Commentary

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Does half a millimetre matter? Root hairs for yield stability. A commentary on 'Significance of root hairs for plant performance under contrasting field conditions and water deficit'

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HALF A MILLIMETRE FOR YIELD STABILITY

Root hairs have been investigated for more than a century, but these single-celled extensions still impress. The vast majority of plant species form these epidermal cell extensions, which are assumed to contribute to water and nutrient uptake; however, few studies examine root hair traits in their natural environment – the soil – and even fewer have attempted to examine their effects on grain yield in actual field trials. Marin *et al.* (2021) do so, comparing two barley varieties with normal root hair development with three mutants with reduced root hair length and densities. The study was conducted in fields with high phosphorus (P) status in two years of differing precipitation, the second year being an unusually dry year. The presence of root hairs did not influence yield – for better or for worse – under favourable conditions in year one, and even a root hairless mutant was able to take up sufficient P from this high-P soil. However, under water deficit conditions of the second year, root hairs increased P uptake, improved plant water status and prevented grain yields from declining relative to the first year. Marin *et al.* (2021) concluded that root hairs contributed to yield stability under water-limited conditions, while not conferring a yield penalty under favourable conditions, which is in line with theoretical work predicting that root hair production should not represent a measurable carbon cost (Lynch and Ho, 2005).

The study of Marin *et al.* (2021) is one of the few studies to date that has investigated the contribution of root hairs to crop yields under field conditions. Earlier, Gahoonia and Nielsen (2004) showed that barley cultivars with longer root hairs had improved grain yield in a P-deficient soil where root hairs are believed to contribute to P uptake by increasing the root surface area involved in P acquisition. Such an effect was not shown by Marin *et al.* (2021) in the year with sufficient precipitation, leading the authors to conclude that the high P availability in their soil eliminated the root hair advantage. However, in a dry year, a 50 % higher P uptake was seen in genotypes with root hairs and, while it was not clear whether the reduction in yield of hairless mutants was primarily driven by reduced water uptake or by a combination of poor P and water uptake, the positive effects of root hairs on the acquisition of both resources was evident. Previously, pot experiments with the same mutant lines showed similar positive effects for the combination of water deficit with low P soil (Brown *et al.*, 2012). This may change how we think about root hairs from a crop improvement point of view. A paradigm in modern agriculture has been to remove yield-limiting factors by the application of fertilizers and other inputs, thereby creating favourable conditions where one may conclude that 'root hairs are dispensable' (Wen and Schnable, 1994). The present study highlights that this paradigm may no longer hold in the age of climate change where more irregular rainfall patterns affect crop productivity directly through water shortages and indirectly through reduced nutrient availability even in fertilized fertile soils.

CAN ROOT HAIRS BE PART OF THE SOLUTION TO IMPROVE ADAPTATION TO CLIMATE CHANGE?

Marin *et al.* (2021) present one more pieces of evidence that root hairs can improve climate resilience of crops. The benefit of longer root hairs for P uptake in dry soils is due to the fact that they counteract the effect of reduced P diffusion as the soil water content decreases. Modelling suggested that doubling hair length from 0.4 mm to 0.8 mm would improve P uptake by 26 % in a moist soil but by 52 % in a dry soil (Zygalakis *et al.*, 2011). In a warmer world, this scenario is expected more often in Europe, even in northern regions such as Scotland, and the need to develop more climate-resilient cereal crops is recognized among the European crop improvement community. Should root hairs be considered a breeding target given their potentially positive contribution? As is so often the case, the answer hinges on the question of whether sufficient natural variation for root hair formation can be found in the larger barley/cereal gene pool. Most studies confirming positive effects of root hairs have used mutants with impaired root hair formation. In breeding, the objective would be to increase root hair length or density above the level already present in the 'wild-type' breeding population. Typical values for root hair length reported by Marin *et al.* (2021) were 0.4–0.7 mm; however, the same genotypes evaluated earlier showed maximum length ranging from 0.7 to 0.9 mm, with reductions to as low as 0.4 mm depending on soil properties (Haling *et al.*, 2014). Such a 2-fold variation in a given genotype in response to soil factors raises several important questions.

(1) To what extent will genotypic differences observed in screening trials be realized in field conditions?

Screening seedlings in artificial media (agar, nutrient solution or filter paper) provides quick and potentially more reproducible results compared with soil-based experiments, and allows for maximum expression of root hair traits. However, root hair density and especially length typically decrease in soil (Nestler *et al.*, 2016; Kant *et al.*, 2018), making it crucial to confirm results from screens in artificial media under realistic soil conditions. Further attention to factors impacting hair development in soil is necessary, especially in terms of genotypic variation (Fig. 1).

(2) Can target root hair traits be set that would justify devoting resources to their pursuit in selection?

Increasing root hair length is predicted to be more beneficial than increasing root hair density, especially in drying soil (Zygalakis *et al.*, 2011), but to what extent donor lines with significantly longer roots hairs compared with existing varieties can be identified remains to be seen.

