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Effects of nitrogen addition and above-ground biomass removal on the growth and interactions between species of xerothermic grasses

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Abstract: Aspects of global change, such as increasing atmospheric nitrogen deposition and changes in land use, promote the increasing dominance of grass in xerothermic grasslands. It is assumed that nutrient addition and land use affect interactions between the expanding *Bromus erectus* and other co-occurring xerothermic species of grass in central Germany. The plant-plant interactions are key factors in the regulation of species composition, productivity, structure and dynamics of plant communities as well as the functioning of ecosystems. A competition experiment between *B. erectus* and the grasses *Brachypodium pinnatum*, *Stipa capillata* and *Stipa tirsa* was carried out using a replacement design, with species cultivated at two densities (9 individuals or 1 individual per pot) and three different species compositions of nine plants in monoculture and mixtures (6:3, 3:6), to study the effect of *B. erectus* on the other three grasses. Treatments included nutrient addition (nutrient-poor vs. nutrient-rich) and above-ground biomass removal (unclipped vs. clipped). Over two consecutive years, each species' growth was documented by measuring both vegetative traits (i.e. above-ground biomass, plant height, specific leaf area (SLA), leaf nitrogen concentration (LNC)) and generative traits (panicle length, number of inflorescences, seed mass). Plant-plant interactions were assessed by calculating the Relative Interaction Index (RII). *Bromus erectus* increases at the detriment of the other three species because of its highest biomass production when nutrients are added. When *B. erectus* was grown alone, biomass production significantly increased when nutrients were added. The effect of intraspecific competition in *B. erectus* was slightly more intensive than interspecific competition, in contrast to the other grasses. Also, *B. erectus* was dominant when nutrients were added, but less so when clipped. As a result, the growth and competitive ability of *B. erectus* affected *S. capillata* and *S. tirsa* more negatively than *B. pinnatum*, which can result an increasing dominance of *B. erectus* under future increasing nitrogen enrichment, leading to displacement of the two rare species of *Stipa*.

Keywords: *Bromus erectus*, *Brachypodium pinnatum*, clipping, functional traits, land-use change, nitrogen addition, growth performance, plant-plant interaction, Relative Interaction Index, *Stipa capillata*, *Stipa tirsa*

Introduction

Global change in terms of deposition of atmospheric nitrogen and changes in land use can affect species richness in xerothermic grasslands (Bobbink et al. 2010, Duprè et al. 2010, Diekmann et al. 2014, Hülber et al. 2017, Kübert et al. 2019). For such grasslands, critical

nitrogen loads range between 14 and 25 kg/ha per year (de Jong et al. 1998) and nitrogen uptake by plants is likely to decline due water stress associated with drought (Homyak et al. 2017), resulting in an increase in plant mortality (Kübert et al. 2019). Human-caused eutrophication has led to changes in nutrient and water cycling and soil conditions (Perring et al. 2018), destabilized primary production in grasslands (Bharath et al. 2020) and losses of typical species of xerothermic grassland in recent decades (Bruelheide et al. 2020), all of which point to changes in the interactions between grass species (Mariotte et al. 2013). In contrast, nitrogen over-fertilization can result in certain grass species becoming dominant (de Malach et al. 2017, Wang et al. 2021) and promote their above-ground biomass production (Bai et al. 2015). Grasses have the competitive advantage of being able to use available nitrogen more efficiently (Hautier et al. 2009, Stevens & Gowing 2014) and produce a lot of litter (Foster & Gross 1998), which inhibits the growth of smaller species along with reducing the amount of light that reaches ground level (Hegedušová & Senko 2011, Ridding et al. 2020). Thus, an increase in the amount of litter can strongly inhibit seed germination and seedling survival (Donath & Eckstein 2010).

