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Root hairs vs. trichomes: Not everyone is straight!

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Abstract

Trichomes show 47 morphological phenotypes, while literature reports only two root hair phenotypes in all plants. However, could hair-like structures exist below-ground in a similar wide range of morphologies like trichomes? Genetic mutants and root hair stress phenotypes point to the possibility of uncharacterized morphological variation existing belowground. For example, such root hairs in Arabidopsis (*Arabidopsis thaliana*) can be wavy, curled, or branched. We found hints in the literature about hair-like structures that emerge before root hairs belowground. As such, these early emerging hair structures can be potential exceptions to the contrasting morphological variation between trichomes and root hairs. Here, we show a previously unreported 'hooked' hair structure growing belowground in common bean. The unique 'hooking' shape distinguishes the 'hooked hair' morphologically from root hairs. Currently, we cannot fully characterize the phenotype of our observation due to the lack of automated methods for phenotyping root hairs. This phenotyping bottleneck also handicaps the discovery of more morphology types that might exist belowground as manual screening across species is slower than computer-assisted high-throughput screening.

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Root hairs, Trichomes, Phenotyping, Morphology, Root.

Introduction

A classic definition of trichome and root hair distinguishes both by above- [1] and below-ground [2] functions and differences in genetic make-up [3]. These often-microscopic extensions of the outermost tissue layer of the shoot and root, play an essential role in a plant's survival. Both help to build resilience against abiotic stresses [**4], provide defense against biotic stresses [5] and resistance against physical forces [6], to name the most commonly reported functions. Moreover, trichome and root hair form endophytic relationships with microbes to exchange carbon and fix nitrogen [7,8]. Yet, trichomes associate with above-ground functions, and root hairs associate with below-ground functions.

Trichomes and root hairs also share genes with similar molecular mechanisms in overlapping differentiation pathways [**9–11] to produce specific patterns of emergence from the epidermis [12]. However, they differ in their morphological variation despite their overlapping genetic pathways and similar functions. Table 1 lists known structure-function relationships for trichomes and root hairs. The large variety of morphological phenotypes in trichomes link to different plant functions [13]. In contrast, root hairs are predominantly reported as straight tubular extensions in all plants [14]. Therefore, we ask in this review if similar morphological variation could exist in root hairs and if the pointers to a much larger variety of root hair morphologies might hide in plain sight. We next identify the technological bottlenecks that inhibit the discovery of morphological variants of root hair and report on a hair-like structure below-ground that exhibits unique 'hooked' morphology in common bean (*Phaseolus vulgaris*).

The huge morphological variation in trichomes and their associated functions

Trichomes are epidermal appendages emerging on the aerial organs of a plant. The presence of glands at the tip of trichomes defines two general types (Figure 1a). If present, glands secrete secondary metabolites that define the glandular trichome type [15]. In contrast, the non-glandular trichome type has no such secretory capabilities [**4].

