highly active enzymes, indicating the presence of slow-growing yet substrate efficient microbes. These microbes add more carbon to biomass, i.e., higher SOC accumulation and less carbon get lost from the soil (Zhang *et al.* 2020a). This shift in microbial behaviour could be due to an increased supply of substrate (exudation) in the presence of root hairs.

Besides carbon input, soil pores of size distribution ranging from 30-150 µm, promote microbial hotspots having higher enzyme activity resulting in carbon sequestration in the rhizosphere (Kravchenko *et al.* 2019). Therefore, root systems with more soil matrix around 30-150 µm pores have increased soil volume available for carbon stabilization through microbial activity (Kravchenko *et al.* 2019). Interestingly, root hairs modify the inter-aggregate pores near the root surface (up to 200 µm) by decreasing the number of bigger pores (near 200 µm) and increasing pores with size below ~160 µm (Koebernick *et al.* 2017, 2019). Therefore, root hairs could also play their part in regulating microbial growth for carbon accrual by modifying soil pore structure in addition to carbon input.

Acquiring the resources: physiological importance of root hairs in water and nutrient uptake

Role of root hairs in water uptake

Root hairs modulate the water uptake dynamics and plant water status in drying soil and/or high evaporative demand. However, root hairs have no significant advantage in water uptake in wet soil and/or low evaporative conditions (Dodd & Diatloff 2016). Thus WT and *brb* mutant (of barley) displayed similar transpiration rates and leaf elongation during well-watered conditions (Dodd & Diatloff 2016). Also, during low evaporative demand, *brb* and WT have similar ability to take up water (Carminati *et al.* 2017). However, in drying soil, *brb* mutant (compared to WT) displayed a sharp increase in xylem suction at high transpiration rates due to their lower ability for water uptake (Carminati *et al.* 2017). Thus, root hairs help to maintain the water uptake in dry conditions, and they do so by extending the effective physiological radius of the root. This increase in radius reduces the decrease in water potential at the root-soil interface during high transpiration (Carminati *et al.* 2017). Further, the water uptake is severely affected in drying soil due to a decrease in soil hydraulic conductivity and matric potential between root-soil interface and bulk soil (Carminati *et al.* 2017). Root hair provides an alternate path for water with increased hydraulic conductivity, lower flow rate, and larger volume, resulting in a small drop in matric potential and sustained water uptake (Carminati *et al.* 2017).

In dry conditions, higher soil-root hydraulic resistance induces stomatal closure to maintain leaf xylem water potential (Abdalla, Carminati, Cai, Javaux & Ahmed 2021) (Figure 5a). Therefore, root hairs, by providing higher hydraulic conductivity, can impact leaf water status. In barley, root hairs reduce drought effects by maintaining higher leaf water potential and lower leaf ABA (abscisic acid), resulting in greater yield stability for WT plants than *nrh*, *brh* and *srh* (*short root hair*) mutants (Figure 5a, b) (Marin *et al.* 2021). Overall, root hairs act as an extended physiological radius of the root where they control the water potential gradient, thereby maintaining leaf water potential in a highly transpiring scenario (Segal, Kushnir, Mualem & Shani 2008; Carminati *et al.* 2017).

Besides root hairs' direct or indirect role in drought mitigation, they can work as sensors for soil drying and activate stress-responsive pathways. In particular, inducing ABA biosynthetic genes in WT (of barley) compared to *rhl1.a* mutant (Kwasniewski *et al.* 2016). But interestingly, during soil drying, *brb* mutant showed no difference in xylem ABA content when compared with WT (Dodd & Diatloff 2016). Most probably, it was difficult to analyze the effect of root hairs in this case as *brb* mutant had higher root biomass that compensated for the absence of root hairs and resulted in similar shoot parameters when compared with WT during soil drying (Dodd & Diatloff 2016). Unlike ABA induction by root hairs, it is very much clear that ABA induces root hair growth during dry conditions. In rice and barley, endogenous ABA induces the formation of rhizosheaths with higher water content by increasing root hair length during soil drying (Zhang *et al.* 2021b a). The barley *Az34* ABA deficient mutant had shorter root hairs both in wet and dry conditions, and exogenous ABA could increase root hair length of *Az34* mutants during soil drying (Zhang *et al.* 2021b). However, full recovery of root hair length phenotype of *Az34* was only possible with exogenous auxin treatment (Zhang *et al.* 2021b). Thus, soil drying-induced ABA promotes root hair growth via auxin mediation, resulting in longer root hairs and larger rhizosheaths (Zhang *et al.* 2021b a).

While drying-induced ABA elongates root hair length in grasses, Arabidopsis and tomato display contrasting behaviour by reducing root hair length in dry conditions (Schnall & Quatrano 1992; Karanja *et al.* 2021). Interestingly, shortening of root hairs in Arabidopsis is also controlled by ABA as ABA insensitive mutants (*abi1* and *abi2*) failed to show this response when treated with exogenous ABA (Schnall & Quatrano 1992). ABA reduces tip growth by suppressing *RSL2* transcription by inducing a transcription factor, OBF BINDING PROTEIN4 (OBP4) (Rymen *et al.* 2017). OBP4 binds on the promoter of *RSL2* to inhibit *RSL2* expression. Among various class II bHLH transcription factors that respond to development and environmental signals like drought and P deficiency, the ABA response of root hairs is specifically governed through RSL2 in Arabidopsis (Rymen *et al.* 2017).

