

## RESEARCH ARTICLE

# Drought effects on root and shoot traits and their decomposability

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## Abstract

1. Drought can induce phenotypic plasticity in a range of plant root and shoot traits. These traits have been shown to explain differences in root and shoot litter decomposability between species. However, it is unknown how drought-induced plasticity of root and shoot traits alters their decomposability.
2. To investigate this issue across a range of species, we grew a grass *Lolium perenne*, a forb *Plantago lanceolata* and a legume *Trifolium repens* common to European temperate grasslands and subjected them to a 5-week moderate drought treatment. We compared morphological and chemical root and shoot traits of the droughted plants to well-watered controls. We then conducted a decomposition assay of the senesced root and shoot material over 16 weeks, with mass loss measurements at five timepoints.
3. Drought had significant and sometimes strong effects on morphological and chemical root and shoot traits of all three species, sometimes similar to differences between species and generally in line with a shift to a more resource-conservative strategy. Drought also increased the labile litter fraction in roots of *Lolium perenne*, which was associated with a substantial increase in non-structural carbohydrates. Drought decreased the labile litter fraction in shoots of *Plantago lanceolata*, but this could not be explained by the traits we measured. Drought effects on litter decomposability were weaker than on plant traits.
4. Our results suggest that plant trait-mediated effects of drought on litter decomposability can either increase or decrease vegetation feedbacks to climate change. They also show that drought-induced plasticity in root and shoot traits does not automatically translate into equivalent changes in litter decomposability.

## KEYWORDS

drought, grassland, intraspecific variation, litter decomposability, non-structural carbohydrates, phenotypic plasticity, plant traits, root traits

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## 1 | INTRODUCTION

Droughts are projected to increase in frequency and severity globally with climate change (Dai, 2013). Ecosystem carbon (C) and nitrogen (N) cycles are affected by drought in a number of ways, including through effects on vegetation (Wu et al., 2011). Studies of plant traits have contributed to a better understanding of both the response of vegetation to environmental variation and the effect of vegetation on ecosystem functions (Funk et al., 2017; Lavorel & Garnier, 2002). Specifically, traits related to the 'resource economic spectrum' can be used to characterize trade-offs between resource-acquisitive and resource-conservative growth strategies (Reich, 2014).

Drought can alter plant community traits by affecting community composition and structure with some species being more susceptible to drought than others (Fry et al., 2013). Additionally, drought can induce trait changes within species due to phenotypic plasticity, the process by which a single genotype presents different forms, phenologies and physiologies depending on the environmental conditions (Sultan, 2000). Phenotypic plasticity can, in turn, have effects on plant-soil C and N cycling (de Vries et al., 2016). Plants have evolved traits that allow them to cope with drought through avoidance and/or tolerance strategies (Lambers et al., 2008) with phenotypic plasticity contributing to their responses (Lozano et al., 2020). Plants with an avoidance strategy have traits that increase water uptake and/or reduce losses, for example: (i) Resource-conservative root and shoot tissues with high leaf/root dry matter content (LDMC/RDMC), high lignin content and low specific leaf area (SLA), specific root length (SRL) and tissue N content can reduce water loss (Fort et al., 2013). (ii) Resource-acquisitive fine roots with a high SRL can improve water uptake (Fort et al., 2013; Padilla et al., 2013). (iii) An accumulation of non-structural carbohydrates (NSCs) in shoots and roots can reduce water loss by lowering plant tissue osmotic potential and also affect morphological traits, for example, increase LDMC and RDMC (Zwicke et al., 2015). (iv) A high root to shoot ratio can increase water uptake (Poorter et al., 2012). Plants with a tolerance strategy have the capacity to re-grow after drought, for example, by accumulating osmoprotectant NSC in tissues, protecting the plant against cell damage and facilitating re-growth (Zwicke et al., 2015). Intense water stress may, however, inhibit plant growth to such a degree that plant trait plasticity is mostly related to reduced growth, rather than being an adaptive response to drought. In this case, drought may lead to higher SLA, lower LDMC/RDMC and higher tissue N content (de Vries et al., 2016). In summary, drought can induce phenotypic trait plasticity in different directions, depending on the plant's drought strategy and on the severity of the drought stress.

Plant trait plasticity can potentially affect ecosystem processes, including litter decomposition. Litter decomposition is an important component of ecosystem C and N cycling, as it influences nutrient availability for plants and microbes and affects microbial community composition and C storage (De Deyn et al., 2008). Rates of litter decomposition depend on several interacting factors, including litter quality, climate, soil conditions and decomposer communities. However, results from a meta-analysis of decomposition

experiments across biomes on six continents suggest that the influence of litter quality is larger than the influence of climatic variation (Cornwell et al., 2008). Even though chemical traits of litter differ from those of fresh plant material due to senescence and nutrient resorption (Orwin et al., 2010; Quedstedt et al., 2003), a considerable part of the variation in root and shoot litter decomposability between species can often be linked to easily measurable traits of fresh plant material, such as LDMC and leaf nitrogen content (Bumb et al., 2018; Cornwell et al., 2008; Fortunel et al., 2009; Kazakou et al., 2009). Additionally, studies have shown a variety of chemical compounds to be important in explaining differences in litter decomposability between species, such as cellulose, lignin and a range of NSCs (Gunnarsson et al., 2008) and plant secondary metabolites (Chomel et al., 2016). Root decomposability is also likely linked to traits, even though less research has been conducted and the results are somewhat conflicting. For example, in Mediterranean herbaceous species, fine root decomposability was related to root chemical traits (phosphorus, NSC and hemicellulose), but not to morphological traits (Birouste et al., 2012). In contrast, temperate tree root decomposition was correlated with root diameter, root hemicellulose and NSC, but not with root lignin (Hobbie et al., 2010).

