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Plant community flood resilience in intensively managed grasslands and the role of the plant economic spectrum

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Abstract

1. The increasing frequency of extreme weather events, such as floods, requires management strategies that promote resilience of grassland productivity. Mixtures of plant species may better resist and recover from flooding than monocultures, as they could combine species with stress-coping and resource acquisition traits. This has not yet been tested in intensively managed grasslands despite its relevance for enhancing agroecosystem resilience.
2. Using intact soil cores from an 18-month-old field experiment, we tested how 11 plant communities (*Festuca arundinacea*, *Lolium perenne*, *Poa trivialis* and *Trifolium repens* in monoculture, two- and four-species mixtures) resist and recover from repeated flooding in a 4-month greenhouse experiment.
3. We found that plant community composition, not whether the community was a mixture or monoculture, influenced the community's resistance to flooding, although most communities were able to resist and recover from both floods.
4. The plant community's position on the leaf economic spectrum in flooded conditions was related to its resistance to and recovery from flooding. Resistance to and recovery from a severe flood were related to flood-induced intraspecific trait variation, causing a shift in the community's position on the leaf resource economic spectrum. In flooded conditions, resource-conservative communities (characterized by low specific leaf area, low leaf nitrogen content and high leaf dry matter content) better resisted and recovered from flooding. The community's position on the root resource economic spectrum was less connected to the community's resistance and recovery.
5. *Synthesis and applications*. Our study shows that in flooded conditions, resource-conservative plant communities are more resilient to flooding than resource-acquisitive communities in an intensively managed grassland. This suggests that plant community position on the leaf economic spectrum, as well as species' flood-induced intraspecific variation, should be considered when designing grasslands to withstand increasing flood frequency and severity.

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KEYWORDS
extreme weather event, flooding, grassland, plant community, plant traits, recovery, resistance, resource economic spectrum

1 | INTRODUCTION

The intensity and frequency of extreme weather events, such as floods, are predicted to increase in the near future due to climate change (IPCC, 2018; Stocker et al., 2013). This jeopardizes agricultural production, with annual flooding damages expected to total 260 million euros in the European Union alone (Rojas, Feyen, & Watkiss, 2013). Flooding can have disastrous effects on intensively managed grasslands both economically (to the farmers who depend on these grasslands for fodder) and ecologically (via nutrient losses to the groundwater and atmosphere; Hopkins & Holz, 2006). These effects could be offset by managing grasslands to maintain productivity and mitigate nutrient losses throughout flooding and re-drying periods.

Plant community's response to perturbation can be separated into two parts: how it withstands a perturbation (*resistance*) and how well it returns to its pre-perturbed state afterwards (*recovery*; Hodgson, McDonald, & Hosken, 2015; Ingrisch & Bahn, 2018). A flood is a complex type of perturbation, which introduces both stress and influx of resources (Wright et al., 2015), being different from perturbations such as drought, which reduces resources (e.g. Tilman & Downing, 1994). One way to predict how a plant community will respond to an intermingling of stress and nutrient enrichment is by considering plant functional traits. Plant functional traits are indicators of plant strategies for resource acquisition, growth and survival (Grime, 2001). Trait-based approaches are frequently used to explain plant community–ecosystem functioning relationships (Lavorel & Garnier, 2002). They can also predict how plant communities resist and recover from perturbation (Díaz & Cabido, 2001) such as flooding (De Boeck et al., 2018). Communities that combine multiple plant species may better withstand perturbations because they include a variety of stress-coping and resource acquisition traits, compared to plant species in monoculture (Yachi & Loreau, 1999). Therefore, increasing the number of plant species in a community can increase resistance to perturbation and yield stability over time (Craven et al., 2018).

Leaf and root traits covary across plant species, indicating their resource uptake strategy (i.e. *the leaf economic spectrum* [LES], Wright et al., 2004 and the *root economic spectrum* [RES], e.g. Fort et al., 2016). On one side of the LES are fast-growing, resource *acquisitive* plant species with high specific leaf area (SLA) and leaf nitrogen (N) and low leaf dry matter content (LDMC). On the other side of the spectrum are slow-growing resource-*conservative* plant species with opposite traits. Below-ground, plant species with high specific root length (SRL) and root N content, and low root tissue density (RTD) are considered acquisitive, while conservative plant species have thicker, denser roots (Fort et al., 2016; Prieto et al., 2015).

A plant community's position on the LES, that is, its strategy based on the traits of the component species, has been linked to plant productivity (Mason et al., 2016), N cycling and losses (Abalos, van Groenigen, & De Deyn, 2018; de Vries & Bardgett, 2016), as well as to response to flood perturbations in semi-natural grasslands (Fischer et al., 2016). Conservative communities may have greater resistance to flooding as slower growth rate and lower respiration could reduce loss of carbohydrates and organ mortality (Bailey-Serres & Colmer, 2014). Contrarily, acquisitive communities may recover faster from flooding due to quicker nutrient uptake and growth after the flood has receded (Wright et al., 2015). How a community's position along the LES or RES influences flood resistance and recovery in intensively managed grasslands remains unknown. Further, a plant community's strategy could be related to its resistance/recovery because of its inherent position on these spectra, or due to flood-induced shifts in plant traits. Plant traits measured in ambient conditions can predict ecosystem response to perturbation (Kimball et al., 2016). Intraspecific shifts in plant trait or changes in the relative abundance of species (species turnover) can also explain a community's response to perturbation (Jung et al., 2014).