Various environmental stresses like soil drying and nutrient deficiencies can aggravate the impact of each other. For example, delay in precipitation or less saturated soil can impede P uptake (Ruiz *et al.* 2020). Similarly, N (nitrogen) and P deficiencies can reduce root hydraulic conductivity for water uptake (Rhee, Chung, Katsuhara & Ahn 2011). Therefore, root hairs often effectively deal with the combined stress of nutrient deficiency and soil drying. In a combined drought and P deficiency condition, barley genotypes harbouring root hairs perform better with sustainable yield than *nrh* and *srh* mutants (Brown *et al.* 2012). Daly, Keyes, Masum & Roose (2016) suggest that root hairs may contribute more (in comparison with roots) to P uptake in low moisture soils due to root hairs' ability to access soil micropores owing to their microscopic dimensions compared to roots. In conclusion, beneficial effects asserted by root hairs in combined stresses could be due to root hairs' multi-dimensional role in both water and nutrient uptake.

Role of root hairs in nutrient uptake

Root hairs facilitate the acquisition of mineral elements – Potassium (K), magnesium (Mg), N, P, and sulfur (S) – by expanding explorative area and root-soil contact (Schiefelbein, Shipley & Rowse 1992; Gahoonia & Nielsen 1998; Babourina, Hawkins, Lew, Newman & Shabala 2001; Ivashikina *et al.* 2001; Nath 2005; Klinsawang, Sumranwanich, Wannaro & Saengwilai 2018; Liu, Zhang, Fang, Zhang & Jin 2018; Kimura *et al.* 2019). Among the mineral elements, root hairs are particularly effective in acquiring immobile or sparingly soluble nutrients (Misra, Alston & Dexter 1988). Hence, root hairs' participation in the uptake of immobile nutrients like P has been repeatedly modelled and explored in detail.

Plants absorb P through two surfaces, root epidermis and root hairs, and each contributes nearly 50% for the total P uptake (Figure 5c) (Keyes *et al.* 2013). P acquisition via root epidermis requires a vast diffusion zone; whereas, root hairs procure P by minute localized gradients near the surface of soil particles (Keyes *et al.* 2013). Thus, root hair traits like length and curvature can be more beneficial for P uptake from the particle surface (facing root hair) in comparison to root hair density (Zygalakis, Kirk, Jones, Wissuwa & Roose 2011; Keyes *et al.* 2013). Denser root hairs can enhance P uptake by forming a sink in the root hair zone. Although, once P concentration drops to a minimum quantity due to higher absorption and competition between the root hairs, further increase in density would have no benefit (Brown, George, Dupuy & White 2013b; Keyes *et al.* 2013). Experimental studies back up these findings, where impaired root hair length had more impact on P uptake than a decrease in root hair density during P deficiency (Bates & Lynch 2000). Especially in dry soil, root hair density has little impact in acquiring P, whereas root hair length plays a significant part (Zygalakis *et al.* 2011)

Root hair traits like density, length, and branching display plasticity in nutrient deficiencies. Both root hair length and density increase many fold in the P deficiency (Bates & Lynch 1996; Ma, Bielenberg, Brown & Lynch 2001a). Despite their varying importance for P uptake, synergistically, these traits provide an extra edge compared to the additive effect of their individual advantages for P acquisition (Ma, Walk, Marcus & Lynch 2001b). The synergistic plastic response of root hairs under P deficiency requires complex molecular pathways and regulations (Figure 5d). Distinct molecular pathways work in forming longer and denser root hairs during P deficiency, and both pathways get activated locally via sensing P depletion in the immediate vicinity (Bhosale *et al.* 2018; Wendrich *et al.* 2020). Once perceived, a P deficiency signal leads to the accumulation of auxin and induces its signaling in columella, lateral root cap cells, and xylem that orchestrates both the responses (Bhosale *et al.* 2018; Giri *et al.* 2018; Wendrich *et al.* 2020). In xylem, induced auxin signaling activates *TARGET OF MONOPTEROS 5/LONESOME HIGHWAY(TMO5/LHW)* transcription factor complex that triggers local biosynthesis of a mobile signal – cytokinin (Wendrich *et al.* 2020). Cytokinin connects P sensing in the vascular region to the root hair density response at epidermal cells by diffusing outward to the epidermal files, where cytokinin modulates trichoblast cell fate and reduces cell length (Wendrich *et al.* 2020), although it is unknown which cell fate governing proteins are regulated by cytokinin. P deficiency elongates root hair length via two distinct phytohormonal pathways of auxin and ethylene that converge to root hair elongation by activating RSL4 and other root hair elongating genes and processes (Song *et al.* 2016; Feng *et al.* 2017; Bhosale *et al.* 2018) (Figure 5d). Besides P deficiency induced plasticity, ethylene and auxin control root hair length response in iron and boron deficiency (Schmidt W & Schikora A 2001; Martin-Rejano *et al.* 2011) and along with NO (nitric oxide) in Mg deficiency (Liu *et al.* 2018). However, molecular mechanisms are largely unknown that are involved in orchestrating root hair response in nutrient deficiencies other than P; thus, efforts are required to fill this knowledge gap. Further, this will pave the path to understanding root hair roles in multiple and combined nutrient deficiencies.

Genetic diversity of root hair traits in crops: a resource for future sustainable agriculture

The target of enhanced food production is becoming more challenging given the impact of climate change on water availability, deteriorating soil quality, reduction in farmland due to urbanisation and the aim to reduce fertiliser inputs to make agriculture more environmentally sustainable (Anwar, Liu, Macadam & Kelly 2013; Johnson, Runge, Senauer, Foley & Polasky 2014; Tigchelaar, Battisti, Naylor & Ray 2018; Raven & Wagner 2021). Crops with beneficial agronomic traits can help mitigate these constraints. Root hairs represent one of such target traits for future sustainable agriculture as they play multifaceted roles in improving soil resource acquisition and maintaining yield under suboptimal conditions.

With this objective, the last two decades have seen increasing numbers of bi- and multi-parental and genome-wide association mapping studies in various crops that have been developed to identify superior germplasms with improved root hair and root hair-related traits and determining underlying QTLs and genes (Table 2) (George *et al.* 2014; Kohli *et al.* 2020). These studies, along with advanced physiological and phenotypic experiments, further improved our understanding that will facilitate the inclusion of root hair traits in future crop improvement programs. Especially the utilization of phenotypic plasticity, interaction among root hair traits and the environment, and identifying trade-offs that can make the selection of root hair traits more precise.