In addition to nitrogen input, changes in traditional land use (e.g. grazing by sheep and goats, annual or biennial mowing in order to prevent encroachment by shrubs) may have an adverse effect on the biodiversity of xerothermic grassland and promote the dominance of certain grass species (Bobbink et al. 2010, Diekmann et al. 2014, 2019, Elias et al. 2018, Bohner et al. 2019, Lemmer et al. 2021). Grasses produce more biomass in xerothermic grasslands than dicotyledonous plants (Del-Val & Crawley 2005, Partzsch et al. 2018) and following changes in land use, their increase has resulted in the conversion of previously species-rich to species-poor grassland communities (Partzsch 2000, Wesche et al. 2012, Rupprecht et al. 2016). Selective defoliation caused by traditional land use induces grasses to produce compensatory growth and partially or completely replace all the lost biomass (Agrawal 2000, Stevens & Gowing 2014). Moreover, the timing of grazing can have an important effect on the competitive ability of grasses, since e.g. with extensive late summer grazing, competitive grasses are less likely to be grazed due to their reduced nutritional value (Dostálek & Frantík 2012, Hejcmanová et al. 2016).

Over the last few centuries, there has been an increase in the dominance of grasses such as *Bromus erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and species of *Stipa* in xerothermic grasslands (Bobbink et al. 1998, Bornkamm 2006, 2008, Meier & Partzsch 2018, Meier et al. 2021), which seems to be a global phenomenon (Chýlová & Münzbergová 2008). In central Germany, within the last two decades the presence of *B. erectus* has significantly increased and its cover in dry and semi-dry grasslands has tripled, while that of *B. pinnatum* and *S. capillata* has remained constant (Meier et al. 2021). These grasses have a longer lifespan than others and are therefore more resistant to environmental changes, and have a competitive and stress-tolerant strategy type (CS) (Grime 2001). Furthermore, *B. erectus*, *B. pinnatum* and species of *Stipa* often occur together in xerothermic grasslands (Bieringer & Sauberer 2001, Meier & Partzsch 2018, Meier et al. 2021) and have been the subject of various experiments on plant-plant interactions, e.g. under nitrogen addition, drought and changes in land use (Corcket et al. 2003, Wang et al. 2021).

Plant-plant interactions can be both positive in the sense of facilitation and negative in the sense of competition between individuals of one species (intraspecific) or individuals of different species (interspecific) (Callaway & Walker 1997, Brooker et al. 2008,

Freckleton et al. 2009, Thorpe et al. 2011, Dohn et al. 2013, Liancourt & Doležal 2021). These interactions depend on environmental conditions and species-specific plant traits (Callaway & Walker 1997, Holmgren et al. 1997, Callaway 2007, Seifan et al. 2010) and are important factors determining the regulation of species composition, productivity, structure and dynamics of plant communities and function of ecosystems (Brooker 2006, Thorpe et al. 2011, Le Bagousse-Pinguet et al. 2014, Tredennick et al. 2018). Also, commonness and status of the plants play an important role. So, rare native plants are less competitive than non-native plants or common native plants (Zhang & van Kleunen 2019). Functional traits such as plant height, specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen concentration (LNC) and seed mass are linked to resource use and competitiveness of plants (Reich 2014, Garnier et al. 2016). However, there are no reports of the interactions between xerothermic species of grass in combination with nutrient supply and above-ground biomass removal and previous studies on the competitive ability of *B. erectus* are rather limited to long-term observations (Bornkamm 1961, 1974, 2006).

The aim of this study is therefore to determine whether *B. erectus*, in particular, becomes more competitive when grown with other species of xerothermic grass when nutrients are added and traditional land use decreases, such as grazing or mowing. Such effects could result in changes in dominance ratios and eventually to a decline in species diversity in xerothermic plant communities, especially since *B. erectus* and species of *Stipa* (e.g. *S. capillata*, *S. tirsa*) are relatively similar in their functional traits, so that competitive exclusion can occur if abiotic conditions change (Meier et al. 2019). In the present study, clipping experiments were used to study the effects of land use on grasses, where the above-ground biomass of a plant is trimmed to stubble height (Kimball & Schiffman 2003), but excluding the influence of livestock trampling and excrement (Li et al. 2015). In order to investigate growth and interactions between *B. erectus* and the grasses *B. pinnatum*, *S. capillata* and *S. tirsa*, we simulated nutrient addition and clipping in a replacement design competition experiment (de Wit 1960) and measured several functional traits.

