Annual Meeting

The elephant underground: Belowground plant traits and their increasing importance in ecological studies

Jacqueline P. Ott[1], Jitka Klimešová[2], Luke McCormack[3], and S. Joseph Tumber-Dávila[4]
[1]Forest and Grassland Research Laboratory, Rocky Mountain Research Station, USDA Forest Service, Rapid City, South Dakota 57702 USA
[2]Department of Experimental and Functional Morphology, Institute of Botany of the Czech Academy of Sciences, Třeboň, 37901 Czech Republic
[3]Center for Tree Science, The Morton Arboretum, Lisle, Illinois 60532 USA
[4]Department of Environmental Studies, Dartmouth College, Hanover, New Hampshire 03755 USA

Key words: *belowground growth organs; bud bank; carbon storage; clonal; perennial plants; root economic space; root system architecture.*

Introduction

Plants are an integral part of the Earth's Critical Zone, linking the atmosphere, hydrosphere, lithosphere, and biosphere (Field et al. 2015). To improve our insights into ecological theory and ecosystem processes, we need a more holistic view of plants that incorporates the "unseen elephant" of belowground plant organs and their traits (Fig. 1). Roots and belowground stems (e.g., rhizomes and tubers) acquire and store nutrients and support belowground buds that enable plants to regenerate following dormant seasons or disturbance (Klimešová and Klimeš 2007). Although belowground plant traits have been increasingly studied and included in databases (e.g., FRED, CLO-PLA, TRY), the understanding of belowground plant traits and the functions that they represent still lag behind aboveground traits and functions (Iversen et al. 2017, Kattge et al. 2020, Ottaviani et al. 2020). At the Ecological Society of America Annual Meeting held in Baltimore, Maryland, USA on 13 August 2025, we held a symposium titled "Belowground Plant Traits and Their Key Functions: An Overview of Roots, Clonal Growth Organs, and Bud Banks and Their Role in Resource Acquisition, Resource Storage

Ott, J. P., J. Klimešová, L. McCormack and S. J. Tumber-Dávila. 2026. The elephant underground: Belowground plant traits and their increasing importance in ecological studies. Bull Ecol Soc Am 0(0):e70085. https://doi.org/10.1002/bes2.70085

Fig. 1. The unseen elephant. Belowground plant traits are unseen and a largely unexplored frontier in ecology (Linograph by Jitka Klimešová).

and Vegetative Regeneration." Our goals were to (1) provide an overview of the current belowground plant trait research, and (2) bring together scientists studying roots, belowground morphological organ types, and bud banks to identify how to better integrate these fields. We first provide overviews of each presentation, and then discuss how areas of research are progressing and may be integrated in the future.

Belowground organ types

Presentation by Jitka Klimešová

From the very beginning of their lives, plants have aboveground shoots bearing leaves for assimilation and buds for branching, and belowground roots providing them with water, nutrients, and anchorage.

While some plants keep this body composition for their whole life, others adjust their body so that buds are located belowground—where they are protected from seasonal adversities and recurrent disturbances—either by placing their stems and associated buds belowground or by forming buds directly on roots (Ott et al. 2019, Klimešová 2025). Forming belowground (or close to the soil surface) storage and bud-bearing organs is crucial for perennial herbs and resprouting shrubs, which are present in forest understories but also dominate the majority of open ecosystems on Earth (Ottaviani et al. 2024). As perennating (i.e., storage, clonal, and bud bearing) organs evolved many times independently (Herben and Klimešová 2020, Klimeš et al. 2022), they are morphologically very diverse so that their functions apart from perennation also differ. For example, stolons are better at space occupation and clonal multiplication, while rhizomes are better protected and contain larger carbohydrate storage (Herben and Klimešová 2020). Belowground perennating organs affect the architecture of aboveground shoots by providing a plant with clonal multiplication, but also affect fine root architecture by adjusting their growth depth or width (Klimešová and Herben 2023). Belowground organ types, therefore, have the potential to affect the distribution of species along environmental gradients.