Drought can induce phenotypic plasticity in the traits that are correlated with differences in decomposition rates, such as LDMC/RDMC, and content of N, lignin, cellulose and NSC. However, to our knowledge, the consequences of drought-induced trait plasticity on litter decomposability have so far only been experimentally tested in one study on the roots of four tree species (Carrillo et al., 2022). The aim of our study was to investigate whether drought-induced plasticity of root and shoot traits alters their decomposability in three common European temperate grassland species, as grasslands cover more than a third of the global land surface (Suttie et al., 2005) and hold large C stocks (Read et al., 2001). We grew a grass *Lolium perenne*, a forb *Plantago lanceolata* and a legume *Trifolium repens* in the greenhouse and subjected them to a 5-week experimental drought. At the end of the drought, a range of root and shoot traits were measured and a decomposition assay of senesced root and shoot material was conducted. The following hypotheses were tested: (1) Shoot traits of all three species will shift to a more resource conservative strategy in response to drought. (2) Root traits will either shift to a more resource conservative strategy or to a more resource acquisitive strategy in response to drought, depending on plant species. (3) A shift to more conservative root or shoot traits will lead to slower litter decomposition while a shift to more acquisitive traits will lead to faster litter decomposition.

## 2 | MATERIALS AND METHODS

### 2.1 | The drought experiment

We selected three plant species common to European temperate grasslands from different functional groups, as research suggests that classifying grassland plants into the broad functional groups

of grasses, forbs and legumes offers a way to understand ecosystem dynamics (Ravenek et al., 2016; Tjoelker et al., 2005), drought response (Lozano et al., 2020; Mackie et al., 2019) and effects on ecosystem functions (Allan et al., 2013; Fornara et al., 2009). The species were *Lolium perenne*, a fine-rooted grass, *Plantago lanceolata*, a rhizomatous forb and *Trifolium repens*, a shallow-rooted, stoloniferous N-fixing legume.

We grew the plants in the greenhouse at 16 h light/8 h dark in soil (silt loam of the Brickfield 2 association, detailed soil characterization see de Vries et al., 2018) collected from a mesotrophic grassland at Hazelrigg field station in northern England (54°10 N, 2°46W, 94m.a.s.l.), sieved to 1 cm and homogenized. No permissions were needed to conduct this fieldwork. Seeds (Emorsgate Seeds, King's Lynn) were germinated in plug trays. After 2 weeks, the seedlings were transplanted into monoculture pots with 7 individuals per pot. The pots were built out of a drain pipe (45 cm height, 18 cm diameter) with a mesh at the bottom and filled with a layer of chippings (1 kg) and 10 kg of field-moist (55% water-holding capacity [WHC]) Hazelrigg soil.

For each of the three species, we set up five replicate pots for the well-watered treatment and five pots for the drought treatment, resulting in 30 pots in total. The pots were arranged in a fully randomized block design with one pot per treatment in every block. During the first 5 weeks, all pots were watered evenly 3–4 times a week. During the following 5 weeks, well-watered pots were kept at 60% WHC and droughted pots at 40% WHC by adjusting gravimetrically 3–4 times a week. These WHC are comparable to previous

drought experiments (de Vries et al., 2016; Lozano et al., 2020). We chose a relatively mild drought at 40% WHC to allow the plants to adjust plastically while not wilting.

At the end of the growth period, when the plants were 12 weeks old, we measured morphological root and shoot traits (see following section). Watering was then stopped and the plants left to senesce for 2 weeks in the greenhouse. Senesced shoots from each pot were cut at the base. We collected senesced roots removing the entire soil mass from the pot, working it gently with gloved hands and a rubber mallet and shaking to remove soil. The senesced roots and shoots were oven-dried at 40°C for 48 h, cut into pieces of max. 4 cm length and homogenized within the sample to be used in the litter decomposition assay.

## 2.2 | Trait measurements

We measured fresh plant traits at the end of the growth period on one randomly selected individual from each pot following standard protocols (Pérez-Harguindeguy et al., 2013). Leaf area (LA), leaf length, SLA, LDMC were measured on five mature leaves per individual. Leaves were scanned using an EPSON flatbed scanner and leaf area was analysed using the software WinRhizo (Regent Instruments Inc., Sainte-Foy-Sillery-Cap-Rouge, QC, Canada). Leaf length was measured with a ruler. Leaves and shoots were weighed before and after drying for 48 h at 65°C.