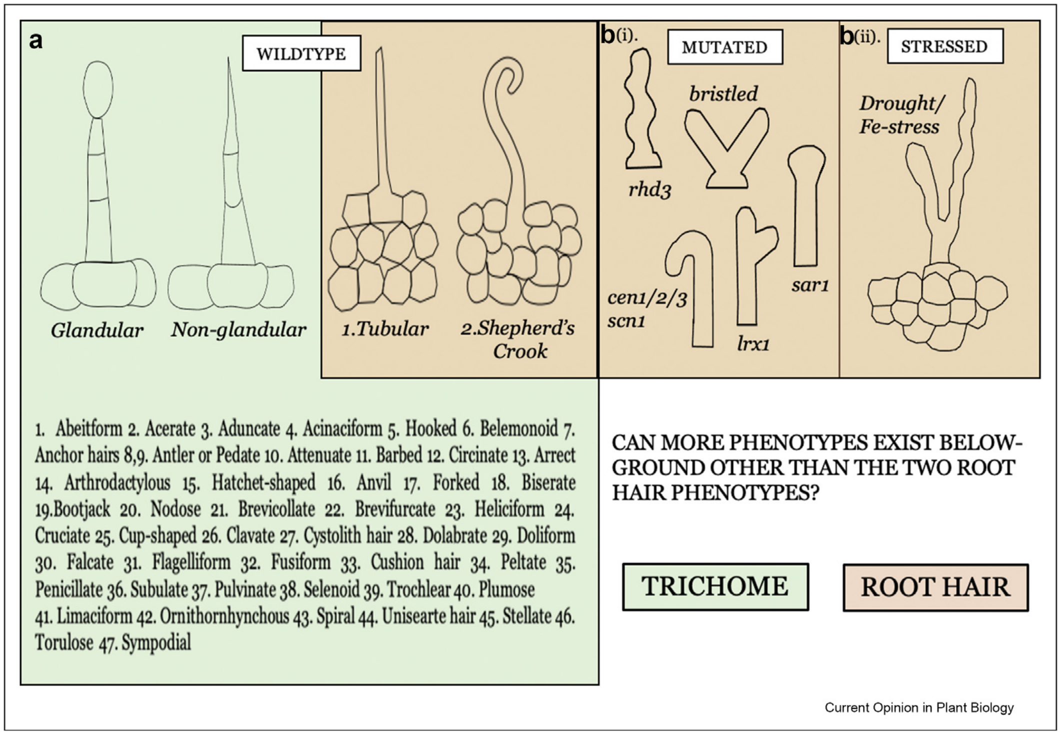
Further classification of trichome morphology defines sub-types for glandular and non-glandular types. The sub-types are powerful tools to identify plant species because they exhibit a tremendous species-specific morphological diversity [16]. As such, trichomes can be short, long, uni- or multicellular and uni-, bi or multiseriate. Both, tubular and branched morphologies are typical for trichomes. Additionally, the observed non-tubular configurations can exist in a wide variety of morphologies represented by 47 morphologies ranging from stellate, hooked, and cup-shaped to forked or trifurcate [17].

Table 1

Overview of known structure–function relations for epidermal hairs. The smaller number of discovered functions for root hairs indicates the potential for more below-ground morphologies.

	Location	Function	Hair Type	Structural Variation
Resilience against abiotic stresses	Above-ground	Sequestration of toxic metals	Trichome	Morphology
	Below-ground	Nutrient/water uptake under stress	Root Hair	Length/Density
Defense against biotic stresses	Above-ground	Chemical defense against pests	Trichome	Morphology
	Above-ground	Physical defense against pests	Trichome	Morphology
	Below-ground	Chemical defense against microbes	Root Hair	Exudate composition
Resistance against physical forces	Above-ground	Regulation of leaf temperature	Trichome	Morphology
	Above-ground	Protection from ozone	Trichome	Morphology
	Above-ground	Protection from UV radiation	Trichome	Morphology
Other vital plant functions	Above-ground	Guide for pollinators	Trichome	Morphology
	Above-ground	Nutrient and water uptake	Trichome	Morphology
	Below-ground	Nutrient mobilization under deficiencies	Root Hair	Exudate composition
	Below-ground	Release of carbon into the rhizosphere	Root Hair	Exudate composition

Figure 1



Current Opinion in Plant Biology

Known morphologies of hair-like plant structures. (a) Comparison of frequently reported morphological phenotypes. Glandular and non-glandular trichomes (green color) collectively can be classified into 47 morphological phenotypes [17]. The two most commonly reported morphological phenotypes of root hair (brown color) are shown. **(b)**(i)Human-induced mutations and (ii) stress conditions that cause atypical and sparsely reported root hair phenotypes which hint towards potentially uncharacterized below-ground phenotypes.