We tested this idea in the flora of Central Europe and found that the various morphological types of belowground organs have different distributions along environmental gradients, even in this moderate climate without extremes (Klimešová and Herben 2024). From our analysis, it is clear that categories like clonal versus nonclonal herbs are too broad, as even nonclonal annuals and perennial nonclonal herbs substantially differ in their habitat preferences. While annual plants prefer severely and frequently disturbed habitats, perennial nonclonal plants avoid such communities. Similar differences were found among different groups of clonal plants. For example, rhizomatous herbs functioned better in stressful environments than root sprouters that excelled in tolerating severe disturbance (Klimešová et al. 2025). Alas, testing these relationships outside of Central Europe is difficult as we lack complete data on the diversity of clonal organs for any other flora (Klimešová et al. 2017). Therefore, a crucial step in our understanding of the functionality of belowground perennating organs for plant performance and ecosystem function is to fill the gap in our knowledge of the morphological diversity of belowground organs in different floras and communities.

Bud banks provide insight into ecological patterns and processes

Presentation by Jacqueline Ott

Although the concept of bud banks was formally introduced by Harper in 1979, bud bank research only increased in the 21st century following their further description (Klimešová and Klimeš 2007) and recognition of their major ecological role in community regeneration (Benson and Hartnett 2006, Ott et al. 2019). Buds can occur on stems or roots, which include modified stem structures such as tubers, rhizomes, and stolons, and are predetermined to become shoots (Klimešová and Klimeš 2007, Ott et al. 2019). Bud availability is driven by inputs (bud natality), outputs (bud mortality or outgrowth), and bud dormancy within the bud bank (Ott et al. 2019). These bud bank dynamics can provide a useful framework for advancing our understanding of potential belowground bud bank traits and also how bud banks respond to disturbance and contribute to observed ecosystem patterns and processes (Ott et al. 2019).

Bud banks often mediate the response of plant communities to disturbance and variable weather. For example, grassland aboveground net primary productivity and its response to interannual

precipitation variability and precipitation legacies have been linked to belowground bud bank density and the age structure of the bud bank (Knapp and Smith 2001, Dalgleish and Hartnett 2006, Ott and Hartnett 2012, Reichmann and Sala 2014). Plant population response to fire depends on the vertical distribution of buds within the soil profile. Fire reduced a species whose vertical bud distribution was shallower as compared to other species within the community, leading to greater bud mortality and lower bud resprouting of the shallow-bud species (Hiers et al. 2021). Species that experience frequent disturbance may maintain greater amounts of buds to be able to resprout following the disturbance, as is demonstrated by species that experience increased inundation in Chinese wetlands (Chen et al. 2015). Bud bank spatial distributions can also be altered by the presence of competition and can be a mechanism by which invasive species outcompete native species (Bam et al. 2023). In grassland restorations, younger grasslands are often of lower species richness and lack the species that rely on belowground clonal growth organs and bud banks (Nerlekar and Veldman 2020, Pornon and Andalo 2023). Therefore, restoration of grasslands and other herbaceous communities may require restoring bud bank density and diversity (e.g., Willand et al. 2013). Many additional opportunities exist to explore bud bank contributions to the functioning of plant populations and communities, such as their role in resistance to aridification (Klimešová et al. 2023) and resilience to herbivory (e.g., Dalgleish and Hartnett 2009, Fidelis et al. 2014, VanderWeide et al. 2014). Belowground bud bank traits will be an important part of further explorations into plant community ecological theory and application (Ott et al. 2019).

Root system architecture and distribution

Presentation by Shersingh Joseph Tumber-Dávila

The spatial extent of a plant's root system—its size and distribution—defines the rhizosphere: the primary zone for resource uptake and a hotspot for plant–soil–microbial interactions. Yet, despite its critical role, root system size remains underexplored compared to fine root traits and especially aboveground size, due in part to the complexity of adequately estimating the spatial extent of plants belowground. The following nonexhaustive list illustrates some of the technical challenges:

1. Plant roots can often be found tens of meters beneath the soil surface (Tumber-Dávila et al. 2022).
2. Excavating and directly observing rooting depth distributions is time-consuming, technically demanding, and costly (Maeght et al. 2013).
3. The distribution of roots is highly plastic across edaphic and hydrological constraints (Fan et al. 2017)—maximum rooting depth alone does not reflect the space occupied by roots and their role in meeting water-uptake demands (Nippert and Holdo 2015).
4. Most studies do not go deeper than 1 m, and much more often stop around 30 cm, and therefore do not capture the true variation in rooting depth distribution, especially in seasonally-dry climates with large woody plants (Germon et al. 2020).
5. Among many other factors, rooting depth is influenced by overall plant strategies across various growth forms to resist, avoid, and confront resource limitations and stress; however, the exact relationship between rooting depth and plant types/strategies is so far difficult to predict (Pierret et al. 2016, Laughlin et al. 2023, Klimešová et al. 2025).