Here, we tested how repeated flooding with increasing intensity affects the resistance and recovery of intensively managed grassland communities (Figure 1). We tested how a community's position

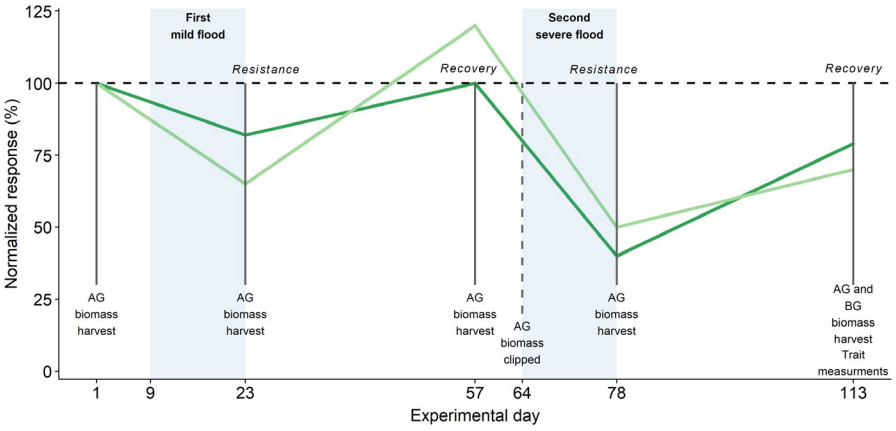


FIGURE 1 Conceptual diagram of flood resistance and recovery (sensu Ingrisch & Bahn, 2018). Resistance and recovery are the above-ground biomass in the flooded monoliths relative to the control monoliths (dynamic baseline at 100%). Two potential scenarios (green lines) show hypothetical normalized responses to flooding. It is important to note that we considered a system for a limited time (see main text), and therefore, full recovery or permanent displacement cannot be derived. AG, above-ground; BG, below-ground

on the LES and RES, predicted from traits in ambient or flooded conditions, related with flood resistance and recovery. We also tested how the change in LES due to intraspecific variation or species turnover related with resistance and recovery. We hypothesize the following:

1. Plant communities will differ in their resistance to and recovery from flooding; mixtures will better resist and recover from flooding than monocultures.
2. Plant communities with a conservative position on the leaf- and root economic spectrum (based on the traits of the plant species within the community) will be more resistant to flooding because of slower energy loss and organ mortality. Acquisitive communities will better recover because of higher nutrient acquisition and growth after the flood has passed.

2 | MATERIALS AND METHODS

2.1 | Experimental design

Intact monoliths (20 cm diameter × 25 cm soil depth) were taken in September 2017 from an established field experiment (sown in March 2016) in Wageningen, The Netherlands (51.9884°N, 5.6616°E). For full details, see Oram, van Groenigen, et al. (2020) and Abalos et al. (n.d., under review). Briefly, the soil is classified as a *typic endoaquoll* (Soil Survey Staff, 1999) with 75% sand, 23% silt and 2% clay. Characteristics of the 0–15 cm soil layer were as follows: pH-$CaCl_2$: 5.1, soil bulk density: 1.42 Mg/m^3, organic matter: 2.2%, total N: 1.30 g/kg. Mean annual rainfall is 780 mm and mean annual temperature 9.4°C (KNMI, 2018). The field experiment included three grasses (*Festuca arundinacea* Schreb., *Lolium perenne* L. and *Poa trivialis* L.) and one legume (*Trifolium repens* L.) grown in monocultures, all combinations of two- and four-species mixtures in 3 × 3 m plots, replicated five times in a completely randomized block design (n = 55 field plots). Two monoliths (intact soil cores) were taken from each field plot (n = 110), sealed, and transferred to the greenhouse.

One monolith per plot was subjected to a flooding treatment; the other monolith (the control) was maintained at 60% water holding capacity (WHC), which is optimal for plant growth. Soil water content and WHC were determined on soil taken from the field plot at the same time as the monolith. Control monoliths were watered throughout the experiment to their weight at 60% WHC.

The flooding treatment consisted of two floods, a first, mild flood, in which 1.28 L of water (equivalent to 45 mm rainfall) was added to the surface of the monoliths (day 9), and a second, severe flood: 2.84 L of water was added to the monoliths, equivalent to 100 mm rainfall (day 64). All monoliths were at 60% WHC when the flood water was added. Both rainfall events, representing a mild (5-year return) and a severe one (50–100 year return; Rajczak, Pall, & Schär, 2013), are realistic and are expected to increase with climate change (KNMI, 2018). Flooded water levels were maintained for 2 weeks, then surface water was removed with a syringe and discarded, and monoliths could recover (maintained at 60% WHC) for 5 weeks (Figure 1). Monoliths were fertilized in line with common management practices in temperate managed grasslands (Sutton et al., 2011), with calcium ammonium nitrate (50 kg N/ha) on days 1 and 57 following above-ground biomass harvest (i.e. 100 kg N/ha in total).

Above-ground biomass was harvested to 2 cm above the soil surface five times: on day 1 to establish if there were initial biomass differences, directly after each flood to quantify *resistance* (days 23 and 78), and after each recovery period to quantify *recovery* (days 57 and 113; Figure 1). Above-ground biomass was sorted per species and dried for 48 hr at 70°C. Immediately prior to the severe flood, above-ground biomass was clipped to facilitate submergence. At the final harvest (day 113), root washing took place by block over the next 4 weeks at which time the monoliths were stored at 4°C in the dark and shoot regrowth was not observed. Roots were washed over a 0.5-mm sieve, and a representative subsample (~1 g) of clean roots was stored in 70% ethanol until morphological trait measurements (Pérez-Harguindeguy et al., 2016). The rest of the roots were dried at 70°C for 72 hr.