The objective of this study was to answer the following questions: (i) How do the vegetative traits of *B. erectus* and the other three grasses differ in the nutrient conditions and clipping treatments? (ii) Do the generative traits of *B. erectus* differ in monoculture and mixtures subject to different nutrient conditions and clipping treatments? (iii) How does *B. erectus* interact with the other three grasses when subjected to different nutrient conditions and clipping treatments?

Materials and methods

Study species

Bromus erectus Huds. (*Poaceae*) is a 30–90 cm tall perennial hemicryptophyte that produces tussocks with slightly ciliate leaf blades and 10–25 cm long panicles (Jäger 2017). The average specific leaf area is 165.7 cm^2/g (Splith et al. 2021), while mean seed mass is 4.4 mg and seed length about 10.9 mm (Klotz et al. 2002).

Brachypodium pinnatum (L.) P. Beauv. (*Poaceae*) is a perennial hemicryptophyte with a creeping rhizome. It is 60–100 cm tall and has 4–25 cm long inflorescences that are

always upright (Jäger 2017) and a mean seed mass of 3.8 mg and seed length of 9.8 mm (Klotz et al. 2002). The specific leaf area is about 183.7 cm²/g (T. Meier, unpubl. data).

Stipa capillata L. and *S. tirsa* Steven (*Poaceae*) are deciduous, perennial hemicrypto-phytes that produces tussocks and reach a height of 30–100 cm. *Stipa capillata* usually has folded leaf blades, while *S. tirsa* has very thin, thread-like and always folded leaf blades that extend into a long bristle-shaped tip. *Stipa capillata* is hairless, while *S. tirsa* has hairy feathered awns up to 50 cm long that form on caryopses (Jäger 2017). Whereas *S. capillata* has a mean seed mass of 9.6 mg and seed length of 11.4 mm, *S. tirsa* has a mean seed mass of 17.8 mg and seed length of 17.4 mm. Their specific leaf areas varied between 72.5 cm²/g and 63 cm²/g (T. Meier, unpubl. data). There are slight local differences in the occurrence of these two species (Meier & Partzsch 2018).

Competition experiment

To study the effect of *B. erectus* on *B. pinnatum* as well as *S. capillata* and *S. tirsa* we used a replacement design wherein the proportion of species within mixtures was varied maintaining a constant density throughout (de Wit 1960). In this experiment, addition of nutrients and above-ground removal were simulated. In summer 2017, we collected mature seeds of the target species from different populations in xerothermic grasslands in Saxony-Anhalt, Germany. The seeds were pooled and the seeds of *S. capillata* and *S. tirsa* were cold-stratified for 10 days to break dormancy (as reported for other species of *Stipa* (Ronnenberg et al. 2008)). In October 2017, seeds of all these grass species were sown in plastic pots containing a compost-sand mixture (3:2, pH value 7.0) and cultivated in a greenhouse.

In April 2018, juvenile plants at the stage of the first primary leaves were transferred to Mitscherlich-pots (diameter 22 cm; height 19 cm) filled with the same substrate (the soil was pretreated with steam to preclude the emergence of other seedlings). All pots were placed outdoors in the Botanical Garden of Halle (Saale). The plants were planted at two density levels of either 9 individuals per pot or 1 individual per pot and in three different species compositions for the 9 plants per pot: monoculture or two mixtures with either a ratio of 6:3 or 3:6. The plants were arranged in three rows of three per pot (plants of the same species placed in one horizontal row). Within the mixtures, the proportion of the two species varied, with the less abundant species being placed in the middle row. In addition, single individuals of each species were planted in order to calculate the plant-plant interaction indices. All monocultures, mixtures and single individuals were grown with and without additional nutrients. Unfertilized pots simulated nutrient-poor conditions, while fertilized pots simulated nutrient-rich conditions by adding 1 g (per pot) of NPK (nitrogen, phosphorus, potassium) slow-release granule fertilizer (Basacote Plus 9M, 15% N, manufactured by COMPO GmbH & KG, Münster, Germany).

