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Weed suppression enhanced by increasing functional trait dispersion and resource capture in forage ley mixtures

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ABSTRACT

Weeds in intensively managed grassland can result in substantial losses of forage yield and quality. We studied whether weeds could be suppressed sustainably by use of functionally diverse grassland mixtures with high resource capture and biomass yield. To this aim, growth of planted phytometers and of spontaneously establishing, unsown species were evaluated.

To represent weeds, seedlings of five model species were grown up as phytometer plants in stands of forage leys under two precipitation regimes. Ley stands comprised monocultures and mixtures of two and four species with distinctly differing plant functional traits (PFTs) related to nitrogen (N) acquisition and rooting depth, including: *Lolium perenne* L. (PFT: non-N_2-fixing, shallow-rooted), *Cichorium intybus* L. (non-N_2-fixing, deep-rooted), *Trifolium repens* L. (N_2-fixing, shallow-rooted), and *Trifolium pratense* L. (N_2-fixing, deep-rooted). Five PFTs were measured from these ley species: leaf dry matter content, specific leaf area, leaf N and carbon (C) content, and the leaf C:N ratio. Survival of phytometer plants and biomass of unsown species was measured under rainfed conditions and during an experimentally induced, nine-week summer drought with complete rain exclusion.

Mixtures with high functional dispersion (calculated from PFTs) and biomass yield suppressed phytometer plants and unsown species significantly more than mixtures with low functional dispersion. Under rainfed conditions, fourteen weeks after planting, survival of phytometer plants was 32% in the four-species mixture with the highest functional dispersion, while survival was 68% averaged across monocultures, the stands with the lowest functional dispersion. Surviving individuals had significantly smaller tiller number and rosette diameter in mixtures than in monocultures. Biomass of unsown species was 3.6 kg ha^{-1} in the four-species mixture, but was 13.0 kg ha^{-1} in averaged monocultures. The suppressive effect was equally apparent under drought conditions, where, at the end of the drought period, phytometer survival was 16% and 47% in the four-species mixture and averaged monocultures, respectively. During a six-week post-drought period, the suppressive effect of ley mixtures on phytometer plants was sustained. The strong suppressive effect of ley mixtures was explained by their superior capture for light and plant-available soil N.

We conclude that cropping functionally diverse grassland mixtures could be a sustainable strategy to enhance weed suppression under rainfed and drought conditions.

1. Introduction

Weeds in managed grassland can lead to substantial losses of forage yield and quality (Naylor, 2002). Although weeds can be controlled by herbicides, such measures have both economic and environmental costs. In mixed grasslands, for example, application of herbicides can affect sward composition (Suter and Lüscher, 2011), e.g. loss of dicotyledons including legumes that positively affect biomass production and nitrogen yield (Nyfeler et al., 2009; Suter et al., 2015).

One strategy to achieve more sustainable grassland management is the use of multi-species mixtures (Lüscher et al., 2014) that significantly increase aboveground biomass yield over monocultures (Finn et al., 2013). Such benefit from mixtures can arise through positive species interactions and complementary resource use (Hoekstra et al., 2015; Nyfeler et al., 2011; van Ruijven and Berendse, 2005), which suggests that high yielding mixtures capture and transform increased amounts of resources into biomass. It is yet to be determined which forage species have to be combined to result in grassland providing multiple ecosystem

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functions beyond yield, including e.g. high forage protein content, high weed suppression, and – in the face of predicted climate change – drought resistance (Goslee et al., 2013; Storkey et al., 2015).

Plant functional traits (PFTs) reflect the resource economy and growth strategy of species. Extensive research on PFTs across the worlds' biomes has demonstrated a close relationship between traits and growth strategies, converging along an axis ranging from fast-growing species with high biomass turnover and rapid nutrient acquisition to slow-growing species with permanent leaf structures and efficient conservation of nutrients (Westoby et al., 2002; Wright et al., 2004). Thus, PFTs seem to consistently reflect plant physiological functions worldwide, meaning that the prevalent "fast-slow axis" of growth should generally apply within and across communities, climate zones, and biomes (Reich, 2014). From the multitude of PFTs, three traits closely reflect a species' resource economy, i.e. the resource exploitation/conservation trade-off: (i) leaf nitrogen content, because of the proteins involved in photosynthesis (Wright et al., 2004), (ii) specific leaf area, which is related to the efficiency with which leaves capture light and carbon dioxide (Reich et al., 1998), and (iii) leaf dry matter content, which reflects a plant's investment in persistent leaf structures and nutrient retention (Wright and Cannon, 2001). Recently, it has been argued that agroecology should adopt the functional trait approach to optimize multiple ecosystem services of grasslands across varying environmental conditions and management regimes (Storkey et al., 2015; Wood et al., 2015). In the light of weed control, one may crop species in mixtures such that a combination of their functional traits results in increased resource capture; this would leave a smaller share of the limited resource pool to weeds and, thus, enhance their suppression. Preferably, this effect would be observed under a range of environmental conditions.

