





ARTICLE

Belowground niche partitioning is maintained under extreme drought

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Funding information

Athene Fellowship of Tübingen University; Ministerium für Wissenschaft, Forschung und Kunst Baden-Württemberg; Akademie Věd České Republiky, Grant/Award Number: RVO 67985939

Handling Editor: Samantha

K. Chapman

Abstract

Belowground niche partitioning presents a key mechanism for maintaining species coexistence and diversity. Its importance is currently reinforced by climate change that alters soil hydrological conditions. However, experimental tests examining the magnitude of its change under climate change are scarce. We combined measurements of oxygen stable isotopes to infer plant water-uptake depths and extreme drought manipulation in grasslands. Belowground niche partitioning was evidenced by different water-uptake depths of co-occurring species under ambient and extreme drought conditions despite an increased overlap among species due to a shift to shallower soil layers under drought. A co-occurrence of contrasting strategies related to the change of species water-uptake depth distribution was likely to be key for species to maintain some extent of belowground niche partitioning and could contribute to stabilizing coexistence under drought. Our results suggest that belowground niche partitioning could mitigate negative effects on diversity imposed by extreme drought under future climate.

KEYWORDS

belowground niche partitioning, climate change, extreme drought, grasslands, hydrological niche segregation, oxygen stable isotopes, rainout shelter, water-uptake depth

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INTRODUCTION

How competing plant species coexist is a major unresolved question in ecology. Niche partitioning, and in particular belowground niche partitioning, has long been hypothesized as the key mechanism promoting species coexistence and diversity by effective resource exploitation and diminishing interference of roots during nutrient and water uptake (Guderle et al., 2018; Herberich et al., 2017; Silvertown, 2004; Silvertown et al., 1999, 2015). Although the importance of this mechanism is largely accepted, experimental tests examining the extent of belowground niche partitioning in natural communities and the magnitude of its change as a response to stress are still scarce. This scarcity of empirical tests is mainly due to the inherent difficulty of observing belowground processes *in situ* without major disturbance to plants, that is, without major interference with the coexistence mechanisms themselves.

The most species-rich communities on a small spatial scale, the seminatural temperate grasslands (Wilson et al., 2012), are composed of species that share a similar life form with a potentially higher overlap in the soil depth utilized for water and nutrient uptake, rendering the niche partitioning potentially more difficult to achieve. Examining belowground niche partitioning as a key mechanism underlying this high diversity of grasslands is crucial to be done *in situ* because controlled experiments conducted in artificial grassland mesocosms with limited species pools have yielded so far conflicting results. These range from no evidence of belowground niche partitioning (Bachmann et al., 2015; Oram et al., 2018) to strong context dependence of belowground niche partitioning on species richness (Braun et al., 2022; Guderle et al., 2018; Hoekstra et al., 2014; Mueller et al., 2013). The existing empirical support of belowground niche partitioning under field conditions has mainly focused on the comparison of species with contrasting growth forms or plant functional types, such as tree and grass species (e.g., Kulmatiski et al., 2020), or C4 and C3 species (e.g., Fargione & Tilman, 2005; Nippert & Knapp, 2007; for a review see Silvertown et al., 2015), where the likelihood of spatial partitioning might be higher.

Understanding the role of belowground niche partitioning for species diversity and coexistence is further reinforced by the predictions of increased regional incidents of extreme drought under climate change (IPCC, 2021). However, it remains unclear whether increased drought will lead to a shift in water-uptake depths, and if yes in which direction. The empirical evidence from grasslands is so far equivocal, with studies documenting a shift in water-uptake depths to the uppermost soil layer (0–10 cm) under experimental summer drought in lowland C3 grasslands on cambisols in Switzerland (Prechsl et al., 2015), no

response to experimental summer drought in subalpine C3 grasslands on humous sandy loam soils in Switzerland (Prechsl et al., 2015), and a shift to the deeper subsoil layers (30–50 cm) under experimentally imposed 4-year extreme drought in mesic alpine C3 grasslands on mollisols on the Tibetan Plateau (Liu et al., 2018). However, the studies documented the belowground responses to extreme drought on a community level, that is, not distinguishing among individual co-occurring species. As such, whether these shifts in water-uptake depths affecting the whole community in either direction will accentuate (decrease overlap among species) or reduce (increase overlap among species) the extent of belowground niche partitioning has yet to be empirically tested.

