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Insight

Tree carbon allocation to root exudates: implications for carbon budgets, soil sequestration and drought response

Melanie Brunn[1,2,*], Carsten W. Mueller[3,4], Nikhil R. Chari[5], Ina C. Meier[6], Sophie Obersteiner[7], Richard P. Phillips[8], Benton Taylor[5], Shersingh Joseph Tumber-Dávila[9,10], Sami Ullah[11] and Tamir Klein[7]

[1]IES, Institute for Environmental Sciences, University of Kaiserslautern-Landau (RPTU), Fortstraße 7, 76829 Landau, Germany
[2]IfIN, Institute for Integrated Natural Sciences, Universität Koblenz, Universitätsstraße 1, 56070 Koblenz, Germany
[3]Institute of Ecology, Chair of Soil Science, Technische Universität Berlin, Ernst-Reuter-Platz 1, 10587 Berlin, Germany
[4]Department for Geosciences and Natural Resource Management, University of Copenhagen, Øster Voldgade 10, 1350 København K, Copenhagen, Denmark
[5]Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford St., Cambridge, MA, USA
[6]Functional Forest Ecology, Universität Hamburg, Ohnhorststraße 18, 22609 Hamburg, Hamburg, Germany
[7]Department of Plant and Environmental Sciences, Nella and Leon Benoziyo Building for Biological Sciences, Weizmann Institute of Science, Rehovot 7610001, Israel
[8]Department of Biology, Indiana University, 1001 E. Third St., Bloomington, IN 47405, USA
[9]Department of Environmental Studies, Dartmouth College, 38 College St, Hanover, NH 03755, USA
[10]Harvard Forest, Harvard University, 324 North Main Street, Petersham, MA 01366-9504, USA
[11]School of Geography, Earth and Environmental Sciences & Birmingham Institute of Forest Research, University of Birmingham, Edgbaston, B15 2TT, Birmingham, UK

*Corresponding author (melanie.brunn@uni-landau.de)

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Root carbon (C) exudation plays a central role in nutrient acquisition, microbially mediated organic matter decomposition and many other critical ecosystem processes. While it is well known that roots respond strongly to belowground resources, we have a limited quantitative understanding about C allocation to exudates and its fate in soil under changing water availability. This review synthesizes the importance of exudate C fluxes, summarizes studies quantifying mass-specific exudation rate (SER), total exudation rate (TER) and root exudate fraction (REF; the proportion of TER in a plant's C allocation), examines drought effects and highlights key research priorities to advance the understanding of C allocation to exudates in forest ecosystems. On average, SER is often <1 mg C $g_{\text{dry root}}{}^{-1}$ day^{-1}, TER is 3.8 Pg C year^{-1} and REF varies between 1 and 17% of net primary production. Spatiotemporal variations in exudation, including seasonal and daily patterns and subsoil exudation, remain critical knowledge gaps. We show that many studies report a 1.2- to 11-fold increase in SER and REF in response to drought. However, TER often remains unchanged, suggesting that absolute exudate C inputs to the soil may stay constant under drought conditions. Disentangling the individual impacts of soil and air drought as well as drought legacy impacts on ecosystem C dynamics are overlooked aspects. By estimating the differences in rhizosphere formation and exudation across various forest biomes, we find that exudate-affected soil volumes are highest in tropical forests and lowest in boreal forests. While current research emphasizes significant C allocation from the canopy to soil via exudates, understanding exudation dynamics and biome-specific responses to drought by using standardized protocols is essential. Expanding these insights is critical for comprehending the role of root exudates in soil organic matter formation, ecosystem resilience and adaptation to climate change.

Keywords: climate change, drought legacy, forest, plant–soil interaction, rhizodeposition, soil organic matter formation.

Introduction

Nearly half of the world's terrestrial carbon (C) is stored in forests, making them an essential ecosystem for providing services like climate change mitigation (Bonan 2008, Pan et al. 2011). Most C in forests resides belowground, with soils storing more C globally than the vegetation and atmosphere combined (Friedlingstein et al. 2023). Photosynthetically fixed C enters the soil through aboveground litter and inputs from living and dead roots. Such inputs from plants form soil organic matter (SOM), which either persists in soil or is metabolized by soil microbes and returned to the atmosphere as CO_2. Given the importance of the feedback by the forest C cycle to global climate, there is a need to quantify and better understand the mechanisms driving plant C allocation and the conversion of C into persistent SOM, as well as their sensitivities to global environmental change.

An important but understudied part of the forest C cycle is root exudation. Root exudation is the process by which soluble low-molecular-weight C compounds released by living roots are deposited into the rhizosphere (Oburger and Jones 2018). By building a dynamic exchange process between the atmosphere, hydrosphere, biosphere and lithosphere, C allocation to exudates has emerged as a crucial nexus for ecosystem C dynamics (Hagedorn et al. 2016, Vetterlein et al. 2020, Mueller et al. 2024). Recent photoassimilates can be rapidly allocated belowground within a few days (Högberg et al. 2008, Gorka et al. 2019, Hikino et al. 2022), where they influence C cycling in various ways once released as root

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exudates. Exudates drive physicochemical and biochemical processes, serve as signaling compounds that mediate biological interactions (Oburger and Jones 2018) and regulate ecosystem functioning across scales, from the molecular level to the entire ecosystem (Bais et al. 2006, Jones et al. 2009).

Given that root exudates are believed to be controlled by rates of C assimilation, genetic variability and source–sink relations in plants, it stands to reason that exudation rates would be affected strongly by factors that influence whole-plant C dynamics, including plant stressors such as drought. Forest ecosystems typically experience decreases in photosynthesis in drier periods (Ciais et al. 2005, Rennenberg et al. 2006, Gampe et al. 2021, Fu et al. 2022). In adapted ecosystems, reductions in tree photosynthesis are closely linked to decreased C inputs into the soil (Hansen et al. 2024) and a diminished C sink capacity in drought-stressed forests (Wardle et al. 2004, Walker et al. 2021, Wolf and Paul-Limoges 2023). However, during short-term drought events, belowground C processes in roots and soil may respond differently than aboveground C assimilation, making it difficult to accurately predict the ecosystem C sink capacity when one value is inferred from the other. This is especially true as short-term climate extremes become more frequent (IPCC 2023).

Despite the well-characterized importance of exudation, investigations of exudation in forest ecosystems are relatively sparse, as there are few appropriate methods for capturing exudates for field-grown mature trees (see Phillips et al. 2008). This review focuses on root C exudation, which describes the movement of C from living plant roots into the soil and provides insights into broad patterns of C cycling and forest ecosystem function. Specifically, we: (i) highlight the quantitative importance of exudation as a critical component of the C cycle; (ii) explore the fate of exudates in soil; and (iii) review the current literature on how drought impacts C allocation to exudates and the potential consequences for soil C sequestration, with an emphasis on overall forest C fluxes.

Root exudation, a quantitatively important component of C cycling

Exudates are among the hardest to measure C fluxes (see Box 1 for challenges), with dry-mass-specific exudation rates (SERs) (Figure 1) often <1 mg C $\mathrm{g}_{\text{dry-root}}^{-1}$ day^{-1} (Gougherty et al. 2018, Meier et al. 2020, Brunn et al. 2022, Chari et al. 2024). Carbon fluxes from single terminal root branches are often used to compare exudation rates among species (Smith 1976, Sun et al. 2017, Gougherty et al. 2018). Estimating the ecosystem flux requires multiplying the SER by the root density of the individual tree per ground surface area to get the total exudation rate (TER) (Figure 1). Yet, quantifiable relationships between exudation and tree C budgets remain poorly understood and, until recently, have been estimated using basic 'budget closure' methods. Given that process-based terrestrial C models indirectly inform international climate change policies via state-of-the-art Earth system models, benchmarking with empirical data on exudation rates is crucial not only for advancing scientific understanding and science-informed policymaking but also for more accurately calculating the net primary production (NPP) of trees (Clark et al. 2001) as the exudation flux is not often included (Harris et al. 2021). Therefore, linking the root exudation C flux with aboveground C fluxes (root exudate fraction (REF = TER/(TER + net primary production, i.e., exudates per NPP)) necessitates comprehensive information on the entire tree or ecosystem (Box 1).

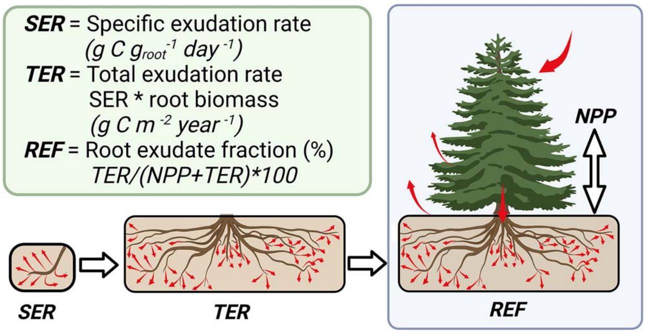

Figure 1. Schematic overview of C fluxes, scales and linkages addressed. Root exudates are examined at the branch level (SER from fine roots), as fine-root exudate C flux per soil surface area (TER, i.e., SER, i.e., upscaled to the fine-root system of an individual tree), and as relative exudation indicating the relationship between the exudate C flux and rate of NPP (REF).

Box 1. Challenges in measuring exudation rates.

Collecting exudates from root branches

Measuring exudates in forest ecosystems is both time-consuming and logistically challenging (Smith 1970, Phillips et al. 2008, Oburger and Jones 2018). The common and widely accepted cuvette-based approach (Phillips et al. 2008) (Figure 2B) enables the capture of exudation from single root branches (mostly first- and second-order roots), providing information on the amount of C released from the terminal part of the absorptive root system (McCormack et al. 2015). The SER is calculated as the amount of C released over an incubation period (typically 24 h to account for a full diurnal cycle) divided by root dry mass or root surface area to obtain the mass-specific or area-specific C flux. This measurement captures net exudation (i.e., gross exudation minus root reabsorption and microbial consumption) (Liese et al. 2018). Yet, there is uncertainty regarding the extent to which sampling protocols need to be adjusted to reflect long-term patterns of exudation, particularly in situations of drought, because the current method requires incubating roots in a dilute nutrient solution, thereby possibly releasing them from water stress. Further, variations in methods related to preparing (root cleaning, equilibration times) and incubating the roots (cuvette volume, pre-equilibration duration, flushing, nutrient solution concentration, etc.) can greatly affect exudation measurements (see supplementary material in Heinzle et al. (2023). Accurately comparing datasets across studies necessitates standardized protocols (Freschet et al. 2021) (see Figure 2 for suggestions).