Functionally, glandular trichomes protect against ozone stress [18] and aid in the sequestration of toxic metals [19]. The secreted exudates also provide active means for insecticidal effects in defense against pests. For example, terpenes secreted in tomatoes (*Solanum habrochaites*) affect the feeding behavior of aphids [20]. Leaf peltate trichomes in cork trees (*Millingtonia hortensis*) accumulate non-volatile phenols to protect young shoots from damage by insects and pathogens [21]. Glandular trichomes prevent the settling of leafhoppers in *Medicago sativa* by diet rejection [22] and show insect antifeedant activity in camphorweed

(*Heterotheca subaxillaris*) [23]. We refer to Schuurink et al. [24] for an extensive review of the biological functions of glandular trichomes.

Non-glandular trichomes associate with functions different from glandular trichomes. As such, they can protect against ultraviolet radiation [**4] and act as guide pollinators [25]. In epiphytes, they even fulfill functions of nutrient and water absorption [26]. The morphology of non-glandular trichomes enables physical defense against insects compared to the chemical defense by glandular trichomes [27]. Hooked non-glandular trichomes are effective in trapping pests [28]. For example, they trap aphids in their hooks during walking or feeding in common bean (*P. vulgaris*) eventually, causing death by starvation or injury. We refer to Bar et al. for a detailed review of the defense mechanisms in non-glandular trichomes [13].

However, there is no rule without exception, and special trichome phenotypes with characteristics of both glandular and non-glandular types have been observed on the leaves of some species in the Lamiaceae family [29]. Unsurprisingly, glandular, and non-glandular trichomes have some identical functions. Both contribute towards regulating leaf temperature to decrease water loss through reflection and reducing leaf wetness thus, affecting transpiration [30].

Is variation in root hair morphology absent or just uncharacterized?

Root hairs are the below-ground counterpart of trichomes at the plant—soil interface, which interact with the surrounding rhizosphere [31]. They are unicellular epidermal modifications of root trichoblasts that grow in the elongation zone of the root tip [32]. The restriction to unicellular architecture might be a biological reason for less morphological variation in root hairs compared to the wide variety reported for trichomes. One non-straight phenotype is the curled morphology of root hairs in legumes. Also known as shepherd's crook, its function is to trap rhizobacteria to form root nodules as means to fixate nitrogen [33]. Besides the reported shepherds crook, root hair studies focus predominantly on the change in root hair length as the morphological variation of individual root hairs. Other reported phenotypes describe changes like density, which associate with a population of root hairs [34] or changes in the composition of exudates released into the soil.

Root hairs change their individual length and population density to acclimatize to nutrient limitations [35]. For example, phosphorus stress triggers longer and denser root hair growth in the topsoil. In Arabidopsis, additional root hairs emerge from atrichoblasts. These extra root hairs appear at locations that do not conform with known emergence patterns from the trichoblasts in the epidermis [36]. Other nutrient limitations elicit a similar response [37]. As such, manganese stress induces additional root hairs on the epidermis [38], while higher magnesium levels progressively decrease root hair development [39]. Potassium deficiency stimulates an increase in root hair length and density in a variety of agriculturally important crops such as pea (*Pisum sativum*), barley (*Hordium vulgare*), and rye *(Secale cerale)* [40]. Similarly, maize genotypes with longer hairs perform better in low phosphorus conditions [41]. Phosphorus uptake is also positively correlated with basal root hair length and density in common bean [42]. Root hairs further respond to drought. Longer and denser root hairs developed in tall fescue plants over 14 days in moderate drought conditions [43]. The often observed duality of simultaneous change in root hair length and density led to the explanation that root hairs increase the surface area of the root [44] in response to nutrient or water stress.

Similar to glandular trichomes, root hairs play an essential role in the release of exudates. For example, johnsongrass (*Sorghum halepense*) releases the phytotoxic compound sorgoleone to gain a competitive advantage by slowing the growth of neighboring plants [45]. Another example is the sensitive root hair of touch-me-not (*Mimosa pudica*) that releases sulphur when the roots get surface contact with skin or soil [46]. Root hairs also increase substrate availability for consumption by microorganisms in the vicinity of the root by releasing organic compounds [47]. The length and density of basal root hairs in common beans correlate positively with root exudates, which facilitate phosphorus uptake [42]. Root exudates also mobilize nutrients by increasing the phosphatase activity in the rhizosphere [48]. Unsurprisingly, drought, nutrient deficiencies, and salt stress associate with altered exudate compositions. For example, drought shifted the exudate composition in holm oak (*Quercus ilex*) towards secondary metabolites (71%) compared to non-drought conditions in which primary metabolites were dominant (81%) [49]. Exudates also help to alleviate nutrient stresses. For example, malate helps to cope with phosphorus-deficient conditions in Arabidopsis [50]. Furthermore, salt stress in *Phragmites Australis* shows a 24-fold increase in amino acid content in exudates compared to the control experiment [51].