Measurements of natural proportions of oxygen stable isotopes in soil water offer a nondestructive solution to exploring belowground niche partitioning by enabling to discriminate from which source and depth plants take up water (Beyer et al., 2020; Chen et al., 2020; Ehleringer & Dawson, 1992; von Freyberg et al., 2020). In short, during short periods without any precipitation events (7–14 days), upper soil layers become gradually drier, and the soil water becomes enriched in the heavier isotope (^{18}O) due to faster evaporation of water containing the lighter ^{16}O (Schwinning, 2008). This process, known as isotopic fractionation, results in a vertical gradient of water isotopic signature in soils (Barnes & Turner, 1998). During the phase of water uptake and transport in roots and in nonphotosynthetic-active tissues (e.g., root crown for herbaceous plants), further fractionation of water isotopes is negligible (Barnard et al., 2006; Chen et al., 2020). Hence, the isotopic signature of water within the xylem sap reflects that in the source (soil depth) from which the plant extracts water (Beyer et al., 2020; Chen et al., 2020; Ehleringer & Dawson, 1992; von Freyberg et al., 2020). Although this method has recently received updates and criticism, it can still provide valuable insight into the water-uptake depth of plants (Chen et al., 2020; von Freyberg et al., 2020, and references therein). The nondestructive approach of stable oxygen isotopes combined with long-term experimental manipulation of drought events *in situ* should provide valuable insights into whether belowground niche partitioning could buffer species diversity under climate change.

Using the oxygen stable isotope approach, we tested for belowground niche partitioning in seminatural temperate mesic grasslands in central Europe under ambient conditions and under experimentally imposed extreme 4-year drought that reduced the precipitation by 50%. We tested (1) the extent of belowground niche partitioning under ambient conditions and (2) whether it may be altered under extreme drought. We hypothesized that as a response to extreme drought, (2a) some plants will shift

their water uptake toward deeper soil layers to avoid drought or (2b) shift their water uptake toward shallower soil layers to use the reduced precipitation more efficiently. We further tested (3) whether the shift in water-uptake depths in either direction as a response to extreme drought will accentuate (decrease overlap among species) or reduce (increase overlap among species) the extent of belowground niche partitioning.

MATERIALS AND METHODS

Study system

The experiment was set up in two sites on the Swabian Jura, a low mountain range in Southern Germany (48°28' N, 9°18' E; 48°30' N, 9°15' E; for further information on sites see also Herberich et al., 2023 and Kramp et al., 2022). During the time of the experiment (2017–2020), mean annual precipitation varied between 546 and 849 mm, and mean annual temperature varied between 9.4 and 10.4°C (DWD, 2020). The two experimental sites (5.1 km apart) were selected to represent similar plant communities belonging to the temperate mesic grasslands of *Arrhenatheretum elatioris* (classified after Wilmanns, 1993) with similar underlying geology of Jurassic shell limestone and a similar slope of 4%. In both sites, mowing was carried out in the experimental plots to mimic the traditional, centuries-long management and thus maintain the original ecosystem structure. The mowing dates during the experiment were set up to be synchronous with the surrounding management practice. At both sites, the soil type according to the WRB reference soil groups was cambisol (IUSS Working Group WRB, 2022), the soil texture was sandy loam with a large proportion of calcareous coarse fragments in the subsoil, and soil depth was between 55 and 70 cm.

Experimental design

The experiment was set up in 2017 and the sampling took place after 4 years in the vegetation season of 2020. In each of the two sites, two replicate plots for ambient conditions and two replicate plots for the 50% rainfall reduction treatment were established (Appendix S1: Figure S1a,b). The plots were 4 × 4 m with an additional 1 m buffer at the edges and they were 10–20 m apart from each other. Within each plot, four subplots of 1 × 1 m were used for the soil and plant sampling (Appendix S1: Figure S1c). Subplots were arranged in a Latin square design. For a detailed description of the rainout shelters and the extreme drought treatment see Appendix S1: Sections S2 and S3.

Study species

Target species were selected based on their relative abundance at both study sites in order to represent the studied communities. This resulted in five forbs: *Galium mollugo*, *Plantago lanceolata*, *Ranunculus acris*, *Taraxacum* sect. Ruderalia, and *Trifolium repens*; and four grasses: *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca rubra*, and *Lolium perenne*. The selected species amounted to 68% and 43% of the total vegetation cover in ambient and extreme drought conditions, respectively. *P. lanceolata* and *T. sect. Ruderalia* have a taproot, *G. mollugo*, *R. acris* and *T. repens* and all grasses have a fibrous rooting system (Kutschera, 1982; Kutschera et al., 1992). All species are perennials with a C3 photosynthetic pathway. Nomenclature follows www.theplantlist.org.

Soil cores

The sampling for soil and plants took place between 24 and 31 July 2020. Each sampling took place at least 7 days after the last rain event. This allowed the establishment of isotopic vertical gradients in soil (Schwinning, 2008). Soil cores for isotope measurements were taken once per subplot, in its middle using a soil auger with a 2 cm diameter (Appendix S1: Figure S1d,e). The cores reached a maximum depth of 55–70 cm, depending on the soil depth. To avoid soil and moisture loss upon extraction, cling film was tightly wrapped around the soil auger while it was pulled out. The cling film was then marked at the depths of 5, 10, 15, 20, 30, and 50 cm. The cling film was then cut open at each of the marked depths and ~2 g of soil was taken out from each sampling depth (±1 cm to extract enough soil needed for the cryodistillation). The soil (without any roots) was immediately transferred into a 12-ml Standard Exetainer vial with a small spatula. The vials were closed with Standard Exetainer caps equipped with a gas-tight chlorobutyl rubber septum, cooled in the field, and then frozen at –20°C until further processing.

