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Review

Building soil sustainability from root–soil interface traits

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Great potential exists to harness plant traits at the root–soil interface, mainly rhizodeposition and root hairs, to 'build' soils with better structure that can trap more carbon and resources, resist climate stresses, and promote a healthy microbiome. These traits appear to have been preserved in modern crop varieties, but scope exists to improve them further because they vary considerably between genotypes and respond to environmental conditions. From emerging evidence, rhizodeposition can act as a disperser, aggregator, and/or hydrogel in soil, and root hairs expand rhizosheath size. Future research should explore impacts of selecting these traits on plants and soils concurrently, expanding from model plants to commercial genotypes, and observing whether impacts currently limited to glasshouse studies occur in the field.

Highlights

Root hairs and rhizodeposits are root traits that vary between plant species and crop genotypes and have a large impact on both plants and soils.

Targeting these traits may benefit both plants and soil, improving food and environmental security at the same time. Soils may store more carbon (greenhouse gas mitigation), trap more water (drought tolerance) and nutrients, and resist erosion.

From limited research, rhizosheath size has been maintained or improved in modern crop varieties, but potential exists to increase it further. Whether this will lead to improved yield or soil properties, however, requires greater field testing to verify.

Laboratory and glasshouse research using root trait ideotypes has found marked impacts on soil biophysical properties. Rhizodeposits vary in behaviour between species from hydrogels to surfactants, and as soil dispersers (miners) or aggregators (builders).

Building soil sustainability from root–soil interface traits

By reversing our thinking of how root–soil interface traits affect the functioning of the **rhizosphere** (see Glossary), there is considerable opportunity to restore degraded soils [1], mitigate greenhouse gases [2], and enhance biodiversity [3]. These are some of the grandest challenges facing humanity [4], which, by focussing on root–soil interface traits, plant breeding may help address while also underpinning another grand challenge – food security. Breeding crop varieties with the target of improving soil health and reducing soil degradation will produce better conditions for crop growth through more efficient resource use and stress tolerance, so a win–win is possible where both yield and soil are improved and could be the cornerstone of regenerative agriculture.

Whilst considerable research has explored root exudation and the rhizosphere microbiome [3,5–7], the lack of integrated research with other disciplines has failed to capture wider benefits of root–soil interface traits on soils. If soils are improved by optimising rhizosphere function, then plants may benefit from both direct and indirect impacts. Direct impacts have been studied extensively, focussed primarily on the suppression of pathogens [3,8] and the capacity of plants to capture resources from soil, such as through manipulation of nutrient cycling by micro-organisms [9]. This review focusses on indirect impacts that are less well studied, specifically on the capacity of roots to restructure soil.

By targeting **soil structure** building root traits, abiotic stress resistance of both plants and soils could increase through microbial habitat formation to improve nutrient cycling, stabilisation of soil against erosion, and a greater capacity of soil to absorb, store, and drain water [10]. Such improvements to soil structure driven by plants may improve carbon storage [11,12] and may mitigate against soil compaction damage that prevents deep-rooting cultivars penetrating through hard layers of soil and capturing otherwise lost resources [13]. Plants are known to have a huge impact on soil properties, but these processes are generally ignored in plant breeding, where the primary focus is yield, either directly from plant productivity or indirectly from biotic

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and abiotic stress tolerance [10]. With the shift towards reduced tillage and smaller inputs of agrochemicals, a plant's capacity to alter soil structure [14] and the rhizosphere microbiome [3] will become increasingly important. Given that root–soil interface traits that benefit soils may also benefit plants, perhaps favourable traits have been inadvertently selected in modern varieties, so we seek evidence from past research.

Plants as architects of soil

The capacity of plants to manipulate soils has been long appreciated, forming the basis of good rotation design and **biological tillage** [15]. A considerable body of research has shown plant roots to be a major driver of the soil microbiome [5,6] and soil physical structure [16]. The mechanisms used by plant roots to navigate and modify structurally heterogeneous soil were discussed by Jin *et al*. [13], who also argued that optimising root–soil interactions could improve food and soil sustainability. Starting at the root tip, compression of soil by an elongating and expanding root can be eased by sloughed-off cells [17] and exuded **mucilage** [18] (Figure 1). Extending along the root, primarily to the elongation zone, **exudates** are released that enhance nutrient capture [19]. All of these compounds secreted by roots provide a major burst of substrate, producing a 'hot spot' or 'hot moment' at the root–soil interface [20]; this has profound effects on the diversity and functioning of the surrounding microbiome [7].

A hot opportunity may exist to manipulate mucilages and exudates from roots to improve soil properties at the root–soil interface, producing a unique biophysical environment and niche for microbes and their functions. These compounds interact with microbial by-products and the physical action of the expanding, drying, and wetting root to form the rhizosphere [14]. Rhizosphere size is difficult to define and varies rapidly over time, but it can have chemical influences extending 3 mm and physical influences extending over 10 mm into the soil. A volume of soil under cereals has been estimated to be 2% roots and about 50% rhizosphere [21], but there is scope through breeding to extend this further. Properties of the rhizosphere can vary markedly to the surrounding soil, with a range of benefits to plant productivity and the environment (Box 1). It forms the interface of all materials captured by the plant from soil and the habitat where micro-organisms interact to cycle plant nutrients and compete against pathogens and is therefore a critical zone of global significance.

Plant breeding and root–soil interface traits

Modern agriculture has degraded soils through depleting soil carbon, acidification, increasing salinity (irrigation and removal of trees), mining of elements, enhancing erosion, and decreasing microbial diversity [4]. To some extent, these threats can be mitigated by improved agronomy, but perhaps plant breeding exacerbated soil degradation by focussing on yield and resource capture in fertilised soils. Fertilisers decrease the benefit of root–soil interface traits such as exudates and **root hairs** [22,23] to capture nutrients, arguably making them more dispensable for the plant. Coupled with this, modern crop cultivars may have root systems that are smaller, steeper, and reach deeper than older varieties [24,25], so they would be expected to return less carbon to soils. However, even when root system biomass has decreased over time with cultivar development, net effects on rhizodeposition may be minimal, and therefore the long-term impact on soil carbon is uncertain [26]. Furthermore, under less ideal conditions of drought [24] or compaction [27], modern varieties may be more responsive at reaching deeper soil [28] where **rhizodeposits** decompose more slowly, resulting in more effective carbon storage [29]. In a study of over 100 wheat genotypes, Mathew *et al*. [30] concluded that root biomass could be selected along with grain yield to satisfy both soil carbon sequestration and food security.