Drought events are expected to increase in frequency and severity in temperate regions due to climate change (Seneviratne et al., 2012). Drought events can substantially impair biomass yield of intensively managed grasslands (Vogel et al., 2012), and can increase the temporary abundance of weeds (Gilgen et al., 2010) and the invasibility to non-resident species (Buckland et al., 2001). Grassland invasibility is not an intrinsic characteristic of a community, but is rather related to multiple and variable factors such as water and nutrient status, disturbance, and community composition (Renne et al., 2006). Thus, the invasibility of a grassland may be enhanced by changes in soil water content and nutrient fluxes in response to drought (Borken and Matzner, 2009), which in turn affect sward density and light interception (Hofer, 2016). It could be hypothesised that grassland invasibility is reduced by enhancing the drought resistance and/or resilience of forage species, e.g. through adapted management, as maintaining high biomass yields maintains high resource capture. Recent results from Hofer et al. (2016) demonstrated high drought resistance and/or resilience of intensively managed experimental grasslands. In particular when non-legumes and legumes were grown in mixtures, significant overyielding (mixture performance greater than the weighted average of the respective monocultures) was apparent even under severe drought, compensating for drought-induced losses in yield observed in species' monocultures. Yet, there is, to our knowledge, no evidence that high yielding grassland can resist weed invasion despite drought-induced disturbance.

In this paper, we investigated suppression of weeds by different types of monocultures and mixtures of forage ley species under two precipitation regimes. Ley species were selected to have distinctly differing PFTs closely related to the species' resource economy and the fast-slow axis of growth. To test for weed suppression, seedlings of five model species were grown as phytometers in ley stands, and phytometers' growth and survival were measured. In addition, biomass of spontaneously establishing, unsown species was evaluated. A nine-week summer drought with complete rain exclusion was simulated to assess the impact of leys on weeds under a severe climatic event. It was our primary aim to evaluate which of the targeted combinations of forage species would result in increased functional trait dispersion and resource capture, and whether this would lead to enhanced weed suppression. The following specific questions were addressed:

1 Are weeds increasingly suppressed in functionally more diverse ley mixtures than in less diverse mixtures and monocultures?
2 Is the suppressive effect of functionally diverse ley mixtures also evident under severe drought?
3 Can weed suppression be explained by the ley species interactions reflecting high resource capture?

2. Materials and methods

2.1. Site conditions and experimental design

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 topsoil composition of 32% sand, 42% silt, 26% clay, and a pH of 7.1. In the experimental year, mean annual temperature was 9.8 °C and annual precipitation 1165 mm (see Table B.1, Appendix B in Supplementary materials, for further climatic data). All plots received 200 kg N ha^{-1} $year^{-1}$ of mineral N fertiliser in six applications (Mg-S-Ammonsalpeter 25%, Lonza, Switzerland), while phosphorus (Triple-Super 46%, CU Agro, Switzerland) and potassium (Kali 60%, CU Agro, Switzerland) were applied once in spring following local fertilisation recommendations for intensively managed grassland.

Four key forage species of productive temperate grasslands worldwide were used to establish leys. The species were selected to have distinctly differing plant functional traits (PFTs) related to nitrogen (N) acquisition and rooting depth: a non-N_2-fixing, shallow-rooted grass: *Lolium perenne* L., cultivar (cv.) Alligator; a non-N_2-fixing, deep-rooted forb: *Cichorium intybus* L., cv. Puna II; a N_2-fixing, shallow-rooted legume: *Trifolium repens* L., cv. Hebe; and a N_2-fixing, deep-rooted legume: *Trifolium pratense* L., cv. Dafila. Hereafter, when referring to the type of N acquisition, *L. perenne* and *C. intybus* are termed "non-legumes".

Plots of 3 m × 5 m were established in monocultures and mixtures of varying species richness in the year prior to experimentation (August 2011) to result in four different monocultures (100% of one species), six types of binary mixtures (50% of each of two species), and a four-species equi-proportional mixture (25% of each of the four species). Two replicates were set up for each of the monocultures and binary mixtures, and three replicates for the four-species mixture. The described set of monocultures and mixtures was established twice, for ambient, rainfed conditions and for drought conditions, for which a summer drought event was simulated. This resulted in a total of 46 plots, which were arranged in an incomplete block design. Rainfed and drought plots of the same type of stand were placed next to each other in pairs to represent a "mainplot", reflecting a split-plot design.

Five phytometer species were used as model species to represent weeds of intensively managed grasslands. Phytometer species were selected to vary widely in growth form (given in parentheses), and consisted of two grasses: *Bromus hordeaceus* L. (tussock) and *Poa trivialis* L. (creeping-stoloniferous), and three forbs: *Leontodon hispidus* L. (rosette), *Rumex obtusifolius* L. (prostrate with rosette), and *Taraxacum officinale* Web. (rosette). These were grown from seeds in the glasshouse in early spring 2012, and eight healthy seedlings per phytometer species were planted into each ley stand in non-competing distances to each other in mid-May.