Upscaling exudation rates

For quantifying TER, a fundamental challenge lies in scaling up processes measured locally at fine scales (e.g., the rhizosphere) to the ecosystem, while accounting for the spatial heterogeneity (vertical and horizontal) and temporal dynamics (intra- and interannual or comparing the growing vs non-growing season) in ecosystems. As we often lack knowledge from deep roots, uniform exudation for the entire root system is assumed, i.e., likely to overestimate TER. In addition, establishing relationships between root morphological traits and exudation (across root orders, types or the root lifecycle and fine roots branching frequency) will likely be needed for the most effective up-scaling (Herz et al. 2018, Gao et al. 2023, Rathore et al. 2023). This requires parsing exudation rates by the different parts of the root system (absorptive fine roots, transport fine roots and coarse roots) and root age across the soil profile. Thus, calculating TER requires comprehensive data necessitating the use of combined, sophisticated and time-intensive methods for accurate and thorough root biomass estimates (Maeght et al. 2013, McCormack et al. 2015, Pregitzer et al. 2002, Hartmann et al. 2020). Deep learning-based workflows are promising tools to simplify image analyzes (Sordo et al. 2024). To estimate root biomass for an entire tree, a combination of soil coring data for reporting root dry biomass and minirhizotron images has proven useful in forest ecosystems (Ostonen et al. 2005, Strand et al. 2008, Brunn et al. 2022). Relying solely on minirhizotron images has limitations because of the challenge of converting two-dimensional images into estimates of root mass within the soil volume (Bernier and Robitaille 2004, Taylor et al. 2014) and due to the fact that very little of the root biomass is captured by the images (Taylor et al. 2013). In addition, soil physical factors may alter root growth at the soil–tube interface (Taylor et al. 1990). Machine learning algorithms trained by a large dataset of in situ measurements to estimate global root biomass in forests are promising (Huang et al. 2021).

The REF has been estimated at 1–17% of NPP in forests globally (Panchal et al. 2022, Chari et al. 2024, Norby et al. 2024, Rog et al. 2024), though there is a high degree of uncertainty with this estimate owing to the limited number of studies that have reported SER. Two recent studies illustrate how estimates of the global exudate flux depend, in part, on how exudation is measured. Chari et al. (2024) synthesized data from cuvette-based solution cultures (roots incubating in a moistened glass bead matrix; see Box 1) and estimated a global average of TER of forest areas being 3.8 Pg C year^{-1}, which represents a REF of about 7% (assuming that NPP of global forests is 50.5 Pg C year^{-1}; Badgley et al. (2019). Panchal et al. (2022), using ^{13}C isotopic labeling, estimated TER at 118.5 g C m^{-2} y^{-1}, which is a REF of 16.7% assuming a net: gross primary production factor of 0.46 (Collalti and Prentice 2019, Chari et al. 2024). The data used to calculate REF in Panchal et al. (2022) came from measurements that capture total rhizodeposition (i.e., root cap and border cells, root lysates, C flux to root-associated microorganisms and mucilage; Jones et al. 2009), which may explain the greater fluxes relative to the soluble exudates measured by Chari et al. (2024). Studies reporting REF in trees show values typically $<$10% of NPP, with local estimates ranging between 1 and 3% in young trees (Liese et al. 2018), 5.2% during the growing season in mature temperate forest (Brunn et al. 2022), 4.2–8.7% in temperate mature forests (Abramoff and Finzi 2016, Norby et al. 2024) and 9.2% (Rog et al. 2024) in Mediterranean forests.

Further complicating the ability to estimate TER and SER is the fact that most of our available data are limited to the shallowest soil layers. The SER is likely to decrease with depth (Finzi et al. 2015, Hicks Pries et al. 2018), with one study in a European beech forest reporting that SER at 1 m depth was 20% of the SER compared with shallow roots (Tückmantel et al. 2017). In line with the call to understand deep soil C storage (Button et al. 2022, Hicks Pries et al. 2023) and deep fine roots (Germon et al. 2020), we emphasize the need to measure SER along soil profiles (see Box 1). While stable-isotope labeling studies have allowed quantifying TER, including deeper roots, they often achieve this by tracing belowground C allocation via microbial activity and soil respiration measurements from the soil surface (Ruehr et al. 2009, Joseph et al. 2020, Gao et al. 2021). These data may differ from TER because exudate fluxes deeper in the soil might not be detectable in CO$_2$ effluxes from the soil, and C tracing data may hide shifts in SER under drought and post-drought conditions.

The fate of exudates in forest soil systems

Numerous studies have reported that soil organisms preferentially assimilate organic matter derived from roots compared with aboveground litter (Rasse et al. 2005, Pollierer et al. 2007, Sokol et al. 2019), which may be the reason why rhizodeposition is so efficiently transformed into SOM (Teixeira et al. 2024). As a key mediator of the interaction between plants and microorganisms, exudates can have immediate effects on SOM formation and quality (Chari and Taylor 2022, Panchal et al. 2022). The type of SOM can be described by two major solid fractions: (i) mineral-associated organic matter (MAOM), which is usually assumed to have a lower bioavailability for microbial decomposition (von Luetzow et al. 2006, Castellano et al. 2015, Angst et al. 2021) and (ii) particulate organic matter (POM), which is often considered a rather labile SOM pool with a wide range of decomposability and turnover times (Lavallee et al. 2020, Witzgall et al. 2021, Angst et al. 2023). Labeling potted *Eucalyptus* spp. seedlings with ^{13}CO$_2$ revealed that 76% of the net rhizodeposition was retained within the MAOM fraction (Teixeira et al. 2024). This is well supported by findings that rhizodeposition has a higher efficiency in forming mineral-associated C (46%) as compared with root biomass (9%) or aboveground biomass inputs (7%) (Villarino et al. 2021). While root biomass turnover can represent a larger input of C into the soil than exudation in many ecosystems (Chari et al. 2024), the relatively high efficiency at which rhizodeposition forms MAOM means that rhizodeposition is likely the dominant pathway for root-derived C to enter the MAOM pool. As POM, including also dead root particles, is a main precursor for MAOM formation (Witzgall et al. 2021, 2024, Angst et al. 2023), it can be assumed that some of the structural C entering the rhizosphere can ultimately end up as rather persistent SOM of the MAOM pool. Therefore, the rhizosphere can be seen as a hotspot controlling the persistence of soil C (Wang et al. 2025, Vidal et al. 2018, Mueller et al. 2024), soil structure formation including aggregate formation (Baumert et al. 2021, Guhra et al. 2022) and important ecosystem functions (Philippot et al. 2013, Vetterlein et al. 2020, Schnepf et al. 2022).

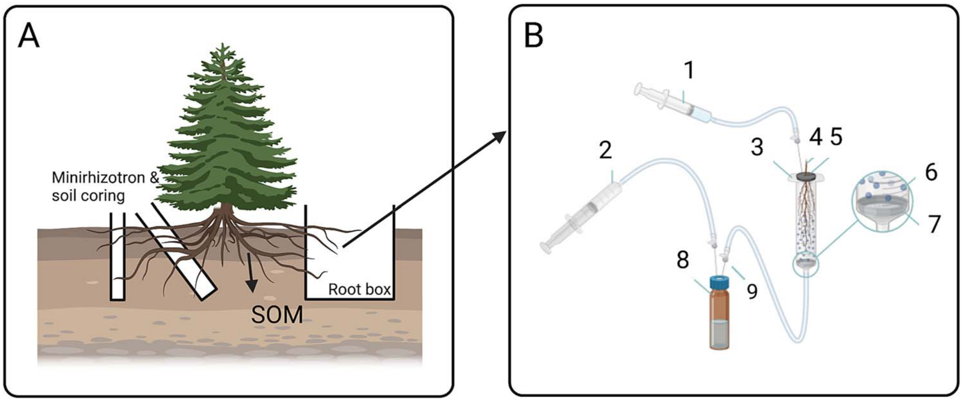

Figure 2. Schematic overview of the exudate collection approach. Root biomass and distribution are accessed, e.g., via root boxes, and distal fine root branches are carefully excavated for exudate collection (A), cleaned with equilibrium solution and forceps, and allowed a pre-equilibration period. The system (B) is flushed at least once before exudate collection, which should span at least one diurnal cycle. Blanks are included for reference and all samples are filtered (pore size 0.22 μm). The exudate collection system (B) consists of several components. Prior to use, all syringes and glass beads are thoroughly cleaned with a muffle furnace and acid washing (preferably nitric acid). The root is immersed in an equilibrium solution (1) to maintain optimal conditions. A syringe or pump (2) is used to induce negative pressure, while another syringe (3) collects the exudates from the cleaned and living root (4). The syringe is sealed by a septum (5) to prevent contamination. Glass beads (6) provide support for the root, separated by a mesh (7). Exudates are collected in a glass vial (8) and passed through a 0.22 μm filter (9). For upscaling exudation rates (i.e., TER), information on root system biomass and distribution can be taken from minirhizotron and soil coring (A).

Detailed quantification of how altered SER patterns along soil profiles affect the surrounding SOM is sparse. Artificial root exudate (ARE) experiments have been used to simulate exudate effects on soils (Drake et al. 2013, Keiluweit et al. 2015, Meier et al. 2017, Chari and Taylor 2022). For instance, it was demonstrated that soil conditions, as well as exudate composition and rate, dictate whether exudation leads to SOM formation or loss (Yin et al. 2014, Baumert et al. 2018, Baumert et al. 2021, Chari and Taylor 2022). Chari and Taylor (2022) found that lower exudation rates promote SOM formation and that bioenergetically favorable simple sugars increase SOM loss, while amino and organic acids induce net accumulation of stable SOM in intact mineral topsoil cores. However, as the microbial respiration response to real exudates is much lower than when the same amount of C is added artificially (Niedeggen et al. 2024), ARE may not fully represent in situ processes under field conditions. In a future atmosphere, i.e., further enriched in CO_2, SOM loss might be favored in forest soil (Terrer et al. 2021), at least in stands with high levels of POM such as those dominated by ectomycorrhizal (ECM) trees. In addition to gaps in our quantitative assessment and understanding of the processes that determine the efficiency of exudates in contributing to the formation of MAOM, the spatiotemporal organization of the rhizosphere, considering also variations with depth in forest soils remains largely unknown.