Plants carry multiple plastic and adaptive traits (e.g., root hair length), which confer superior fitness in adverse environmental conditions. Adaptive plasticity is a trait itself and has its own characteristics: i) it is a property of a genotype, ii) therefore, carries heritable variation among the population, iii) as variation is associated with fitness, the plastic trait evolves by natural selection (Richards, Bossdorf, Muth, Gurevitch & Pigliucci 2006). Thereby, adaptive plastic traits can be selected and introgressed to develop varieties resilient to challenging environmental conditions. For instance, an increase in root hair length and density can significantly improve tolerance to soil P deficiency. However, these traits are controlled by complex molecular pathways and show significant variability in the G x E (genotype x environment) interactions context. For example, natural accessions of Arabidopsis and chickpea display phenotypic variation for change in root hair length from fertile to P deficient conditions. Many of their accessions also show an opposite trend of reduced root hair length in P deficiency (Stetter, Schmid & Ludewig 2015; Kohli *et al.* 2020), consistent with the similar observations in a small number of genotypes in soybean and rice (Vandamme *et al.* 2013; Vejchasarn, Lynch & Brown 2016). Apart from natural accessions, with 169 RILs of maize, Zhu *et al.* (2005) calculated significant G x E interaction for root hair length change, and the population showed 60% heritability for the plasticity depicting the heritable nature of the trait. Also, plastic and long root hair RILs had higher fitness than short root hair in P deficiency (Zhu, Zhang & Lynch 2010).

Adaptive plasticity gets selected in a population because of superior fitness in adverse conditions and similar/low cost of phenotype in a normal scenario (Murren *et al.* 2015). In general, longer root hairs are carbon inexpensive and can provide higher payoffs than more expensive roots (Lynch & Ho 2005; Gonzalez, Postma & Wissuwa 2021). For example, in barley, longer root hairs in normal conditions give similar yield and comparable fitness with *srh* mutant (Marin *et al.* 2021). Therefore, plasticity for root hair traits needs to be modelled and evaluated in a more comprehensive genetic pool across a wider range of environments, for which quantitative genetics approaches like Finlay–Wilkinson regression is ideal (Walsh 2017).

The scenario becomes more complex in the case of root hairs, as trade-offs can happen for thin laterals or mycorrhizal associations (Nestler & Wissuwa 2016; Ma, Li & Ludewig 2021). Due to such trade-offs, the advantage that root hairs provide can vary among different crops. For example, maize (~4 mm) (Zhu *et al.* 2005), wheat (~2.5 mm) (Liu *et al.* 2017), and barley (~2.5 mm) (George *et al.* 2014) displayed longer root hair lengths than rice (~0.6 mm) (Nestler & Wissuwa 2016) and some of the P efficient genotypes of rice do not count on root hairs for the higher fitness in low P soils (Nestler & Wissuwa 2016). Nestler *et al.* (2016) suggested thin laterals (s-type) and second-order laterals as “super root hairs” that could compensate for short root hairs for P uptake in rice. Although, the competition and trade-off between thin laterals and root hairs are not yet defined properly in rice. However, in maize under P deficiency, *rth3* and *rth2* mutants compensate partly and fully respectively for the absence of root hairs with more laterals (Klamer *et al.* 2019; Wang, Li, Mang, Ludewig & Shen 2021). Other than lateral roots, root hairs can be traded-off by mycorrhizal association, but the advantage of trade-offs by mycorrhizal associations displays species specificity. For example, in barley, arbuscular mycorrhizal fungi (AMF) has detrimental results under P deficiency (Brown, George, Barrett, Hubbard & White 2013a), whereas maize has 33% more growth dependency of AMF than root hairs; thus, AMF outcompetes root hairs under low P in maize (Ma *et al.* 2021). Interestingly, *rth3* has higher AMF colonization and induced gene expression of phosphate transporters than WT, but both displayed similar P uptake and biomass under P deficiency (Ma *et al.* 2021). It shows that in the case of WT, the cumulative advantage of both AMF and root hairs is absent and both the traits are competing with each other.

Apart from trade-offs, traits can exhibit variable fitness due to synergistic and holistic interactions with other traits, especially in stress conditions. In common bean, genotypes display twice the increase in shoot biomass that carry denser and longer root hairs along with shallow basal root growth angle compared to the additive increase of each trait (Miguel, Postma & Lynch 2015). Shallow root growth angle is beneficial in phosphorus uptake as phosphorus being immobile, stays in the upper layers of soil (Lynch & Brown 2001). In addition to shallow root growth angle, an increase in root exudation of organic acids and acid phosphatases can increase available phosphate for uptake by root hairs and could act synergistically (Wang *et al.* 2015; Mehra, Pandey & Giri 2017; Gaviglio, Shields & Mondala 2019; Panchal, Miller & Giri 2021; Bhadouria & Giri 2021). Therefore, along with holistic roles of root hair traits (density, length, and longevity), synergistic interactions with root exudation and root growth angle could have higher positive cumulative effects. These factors make selection of root hair traits more challenging and requires a thorough investigation before breeding, especially when targeting stress conditions where plasticity, trade-offs and synergism play a significant role.

Conclusion and future perspective

Root hairs significantly contribute to plant survival as an active physiological rooting structure by performing resource acquisition, providing anchorage, and constructing the rhizosphere with desirable physical, chemical, and biological properties (Gahoonia & Nielsen 1998; Bengough *et al.* 2016; Robertson-Albertyn *et al.* 2017; Holz *et al.* 2018; Burak *et al.* 2021). Thus, root hairs play a crucial role in maintaining plant fitness and have wider ecological relevance in terms of plant-environment interactions, especially with abiotic and biotic components of soil (Brown *et al.* 2017; Robertson-Albertyn *et al.* 2017). Therefore, root hairs can be of great importance towards developing sustainable agroecosystems.

