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in

Baumont R. (ed.), Carrère P. (ed.), Jouven M. (ed.), Lombardi G. (ed.), López-Francos A. (ed.), Martin B. (ed.), Peeters A. (ed.), Porqueddu C. (ed.).
Forage resources and ecosystem services provided by Mountain and Mediterranean grasslands and rangelands

Zaragoza : CIHEAM / INRA / FAO / VetAgro Sup Clermont-Ferrand / Montpellier SupAgro
Options Méditerranéennes : Série A. Séminaires Méditerranéens; n. 109

2014
pages 489-493

Effects of extreme drought on grasslands
Evaluation of the buffering effect of plant diversity using an experimental approach

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Abstract. The frequency and magnitude of extreme drought events are expected to increase with climate change. Consequently, it is important to assess the ability of temperate grassland to resist and recover from more frequent and intense drought stress. To study this topic, we established a mesocosm experiment in autumn 2012: large pots (100 L) containing combinations of grassland species (1, 2 or 5 species) were placed on weighing scales to continuously measure the actual evapotranspiration of the plant canopy. Species selected (four grasses and one legume) were representative of temperate upland grasslands on fertile soils. An extreme summer drought was applied to half the pots and plant recovery following rewetting was monitored. Total biomass and evapotranspiration were analyzed to test the effects of species diversity on the resistance and recovery of grasslands to extreme drought. As expected, drought dramatically reduced by 79% biomass of all mixtures. The 5 species mixtures showed higher drought avoidance by maintaining integrated water-use efficiency and took up water at deeper soil layers than the less diverse mixtures during drought. These findings indicated that buffering effect of diversity during drought occurs for the 5-species mixtures, possibly due to below-ground niche differentiation. This study emphasizes the high capacity of grass species mixtures to recover after an extreme drought.

Keywords. Drought – Resistance – Resilience – Plant diversity – Functional complementarity.

Effet d'une sécheresse extrême sur l'écosystème prairial : évaluation du rôle tampon de la diversité végétale par approche expérimentale

Résumé. *Avec le changement climatique la fréquence et l'ampleur des phénomènes extrêmes de type sécheresse devraient augmenter. Dans ces conditions, il est important d'évaluer la capacité des prairies de moyenne montagne à résister et à récupérer de stress plus fréquents et plus intenses. Une expérience en mésocosmes a donc été mise en place à l'automne 2012 : de grands pots (100 L) contenant des cultures d'espèces prairiales (1, 2 ou 5 espèces) ont été placés sur des balances permettant de mesurer en continu l'évapotranspiration réelle du couvert végétal. Les espèces sélectionnées (quatre graminées et une légumineuse) sont représentatives des prairies permanentes fertiles de moyenne montagne. Une sécheresse extrême estivale a été simulée sur la moitié des pots, puis les cultures ont été réhydratées pour suivre leur capacité de récupération. La biomasse totale et l'évapotranspiration ont été analysées pour tester les effets de la diversité en espèces sur la résistance et la récupération des prairies à une sécheresse extrême. Comme attendu, la sécheresse a considérablement affecté tous les mélanges avec une réduction de biomasse de 79%. Pendant la période de sécheresse les mélanges à 5 espèces montrent un évitement plus marqué que les mélanges moins diversifiés notamment avec un maintien de leur efficience d'utilisation de l'eau et un prélèvement de l'eau dans des couches plus profondes du sol. Ces résultats indiquent que l'effet tampon de la diversité lors de la sécheresse apparaît pour les mélanges 5 espèces, probablement en raison de la différenciation de niches au niveau souterrain. Cette étude souligne la grande capacité de récupération des mélanges d'espèces prairiales après un évènement de sécheresse extrême.*

Mots-clés. *Sécheresse – Résistance – Résilience – Diversité – Complémentarité fonctionnelle.*

I – Introduction

The frequency and magnitude of extreme drought events are expected to increase with climate change. Beyond a certain threshold, these extreme events can alter the resistance and resilience of grasslands, modifying grassland productivity and/or forage quality. However, the ability of grassland communities to resist and recover from more frequent and intense drought stress events remains unclear. According to the insurance hypothesis (Yachi and Loreau, 1999), diversity promotes resistance and resilience to stress, and this effect should be maintained under climate change (Vogel *et al*., 2012). In the present experiment, we assess the buffering effects of species diversity on the resistance and recovery of grasslands to extreme drought, and examine the mechanisms involved (between-plant facilitation or complementarity).

