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The effect of root hairs under drought in open field conditions

Maria Marin^{1,2}, Deborah S Feeney^{2,3}, Lawrie K Brown², Muhammad Naveed^{1,4}, Siul Ruiz⁵, Nicolai Koebernick^{5,6}, Anthony G Bengough^{2,3}, Paul D Hallett¹, Tiina Roose⁵, Jaime Puértolas⁷, Ian C Dodd⁷, and Timothy S George²

¹School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 3UU, UK (maria.marin@abdn.ac.uk; paul.hallett@abdn.ac.uk)

²The James Hutton Institute, Invergowrie, Dundee, DD2 5DA, UK (lawrie.brown@hutton.ac.uk; tim.george@hutton.ac.uk)

³School of Science and Engineering, University of Dundee, Dundee, DD1 4HN, UK (A.Bengough@dundee.ac.uk)

⁴School of Computing and Engineering, University of West London, London W5 5RF (Muhammad.Naveed@uwl.ac.uk)

⁵School of Engineering, University of Southampton, Southampton, SO17 1BJ, UK (S.A.Ruiz@soton.ac.uk; T.Roose@soton.ac.uk)

⁶Institute of Agricultural and Nutritional Sciences, Martin Luther University Halle-Wittenberg, 06108 Halle (Saale), Germany (nicolai.koebernick@landw.uni-halle.de)

⁷The Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK (j.puertolas@lancaster.ac.uk; i.dodd@lancaster.ac.uk)

Root hairs represent an attractive target for future crop breeding, to improve resource use efficiency and stress tolerance. Most studies investigating root hairs have focused on plant tolerance to phosphorus deficiency and rhizosheath formation under controlled conditions. However, data on the interplay between root hairs and open-field systems, under contrasting soils and climate conditions, are limited. Although root hairs and rhizosphere are assumed to play a key role in regulating plant water relations, their effect on plant water uptake has been rarely investigated. As such, this study aimed to experimentally elucidate some of the impacts that root hairs have on plant performance under field conditions and water deficit. A field experiment was set up in Scotland for two consecutive years, in 2017 (a typical year) and 2018 (the driest growing season ever recorded at this site), under different soil textures (i.e., clay loam vs. sandy loam). Five barley (*Hordeum vulgare*) genotypes exhibiting variation in root hair length and density were used in the study. Measurements of root hair density, length and its correlation with rhizosheath weight highlighted trait robustness in the field under variable environmental conditions. Root hairs did not confer a notable advantage to barley under optimal conditions, but under soil water deficit root hairs enhanced plant water status and stress tolerance. This resulted in less negative leaf water potential and lower leaf abscisic acid concentration, while promoting shoot phosphorus accumulation. Specifically, minimum leaf water potential differed significantly ($P = 0.021$) between the wild type (-1.43 MPa) and its hairless mutant (-1.76 MPa) grown in clay loam, with the mutant exhibiting greater water stress. In agreement with leaf water potential measurements, at the peak of water stress, leaf abscisic acid concentration was significantly ($P = 0.023$) greater for the hairless mutant (394 ng g^{-1}) than the wild type (250 ng g^{-1}) grown in clay loam soil. Under water deficit conditions, in clay loam soil, shoot phosphorus accumulation in the wild type ($2.49 \text{ mg P shoot}^{-1}$)

was over twice that in the hairless mutant ($1.10 \text{ mg P shoot}^{-1}$). Furthermore, the presence of root hairs did not decrease yield under optimal conditions, while root hairs enhanced yield stability under drought. While yield of the hairless mutant significantly ($P = 0.012$) decreased from 2017 to 2018 in both clay (-26%) and sandy (-33%) loam soils, no significant differences were found between years in the yield of the wild type. Therefore, selecting for beneficial root hair traits can enhance yield stability without diminishing yield potential, overcoming the breeder's dilemma of trying to simultaneously enhance both productivity and resilience. To our knowledge, the present findings provide the first evidence of the effect of root hairs under drought in open field conditions (i.e., real agricultural system). Therefore, along with the well-recognized role for P uptake, maintenance or enhancement of root hairs can represent a key trait for breeding the next generation of crops for improved drought tolerance in relation to climate change.