To improve root hair traits in modern cultivars, we need to know the impact of domestication, especially after improved irrigation and chemical fertilizers. Screening genetic resources like wild species and landraces is a way forward, though large-scale screening for root hair traits is challenging due to demanding and rigorous phenotyping. Additionally, root hair phenotyping becomes more cumbersome and requires diligence due to the plastic nature of root hairs in different phenotyping systems (hydroponics vs. soil) and between different roots of the same plant (Nestler & Wissuwa 2016; Nestler *et al.* 2016). Therefore, large-scale screening requires the development of root hair compatible invasive or non-invasive high throughput phenotyping systems or identification of easily phenotyped proxy traits like rhizosheath that can be measured in place of root hairs (Liu *et al.* 2017; Wissuwa & Kant 2021). These phenotyping systems should be relevant for screening in stress conditions to be employed in crop research for stress-resilient agriculture.

Screening of root hairs is largely done in controlled conditions, which often fail to replicate complex field environments. In natural conditions, variables like soil, water and nutrients interact with each other; therefore, irregularities in them often aggravate the situation to combinatorial and multiple stresses. In combined drought and P deficiency, root hairs are highly beneficial in mitigating both the stresses (Marin *et al.* 2021). Concomitantly, the presence of root hairs benefits the plant in high-strength soils for P uptake during its deficiency (Haling *et al.* 2013). Therefore, phenotypic screenings of available genetic resources in field conditions under combined stresses are required to incorporate root hairs in breeding programs for stress resilience.

Further, to include root hairs in crop improvement programs, we need to widen our understanding of mechanistic details of root hair-environment interactions, particularly for root hair trait plasticity and trade-offs, interactions with soil and its microbiota, and the role of root hairs in carbon sequestration. The plastic nature of root hairs is well-defined for nutrient deficiencies; however, the molecular pathways involved in controlling root hair morphology are largely unknown other than P deficiency. Moreover, root hair plasticity under water stress is highly diverse; for instance, grasses increase root hair length (Zhang *et al.* 2021b a), while tomato and Arabidopsis shorten their root hairs (Schnall & Quatrano 1992; Karanja *et al.* 2021). Similarly, variability is present in trade-offs for root hairs, especially with arbuscular mycorrhizal fungi under P deficiency, like in maize, root hairs are traded off with arbuscular mycorrhizal fungi, and in barley, root hairs (not mycorrhiza) play a major role in nutrient deficiency mitigation (Brown *et al.* 2013a; Ma *et al.* 2021). These variabilities are largely unexplained in the context of plant physiology, stress resilience and underlying molecular pathways, which need further attention.

Recently, root hairs have also been shown to modulate rhizosphere microbiota; however, how root hairs do it is largely unknown (Robertson-Albertyn *et al.* 2017). Exudation and root hairs' influence on soil matrix are probable reasons, but things are yet to be explored at this stage. Due to root hairs' influence on exudation and interaction with soil microbiota, it would be interesting to investigate whether root hairs have any possible direct or indirect role in kin recognition and plant-plant interactions. Moreover, it is also important to probe further how these interactions will shape soil structure and plant health, leading to a better understanding for restoring degraded ecosystems.

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Conflict of Interest

The authors declare no conflicting interest.

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Authors' contributions

JG conceived the study; PSK collected the literature with help of KM and wrote the first draft; PSK, JKT, RB, and JG corrected the draft and finalized the manuscript.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Summary Statement

Root hairs contribute to plant survival and assist in maintaining a holistic plant ecosystem through a coordinated interplay with various abiotic (edaphic, water, and mineral nutrients) and biotic (microorganisms) components.

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Figures

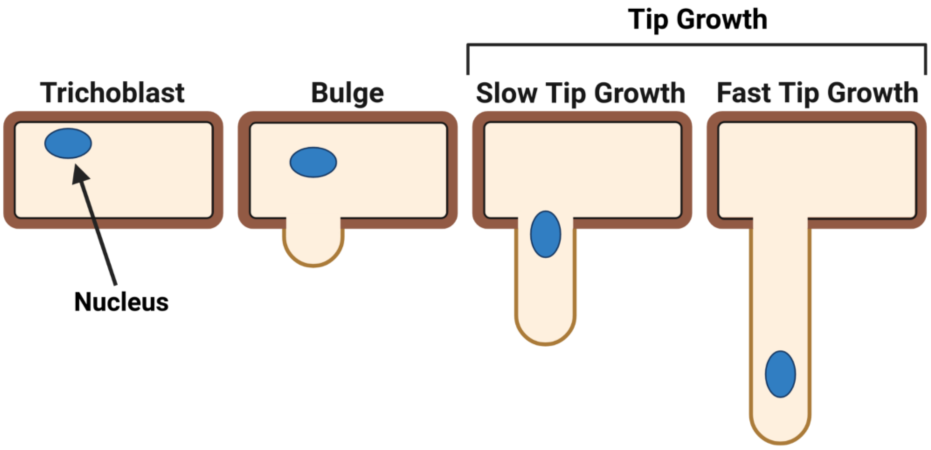

Figure 1. Stages of root hair development. Growth of the root hair can be divided into morphologically distinct three stages. First, the appearance of a bulge on the basal region of the trichoblast cell (root hair initiation). The initial bulge precedes a slow growth phase which transits to a fast growth phase. Together both these growth phases are considered as root hair tip growth (Dolan *et al.* 1994) . Before root hair initiation, the epidermal cell nucleus gets migrates to the region where bulge formation occurs. During the transition and slow growth phase, the nucleus enters the root hair and remains near the shank. After the transition phase, i.e., in fast growth, the nucleus enters the growing root hair cell and maintains a certain distance from the growing tip until root hair achieves a certain length (Ketelaar *et al.* 2002).