The following 14 density-composition levels were used: (i) monocultures: Be9 (*B. erectus*, 9 individuals), Bp9 (*B. pinnatum*, 9 individuals), Sc9 (*S. capillata*, 9 individuals), St9 (*S. tirsa*, 9 individuals); (ii) mixtures: Be6Bp3 (*B. erectus*, 6 individuals and *B. pinnatum*, 3 individuals), Be3Bp6 (*B. erectus*, 3 individuals and *B. pinnatum*, 6 individuals), Be6Sc3 (*B. erectus*, 6 individuals and *S. capillata*, 3 individuals), Be3Sc6 (*B. erectus*, 3 individuals and *S. capillata*, 6 individuals), Be6St3 (*B. erectus*, 6 individuals and *S. tirsa*, 3 individuals), Be3St6 (*B. erectus*, 3 individuals and *S. tirsa*, 6 individuals);

(iii) low-density level: Be1 (*B. erectus*, 1 individual), Bp1 (*B. pinnatum*, 1 individual), Sc1 (*S. capillata*, 1 individual), St1 (*S. tirsa*, 1 individual). Each density-composition level was replicated 16-times (448 pots: 224 unfertilized, 224 fertilized; total of 3008 individuals) and all pots were located randomly, with their positions changed every 2–3 weeks throughout the vegetation period. The plants in the pots were watered as required and any weeds removed.

In July 2018, the following growth and fitness traits were measured per individual: plant height [cm], leaf area [mm^2], leaf dry mass [mg], SLA [mm^2·mg^{-1}], LDMC [mg·g^{-1}], leaf carbon concentration (LCC) [%], leaf nitrogen concentration (LNC) [%] and C/N ratio. These traits were quick and easy to measure and are closely linked to resource utilization and competitiveness (Garnier et al. 2016). Plant height was measured as the distance between the highest photosynthetic organ and the base of the plant (Weiher et al. 1999); thus, inflorescences were not considered. One well-developed leaf of each individual per pot was taken and kept moist in plastic bags with water and stored in a cool box for further analysis (Pérez-Harguindeguy et al. 2013). In the laboratory, the leaves were then scanned (resolution: 300 dpi) and their areas analysed using the program WinFOLIA Pro (S). They were weighed, then dried at 80 °C for 24 h and weighed again to determine their leaf dry mass. The data were used to calculate SLA (ratio between leaf area and leaf dry mass) and LDMC (ratio between leaf dry mass and water-saturated fresh mass of the leaf). Afterwards, the leaf samples were milled (Vibratory Mill MM 400, Retsch GmbH) and transferred to a C/N analyser (vario EL cube, Elementar Analysensysteme GmbH). Only mixed leaf samples were examined, i.e. one sample for each species per pot (monocultures: one sample, mixtures: two samples). As a result, LCC and LNC can be determined and the C/N ratio analysed.

Subsequently (end of July 2018), to simulate above-ground removal, plants from eight replications of each nutrient condition per density-composition level were clipped (clipping time for nutrient-poor grasslands at the beginning of July or later; Briemle 2004). The individuals were clipped at 3–5 cm above the soil surface to avoid any damage to the meristem (standard cutting height of 5 cm in agriculture; lower cutting height possible for grasses; Löbbert 1998). The above-ground biomass [g] was dried at 80 °C for 24 h and then weighed. As a control, the plants from the other eight replications of each nutrient condition per density level remained unclipped. Therefore, the following four treatments (112 pots per treatment) of the 14 density-composition levels were carried out: (i) unclipped, no fertilizer; (ii) unclipped, with fertilizer; (iii) clipped, no fertilizer; (iv) clipped, with fertilizer. One year later, in July 2019 (without further application of fertilizer and clipping), the same parameters were recorded and, additionally for *B. erectus*, the generative traits per individual: panicle length [cm], number of inflorescences [n] and seed mass [mg]. To determine the seed mass, 10 seeds were taken from each individual, weighed separately and the mean value calculated. After the end of the experiment (end of July 2019), the above-ground biomass produced in all treatments (unclipped and clipped) was harvested (biomass in the second year was cut at the same level as in half of the pots in the first year) and dry weighed. The experiment was run over two consecutive years, as the combined effects of nutrient addition and clipping could only be investigated in the second year and growth performance and plant-plant interactions can change over time (Kikvidze et al. 2006).