2.2 | Plant traits

Plant traits measurements are described in Oram, van Groenigen, et al. (2020), which were carried out according to Pérez-Harguindeguy et al. (2016). We measured SLA (leaf area/leaf dry weight) and LDMC (leaf saturated weight/leaf dry weight) of the youngest fully expanded leaf of five individuals per species in each monolith at the final harvest (day 113). Below-ground, we estimated root length and volume of scanned roots with WinRhizo (Regent Instruments Inc.), and determined SRL (root length/root dry weight) and RTD (root dry weight/root volume). Carbon (C) and N content were determined in leaves (species level) and roots (community level) from the final harvest at the UC Davis Stable Isotope Facility (California, USA) using an elemental analyser (PDZ Europa ANCA-GSL, Sercon Ltd.) interfaced to a continuous flow isotope ratio mass spectrometer (IRMS).

Above-ground traits, and the community LES, were calculated as the community weighted mean (CWM, Equation 1, Garnier et al., 2004):

$$\mathrm{CWM} = \sum_{i=1}^{s} w_i \cdot x_i, \quad (1)$$

where w_i is the relative abundance of above-ground biomass (g/m^2) over the entire experiment of species i, and x_i is the trait value for species i. To determine if flood-induced trait shifts were due to changes in the relative abundance of species (species turnover) or intraspecific trait changes, we followed the method of Jung et al. (2014) to calculate the $CWM_{Control}$ and CWM_{Flood} using the relative abundance of species (w_i) and species above-ground traits (x_i) in each control or flooded monolith, respectively. We then calculated $CWM_{Predicted}$, using the

relative abundance (w_i) of species in flooded monoliths, and the traits (x_i) of species grown in the control monolith originating from the same field plot. Below-ground traits were measured at the community level. Functional dispersion (FDis), a measure of functional trait diversity, was calculated according to Laliberté and Legendre (2010), using the leaf traits measured in monoculture (SLA, LDMC, leaf N concentration) weighted by the relative abundance of above-ground biomass per species in mixtures over the entire experiment.

2.3 | Quantifying resilience

We incorporated components of the framework of Ingrisch and Bahn (2018) into our characterization of resilience (Figure 1). This framework integrates resistance and recovery, compares a perturbed plant community with a dynamic baseline, and corrects for initial differences between perturbed and control treatments. We compare flooded plant communities with the control from the same field plot (a dynamic baseline). Resistance is the baseline normalized biomass of the flooded monoliths directly after a 2-week flood. Recovery is the baseline normalized biomass of the flooded monoliths 5 weeks after the flood. All baseline normalized values were corrected for initial biomass differences between paired control and flood monoliths (i.e. at time 0, t_0), Equation 2.

$$\text{Resistance or Recovery} = \frac{\text{Biomass Flood } t_x}{\text{Biomass Control } t_x} \Big/ \frac{\text{Biomass Flood } t_0}{\text{Biomass Control } t_0}. \quad (2)$$

2.4 | Statistical analysis

The effects of plant community composition (11 communities), plant species richness (1, 2 or 4 species) or culture (mixture or monoculture) on plant community resistance and recovery were tested with linear mixed effects models using the function lme{nlme} (Pinheiro, Bates, DebRoy, Sarka, & R Core Team, 2016) with block (5 blocks) as a random factor, fitted with a type III SS ANOVA, anova{base}. For all analyses, baseline normalized resistance and recovery were log transformed to meet assumptions of normality. The effects of plant community composition, flooding (flood or control) and their interaction on above-ground biomass were tested with an lme model (as above) with field plot nested within block as a random structure to account for two monoliths taken from the same field plot. Variance structures, varIdent{nlme}, were included in models with heterogenous variances between treatments. Models with the variance structures were accepted when they had a significantly lower Akaike information criterion than the model without (tested with ANOVA).

The change in traits ($CWM_{Control}$ vs. CWM_{Flood}) was tested with an lme model and ANOVA (as above) including treatment, plant community composition and their interaction. In mixtures, we tested trait shifts due to species turnover ($CWM_{Control}$ vs. $CWM_{Predicted}$) and intraspecific variation (CWM_{Flood} vs. $CWM_{Predicted}$) with trait type ($CWM_{Control}$, CWM_{Flood}, $CWM_{Predicted}$), plant community composition and their interaction as explanatory variables. All models included block/field plot as a random structure. A Tukey post-hoc test was used to determine significance levels of explanatory variables using the function emmeans{emmeans} (Lenth, 2018).

The LES and RES based on community-level traits ($CWM_{Control}$, CWM_{Flood}, $CWM_{Predicted}$ above-ground and community-level traits from control and flooded monoliths below-ground) were determined with principle component analysis (PCA) using the function rda{vegan} (Oksanen et al., 2017). Traits were first scaled (M 0, SD ± 1) using the function scale{base}. Above-ground and below-ground traits were first considered together, and as they were decoupled (i.e. morphological traits of leaves and roots were orthogonal) were subsequently analysed separately. The LES included CWM for SLA, LDMC and leaf N concentration similar to Vogel et al. (2019). Using species-level traits as the input for the PCA and then weighting the PCA scores by species relative abundance resulted in similar CWM trait values (R^2 = 0.98, details not shown). The RES included SRL, RTD and root N concentration (Freschet, Cornelissen, van Logtestijn, & Aerts, 2010). The FDis above-ground (SLA, LDMC, leaf N) in mixtures was calculated using the FD package on scaled traits (Laliberté & Legendre, 2010).