**TABLE 1** Main and interactive effects of plant species and drought treatment on shoot and root plant traits, tested by two-way ANOVA. Bold values indicate significant effects ( $p < 0.05$ ). DMD, dry matter digestibility; NSC, non-structural carbohydrates

Shoots							
Factor	Statistic	Morphological traits				Shoot dry weight	
		Leaf dry matter content	Specific leaf area	Leaf area	Leaf length		
Species ( $df = 2$ )	<i>F</i>	<b>7.16</b>	<b>31.49</b>	<b>55.39</b>	<b>63.08</b>	2.92	
	<i>p</i>	<b>0.003</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.074	
Drought treatment ( $df = 1$ )	<i>F</i>	<b>14.62</b>	<b>18.33</b>	<b>10.25</b>	<b>27.65</b>	3.47	
	<i>p</i>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.004</b>	<b>&lt;0.001</b>	0.075	
Species × drought treatment ( $df = 2$ )	<i>F</i>	0.28	1.31	0.40	0.64	0.65	
	<i>p</i>	0.759	0.287	0.677	0.536	0.530	
Roots							
Factor	Statistic	Morphological traits					Root: shoot ratio
		Root dry matter content	Root diameter	Specific root length	Root tissue density	Root dry weight	
Species ( $df = 2$ )	<i>F</i>	<b>11.38</b>	<b>5.04</b>	<b>30.00</b>	<b>8.23</b>	<b>28.41</b>	<b>26.90</b>
	<i>p</i>	<b>&lt;0.001</b>	<b>0.015</b>	<b>&lt;0.001</b>	<b>0.002</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Drought treatment ( $df = 1$ )	<i>F</i>	<b>55.15</b>	4.18	1.61	0.01	<b>5.31</b>	<b>14.07</b>
	<i>p</i>	<b>&lt;0.001</b>	0.052	0.217	0.929	<b>0.030</b>	<b>&lt;0.001</b>
Species × drought treatment ( $df = 2$ )	<i>F</i>	0.96	0.04	0.16	0.84	0.48	0.85
	<i>p</i>	0.398	0.960	0.851	0.445	0.627	0.441

To determine root dry weight, SRL, root diameter, root tissue density (RTD) and RDMC, we took a soil core (3 cm diameter) centred on the harvested individual to the full depth of each pot. The roots were washed, scanned using an EPSON flatbed scanner and weighed before and after drying at 65°C for 48 h. The scanned images were analysed using WinRhizo.

Chemical traits were determined on senesced material. A dried sub-sample of litter from each root and shoot sample was ground with a ball mill and approximately 3 mg (for shoots) or 4 mg (for roots) were used to analyse C and N content with an elemental analyser (EA 1108, Carlo Erba Instruments). Fibre fractions and dry matter digestibility (DMD) were analysed using near infrared reflectance spectroscopy (NIRS), following the method outlined by Bumb et al. (2016). Samples were ground in a knife-mill with a 1 mm screen and packed in ring cells equipped with a quartz glass. Spectra were collected in duplicate (different cup fillings) using a monochromator spectrometer (FOSS NIRSystems 5000), at wavelengths between 1100 and 2500 nm with a 2 nm step. NIRS calibrations used for predictions were based on databases available at the laboratory, updated by conducting reference measurements of chemical traits on 12 samples. NIRS calibration was performed using modified partial least square regression with the software WINISI (Version 4, Infrasoft International). The reference method for fibre fractions was the Van Soest sequential analysis (Van Soest et al., 1991) which provides measures for neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL). Hemicellulose was estimated as (NDF – ADF) and cellulose as (ADF

– ADL). The Kjeldahl method was used for crude protein (CP = N \* 6.25) while ash was determined by combustion in a muffle furnace at 550°C. The in vitro pepsin–cellulase method (Aufrère et al., 2007) was used as reference for DMD. NSC was estimated by difference as (100 – [ash + CP + NDF]).

### 2.3 | Litter decomposition assay

The litter decomposition assay followed an approach developed by Wardle et al. (1998). For each assay, we filled a Petri dish with 30 g field-moist Hazelrigg soil that had been sieved to 2 mm. The soil was covered with a circle of nylon mesh (1 mm), that was cut to the diameter of the Petri dish and a 0.5 g sample of dried senesced plant material was spread out on top. To allow destructive harvesting over time, we took five sub-samples of 0.5 g senesced shoot material per plant pot and placed them in individual Petri dishes to be incubated for 2, 4, 8, 12 or 16 weeks. For *Lolium* and *Plantago*, we also took five sub-samples of 0.5 g senesced root material per plant pot and placed them in Petri dishes to be incubated for 2, 4, 8, 12 or 16 weeks. *Trifolium* had less root material, so we only took two sub-samples to be incubated for 4 or 16 weeks.

This resulted in: (5 timepoints × 5 replicate pots × 5 litter types [3 species for shoots and 2 species for roots] × 2 watering treatments) + (2 timepoints × 5 replicate pots × 1 litter type [*Trifolium* roots] × 2 watering treatments) = 540 Petri dishes.