Data analysis

In order to assess plant-plant interactions between the xerothermic grasses, the Relative Interaction Index (RII) was calculated (Armas et al. 2004): $RII = (P_{+N} - P_{-N}) / (P_{+N} + P_{-N})$. P_{+N} is the performance of a target plant in the presence of neighbouring plants ($\triangleq$ individuals of the monocultures or mixtures), while P_{-N} is the performance of a target plant in the absence of neighbouring plants ($\triangleq$ single individual (low-density level); data shown in Supplementary Table S1). The RII values are in the range –1 to +1; positive values correspond to facilitation and negative values to competition. We only calculated the RII for above-ground biomass per individual as a measure of growth performance.

All the plant parameters recorded were checked for normality and variance homogeneity (Crawley 2007) and transformed logarithmically for the subsequent analyses. With the help of the Bartlett test, it was confirmed that there were no serious deviations from the assumption of an analysis of variance (ANOVA). Using two-way ANOVA, it was possible to check for differences and interactions in the first-year growth performance between the three species compositions (9, 6:3, 3:6) and nutrient conditions (without nutrients (N–) and with nutrients (N+)). Three-way ANOVA were carried out to determine differences and interactions in the second-year growth performance between species compositions, nutrient conditions and clipping treatments (unclipped and clipped). Finally, for all grasses, a general comparison was performed between the two nutrient conditions, comparing the biomass of single individuals (without interaction), and plant interactions (intraspecific = species composition in monocultures (9); interspecific = species composition in mixtures (6:3, 3:6)) using RII. Therefore, first- and second-year above-ground biomass data were pooled without differentiating between clipped and unclipped treatments in the second year, while species compositions (6:3, 3:6) were pooled for interspecific interactions. Mean values of species above-ground biomass were compared between nutrient-poor and nutrient-rich conditions using pairwise t-tests (single individuals) or two-way ANOVA with subsequent Tukey post-hoc tests (plant interactions). The various plant parameters are the dependent variables. The different species compositions and nutrient conditions as well as effects of clipping (second year) were treated as independent variables. The probability of error (P) of the independent variables was checked using an F-test, where $P < 0.05$ was considered significant. Statistical analyses were performed using R 3.6.0 (R Core Team 2019).