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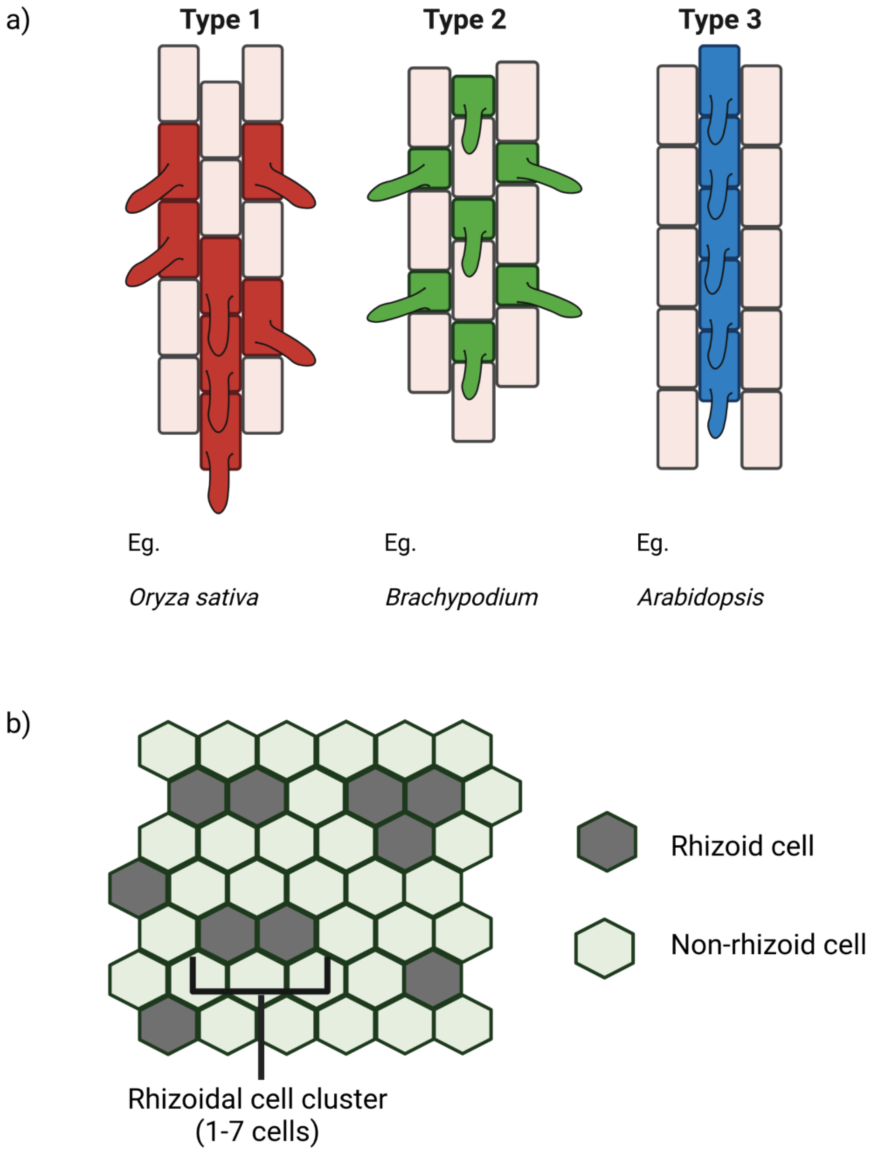

Figure 2. Epidermal cell patterning of the root of angiosperms and gemma of *Marchantia polymorpha*. a) Angiosperms mainly consist of three types of arrangement: in type 1, there is no distinction between the hair and nonhair forming cell; any of the epidermal cells can form root hair. Type 2 patterns have hair and nonhair cells present in the same longitudinal epidermal files. This arrangement results from an asymmetric division in which shorter cell forms a root hair and larger remains as a nonhair cell. In Type 3, alternate longitudinal epidermal files of trichoblasts and nonhair cells are present, and the fate of epidermal cells is decided early in the rootward region of the meristem (Adapted from Datta *et al.* 2011). b) Gemma of *Marchantia* consists of a single or group (up to 7) of rhizoidal cells surrounded by flat epidermal cells/non-rhizoid cells (Adapted from Thamm *et al.* 2020).

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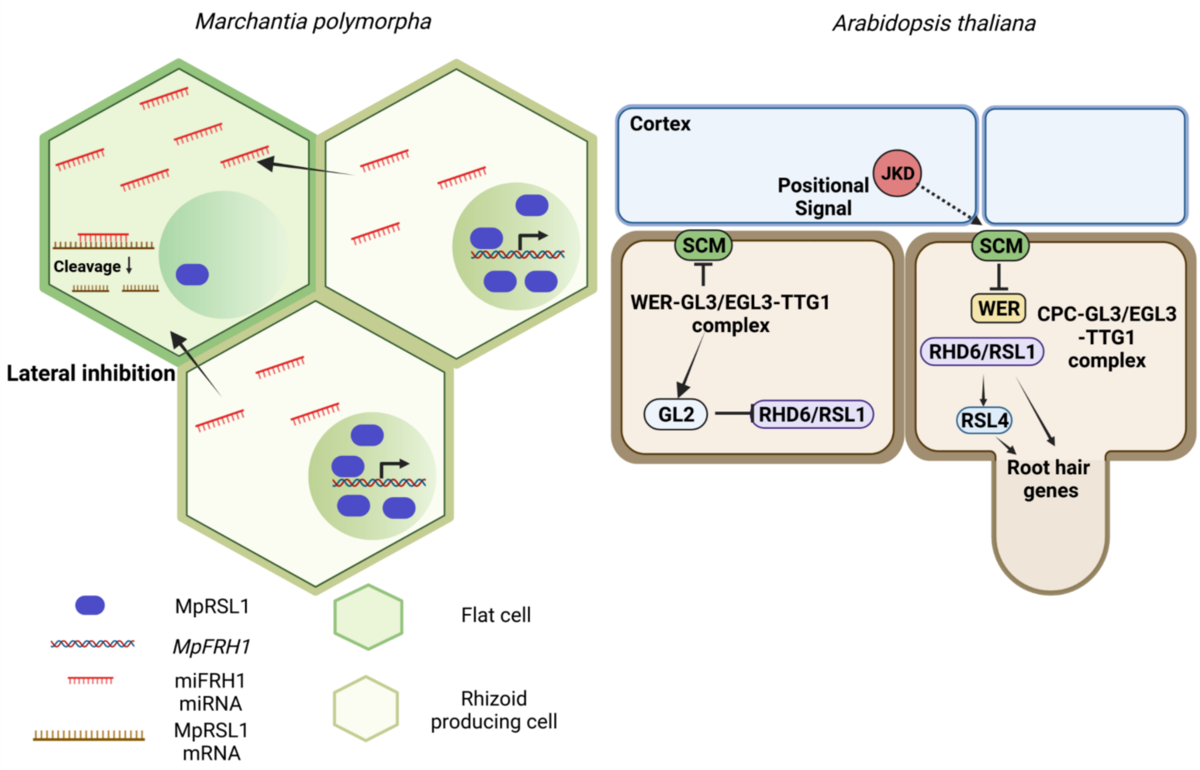