Root crowns

Plant root crowns were collected in each subplot as close as possible to the soil core allowing a maximum distance of 50 cm between plant individuals and the soil core (Appendix S1: Figure S1d). Root crowns, the part of a plant connecting the root and the stem (Appendix S1: Figure S1f), have no photosynthetic tissue and are usually white. Barnard et al. (2006) identified the root crown to best reflect the isotope compositions of the root water, and therefore of the soil water in the depth from which it

is taken up by the plant. Between three to five individuals (or ramets for the grass) for the larger species *D. glomerata*, *P. lanceolata*, *R. acris*, *T. repens* and *T. sect. Ruderalia*, ~10 individuals of *G. mollugo*, ca. 13 ramets of *L. perenne*, ca. 20 ramets of *A. elatius* and ~30 stalks of *F. rubra* were collected as one sample in each subplot. This resulted in 0.15–0.5 g of fresh biomass per plant species per subplot, which is the amount needed to later extract a sufficient amount of water by the cryodistillation for the stable isotope analyses (sufficient amount of plant material was established by preliminary experiments). The root crowns were placed in a 12-ml Standard Exetainers vial, closed with Standard Exetainer caps equipped with a gas-tight chlorobutyl rubber septum, cooled in the field, and then frozen at -20°C until further processing.

In each subplot, belowground biomass in the upper 10 cm of the soil, where most of the roots are present in the grassland system, was measured (for a detailed description of methods see Appendix S1: Section S4).

Cryodistillation

Water was extracted from the soil and plant samples by cryogenic vacuum distillation (cryodistillation). Each Exetainer vial containing a sample was coupled with another empty 12-ml Exetainer vial using a custom-made (3D printed) threaded connecting piece. Such pairs of vials were vacuumed using an oil pump for about 10 s to reach a pressure of about 100 Pa and then closed. To reach pressure below the water triple point and to reduce water loss during the evacuation, the lower vials containing the plant or soil samples were kept frozen at -20°C . The upper vials served to trap the water during the cryodistillation. During the cryodistillation process, the lower vials were heated in a common heating block at 100°C , while the upper vials were cooled in a custom-made bath filled with liquid nitrogen. The low air pressure established by the vacuum pump, the low water vapor pressure maintained by water desublimation, and the increased temperature of the samples allowed fast water transfer from the sample to the upper vial. The cryodistillation took 2.5 h. Such time was sufficient to extract all water from the sample; based on previous trials, the cryodistillation of the largest samples (about 0.5 ml of water) took less than 1 h. We compared the amount of collected water with the original water content in the sample by weighting the samples before and after the cryodistillation process and by re-heating and re-weighting the samples. This allowed us to identify a few samples in which the cryodistillation failed due to water loss (leaking of the connecting piece) or incomplete sample drying (failure of the tube vacuuming). Such samples also

deviated in the isotopic composition and were removed from the data set. Up to 250 μl of the collected water was pipetted into airtight PP screw thread autosampler vials.

Analysis of oxygen stable isotopes

The stable isotope analysis of the water oxygen was performed using an isotope-ratio mass spectrometer (IRMS) DELTAplus XL coupled to a high-temperature conversion elemental analyzer TC/EA (ThermoFinnigan, Bremen, Germany). A standard with known isotopic composition was analyzed for every tenth sample. The stable isotope of oxygen composition was expressed as the isotope ratios relative to Vienna Standard Mean Ocean Water, that is, $\delta^{18}\text{O}$ (‰). The analysis of oxygen isotope was chosen over the hydrogen isotope due to its higher reliability (Chen et al., 2020).

Statistical analyses

We approximated the water-uptake depth by comparing the $\delta^{18}\text{O}$ of the water extracted from the root crowns with the $\delta^{18}\text{O}$ of the soil water along the soil profile, following the assumption that fractionation of oxygen isotopes is negligible inside plants (Barnard et al., 2006; Chen et al., 2020). For that, we fitted a logarithmic approximation curve on the soil $\delta^{18}\text{O}$ gradient, that is, a log-linear function between soil depth (in centimeters) and soil $\delta^{18}\text{O}$ (in per mille), for each of the plots using the mean (across the four subplots of each plot) of the $\delta^{18}\text{O}$ isotope values of each depth. This approach was chosen to account for missing values for some depths and subplots as well as to account for the microheterogeneity within each plot. The equation of the logarithmic approximation curve was then used to calculate the water-uptake depth of the plants sampled within each given plot by inserting the isotope value of their root crown into this equation. Because of the generally high explanatory power of the logarithmic approximation curves ($R^2 = 0.94\text{--}0.95$; Appendix S1: Section S5, Figures S4 and S5), the resulting water-uptake depth values (in centimeters) for each species in each subplot were used for all following statistical analyses, except for determining the relative proportion of water-uptake from the different soil layers.

