Species Richness Increased Yield Stability in Intensively Managed Grasslands Subjected to Experimental Drought

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Abstract
Climate change is expected to cause an increase in the frequency and intensity of drought events. Over two years we investigated the effects of experimentally imposed drought on intensively managed grassland communities (5 m x 6 m plots) of varying richness (1, 2 and 4 species), and comprising four species (*Lolium perenne* L., *Cichorium intybus* L., *Trifolium repens* L., *Trifolium pratense* L.). In each year a summer drought period of nine weeks with complete exclusion of precipitation was simulated, inducing severe drought stress at Reckenholz (Zürich, Switzerland), and extreme drought stress at Wexford (Ireland). Mean yield and plot-to-plot variance of yield were measured across harvests during drought and after a subsequent post-drought recovery period. At both sites, there was a positive relationship between species richness and yield under both the rainfed control conditions and under drought. At both sites, four-species communities had lower plot-to-plot variance of yield compared to monoculture or two-species communities under both rainfed (-49% smaller standard deviation) and drought conditions (-24%), which demonstrates higher yield stability in four-species communities. At the Swiss but not the Irish site, a high degree of species asynchrony could be identified as a mechanism underlying increased temporal stability in four-species communities.

Introduction
Climate change is expected to cause an increase in the frequency and intensity of drought events, which have strong negative effects on the aboveground biomass (yield) of grassland ecosystems (IPCC 2013). In intensively managed grasslands, even modest increases in species richness can result in strong yield benefits, when species are specifically selected for complementary traits (Nyfeler *et al*. 2009, Finn *et al*. 2013); however, there are remarkably few examples relating diversity to yield stability, for unperturbed or perturbed conditions. This is despite their high economic importance and threats to food security that can be expected from related climate change effects on grasslands. We investigated the use of multi-species mixtures in intensively managed grasslands as a practical adaptation strategy for increasing yield stability of intensively managed grasslands under drought.

Methods and Study Site
A field experiment was established at two sites (i) Wexford, Ireland and (ii) Zürich, Switzerland. Four agricultural grassland species were selected based on the factorial combination of nitrogen-fixing (N2-fixing) and root-depth traits; two non-fixing species, *Lolium perenne* L. (shallow-rooted grass) and *Cichorium intybus* L. (deep-rooted forb), and two N2-fixing species, *Trifolium repens* L. (shallow-rooted legume) and *Trifolium pratense* L. (deep-rooted legume). Main-plots (5 m x 6 m) were sown following a simplex design (Hofer et al. 2016), such that there were: monocultures of each 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). At each site, a total of 35 main-plots were arranged according to a randomised incomplete block design.

A summer drought of nine to ten weeks was simulated at each site over two years (see Hofer et al., 2016). Precipitation was completely excluded from one randomly selected half (split-plot) of the main-plot by using rain-out shelters. Aboveground biomass was harvested five times annually at Wexford and six times at Zürich. Plots received mineral nitrogen (N) fertiliser at a rate of 130 kg N ha^{-1} y^{-1} (year 1) and 150 kg N ha^{-1} y^{-1} (year 2) at Wexford, and 200 kg N ha^{-1} y^{-1}in both years at Zürich. At each harvest, dry matter content of each split-plot yield was determined by drying a subsample of the harvested fresh biomass.

Analysis of the yield responses to experimental drought only included data from the control and drought treatment for the three harvests: mid-drought, end-of-drought and post-drought harvests in each year (the post-drought comprised the first harvest after the removal of rain-out shelters). Mean yield across all harvests, plot-to-plot variance of yield (per level of species richness and drought treatment), and the stability index S (yield mean / standard deviation across harvests) were measured across harvests during drought and after a subsequent post-drought recovery period. To investigate a potential mechanism underlying the observed levels of yield stability, an analysis of species asynchrony was conducted for the mixtures (see Haughey *et al*. 2018 for details). The smaller the value, the more asynchronous the temporal pattern of growth across species in the community.

Results

At both sites, there was a positive relationship between species richness and yield. Under rainfed control conditions, mean yields of four-species communities were 32% (Wexford, Ireland) and 51% (Zürich, Switzerland) higher than the average of the four monocultures ($P < 0.001$ both sites). This positive relationship was also evident under drought, despite significant average yield reductions due to drought (-27% at Wexford; -21% at Zürich). At both sites, four-species communities had lower plot-to-plot variance of yield compared to monoculture or two-species communities under both rainfed (-49% smaller standard deviation) and drought conditions (-24%), which demonstrates higher yield stability in four-species communities.