Figure 3. Comparative molecular control of epidermal cell patterning between *Marchantia polymorpha* and *Arabidopsis thaliana*. Epidermal cell patterning in *M. polymorpha* and *A. thaliana*. Epidermal cell patterning exhibits independent evolution in different plant lineages. In *Marchantia*, a miRNA FEW RHIZOIDS1 (MpFRH1) inhibits MpRSL1, whereas GL2 inhibits AtRHD6 in Arabidopsis. Positional developmental signals decide the cell fate of epidermal cells early in the root development of Arabidopsis through a non-cell autonomous mechanism. On the contrary, lateral inhibition guides the cell fate in *Marchantia* (Hassan, Scheres & Blilou 2010; Lin *et al.* 2015b; Honkanen *et al.* 2018; Thamm *et al.* 2020). JKD-JACKDAW; SCM-SCRAMBLED; WER-WEREWOLF

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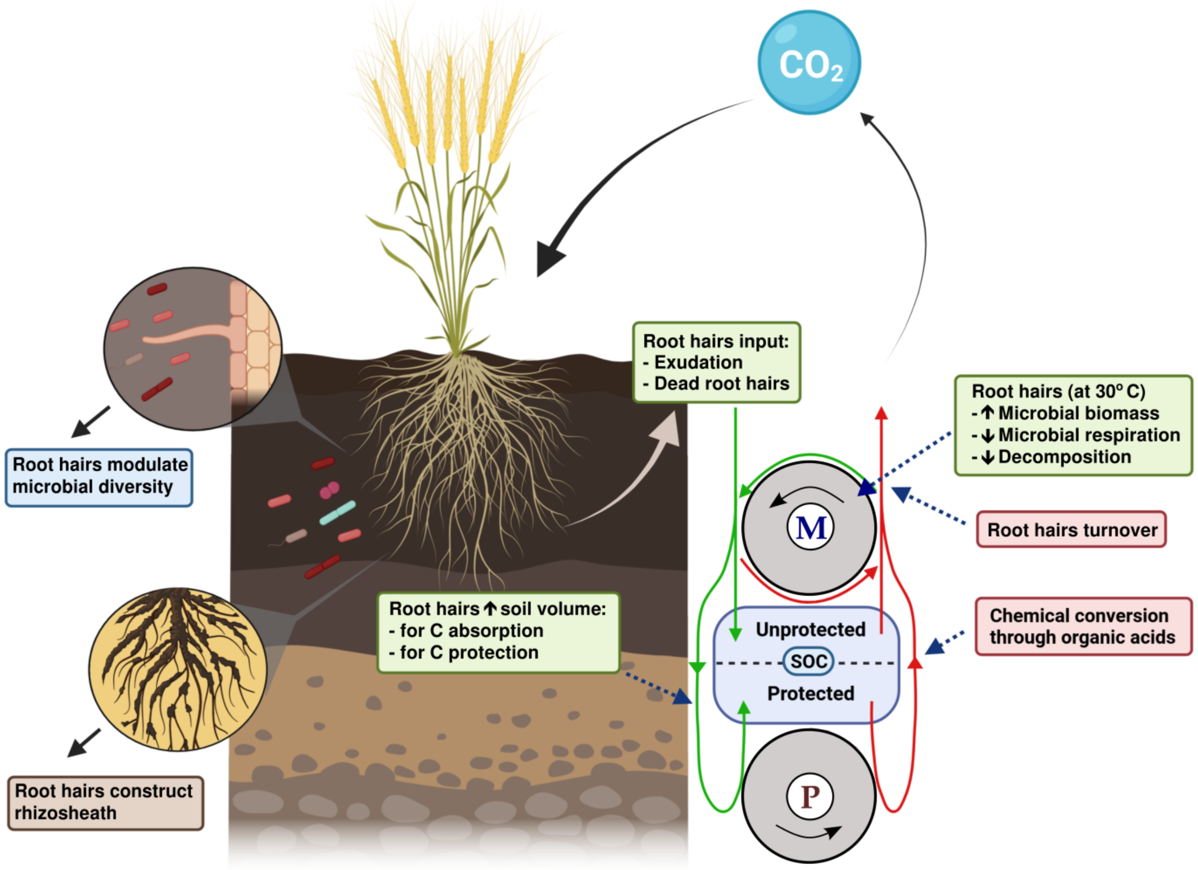

Figure 4. Contribution of root hairs in influencing physical, chemical, and biological components of the rhizosphere. Root hairs' actions influence the rhizo-engine framework for soil organic carbon (SOC) (proposed by Dijkstra *et al.* (2021) . Root hairs modulate the SOC pool towards sequestration through their input as exudates and actions on soil microbes (M) and soil physio-chemical matrix (P). Green boxes indicate root hair actions that contribute to SOC, and red boxes include actions that add to the conversion of SOC to CO$_2$ (Adapted from Dijkstra *et al.* (2021). Further, root hair influences microbial diversity of the rhizosphere by enriching plant growth-promoting rhizobacteria (PGPR) (Robertson-Albertyn *et al.* 2017) and are instrumental in forming rhizosheath (Haling *et al.* 2014; Brown *et al.* 2017).