We tested the belowground niche partitioning and the response of plants in their water-uptake depths to extreme drought with generalized linear mixed models (GLMM) with a Gamma distribution and an inverse link function (package lme4; Bates et al., 2015). The gamma distribution was chosen to account for the nature of our data, which has a right-skewed distribution with a

biologically set upper limit at 0 cm soil depth and a long tail toward deeper soil layers. The models included water-uptake depths (calculated from the logarithmic approximation curves) as response variable, species, treatment (ambient conditions and extreme drought), and their interaction as fixed effects, and plot nested within sites as a random effect. We then used planned comparisons (“contrasts”) to specifically test for the differences in water-uptake depths (1) among species in the ambient conditions, (2) among species in the extreme drought conditions, and, (3) differences within each species between ambient and extreme drought conditions (package *emmeans*; Lenth, 2021).

We further calculated the overlap in water-uptake depths among species under the ambient and under extreme drought conditions (package *overlapping*; Pastore, 2018). The overlap quantifies the similarity between two empirical distributions, in our case distributions of the water-uptake depths (calculated from the logarithmic approximation curve; Pastore, 2018; see also Gross et al., 2021). We tested the differences in species overlap between the treatments using a GLMM with a Gamma distribution and an inverse link function, including the overlap as the response variable, treatment as a fixed effect, and site as a random effect. To evaluate the response to extreme drought of each species individually, we then calculated the overlap between ambient and extreme drought conditions for each species separately.

We additionally determined the relative proportion of water uptake from the different soil layers by using the Bayesian mixing model *MixSIAR* (Stock et al., 2018). The $\delta^{18}\text{O}$ mean value and standard deviation of the isotopic composition of the soil water (source data) and the $\delta^{18}\text{O}$ raw plant xylem water (mixture data) were used in two different models. The discrimination values were set to zero for $\delta^{18}\text{O}$, mainly because there was negligible isotope fractionation during plant water uptake (von Freyberg et al., 2020). The run length of the Markov chain Monte Carlo (MCMC) was set as “normal” with the model parameters being set as follows: iterations = 100,000, burn-in = 50,000, thin = 50, and number of chains = 3. The model error was evaluated by residual and process error. “Gelman–Rubin” and “Geweke” diagnostics were used to determine the convergence of the model.

We also tested for differences in water uptake depths (calculated from the logarithmic approximation curves) between rooting systems (fibrous and taproot) and growth forms (forbs and grasses; for a detailed description see Appendix S1: Section S6).

All analyses were performed in R Software v.4.0.3 (R Core Team, 2020).

RESULTS

Plant water-uptake depths differed significantly among the studied grassland species under both ambient and extreme drought conditions (Table 1; Figure 1). The overlap in water-uptake depths among all co-occurring species increased significantly from 22% under ambient to 30% under extreme drought conditions ($\chi^2 = 6.19$, $df = 1$, $p = 0.013$; Figure 2).

As a response to extreme drought, all plants shifted their water uptake toward shallower soil layers (Table 1; Figures 1, 3, and 4), that is, species relied more heavily on water from the shallowest depth (5 cm) under extreme drought conditions than under ambient conditions (Figure 3; Appendix S1: Section S7, Table S5, Figure S7). However, the magnitude of the upward water-uptake shift to shallower soil layers was species-specific (Table 1). The results of the Bayesian mixing model *MixSIAR* supported the results from logarithmic approximation curve analysis and offered a more detailed insight into the contribution of the different soil layers to the total water-uptake depths of the target species (Figure 3; for a detailed description see Appendix S1: Section S7, Table S5, Figure S7).

We observed three types of responses to extreme drought that were captured by the changes in distribution and the overlap in the water-uptake depths for each species separately between the ambient and the extreme drought conditions (Figure 4). Namely, we observed a narrower and more right-skewed distribution of the water-uptake depths under extreme drought compared to a broader and more unimodal distribution under the ambient conditions for *Festuca rubra*, *Ranunculus acris*, *Arrhenatherum elatius* and *Trifolium repens* (overlap between distributions <50%; Figure 4). For *Galium mollugo*, *Plantago lanceolata*, *Taraxacum* sect. *Ruderalia* and *Lolium perenne*, the distributions remained more similar between the treatments (overlap between distribution >50%; Figure 4). For the deepest rooting species

TABLE 1 Results of the generalized linear mixed models with Gamma distribution testing the differences in the water-uptake depths among nine co-occurring grassland species in the ambient and the extreme drought conditions (“Treatment”) and their interaction.

Fixed effect	df	χ^2 value	p-value
Species	8	58.75	<0.001
Treatment	1	3.87	0.049
Species × Treatment	8	16.20	0.040

Note: Significant differences at $\alpha = 0.05$ are marked in bold.

