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Commentary

Root traits catching up

The belowground world is one of the final frontiers in terrestrial ecology. Over the years, *New Phytologist* has served as a hotspot for scientists to present and discuss their science on the interplay among belowground plant traits, microbial activity, and edaphic and environmental conditions from biomes around the world (Iversen & McCormack, 2021). Here, the new paper published in this issue of *New Phytologist* by Tumber-Dávila *et al.* (2022; pp. 1032–1056) fits well and is perfectly complementary, as it focuses on the sizes of root systems (rooting depth, root system width) and their relationship with shoot size (plant height, canopy width) – aspects of major ecological relevance that are not often addressed. The analyses are based on the new release of the Root Systems of Individual Plants (RSIP) database: since 2002, globally, this has been the primary resource for rooting depth, and has now more than doubled the number of trait records compared to its last release in 2005. Tumber-Dávila *et al.* show that trait records in the RSIP database are well distributed across climate regimes, plant phylogeny and plant functional types. Based on the increase in data availability, their findings substantially improve our knowledge about root system sizes and plant shapes with implications for a wide range of different aspects of ecology:

(**1**) The results confirm that root systems sizes covary strongly with shoot sizes. Water availability and growth form greatly influence shoot size, and shoot size is the strongest predictor of root system width; however, rooting depth is influenced primarily by temperature seasonality. In consequence, the geometries of plants differ considerably across climates, with woody plants in more arid climates having shorter shoots but deeper, narrower root systems.

(**2**) The results confirm a strong phylogenetic signal on plant sizes and geometry, but this signal is interpreted as a result of eco-evolutionary sorting rather than being a direct consequence of phylogenetic constraints.

(**3**) Most importantly, the results indicate that rooting depth and width are systematically underestimated globally. In contrast to the general assumption that canopy width and root system width would be about equal, root system width is, on average, about two times wider than canopy width. This has substantial implications for our understanding of interactions between plant individuals and community assembly processes. The additional overlap of the root systems of different individuals allows for much more intense interactions with respect to competition for nutrient and water uptake, but also facilitation via, for example, nutrient and water redistribution and sharing of information. The network of mycorrhizal fungi amplifies these interactions.

The underestimation of rooting depth substantially confounds our understanding and modelling of carbon–water interactions. The information density in the new RSIP database now appears sufficiently high, and its relationship to plant functional types and climate gradients seems sufficiently consistent to substantially improve the representation of rooting depth, and to furthermore implement it as a dynamic response to climate variations. This implementation might constitute essential progress in predicting species, vegetation and ecosystem responses to climate change. Although we might expect deeper roots to improve species or ecosystem resilience, we must acknowledge that the already observed and ongoing effects of climate change are happening despite them.

> *‘The integration of root traits into a whole plant perspective seems more complex and nuanced and, thus, more interesting than expected.’*

In addition, the new RSIP database will substantially improve our knowledge about the multivariate trait–trait correlations across the different organs of vascular plants and contribute to extending the aboveground-only perspective of, for example, Díaz *et al.* (2016) to the whole plant. In a global analysis of six aboveground traits, Díaz *et al.* (2016) identified two major axes of variation: the first axis is related to plant size, with plant height as the leading trait, and the second is associated with the leaf economics spectrum (Wright *et al.*, 2004), defining fast vs slow growth strategies. This 2D correlation structure, the ‘global spectrum of plant form and function’, has been confirmed in several analyses, for example, with more traits (Joswig *et al.*, 2022) or at the community level (Bruelheide *et al.*, 2018). There also was an implicit expectation that the two major axes persist in a whole-plant context: the general correlation of above- and belowground plant sizes seems obvious and has been confirmed by Tumber-Dávila *et al.* and the consistency of the fast- vs slow-growth strategy across the whole plant has been postulated by Peter Reich (2014). Recently, two publications added root traits to the global spectrum of plant form and function – but with inconclusive results (Carmona *et al.*, 2021; Weigelt *et al.*, 2021). Weigelt *et al.* (2021) found the predicted match between leaf and fine-root fast- vs slow-growth strategies, yet this match did not emerge in the analysis by Carmona *et al.* (2021). The expected general correlation of above- and belowground sizes was not detected by Weigelt *et al.* (2021), and the assumption that tall plants also root deeply was not supported. However, these findings of Weigelt *et al.* (2021) are consistent with the results of Tumber-Dávila *et al.* indicating that root system width is the more consistent analogue to aboveground plant size. In conclusion, the integration