Despite vertical variation in soil profiles, the direct average influence of exudates is limited to small spatiotemporal zones that surround root apices (Dennis et al. 2010) and consequently, it is questionable how processes within these small volumes can directly affect SOM quantity and quality at larger scales. Using global estimates, the recent rhizosphere fraction is approximately 1% throughout the entire soil profile, with the active rhizosphere (the rhizosphere volume around absorptive fine roots) likely smaller (Box 2). In a study conducted in a temperate *Fagus sylvatica* and *Picea abies* forest, the mean rhizosphere volume was estimated to be 2.4% in soil profiles including top and subsoil (Brunn et al. 2022). Although the rhizosphere occupies a small physical space, its impact on soil C dynamics can be assumed to be disproportionately large due to the complex interactions and transformations that occur there. In addition, these interactions are spatially not static, but change over the course of the stand age and seasonally throughout the growing season. Further, through the hyphosphere, fungal hyphae and the zone they influence, exudates may affect the surrounding soil beyond the rhizosphere (Meier et al. 2015, Vidal et al. 2018, See et al. 2022). This is of particular importance when comparing forest biomes globally, associated with different mycorrhizal fungi, for instance, arbuscular fungi (AM) in the tropics, whereas boreal roots typically associate with ECM.

Box 2. Root exudate and rhizosphere dynamics in different forest biomes.

The root surface itself is widely recognized as a hotspot for C allocation (Schmidt et al. 2018). Soil that adheres to the root after it is removed from the bulk soil and shaken is often methodologically defined as rhizosphere for subsequent measurements (Girardi et al. 2022). Technological advancements and improved visualization techniques are essential to gain deeper insights into the spatial extension and processes occurring within the rhizosphere (Holz et al. 2020, Lohse et al. 2021, Schlüter et al. 2022, Garcia Arredondo et al. 2023). Given the distribution of microbial activity and various factors like pH, CO_2 and O_2 concentrations, redox potential, enzyme activities, water and nutrient contents (Kuzyakov and Razavi 2019), it is reasonable to assume that exudates have their greatest impact within the first 2 mm surrounding the root surface (Finzi et al. 2015); however, up to 10 mm as a zone of influence have been reported (Kuzyakov and Blagodatskaya 2015). Considering this, the current rhizosphere volume affected by exudates constitutes only a small fraction of the entire soil volume. By using global data on root surface areas from Jackson et al. (1997) and approximated rooting depths from Jackson et al. (1996)

and assuming that the rhizosphere extends 2 mm around fine roots (Kuzyakov and Razavi 2019), this fraction is estimated for forests to be roughly 1%. As absorptive fine roots, located at the terminal end of root branches and comprising first- and second-order roots (Pregitzer et al. 2002, McCormack et al. 2015), are known as the primary area of exudation (Canarini et al. 2019), the 'active rhizosphere', thus, the rhizosphere around absorptive fine roots only, is 0.3% of the entire soil volume. How well these data reflect the natural variation in the environment will require clear edaphic relationships between, e.g., soil texture and rhizosphere evolution and accurately quantifying the absorptive fine-root fraction from total fine roots (absorptive plus transport), which is time-consuming and often impractical. Although the volume of soil influenced by roots at any given time is limited, over years and centuries nearly all soil in a forest likely transitions into a rhizosphere to some extent. This transformation varies significantly with the growing season, stand age and across biomes. For instance, fine-root turnover and decomposition decreases, and root longevity increases in colder regions (Vogt et al. 1986, Solly et al. 2018). With root biomass decomposition taking about seven times longer in boreal regions than in tropical forests (Vogt et al. 1986), root–soil interactions are less dynamic in boreal ecosystems. The potential soil volumes affected by exudates are highest in tropical forests and lowest in boreal forests: within 10 years, approximately 17% of the soil volume may be influenced in the tropics (to a depth of 150 cm), 8% in temperate forests (190 cm soil depth), 3% in Mediterranean forest (200 cm soil depth) and only 1% in boreal forests (100 cm soil depth) (Figure 3).

How drought influences root exudation

The recent and projected increase in drought stress across forested ecosystems, such as the severe drought events of the past two decades in Central Europe, has underscored the urgent need to study how ecosystems respond to prolonged drought (Schuldt et al. 2020). Drought is typically investigated by examining processes occurring when soil water content (SWC) decreases—a direct consequence of reduced precipitation.

Despite reductions in photosynthesis under drought, Rog et al. (2024) recently showed that the total C flux at the tree level remains stable, suggesting significant changes in the partitioning of C within the plant, including higher REF. While there have been some reports of downregulation of SER in dry soil (Preece et al. 2021, Staszel et al. 2022, Jiang et al. 2023), roots more often respond to drought by upregulating SER (Karst et al. 2017, Preece et al. 2018, de Vries et al. 2019, Jakoby et al. 2020, Lv et al. 2023, Yin et al. 2023) and REF (Liese et al. 2018, Brunn et al. 2022, Preece et al. 2024, Rog et al. 2024) (Table 1). For instance, in a semiarid Mediterranean forest, SER was found to increase 4–11 times under drought (Jakoby et al. 2020). Controlled greenhouse experiments with saplings (Preece et al. 2018) and various grassland species grown under reduced water supply have also demonstrated elevated SER, increasing by at least a factor of 1.2 (de Vries et al. 2019). Similarly, a large range of different temperate deciduous species showed an increased SER by a factor of 1.7 (Liese et al. 2018). In contrast, SER may decrease under extremely low SWC (Williams and de Vries 2020), particularly when roots lose contact with the soil, indicating extreme stress when drought exceeds natural maximum values (Sáez-Sandino et al. 2024). However, in contrast to results from individual studies, we found that response ratios (RR) of neither SER, TER nor REF were significantly different than 0 (Table 1). Although most of the reactions were positive

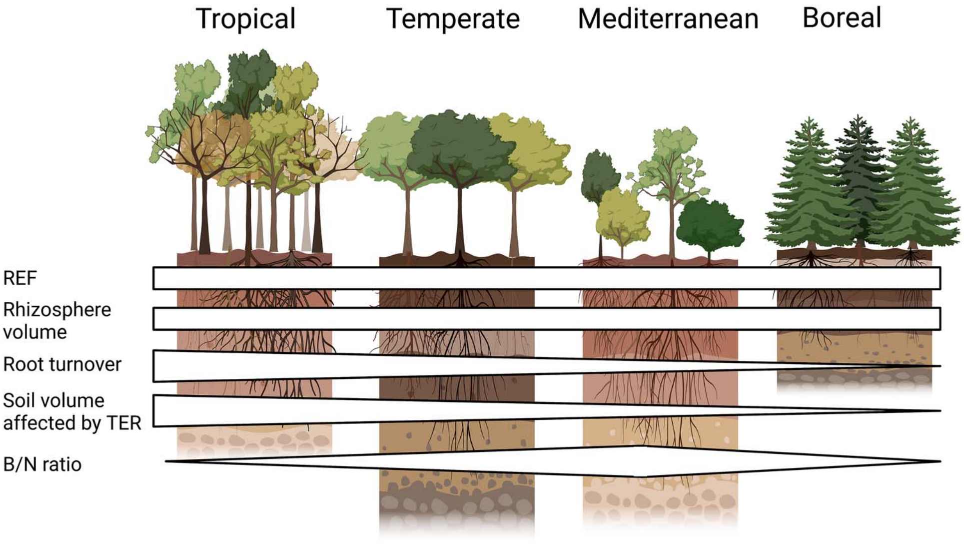

Figure 3. Exudation and rhizosphere volumes in contrasting biomes. Root exudation fractions are taken from Chari et al. (2024). Rhizosphere volumes were estimated using data from Jackson et al. (1997) and approximate rooting depths from Jackson et al. (1996), assuming that the rhizosphere extends 2 mm around fine roots (Kuzyakov and Razavi 2019). Root turnover times are based on Vogt et al. (1986) and Finér et al. (2011) with the soil volume affected by root–soil interactions calculated for a fictive time of 10 years (soil volume affected by TER = 10/root turnover × rhizosphere volume). Biomass/necromass ratios (B/N) are taken from Wang et al. (2018). Data for Mediterranean forests are from Yatir forest (*Pinus halepensis*, 280 mm annual precipitation), where fine root growth and mortality were monitored using minirhizotron cameras (T. Klein et al., unpublished). Growth averaged 400 mm per tube in winter, decreasing to 350 mm in spring, with a 12.5% mortality. This implies an average turnover time of 4 years.

Table 1. Response of root exudation to drought across various biomes, presented as RR (LOG(drought/control)) (Hedges et al. 1999). The data include different scales of root exudation: mass-SER, TER and REF. Positive values indicate higher exudation under drought conditions.