Chemical traits of senesced material						
Carbon	Nitrogen	Cellulose	Hemi-cellulose	Lignin	NSC	DMD
5.90	796.98	909.57	1267.60	344.11	533.44	390.76
0.009	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
0.01	0.27	44.34	1.35	0.28	17.68	27.48
0.914	0.606	<0.001	0.257	0.601	0.0003	<0.001
1.31	4.82	7.78	10.97	1.68	6.18	9.64
0.289	0.018	0.002	<0.001	0.207	0.007	<0.001
Chemical traits of senesced material						
Carbon	Nitrogen	Cellulose	Hemi-cellulose	Lignin	NSC	DMD
5.39	1336.50	61.67	462.39	25.96	175.22	134.02
0.012	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
6.17	0.56	18.77	0.07	20.95	26.08	26.85
0.020	0.461	<0.001	0.799	<0.001	<0.001	<0.001
0.78	0.30	0.44	3.59	2.07	4.52	4.26
0.468	0.741	0.648	0.043	0.148	0.021	0.026

Petri dishes were sealed with electrical tape leaving a small gap to allow air circulation and incubated at 15°C (the mean summer month temperature in Hazelrigg 2008–2018) in the dark. Once a month, we re-adjusted the moisture gravimetrically with sterile deionized water. At each destructive sampling (2, 4, 8, 12, 16 weeks), the remaining litter was collected with tweezers, dried at 65°C for 48 h and weighed.

## 2.4 | Statistical analyses

Statistical analyses were conducted in R version 3.6.1 (R Core Team, 2019). To test our first hypothesis, we determined species differences and drought effects for all plant traits using two-way analysis of variance (ANOVA). Trait data were  $\log_{10}$ -transformed where necessary to fulfil model assumptions. Pairwise comparisons of significant effects were assessed using Tukey post hoc tests.

To compare magnitudes and directions of drought effects on different plant traits, we computed the log response ratios (LRR) for each trait  $x$ :

$$\text{LRR}_x = \ln\left(\frac{\bar{x}_{\text{drought}}}{\bar{x}_{\text{well-watered}}}\right), \quad (1)$$

where  $\bar{x}$  is the mean of trait  $x$ . The LRR was chosen as a measure as it standardizes drought effects on different traits to the same unit, and also separates positive and negative drought effects on a comparable scale.

We computed the standard error  $SE_{\text{LRR}_x}$  of the LRR of each trait  $x$  as:

$$SE_{\text{LRR}_x} = \sqrt{\left(\frac{SE_{x \text{ drought}}}{\bar{x}_{\text{drought}}}\right)^2 + \left(\frac{SE_{x \text{ well-watered}}}{\bar{x}_{\text{well-watered}}}\right)^2}, \quad (2)$$

Where  $SE_x$  is the standard error of the mean. [Corrections added on 15 March 2023, after first online publication: The equation 2 has been corrected].

To assess litter decomposability, we fitted models to the data of remaining litter mass after 2, 4, 8, 12 and 16 weeks using nonlinear least squares regression. This was done for root and shoot litter from each pot separately using a modified version of the R code provided by Adair et al. (2010). First, we fitted a simple exponential model (Olson, 1963):

$$\text{Simple exponential model: } X(t) = e^{-kt}, \quad (3)$$

where  $X(t)$  is the proportion of litter mass remaining at time  $t$  and  $k$  is the decomposition rate.

As this type of model can have a poor fit (Adair et al., 2010), we additionally fitted an asymptotic exponential model and a double exponential model, as described in Wieder and Lang (1982):

$$\text{Asymptotic exponential model: } X(t) = A + (1 - A)e^{-kt}, \quad (4)$$

$$\text{Double exponential model: } X(t) = Ae^{-lt} + (1 - A)e^{-kt}. \quad (5)$$

(1-A) is a labile litter fraction that decomposes at rate  $k$  and  $A$  is a residual litter fraction with a decomposition rate of zero (at least, over the period of the study) in case of the asymptotic model, and with a decomposition rate of  $l$  in case of the double exponential model. We used Akaike's information criterion modified for small sample sizes (AICc) to select the best decomposition model.

To test our second hypothesis, we determined the effect of species differences and drought effects on the decomposition model parameters using two-way ANOVAs with log-transformation of variables where necessary to fulfil model assumptions. Pairwise comparisons of significant effects were assessed using Tukey post hoc tests. For *Trifolium* root litter, we tested the effect of drought on remaining mass % after 4 and 16 weeks directly using t-tests, as data were insufficient to fit the decomposition models.

All figures were produced using the packages `GGPLOT2` (Wickham, 2016) and `PATCHWORK` (Pedersen, 2019).