Glossary

Biological tillage: fragmentation and aggregation of soil through the action of plant roots, soil fauna, and micro-organisms.

Exudates: substances secreted by roots, composed of a mix of sugars, amino acids, organic acids, and other organic substances.

Microhydrological niches: discrete spatial regions in soil where biological compounds alter water holding and transport properties.

Mucilage: polysaccharide-rich compounds secreted at the root tip that are viscous.

Quantitative trait loci (QTLs): genes that influence specific traits.

Rhizodeposits: collective term for all materials exchanged from the plant to soil, dominated by exudates, mucilages, and sloughed cells.

Rhizosheath: soil that adheres strongly to the root through the action of root hairs and rhizodeposits. It provides a rapid and easy approach to sample soil affected by plant roots.

Rhizosphere: soil at the interface of plant roots that has been influenced by rhizodeposits. All resources capture by a plant from soil enters through the rhizosphere. It generally has greater carbon, biological activity, and stability than surrounding soil.

Root hairs: single-cell outgrowths from the root epidermis that increase root surface area and soil exploration.

Soil structure: the spatial arrangement of soil particles and pores, driven primarily by aggregation and dispersion from roots and soil biology.

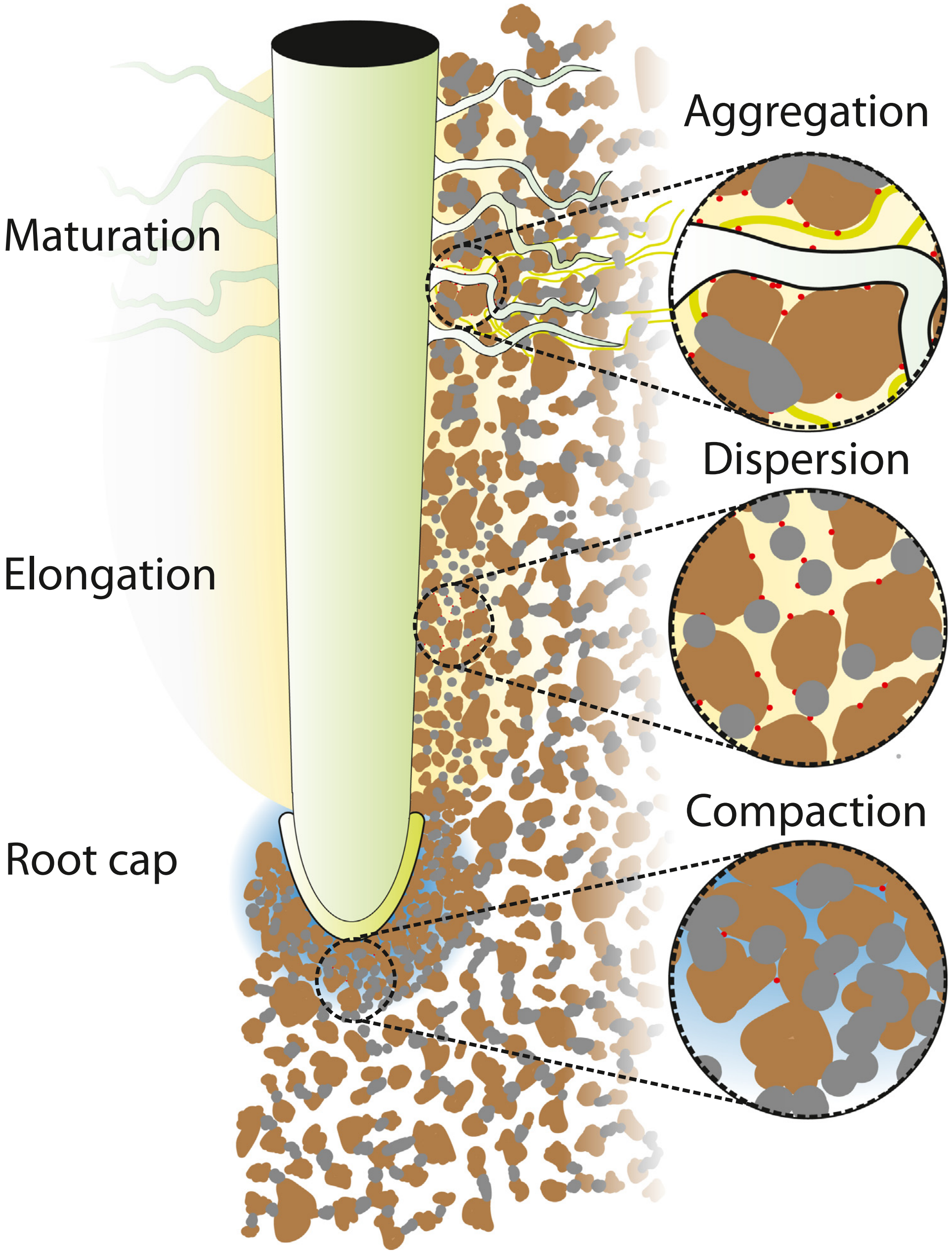

Figure 1. Formation of the physical environment at the root–soil interface through the combined impacts of root hairs, root tip mucilage (*blue*), and root exudates (*yellow*). Bacteria (*red dots*) and arbuscular mycorrhizal fungi (*green lines*) populations increase along the root and produce secondary compounds from rhizodeposits that have further physical impacts.

By growing deeper in soil, root architecture offers exciting opportunities to improve crop resistance to stress and soil carbon storage at the same time [28]. This comes at a metabolic cost, so there is emerging interest in altering root anatomy such as tissue structure for greater metabolic efficiency [31]. Compared with system architecture, however, root–soil interface traits can offer far greater metabolic efficiency for capturing resources from soil [32,33]. Under constrained

Box 1. Rhizosphere traits that benefit plants and soils

Plant roots are ecosystem engineers that are highly responsive to the soil environment [13]. Through rhizodeposition, roots massively influence a thin zone of soil at their surface that is expanded by root hairs (Figure I). Improved properties for plants emerge in the rhizosphere, which is teeming with microbial life in mutualistic, symbiotic, and parasitic interactions with plants [3]. Everything a plant captures from soil passes through the rhizosphere, which also serves as a store that captures and releases water and nutrients better than the surrounding soil [70].