II – Materials and methods

The mesocosm experiment was established in autumn 2012. Large cylindrical pots (100 L, 93 cm deep and 37.5 cm diameter) were filled with grassland soil and equipped with soil water content sensors (ECHO-5, Decagon, USA) at three depths (15, 30, 50 cm). Monocultures, binary and five-species mixtures were established by planting mature plants in autumn. Species selected were representative of temperate fertile upland grasslands: *Dactylis glomerata*, *Festuca arundinacea*, *Poa pratensis*, *Trisetum flavescens* and *Trifolium repens*. Five types of monocultures, ten types of binary and one mixture of five species were established, each pot initially containing 30 individuals with an equal proportion between species in mixtures. In spring of the following year, the pots were placed on weighing scales to continuously measure the evapotranspiration of the plant canopy. In total, 96 pots were set up: two treatments (control and drought) and six replicates by type of mixture. Following mesocosm establishment, all pots were maintained at 80% of the field capacity by watering or rainfall for eight months. In June 2013, an extreme summer drought lasting two months was applied to half of the pots (3 pots by type of mixture). This extreme event was simulated by a total rainfall interception from mid-June to mid-August (Fig. 1). The remaining pots (control treatment) were irrigated to maintain soil water content at 80% of field capacity for the duration of the experiment. Mesocosms were managed by cutting to 5 cm at five dates from April to October (Fig. 1). During the drought (July cutting date), only the control pots were cut. All biomass samples were oven-dried (48 h, 60°C) and weighed.

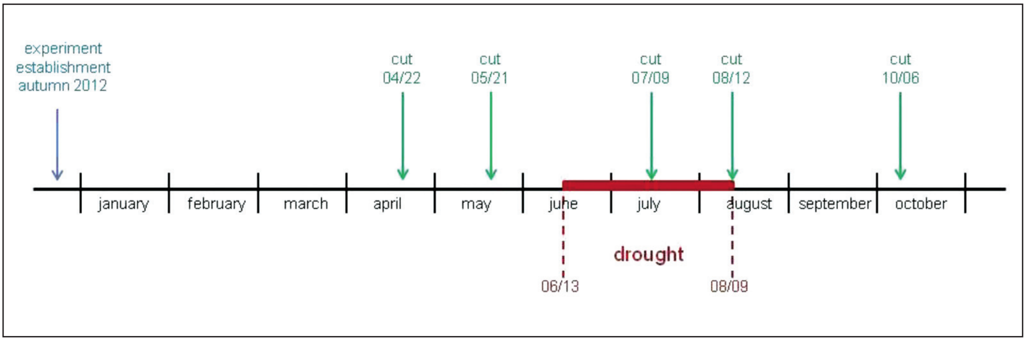

Fig. 1. Time course of the experiment. Red bar corresponds to period of drought.

Cutting dates were used to define three major periods of vegetation biomass production (g m^{-2}) during the experiment: before the drought (between 04/22 and 05/21), during the drought (between 05/21 and 08/12) and after the drought (between 08/12 and 10/06). Integrated water-use efficiency (WUE, g kg^{-1}) was calculated as the ratio of biomass to cumulative evapotranspiration for each period. Data on biomass production, evapotranspiration, WUE and soil moisture were used to assess the resistance and recovery of the different mixtures to a severe drought, and to study the potential buffer role of plant diversity. Statistical analyses were performed using mixed effect models with the software R (R Development Core Team, 2009).