Biome	Drought	Tree species	RR SER	RR TER	RR REF	Reference
Studies in mature forest						
Temperate	Throughfall exclusion (70%)	*Fagus sylvatica*, *Picea abies*	0.43	0.07	0.46	Brunn et al. (2022)
Temperate	Not defined	*Fraxinus mandshurica*, *Juglans mandshurica*, *Betula platyphylla*, *Larix olgensis* and *Pinus sylvestris*	0.09			Lv et al. (2023)
Subtropics	Throughfall exclusion (70%)	*Schima superba*, *Lithocarpus glaber Castanopsis*	−0.09			Jiang et al. (2023)
Mediterranean	Dry (0 mm) vs wet (510 mm) season	*Pinus halepensis*, *Cupressus sempervirens*, *Quercus calliprinos*, *Ceratonia siliqua* and *Pistacia lentiscus*		0.08	0.04	Rog et al. (2024)
Studies with young plants in pots						
Boreal	Reduced watering (90% reduction)	*Populus tremuloides*	0.38			Karst et al. (2017)
Temperate	25% humidity vs 55% humidity	*Quercus petraea*	−0.48			Staszel et al. (2022)
Temperate	5% SWC (v/v) vs 10% SWC (v/v)	*Fraxinus excelsior*, *Acer pseudoplatanus*, *Acer platanoides*, *Prunus avium*, *Fagus sylvatica*, *Quercus robur*, *Tilia cordata* and *Carpinus betulus*	0.23		0.86	Liese et al. (2018)
Mediterranean	Reduced watering (100% reduction)	*Quercus ilex*	0.08			Preece et al. (2018)

Response ratios for the SER were on average 0.09 and did not differ from 0 (one sample t-test; $t = 0.79$, $df = 6$, $P = 0.46$), suggesting that SER does not change with drought across the investigated studies. Response ratios for the REF were on average 0.46 and did not differ from 0 (one sample $t = 1.94$, $df = 2$, $P = 0.19$), suggesting that TEF does not change with drought across the investigated studies.

(increasing exudation with drought), the data were highly variable. One factor that may contribute to these observations is the lack of a clear integration of the plant's physiological response, which could explain why different species respond differently to reduce SWC, particularly in pot experiments. Additionally, there are strong differences in how 'drought' is defined and reported across studies, further complicating comparisons and synthesis. Moreover, part of the studies included in Table 1 were those that reported data on controls, a prerequisite for calculating RR. We recommend employing multi-method approaches for determining water stress levels as well as for collecting exudates to improve the robustness of future studies. Several potential mechanisms have been proposed to explain why trees might increase SER and likely REF and, thus, increase C investment belowground during drought. Despite higher root-mass fractions in dryer areas globally (Ma et al. 2021) translating into an increasing root-to-shoot ratio as an adaptation to long-term drought, root growth can decline under a short-term reduction of SWC (Gaul et al. 2008, Brunner et al. 2015). Physiologically, exudates may be a consequence of maintained C supply despite reduced growth in stressful situations (Körner 2015). In an experiment investigating root elongation under low SWC, root elongation was reduced at greater rates than C supply (Muller et al. 2011). A reduced root growth combined with continued C supply has led Prescott et al. (2020) to postulate the surplus C theory that suggests that exudates may be a consequence of maintained C supply despite reduced growth at the onset of environmental stress, suggesting that exudates are a mechanism for offloading a tree's C surplus in stressful situations. We used this concept to describe ecosystem resilience to estimated trajectories of SER post-drought (Box 3). Additionally, several other processes could explain increased SER, such as the mobilization of non-structural carbohydrates during drought (Kannenberg et al. 2017), increased mucilage production (Ahmed et al. 2014), reduced membrane integrity resulting in C leakage from the root cortex (Preece et al. 2018), methodological constraints (Box 1) or hydraulic redistribution that can contribute to higher exudation by facilitating the passive movement of C compounds alongside the redistributed water, particularly under dry soil conditions where microbial activity is low. Yet, the clear relationship between whether and how exudates enhance resilience has not been proven in mature forest settings (Suseela et al. 2022). However, results from potted cultures suggest significant plant–soil feedbacks, where plant productivity was maintained through changes in exudation patterns during drought (van der Putten et al. 2016, Semchenko et al. 2022, de Vries et al. 2023).

Box 3. Shallow and deep roots differently respond to and recover from drought.

When considering SER of both surface and deep roots together, there was no observable change in TER but vertical shifts, with water-limited *P. abies* releasing two-thirds of TER into the surface soil (Brunn et al. 2022). Other studies revealed that TER could be maintained by alterations in fine-root biomass (Holz et al. 2018, Heinzle et al. 2023, Preece et al. 2024). Deeper roots generally respond differently to environmental stresses than shallow roots (Iversen 2010, Germon et al. 2020, Shakas et al. 2025a), e.g., only roots in the surface soil respond to drought with elevated SER, while deeper roots exhibit the opposite response with decreasing SER in subsoil (Brunn et al. 2022). Thus, significant consequences for the redistribution of C in soil and probably how ecosystems respond to recurrent drought situations can be expected (Borken and Matzner 2009, Bardgett et al. 2013, Göransson et al. 2013). Drought legacies have been shown to significantly impact the forest C cycle toward decreasing C stocks (Reichstein et al. 2013, Kannenberg et al. 2020, Müller and Bahn 2022). However, quantitative analyses of drought legacy responses in forest ecosystems have predominantly focused on aboveground C fluxes (Müller and Bahn 2022, Vilonen et al. 2022), although drought adjustments include the response of both above- and below–ground traits (Rowland et al. 2023). An open question is how SER changes along soil profiles under repeated drying-rewetting cycles. By applying normalized system-state indices (Ingrisch and Bahn 2018) to describe ecosystem resilience to estimated trajectories of SER post-drought, we find that shallow roots respond oppositely to deeper roots (Figure 4). Our underlying concept is that root biomass controls SER in different soil depth sections with varying SWC. During drought, higher root mortality typically occurs in the shallow soil, and based on potential growth–exudation relationships, leads to higher SER, while root growth is maintained in the subsoil, resulting in less exudation. If this relation continues post-drought over several years, with more roots growing in the topsoil during the recovery phase, the consequence would be a lower SER in shallow soil. Conversely, if sufficient water and more nutrients are available in the topsoil, the relative contribution of roots in deeper soil decreases, resulting in an increasing SER in the subsoil.

Understanding whether root C exudation is balanced between shallow soil and sub-soil, and accurately quantifying TER across drought and recovery phases, could help determine if the reduced C inputs during recovery offset the increased inputs during drought, or if there is a mismatch due to altered vertical patterns in SER (Figure 4). Given the essential role of deep roots in water uptake (Davidson et al. 2011, Shakas et al. 2025b) and in mitigating drought impacts, especially in tropical trees (Werner et al. 2021, Kühnhammer et al. 2023, Yaffar et al. 2024), significant shifts in plant–soil interactions are likely to occur under future climate scenarios.

Disentangling the individual impacts of vapor pressure deficit and SWC on ecosystem C dynamics is an often overlooked aspect (Grossiord et al. 2020, Treydte et al. 2024), particularly in mesic, yet increasingly drought-stressed forests (Novick et al. 2016). As there are only a few greenhouse studies that measured the effects of changed VPD on exudates (Sell et al. 2021), the focus of this review was primarily on the response of exudates to reduced SWC (referred to as drought) compared with a control, whether simulated in field or pot experiments or resulting from seasonal variations. We did not separate between adapted and non-adapted ecosystems and focused on both, the short-term response to reduced SWC and the longer-term response when seasons were compared.

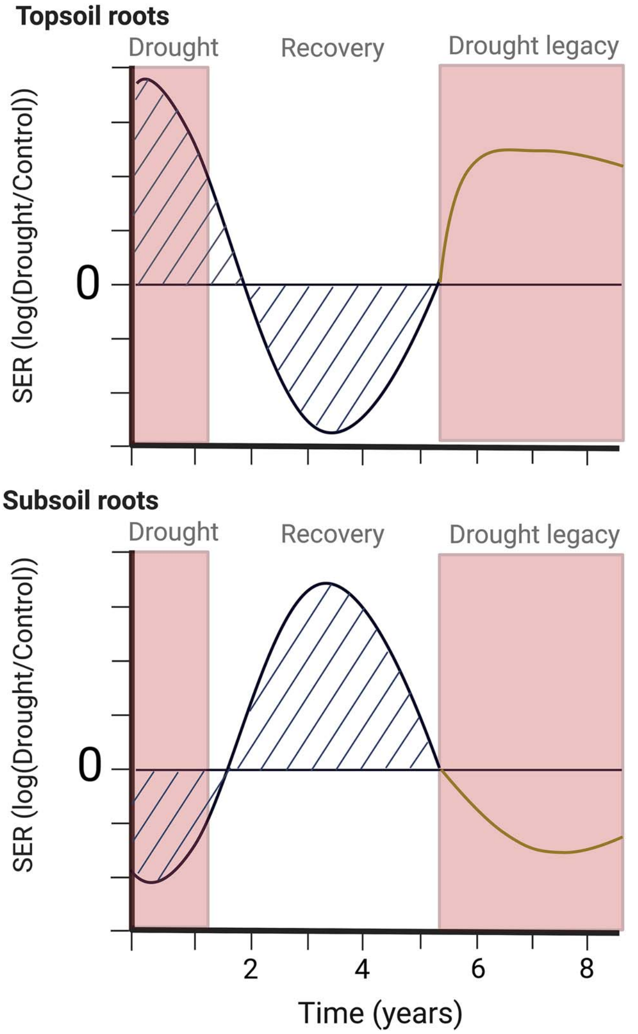

Figure 4. Expected response of mass-SERs to drought either exposed to first-time drought or drought-legacy. Exudation rates are shown for surface and deep roots and are displayed as relative drought response, i.e., the log-transformed ratio between exudation under treatment and control conditions. Values > 0 indicate an upregulation and values < 0 a downregulation of SER. Numerical integration is indicated as shaded lines and serves to calculate balances of exudation fluxes.

Knowledge gaps and outstanding questions

How plastic is root exudation?

Exudation is highly responsive to the plant's C balance and the surrounding soil environment, yet the lack of standardized methodologies hampers meaningful cross-study comparisons. For instance, water is often used as a trap solution to minimize interference during metabolomic analyzes or to quantify nitrogen exudation. However, the potential effects of the trap solution on exudation dynamics under varying environmental conditions remain largely unexplored. When testing SER in soils with contrasting phosphorus (P) availability using a standard trap solution and a P-free solution, significant variability was observed (M. Brunn and T. Klein, unpublished). Roots from high-P soils displayed consistent exudation rates, whereas roots from low-P soils exhibited greater variability and up to a threefold change in exudation depending on the solution composition and incubation duration. These findings highlight the critical importance of accounting for root pre-equilibration, trap solution composition, incubation time and edaphic conditions to improve the comparability and reliability of SER measurements.

Is the available method constrained in dry soil?