Given the ever-important role that roots play in maintaining the plant-water balance, and the growing need to understand how ecosystems and plant communities will respond to changing hydrological regimes, a renewed focus on unearthing the spatiotemporal (across both depth and time) dynamics of root system size is urgently needed (Binkley 2015, Tumber-Dávila and Malhotra 2020, Miguez-Macho and Fan 2021, Stocker et al. 2023).

Root system architecture not only influences access to water and nutrients, but also mediates plant performance, resilience to stress, and carbon allocation strategies. To demonstrate the role of root system architecture and distribution, we synthesized global data on root system dimensions across growth forms, ecosystems, disturbance regimes, and climates. We showed that the size of the rhizosphere—based on the maximum lateral extent and rooting depth of plants—exhibits high plasticity both within and among species, even if highly linked to total aboveground size, responding dynamically to environmental limitations such as water stress—especially for rooting depth (Tumber-Dávila et al. 2022). These results revealed broad variation in root system investment strategies, complementing more commonly studied fine root traits such as specific root length, root diameter, root nitrogen, or root tissue density. We argued that a renewed focus on the structural aspects of root systems is needed to advance our understanding of belowground functional strategies. While fine root traits provide critical insight into root economics, these morphological and chemical traits tended to be relatively more conserved within species, when compared to patterns of space occupancy and allocation to roots and other belowground carbon pools (i.e., exudation and mycorrhizal symbionts; Freschet et al. 2021, Matthus et al. 2025). However, root system size and distribution demonstrated far more plasticity and may better reflect whole-plant responses to spatial and temporal heterogeneity in resources (Schenk 2008, Iversen 2010). For example, deeper rooting and greater belowground carbon allocation are frequently observed under water-limited conditions, suggesting strong adaptive advantages tied to rhizosphere expansion (Canadell et al. 1996, Schenk and Jackson 2002, Tumber-Dávila et al. 2022). While most root biomass still lies in the shallower (<30 cm) portion of the soil, even in water-limited environments, a substantial increase in root biomass at deeper depths has been observed across many ecosystems (Lu et al. 2025), and those deeper roots, when present, may provide a lifeline for plants under periods of water limitation (Bachofen et al. 2024).

While we demonstrate the dynamic role of root system distributions across environmental gradients, further research is needed to evaluate trade-offs between carbon investment in structural and acquisitive roots versus alternative foraging strategies such as clonal growth organs, mycorrhizal associations, or root exudation to meet resource demands across environmental gradients.

The root economic space

Presentation by Luke McCormack

Concepts of plant economics and economic traits are longstanding in the field of plant ecology. These were largely advanced from an aboveground perspective, focusing first on leaves and later wood, and eventually integrated into whole-plant concepts (Wright et al. 2004, Chave et al. 2009, Reich 2014). However, application of these same principles lagged behind for fine roots belowground, owing largely to a paucity of data. Roughly a decade ago, several teams began to synthesize curated data sets, some built upon previously published data (Freschet et al. 2017, Valverde-Barrantes

et al. 2017) and others developed largely by single research teams (Chen et al. 2013, Kong et al. 2014, Ma et al. 2018). These efforts culminated with the synthesis of a large, globally-relevant and freely-available database of fine-root traits dubbed the Fine-Root Ecology Database (FRED; Iversen et al. 2017). Since its initial release, FRED has enabled a veritable explosion of novel belowground research, much of it focused on understanding how fine-root traits are integrated to create unique belowground resource acquisition strategies. Multiple studies have now tested core economic principles in roots first derived in leaves, with several core concepts seeming to reasonably apply to both leaves and roots. In particular, concepts relating to "fast" vs. "slow" strategies, or similarly "acquisitive" vs. "conservative" strategies, have found a home belowground when describing the core economic root traits of root diameter, specific root length, root tissue density, and root nitrogen content. However, there is a major difference when comparing leaves to fine roots, in that while most leaf economic strategies fall along a single spectrum, root economic strategies clearly organize in multiple dimensions. The multidimensionality of fine-root traits was demonstrated in several key studies (Kong et al. 2014, Kramer-Walter et al. 2016, Weemstra et al. 2016, Ma et al. 2018, McCormack and Iversen 2019), but was not formalized as the root economic space (RES) until the publication by Bergmann et al. (2020).