The benefits to the plant from the rhizosphere also benefit the soil. Carbon is the primary driver, which provides a substrate for microbial activity that underpins nutrient cycling and particle aggregation [6]. A range of root and microbially derived compounds aggregate soil, capture water as hydrogels, and ease water extraction by their surface activity. Root hairs further bind the soil together, improving the anchorage of roots and possibly soil resistance to erosion.

Between different genotypes of the same crop, rhizodeposition and root hair properties differ, and the QTLs driving these traits are being identified [41]. Rhizodeposition and root hairs also adapt to the soil environment, increasing plant resistance to drought [5] and nutrient capture when fertility is poor [38]. Targeting root traits that influence the rhizosphere could therefore make both soils and food production more sustainable.

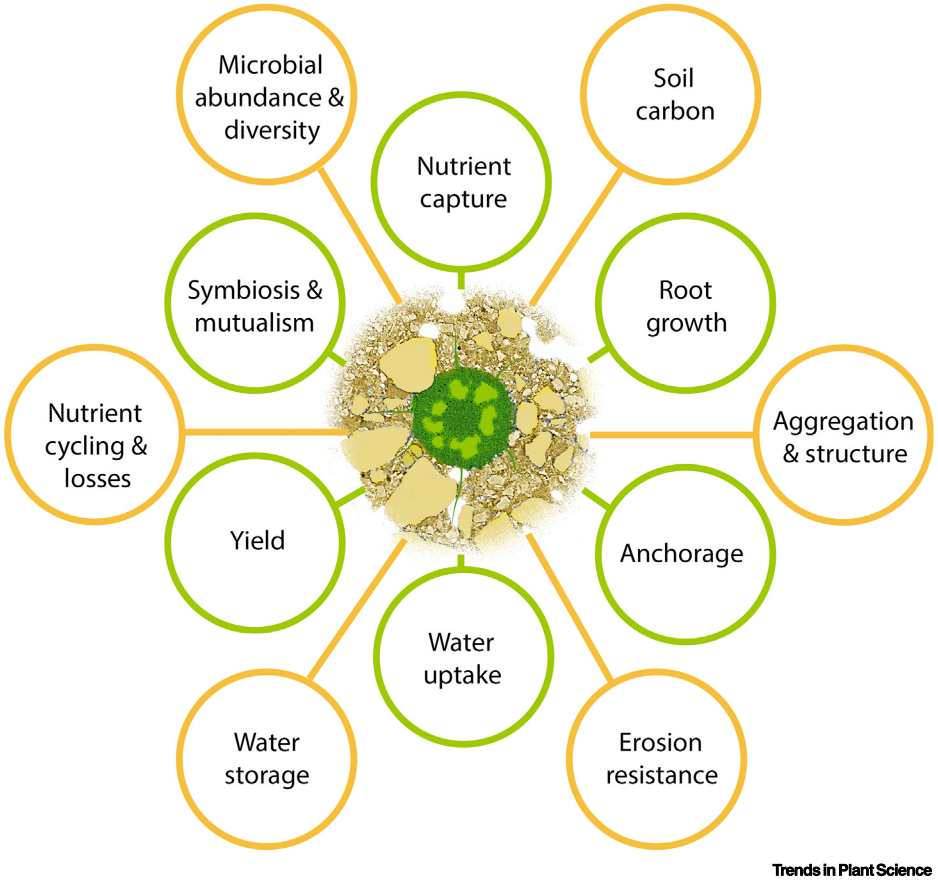

Figure I. How root surface traits influence soils.

conditions of nutrients, water, or temperature, root hair abundance increases [34], and exudates containing more efficient enzyme signatures can be produced [35]. Exudates and root hairs work in tandem to improve metabolic efficiency [12], driving improved soil conditions for the plant in the rhizosphere [36].

As the rhizosphere is difficult to define and separate from soil, soil that adheres to roots to form a **rhizosheath** [14] is often measured because it has defined boundaries and is easier to sample. While this operationally defined trait does not encompass the entire rhizosphere, it is a good proxy for rhizosphere size and properties [37]. From the little data that exist comparing landraces with different eras in modern crop breeding, it appears that rhizosheath size has been maintained or improved over time (Table 1).

The size of the rhizosheath differs considerably between species [38] and also between genotypes of the same species. But would targeting rhizosheath size in breeding lead to a yield reduction? A comparison of rhizosheath size with yield finds little impact (Figure 2), and one of the few field studies on root hair impacts on rhizosheath size found a positive impact on yield in dry years [39]. Potential therefore exists to target genotypes with a greater ability to physically manipulate soils, possibly with improved crop productivity too.

Could this offer a new tool in a plant breeders' arsenal? **Quantitative trait loci (QTLs)** related to rhizosheath size have been found, and the genetic controls may be relatively simple [40]. Between 144 elite genotypes of *Hordeum vulgare* grown in soil mesocosms, rhizosheath size was found to vary by over 500%, with the upper quartile varying by about 175% [41]. However, it is not only the genotype but also the environment that affects rhizosheath size. Poor soil phosphorus availability and root–soil contact tends to create larger rhizosheaths [42], so selecting crops for rhizosheath size could infer greater abiotic stress resistance with plasticity from responsiveness in degraded soils. Drought can increase rhizosheath size and its ability to store and transmit water, particularly in drought-tolerant genotypes [16]. Investment in the rhizosheath or rhizosphere may give a direct payoff to the plant through improved resource acquisition to counteract stress [5,12,16,43], but it may also indirectly pay off by improving soil structure. It is interesting to note that the species which were first noted for having rhizosheaths were desert grasses that survived in extremely poor soils low in organic matter content [44]. Plants appear to be investing in improving their soil conditions at the root–soil interface and buffering themselves against hostile environments.