Measuring exudation under drought conditions presents unique challenges regarding incubation moisture levels. Our experiments indicate that incubating roots at high moisture levels or full saturation leads to higher SER values; thus, it is important to standardize moisture levels in the cuvettes. It is unknown whether exudation correlates more closely with soil water potential than SWC. Ideally, the water potential in the cuvettes reflects that of the rhizosphere, which might be impossible to adjust, especially if roots from fine-textured soils are investigated. The syringe environment mimics a very coarse soil that holds minimal water at field capacity. As studies have reported higher SWC in the rhizosphere compared with the detritusphere, drought relief in the cuvette might not be as significant as assumed, especially for first- and second-order roots residing in soil pores, which often maintain access to water.

How do species mixing and root longevity influence exudation rates?

Mixed-species forests tend to exhibit greater productivity, with overyielding occurring when species mixtures outperform monocultures (Ammer 2019). Based on simple biomass-exudation relationships, increased root growth could lead to lower exudation. Interestingly, studies on potted grassland species have shown the opposite: higher diversity tends to increase rhizodeposition (Semchenko et al. 2021) and boost SOM stocks, particularly in subsoils (Lange et al. 2015). Whether these dynamics hold true for species mixtures in forests in terms of exudation and soil C sequestration remains unclear. Rhizodeposition is influenced not only by root growth but also by the lifecycle of roots. Root lifespan is a variable trait affected by belowground resource availability (Strand et al. 2008) and can vary widely between and within species, ranging from days to weeks to years (Solly et al. 2018). For example, throughfall exclusion in a mature forest has been shown to extend the lifespan of *P. abies* roots and maintain fine-root production in species mixtures (Zwetsloot and Bauerle 2021), which was likely related to the observed increased exudation (Brunn et al. 2022, 2023).

Can we approach gross exudation rates?

Current research primarily reports net exudation fluxes, excluding C re-uptake by roots (Jones and Darrah 1993), microorganisms and mycorrhizae, leaving gross exudation rates poorly understood. Species with greater reliance on mycorrhizal associations, often classified as ‘collaborative’ species, tend to exude more C (Sun et al. 2021, Williams et al. 2021) and higher photosynthetic C costs of exudation were found in ECM tree species than in AM tree species under drought (Liese et al. 2018). However, quantifying the exchange of C at the root–mycorrhiza–soil interface remains a significant challenge. Advancing methods to isolate and quantify gross exudation fluxes would provide more accurate insights into the role of exudation in forest C cycling.

How can we improve global estimates?

Global estimates of TER and REF are limited by spatial gaps, particularly in Africa, Central America and South America (Chari et al. 2024), with savanna being underrepresented. Additionally, winter measurements are scarce despite evidence of significant root activity during this season (Malyshev et al. 2023). Understanding whether TER persists during periods of reduced photosynthesis is critical, as it would substantially alter REF calculations. Developing reliable proxies could enhance upscaling efforts and improve our understanding of exudation dynamics on a global scale.

Conclusion

Root exudates are central to forest ecosystem functioning, shaping soil physicochemical properties, biochemical processes and biological interactions. Despite their importance, significant knowledge gaps remain about how abiotic factors like drought (air and soil) influence C exchange between plants and soil and its relation to and implications for NPP and soil C sequestration.

Drought often increases SER and REF, reallocating photosynthetically fixed C in soil depth profiles toward topsoils. The rhizosphere acts as a hotspot for SOM accumulation and loss, driven by complex root–microbe–soil interactions. However, its influence likely transcends the immediate rhizosphere, requiring a broader perspective on how root exudates shape soil processes spatiotemporally. Transient and spatially variable, root exudation forms dynamic zones of activity that disproportionately affect SOM formation and degradation at ecosystem scales.

As climate change drives more frequent droughts, the response of exudation across depths, seasons and forest ecosystems will be pivotal for understanding ecosystem resilience. Accurately quantifying TER during drought and recovery phases—and understanding whether exudation is balanced between shallow and subsoil—could reveal whether potentially reduced C inputs during recovery offset the increased inputs during drought. Exudates are collected with trap solutions from excavated and washed living roots and are often lower than the amounts reported for rhizodeposition. For cross-study comparisons, standardized protocols are essential.

Ultimately, exudates are pivotal for nutrient acquisition, microbially mediated decomposition and the formation and persistence of SOM—all of which are crucial for sustaining ecosystem functions. Closing the existing knowledge gaps in root exudation research will be vital for enhancing our predictive capabilities in forest C cycling under future environmental scenarios.

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Authors' contributions

M.B., T.K. and C.W.M. designed the idea of the study. M.B. developed hypotheses and the concept of the manuscript, and wrote the manuscript. All co-authors contributed to the development of the manuscript and thoroughly revised and edited manuscript drafts.

Conflict of interest

None declared.

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Data availability

All data discussed in this review are publicly available from previously published sources. No new data were generated in support of this research.

References

Abramoff RZ, Finzi AC (2016) Seasonality and partitioning of root allocation to rhizosphere soils in a midlatitude forest. Ecosphere 7:20. https://doi.org/10.1002/ecs2.1547.

Ahmed MA, Kroener E, Holz M, Zarebanadkouki M, Carminati A (2014) Mucilage exudation facilitates root water uptake in dry soils. Funct Plant Biol 41:1129–1137. https://doi.org/10.1071/FP13330.

Ammer C (2019) Diversity and forest productivity in a changing climate. New Phytol 221:50–66. https://doi.org/10.1111/nph.15263.

Angst G, Mueller KE, Nierop KGJ, Simpson MJ (2021) Plant- or microbial-derived? A review on the molecular composition of stabilized soil organic matter. Soil Biol Biochem 156:108189. https://doi.org/10.1016/j.soilbio.2021.108189.

Angst G, Mueller KE, Castellano MJ, Vogel C, Wiesmeier M, Mueller CW (2023) Unlocking complex soil systems as carbon sinks: multi-pool management as the key. Nat Commun 14:2967. https://doi.org/10.1038/s41467-023-38700-5.

Badgley G, Anderegg LDL, Berry JA, Field CB (2019) Terrestrial gross primary production: using NIRV to scale from site to globe. Glob Chang Biol 25:3731–3740. https://doi.org/10.1111/gcb.14729.

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol 57:233–266. https://doi.org/10.1146/annurev.arplant.57.032905.105159.

Bardgett RD, Manning P, Morriën E, De Vries FT (2013) Hierarchical responses of plant–soil interactions to climate change: consequences for the global carbon cycle. J Ecol 101:334–343.

Baumert VL, Vasilyeva NA, Vladimirov AA, Meier IC, Kögel-Knabner I, Mueller CW (2018) Root exudates induce soil macroaggregation facilitated by fungi in subsoil. Front Environ Sci 6:17. https://doi.org/10.3389/fenvs.2018.00140.

Baumert VL, Forstner SJ, Zethof JHT, Vogel C, Heitkötter J, Schulz S, Kögel-Knabner I, Mueller CW (2021) Root-induced fungal growth triggers macroaggregation in forest subsoils. Soil Biol Biochem 157:108244. https://doi.org/10.1016/j.soilbio.2021.108244.

Bernier PY, Robitaille G (2004) A plane intersect method for estimating fine root productivity of trees from minirhizotron images. Plant Soil 265:165–173.

Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320:1444–1449. https://doi.org/10.1126/science.1155121.

Borken W, Matzner E (2009) Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Glob Chang Biol 15:808–824.

Brunn M, Hafner BD, Zwetsloot MJ, Weikl F, Pritsch K, Hikino K, Ruehr NK, Sayer EJ, Bauerle TL (2022) Carbon allocation to root exudates is maintained in mature temperate tree species under drought. New Phytol 235:965–977. https://doi.org/10.1111/nph.18157.

Brunn M, Krüger J, Lang F (2023) Experimental drought increased the belowground sink strength towards higher topsoil organic carbon stocks in a temperate mature forest. Geoderma 431:116356. https://doi.org/10.1016/j.geoderma.2023.116356.

Brunner I, Herzog C, Dawes MA, Arend M, Sperisen C (2015) How tree roots respond to drought. Front Plant Sci 6:1–16. https://doi.org/10.3389/fpls.2015.00547.

Button ES, Pett-Ridge J, Murphy DV, Kuzyakov Y, Chadwick DR, Jones DL (2022) Deep-C storage: biological, chemical and physical strategies to enhance carbon stocks in agricultural subsoils. Soil Biol Biochem 170:108697. https://doi.org/10.1016/j.soilbio.2022.108697.

Canarini A, Kaiser C, Merchant A, Richter A, Wanek W (2019) Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. Front Plant Sci 10:19.

Castellano MJ, Mueller KE, Olk DC, Sawyer JE, Six J (2015) Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept. Glob Chang Biol 21:3200–3209. https://doi.org/10.1111/gcb.12982.

Chari NR, Taylor BN (2022) Soil organic matter formation and loss are mediated by root exudates in a temperate forest. Nat Geosci 15: 1011–1016. https://doi.org/10.1038/s41561-022-01079-x.

Chari NR, Tumber-Dávila SJ, Phillips RP et al. (2024) Estimating the global root exudate carbon flux. Biogeochemistry 167:895–908. https://doi.org/10.1007/s10533-024-01161-z.

Ciais P, Reichstein M, Viovy N et al. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533. https://doi.org/10.1038/nature03972.

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J (2001) Measuring net primary production IN forests: concepts and field methods. Ecol Appl 11:356–370. https://doi.org/10.1890/1051-0761(2001)011[0356:MNPPIF]2.0.CO;2.

Collalti A, Prentice IC (2019) Is NPP proportional to GPP? Waring's hypothesis 20 years on. Tree Physiol 39:1473–1483. https://doi.org/10.1093/treephys/tpz034.

Davidson E, Lefebvre PA, Brando PM, Ray DM, Trumbore SE, Solorzano LA, Ferreira JN, Bustamante MMC, Nepstad DC (2011) Carbon inputs and water uptake in deep soils of an eastern Amazon Forest. For Sci 57:51–58.

de Vries FT, Williams A, Stringer F, Willcocks R, McEwing R, Langridge H, Straathof AL (2019) Changes in root-exudate-induced respiration reveal a novel mechanism through which drought affects ecosystem carbon cycling. New Phytol 224:132–145. https://doi.org/10.1111/nph.16001.

de Vries F, Lau J, Hawkes C, Semchenko M (2023) Plant-soil feedback under drought: does history shape the future? Trends Ecol Evol 38: 708–718. https://doi.org/10.1016/j.tree.2023.03.001.