While most recent studies have broadly supported the core RES, it is important to mention that identifying the limitations of the RES is also critically important. Indeed, by discovering and understanding its limitations, we can much more robustly interpret the utility and extensions of the RES (Matthus et al. 2025). For example, previous studies highlighted that fine-root diameter, a core trait within the RES, was closely related to plant evolutionary history, with older lineages tending towards thicker roots while younger lineages had thinner roots (Comas et al. 2012, Ma et al. 2018). However, these studies were largely focused on angiosperm species. A recent study focusing on gymnosperms found no relationship between root diameter and evolutionary history (Langguth et al. 2024). In a different study, relationships among RES traits were compared between a phylogenetically diverse set of tree species that largely reflected the standard RES, and a phylogenetically narrow set of species (i.e., all within the *Quercus* genus; McCormack et al. 2020). Here, relationships among RES traits within the single genus notably diverged from those determined among diverse species. Recognizing and understanding different evolutionary trajectories of RES traits among major clades allows us to predict trait variation more accurately in previously unstudied species.

Understanding the functional implication of fine-root trait variation is an important next step. Excitingly, recent studies have highlighted tangible connections between RES traits and species occurrence along environmental gradients and local ecosystem properties (Laughlin et al. 2021, Barry et al. 2025). However, the explanatory power of RES traits to predict species occurrence or ecosystem services was generally weak, reminding us that root economic traits are still, at best, only part of the story. Additionally, a core tenet of the collaboration gradient defined by the RES is a prominent positive relationship between root diameter and colonization rates by mycorrhizal fungi, which are responsible for many "root" functions, including uptake and transport of soil resources. Here, thicker roots are expected to have higher mycorrhizal colonization and greater reliance on mycorrhizal fungi compared to plant species with thinner roots. However, closer inspection has highlighted that this trend may not be universal, as the positive diameter-colonization relationship is driven primarily by symbioses between plants and arbuscular mycorrhizal fungi, while plants that associate with ectomycorrhizal fungi generally do not follow this same trend (McCormack and Iversen 2019). Altogether, the core RES concepts have shown to be useful, yet recognizing limitations of the

RES helps shed light on new opportunities to understand how roots, fungi, and whole-plants are uniquely integrated to thrive in a wide range of environmental conditions.

Future opportunities to integrate belowground ecology across dimensions

A more holistic approach that considers the entire sum of belowground organs is needed to obtain the whole picture of belowground plant function. Incorporating the connection between root architecture and perennating organs can provide a more comprehensive picture of nutrient acquisition and storage from a whole-plant perspective. Workshops that bring together scientists from across the belowground functional trait expertise, similar to *Go Belowground!* offered by the Institute of Botany- Czech Academy of Science, can provide opportunities for synergies between the respective fields of woody and nonwoody roots, clonal and perennating growth organs, bud banks, and whole plants. Early results of these synergies have enabled efforts that have connected shoot and root economic spectrums (Weigelt et al. 2021), and more work can result if we only imagine the possibilities (Box 1).

Both seasonal (i.e., phenological) and developmental (i.e., ontogenic) timing of natality, growth, mortality, and decomposition of belowground plant organs and associated organisms (such as fine roots, root-associated fungi, rhizomes, buds) will be critical to the next steps in exploring belowground plant biology and ecology. Ontogenic development of root and clonal traits is not well known and may be important to understand

Box 1. Potential belowground plant ecology questions that can help us uncover the "unseen elephant."