The relationships between the LES or RES and resistance/recovery were tested with lme models using the PCA axis 1 projection scores (see Figure 4, Section 3) as an explanatory variable. To determine whether the relationship between resistance/recovery and the LES was due to flood-induced shifts and the underlying traits due to intraspecific variation or species turnover, we calculated C_{Intra} and C_{Turn} in line with Jung et al. (2014):

$$C_{Intra} = LES_{Flood} - LES_{Predicted}, \quad (3)$$

$$C_{Turn} = LES_{Predicted} - LES_{Control}, \quad (4)$$

where LES_{Flood} is the PCA axis 1 of CWM_{Flood} traits, $LES_{Control}$ is the PCA axis 1 of $CWM_{Control}$ traits and $LES_{Predicted}$ is the PCA axis 1 of $CWM_{Predicted}$ traits. C_{Intra} considers all monoliths, C_{Turn} considers mixtures as there is no species turnover in monocultures. A constant number was added to all PCA scores to make them positive first. Higher C_{Intra} or C_{Turn} values indicate a shift to a more conservative community.

All statistical analysis was performed in R version 3.6.2 (R Core Team, 2019). Figures were made using the packages GGPLOT2 (Wickham, 2016) and COWPLOT (Wilke, 2019).

3 | RESULTS

3.1 | Flood and plant community effects on above-ground biomass

Before flooding, above-ground biomass depended on plant community composition (main effect $F_{10,40}$ = 7.34, p < 0.001), and one community (*F. arundinacea* + *P. trivialis*) had higher above-ground biomass in the future flooded monoliths than in the control monoliths (interaction flooding: plant community composition $F_{10,44}$ = 3.14, p < 0.05).

There was no main effect of flooding (Figure S1). Immediately after the first, mild flood, above-ground biomass differed between plant communities (main effect: $F_{10,40}$ = 8.96, p < 0.001), as the *P. trivialis* monoculture had lower biomass than the other plant communities (Figure 2A). Above-ground biomass did not differ between control and flooded monoliths (Figure 2A). After a 5-week recovery from the first flood, above-ground biomass depended on the interaction between plant community composition and flooding ($F_{10,44}$ = 3.17, p < 0.01). The above-ground biomass of the *P. trivialis* monoculture was significantly higher in flooded than control monoliths (Figure 2B). The second, severe flood significantly reduced above-ground biomass compared to the control ($F_{1,44}$ = 7.91, p < 0.01, Figure 2C), the extent to which depended on the plant community composition (interaction flooding: plant community composition, $F_{10,44}$ = 2.37, p < 0.05, Figure 2C). After a 5-week recovery from the second flood, above-ground biomass depended on an interaction between plant community composition and flooding ($F_{10,44}$ = 3.55, p < 0.01, Figure 2D).

3.2 | Plant community effects on flood resilience

Plant community response to the first flood depended on plant community composition (resistance $F_{10,40}$ = 7.07, p < 0.001, Figure 3A; recovery $F_{10,40}$ = 4.57, p < 0.001, Figure 3B). Most communities were able to resist the first, mild flood, with the baseline normalized resistance near 100% (Figure 3A). The four-species mixture was significantly less resistant than the *L. perenne* monoculture and the *L. perenne* + *P. trivialis* mixture (Figure 3A). However, as the above-ground biomass of *P. trivialis* made up less than ~5% of this mixture, it was almost a monoculture of *L. perenne* (Figure S2). Plant communities showed similar recovery to the first flood, except for the *P. trivialis* monoculture that produced more biomass during the recovery period in the flooded than the control monoliths (Figure 3B). During the second, severe flood, plant community composition tended to influence resistance ($F_{10,40}$ = 1.92, p = 0.07, Figure 3D), and significantly influenced recovery ($F_{10,40}$ = 2.45, p < 0.05, Figure 3E). However, due to high variation, the post-hoc test showed no significant differences between plant communities' baseline normalized