III – Results and discussion

Before drought, biomass and WUE were similar for 1, 2 and 5 species mixtures (Fig. 2a). As expected, biomass produced during the drought was significantly lower in the drought treatment compared with the control (average -79%). Diversity treatments had no significant effect on biomass production during drought (Fig. 2b).

Unlike biomass, WUE showed a significant drought x diversity interaction, with smaller drought-induced decreases in WUE in the 5-species mixture (Fig. 2f). This result could indicate a greater resistance to drought for 5-species mixtures in terms of WUE, and is consistent with the idea of a buffering effect at high species diversity.

In the control treatment, 5-species mixtures had lower soil moisture values at 15 cm (P1) soil depth throughout the experiment compared with the 1 and 2 diversity levels (Fig. 3). But during the drought, the largest decrease of soil moisture was observed at 30 cm (P2) and 50 cm (P3) for the 5 species mixture (Fig. 3.c). In case of less diverse mixtures, this decrease was more important at P1 and P2 (Fig. 3.a, 3.b). These findings indicate that the more diverse mixture took up water deeper, suggesting the presence of deeper active roots in diverse mixtures. Higher competition for water in the shallow soil in diverse mixtures could have promoted a differentiation in root depth between species. Mechanisms of complementarity by niche differentiation could involve better resource partitioning and increased water use efficiency, resulting in higher drought resistance for high diversity mixtures (Cardinale *et al*., 2007; Verheyen *et al*., 2008).

During the recovery period after drought, biomass and WUE of droughted-mixtures reached the same levels as the control (Fig. 2c, 2g), which highlights a strong and fast capacity of recovery in terms of biomass production and WUE. However, diversity treatments had no significant effect on biomass production or WUE during the recovery period.

The belowground species complementarity seems to appear for high levels of diversity (5 species) and could involve a better resistance to stress. However for the 5 species mixtures we observed a decrease of species richness to 3 or 4 species during the recovery period due to species mortality (low or absence of recovery for *Festuca arundinacea* and *Trifolium repens*). The observation of a positive diversity effect at the community level for the 5 species mixtures should be mitigated by this mortality observed at the species level.

IV – Conclusions

Our experiment shows that a buffering effect of species diversity during drought occurs for WUE of the 5-species mixtures, possibly due to below-ground niche differentiation. However this effect was transitory as it disappeared during the recovery period. Finally our results highlighted the high capacity of grass mixtures to recover after an extreme drought, although some species like *Festuca arundinacea* or *Trifolium repens* did not. Further analyses will explore differential specific response of the mixtures to drought and after rehydration.