The rare but special morphologies of root hairs raise questions

There is little evidence in the literature for hair-like extensions below-ground other than the straight, tubular or the shepherd's crook phenotype. Human-induced mutations, certain stress conditions [34], and the phase of early root development point at the possibility of additional morphological phenotypes in individual hairs. Root hair mutants in Arabidopsis are examples of such morphological variants (Figure 1b(i)). For example, long and branched (*lrx1*), short and branched (*bristled1*), short with either a wide base, curled or branched (*cen1/2/3, scn1*), wavy (*rhd3*), stunted and swollen (*keule*) hair types in Arabidopsis [52]. Other examples of such morphological phenotypes are short (*rth1/2/3*) [53] in maize (*Zea mays*), short (*Osrhl1 Osrhl2*) [54] and stunted *(OsexpA17)* [55] in rice (*Oryza sativa*), branched (*scarn*) [56], swollen (*crinkle*) [57], short (*LjSRH*), petite (*LjPRH*), and variable root hair length (*LjVRH*) in birdsfoot trefoil (*Lotus japonicus*) [58]. Moreover, the *scarn* and *crinkle* phenotypes in *L. japonicus* fail to establish legume-rhizobia symbiosis.

These morphological phenotypes are pointers to more root hair variation because they are known stress responses in natural environments. For example, root hair branching increases the absorptive surface area under Fe stress in Arabidopsis [59] and under progressive drought, up to 8.27% of all root hairs were branched [60] (Figure 1b(ii)). Besides abiotic stress responses, hair-like structures exist in early root development. When a seedling navigates its way, penetrating the ground, it is devoid of root hairs. Yet, hair-like structures emerge on the young root instead to fulfill root hair functions [61] to support seedling establishment [62] and geotropism [63]. In terrestrial plants, they may protect against herbivory and increase water uptake [64]. Recent research also discusses the ecological importance of hypocotyl hairs in swamp paperback (*Melaleuca ericifolia*). As such, the phenotype of hypocotyl hairs is significantly longer than observed for root hairs (~20 mm × 30 μm vs. ~5 mm × 15 μm) [65]. Similarly, collet hairs develop on the hypocotyl-radicle junction in Arabidopsis during the first few days of development. Collet hairs differ in patterning such that every epidermal cell develops into a collet hair in contrast to the alternate patterning of root hairs [66]. These early hair-like structures contribute to biological functions such as anchorage and uptake from the soil under non-limiting conditions, which are important for survival [67].