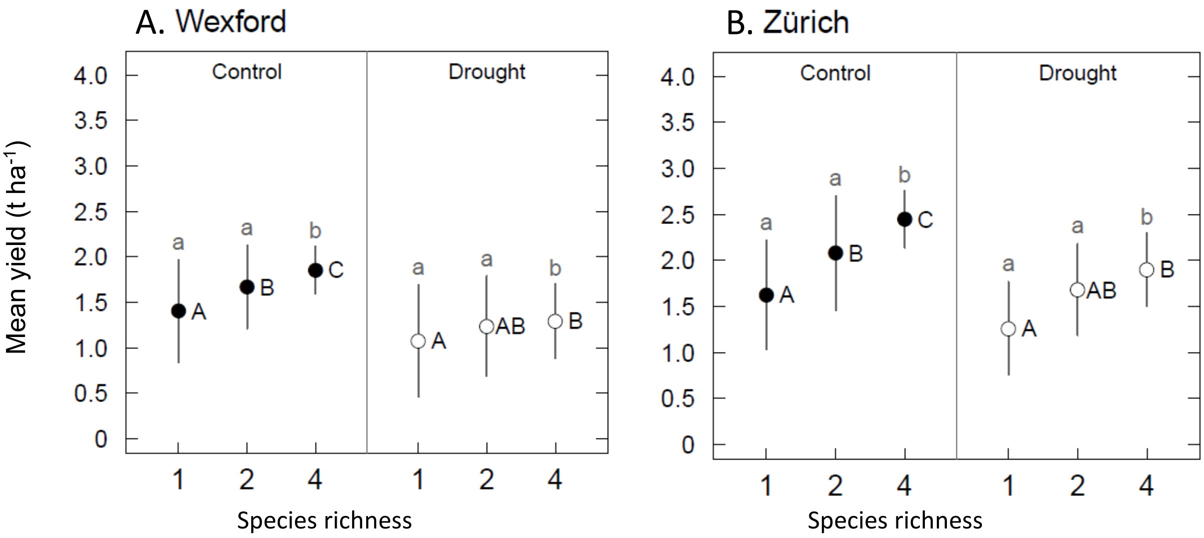

Figure 1. Effects of species richness and drought on yield mean across harvests and plot-to-plot standard deviation under rainfed control and drought conditions at Wexford (A) and Zürich (B). Within each site and treatment, different letters indicate a difference at $P < 0.05$ based on regression analysis, except SD under drought at Zürich, which is at $P < 0.1$ (means: inference in black upper-case letters; SD: inference in grey lower case letters). Reproduced from Haughey et al. (2018), and refer therein for details.

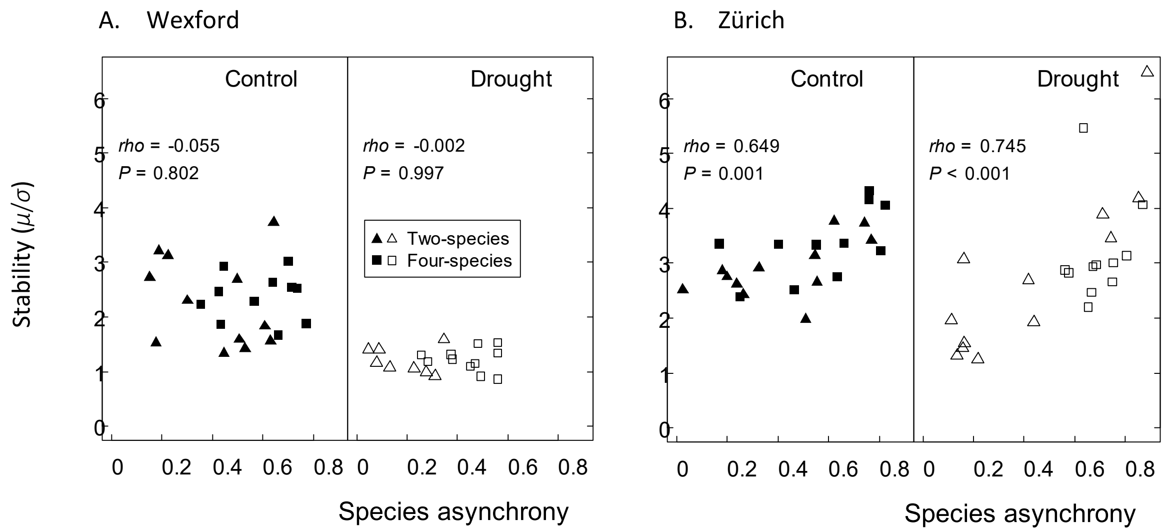

Figure 2. Relationship between species asynchrony and yield stability at Wexford (A) and Zürich (B), under rainfed control and drought conditions. The stability index S = μ/σ was computed with μ and σ being the mean and the standard deviation across all harvests. *Rho*: spearman rank correlation.

A significant positive correlation between the stability index S and species asynchrony was identified at Zürich under both control (rho = 0.649) and drought conditions (rho = 0.745, Fig. 2), but not in Wexford. At Wexford, species asynchrony was strongly reduced by drought ($P < 0.001$), resulting in a distinctly reduced stability under drought at this site. Overall, while the asynchrony-stability correlation was driven by drought at Wexford (overall rho = 0.304, $P = 0.051$), the asynchrony-stability relationship was more affected by species richness at Zürich.

Discussion

Lüscher *et al.* (2014) listed the potential contribution of legumes to the key challenges of sustainable intensification as: (i) increasing forage yield, (ii) substituting inorganic N-fertilizer inputs with symbiotic N_2 fixation, (iii) supporting mitigation and adaptation to climate change and (iv) increasing the nutritive value and conversion efficiency of herbage. In addition to these arguments, our results show that higher plant diversity increased yield stability of forage production, even under drought events, and further highlight the potential of legume-based mixtures to contribute to sustainable intensification (see also Hofer *et al*. 2016). Improved understanding of species-specific responses to severe weather events could help further improve species and cultivar selection for use in multi-species grasslands, and so better inform practical agricultural strategies to adapt grasslands to a climate with a higher frequency of severe events.

In summary, we found a positive relationship between species richness (1, 2 and 4 species) and yield, and a negative relationship between species richness and yield variation. This demonstrates higher yield stability in four-species grassland communities under both rainfed control and drought treatments. These results indicate the high potential of multi-species grasslands as an adaptation strategy against drought events and that mixtures can help achieve sustainable intensification under both unperturbed and perturbed environmental conditions.

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