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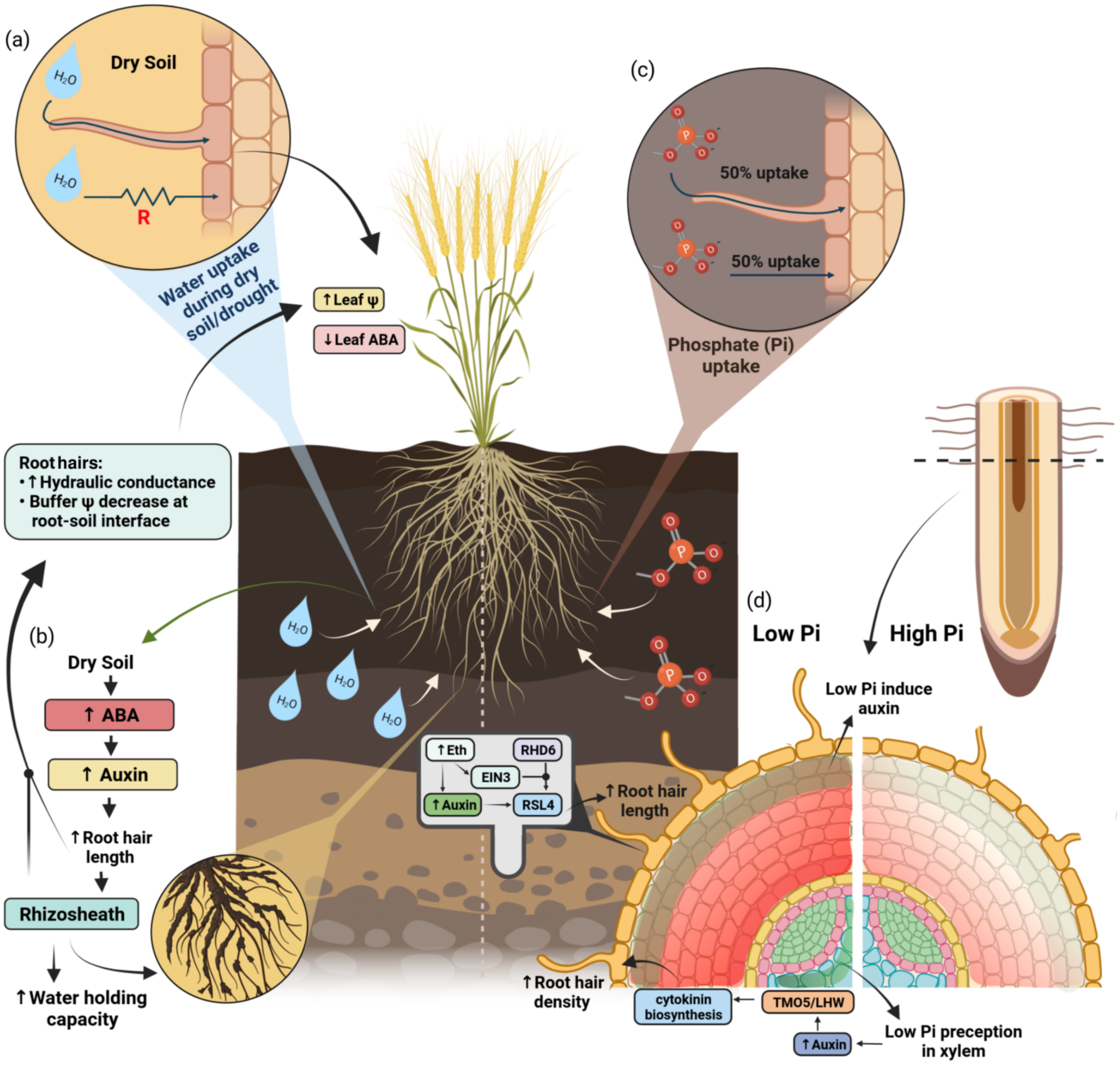

Figure 5. Roles of root hairs in water and phosphate (Pi) acquisition and their response in dry and Pi deficiency conditions. (a) During dry conditions, root hairs provide better hydraulic conductance than dry soil, and buffer water potential (ψ) decrease at root-soil interface (Carminati *et al.* 2017); leads to lower leaf abscisic acid (ABA) and higher leaf ψ (Marin *et al.* 2020). (b) ABA synthesis during drought in barley and rice leads to longer root hairs and increase in rhizosheath size. Rhizosheath helps in dry conditions as it has more water holding capacity than bulk soil (Zhang *et al.* 2020b, 2021b); (c) Root hairs acquire half of the total Pi from the soil (Keyes *et al.* 2013) and; (d) during Pi deficiency root hair length and the number increases through complex molecular and phytohormonal interplay (Feng *et al.* 2017; Bhosale *et al.* 2018; Wendrich *et al.* 2020). Auxin near epidermal cells and in the xylem is represented by green; Cytokinin gradient extends from stele to epidermal cells in red. ↑-Increase, ↓-Decrease, Eth-ethylene

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Table 1. List of selected root hair mutants in monocots used for understanding root hair physiology