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of root traits into a whole-plant perspective seems more complex and nuanced and, thus, more interesting than expected.

The two approaches, Carmona *et al.* (2021) and Weigelt *et al.* (2021), are based on fine-root trait data compiled in the Fine Root Ecology Database (FRED; Iversen *et al.*, 2017, 2021). The FRED database was initiated in 2014 as a response to the poor coverage of fine-root traits in the global trait database TRY (Kattge *et al.*, 2011). To facilitate whole-plant trait investigations, each new version of FRED is submitted to the TRY plant trait database. As a consequence, together with other root trait contributions, the representation of root traits in TRY increased from 14 000 trait records in 2009 to 240 000 records in 2020 (Kattge *et al.*, 2020). In parallel, leading fine-root traits with high ecological information content and good data coverage in FRED have been identified and were further complemented and consolidated for easy application in the Global Root Traits database (GRooT; Guerrero-Ramírez *et al.*, 2021). A first application of the GRooT database shows that fine-root economics are more complicated than the leaf economics spectrum: in addition to the 'fast vs slow' growth strategy of the leaf economics spectrum, fine-root economics are determined by a mycorrhiza association gradient, which allows the outsourcing of resource uptake to mycorrhizal fungi (Bergmann *et al.*, 2020).

These results indicate three major aspects of root trait research supported by data collection and integration: root system size (supported by RSIP), fine-root morphology and physiology (supported by, e.g., FRED and GRooT), and symbiotic associations (supported by, e.g., the FungalRoot database; Soudzilovskaia *et al.*, 2020). The RSIP, FRED and GRooT databases cover *c.* 1500–3000 species per key trait. They have thus achieved sizes similar to the characterization of the leaf economics spectrum (Wright *et al.*, 2004; 2021 species) or the global spectrum of plant form and function (Díaz *et al.*, 2016; 2214 species with full trait coverage). The FungalRoot database contains mycorrhiza associations for 14 870 plant species, which is similar to (semi-) categorical aboveground traits in the TRY database (Kattge *et al.*, 2020). For more comprehensive overviews of root traits as drivers of plant and ecosystem functioning and root trait-related databases, see Freschet *et al.* (2021) and Iversen & McCormack (2021).

However, in advancing from only aboveground or only belowground analyses towards a whole-plant perspective, the number of relevant traits to be included in multivariate analyses essentially doubles. Given the current state of trait data coverage, the number of species with full trait coverage, as needed for, for example, PCA analyses, is reduced by *c.* 50% with each additional trait (Kattge *et al.*, 2020). Therefore, statistical gap-filling seems unavoidable to enable multivariate analyses based on complete datasets of above- and belowground traits. Here, phylogenetically or taxonomically constrained gap-filling algorithms have proven powerful in allowing the characterization of species mean traits and trait–trait correlations (Johnson *et al.*, 2021).

These developments have become possible because the perception of trait data records in the plant trait community has changed from a protective toward an open sharing approach. This was initiated by the tremendous success of the Glopnet initiative, headed by Peter Reich, David Ackerly, Mark Westoby and Ian Wright. At about the same time, and arguably as relevant for our general understanding of plant form and function, Jochen Schenk and Robert Jackson at Stanford University started to systematically compile the literature on plant rooting depth and developed the RSIP database, which was first published in 2002 and is now available in its third and substantially extended version in the context of the paper by Tumber-Dávila *et al.*

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