- What is the relationship of belowground traits with one another (clonal growth organs, roots, and buds)?
- How do belowground traits and root functions differ spatiotemporally (both phenologically and across the soil profile)? (Which traits are more fixed/conserved at shorter timescales?)
- How do storage organs affect aboveground phenology?
- How do individual traits and cohesive belowground strategies change with plant ontogeny from seedling to mature and overmature life stages?
- How do you measure annual biomass production of belowground clonal organs and tradeoffs with aboveground biomass?
- How does carbohydrate storage interact with root exudation?
- How do coarse belowground organs contribute to carbon cycling?
- How do plant–soil interactions and belowground traits influence ecosystem carbon dynamics and overall soil biogeochemistry?
- Is the relationship between clonal traits and environmental factors the same on all continents and biomes?
- How do bud banks contribute to community resilience to disturbance?
- How do mechanisms of competition and facilitation structure rhizosphere microbiomes, including fungal, bacterial, and other members?
- What organisms, and to what extent can rhizosphere communities enable resource or information transfer between plant hosts?
- How do belowground traits respond to global change drivers and other stressors?

in relation to aboveground plant ontogenic development (e.g., flowering; Martínková et al. 2025a). By understanding the phenology of these organs (e.g., timing of initial construction and later senescence, see for example, Martínková et al. 2025b, da Silva et al. 2026), we will be better able to time sampling campaigns but also to identify the critical periods when these organs are present, most active, and most impacted by abiotic and biotic factors. Belowground plant organ phenology and cycling will also help inform ecosystem functioning, for example, belowground carbon dynamics.

As the belowground plant trait field expands, increased coordination of herbaceous, shrub, and tree belowground trait research is needed. Belowground morphological organ types and bud bank research have been heavily focused on herbaceous plant communities, while fine root trait research with an ecological focus has been somewhat biased towards woody plants. Bridging belowground trait concepts and methodologies across these fields will be important for answering future belowground plant trait questions. In woody plants, it would be beneficial to link our knowledge of belowground horizontal clonal growth in herbs to better understand clonal growth in woody plants (DeWoody et al. 2008, Ratajczak et al. 2011).

In summary, belowground plant traits of both woody and herbaceous species can offer insight into ecosystem function and response to disturbance. We need further exploration of this "unseen elephant" in ecology (Fig. 1). Increasing collaboration across belowground plant organs and plant functional types and further examination of belowground organ dynamics will help us achieve a deeper understanding of our worldwide ecosystems.

Acknowledgments

This research has been supported by the USDA National Institute of Food and Agriculture—Agriculture and Food Research Initiative Grant #2024-67019-43719 and the USDA Forest Service Rocky Mountain Research Station to JPO, by US DOE award #DE-SC0023480 to MLM, and by Praemium Academiae (Czech Academy of Sciences) to JK. Opinions, findings, conclusions, or recommendations expressed in the material are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

Conflicts of Interest

The authors have no competing interests to declare that are relevant to the content of this article.

Literature Cited

Bachofen, C., S. J. Tumber-Dávila, D. S. Mackay, N. G. McDowell, A. Carminati, T. Klein, B. D. Stocker, M. Mencuccini, and C. Grossiord. 2024. Tree water uptake patterns across the globe. New Phytologist 242:1891–1910.

Bam, S., J. P. Ott, J. L. Butler, and L. Xu. 2023. Belowground growth strategies of native and invasive rhizomatous perennial grasses in response to precipitation variability, clipping, and competition. Folia Geobotanica 58:13.

Barry, K. E., J. Hennecke, A. Weigelt, J. Bergmann, H. Bruelheide, G. T. Freschet, C. M. Iversen, T. W. Kuyper, D. C. Laughlin, and M. L. McCormack. 2025. Rooting for function: community-level fine-root traits relate to many ecosystem functions. New Phytologist 248:3221–3239.

Benson, E. J., and D. C. Hartnett. 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. Plant Ecology 187:163–177.

Bergmann, J., et al. 2020. The fungal collaboration gradient dominates the root economics space in plants. Science Advances 6:eaba3756.

Binkley, D. 2015. Ecosystems in four dimensions. New Phytologist 206:883–885.

Canadell, J., R. B. Jackson, J. B. Ehleringer, H. A. Mooney, O. E. Sala, and E.-D. Schulze. 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583–595.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. Ecology Letters 12:351–366.

Chen, W., H. Zeng, D. M. Eissenstat, and D. Guo. 2013. Variation of first-order root traits across climatic gradients and evolutionary trends in geological time. Global Ecology and Biogeography 22:846–856.