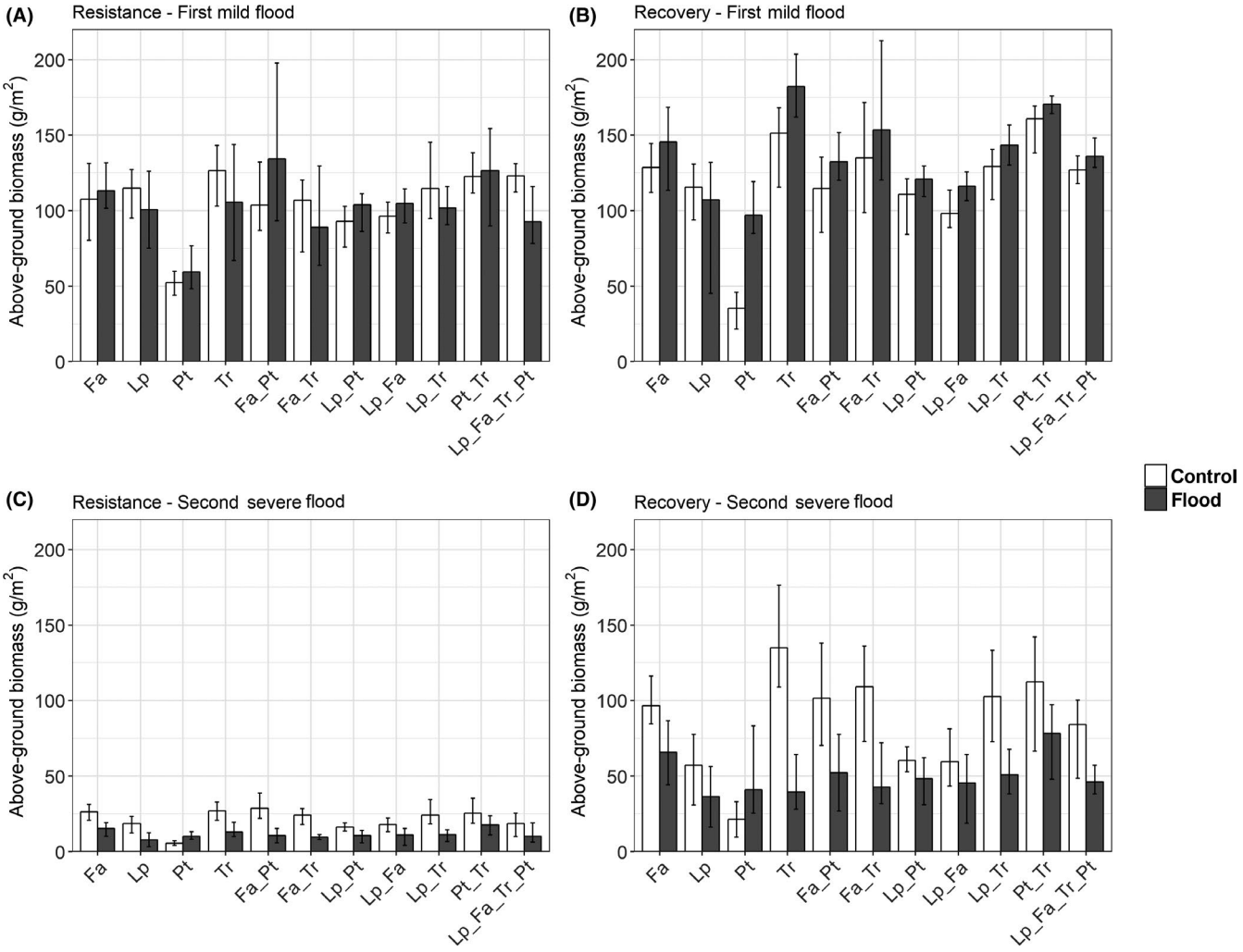


FIGURE 2 Above-ground biomass of plant communities directly after (A) the first flood and (C) the second flood, and after a 5-week period from (B) the first flood and (D) the second flood. Bars indicate mean ± confidence interval (n = 5 per bar), thus if they do not overlap the difference between the bars is significant. *Festuca arundinacea* (Fa), *Lolium perenne* (Lp), *Poa trivialis* (Pt) and *Trifolium repens* (Tr)

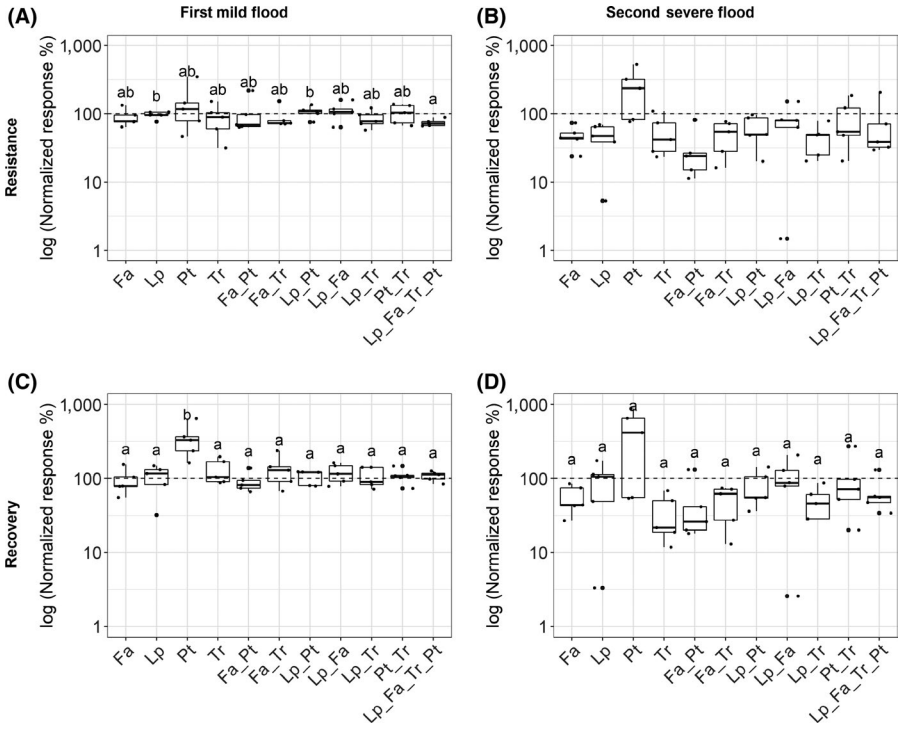


FIGURE 3 Plant community composition effect on resistance to (A) the first flood, (B) the second flood, recovery from (C) the first flood, (D) the second flood. *Festuca arundinacea* (Fa), *Lolium perenne* (Lp), *Poa trivialis* (Pt) and *Trifolium repens* (Tr). The response is the above-ground biomass of flooded compared to control monoliths (100% indicates no difference between flooded and control monoliths). Letters indicate significant differences based on a Tukey post-hoc test