Dactylis glomerata, the distribution changed from unimodal to a distribution with several peaks (Figure 4).

We found no differences in water-uptake depth between the different rooting systems (fibrous and tap-root), nor between the two growth forms (forbs and grasses; Appendix S1: Section S6, Tables S3 and S4, Figure S6). Belowground biomass of the upper 10 cm did not differ between ambient and extreme drought conditions (Appendix S1: Section S4, Figure S3).

DISCUSSION

We found evidence of belowground niche partitioning in grassland communities under both ambient and extreme drought conditions. Under extreme drought, plants shifted their water-uptake depths toward shallower soil layers. Despite the reduction of range and distribution of

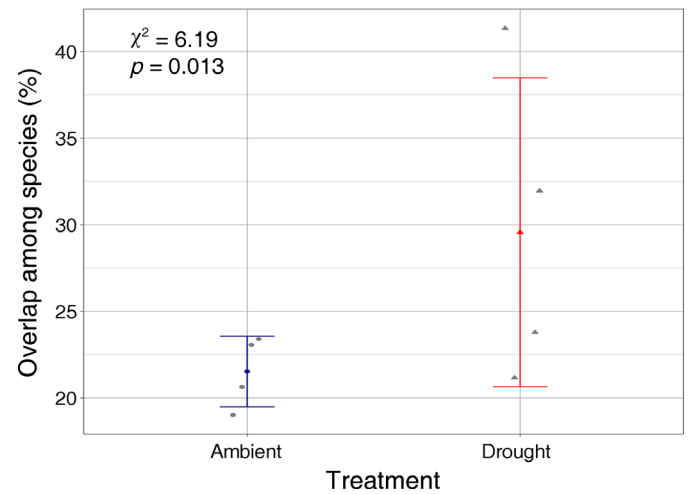


FIGURE 2 Overlap in water-uptake depths (mean \pm 95% CI) among species under ambient and extreme drought conditions (four plots per treatment).