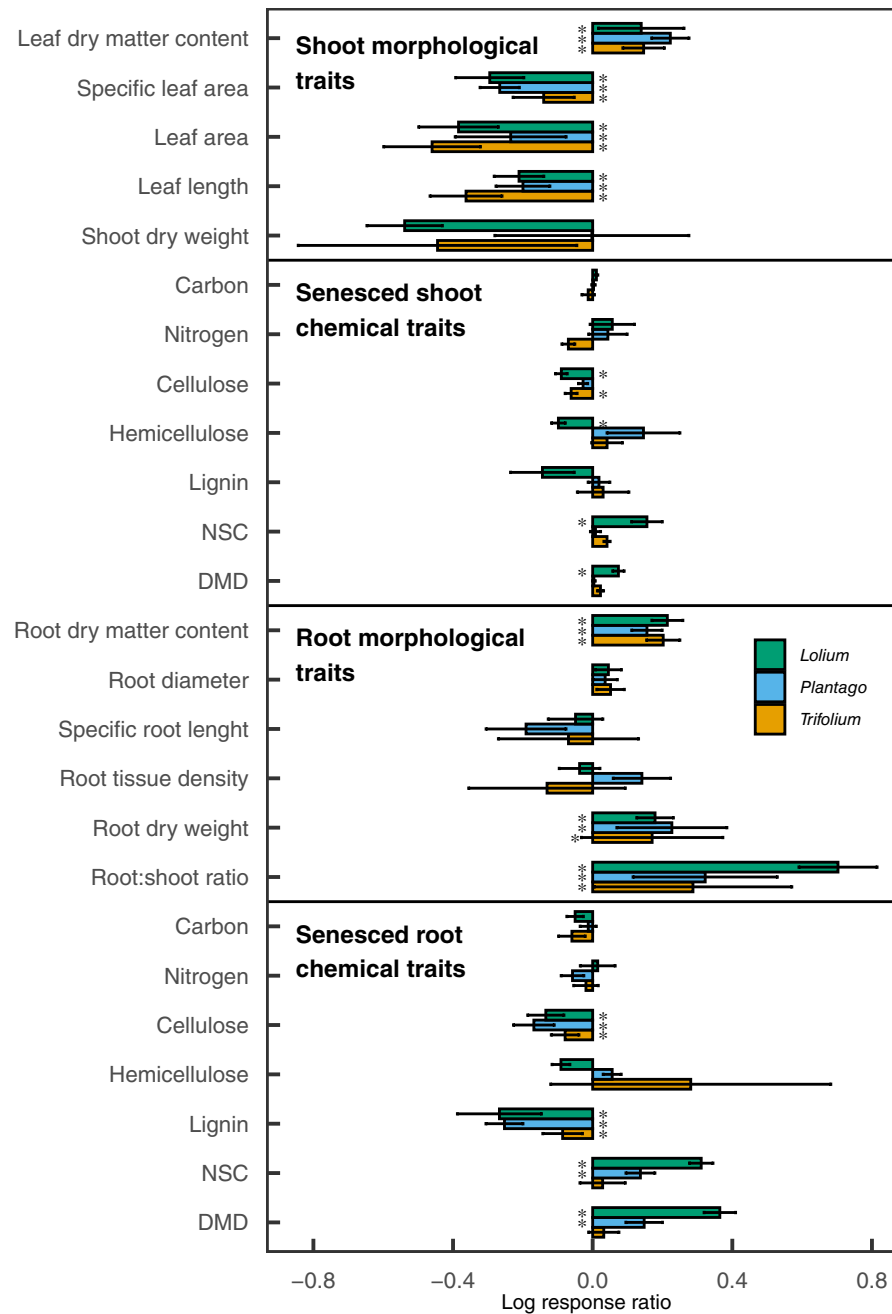
## 3 | RESULTS

### 3.1 | Plant traits

The three species differed significantly ( $p < 0.05$ ) in all plant traits measured, except shoot dry weight, where  $p = 0.074$  (Figures S1 and S2, Table 1). A range of root and shoot morphological traits, as well as root chemical traits were affected significantly by drought across all species (Table 1, Figure 1). Drought increased LDMC, RDMC, root dry weight and root:shoot ratio ( $p < 0.05$ ) for all species. Drought also tended to increase root diameter ( $p = 0.052$ ). Drought decreased SLA, LA, leaf length, as well as root cellulose and lignin ( $p < 0.05$ ) across species. For some chemical traits, the drought effect varied between species (species  $\times$  drought, Table 1, Figure 1). *Lolium* had the most traits affected at  $p < 0.05$ : drought additionally decreased shoot cellulose and hemicellulose, and increased root and shoot NSC and DMD. Shoot cellulose was decreased by drought in *Trifolium*, and root NSC and DMD increased by drought in *Plantago*. LRRs (see Figure 1) showed that, in general, drought had the strongest effects on shoot morphological traits and weaker effects on root traits. Effects on shoot chemical traits were generally weakest. Effects on root chemical traits were generally stronger than effects on shoot chemical traits; almost as strong as the effects on root morphological traits.

### 3.2 | Litter decomposition

AICc comparison showed that the asymptotic exponential model provided a better fit than the simple exponential model (AICc difference  $> 2$ ) for 44 cases, a similar fit for 5 cases (AICc difference  $< 2$  and  $> -2$ ) and a worse fit (AICc difference  $< -2$ ) for only one case, which contained an outlier (Table S1a,b, Figure S3). The double exponential model provided a better fit than the asymptotic model in 11 cases, a similar fit in 6 cases and a worse fit in 33 cases (Table S1b,c). In some cases, the double exponential model contained biologically unrealistic parameters,



**FIGURE 1** Log response ratios (LRR) for drought effects on plant traits, see Equation 1. If  $LRR > 0$  there was a positive drought effect, if  $LRR < 0$  there was a negative drought effect. Error bars represent  $\pm 1$  standard error. \* at the base of the bar plots indicate significant drought effects ( $p < 0.05$ ) on plant traits, determined by multiple comparisons through Tukey post hoc tests if there was a significant effect of drought and/or species  $\times$  drought on the plant trait (see Table 1). NSC, non-structural carbohydrates; DMD, dry matter digestibility [Corrections added on 15 March 2023, after first online publication: The bars in figure 1 have been corrected].

