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Short communication

Greater gains in annual yields from increased plant diversity than losses from experimental drought in two temperate grasslands

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ABSTRACT

Climate change is predicted to result in more severe weather events, including drought, which will affect forage production in agricultural grasslands. We evaluated the effects of an experimentally imposed drought on yields of monocultures and mixtures of intensively managed grassland communities comprising four species with contrasting functional traits (*Lolium perenne* L., *Cichorium intybus* L., *Trifolium repens* L., *Trifolium pratense* L.). Complete exclusion of precipitation was implemented in a common field experiment at two sites, resulting in an experimental drought at Wexford (Ireland) and Zürich (Switzerland). In the individual harvest at the end of the drought event, very strong yield reductions (up to −87%) occurred across all communities. In contrast, drought effects on annual yields of averaged monocultures and the equi-proportional four-species mixture were only −9% and −12%, respectively. These losses were much smaller than the yield advantage due to mixtures, which were 31% under drought and 34% under rainfed conditions. The large effect of mixtures on annual yield is attributed to complementarity among species with contrasting functional traits, and to mixture effects being active over the whole growing season and under drought. We attribute these relatively small drought effects on annual yield to the immediate recovery in harvest yields when soil water supply increased after the drought (resilience), the buffering effect of soil water at the beginning of rain exclusion, and the relatively long growing season that diluted the short-term effect of the drought event.

1. Introduction

Climate change is predicted to result in increased climate variability (Orlowsky and Seneviratne, 2012). The combined effects of increased variability in precipitation and the amount of precipitation per event (e.g. prolonged periods of drought or waterlogging) can result in reduced yields in grassland systems (Swemmer et al., 2007; Hofer et al., 2016; Volaire et al., 2014). Results from natural events and manipulation experiments show that plant diversity can improve the resistance and/or resilience of extensively managed grasslands to drought (e.g. Van Ruijven and Berendse, 2010; Vogel et al., 2012; Volaire et al., 2014; Isbell et al., 2015). Drought effects on yield can depend on environmental conditions that include the intensity of agricultural management (Gilgen and Buchmann, 2009; Vogel et al., 2012; Zwicke et al., 2013) as well as pre-drought conditions and soil type (especially soil moisture retention properties, e.g. Hofer et al., 2016).

In intensively managed grasslands, there is strong evidence for yield advantages of multi-species mixtures that may even be sufficiently strong to out-yield the best-performing monoculture (Nyfeler et al., 2009; Finn et al., 2013). Surprisingly, there have been remarkably few experimental investigations of whether the use of multi-species mixtures in intensively managed grasslands is an effective option to reduce the impact of drought on yield (resistance), and/or to enhance the recovery of affected grasslands (resilience) (but see Hofer et al., 2016). Intensively managed grasslands are widely distributed and economically important, but typically have a small number of more productive species and are potentially more prone to environmental disturbances. For example, drought events can impose greater economic losses on intensively managed compared to less intensively or extensively managed grassland (Finger et al., 2013).

We previously showed strong short-term effects of drought on yields in one year of investigation in intensively managed grasslands; yet, there was no influence of plant diversity on resistance to drought (Hofer et al., 2016). Annual yield is also important, however, and there is significant practical importance attached to the effect of severe weather events on annual yield. For example, farm-scale decision-making about

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appropriate adaptation strategies to maintain forage supply will be determined by factors that include the duration of drought effects on individual harvests, and the aggregate effect on annual yields. Here, we build on our previous work on effects of drought on individual regrowth periods in one year (Hofer et al., 2016); we include two years of investigation in the present study, directly address knowledge gaps about the persistence of drought impacts on yields in intensively managed grasslands, and scale up to aggregated effects across harvests and years. For example, although drought can impact on short-term yields during the drought period itself, what is the aggregate effect on the annual yield of biomass? What is the aggregate effect over consecutive years? Such knowledge is crucial to inform the choice of mitigation and adaptation strategies to maintain security of supply of forage from intensively managed grasslands. As part of a plot-scale manipulation experiment, we investigated the following research questions:

1. What is the effect of simulated drought on individual harvests and how does it translate into the annual yields of monocultures and mixtures of grassland species?
2. What is the effect of simulated drought on the yield benefits from mixing plant species during individual harvests and over the whole year, and how does it compare to the size of drought effects on yield?