Searching for more morphological variation in root hairs

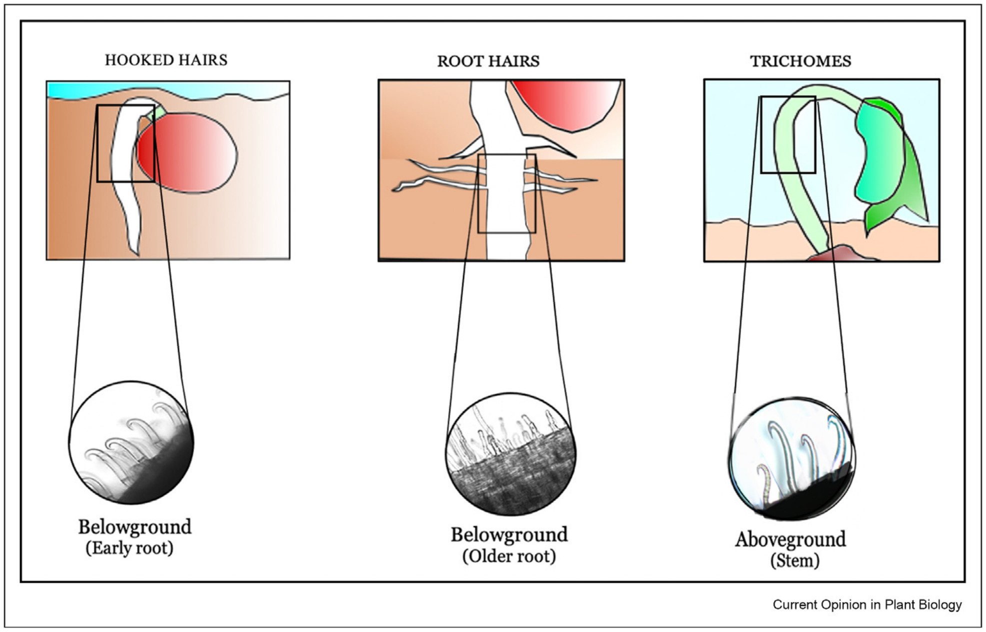
Plant trichomes exhibit 47 variants of functionally relevant morphological phenotypes. These 47 phenotypes compare to only two relevant morphological phenotypes in root hairs among all plants – either tubular-straight or the shepherd's crook. Nevertheless, sparsely found mutant studies in lab experiments indicate that root hairs have the potential for more morphological phenotypes. Prior research has shown that morphology can alter under abiotic stresses, which raises the question of why these root hair phenotypes do not occur in non-limiting conditions. One can argue that the collet and hypocotyl hairs, which only exist during early development, should be classified as root hairs. However, these hair-like structures indeed constitute an exception in morphological variation below-ground.

It seems unlikely to find unreported root hair phenotypes that mirror the diversity and generality present in trichomes. Yet, from our literature research, we hypothesize that a species-specific likelihood for unreported hair-like morphologies below-ground exists. The similarity of the genetic make-up and the environmental cues altering root hair and trichome phenotype support our hypothesis. It seems likely that the reason for the sparse coverage of early hair-like morphologies lies in their transitory characteristic. As such, hypocotyl hairs disappear within a few weeks after germination [61]. Consequently, they were either being overlooked or mistaken for root hairs and for that reason may have remained understudied across species.

Common bean (*P. vulgaris*) caught our attention for a first hypothesis forming test because its hooked leaf trichomes could serve as a template for early below-ground hairs with undiscovered morphology. In a first observation, we found 'hooked' hairs during early root development in common beans (Figure 2). The observed 'hooking' morphology is visually distinct from the shepherd's crook observed during nodulation. The observation was first made in a hydroponics set-up and replicated in simple vermiculite-perlite and soil-based growth systems.

We cannot exclude the possibility of an uncharacterized phenotype because of these hair-like structures' below-ground location. Their location on the young root right above the first emerging basal roots makes it hard to think of these hair-like structures as trichomes that grow out of the ground during development. However, it is impossible to distinguish the observed hair-like structure from a trichome visually. Our inability to visually differentiate a trichome from the 'hooked hair' raises questions about the function and classification of the newly observed phenotype. Is it a below-ground trichome or a root hair phenotype? Or is it an intermediate phenotype between root hair and trichome? Hooked hairs are the first structures to emerge below-ground on the young root within the first 3–5 days after planting for our growth system (Supplemental Material 1). We observed that hooked hairs emerge before root hairs. However, the number of days until hooked hairs emerge most likely varies with environmental conditions which can affect the growth rate of seedlings (Supplemental Material 2). Trichomes, on the contrary, can be observed above-ground on the stem after the cotyledons emerge from below the soil. Location (root/shoot transition zone vs. tap/basal roots vs. stem/leaves) and stage of development differentiate the observed hooked hair from root hair and trichome. However, phenotypic characterization of the morphology to distinguish the hooking shape and

Figure 2



Distinction between hair-like structures. Location and emergence of hooked hair, root hair, and trichome in common bean and an example image taken under the microscope with 10x resolution. Important to recognize are the differences between hooked hairs, root hairs, and trichomes in traits like morphology and length distribution. Notably, the hooked hair-like structures will stay below ground during development.

form quantitatively demands new technological developments in root hair phenotyping.

