



Évora, Portugal
13–16 April 2026

Challenges and innovations for grasslands resilience

Edited by

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Volume 31
Grassland Science in Europe

Drought tolerance and productivity in *Plantago lanceolata* cultivars under controlled conditions

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Abstract

In a mesocosm pot experiment, seven cultivars of *Plantago lanceolata* (ribwort plantain) were subjected to a drought stress with six replicates per cultivar. The experiment included two drought stress phases, each followed by a recovery phase. Four harvests were conducted: after the first drought phase, after the first recovery phase, after the second drought phase, and after the final recovery phase. A significant cultivar \times treatment \times harvest interaction was found for the dry matter yield ($F_{18,275} = 7.80$, $P < 0.0001$), indicating that cultivar responses to drought differed across harvests. On average, drought stress reduced total biomass yield by 26.7% across cultivars, with losses ranging from 3% in ‘Ecotain’ to over 45% in ‘Captain’. Stomatal conductance (g_s) decreased significantly under drought stress across cultivars ($P < 0.001$), indicating a clear physiological response to water limitation. These results reveal short-term resilience in *P. lanceolata* following moderate drought events.

Introduction

Climate change increasingly challenges forage production due to the rising frequency of drought events (Trnka *et al.*, 2014). To secure productivity in grassland systems, drought-tolerant species such as *P. lanceolata* (ribwort plantain) have gained attention as functional components in forage mixtures (Stewart, 1996; Lee *et al.*, 2015). Stomatal conductance (g_s) is widely recognized as a key physiological indicator of plant response to drought stress (Flexas *et al.*, 2004). Previous studies in crops such as maize and barley have demonstrated cultivar-specific physiological adaptations to drought, including differences in g_s (Li *et al.*, 2021; Lv *et al.*, 2023). The present study aimed to evaluate seven *P. lanceolata* cultivars, including two wild accessions, under drought and control conditions, focusing on productivity and g_s . We hypothesized that (1) cultivars differ in drought tolerance, and (2) stress responses are reflected in physiological adaptation in terms of g_s .

Materials and methods

A two-factorial mesocosm experiment considering the *P. lanceolata* cultivar and drought stress was conducted from September 2023 to December 2024 at the mesocosm station of the Hessen Department of Agricultural Affairs in Central Germany. A total of 84 mesocosms (25.2 cm diameter, 28 cm height, 14–18 kg soil per mesocosm) were used in a randomized complete block design with six replications. The used soil consisted of a silty sand (63.8% sand, 28.0% silt, 8.2% clay) with a pH of 7.3. Seven accessions of *P. lanceolata* were tested, including five commercial cultivars (‘Captain’, ‘Ceres Tonic’, ‘Diversity’, ‘Hercules’, ‘Ecotain’) and two wild accessions. Sowing took place on 12 September 2023, with 50 seeds per pot (equivalent to 1000 seeds m^{-2}) sown without pretreatment. No thinning was conducted, and approximately 20 plants per pot remained on average after winter. In early April 2024, each pot received 0.5 g N, 1.5 g P_2O_5 and 3.0 g K_2O (equivalent to approximately 100, 300 and 600 kg ha^{-1} , respectively). After the first three harvests, additional nitrogen was applied as urea

solution on 19 June, 23 August and 2 October 2024 (0.5 g, 1.0 g and 0.5 g per pot, respectively; = 400 kg N ha⁻¹ total seasonal input).

After successful overwintering, plants were harvested once on 8 May 2024 to 6 cm stubble height. Immediately after this harvest, drought stress was induced in the drought stress treatment by completely withholding irrigation, while control pots remained irrigated and were re-filled to their initial mesocosm weight. The first drought phase lasted for 36 days (9 May–14 June 2024), during which soil moisture declined by approximately 60%, and visible wilting occurred after about 14 days. After the drought phase, all pots were fertilized and fully irrigated to allow recovery. In total, four harvests were conducted: after the first drought, first recovery, second drought, and final recovery phases (December 2024). Plants were cut at 6 cm, separated into leaves and stems, and fresh and dry weights were recorded after drying at 60°C for 48 h to record the dry matter yield (DMY). Stomatal conductance (g_s) was measured weekly on six dates during the first drought stress period using a LI-600 (LI-Cor) with three readings per mesocosm. The mean g_s per mesocosm across dates was used for analysis. The statistical analyses were performed in R studio using linear mixed effects models with cultivar, treatment, and their interaction as fixed and block as random effects. Model formulae were: $DMY \sim \text{cultivar} \times \text{treatment} \times \text{harvest} + (1 | \text{block})$ and $g_s \sim \text{cultivar} \times \text{treatment} + (1 | \text{block})$. Comparisons of means were performed post hoc using Tukey's HSD method. To complement significance testing, compact effect sizes are reported as percent DMY change between drought and control per cultivar across harvests