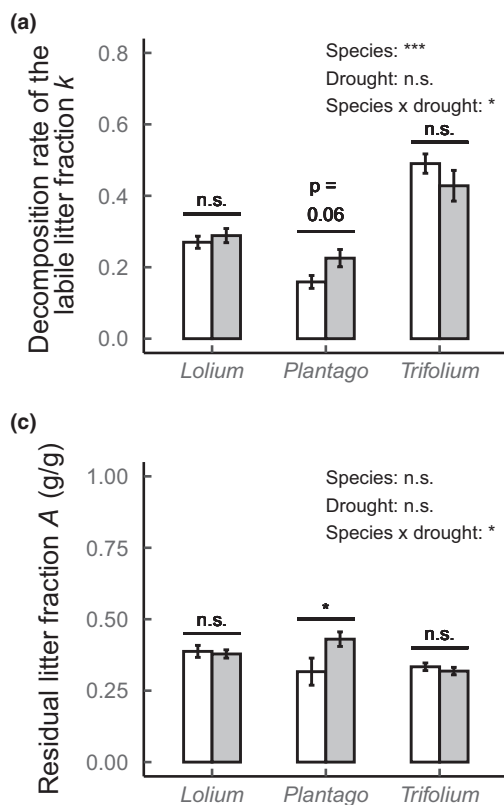
that is, negative decomposition rates. Based on this and to ensure consistency, the asymptotic exponential model was fitted to all decomposition curves with the exception of *Trifolium* root litter, for which only two time points were available due to its smaller root biomass (Figure S3). Pearson correlation coefficients between measured and modelled values of remaining mass ranged between 0.974 and 0.999.

The decomposition rate  $k$  of the labile litter fraction  $1-A$  was significantly different between species for shoots ( $p < 0.001$ ), while the drought effect varied between species (Figure 2). Post-hoc testing

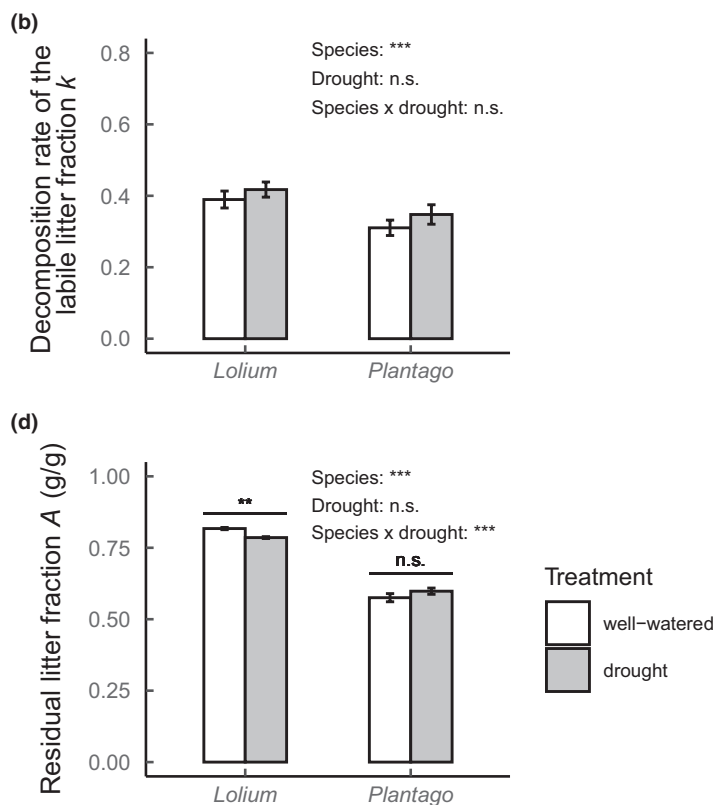
revealed that drought tended to increase  $k$  from 0.16 to 0.23 weeks<sup>-1</sup> in *Plantago* at  $p = 0.06$ , but did not affect  $k$  in *Lolium* and *Trifolium*. For roots,  $k$  differed between species ( $p < 0.001$ ) in droughted and well-watered treatments with a lower rate of decomposition in *Plantago* compared to *Lolium*.