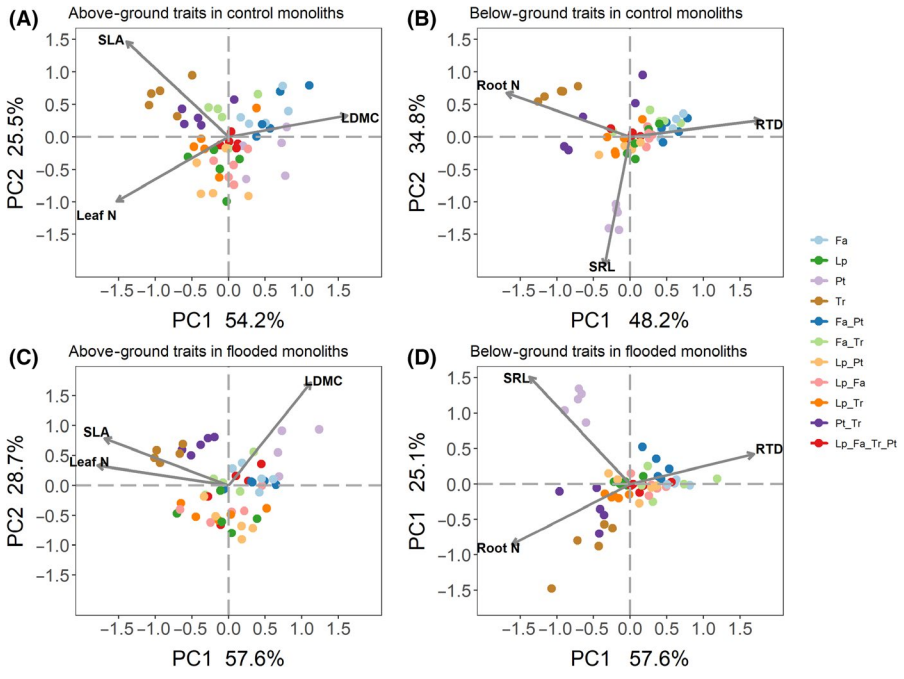


FIGURE 4 (A) Community-level specific leaf area (SLA, cm^2/g), leaf dry matter content (LDMC mg/g) and leaf nitrogen concentration (leaf N, mg/g) of plants grown in control conditions and (C) flooded conditions. Root tissue density (RTD g root/cm^3 root), specific root length (SRL m/g) and root nitrogen content (root N mg/g) grown in (B) control conditions and (D) flooded conditions. *Festuca arundinacea* (Fa), *Lolium perenne* (Lp), *Poa trivialis* (Pt) and *Trifolium repens* (Tr)

recovery (Figure 3D). The number of plant species or whether the community was a monoculture or mixture did not affect flood resistance or recovery.

3.3 | The resource economic spectrum and resistance and recovery

The LES and RES based on plant traits of plants growing in control or flooded monoliths were decoupled (Figure S3), and thus the LES and RES are considered separately. Communities with a conservative position on the LES or RES had higher PCA axis 1 scores (Figure 4).

The LES did not differ between control and flooded conditions (Figure S4D), while flood effects on the RES depended on plant community composition (Figure S4H). The *P. trivialis* monoculture and the *P. trivialis* + *F. arundinacea* mixture became more acquisitive below-ground (lower RES PCA 1) in flooded conditions, while the other communities were not affected. The interaction between plant community composition and flooding affected SLA (Figure S4A), LDMC