Dennis PG, Miller AJ, Hirsch PR (2010) Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? FEMS Microbiol Ecol 72:313–327. https://doi.org/10.1111/j.1574-6941.2010.00860.x.

Drake JE, Darby BA, Giasson MA, Kramer MA, Phillips RP, Finzi AC (2013) Stoichiometry constrains microbial response to root exudation-insights from a model and a field experiment in a temperate forest. Biogeosciences 10:821–838. https://doi.org/10.5194/bg-10-821-2013.

Finér L, Ohashi M, Noguchi K, Hirano Y (2011) Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. For Ecol Manage 262:2008–2023. https://doi.org/10.1016/j.foreco.2011.08.042.

Finzi AC, Abramoff RZ, Spiller KS, Brzostek ER, Darby BA, Kramer MA, Phillips RP (2015) Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. Glob Chang Biol 21:2082–2094. https://doi.org/10.1111/gcb.12816.

Freschet GT, Pagès L, Iversen CM et al. (2021) A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. New Phytol 232:973–1122.

Friedlingstein P, O'Sullivan M, Jones MW et al. (2023) Global carbon budget 2023. Earth Syst Sci Data 15:5301–5369. https://doi.org/10.5194/essd-15-5301-2023.

Fu Z, Ciais P, Prentice IC et al. (2022) Atmospheric dryness reduces photosynthesis along a large range of soil water deficits. Nat Commun 13:1–10. https://doi.org/10.1038/s41467-022-28652-7.

Gampe D, Zscheischler J, Reichstein M, O'Sullivan M, Smith WK, Sitch S, Buermann W (2021) Increasing impact of warm droughts on northern ecosystem productivity over recent decades. Nat Clim Change 11:772–779. https://doi.org/10.1038/s41558-021-01112-8.

Gao J, Joseph RA, Werner I et al. (2021) Drought alters the carbon footprint of trees in soils-tracking the spatio-temporal fate of C-13-labelled assimilates in the soil of an old-growth pine forest. Glob Chang Biol 27:2491–2506. https://doi.org/10.1111/gcb.15557.

Gao Y, Wang H, Yang F, Dai X, Meng S, Hu M, Kou L, Fu X (2023) Relationships between root exudation and root morphological and architectural traits vary with growing season. Tree Physiology 44.

Garcia Arredondo M, Fang Y, Jones M, Yabusaki S, Cardon Z, Keiluweit M (2023) Resolving dynamic mineral-organic interactions in the rhizosphere by combining in-situ microsensors with plant-soil reactive transport modeling. Soil Biol Biochem 184:109097.

Gaul D, Hertel D, Borken W, Matzner E, Leuschner C (2008) Effects of experimental drought on the fine root system of mature Norway spruce. For Ecol Manage 256:1151–1159. https://doi.org/10.1016/j.foreco.2008.06.016.

Germon A, Laclau J-P, Robin A, Jourdan C (2020) Tamm review: deep fine roots in forest ecosystems: why dig deeper? For Ecol Manage 466:118135. https://doi.org/10.1016/j.foreco.2020.118135.

Girardi JP, Korz S, Muñoz K et al. (2022) Nitrification inhibition by polyphenols from invasive Fallopia japonica under copper stress. J Plant Nutr Soil Sci 185:923–934.

Göransson H, Godbold DL, Jones DL, Rousk J (2013) Bacterial growth and respiration responses upon rewetting dry forest soils: impact of drought-legacy. Soil Biol Biochem 57:477–486.

Gorka S, Dietrich M, Mayerhofer W et al. (2019) Rapid transfer of plant photosynthates to soil bacteria via ectomycorrhizal hyphae and its interaction with nitrogen availability. Front Microbiol 10:20. https://doi.org/10.3389/fmicb.2019.00168.

Gougherty SW, Bauer JE, Pohlman JW (2018) Exudation rates and δ13C signatures of tree root soluble organic carbon in a riparian forest. Biogeochemistry 137:235–252. https://doi.org/10.1007/s10533-017-0415-9.

Grossiord C, Buckley TN, Cernusak LA, Novick KA, Poulter B, Siegwolf RTW, Sperry JS, McDowell NG (2020) Plant responses to rising vapor pressure deficit. New Phytol 226:1550–1566. https://doi.org/10.1111/nph.16485.

Guhra T, Stolze K, Totsche KU (2022) Pathways of biogenically excreted organic matter into soil aggregates. Soil Biol Biochem 164:108483. https://doi.org/10.1016/j.soilbio.2021.108483.

Hagedorn F, Joseph J, Peter M et al. (2016) Recovery of trees from drought depends on belowground sink control. Nat Plants 2:5. https://doi.org/10.1038/nplants.2016.111.

Hansen PM, Even R, King AE, Lavallee J, Schipanski M, Cotrufo MF (2024) Distinct, direct and climate-mediated environmental controls on global particulate and mineral-associated organic carbon storage. Glob Chang Biol 30:e17080. https://doi.org/10.1111/gcb.17080.

Hartmann H, Bahn M, Carbone M, Richardson AD (2020) Plant carbon allocation in a changing world – challenges and progress: introduction to a Virtual Issue on carbon allocation. New Phytol 227:981–988.

Harris NL, Gibbs DA, Baccini A et al. (2021) Global maps of twenty-first century forest carbon fluxes. Nat Clim Change 11:234–240. https://doi.org/10.1038/s41558-020-00976-6.

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2.

Heinzle J, Liu XF, Tian Y et al. (2023) Increase in fine root biomass enhances root exudation by long-term soil warming in a temperate forest. Frontiers in forests and global. Change 6.

Herz K, Dietz S, Gorzolka K, Haider S, Jandt U, Scheel D, Bruelheide H (2018) Linking root exudates to functional plant traits. PLOS ONE 13:e0204128.

Hicks Pries CE, Sulman BN, West C et al. (2018) Root litter decomposition slows with soil depth. Soil Biol Biochem 125:103–114. https://doi.org/10.1016/j.soilbio.2018.07.002.

Hicks Pries CE, Ryals R, Zhu B, Min K, Cooper A, Goldsmith S, Pett-Ridge J, Torn M, Berhe AA (2023) The deep soil organic carbon response to global change. Annu Rev Ecol Evol Syst 54:375–401. https://doi.org/10.1146/annurev-ecolsys-102320-085332.

Hikino K, Danzberger J, Riedel VP et al. (2022) Dynamics of initial carbon allocation after drought release in mature Norway spruce—increased belowground allocation of current photoassimilates covers only half of the carbon used for fine-root growth. Glob Chang Biol 28:6889–6905. https://doi.org/10.1111/gcb.16388.

Högberg P, Högberg MN, Göttlicher SG et al. (2008) High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. New Phytol 177:220–228. https://doi.org/10.1111/j.1469-8137.2007.02238.x.

Holz M, Zarebanadkouki M, Kaestner A, Kuzyakov Y, Carminati A (2018) Rhizodeposition under drought is controlled by root growth rate and rhizosphere water content. Plant and Soil 423: 429–442.

Holz M, Becker JN, Daudin G, Oburger E (2020) Application of planar optodes to measure CO2 gradients in the rhizosphere of unsaturated soils. Rhizosphere 16:100266.

Huang Y, Ciais P, Santoro M et al. (2021) A global map of root biomass across the world's forests. Earth Syst Sci Data 13:4263–4274.

IPCC (2023) Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. In: Lee H, Romero J (eds.) Summary for policymakers. Core Writing Team, Geneva, Switzerland, pp 1–34.

Ingrisch J, Bahn M (2018) Towards a comparable quantification of resilience. Trends Ecol Evol 33:251–259.

Iversen CM (2010) Digging deeper: fine-root responses to rising atmospheric CO2 concentration in forested ecosystems. New Phytol 186:346–357.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411. https://doi.org/10.1007/BF00333714.

Jackson RB, Mooney HA, Schulze E-D (1997) A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci U S A 94:7362–7366. https://doi.org/10.1073/pnas.94.14.7362.

Jakoby G, Rog I, Megidish S, Klein T (2020) Enhanced root exudation of mature broadleaf and conifer trees in a Mediterranean forest during the dry season. Tree Physiol 40:1595–1605. https://doi.org/10.1093/treephys/tpaa092.

Jiang Z, Fu YL, Zhou LY et al. (2023) Plant growth strategy determines the magnitude and direction of drought-induced changes in root exudates in subtropical forests. Glob Chang Biol 29:3476–3488. https://doi.org/10.1111/gcb.16685.

Jones DL, Darrah PR (1993) Re-sorption of organic compounds by roots of *Zea mays* L. and its consequences in the rhizosphere. Plant Soil 153:47–59. https://doi.org/10.1007/BF00010543.

Jones DL, Nguyen C, Finlay RD (2009) Carbon flow in the rhizosphere: carbon trading at the soil–root interface. Plant Soil 321: 5–33. https://doi.org/10.1007/s11104-009-9925-0.

Joseph J, Gao D, Backes B et al. (2020) Rhizosphere activity in an old-growth forest reacts rapidly to changes in soil moisture and shapes whole-tree carbon allocation. Proc Natl Acad Sci U S A 117: 24885–24892. https://doi.org/10.1073/pnas.2014084117.

Kannenberg SA, Novick KA, Phillips RP (2017) Coarse roots prevent declines in whole-tree non-structural carbohydrate pools during drought in an isohydric and an anisohydric species. Tree Physiol 38: 582–590. https://doi.org/10.1093/treephys/tpx119.

Kannenberg SA, Schwalm CR, Anderegg WRL (2020) Ghosts of the past: how drought legacy effects shape forest functioning and carbon cycling. Ecol Lett 23:891–901.

Karst J, Gaster J, Wiley E, Landhäusser SM (2017) Stress differentially causes roots of tree seedlings to exude carbon. Tree Physiol 37: 154–164. https://doi.org/10.1093/treephys/tpw090.

