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Nitrogen status of functionally different forage species explains resistance to severe drought and post-drought overcompensation

Daniel Hofer[a,b], Matthias Suter[a], Nina Buchmann[b], Andreas Lüscher[a,*]

[a] Agroscope, Institute for Sustainability Sciences ISS, Reckenholzstrasse 191, CH-8046 Zürich, Switzerland
[b] ETH Zürich, Institute of Agricultural Sciences, Universitätstrasse 2, CH-8092 Zürich, Switzerland

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ABSTRACT

Forage species of intensively managed temperate grassland differ substantially in their drought responses. We investigated whether differences in resistance and resilience, based on biomass yield, are related to species nitrogen (N) acquisition and drought-induced N deficiency.

A three-factorial field experiment was established with monocultures of four species (first factor) that differed in functional traits regarding N acquisition and rooting depth: *Lolium perenne* L. (shallow-rooted non-legume), *Cichorium intybus* L. (deep-rooted non-legume), *Trifolium repens* L. (shallow-rooted legume), and *Trifolium pratense* L. (deep-rooted legume). A ten-week summer drought was simulated (second factor) and compared to a rainfed control during two regrowths under drought and one regrowth during a subsequent six-week post-drought period. The distribution of applied fertiliser N (200 kg ha^{-1} $year^{-1}$ in total) was manipulated (third factor) with plots receiving no N during drought or 60 kg N ha^{-1}.

Soil water availability during drought became increasingly restricted over time. Plant-available soil N was reduced up to 4- and 12-fold during the first and second regrowths under drought, respectively, but was increased up to 4-fold during the post-drought regrowth, compared to rainfed control conditions. Legumes were consistently less N-limited than non-legumes ($P < 0.001$). Nitrogen derived from the atmosphere (Ndfa) in the legume *T. repens* was 72% under severe drought (first regrowth under drought). Here, legumes were rather drought-resistant (biomass yield under drought was −22% compared to the rainfed control), while non-legumes were not (−41%). Further, N fertilisation mitigated the negative drought effect on biomass yield of non-legumes from −41% (no N under drought) to 23% (N under drought). Under extreme drought (second regrowth under drought), all species were strongly impaired, irrespective of N fertilisation (−75% on average); yet, Ndfa in *T. repens* was still 56%. During the post-drought regrowth, former drought-stressed non-legumes overcompensated and revealed +53% higher yield than the control.

The interspecific differences in plant species responses to drought suggest a shift from N limitation under severe drought to water limitation under extreme drought. Because legumes were able to compensate for drought-induced restrictions in yield through symbiotic N_2 fixation, and non-legumes overcompensated during post-drought, cropping selected legumes in mixtures with non-legumes could improve resistance and resilience of forage swards against severe drought events.

1. Introduction

Drought events are projected to increase in frequency and severity in many regions worldwide due to climate change (Seneviratne et al., 2012; Trenberth et al., 2014). Droughts are expected to threaten widespread, grassland-based livestock farming by impairing forage production (Olesen et al., 2011), especially where biomass yield is currently high (Wang et al., 2007). Most studies to date have found that drought events reduce forage yields in extensively (e.g. Grant et al., 2014; Hoover et al., 2014), as well as intensively managed grassland (e.g. Zwicke et al., 2013; Hofer et al., 2016). However, the degree of drought impairment differs substantially depending on management type (Deléglise et al., 2015) and intensity (Gilgen and Buchmann, 2009), cutting frequency (Vogel et al., 2012), species richness (Isbell et al., 2015), and species identity (Hofer et al., 2016).

* Corresponding author at: Reckenholzstrasse 191, 8046 Zürich, Switzerland.
E-mail addresses: matthias.suter@agroscope.admin.ch (M. Suter), nina.buchmann@usys.ethz.ch (N. Buchmann), andreas.luescher@agroscope.admin.ch (A. Lüscher).

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Drought induces not only pure water stress but can severely constrain the availability of soil nutrients, particularly soil nitrogen (N) by restricting mineral N fluxes (Cassman and Munns, 1980; Durand et al., 2010). Indeed, soil N uptake by forage species was found to be reduced due to drought (Dijkstra et al., 2015; Hoekstra et al., 2015). However, it remains open whether plant N uptake is reduced due to drought-induced N limitation in the soil or due to low N demand of the plants resulting from growth limitation in response to water scarcity. Because legumes do not depend solely on soil N (due to their benefit from symbiotic dinitrogen (N_2) fixation; Hartwig, 1998), they may increasingly rely on N_2 fixation with an increasing limitation of soil N availability under drought. Cropping forage legumes in grassland mixtures could thus promote drought resistance in biomass yield (resistance defined as the degree of impairment during a drought event; Pimm, 1984). The longer N_2 fixation is maintained under persisting drought, the longer legumes could continue to produce biomass. Drought resistance in legumes may therefore depend on whether water or N is the primary limiting resource.