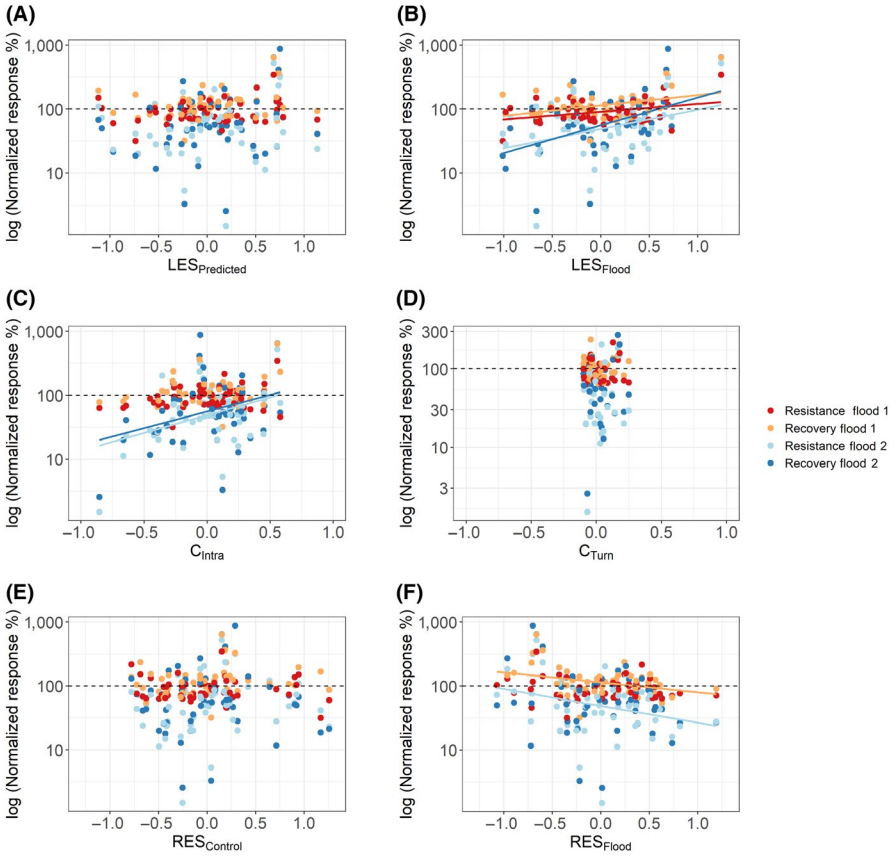


FIGURE 5 Relation between plant community response to flooding and the leaf economic spectrum (LES) and root economic spectrum (RES). The LES was based on the leaf traits (specific leaf area, leaf dry matter content, leaf N) measured in (A) control monoliths (LES$_{Predicted}$) and (B) flooded monoliths (LES$_{Flood}$). A higher value on the spectrum indicates a more conservative plant community (PCA 1, Figure 4). (C) Flood-induced shifts in the LES due to intraspecific variation (C$_{Intra}$) were related to resistance to and recovery from the second flood, while (D) shifts due to species turnover (C$_{Turn}$) were not. Below-ground, the RES (specific root length, Root tissue density, root N) in (E) control monoliths (RES$_{Control}$) and (F) flooded monoliths (RES$_{Flood}$). A normalized response of 100% indicates that the flooded communities produced the same above-ground biomass as the control communities. Lines indicate a significant relationship

(Figure S4B) and leaf *N* (Figure S4C). In the mixtures, shifts in SLA were small, and species turnover contributed to the decrease in SLA in the *F. arundinacea* + *P. trivialis* community (Figure S5A). Decreases in LDMC and leaf N concentration were due to intraspecific variation (Figure S5B,C) and species turnover also contributed to the decrease in leaf N of the *L. perenne* + *P. trivialis* community (Figure S5C). Below-ground, flooding decreased RTD (Figure S4F) and the root N of the *T. repens* monoculture (Figure S4G) but did not affect SRL (Figure S4E).

A community's position along the LES, based on traits measured in control monoliths (LES$_{Predicted}$), was not related to flood resistance or recovery (Figure 5A). Communities with a conservative position on the LES, based on traits in flooded monoliths (LES$_{Flood}$, Figure 4C), were more resistant to the first flood ($F_{1,49}$ = 5.78, p < 0.05), the second flood ($F_{1,49}$ = 7.33, p < 0.01) and recovery from the first ($F_{1,49}$ = 8.63, p < 0.01) and the second flood ($F_{1,49}$ = 14.28, p < 0.001) than acquisitive communities (Figure 5B). The shift in LES due to intraspecific variation (C$_{Intra}$) was related with resistance to ($F_{1,49}$ = 10.87, p < 0.01) and recovery from ($F_{1,49}$ = 7.50, p < 0.01) the second flood (Figure 5C). Shifts in LES due to species turnover (C$_{Turn}$) were not related to resistance or recovery (Figure 5D).

The RES of control monoliths (Figure 4B) did not relate to community resistance or recovery (Figure 5E). However, the RES of flooded monoliths (Figure 4D) was significantly related to the community recovery from the first flood ($F_{1,49}$ = 7.99, p < 0.01, Figure 5E) and resistance to the second flood ($F_{1,49}$ = 5.48, p < 0.05, Figure 5F). Contrary to the LES, communities with an acquisitive position on the RES recovered better from the first flood and resistance to the severe flood.

The FDis of leaf traits (SLA, LDMC, leaf N) was not related to flood resistance or recovery of the species mixtures (Figure S6).

4 | DISCUSSION

4.1 | Plant community composition and flood resilience

Plant community response to flooding depended on plant species composition but was not affected by the number of plant species. The differences between plant communities were mainly driven by a few communities, that is, the four-species mixture was less resistant to the first flood than the *L. perenne* monoculture, and the *P. trivialis* monoculture benefited from a previous mild flood, compared to the other plant communities. Although not statistically significant, our results suggest that *P. trivialis* benefitted from the second, severe flood, producing more biomass in flooded than in control monoliths. However, *P. trivialis* did not contribute to increased flood resistance or recovery of mixtures in which it was present. This is likely because of its poor growth in mixtures, and low biomass production overall. As above-ground biomass is important in intensively managed grasslands, we would not suggest including *P. trivialis* in this system.

4.2 | Flood effects on plant traits

We found that in general, flood-induced shifts in above-ground traits were due to intraspecific variation rather than species turnover. Flooding reduced SLA in the *P. trivialis* and *T. repens* monocultures, which could be caused by reduced water uptake in anaerobic soils (Poorter, Niinemets, Poorter, Wright, & Villar, 2009) or an energetic trade-off with other structural or physiological traits (Moor et al., 2017). In mixtures, the reduction in SLA in the *F. arundinacea* + *P. trivialis* mixture was due to species turnover (an increase in *P. trivialis*). Increasing abundance of flood tolerant species (with low SLA) have been found to lead to a decrease in SLA with increasing wetness (Fu et al., 2014). However, we did not find that species turnover affected the SLA of any other mixture. Decreases in LDMC in flooded conditions were attributed to intraspecific trait shifts. Flooding reduced leaf N content of most communities due to intraspecific trait shifts, that is, a decrease in N uptake in flooded conditions, which is in line with previous studies (Wright & Sutton-Grier, 2012). However, these shifts in traits did not significantly affect the LES; overall, communities did not become more conservative in flooded conditions. Below-ground, flooding reduced RTD, which is in line with findings that in wet environments, grasses have lower RTD than those in drier environments (Craine & Lee, 2003). Overall, differences in plant traits between plant communities were larger than differences between flooded and control treatments.