Species Name	Mutant	Gene	Phenotype	Identified root hair functions	References
Oryza sativa	*rhl1,2 (root hair less1,2)*	*OsRHL1* (bHLH transcriptional factor)	Shorter root hairs	Rhizosheath development, water uptake/deficiency	(Ding *et al.* 2009; Zhang *et al.* 2021a)
	OsexpA17	*OsEXPA17* (Expansin)	Shorter root hairs	Rhizosheath development, water uptake/deficiency	(Yu *et al.* 2011; Zhang *et al.* 2021a)
Zea mays	*rth2 (root hairless 2)*	N.I	Shorter root hairs	P uptake/deficiency	(Wen Tsui Jung & Schnable 1994; Klamer *et al.* 2019)
	rth3 (root hairless 3)	*ZmRTH3* (COBRA Like Protein)	Shorter root hairs	Microbial interaction, P uptake/deficiency, root penetration, rhizosheath development	(Wen Tsui Jung & Schnable 1994; Hochholdinger *et al.* 2008; Bengough *et al.* 2016; Kumar *et al.* 2019; Zhang *et al.* 2020a; Gebauer *et al.* 2021; Burak *et al.* 2021)
Hordeum vulgare	*rhp1.b (root hair primodia1.b)*	N.I	Root hair bulge	Microbial interaction	(Szarejko *et al.* 2005; Robertson-Albertyn *et al.* 2017)

	nrh *(no root hair)*	N.I	Root hairless	Root penetration, P uptake/deficiency, microbial interaction, water uptake/deficiency, soil pore structure, rhizosheath development	Brown *et al.* 2012, 2013; Haling *et al.* 2013, 2014; George *et al.* 2014; Koebernick *et al.* 2019; Marin *et al.* 2020; Zhang *et al.* 2021b)
	srh *(short root hair)*	N.I	Shorter root hairs	Water uptake/deficiency, rhizosheath development, P uptake/deficiency, microbial interaction	(Brown *et al.* 2012, 2013; George *et al.* 2014; Haling *et al.* 2014)
	brh *(bud root hair)*	N.I	Root hair bulge	Water uptake/deficiency, rhizosheath	(Brown *et al.* 2012; Haling *et al.* 2014; Marin *et al.* 2020)
	brb *(bald root barley)*	N.I	Root hairless	Rhizosheath development, exudation, carbon sequestration, water uptake/deficiency, rhizosphere priming, P uptake/deficiency, microbial interaction	(Gahoonia *et al.* 2002; Gahoonia & Nielsen 2003; Haling *et al.* 2010; Pausch *et al.* 2016; Carminati *et al.* 2017; Holz *et al.* 2018; Burak *et al.* 2021)
	rhl1.a *(root hairless 1.a)*	N.I	Root hairless	Water uptake/deficiency, microbial interaction	(Szarejko *et al.* 2005; Kwasniewski *et al.* 2016; Robertson-Albertyn *et al.* 2017)

N.I – Not Identified

Table 2. QTL mapping studies for root hair-associated traits in diverse crops

S.N	Species	Growth met	Parents	Cross	Population	Condition	Trait	QTLs Ide	LOD	PVE %	Reference
1.	*Triticum aestivum* L.	Nutrient agar	Zhou 8425B; Chinese Spring	Biparental RILs	227	Control	RHL	Major: 4	3.96-2.77	6.52-4.56	(Huang *et al.* 2020)
								Minor: 4	2.31-2.09	3.68-3.32	
2.	*Triticum aestivum* L.	Pot soil	EGA Burke; Fronteira	Biparental RILs	139	Control (Acidic soil)	Rhizosheath size	5	15.78-3.06	34.1-6.8	(James *et al.* 2016)
3.	*Triticum aestivum* L.	Pot soil	Yitpi; Baxter; Chara; Westonia	MAGIC	466	Control	Rhizosheath size	Major:	9.65-	9.7 -	(Delhaize, Rathjen & Cavanagh 2015)
								Minor:	2.69-1	3.1 -	
4.	*Triticum aestivum* L.	Nutrient phytagel	Spark; Rialto	Biparent-	115	Control	RHL	3	2.7 -	8.2 -	(Horn, Wingen, Snape & Dolan 2016)
			Charger ; Badg-	Biparent-	95	Control	RHL	1	3.8	17.6	
5.	*Hordeum vulgare*	Pot soil	Commander; Fleet	Biparental DHs	175	Control	Rhizosheath size	5	4.91-2.95	11.96-7.94	(Gong & McDonald 2017)
6.	*Zea mays* L.	Paper roll	B73; Mo17	Biparental RILs	169	Control	RHL	3	4.55-	14.7-	(Zhu, Kaeppler & Lynch 2005)
						P deficiency	RHL	1	4.04	10.4	
							RHL	1	5.86	9.6	
7.	*Phaseolus*	Hydrop	DOR364;	Biparent-	86	P defi-	RHL-	2	4.18-	14.5-	(Yan, Liao,

	vulgaris L.	onics	G19833	al RILs		ciency	RHL-tr	3	5.43-2.5	28.6-8.5	Beebe, Blair & Lynch 2004)
							RHD-	3	5.55-	20.0-	
8.	*Oryza sativa*	Field condi-	Aus276/3;IR64	Backcross (BC_2F_1)	206	Drought (Direct	RHL	1	-	7.1-6.8	(Sandhu *et al.* 2015)
							RHD	2	-	6.6-6.3	
			Aus276/3;MTU1010	Backcross (BC_2F_1)	116	Drought (Direct	RHL	1	-	6.9-6.6	
							RHD	1	-	6.7-6.3	

RIL - Recombinant inbred lines; DH- Double haploid; RHL- Root hair length; P- phosphorus; MAGIC- *multi-parent advanced generation intercross; PVE- Percentage variation explained; RHL-br - Root hair length of basal roots; RHL-tr - Root hair length of tap roots; RHD-br - Root hair density of basal roots*