Chen, X. S., Z. M. Deng, Y. H. Xie, F. Li, Z. Y. Hou, and X. Li. 2015. Belowground bud banks of four dominant macrophytes along a small-scale elevational gradient in Dongting Lake wetlands, China. Aquatic Botany 122:9–14.

Comas, L. H., K. E. Mueller, L. L. Taylor, P. E. Midford, H. S. Callahan, and D. J. Beerling. 2012. Evolutionary patterns and biogeochemical significance of angiosperm root traits. International Journal of Plant Sciences 173:584–595.

da Silva, G. S., T. Harris, A. Ferraro, M. Millan, and J. Klimešová. 2026. Throwing away to survive: rhizome senescence as a strategy adopted by a herbaceous clonal plant to remain young forever. Annals of Botany:mcag004.

Dalgleish, H. J., and D. C. Hartnett. 2006. Below-ground bud banks increase along a precipitation gradient of the north American Great Plains: a test of the meristem limitation hypothesis. New Phytologist 171:81–89.

Dalgleish, H. J., and D. C. Hartnett. 2009. The effects of fire frequency and grazing on tallgrass prairie productivity and plant composition are mediated through bud bank demography. Plant Ecology 201:411–420.

DeWoody, J., C. A. Rowe, V. D. Hipkins, and K. E. Mock. 2008. "Pando" lives: molecular genetic evidence of a giant aspen clone in central Utah. Western North American Naturalist 68:493–497.

Fan, Y., G. Miguez-Macho, E. G. Jobbágy, R. B. Jackson, and C. Otero-Casal. 2017. Hydrologic regulation of plant rooting depth. Proceedings of the National Academy of Sciences 114:10572–10577.

Fidelis, A., B. Appezzato-da-Gloria, V. D. Pillar, and J. Pfadenhauer. 2014. Does disturbance affect bud bank size and belowground structures diversity in Brazilian subtropical grasslands? Flora 209:110–116.

Field, J. P., et al. 2015. Critical zone services: expanding context, constraints, and currency beyond ecosystem services. Vadose Zone Journal 14:vzj2014-10.

Freschet, G. T., et al. 2021. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. New Phytologist 232:1123–1158.

Freschet, G. T., et al. 2017. Climate, soil and plant functional types as drivers of global fine-root trait variation. Journal of Ecology 105:1182–1196.

Germon, A., J.-P. Laclau, A. Robin, and C. Jourdan. 2020. Tamm review: deep fine roots in forest ecosystems: why dig deeper? Forest Ecology and Management 466:118135.

Harper, J. L. 1979. Population biology of plants. Academic Press, London, United Kingdom.

Herben, T., and J. Klimešová. 2020. Evolution of clonal growth forms in angiosperms. New Phytologist 225:999–1010.

Hiers, Q. A., M. L. Treadwell, M. B. Dickinson, K. L. Kavanagh, A. G. Lodge, H. D. Starns, D. R. Tolleson, D. Twidwell, C. L. Wonkka, and W. E. Rogers. 2021. Grass bud responses to fire in a semiarid savanna system. Ecology and Evolution 11:6620–6633.

Iversen, C. M. 2010. Digging deeper: fine-root responses to rising atmospheric CO2 concentration in forested ecosystems. New Phytologist 186:346–357.

Iversen, C. M., M. L. McCormack, A. S. Powell, C. B. Blackwood, G. T. Freschet, J. Kattge, C. Roumet, D. B. Stover, N. A. Soudzilovskaia, and O. J. Valverde-Barrantes. 2017. A global fine-root ecology database to address below-ground challenges in plant ecology. New Phytologist 215:15–26.

Kattge, J., et al. 2020. TRY plant trait database – enhanced coverage and open access. Global Change Biology 26:119–188.

Klimeš, A., I. Šímová, A. Zizka, A. Antonelli, and T. Herben. 2022. The ecological drivers of growth form evolution in flowering plants. Journal of Ecology 110:1525–1536.

Klimešová, J. 2025. Plant bodies: how plant structures contribute to our comprehension of their life-history strategy. Springer Nature, Switzerland.

Klimešová, J., J. Danihelka, J. Chrtek, F. de Bello, and T. Herben. 2017. CLO-PLA: a database of clonal and bud-bank traits of the central European flora. Ecology 98:1179.