The technological barrier to discovering new hair-like phenotypes

Phenotyping is the quantitative characterization of plant traits [*68] which is inherently difficult for root hairs due to their underground location and microscopic size. Characterizing root phenotypes is a challenging task in itself [*69], but root architecture is multiple scales larger than the cellular scale of a root hair. Bridging multiple scales of organization has been identified as a challenge in the phenotyping community [70] and only very few research projects have developed tools to phenotype root hairs. Semi-automated software plugins like Root Hair Sizer [71] are available in ImageJ [72] to measure root hair length. To our best knowledge, only one other software exists for quantifying root hair growth in soil-grown roots in the form of an R script which implements a logistic regression model for measuring root hair area from images [73]. However, none of these tools has the automatization level needed to discover new morphological phenotypes in root hairs and other hair-like structures. Thus, to date, root hair analysis is a tedious manual process for simple traits like length and density.

As such only a limited amount of software supported phenotyping studies for root hairs exists. For example, root hair length was measured in ImageJ in a study investigating the effects of soil properties on root hairs in barley (*Hordeum vulgare* L.) [74]. Another study measured root hairs manually using a micrometer scale under a light microscope to characterize the response of canola (*Brassica napus*) to salinity stress [75]. However, quantifying and interpreting the newly observed hooked hair phenotype requires tools to evaluate curvature, area, and perimeter of root hairs in addition to length. Such a characterization is infeasible manually because of the number of samples needed to obtain statistically significant results. Root hair phenotyping is, therefore, a technological barrier to evaluate stress responses, variation, and patterning. As such, discovering and investigating hair-like phenotypes below-ground requires technology to facilitate high-throughput analysis of thousands of microscopy images.

Discussion

We hypothesized in our literature review that belowground epidermal extensions other than the well-known straight and tubular, and the shepherd's crook phenotypes of root hairs could exist. Yet, their morphological variation is most likely limited to specific plant species and less diverse than the variation observed for trichomes. Our review identified abiotic stresses as a potential natural trigger for branched and curved phenotypes. Early root development was identified as an understudied area where non-tubular phenotypes might exist in some plant species. We tested this idea by investigating early root development in common beans. As hypothesized, we observed a previously unreported hooked hair that grows below ground on common bean seedlings. We believe that the observation is species-specific because we did not observe the hooked hair phenotype in soybean (*Glycine max*) (Supplemental Material 3).

We could not find initial answers in literature to why root hairs have less morphological variation than trichomes. However, we will investigate the newly observed hair-like structures for their ability to respond to abiotic stresses for their potential to function as a root hair in early development. For example, we could not exclude experimentally the possibility that a hooked hair could nodulate like a straight and tubular root hair. Therefore, we plan to combine these functional studies with detailed geometric characterization of the hooked hairs' morphology to statistically distinguish its shape from trichomes. Together, our planned studies might yield insight into the fitness benefits of morphological variation in hair-like structures below ground.

We identified automated phenotyping methods as an essential tool to distinguish the observed hooked hairs from root hairs and trichomes. However, there is a substantial lack of methods and tools to characterize the morphology of hair-like structures. Currently, no tool exists with the capability to quantify the shape and form of single cell elongations. This lack of automated high-throughput tools also handicaps efficient large-scale and high-throughput screening to discover rare phenotypes and their characterization at various developmental stages and across possible combinations of stresses. It could be that these hair-like structures play a beneficial role in plant survival during early development [67]. We believe that such uncharacterized morphologies can be discovered by developing new high-throughput phenotyping methods that automate the measurement of hair-like structures in thousands of microscopy images.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pbi.2021.102151.

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