Results and discussion

We detected a significant three-way interaction (cultivar \times treatment \times harvest; $F_{18,275} = 7.80$, $P < 0.0001$) for the DMY. This indicates that cultivar responses to drought depended on the harvest (i.e., response patterns varied across the four harvest dates). Percent DMY change between drought and control per cultivar across harvests ranged between -45.7% for 'Captain' and -3.0% for 'Ecotain' (Table 1). These percentage changes summarise the practical magnitude of cultivar responses. The drought treatment had a significant main effect on g_s ($F_{1,50} = 20.68$, $P < 0.001$), with mean g_s decreasing by approximately 18% under drought conditions compared to the control. No significant cultivar \times treatment interaction was observed for g_s , indicating that cultivars responded similarly to drought stress in terms of stomatal regulation although considerable variation was found when comparing means for this interaction (Table 1).

On average, cultivars with significant reductions showed a 19% decline in g_s , while stable cultivars decreased by only 4% (Table 1). This finding indicates some variation in stomatal behaviour among cultivars, although the overall response to drought was consistent. The g_s aligns with the Ball–Berry model, where reduced g_s under drought reflects decreased photosynthesis (Ball *et al.*, 1987). Cultivars with more flexible g_s control may better balance CO₂ uptake and water conservation (Flexas *et al.*, 2004). Although absolute g_s values varied slightly among cultivars, their relative response to drought was consistent. However, in some cultivars g_s did not decline under drought which points to genotypic variability in physiological drought-stress adaptation.

These findings support our hypothesis of cultivar-specific reactions to drought stress and highlight better-performing cultivars such as 'Ecotain' and 'Hercules'. However, differences among cultivars were not linked to g_s and may be related to other physiological or morphological adaptations, such as root allocation, which requires further studies. The wild accessions exhibited lower DMY, likely due to genetic background and lack of breeding selection.

Table 1. Total dry matter yield (DMY, g mesocosm⁻¹ ±SE) and mean stomatal conductance (g_s , mol m⁻² s⁻¹ mean ±SE) of seven *Plantago lanceolata* cultivars under control and drought stress conditions.

| Cultivar | Treatment | Total DMY | g_s |
|-------------|----------------|---------------|----------------|
| Captain | Control | 9.4 ± 0.3 Aab | 0.29 ± 0.02 aB |
| | Drought stress | 5.1 ± 0.2 Bbc | 0.22 ± 0.02 aA |
| Ceres Tonic | Control | 8.7 ± 0.2 Aab | 0.33 ± 0.02 aB |
| | Drought stress | 5.0 ± 0.2 Bbc | 0.27 ± 0.02 aA |
| Diversity | Control | 9.1 ± 0.3 Aab | 0.29 ± 0.02 aB |
| | Drought stress | 5.2 ± 0.3 Bbc | 0.23 ± 0.02 aA |
| Ecotain | Control | 10.0 ± 0.2 Aa | 0.29 ± 0.02 aA |
| | Drought stress | 9.7 ± 0.3 Aa | 0.26 ± 0.02 aA |
| Hercules | Control | 6.5 ± 0.3 Abc | 0.29 ± 0.02 aA |
| | Drought stress | 6.1 ± 0.2 Ab | 0.28 ± 0.02 aA |
| Wildtype 1 | Control | 5.7 ± 0.2 Ac | 0.31 ± 0.02 aB |
| | Drought stress | 4.8 ± 0.2 Bbc | 0.26 ± 0.02 aA |
| Wildtype 2 | Control | 5.9 ± 0.2 Ac | 0.27 ± 0.02 aA |
| | Drought stress | 4.2 ± 0.2 Bbc | 0.26 ± 0.02 aA |

Different lowercase letters indicate cultivar differences within a treatment; uppercase letters indicate treatment differences within a cultivar (Tukey's HSD, $P < 0.05$).

Conclusion

This study confirms significant cultivar-specific variation in drought tolerance among *P. lanceolata* cultivars, with cultivars like 'Ecotain' maintaining physiological integrity and productivity under water stress. The results indicate potential to use drought-tolerant *P. lanceolata* cultivars in climate-resilient forage systems.

Acknowledgements

The project was supported by funds from the Federal Ministry of Agriculture, Food and Regional Identity (BMLEH) based on a decision of the Parliament of the Federal Republic of Germany via the Federal Office for Agriculture and Food (BLE) under the Innovation Support Programme (FKZ: 281C702A21). We thank Ralph Dittmann for major support in sampling.

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