4.3 | The resource economic spectrum and flood resilience

We found that the LES based on plant traits measured on flooded monoliths (LES_{Flood}) related with resistance and recovery, while the LES based on traits measured in control monoliths ($LES_{Predicted}$) did not. This shows that leaf traits measured in ambient conditions may not be good predictors of a plant community's response to flooding. In flooded conditions, conservative communities were better able to resist and recover from both floods, compared to acquisitive communities. Communities dominated by slow-growing plant species have been found to enhance ecosystem stability (Craven et al., 2018), which demonstrates that conservative species are less negatively affected by extreme or unusual weather events, maintaining biomass production. In wetter environments, plants with competitive and stress-tolerant strategies have been shown to increase in prevalence (Zelnik & Čarni, 2008), suggesting that in wet environments, traits such as low SLA and high LDMC are favoured (Moor et al., 2017). Conservative communities are slower growing with lower rates of photosynthesis and respiration (Wright et al., 2004), which may allow them to 'sit and wait', conserving their resources during the flood, and continuing to grow afterwards (Colmer & Voesenek, 2009). Semi-natural grasslands with a higher proportion of conservative plant species were shown to benefit from flooding, producing more biomass after the flood receded than before the flood (Fischer et al., 2016).

Conservative plant communities may better tolerate flooding because of their inherent traits, and how they shift their traits in response to flooding. We found intraspecific trait shifts (C_{Intra}) to become more conservative related with resistance to and recovery from the second, severe flood. This is broadly in line with findings from Jung et al. (2014) who showed that intraspecific trait variation played an important role in plant community response to extreme drought. The first, mild flood in our study may not have been intense enough to illicit a shift in traits. Shifts in the LES due to species turnover (C_{Turn}) were not related to flood resistance or recovery. This differs from studies showing that trait shifts due to species turnover facilitate stability to repeated flooding (Brotherton & Joyce, 2015) or across environmental gradients (Kichenin, Wardle, Peltzer, Morse, & Freschet, 2013). The discrepancy could be due to the limited number of species in our experiment, and the relatively short (4 months) timeframe of our experiment. Monitoring the relations between traits and resistance/recovery over a longer timeframe, and across grasslands with more plant species will give a more comprehensive view of how shifts in traits due to intraspecific variation and species turnover affect community response to extreme weather events.

Unexpectedly, the relation between the RES in flooded monoliths and plant community response to flooding was opposite: acquisitive communities were better able to recover from the first, mild flood, and to resist the second, severe flood. Communities with finer, less dense roots (high SRL, low RTD) may have begun taking up nutrients sooner after the stress of the mild flood passed, benefitting their recovery. Low RTD (related with an acquisitive strategy) is typical in grass species from wet, compared to drier, environments (Craine & Lee, 2003). Communities with low RTD may be more resistant to flooding because low RTD could be related with the formation of aerenchyma: porous, gas-filled spaces in the root tissue which form in response to low O_2 stress during submergence (e.g. Bailey-Serres & Voesenek, 2008), increasing O_2 transport (e.g. Voesenek & Bailey-Serres, 2015). However, this is speculative, as we did not measure aerenchyma in this experiment, and further research is required to test the relationship between RTD and root aerenchyma formation in flooded conditions.

4.4 | Towards flood resilient intensively managed grasslands

Our results indicate that a community's position on the LES can help explain variation in flood resistance and recovery. Thus, consideration of plant traits related to resource economies can inform management decisions regarding the choice of plant species to improve the flood tolerance of intensively managed grasslands. These grasslands are commonly ploughed and re-seeded, for example, every 5 years in the Netherlands (Velthof et al., 2010). By choosing plant species based on their traits related to resource economies, farmers can sow grasslands that are better able to resist and recover from extreme rainfall events, potentially prolonging the time between re-sowing and increasing yield stability. It should be noted that extrapolation of our findings to

the field must be done with caution. Although the plant communities in our experiment developed for 18 months in the field before our 4-month greenhouse experiment, a longer timeframe is necessary to fully understand the recovery dynamics of plant communities. Finally, although we considered four plant species that are relevant in the context of intensively managed grasslands in Central and Northern Europe (Abalos, De Deyn, Kuyper, & van Groenigen, 2014; Finn et al., 2013), consideration of more plant species with a broader range in functional traits and strategies is needed to be able to design grasslands that safeguard ecosystem services in the face of extreme weather events.

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AUTHORS' CONTRIBUTIONS

N.J.O., G.B.D.D., P.L.E.B., J.H.C.C., J.W.v.G. and D.A. designed the experiment; N.J.O. and D.A. conducted the experiment with input from G.B.D.D., P.L.E.B., J.H.C.C. and J.W.v.G.; N.J.O. analysed the data and wrote the manuscript with extensive input from G.B.D.D., P.L.E.B., J.H.C.C., J.W.v.G. and D.A.

DATA AVAILABILITY STATEMENT

Data are available in DANS Easy Data Repository: https://doi.org/10.17026/dans-xck-d6jq (Oram, De Deyn, et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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