Keiluweit M, Bougoure JJ, Nico PS, Pett-Ridge J, Weber PK, Kleber M (2015) Mineral protection of soil carbon counteracted by root exudates. Nat Clim Change 5:588–595. https://doi.org/10.1038/nclimate2580.

Körner C (2015) Paradigm shift in plant growth control. Curr Opin Plant Biol 25:107–114. https://doi.org/10.1016/j.pbi.2015.05.003.

Kühnhammer K, van Haren J, Kübert A et al. (2023) Deep roots mitigate drought impacts on tropical trees despite limited quantitative contribution to transpiration. Sci Total Environ 893:164763.

Kuzyakov Y, Blagodatskaya E (2015) Microbial hotspots and hot moments in soil: concept & review. Soil Biol Biochem 83:184–199.

Kuzyakov Y, Razavi BS (2019) Rhizosphere size and shape: temporal dynamics and spatial stationarity. Soil Biol Biochem 135:343–360. https://doi.org/10.1016/j.soilbio.2019.05.011.

Lange M, Eisenhauer N, Sierra CA et al. (2015) Plant diversity increases soil microbial activity and soil carbon storage. Nat Commun 6:6707. https://doi.org/10.1038/ncomms7707.

Lavallee JM, Soong JL, Cotrufo MF (2020) Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. Glob Chang Biol 26:261–273. https://doi.org/10.1111/gcb.14859.

Liese R, Lubbe T, Albers NW, Meier IC (2018) The mycorrhizal type governs root exudation and nitrogen uptake of temperate tree species. Tree Physiol 38:83–95. https://doi.org/10.1093/treephys/tpx131.

Lohse M, Haag R, Lippold E, Vetterlein D, Reemtsma T, Lechtenfeld OJ (2021) Direct imaging of plant metabolites in the rhizosphere using laser desorption ionization ultra-high resolution mass spectrometry. Frontiers. Plant Sci 12.

Lv C, Wang C, Li Y, Zhou Z (2023) Coordination among root exudation C, mycorrhizal colonization, and functional traits and their responses to drought in five temperate tree species. For Ecol Manage 546:121316. https://doi.org/10.1016/j.foreco.2023.121316.

Ma H, Mo L, Crowther TW, Maynard DS, van den Hoogen, Stocker BD, Terrer C, Zohner CM (2021) The global distribution and environmental drivers of aboveground versus belowground plant biomass. Nat Ecol Evol 5:1110–1122. https://doi.org/10.1038/s41559-021-01485-1.

Maeght JL, Rewald B, Pierret A (2013) How to study deep roots - and why it matters. Frontiers in Plant Science 4:14.

Malyshev AV, Blume-Werry G, Spiller O et al. (2023) Warming nondormant tree roots advances aboveground spring phenology in temperate trees. New Phytol 240:2276–2287. https://doi.org/10.1111/nph.19304.

McCormack ML, Dickie IA, Eissenstat DM et al. (2015) Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. New Phytol 207:505–518.

Meier IC, Pritchard SG, Brzostek ER, McCormack ML, Phillips RP (2015) The rhizosphere and hyphosphere differ in their impacts on carbon and nitrogen cycling in forests exposed to elevated CO_2. New Phytol 205:1164–1174. https://doi.org/10.1111/nph.13122.

Meier IC, Finzi AC, Phillips RP (2017) Root exudates increase N availability by stimulating microbial turnover of fast-cycling N pools. Soil Biol Biochem 106:119–128. https://doi.org/10.1016/j.soilbio.2016.12.004.

Meier IC, Tückmantel T, Heitkotter J, Müller K, Preusser S, Wrobel TJ, Kandeler E, Marschner B, Leuschner C (2020) Root exudation of mature beech forests across a nutrient availability gradient: the role of root morphology and fungal activity. New Phytol 226:583–594. https://doi.org/10.1111/nph.16389.

Müller LM, Bahn M (2022) Drought legacies and ecosystem responses to subsequent drought. Glob Chang Biol 28:5086–5103.

Mueller CW, Baumert V, Carminati A et al. (2024) From rhizosphere to detritusphere—soil structure formation driven by plant roots and the interactions with soil biota. Soil Biol Biochem 193:109396. https://doi.org/10.1016/j.soilbio.2024.109396.

Muller B, Pantin F, Génard M, Turc O, Freixes S, Piques M, Gibon Y (2011) Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. J Exp Bot 62:1715–1729. https://doi.org/10.1093/jxb/erq438.

Niedeggen D, Rüger L, Oburger E, Santangeli M, Ahmed M, Vetterlein D, Blagodatsky S, Bonkowski M (2024) Microbial utilisation of maize rhizodeposits applied to agricultural soil at a range of concentrations. Eur J Soil Sci 75:e13530. https://doi.org/10.1111/ejss.13530.

Norby RJ, Loader NJ, Mayoral C et al. (2024) Enhanced woody biomass production in a mature temperate forest under elevated CO_2. Nat Clim Change 14:983–988. https://doi.org/10.1038/s41558-024-02090-3.

Novick KA, Ficklin DL, Stoy PC et al. (2016) The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. Nat Clim Change 6:1023–1027. https://doi.org/10.1038/nclimate3114.

Oburger E, Jones DL (2018) Sampling root exudates—mission impossible? Rhizosphere 6:116–133. https://doi.org/10.1016/j.rhisph.2018.06.004.

Ostonen I, Lõhmus K, Pajuste K (2005) Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: Comparison of soil core and ingrowth core methods. For Ecol Manage 212:264–277.

Pan Y, Birdsey Richard A, Fang J et al. (2011) A large and persistent carbon sink in the world's forests. Science 333:988–993. https://doi.org/10.1126/science.1201609.

Panchal P, Preece C, Peñuelas J, Giri J (2022) Soil carbon sequestration by root exudates. Trends Plant Sci 27:749–757. https://doi.org/10.1016/j.tplants.2022.04.009.

Philippot L, Raaijmakers JM, Lemanceau P, van der Putten (2013) Going back to the roots: the microbial ecology of the rhizosphere. Nat Rev Microbiol 11:789–799. https://doi.org/10.1038/nrmicro3109.

Phillips RP, Erlitz Y, Bier R, Bernhardt ES (2008) New approach for capturing soluble root exudates in forest soils. Funct Ecol 22: 990–999. https://doi.org/10.1111/j.1365-2435.2008.01495.x.

Pollierer MM, Langel R, Körner C, Maraun M, Scheu S (2007) The underestimated importance of belowground carbon input for forest soil animal food webs. Ecol Lett 10:729–736. https://doi.org/10.1111/j.1461-0248.2007.01064.x.

Preece C, Farré-Armengol G, Llusià J, Peñuelas J (2018) Thirsty tree roots exude more carbon. Tree Physiol 38:690–695. https://doi.org/10.1093/treephys/tpx163.

Preece C, Farré-Armengol G, Verbruggen E, Peñuelas J (2021) Interactive effects of soil water content and nutrients on root exudation in two Mediterranean tree species. Soil Biol Biochem 163:108453. https://doi.org/10.1016/j.soilbio.2021.108453.

Preece C, Yang K, Llusià J, Winkler JB, Schnitzler J-P, Peñuelas J (2024) Combined effects of drought and simulated pathogen attack on root exudation rates of tomatoes. Plant Soil 497:629–645. https://doi.org/10.1007/s11104-023-06421-9.

Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL (2002) Fine root architecture of nine north American trees. Ecological monographs 72:293–309.

Prescott CE, Grayston SJ, Helmisaari H-S, Kaštovská E, Körner C, Lambers H, Meier IC, Millard P, Ostonen I (2020) Surplus carbon drives allocation and plant–soil interactions. Trends Ecol Evol 35: 1110–1118. https://doi.org/10.1016/j.tree.2020.08.007.

Rasse DP, Rumpel C, Dignac M-F (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. Plant Soil 269: 341–356. https://doi.org/10.1007/s11104-004-0907-y.

Rathore N, Hanzelková V, Dostálek T, Semerád J, Schnablová R, Cajthaml T, Münzbergova Z (2023) Species phylogeny, ecology, and root traits as predictors of root exudate composition. New Phytol 239:1212–1224.

Reichstein M, Bahn M, Ciais P et al. (2013) Climate extremes and the carbon cycle. Nature 500:287–295.

Rennenberg H, Loreto F, Polle A, Brilli F, Fares S, Beniwal RS, Gessler A (2006) Physiological responses of forest trees to heat and drought. Plant Biol (Stuttg) 8:556–571. https://doi.org/10.1055/s-2006-924084.

Rog I, Hilman B, Fox H, Yalin D, Qubaja R, Klein T (2024) Increased belowground tree carbon allocation in a mature mixed forest in a dry versus a wet year. Glob Chang Biol 30:e17172. https://doi.org/10.1111/gcb.17172.

Rowland L, Ramírez-Valiente J-A, Hartley IP, Mencuccini M (2023) How woody plants adjust above- and below-ground traits in response to sustained drought. New Phytol 239:1173–1189.

Ruehr NK, Offermann CA, Gessler A, Winkler JB, Ferrio JP, Buchmann N, Barnard RL (2009) Drought effects on allocation of recent carbon: from beech leaves to soil CO_2 efflux. New Phytol 184: 950–961. https://doi.org/10.1111/j.1469-8137.2009.03044.x.

Sáez-Sandino T, Maestre FT, Berdugo M et al. (2024) Increasing numbers of global change stressors reduce soil carbon worldwide. Nat Clim Change 14:740–745. https://doi.org/10.1038/s41558-024-02019-w.

Schlüter S, Leuther F, Albrecht L et al. (2022) Microscale carbon distribution around pores and particulate organic matter varies with soil moisture regime. Nat Commun 13:2098.

Schmidt H, Nunan N, Höck A, Eickhorst T, Kaiser C, Woebken D, Raynaud X (2018) Recognizing patterns: spatial analysis of observed microbial colonization on root surfaces. Front Environ Sci 6.

Schnepf A, Carminati A, Ahmed MA et al. (2022) Linking rhizosphere processes across scales: opinion. Plant Soil 478:5–42. https://doi.org/10.1007/s11104-022-05306-7.