Cropping deep-rooted species that reach deeper and moist soil layers have been suggested as a drought mitigation option in temperate grassland (e.g. Kemp and Culvenor, 1994; Skinner et al., 2004). Although the main uptake of soil water and nutrients in drought-stressed, intensively managed grassland occurs within the most superficial soil layer down to 30 cm (Hoekstra et al., 2014, 2015; Prechsl et al., 2015), forage species could increase resource uptake by short-term root growth in the course of the drought event, as indicated by increased root biomass (Dreesen et al., 2012) or higher proportion of root biomass at deeper soil layers under drought conditions (Wedderburn et al., 2010). While such evidence comes mainly from rhizotrons or container experiments, root growth data from forage species in the field is rare (but see Prechsl et al., 2015).

Fertiliser application by farmers is a common strategy to counteract nutrient deficiency in managed grassland (Bélanger et al., 1992). Nitrogen fertilisation could therefore also help to overcome drought enhanced N limitation, although the growth response to N fertiliser might decline with decreasing soil moisture (Colman and Lazenby, 1975). In a multisite field experiment, we recently found drought-stressed forage species to be significantly impaired despite of N fertilisation. However, species were highly resilient after the drought event, and formerly drought-stressed non-legumes even overcompensated by producing more above-ground biomass than the non-stressed controls (Hofer et al., 2016). The underlying cause of such overcompensation remains unknown. Measuring plant-available mineral N in the soil during drought and post-drought periods could reveal to which degree soil and fertiliser N is accessible to plants and whether N resources not taken up during drought would become plant-available during the post-drought period given adequate water supply.

Understanding the drought response of high-yielding and functionally different forage species can promote the development of farming options to adapt forage production to future climate conditions. To this aim, we simulated a ten-week summer drought event on monocultures of four key species of intensively managed temperate grassland, which differ in their functional traits regarding N acquisition and rooting depth. The species' biomass response was examined under increasing drought severity during the course of a ten-week drought period and a subsequent six-week post-drought period with ample water supply. We were primarily interested in the interacting effects of water scarcity and soil N availability on plant N status and biomass yield. We also investigated whether drought-induced N deficiency could be overcome by symbiotic N_2 fixation of legumes or additional N fertilisation of non-legumes, and whether species' root growth could increase resource acquisition. We are aware that drought may also limit C assimilation through stomatal closure (Bollig and Feller, 2014); however, here, we focus on the feedback effect of water stress on N availability in the soil and its significance for the plants responses to drought. The following hypotheses were addressed:

i Resistance of forage species' biomass to drought depends on their functional traits to overcome various degrees of soil water and N limitation.
ii Symbiotic N_2 fixation in legumes promotes drought resistance by preventing plant N limitation.
iii Nitrogen fertiliser application during drought increases drought resistance, especially in non-legumes, and/or contributes to a legacy effect to the post-drought regrowth, leading to increased resilience.
iv Increased root growth especially at deeper soil layers improves drought resistance, particularly for deep-rooted species.

2. Material and methods

2.1. Site conditions and experimental setup

The field experiment was carried out in the North-East of Switzerland at Zürich-Reckenholz (47° 26′ 12″ N, 8° 31′ 51″ E, 479 m a.s.l.). The soil at the site is classified as brown earth, with a top soil composition of 32% sand, 42% silt, 26% clay, containing 2.8% humus, 46 mg kg^{-1} phosphorus (P), 125 mg kg^{-1} potassium, 185 mg kg^{-1} magnesium, and with a pH of 6.9. Experimental plots were established in August 2011, and data presented here refer to 2013, the second year after sowing. In 2013, mean annual temperature was 9.4 °C and annual precipitation was 1068 mm.

A three-factorial experiment was carried out. Monocultures of four key forage species of intensively managed temperate grassland widely used in ruminant production were selected for investigation (first factor). Species differed in their N acquisition (non-N_2-fixing for non-legumes and N_2 fixing for legumes) and rooting depth: *Lolium perenne* L. (shallow-rooted non-legume, cultivar (cv.) Alligator), *Cichorium intybus* L. (deep-rooted non-legume, cv. Puna II), *Trifolium repens* L. (shallow-rooted legume, cv. Hebe), and *Trifolium pratense* L. (deep-rooted legume, cv. Dafila). Species were sown into plots of 5 m × 3 m and two further treatments were established: precipitation was manipulated, consisting of sheltered and rainfed control plots (second factor), and N fertiliser was varied, consisting of plots that were N fertilised during drought, and plots not fertilised during the drought period (third factor; see Section 2.2 for details on the treatments). All plots that received N during drought were replicated three times, while plots that received no N during drought were replicated twice. This resulted in a total of 40 plots that were arranged in an incomplete block design.

2.2. Drought and N fertilisation treatments

An extraordinarily strong summer drought event with complete rain exclusion was simulated for ten weeks from June 5th to August 14th (see Table B.1., Appendix B in Supplementary file). Precipitation was excluded by placing rainout shelters (5.5 m × 3 m) on the plots of the drought treatment, which were covered by a transparent, ultraviolet light-transmissible plastic foil (Gewächshausfolie UV5, 200 μm, Folitec Agrarfolien-Vertrieb, Germany) (see Hofer et al., 2016 for technical details of rainout shelters). The drought treatment excluded 184 mm of precipitation, which resulted in a simulated summer precipitation of 220 mm during June, July, August (see Table B.2. and Fig. B.1., Appendix B in Supplementary file, for further climatic data related to the