The recent surge in understanding of how specific root–soil interface traits manipulate root–soil interactions has been enabled by a range of new technologies. From milligram samples of precisely extracted rhizosphere soil, molecular approaches have unravelled contrasting microbiomes between plant species and genotypes [6,8]. Rhizosphere properties can be measured in intact soil samples using high-resolution physical and chemical measurements [45], including 3D visualisation of how root traits impact soil pore structure [46]. By combining the technologies enabling shoot-root phenotyping [47] with molecular biology of plants and soil microorganisms [6], studies

Table 1. Rhizosheath size of landraces and released varieties of four crop species, along with the data source

Species	Rhizosheath size (g m^{-1})[a]			Soil		Soil pH	Soil P (mg kg^{-1})	Soil water content	Refs
	Era I	Era II	Era III	WRB	Texture				
Zea mays	2.38	2.58	2.09	Acrisols	Sandy loam	6.1	26.1	70% FC	[77]
Hordeum vulgare	4.37	4.54	4.37	Luvisols	Sandy loam	9.2	5 (Colwell P)	75% FC	[78]
Triticum aestivum	–	4.60	3.86	Acrisols	N/A	6.2	N/A	90% FC	[79,80]
Triticum aestivum	1.69	–	1.13–2.54	Andosols	N/A	N/A	14.4	80% FC	[81]
Panicum virgatum	–	0.80	2.40	N/A	N/A	N/A	N/A	30% FC	[82]

[a] Rhizosheaths are expressed as gram per metre of root, including weights of both the fresh root and the moist soil. Era I = landraces; Era II = earlier varieties of *Zea mays* (1983–1998), *Hordeum vulgare* (1951–1986), *Triticum aestivum* (1932–1972), and *Panicum virgatum* (1963); Era III = later varieties of *Zea mays* (2006–2013), *Hordeum vulgare* (1996–2013), *Triticum aestivum* (1993–2006), and *Panicum virgatum* (1973–1978). WRB is the Reference Soil Group of the World Reference Base for soil resources. N/A means data are not available. Soil P is measured by the Olsen method unless another approach is listed. FC is field capacity, the water content of soil after free drainage ceases.

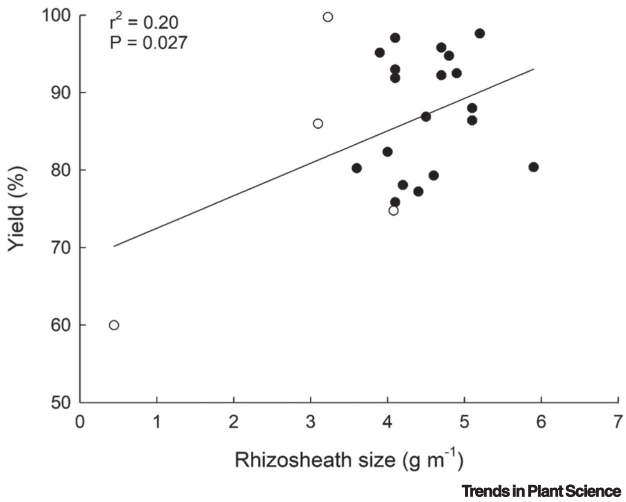

Figure 2. Relationship between rhizosheath size and yield of *Hordeum vulgare*, including 20 varieties from McDonald *et al*. [78] (*black circles*) and 4 genotypes differing in root hair length of cv. Optic from Brown *et al*. [83] (*white circles*). Each genotype under P-limited conditions is represented as a percentage of achievable yield for the same genotype under unlimited P conditions.

of the rhizosphere offer a great opportunity to understand below-ground interactions and their genetic drivers that could be harnessed to improve soil conditions at a spatially and temporally meaningful scale.

Root–soil interface traits for more sustainable plants

The emerging understanding of root–soil interface traits demonstrates the great capacity of plants to manipulate the soil environment and has potential to inform new crop genotypes. Roots produce larger and more stable volumes of soil at their surface, mainly by root hairs and rhizodeposits (Figure 1), that work together to affect the environment surrounding the root, producing the equivalent of intestinal villi and secretions to enhance nutrient capture and support a microbiome. Jethro Tull's [48] assertion 250 years ago that 'roots are but as guts inverted ... that spew out what is superfluous' captures these processes eloquently, although mucilages and exudates are certainly not superfluous.

Compared with the study of the gastrointestinal tract, however, the presence of soil creates a major challenge to the study of root traits. Gut biology is complicated, but the 3D dynamic pore structure, diverse chemistry, and vast biodiversity of soil produces a much more complex system. Just as in gut biology, rhizosphere research focuses on the microbiome [6], but unlike gut biology, where habitat is fixed by organ structure, the rhizosphere microbiome interacts with soil particles, the growing root, root hairs, and rhizodeposits to continuously produce new habitat over time and space. With emerging evidence of the underlying processes that drive this habitat creation comes growing confidence that crop genotypes or species can be selected for their ability to physically manipulate soils. One impact is decreased abiotic stress from drought through rhizodeposits restructuring soil to trap more water [13] and easing deep root penetration through compacted soil [18]. Water stress alters rhizodeposit chemistry, thus influencing microbial diversity [5] and function such as exopolysaccharide production by roots and microbes improving water retention [49].

However, the understanding of the physical processes underpinning rhizosphere formation and its impacts on plants is only just emerging and is constrained by the challenge of direct sampling of rhizodeposits from soil [19]. An alternative is to harvest exudates and other rhizodeposits in soil-free systems such as hydroponics [50], sterile and inert matrices to simulate soil [51], or directly from exuding brace roots or seedling root tips [52,53]. Measurements of directly harvested rhizodeposits have helped to unravel processes that lead to the development and functioning of the rhizosphere. Building on research exploring the chemistry of root mucilage, Read and Gregory [54] found that these compounds were highly surface active and viscous. By being surface active, root mucilage can decrease the surface tension of water by over 30%, with an expected easing of water capture from surrounding soil [55]. Viscous rhizodeposits, on the other hand, are more resistant to drainage. This may aid water uptake [33] and produce **microhydrological niches** that could buffer roots and micro-organisms from the wetting and drying stresses of surrounding soil [56]. Viscous rhizodeposits may also help fill gaps that emerge between drying roots and soil [57], further enabling greater water uptake [56] but potentially leading to the development of a hydrophobic rhizosphere that rewets poorly following drought [58]. The surface activity of other rhizodeposits can help mitigate hydrophobicity, producing greater rewetting rates [43]. Experimental evidence using model rhizodeposits has suggested that they may also decrease water movement rates in dry soil [59], although much of this has been limited to sandy soils where this impact is exacerbated [55].