The residual litter fraction  $A$  did not differ between species for shoots, but the drought effect varied between species (species  $\times$  drought,  $p < 0.05$ , Figure 2). Post-hoc testing revealed that drought increased the mean  $A$  from 0.316 to 0.430 g/g in shoots of

## Shoot decomposition



## Root decomposition



**FIGURE 2** The effect of drought and plant species on the decomposition rate of the labile litter fraction  $k$  (weeks<sup>-1</sup>, a, b) and the residual litter fraction A (g/g, c, d). Bars represent mean  $\pm$  1 standard error.  $k$  and A were determined by fitting Equation 2 to remaining litter mass after 2, 4, 8, 12 and 16 weeks using nonlinear least squares regression. Significance of main and interactive effects of species and drought treatment were assessed using ANOVA with subsequent Tukey post hoc tests. Significance is indicated as:  $p < 0.001$  \*\*\*,  $p < 0.01$  \*\*,  $p < 0.05$  \*

*Plantago* ( $p < 0.05$ ), but did not affect A in *Lolium* and *Trifolium*. For roots, A differed between species ( $p < 0.001$ ) and also the drought effect on A varied between species ( $p < 0.001$ ). Post-hoc testing revealed that drought decreased mean A from 0.817 to 0.786 g/g in *Lolium* ( $p < 0.01$ ) but had no effect on A in *Plantago* roots.

For *Trifolium* roots, there was no significant effect of drought on mass loss after 4 and 16 months ( $p > 0.05$ ). Mean remaining mass after 16 weeks for *Trifolium* roots was 35.5% for the well-watered treatment and 34.2% for the drought treatment.

## 4 | DISCUSSION

The aim of this study was to investigate whether drought effects on root and shoot traits alter litter decomposability in three grassland species. Drought had significant strong effects on many morphological and chemical root and shoot traits of all three temperate grassland plant species. Morphological shoot traits were the most strongly affected by drought. For example, negative effects of drought on LDMC and SLA were of similar magnitude as differences between species. Drought also affected decomposition in two species, accelerating decomposition of the labile litter fraction and

either increasing or decreasing the residual litter fraction. However, drought effects on litter decomposability were fewer and much weaker than drought effects on traits.

### 4.1 | Drought effects on plant traits

In accordance with hypothesis (1) and partly hypothesis (2), drought effects on root and shoot morphological traits (increased LDMC, RDMC and root diameter and decreased SLA, LA and leaf length) were consistent with a shift towards a more resource conservative strategy in all three species. These results confirm other published evidence on the effect of drought on traits of temperate grassland species. Similar trait responses were observed with a more severe drought (2 months at 30% WHC), the same three species, in that drought generally increased LDMC, RDMC and root diameter and decreased SLA (Lozano et al., 2020). Also, a shift to more conservative root traits was observed in grassland species as a response to a two-week drought at 30% WHC (de Vries et al., 2016).

Resource-conservative morphological traits have been found to be associated with higher lignin and fibre content found in larger-scale studies, which has been suggested to be related to fundamental trade-offs

at these scales, both in leaf traits (Onoda et al., 2017) and in root traits (Prieto et al., 2015). However, in our study, we found that despite the shift to more resource-conservative morphological traits, fibre fractions (cellulose, hemicellulose, lignin) and C content were either decreased or not affected by drought, while NSC content was increased in some species. This suggests that the shift in morphological traits was not due to developing tougher, more resource-conservative tissues, but instead may have been due to NSC accumulation for osmotic regulation. We measured NSC content in senesced material and it is possible that higher levels and differences between droughted and control plants would have been found in fresh tissues, as root and shoot tissues lose NSCs through resorption and leaching while senescing (Vergutz et al., 2012). A drought-induced increase in NSC has also been observed in other studies (e.g. Brunner et al., 2015; Zwicke et al., 2015). It is surprising that despite a drought effect on RDMC, there was no significant effect of drought on RTD, but effects might be explained by a higher density in the dry fraction of the root biomass due to NSC accumulation.

Other studies have investigated the effect of drought on plant chemical traits. For example, drought by withholding water for 2 weeks increased levels of NSC in leaves of *Lolium perenne*, but did not affect lignin content (Abdelgawad et al., 2014), which is consistent with our study. Also, feedstock species generally showed increased NSC content and decreased lignin content in a year of drought compared to a non-drought year (Emerson et al., 2014). In contrast to our study, *Trifolium repens* leaf lignin content increased after 12 days of withholding water (Li et al., 2013). Also, in a meta-analysis, Dumont et al. (2015) found on average a small increase in lignin content of grassland shoots as a response to drought, but also a small increase in digestibility, and high variation between experiments. The contrasting results of these studies indicate that plant chemical responses to drought are variable, possibly depending on interspecific and intraspecific differences and on duration and intensity of drought.

LRRs revealed that, generally, shoots had a slightly greater drought response in morphological traits than roots. This might be due to the fact that root morphological traits are more physically constrained by the soil. On the other hand, chemical traits of senesced plants showed a stronger drought response in roots than in shoots. A reason for this might be that roots undertake water acquisition and are directly in contact with the soil. Also, the drought-induced increase in root:shoot ratio in all species implies that more C was allocated to roots under drought, giving more opportunity for plasticity.

## 4.2 | Drought effects on litter decomposability

Hypothesis (3) was supported only for *Plantago* shoots, for which the shift to more conservative morphological traits was associated with a larger residual litter fraction A, indicating slowed decomposition. For *Lolium* roots, the residual litter fraction A was decreased, indicating faster decomposition, and in all other litter types decomposability was not affected by drought. On the whole, the drought effects on litter decomposability we observed were not very large given the magnitude of drought-induced trait

changes and there was no general relation to a shift in resource economic strategy.