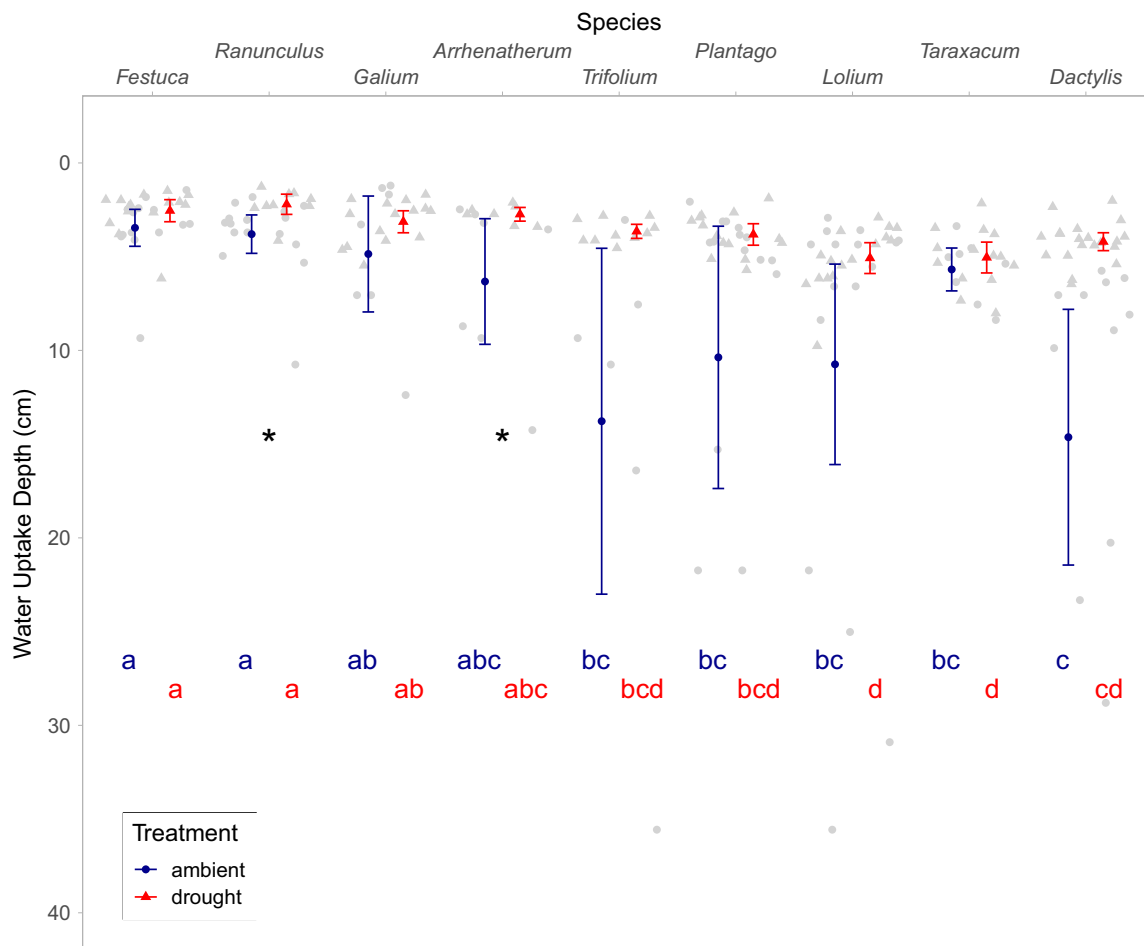


FIGURE 1 Water-uptake depths (mean \pm 95% CI) of plant species under ambient and extreme drought conditions. Planned comparisons were used to specifically test for the differences in water-uptake depths (1) among species in the ambient conditions (letters in blue), (2) among species in the extreme drought conditions (letters in red), and (3) within each species between ambient and extreme drought conditions (asterisk in black). Significant differences at $\alpha = 0.05$ are denoted either by different letters within a color or by an asterisk. For full species names see *Methods: Study species*.

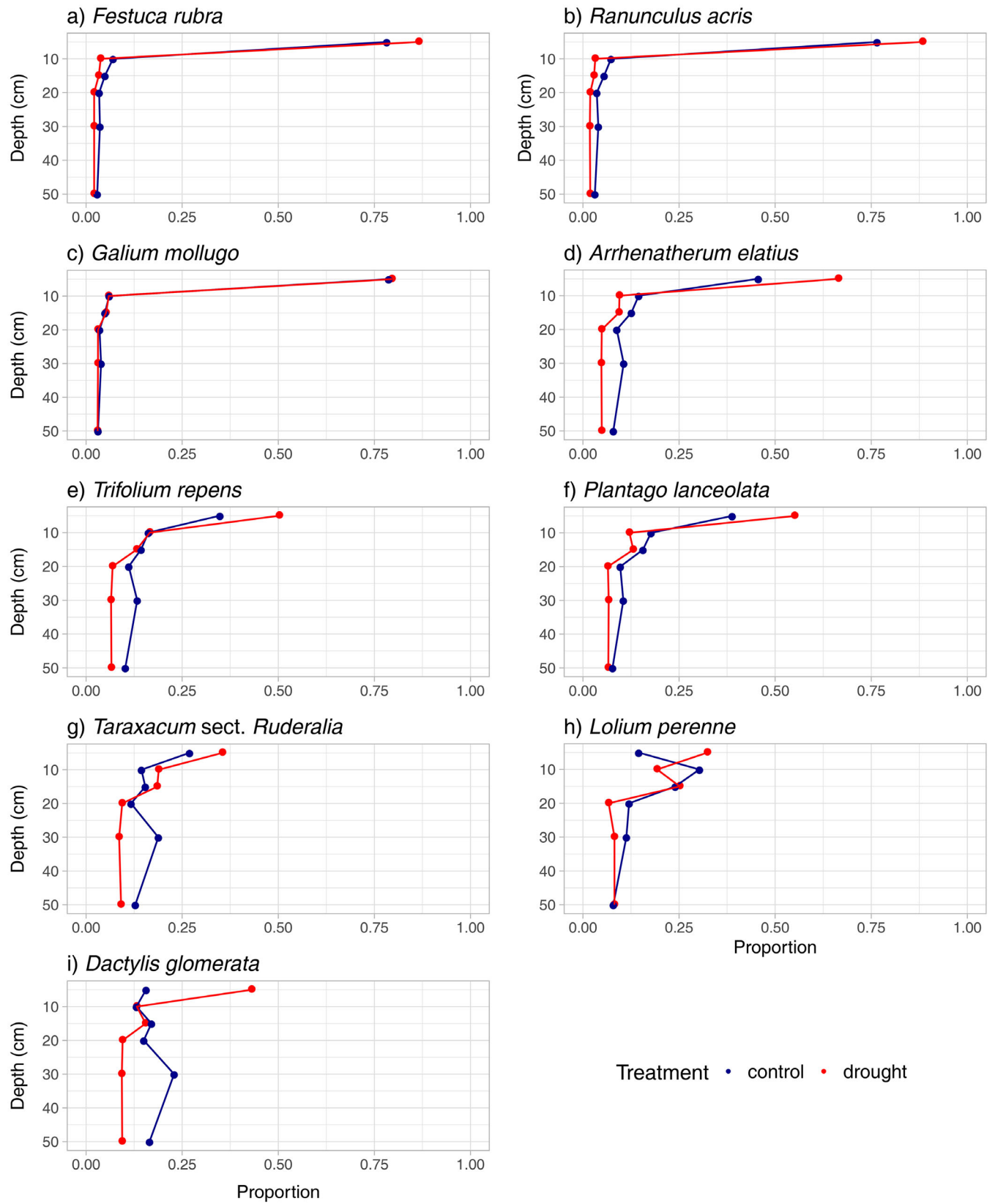


FIGURE 3 Median proportional contribution of soil water from six different layers to the plant xylem water of the nine study species based on the $\delta^{18}\text{O}$ values, calculated with the Bayesian mixing model MixSIAR.