So, it is not just the chemical composition of rhizodeposits that improves root–soil interactions but also their physical properties, and this needs to be considered when exploring root traits. The viscosity and surface activity of rhizodeposits varies between plant species [54,55], resulting in different impacts to soil [60]. *H. vulgare* has a greater proportion of organic acids to sugars in its rhizodeposits than does *Zea mays*, resulting in a lower viscosity and greater surface activity [50]. This suggests that when these rhizodesposits are added to soil, *H. vulgare* eases water extraction by its exudates acting as a surfactant, whereas *Z. mays* exudates improve water storage by acting as a hydrogel [60]. Mechanical measurements of soils amended with these rhizodeposits found *H. vulgare* to weaken and disperse soil particle bonds, which has been speculated to improve nutrient release, ease root growth, and catalyse changes to the rhizosphere [50]. *Z. mays* rhizodeposits have the opposite effect of strengthening and gelling soil particle bonds. Rapid microbial degradation of rhizodeposits produces secondary compounds [19,49], so their physical impacts may change quickly. Microbes have been found to change *H. vulgare* rhizodeposits from dispersing into gelling compounds [50] with diminished surface activity [60] that aggregate soil to create more favourable habitats for microbes and plants. This might improve the sustainability of soil as a more stable and aggregated structure will be more effective at storing and cycling water, carbon, and nutrients.

The different properties of *Z. mays* and *H. vulgare* rhizodeposits could reflect the environments where they evolved. It is fascinating to think that environmental variability may have played out in subtle changes to exudate quality that led to opposing strategies to cope with a deficit of water or nutrients, giving us a range of rhizosphere strategies to challenge the problems posed by drought and soil degradation. Likewise, desert plants are being used to inform QTLs controlling rhizosheath formation [44,49], which could be extended to common crop species as more evidence of contrasting rhizodeposit properties emerges. Harvesting of rhizodeposits and performing quick measurements of their physical behaviour augmented by modelling approaches of root-water uptake could provide a high-throughput approach to screen large numbers of genotypes to identify favourable traits. This would complement emerging understanding of chemical components of rhizodeposits [36] and rapid screens to assess their adhesive properties that aggregate soil [61].

These direct physical measurements of the capacity of rhizodeposits to disperse and aggregate soils were visually apparent in decades-old scanning electron micrographs of the rhizosphere [62]. With the emergence of noninvasive 3D imaging of root–soil interactions, coupled with increased computing power, leaps in understanding should eventually inform crop breeding

[16,47]. For example, synchrotron imaging at submicrometer resolution has visualised the tortuous pathways through soil pores that root hairs penetrate to increase the zone of influence of the root and its capacity to capture resources [46,63]. Such technology is unravelling how traits such as increased root hair length lead to greater P capture [42] and yield under limited conditions (Figure 3) [64]. Sophisticated numerical models can use synchrotron imaging of the submicrometer scale 3D structure of root hairs [65] and their interaction with soil pores [46] to predict resource capture. Other models begin to explore how microbial traits interact with the physical, chemical, and biological properties at these pore scales [66]. The combined experimental knowledge and modelling approaches will deepen our understanding of rhizosphere properties, potentially offering an exciting new tool to simulate optimum root trait ideotypes.

High-resolution 3D imaging has also revealed that root hairs can restructure the root–soil interface to counteract compaction from roots expanding radially and axially as they grow [46]. This early work visualising how root hairs and soil structure interact has been limited to seedlings of *H. vulgare* and *Triticum aestivum* [65] and different water stresses. Findings have been contradictory [46,63], likely due to soil properties, and different genotypes have yet to be explored, so considerable potential exists for follow-on research. Direct visualisation of root hairs in soil has also questioned the value of measuring root hairs in artificial conditions because there may be limited similarity to abundance and length when grown in soil [67]. Processes leading to greater resource capture by root hairs also require greater investigation. In an elegant study using a root pressure chamber [68], root hairs were found to buffer the drying gradient (water potential flux) at the root–soil interface, enabling greater transpiration rates from drying soil [69]. This led to questioning of accepted concepts of plant hydraulics, where stomatal closure under water stress has been argued to be driven by soil hydraulic properties at the root–soil interface rather than xylem vulnerability [70]. Expanding the zone of soil influenced by roots through root hairs may therefore offer another plant trait to improve drought tolerance.

Root hairs also improve anchorage between roots and surrounding soil [34]. This has been observed to increase pull-out resistance, potentially decreasing root lodging by wind, uplifting by grazing animals, and improved establishment of seedlings upon soil disruption [61,71,72]. Another role of root hairs is bracing the root against soil, improving penetration into compacted

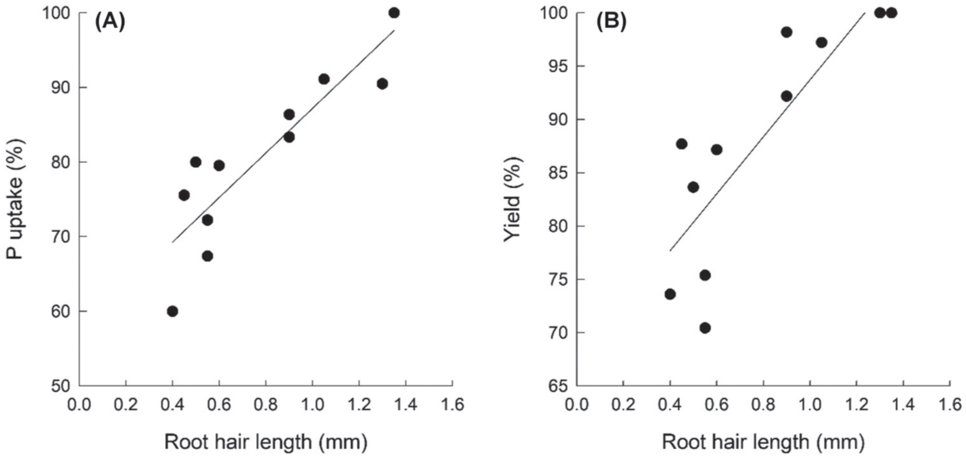

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Figure 3. Relationship between root hair length and P uptake (A) and yield (B) for 11 cultivars of *Hordeum vulgare* under P-limited conditions, from Gahoonia and Nielsen [64]. Each cultivar under P-limited conditions is represented as a percentage of achievable P uptake/yield for the same cultivar under unlimited P conditions.

soils [73]. From the perspective of the plant, root hairs improve nutrient and water capture, anchorage, and penetration, but from the perspective of soil, there are further potential positive impacts, summarised in Box 1.