Drought responses in morphological and chemical traits of *Plantago* shoots were not greater than for the other two species, which means that the drought effect on decomposability in *Plantago* shoots cannot be directly explained by the traits measured. An explanation could be that *Plantago* leaves were much larger than leaves of *Lolium* and *Trifolium*, so the decrease in SLA and LA could have led to a larger decrease in the total leaf surface area that can be accessed by microbes (Hanlon, 1981).

Drought decreased the residual litter fraction A for *Lolium* roots, which means that the initial slope of the mass loss trajectory was higher and the residual litter fraction was smaller. This is consistent with the drought response in chemical traits—drought increased senesced root NSC content and DMD and decreased lignin and cellulose content, indicating a larger labile and a smaller recalcitrant litter fraction. The drought effect on NSC and DMD was much larger in *Lolium* roots than in the other two species, which might explain why drought affected decomposition only in *Lolium* roots, especially as DMD has been shown to be a good predictor of decomposability (Bumb et al., 2018).

Litter decomposition was best described by an asymptotic exponential model rather than a single or double exponential model. Even though a non-decomposable litter fraction is unrealistic under field conditions, a good fit of this model has been found in other studies which also excluded larger decomposer organisms (Hobbie et al., 2010; Howard & Howard, 1974).

Our findings are consistent with results of the few available previous studies on intraspecific plant trait variability and decomposability, showing that morphological traits do not predict differences in litter decomposition within species well, even though they can be good predictors of differences between species (Carrillo et al., 2022; Jackson et al., 2013; Kazakou et al., 2009, 2019). Drought-induced increases in early stage root decomposability could be linked to increased N and P content, but drought effects on morphological root traits did not consistently alter decomposability in a study on four tree species (Carrillo et al., 2022). LDMC, SLA and leaf/litter C, N and P could not explain the considerable within-species variation in leaf litter decomposability in 16 temperate rain forest species from sites differing in soil nutrient status (Jackson et al., 2013). However, more detailed chemical litter traits were not measured in this study. Nitrogen addition induced phenotypic trait changes in herbaceous species in a French Mediterranean old-field succession, but these did not translate in changes in decomposition rates (Kazakou et al., 2009). Furthermore, decomposition rates between genotypes of *Arabidopsis thaliana* were strongly correlated with secondary metabolites, but only weakly with morphophysiological traits (Kazakou et al., 2019).

## 4.3 | Future work

There are some caveats to this study which suggest avenues for future research. In the framing of this study, the best solution to



producing sufficient amounts of litter was to let plants die by imposing an additional fatal drought at the end of the experiment. Even though the fatal drought was much shorter and more severe than the main experimental drought, this may have diminished the observed drought effect, as all plants may have had an additional plastic response. Consequently, drought effects might be larger for decomposition in real-world ecosystems. On the other hand, the plants in our study were relatively young and plasticity may decline in later growth stages (Westerband et al., 2021). Drought might also affect litter decomposition through other mechanisms than changes in litter quality, such as a changes in litter quantity, root:shoot ratio (Poorter et al., 2012), the soil physical environment and in the microbial community and its activity. Further studies are needed to better understand the full effects of drought on decomposition under field conditions. They could include litter from a larger number of species and possibly species mixtures, as studies have shown non-additive decomposition dynamics in mixed-species leaf litter decomposition (Handa et al., 2014). Based on the results of this study, further studies should include not only include morphological traits, but also chemical traits, especially NSC.

## 5 | CONCLUSIONS

Our results indicate that drought-induced plasticity of root and shoot traits can affect litter decomposability in some European temperate grassland species. Drought can alter the ratio between labile and recalcitrant litter fractions, possibly due to drought-induced accumulation of easily decomposable NSCs. These changes could affect ecosystem C storage and also amplify the commonly observed flush of microbial activity after rewetting soils following drought. However, drought had much stronger effects on root and shoot traits than on litter decomposability, generally shifting traits consistent with a more resource conservative strategy. Especially for morphological traits, drought effects on plant traits could be as strong as differences between species. Drought effects on decomposability were much weaker than differences between species and could not generally be explained by a shift in resource economic strategy. This suggests that litter decomposability is less affected by drought than might be assumed based on drought-induced plant trait plasticity.

## AUTHOR CONTRIBUTIONS

Laura Reinelt, Jeanette Whitaker, James Bullock and Nicholas J. Ostle designed the experiment. Laura Reinelt conducted the greenhouse experiment and laboratory work. Laura Reinelt and Laurent Bonnal conducted litter chemical analyses in consultation with Denis Bastianelli. Laura Reinelt conducted data analyses in consultation with Jeanette Whitaker, Elena Kazakou, James Bullock and Nicholas J. Ostle. Laura Reinelt wrote the manuscript with contributions from all co-authors.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.r2280gbhc>, (Reinelt et al., 2022).

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## SUPPORTING INFORMATION

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

### Figure S1.

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