Klimešová, J., and T. Herben. 2023. The hidden half of the fine root differentiation in herbs: nonacquisitive belowground organs determine fine-root traits. Oikos 2023:e08794.

Klimešová, J., and T. Herben. 2024. Belowground morphology as a clue for plant response to disturbance and productivity in a temperate flora. New Phytologist 242:61–76.

Klimešová, J., and L. Klimeš. 2007. Bud banks and their role in vegetative regeneration - a literature review and proposal for simple classification and assessment. Perspectives in Plant Ecology, Evolution and Systematics 8:115–129.

Klimešová, J., et al. 2025. Belowground persistence types relevant to severe disturbance. Trends in Plant Science 30:992–1001.

Klimešová, J., J. Martínková, A. Bartusková, and J. P. Ott. 2023. Belowground plant traits and their ecosystem functions along aridity gradients in grasslands. Plant and Soil 487:39–48.

Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291:481–484.

Kong, D. L., C. G. Ma, Q. Zhang, L. Li, X. Y. Chen, H. Zeng, and D. L. Guo. 2014. Leading dimensions in absorptive root trait variation across 96 subtropical forest species. New Phytologist 203:863–872.

Kramer-Walter, K. R., P. J. Bellingham, T. R. Millar, R. D. Smissen, S. J. Richardson, and D. C. Laughlin. 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. Journal of Ecology 104:1299–1310.

Langguth, J., M. Zadworny, K. Andraczek, M. Lo, N. Tran, K. Patrick, J. Mucha, K. E. Mueller, and M. L. McCormack. 2024. Gymnosperms demonstrate patterns of fine-root trait coordination consistent with the global root economics space. Journal of Ecology 112:1425–1439.

Laughlin, D. C., L. Mommer, F. M. Sabatini, H. Bruelheide, T. W. Kuyper, M. L. McCormack, J. Bergmann, G. T. Freschet, N. R. Guerrero-Ramírez, and C. M. Iversen. 2021. Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. Nature Ecology & Evolution 5:1123–1134.

Laughlin, D. C., et al. 2023. Rooting depth and xylem vulnerability are independent woody plant traits jointly selected by aridity, seasonality, and water table depth. New Phytologist 240:1774–1787.

Lu, M., S. Wang, A. Malhotra, S. J. Tumber-Dávila, S. Weintraub-Leff, M. L. McCormack, X. T. Wang, and R. B. Jackson. 2025. A continental scale analysis reveals widespread root bimodality. Nature Communications 16:5281.
Ma, Z., D. Guo, X. Xu, M. Lu, R. D. Bardgett, D. M. Eissenstat, M. L. McCormack, and L. O. Hedin. 2018. Evolutionary history resolves global organization of root functional traits. Nature 555:94–97.
Maeght, J.-L., B. Rewald, and A. Pierret. 2013. How to study deep roots—and why it matters. Frontiers in Plant Science 4:299.
Martínková, J., A. Klimeš, and J. Klimešová. 2025b. The establishment growth and clonal growth organs. Perspectives in Plant Ecology, Evolution and Systematics 67:125869.
Martínková, J., A. Klimeš, I. Marešová, and J. Klimešová. 2025a. The hidden half of ontogeny and seasonal dynamics in perennial herbs. Journal of Ecology 113:713–726.
Matthus, E., M. Zwetsloot, B. M. Delory, J. Hennecke, K. Andraczek, T. Henning, L. Mommer, A. Weigelt, and J. Bergmann. 2025. Revisiting the root economics space—its applications, extensions and nuances advance our understanding of fine-root functioning. Plant and Soil 514:1–27.
McCormack, M. L., and C. M. Iversen. 2019. Physical and functional constraints on viable belowground acquisition strategies. Frontiers in Plant Science 10:1215.
McCormack, M. L., M. A. Kaproth, J. Cavender-Bares, E. Carlson, A. L. Hipp, Y. Han, and P. G. Kennedy. 2020. Climate and phylogenetic history structure morphological and architectural trait variation among fine-root orders. The New Phytologist 228:1824–1834.
Miguez-Macho, G., and Y. Fan. 2021. Spatiotemporal origin of soil water taken up by vegetation. Nature 598:624–628.
Nerlekar, A. N., and J. W. Veldman. 2020. High plant diversity and slow assembly of old-growth grasslands. Proceedings of the National Academy of Sciences of the United States of America 117:18550–18556.
Nippert, J. B., and R. M. Holdo. 2015. Challenging the maximum rooting depth paradigm in grasslands and savannas. Functional Ecology 29:739–745.
Ott, J. P., and D. C. Hartnett. 2012. Contrasting bud bank dynamics of two co-occurring grasses in tallgrass prairie: implications for grassland dynamics. Plant Ecology 213:1437–1448.
Ott, J. P., J. Klimešová, and D. C. Hartnett. 2019. The ecology and significance of below-ground bud banks in plants. Annals of Botany 123:1099–1118.
Ottaviani, G., R. Molina-Venegas, T. Charles-Dominique, S. Chelli, G. Campetella, R. Canullo, and J. Klimešová. 2020. The neglected belowground dimension of plant dominance. Trends in Ecology & Evolution 35(9):763–766. https://doi.org/10.1016/j.tree.2020.06.006
Ottaviani, G., J. Klimešová, T. Charles-Dominique, M. Millan, T. Harris, and F. A. Silveira. 2024. The underestimated global importance of plant belowground coarse organs in open biomes for ecosystem functioning and conservation. Perspectives in Ecology and Conservation 22:118–121. https://doi.org/10.1016/j.pecon.2024.01.008
Pierret, A., J.-L. Maeght, C. Clément, J.-P. Montoroi, C. Hartmann, and S. Gonkhamdee. 2016. Understanding deep roots and their functions in ecosystems: an advocacy for more unconventional research. Annals of Botany 118:621–635.
Pornon, A., and C. Andalo. 2023. Using the old-growth concept to identify old species-rich semi-natural grasslands. Ecological Indicators 155:110953.
Ratajczak, Z., J. B. Nippert, J. C. Hartman, and T. W. Ocheltree. 2011. Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. Ecosphere 2:14.
Reich, P. B. 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. Journal of Ecology 102:275–301.