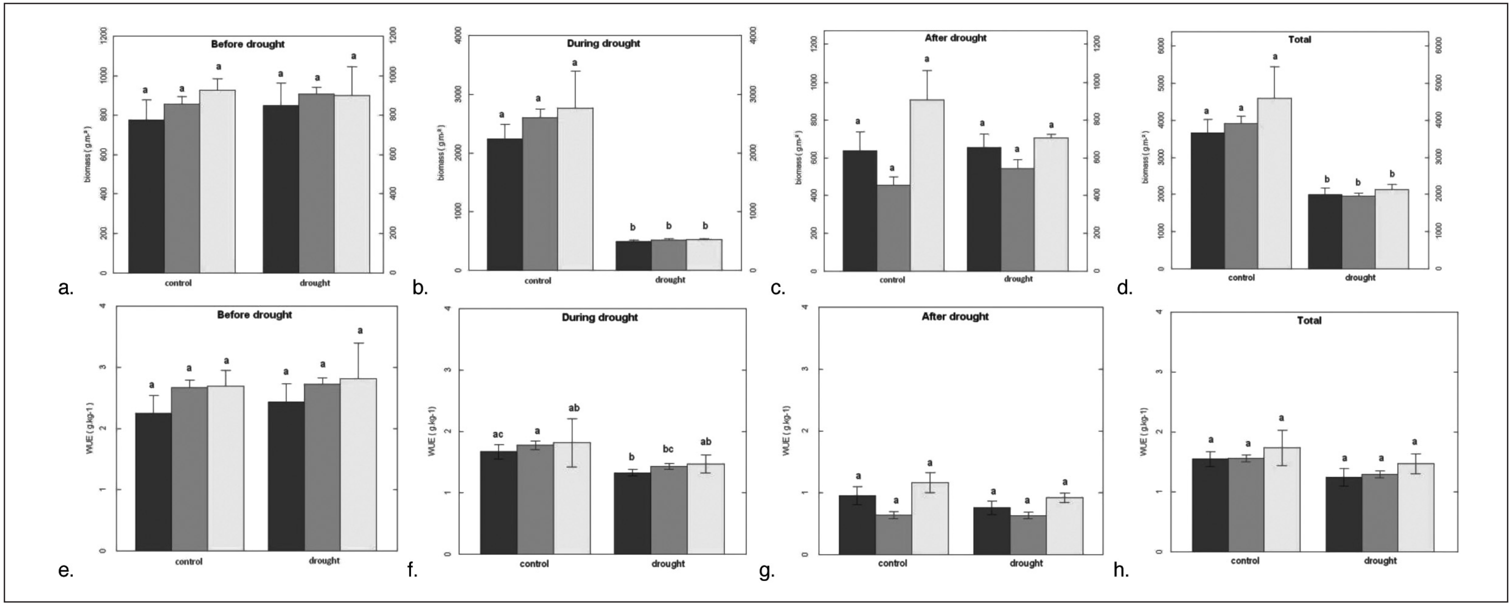

Fig. 2. Biomass (a),(b),(c),(d) and WUE (e),(f),(g),(h) of the three diversity levels: monocultures in black, binary in dark grey, and mixtures of 5 species in light grey. Means ± standard errors are shown. Letters represent the post-hoc Tukey tests performed after ANOVA.

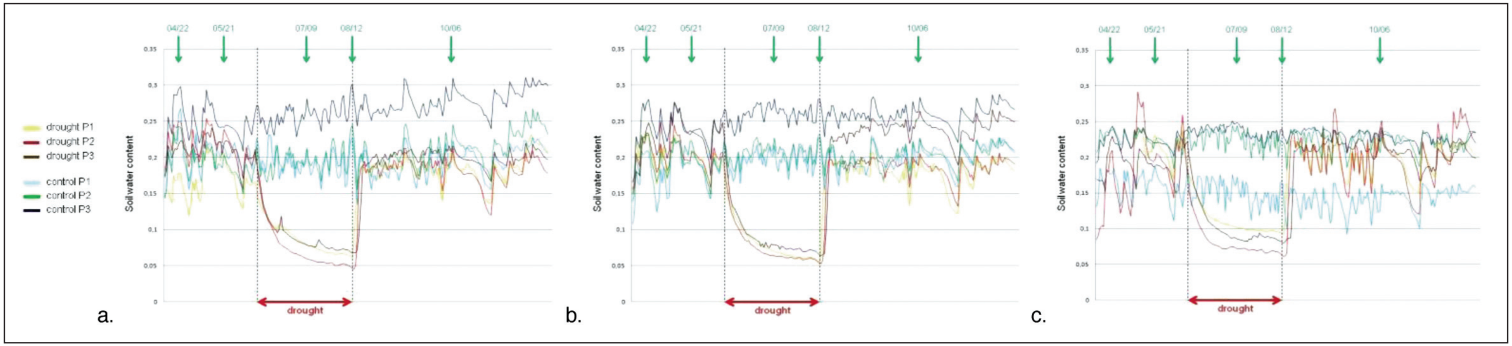

Fig. 3. Time course of soil water content for monocultures (a), binary (b) and 5 species mixtures (c), measured at three depths (P1: 15 cm; P2: 30 cm; P3: 50 cm). Green arrows correspond to cut dates.

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