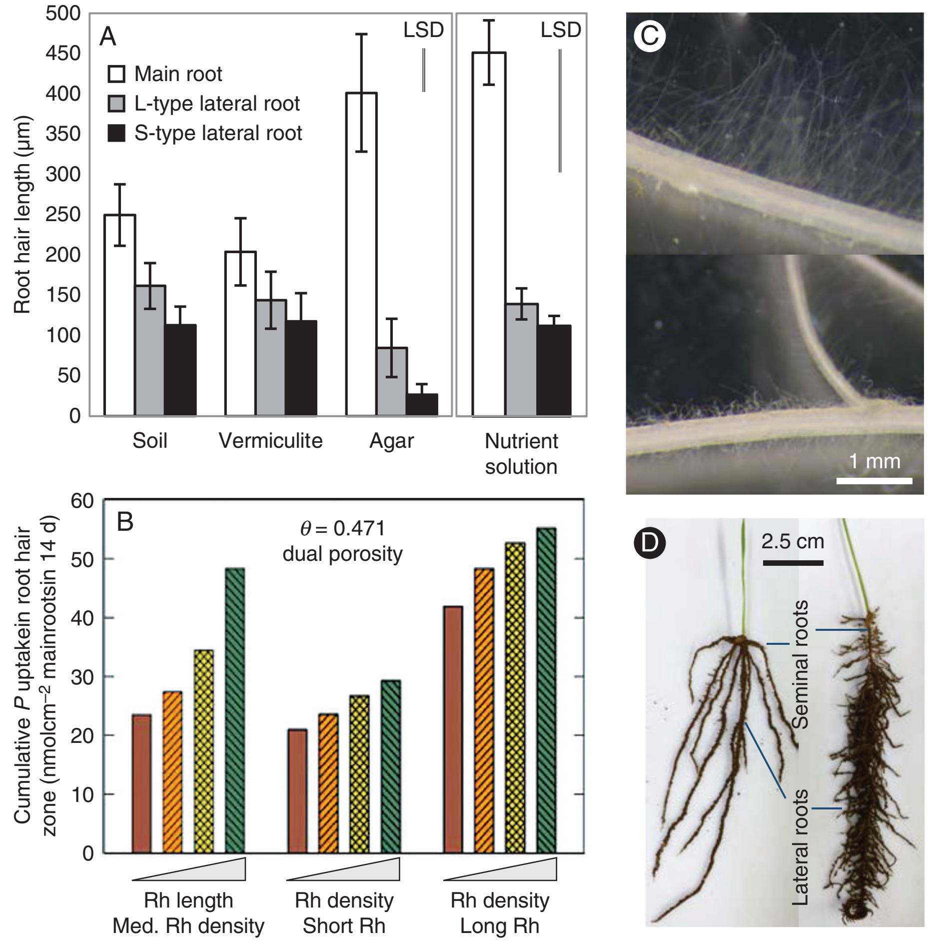

FIG. 1. Variation in root hair traits and their effects. (A) Rice root hair length when grown in different media shows that trait stability is low from lab to field (from Kant *et al.*, 2018). (B) The modelled potential P uptake is more dependent on root hair length than on density (from Zygalakis *et al.*, 2011). (C) Variation in wheat root hair length in high-yielding varieties. (D) Visualization of rhizosheath formation (from Kant *et al.*, 2018).

(3) Are certain gene pools more likely to harbour donors with extreme root hair phenotypes?

Barley is grown in Mediterranean and desert environments, and one may therefore hypothesize that selection in such drought-prone environments has produced breeding lines with desirable root hair traits. Furthermore, a trend has been observed (J. Kant, unpubl. res.) of increasing root hair length in older wheat varieties bred before P fertilizer application reduced the advantage that roots hairs provided.

(4) Do indirect screening methods exist that are adaptable to the throughput requirements in breeding, yet capable of capturing the relevant realized variation for root hair traits in a field?

For root hair traits to be adapted as breeding targets, phenotyping has to move away from microscopic evaluation to a simpler proxy trait correlating with root hair formation. Marin *et al.* (2021) show rhizosheath weight to have a positive correlation with root hair length, but this association was variable and potentially inflated by the presence of an extreme genotype (hairless mutants). A better understanding of the factors contributing to rhizosheath weight other than root hair traits is required to ensure selection does not introduce some negative aspect. Should mucilage excretion indeed be responsible for increasing rhizosheath weight and should mucilage itself contribute positively to intermittent drought tolerance, one could expect positive synergistic effects from employing rhizosheath weight as an indirect selection criterion.

The potential of longer root hairs as a ‘cheap’ solution to protect farmers from yield – and therefore income – loss due to reduced rainfall is tempting; however, targeted breeding for positive root hair traits will be challenging, and a main task at hand is the identification of donors with significantly longer hairs than are already present in breeding populations, combined with a demonstration that such an increase above the present level does have the desired effects.

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