2. Materials and methods

A common field experiment to manipulate precipitation was established at two sites. Sites were located near Zürich in Switzerland and at Wexford in Ireland. We selected the following commercially available cultivars (cv.) of four commonly used forage species based on the factorial combination of their functional traits related to rooting depth and nitrogen (N) acquisition: a shallow-rooted non-legume (*Lolium perenne* L., cv. Alligator), a deep-rooted non-legume (*Cichorium intybus* L., cv. Puna II), a shallow-rooted legume (*Trifolium repens* L., cv. Hebe), and a deep-rooted legume (*Trifolium pratense* L., cv. Dafila). Using these four species, plots (5 m × 3 m) were established in monocultures and mixtures that were sown with systematically varying proportions of the four species: six binary combinations (50% of each of two species), an equi-proportional mixture (25% of each of the four species), and four-species mixtures dominated by each species in turn (79% of one species, 7% of the other three). There were three replicates of each monoculture species and the equi-proportional four-species mixture, and two replicates of all other mixtures. At each site, a total of 35 main-plots were arranged according to a randomised incomplete block design. Each main-plot was split into two sub-plots, to which the two treatments (rainfed and sheltered) were randomly allocated. Thus, each plant community (used to denote monocultures and mixtures) was grown under rainfed conditions (control treatment) and under a drought treatment, in which a summer drought event of nine weeks was implemented at both sites using rainout shelters. The annual yields comprised five harvests at Wexford and six harvests at Reckenholz; there were generally two regrowth periods during the drought treatment, and one post-drought harvest. All plots of a site received the same amount of mineral N fertiliser: 130 kg N ha^{-1} $year^{-1}$ (year 1) and 150 kg N ha^{-1} $year^{-1}$ (year 2) at Wexford and 200 kg N ha^{-1} $year^{-1}$ in both years at Zürich. Soil moisture content was measured weekly at 10 cm and 40 cm soil depth at Wexford and was measured hourly at 5 cm and 40 cm soil depth at Zürich (see Hofer et al., 2016 for full details). After two years, all four species were present in four-species mixtures (Fig. A.1, Appendix A in Supplementary file), although *T. repens* in Zürich comprised only 1%. More importantly, the summed proportions of legume and non-legume species were more than 14% for each group at both sites and under rainfed control and drought treatments, suggesting a sustained potential for significant interactions between legume and non-legume species.

2.1. Data analyses

Drought effects on annual yields, overyielding of mixtures, and the seasonal trajectory of yield were analysed using a regression-based approach following Kirwan et al. (2009). Annual dry matter yield (DMY) of each community was regressed on the proportional contributions of the four species and the drought treatment, as follows:

$$\begin{aligned} \text{DMY} = {} & \beta_1 P_{\text{Lp}} + \beta_2 P_{\text{Ci}} + \beta_3 P_{\text{Tr}} + \beta_4 P_{\text{Tp}} + \delta D_{\text{AVE}} + \gamma_1 P_{\text{Lp}}\text{Drt\_Treat} \\ & + \gamma_2 P_{\text{Ci}}\text{Drt\_Treat} + \gamma_3 P_{\text{Tr}}\text{Drt\_Treat} + \gamma_4 P_{\text{Tp}}\text{Drt\_Treat} \\ & + \gamma_5 D_{\text{AVE}}\text{Drt\_Treat} + \varepsilon \end{aligned} \quad (1)$$

where P represents the sown species proportions (Lp = L. perenne, Ci = C. intybus, Tr = T. repens, Tp = T. pratense) in a community for the analysis of DMY in experimental year 1. In year 2, the observed species proportions of the first experimental year were used as regression predictor. The identity effect of each species is thus estimated by β_1 to β_4, and, if P = 1, β coefficients estimate DMY of a species grown in monoculture. D_{Ave} is related to the average diversity effect calculated from the sum of all pairwise interactions of species:

$$D_{\text{Ave}} = P_{\text{Lp}}P_{\text{Ci}} + P_{\text{Lp}}P_{\text{Tr}} + P_{\text{Lp}}P_{\text{Tp}} + P_{\text{Ci}}P_{\text{Tr}} + P_{\text{Ci}}P_{\text{Tp}} + P_{\text{Tr}}P_{\text{Tp}} \quad (2)$$

The δ coefficient therefore estimates the strength of the average diversity effect (i.e. net interaction) from all pairwise species interactions. Notably, overyielding (mixture yield greater than the weighted average yield of the monocultures) can be directly derived from the δ coefficient. The effect of the drought treatment (Drt_Treat: factor with two levels: 0 for control, 1 for drought) on the species' identity effects is estimated by coefficients γ_1 to γ_4, while the interaction of the drought treatment with the diversity effect is estimated by γ_5 (see Kirwan et al. (2009) for full details of the regression approach). To account for the split-plot structure of the design, Eq. (1) was extended to a linear mixed model (Pinheiro & Bates 2000) by specifying each pair of rainfed control and drought sub-plots as a random unit (modelled as random intercept). The error ε is assumed to be normally distributed with zero mean and variance σ^2. Eq. (1) was applied to annual yield at each of two experimental sites and years. The R^2 of observed *versus* predicted values from these models ranged between 0.81 and 0.98, suggesting that yield predictions based on Eq. (1) were highly reliable (see Fig. A.2). To assess the seasonal trajectory of yield, drought effects, and overyielding at individual harvests, Eq. (1) was extended to a model where all parameters were estimated for each individual harvest (see Appendix A in Supplementary file for the regression equation). We generally compared the modelled estimates of the effect of drought on annual yield for the monocultures and the equi-proportional four-species mixture (as a reference mixture). All inference on specific contrasts related to our research questions was derived from the regression models.

3. Results

At both sites and years, and at both soil depths, soil moisture content levels were lower under the drought than under the rainfed control treatment and were generally smaller than the threshold of plant-available soil water at −1.5 MPa for more than half of the drought period, indicating severe water deficits for plants (Table A.1, Appendix A in Supplementary file). Consequently, in the individual harvest at the end of the drought event, across sites and years, monocultures had drought-induced yield reductions of −67%, while the equi-proportional four-species mixtures had yield reductions of −65% (Figs. 1 and 2). Despite these strong yield impairments at the end of drought, across sites and years, the average effect of drought on annual yields of monocultures and the four-species mixture was only −9% and −12% respectively (Fig. 3).

There was considerable variation in yield over harvests; nevertheless, we generally found similar patterns of seasonal yield and effects