Root–soil interface traits for more sustainable soils

An overarching impact of root hairs and rhizodeposition traits on soil is carbon [11,12], which underpins a broad range of environmental processes that feed back to plant productivity and stress tolerance. It has been estimated that 2.4 times more carbon is contributed by roots than shoots to soils [29]. Between different genotypes of the same crop, rhizodeposition chemistry and its knock-on impact to soil carbon storage can vary markedly [74]. Just as dabbing paint with a brush allows it to penetrate into nooks and crannies on surfaces, root hairs can aid the influence of plant roots by penetrating into soil pores that are too small for roots and distributing rhizodeposits into a greater volume of soil [29]. This creates the adhered soil that makes up the rhizosheath [75], which is postulated to be a major process that aggregates carbon and makes it more recalcitrant to decomposition by micro-organisms [29].

The studies discussed thus far provide convincing arguments of the potential to select rhizodeposition and root hairs to build more stable and aggregated soils. However, it is less clear if they result in meaningful impacts in the field. Even in a laboratory study, hairless root mutants of *H. vulgare* had a capacity to stabilise soil against erosion similar to that of their wild-type parent, but root system architecture confounded interpretation [76]. As in this work, many other studies have used hairless mutants to disentangle mechanisms, but meaningful data for crop breeders needs to contrast commercially viable varieties with differing root hairs and rhizodeposition [22]. One of the few field studies exploring root hairs compared two commercial *H. vulgare* varieties with a range of root hair mutants of one of the varieties [39]. Longer root hairs were correlated with bigger rhizosheaths, but the commercial varieties did not differ enough to provide a contrast. Further field experiments using a broader range of contrasting rhizosphere trait genotypes of different crops are needed to verify that postulated impacts from laboratory studies have meaningful impact. These experiments need to consider longer-term impacts to soil, particularly carbon dynamics, physical structure, and microbial populations that are the cornerstone of soil health.

Concluding remarks and future perspectives

Modern varieties and crop-breeding lines can have vastly different root hair and rhizodeposit properties that need to be scrutinised more closely for their combined impacts on plants and soils (see Outstanding questions). Studies on the microbiology, chemistry, and physical properties of the rhizosphere have shown large plasticity caused by stresses from drought, soil compaction, or nutrient availability. A genotype's capacity to engineer favourable soil properties at the root surface could enhance its fitness under variable field conditions.

We have shown evidence that selecting genotypes for favourable root–soil interface traits can also improve yield with minimal metabolic cost. There is potential through crop rotation for the root–soil interactions of preceding crops to benefit follow-on crops. Moreover, longer-term improvements to soil could result that benefit both the crop and the environment. The impact of plant roots on soils has been appreciated for centuries, but it is only now that new emerging technologies are unravelling the mechanistic processes of how plant root traits form the rhizosphere and impact both plants and soils. We are only at the beginning of understanding whether rhizodeposition and root hairs could be selected for more sustainable soils, but the emerging evidence is positive and compelling (see also Outstanding questions).

Outstanding questions

Are root traits influencing rhizosphere characteristics improved or degraded in modern crops compared with landraces?

What are the fundamental processes driving the biophysical structuring of rhizosphere properties, and how are they influenced by root traits?

Can we improve root–soil interactions for crops by learning from wild plants that have evolved in contrasting environments?

Are there specific QTLs to link crop genotypic and root–soil interface traits that can benefit breeding programmes?

Can we integrate the complex information on rhizospheres, plant physiology, and the soil environment to develop models to identify traits that benefit both plants and soils?

How does the plasticity of root hair growth, rhizodeposition, and the rhizosphere microbiome to environmental stress alter the biophysical properties of soil?

How do root traits and rhizospheres impact soils and ecosystem services such as water, nutrient, and carbon storage over the long term in the field?

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Declaration of interests

The authors have no interests to declare.