Schuldt B, Buras A, Arend M et al. (2020) A first assessment of the impact of the extreme 2018 summer drought on central European forests. Basic Appl Ecol 45:86–103. https://doi.org/10.1016/j.baae.2020.04.003.

See CR, Keller AB, Hobbie SE, Kennedy PG, Weber PK, Pett-Ridge J (2022) Hyphae move matter and microbes to mineral microsites: integrating the hyphosphere into conceptual models of soil organic matter stabilization. Glob Chang Biol 28:2527–2540. https://doi.org/10.1111/gcb.16073.

Sell M, Ostonen I, Rohula-Okunev G, Rusalepp L, Rezapour A, Kupper P (2021) Responses of fine root exudation, respiration and morphology in three early successional tree species to increased air humidity and different soil nitrogen sources. Tree Physiol 42:557–569. https://doi.org/10.1093/treephys/tpab118.

Semchenko M, Xue PA, Leigh T (2021) Functional diversity and identity of plant genotypes regulate rhizodeposition and soil microbial activity. New Phytol 232:776–787. https://doi.org/10.1111/nph.17604.

Semchenko M, Barry KE, de Vries, Mommer L, Moora M, Maciá-Vicente JG (2022) Deciphering the role of specialist and generalist plant–microbial interactions as drivers of plant–soil feedback. New Phytol 234:1929–1944. https://doi.org/10.1111/nph.18118.

Shakas A, Hediger R, Gessler A et al. (2025a) Does optimality partitioning theory fail for belowground traits? Insights from geophysical imaging of a drought-release experiment in a scots pine forest. New Phytol 245:546–558.

Shakas A, Hediger R, Gessler A et al. (2025b) Does optimality partitioning theory fail for belowground traits? Insights from geophysical imaging of a drought-release experiment in a scots pine forest. New Phytol 245:546–558.

Smith WH (1970) Technique for collection of root exudates from mature trees. Plant Soil 32:238–241.

Smith WH (1976) Character and significance of forest tree root exudates. Ecology 57:324–331. https://doi.org/10.2307/1934820.

Sokol NW, Kuebbing SE, Karlsen-Ayala E, Bradford MA (2019) Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. New Phytol 221:233–246. https://doi.org/10.1111/nph.15361.

Solly EF, Brunner I, Helmisaari H-S et al. (2018) Unravelling the age of fine roots of temperate and boreal forests. Nat Commun 9:3006. https://doi.org/10.1038/s41467-018-05460-6.

Sordo Z, Andeer P, Sethian J, Northen T, Ushizima D (2024) RhizoNet segments plant roots to assess biomass and growth for enabling self-driving labs. Scientific Reports 14:12907.

Staszel K, Lasota J, Błońska E (2022) Effect of drought on root exudates from *Quercus petraea* and enzymatic activity of soil. Sci Rep 12:7635. https://doi.org/10.1038/s41598-022-11754-z.

Strand AE, Pritchard SG, McCormack ML, Davis MA, Oren R (2008) Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319:456–458. https://doi.org/10.1126/science.1151382.

Sun L, Ataka M, Kominami Y, Yoshimura K (2017) Relationship between fine-root exudation and respiration of two *Quercus* species in a Japanese temperate forest. Tree Physiol 37:1011–1020. https://doi.org/10.1093/treephys/tpx026.

Sun L, Ataka M, Han M, Han Y, Gan D, Xu T, Guo Y, Zhu B (2021) Root exudation as a major competitive fine-root functional trait of 18 coexisting species in a subtropical forest. New Phytol 229: 259–271. https://doi.org/10.1111/nph.16865.

Suseela V, Williams A, Gao C, Schneider H, Zhang Z (2022) Root and rhizosphere processes under drought: digging deeper to enhance ecosystem resilience. Bull Ecol Soc Am 103:e01970. https://doi.org/10.1002/bes2.1970.

Taylor BN, Beidler KV, Cooper ER, Strand AE, Pritchard SG (2013) Sampling volume in root studies: the pitfalls of under-sampling exposed using accumulation curves. Ecol Lett 16:862–869.

Taylor BN, Beidler KV, Strand AE, Pritchard SG (2014) Improved scaling of minirhizotron data using an empirically-derived depth of field and correcting for the underestimation of root diameters. Plant Soil 374:941–948.

Taylor HM, Upchurch DR, McMichael BL (1990) Applications and limitations of rhizotrons and minirhizotrons for root studies. Plant Soil 129:29–35.

Teixeira PPC, Vidal A, Teixeira APM et al. (2024) Decoding the rhizodeposit-derived carbon's journey into soil organic matter. Geoderma 443:116811. https://doi.org/10.1016/j.geoderma.2024.116811.

Terrer C, Phillips RP, Hungate BA et al. (2021) A trade-off between plant and soil carbon storage under elevated CO_2. Nature 591: 599–603. https://doi.org/10.1038/s41586-021-03306-8.

Treydte K, Liu L, Padrón RS et al. (2024) Recent human-induced atmospheric drying across Europe unprecedented in the last 400 years. Nat Geosci 17:58–65.

Tückmantel T, Leuschner C, Preusser S, Kandeler E, Angst G, Mueller CW, Meier IC (2017) Root exudation patterns in a beech forest: dependence on soil depth, root morphology, and environment. Soil Biol Biochem 107:188–197. https://doi.org/10.1016/j.soilbio.2017.01.006.

van der Putten WH, Bradford MA, Brinkman EP, van de Voorde, Veen GF (2016) Where, when and how plant-soil feedback matters in a changing world. Funct Ecol 30:1109–1121. https://doi.org/10.1111/1365-2435.12657.

Vetterlein D, Carminati A, Kögel-Knabner I et al. (2020) Rhizosphere spatiotemporal organization-a key to rhizosphere functions. Front Agron 2:1–22. https://doi.org/10.3389/fagro.2020.00008.

Vidal A, Hirte J, Bender SF, Mayer J, Gattinger A, Höschen C, Schädler S, Iqbal TM, Mueller CW (2018) Linking 3D soil structure and plant-microbe-soil carbon transfer in the rhizosphere. Front Environ Sci 6:1–14. https://doi.org/10.3389/fenvs.2018.00009.

Villarino SH, Pinto P, Jackson RB, Piñeiro G (2021) Plant rhizodeposition: a key factor for soil organic matter formation in stable fractions. Sci Adv 7:eabd3176. https://doi.org/10.1126/sciadv.abd3176.

Vilonen L, Ross M, Smith MD (2022) What happens after drought ends: synthesizing terms and definitions. New Phytol 235:420–431.

Vogt KA, Grier CC, Vogt DJ (1986) Production, turnover, and nutrient dynamics of aboveground and belowground detritus of world forests. Adv Ecol Res 15:303–377. https://doi.org/10.1016/S0065-2504(08)60122-1.

von Luetzow M, Kogel-Knabner I, Ekschmitt K, Matzner E, Guggenberger G, Marschner B, Flessa H (2006) Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions—a review. Eur J Soil Sci 57:426–445. https://doi.org/10.1111/j.1365-2389.2006.00809.x.

Walker AP, De Kauwe, Bastos A et al. (2021) Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO_2. New Phytol 229:2413–2445. https://doi.org/10.1111/nph.16866.

Wang C, Chen Z, Yin H et al. (2018) The responses of forest fine root biomass/necromass ratio to environmental factors depend on mycorrhizal type and latitudinal region. J Geophys Res Biogeosci 123:1769–1788. https://doi.org/10.1029/2017JG004308.

Wang Q, Ding J, Zhang Z et al. (2025) Rhizosphere as a hotspot for microbial necromass deposition into the soil carbon pool. J Ecol 113:168–179. https://doi.org/10.1111/1365-2745.14448.

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten, Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304:1629–1633. https://doi.org/10.1126/science.1094875.

Werner C, Meredith Laura K, Ladd SN et al. (2021) Ecosystem fluxes during drought and recovery in an experimental forest. Science 374:1514–1518.

Williams A, de Vries FT (2020) Plant root exudation under drought: implications for ecosystem functioning. New Phytol 225: 1899–1905. https://doi.org/10.1111/nph.16223.

Williams A, Langridge H, Straathof AL, Muhamadali H, Hollywood KA, Goodacre R, de Vries FT (2021) Root functional traits explain root exudation rate and composition across a range of grassland species. J Ecol 110:21–33. https://doi.org/10.1111/1365-2745.13630.

Witzgall K, Vidal A, Schubert DI, Hoschen C, Schweizer SA, Buegger F, Pouteau V, Chenu C, Mueller CW (2021) Particulate organic matter as a functional soil component for persistent soil organic carbon. Nat Commun 12:10. https://doi.org/10.1038/s41467-021-24192-8.

Witzgall K, Steiner FA, Hesse BD et al. (2024) Living and decaying roots as regulators of soil aggregation and organic matter formation—from the rhizosphere to the detritusphere. Soil Biol Biochem 197:109503. https://doi.org/10.1016/j.soilbio.2024.109503.

Wolf S, Paul-Limoges E (2023) Drought and heat reduce forest carbon uptake. Nat Commun 14:6217. https://doi.org/10.1038/s41467-023-41854-x.

Yin HJ, Wheeler E, Phillips RP (2014) Root-induced changes in nutrient cycling in forests depend on exudation rates. Soil Biol Biochem 78: 213–221. https://doi.org/10.1016/j.soilbio.2014.07.022.

Yaffar D, Lugli LF, Wong MY et al. (2024) Tropical root responses to global changes: a synthesis. Glob Chang Biol 30:e17420.

Yin S, Wang C, Lv C, Zhou Z (2023) Short-term responses of root traits and carbon exudation to drought in a *Larix gmelinii* plantation. Plant Soil 484:393–405. https://doi.org/10.1007/s11104-022-05800-y.

Zwetsloot MJ, Bauerle TL (2021) Repetitive seasonal drought causes substantial species-specific shifts in fine-root longevity and spatiotemporal production patterns in mature temperate forest trees. New Phytol 231:974–986. https://doi.org/10.1111/nph.17432.

Tree Physiology, 2025, 45, tpaf026
https://doi.org/10.1093/treephys/tpaf026
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