Reichmann, L. G., and O. E. Sala. 2014. Differential sensitivities of grassland structural components to changes in precipitation mediate productivity response in a desert ecosystem. Functional Ecology 28:1292–1298.

Schenk, H. J. 2008. The shallowest possible water extraction profile: a null model for global root distributions. Vadose Zone Journal 7:1119–1124.

Schenk, H. J., and R. B. Jackson. 2002. The global biogeography of roots. Ecological Monographs 72:311–328.

Stocker, B. D., S. J. Tumber-Dávila, A. G. Konings, M. C. Anderson, C. Hain, and R. B. Jackson. 2023. Global patterns of water storage in the rooting zones of vegetation. Nature Geoscience 16:250–256.

Tumber-Dávila, S. J., and A. Malhotra. 2020. Fast plants in deep water: introducing the whole-soil column perspective. New Phytologist 225:7–9.

Tumber-Dávila, S. J., H. J. Schenk, E. Du, and R. B. Jackson. 2022. Plant sizes and shapes above and belowground and their interactions with climate. New Phytologist 235:1032–1056.

Valverde-Barrantes, O. J., G. T. Freschet, C. Roumet, and C. B. Blackwood. 2017. A worldview of root traits: the influence of ancestry, growth form, climate and mycorrhizal association on the functional trait variation of fine-root tissues in seed plants. New Phytologist 215:1562–1573.

VanderWeide, B. L., D. C. Hartnett, and D. L. Carter. 2014. Belowground bud banks of tallgrass prairie are insensitive to multi-year, growing-season drought. Ecosphere 5:1–17.

Weemstra, M., L. Mommer, E. J. Visser, J. Ruijven, T. W. Kuyper, G. M. Mohren, and F. J. Sterck. 2016. Towards a multidimensional root trait framework: a tree root review. New Phytologist 211:1159–1169.

Weigelt, A., L. Mommer, K. Andraczek, C. M. Iversen, J. Bergmann, H. Bruelheide, Y. Fan, G. T. Freschet, N. R. Guerrero-Ramírez, and J. Kattge. 2021. An integrated framework of plant form and function: the belowground perspective. New Phytologist 232:42–59.

Willand, J. E., S. G. Baer, D. J. Gibson, and R. P. Klopf. 2013. Temporal dynamics of plant community regeneration sources during tallgrass prairie restoration. Plant Ecology 214:1169–1180.

Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.