References

1. Brainard, J. (2018) Alarm over land degradation. *Science* 359, 1444
2. Rumpel, C. *et al.* (2018) Boost soil carbon for food and climate. *Nature* 553, 27
3. Mauchline, T.H. and Malone, J.G. (2017) Life in earth – the root microbiome to the rescue? *Curr. Opin. Microbiol.* 37, 23–28
4. Scherer, L. *et al.* (2020) Global priorities of environmental issues to combat food insecurity and biodiversity loss. *Sci. Total Environ.* 730, 139096
5. Williams, A. and de Vries, F.T. (2020) Plant root exudation under drought: implications for ecosystem functioning. *New Phytol.* 225, 1899–1905
6. Sasse, J. *et al.* (2018) Feed your friends: do plant exudates shape the root microbiome? *Trends Plant Sci.* 23, 25–41
7. Pieterse, C.M.J. *et al.* (2016) The soil-borne supremacy. *Trends Plant Sci.* 21, 171–173
8. Hilton, S. *et al.* (2018) Preceding crop and seasonal effects influence fungal, bacterial and nematode diversity in wheat and oilseed rape rhizosphere and soil. *Appl. Soil Ecol.* 126, 34–46
9. Schmidt, J.E. *et al.* (2020) Impacts of directed evolution and soil management legacy on the maize rhizobiome. *Soil Biol. Biochem.* 145, 107794
10. Gregory, P.J. *et al.* (2013) Rhizosphere engineering by plants: Quantifying soil–root interactions. In *Enhancing Understanding and Quantification of Soil–Root Growth Interactions* (Vol. 4) (Timlin, D. and Ahuja, L.R., eds), pp. 1–30, American Society of Agronomy, Crop Science Society of America, Soil Science Society of America
11. Pausch, J. and Kuzyakov, Y. (2018) Carbon input by roots into the soil: Quantification of rhizodeposition from root to ecosystem scale. *Glob. Chang. Biol.* 24, 1–12
12. Holz, M. *et al.* (2018) Root hairs increase rhizosphere extension and carbon input to soil. *Ann. Bot.* 121, 61–69
13. Jin, K.M. *et al.* (2017) Shaping an optimal soil by root-soil interaction. *Trends Plant Sci.* 22, 823–829
14. York, L.M. *et al.* (2016) The holistic rhizosphere: integrating zones, processes, and semantics in the soil influenced by roots. *J. Exp. Bot.* 67, 3629–3643
15. Chen, G.H. and Weil, R.R. (2010) Penetration of cover crop roots through compacted soils. *Plant Soil* 331, 31–43
16. Rabbi, S.M.F. *et al.* (2018) Plant roots redesign the rhizosphere to alter the three-dimensional physical architecture and water dynamics. *New Phytol.* 219, 542–550
17. Bengough, A.G. *et al.* (2011) Root elongation, water stress, and mechanical impedance: A review of limiting stresses and beneficial root tip traits. *J. Exp. Bot.* 62, 59–68
18. Oleghe, E. *et al.* (2017) Plant exudates improve the mechanical conditions for root penetration through compacted soils. *Plant Soil* 421, 19–30
19. Oburger, E. and Jones, D.L. (2018) Sampling root exudates – mission impossible? *Rhizosphere* 6, 116–133
20. Kuzyakov, Y. and Blagodatskaya, E. (2015) Microbial hotspots and hot moments in soil: Concept & review. *Soil Biol. Biochem.* 83, 184–199
21. Bengough, A.G. (2012) Water dynamics of the root zone: rhizosphere biophysics and its control on soil hydrology. *Vadose Zone J.* 11, vzj2011.0111
22. Wissuwa, M. and Kant, J. (2021) 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.'. *Ann. Bot.* 128, iii–v
23. Wen, T.J. and Schnable, P.S. (1994) Analyses of mutants of 3 genes that influence root hair development in *Zea-mays* (Gramineae) suggest that root hairs are dispensable. *Am. J. Bot.* 81, 833–842
24. Friedli, C.N. *et al.* (2019) Modern wheat semi-dwarfs root deep on demand: Response of rooting depth to drought in a set of Swiss era wheats covering 100 years of breeding. *Euphytica* 215, 85
25. Aziz, M.M. *et al.* (2017) Five decades of selection for yield reduced root length density and increased nitrogen uptake per unit root length in Australian wheat varieties. *Plant Soil* 413, 181–192
26. Van de Broek, M. *et al.* (2020) The soil organic carbon stabilization potential of old and new wheat cultivars: A $^{13}CO_2$-labeling study. *Biogeosciences* 17, 2971–2986
27. Correa, J. *et al.* (2019) Soil compaction and the architectural plasticity of root systems. *J. Exp. Bot.* 70, 6019–6034
28. Thorup-Kristensen, K. *et al.* (2020) Digging deeper for agricultural resources, the value of deep rooting. *Trends Plant Sci.* 25, 406–417
29. Rasse, D.P. *et al.* (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant Soil* 269, 341–356
30. Mathew, I. *et al.* (2019) Selection of wheat genotypes for biomass allocation to improve drought tolerance and carbon sequestration into soils. *J. Agron. Crop Sci.* 205, 385–400
31. Lynch, J.P. *et al.* (2021) Root anatomy and soil resource capture. *Plant Soil* 466, 21–63
32. Brown, L.K. *et al.* (2013) A conceptual model of root hair ideotypes for future agricultural environments: what combination of traits should be targeted to cope with limited P availability? *Ann. Bot.* 112, 317–330
33. Ahmed, M.A. *et al.* (2014) Mucilage exudation facilitates root water uptake in dry soils. *Funct. Plant Biol.* 41, 1129–1137
34. Vissenberg, K. *et al.* (2020) Hormonal regulation of root hair growth and responses to the environment in Arabidopsis. *J. Exp. Bot.* 71, 2412–2427
35. Zhang, X.C. *et al.* (2020) Rhizosphere hotspots: Root hairs and warming control microbial efficiency, carbon utilization and energy production. *Soil Biol. Biochem.* 148, 107872
36. Galloway, A.F. *et al.* (2020) Cereal root exudates contain highly structurally complex polysaccharides with soil-binding properties. *Plant J.* 103, 1666–1678
37. Pang, J.Y. *et al.* (2017) Unwrapping the rhizosheath. *Plant Soil* 418, 129–139
38. Brown, L.K. *et al.* (2017) The rhizosheath – a potential trait for future agricultural sustainability occurs in orders throughout the angiosperms. *Plant Soil* 418, 115–128
39. Marin, M. *et al.* (2021) Significance of root hairs for plant performance under contrasting field conditions and water deficit. *Ann. Bot.* 128, 1–16
40. James, R.A. *et al.* (2016) Rhizosheaths on wheat grown in acid soils: phosphorus acquisition efficiency and genetic control. *J. Exp. Bot.* 67, 3709–3718
41. George, T.S. *et al.* (2014) Understanding the genetic control and physiological traits associated with rhizosheath production by barley (*Hordeum vulgare*). *New Phytol.* 203, 195–205
42. Haling, R.E. *et al.* (2013) Root hairs improve root penetration, rootsoil contact, and phosphorus acquisition in soils of different strength. *J. Exp. Bot.* 64, 3711–3721
43. Ahmed, M.A. *et al.* (2018) Engineering rhizosphere hydraulics: pathways to improve plant adaptation to drought. *Vadose Zone J.* 17, 1–12