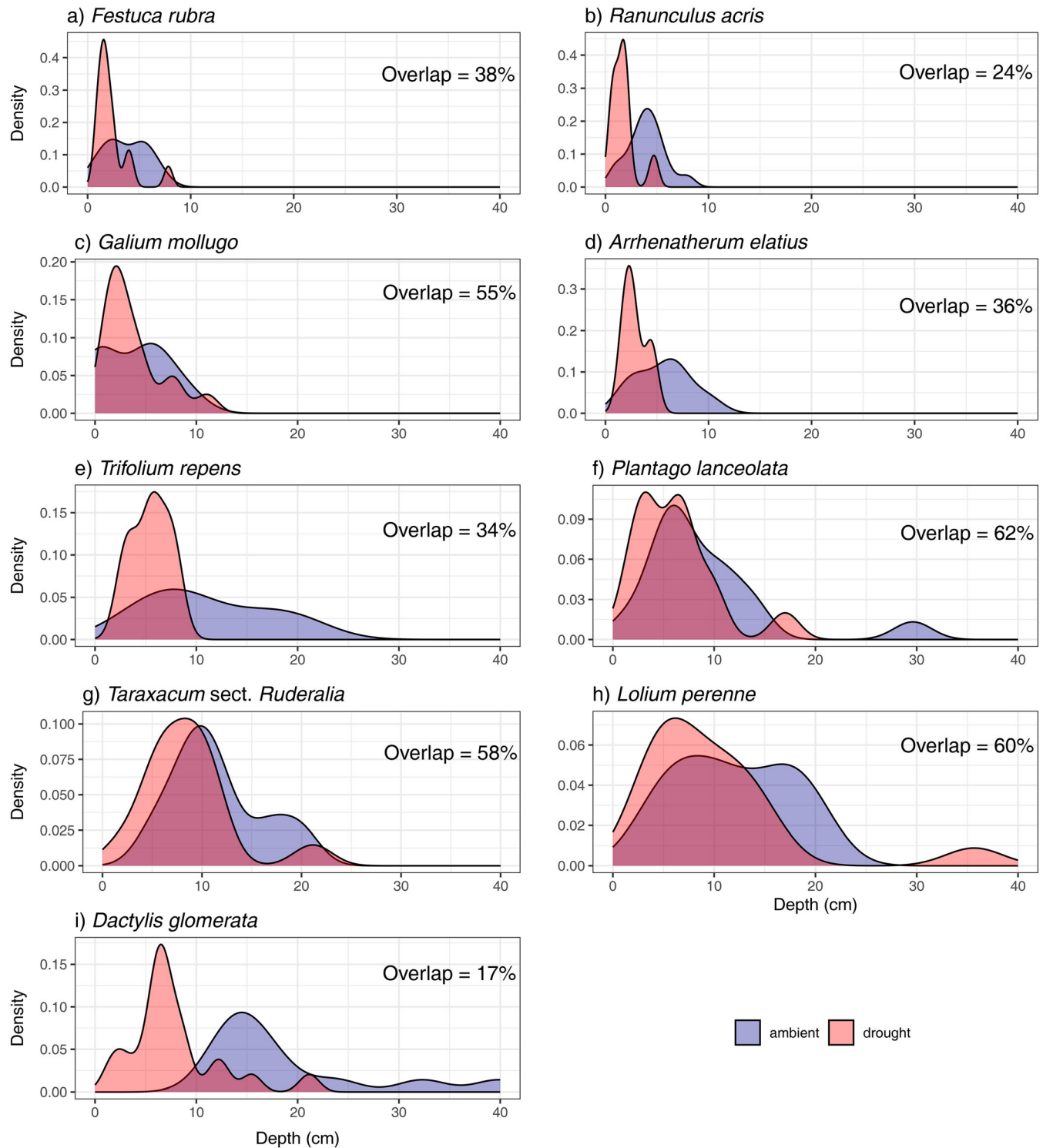


FIGURE 4 Overlap in water-uptake depths between ambient and extreme drought conditions within each species.

water-uptake depths and an increased overlap among species, belowground niche partitioning was maintained under extreme drought. Species showed distinct strategies related to the change of their range and distribution of water-uptake depths as a response to extreme drought.

Under extreme drought, grassland plants showed an overall shift of their water-uptake depths to shallower soil

layers. Our results are consistent with the results of a study conducted on similar plant communities (lowland C3 grasslands in Switzerland) with similar soil conditions (cambisols), where a shift toward the topsoil layer (0–10 cm) under summer drought was observed on the community level (Prechsl et al., 2015). In cambisols, the cambic horizon (b-horizon) is per definition located

quite shallow under the soil surface and has a relatively high water-holding capacity (IUSS Working Group WRB, 2022). This could lead to the shallower cambic horizon being the soil layer storing most water under drought conditions and could explain the upward shift in plant water uptake under extreme drought. Our findings contradict the results of studies conducted in different plant communities with different soil types, that is, subalpine grasslands on humous sandy loam soils in the Swiss Alps (Prechsl et al., 2015) and alpine grasslands on mollisols on the Tibetan Plateau (Liu et al., 2018). These results together suggest that soil physical and hydrological features may play an important role in determining plants' response to extreme drought in terms of their water-uptake depths.