44. Price, S.R. (1911) The roots of some north african desert-grasses. *New Phytol.* 10, 328–340
45. Veelen, A. *et al.* (2020) Root-induced soil deformation influences Fe, S and P: rhizosphere chemistry investigated using synchrotron XRF and XANES. *New Phytol.* 225, 1476–1490
46. Koebernick, N. *et al.* (2017) High-resolution synchrotron imaging shows that root hairs influence rhizosphere soil structure formation. *New Phytol.* 216, 124–135
47. Tracy, S.R. *et al.* (2020) Crop improvement from phenotyping roots: Highlights reveal expanding opportunities. *Trends Plant Sci.* 25, 105–118
48. Tull, J. (1762) *Horse-hoeing husbandry: or, an essay on the principles of vegetation and tillage*, A. Millar
49. Ndour, P.M.S. *et al.* (2020) The rhizosheath: From desert plants adaptation to crop breeding. *Plant Soil* 456, 1–13
50. Naveed, M. *et al.* (2017) Plant exudates may stabilize or weaken soil depending on species, origin and time. *Eur. J. Soil Sci.* 68, 806–816
51. Boeuftremblay, V. *et al.* (1995) Influence of mechanical impedance on root exudation of maize seedlings at 2 development stages. *Plant Soil* 172, 279–287
52. Zickenrott, I.M. *et al.* (2016) An efficient method for the collection of root mucilage from different plant species – a case study on the effect of mucilage on soil water repellency. *J. Plant Nutr. Soil Sci.* 179, 294–302
53. Read, D.B. *et al.* (1999) Physical properties of axenic maize root mucilage. *Plant Soil* 211, 87–91
54. Read, D.B. and Gregory, P.J. (1997) Surface tension and viscosity of axenic maize and lupin root mucilages. *New Phytol.* 137, 623–628
55. Read, D.B. *et al.* (2003) Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. *New Phytol.* 157, 315–326
56. Benard, P. *et al.* (2019) Microhydrological niches in soils: how mucilage and eps alter the biophysical properties of the rhizosphere and other biological hotspots. *Vadose Zone J.* 18, 1–10
57. Carminati, A. *et al.* (2009) When roots lose contact. *Vadose Zone J.* 8, 805–809
58. Ahmed, M.A. *et al.* (2016) Drying of mucilage causes water repellency in the rhizosphere of maize: Measurements and modelling. *Plant Soil* 407, 161–171
59. Zhang, W.C. *et al.* (2021) Physical properties of a sandy soil as affected by incubation with a synthetic root exudate: Strength, thermal and hydraulic conductivity, and evaporation. *Eur. J. Soil Sci.* 72, 782–792
60. Naveed, M. *et al.* (2019) Surface tension, rheology and hydrophobicity of rhizodeposits and seed mucilage influence soil water retention and hysteresis. *Plant Soil* 437, 65–81
61. Eldridge, B.M. *et al.* (2021) A centrifuge-based method for identifying novel genetic traits that affect root-substrate adhesion in *Arabidopsis thaliana*. *Front. Plant Sci.* 12, 13
62. Dorioz, J.M. *et al.* (1993) The role of roots, fungi and bacteria on clay particle organization – an experimental approach. *Geoderma* 56, 179–194
63. Koebernick, N. *et al.* (2019) Imaging microstructure of the barley rhizosphere: Particle packing and root hair influences. *New Phytol.* 221, 1878–1889
64. Gahoonia, T.S. and Nielsen, N.E. (2004) Barley genotypes with long root hairs sustain high grain yields in low-P field. *Plant Soil* 262, 55–62
65. Keyes, S.D. *et al.* (2013) High resolution synchrotron imaging of wheat root hairs growing in soil and image based modelling of phosphate uptake. *New Phytol.* 198, 1023–1029
66. Portell, X. *et al.* (2018) Microscale heterogeneity of the spatial distribution of organic matter can promote bacterial biodiversity in soils: Insights from computer simulations. *Front. Microbiol.* 9, 16
67. Nestler, J. *et al.* (2016) Root hair formation in rice (*Oryza sativa* L.) differs between root types and is altered in artificial growth conditions. *J. Exp. Bot.* 67, 3699–3708
68. Deery, D.M. *et al.* (2013) Uptake of water from a Kandosol subsoil. II. Control of water uptake by roots. *Plant Soil* 368, 649–667
69. Carminati, A. *et al.* (2017) Root hairs enable high transpiration rates in drying soils. *New Phytol.* 216, 771–781
70. Carminati, A. and Javaux, M. (2020) Soil rather than xylem vulnerability controls stomatal response to drought. *Trends Plant Sci.* 25, 868–880
71. Choi, H.S. and Cho, H.T. (2019) Root hairs enhance *Arabidopsis* seedling survival upon soil disruption. *Sci. Rep.* 9, 11181
72. Zenone, A. *et al.* (2020) Biological adhesion in seagrasses: The role of substrate roughness in *Posidonia oceanica* (L.) Delile seedling anchorage via adhesive root hairs. *Mar. Environ. Res.* 160, 105012
73. Bengough, A.G. *et al.* (2016) Root hairs aid soil penetration by anchoring the root surface to pore walls. *J. Exp. Bot.* 67, 1071–1078
74. Mwafulirwa, L. *et al.* (2016) Barley genotype influences stabilization of rhizodeposition-derived C and soil organic matter mineralization. *Soil Biol. Biochem.* 95, 60–69
75. Burak, E. *et al.* (2021) Root hairs are the most important root trait for rhizosheath formation of barley (*Hordeum vulgare*), maize (*Zea mays*) and *Lotus japonicus* (Gifu). *Ann. Bot.* 128, 45–57
76. Burak, E. *et al.* (2021) A mesocosm-based assessment of whether root hairs affect soil erosion by simulated rainfall. *Eur. J. Soil Sci.* 72, 2372–2380
77. Adu, M.O. *et al.* (2017) Quantifying variations in rhizosheath and root system phenotypes of landraces and improved varieties of juvenile maize. *Rhizosphere* 3, 29–39
78. McDonald, G.K. *et al.* (2018) Responses to phosphorus among barley genotypes. *Crop Pasture Sci.* 69, 574–586
79. Delhaize, E. *et al.* (2015) The genetics of rhizosheath size in a multiparent mapping population of wheat. *J. Exp. Bot.* 66, 4527–4536
80. Delhaize, E. *et al.* (2012) Aluminium tolerance of root hairs underlies genotypic differences in rhizosheath size of wheat (*Triticum aestivum*) grown on acid soil. *New Phytol.* 195, 609–619
81. Okano, N. *et al.* (2020) Spanish spelt is unique germplasm for improvement of root hair length in hexaploid wheat. *Plant Soil* 452, 171–184
82. Liu, T.Y. *et al.* (2019) Comparative metabolite profiling of two switchgrass ecotypes reveals differences in drought stress responses and rhizosheath weight. *Planta* 250, 1355–1369
83. Brown, L.K. *et al.* (2012) What are the implications of variation in root hair length on tolerance to phosphorus deficiency in combination with water stress in barley (*Hordeum vulgare*)? *Ann. Bot.* 110, 319–328