Another possible explanation of the observed upward shift in water-uptake depths in the temperate lowland grasslands in both our study and the study of Prechsl et al. (2015) could be related to the recent findings of Schlaepfer et al. (2017), who used ecosystem water balance simulation models to assess the interannual duration and distribution of ecological droughts worldwide. They showed that, in temperate drylands, droughts occurring during the growing season will mostly intensify in deeper soil layers (>20 cm), suggesting that plants will potentially rely on water uptake from shallower soil layers.

The reduction in belowground niche partitioning, that is, an increase in overlap in the water-uptake depths, under extreme drought in comparison with ambient conditions demonstrates that its extent depends on the abiotic context (Michalet et al., 2021). However, the fact that, despite a certain reduction, we still found significant differences in water-uptake depths among co-occurring species to maintain belowground niche partitioning under extreme drought suggests that competition plays an important role also under more stressful conditions (but see Lamb & Cahill Jr., 2008). This is further supported by the fact that the overall shift of water-uptake depth to shallower soil layers was not associated with a change in belowground biomass in the upper 10 cm of the soil, that is, in the soil layer where most plants took the water from under extreme drought.

We found evidence of three distinct strategies related to the shift in water-uptake depths under extreme drought. First, four species (*F. rubra*, *R. acris*, *A. elatius*, and *T. pratense*) had a considerably narrower distribution of water-uptake depths under drought than under ambient conditions. In contrast, four species (*G. mollugo*, *P. lanceolata*, *T. sect. Ruderalia*, and *L. perenne*) had a similarly broad distribution of water-uptake depths, that is, utilizing a similar range of water-uptake depths under ambient and drought

conditions. In both the aforementioned cases, the strategies were not related to the differences between forbs and grasses or between fibrous and taproot rooting systems. A third strategy points toward a so-called dynamic rooting system, that is, a broad distribution of water-uptake depths with the ability to access different rooting depths and switch between the water sources depending on the environmental conditions (Guderle et al., 2018), in our case employed by *Dactylis glomerata* under extreme drought. Because *D. glomerata* is known to cope well with drought due to its high plasticity in root traits (Bristiel et al., 2019), a dynamic rooting system might be an indication of a strategy successful under drought stress. Altogether, the co-occurrence of these three contrasting strategies is likely to be key for species to maintain some extent of belowground niche partitioning and could contribute to stabilizing coexistence under extreme drought.

CONCLUSION

Our empirical demonstration of belowground niche partitioning in natural communities and its change as a response to extreme drought has important implications for species coexistence and the maintenance of species diversity in the context of climate change. As such, our results suggest that belowground niche partitioning could help to mitigate the negative effects of extreme drought on species coexistence and diversity under future climate change scenarios.

AUTHOR CONTRIBUTIONS

Maria Májeková and Pierre Liancourt conceived the idea. Maria Májeková, Sophie E. Weides, Tomáš Hájek, Maximiliane M. Herberich, and Pierre Liancourt designed the study. Katja Tielbörger designed the drought experiment. Sophie E. Weides, Rosa E. Kramp, Tomáš Hájek, and Maria Májeková collected the data. Sophie E. Weides, Maria Májeková, Tomáš Hájek, Pierre Liancourt, L. Camila Pacheco-Riaño, and Sara Tomiolo analyzed the data. Sophie E. Weides and Maria Májeková wrote the first draft of the manuscript and all authors contributed to the revisions.

ACKNOWLEDGMENTS

This work was supported by a grant from the Baden-Württemberg Ministry of Science, Research and Arts to Katja Tielbörger via the project DRiER (Drought impacts, processes and resilience: making the invisible visible) and the Athene Fellowship of Tübingen University to Maria Májeková. Tomáš Hájek and Pierre Liancourt were supported by the long-term research development project no. RVO 67985939 of the Czech

Academy of Sciences. Open Access funding enabled and organized by Projekt DEAL.


CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Weides et al., 2023) are available in Dryad at <https://doi.org/10.5061/dryad.f7m0cfz33>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Weides, Sophie E., Tomáš Hájek, Pierre Liancourt, Maximiliane M. Herberich, Rosa E. Kramp, Sara Tomiolo, L. Camila Pacheco-Riaño, Katja Tielbörger, and Maria Májková. 2024. "Belowground Niche Partitioning is Maintained under Extreme Drought." *Ecology* 105(1): e4198. <https://doi.org/10.1002/ecy.4198>