Results

Vegetative performance of plants

Generally, the biomass of *B. erectus* was greater in monocultures and mixtures than that of the other three species of grass in the first and second year. In the second year, there were significant differences recorded for *B. erectus* in the clipping treatment, nutrient condition and species composition (exception: mixtures with *B. pinnatum*) (Fig. 1, Table 1). In mixtures with *S. capillata* and *S. tirsa*, *B. erectus* had the significantly highest increase in biomass in the nutrient addition and unclipped treatments Be3Sc6 and Be3St6. The biomass of *B. pinnatum* was significantly higher in the monoculture in the nutrient addition and unclipped treatments, whereas for *S. capillata* there were only significant differences
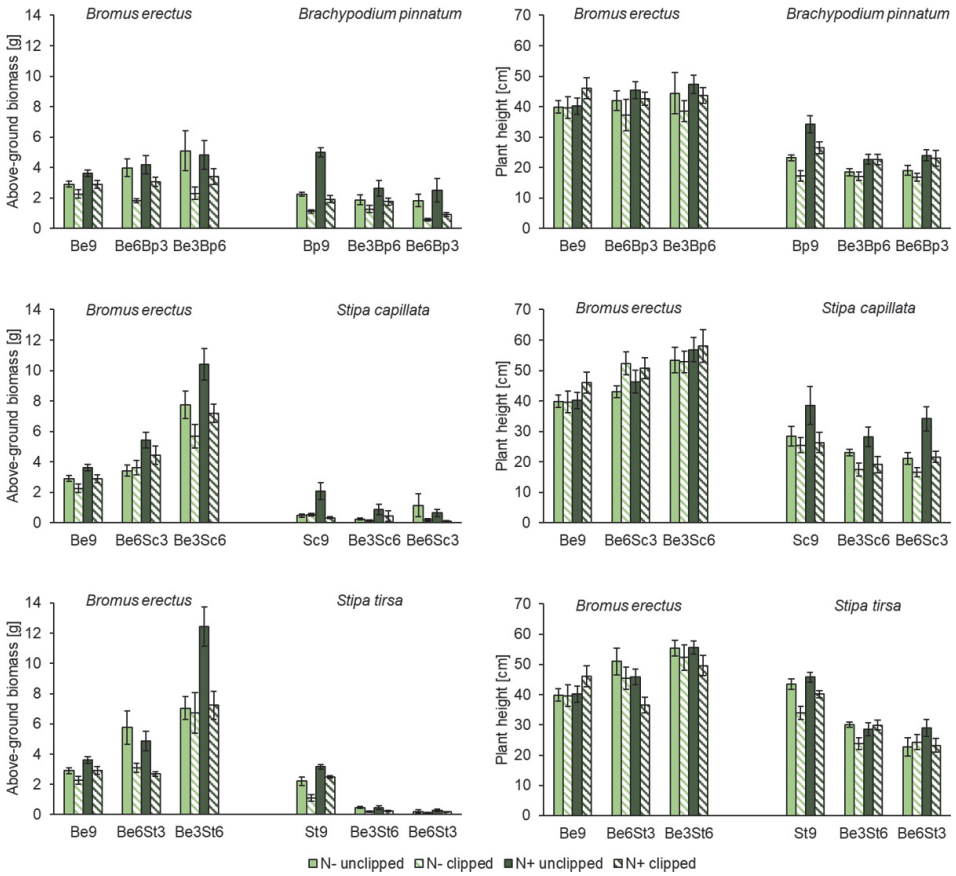
Fig. 1. Second-year performance in terms of the above-ground biomass (left) and plant height (right) per individual of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). The different coloured bars (mean+SE) represent the different species compositions (9, 6:3, 3:6) in the different combinations of nutrient conditions and clipping treatments. Using three-way ANOVA for testing mean differences (see Table 1).

between clipping treatment and species composition, Sc9 and Be3Sc6. The monocultures of *S. tirsa* produced a significantly higher biomass than the mixtures Be3St6 and Be6St3 in all nutrient conditions and clipping treatments. *Bromus erectus* reached the highest plant height in monoculture and mixtures. In Be3Bp6, *B. erectus* was significantly taller in the nutrient addition and unclipped treatments (Fig. 1, Table 1), while in mixtures with *S. capillata* and *S. tirsa*, it significantly increased in plant height with decrease in density in the pots. For the other three grasses, no significant differences resulting from the clipping, nutrient and species composition treatments were detected. The plants in monocultures Bp9, Sc9 and St9 were taller, especially in the nutrient addition and unclipped treatments. The SLA of *Brachypodium pinnatum* was higher than that of the other species and there were no significant differences in the SLAs of all the grasses, except for *B. erectus* in the mixture with *S. tirsa*, when its SLA was significantly higher in the nutrient and clipping treatments (Fig. 2, Table 1). The four grasses had a relatively similar LNCs, and

Table 1. Results of the three-way ANOVA of above-ground biomass, plant height, SLA, LNC and RII in the competition experiment: *Bromus erectus* in combination with (1) *Brachypodium pinnatum*, (2) *Stipa capillata* and (3) *S. tirsa* in the second year (clipping treatment: unclipped/clipped; nutrient condition: nutrient poor/nutrient rich; species composition: 9, 6:3, 3:6). Degrees of freedom (df), F-values and error probabilities (* $P < 0.05$, ** $P < 0.1$, *** $P < 0.001$) are given. Abbreviations: CT = clipping treatment; NC = nutrient condition; SC = species composition; E = error; ns = not significant.

| Source of variation	Biomass [g]			Plant height [cm]			SLA [mm²/mg]			LNC [%]			RII		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
1. *B. erectus* in combination with *B. pinnatum*															
B. erectus															
CT	1	20.31	***	1	0.91	ns	1	2.57	ns	1	0.66	ns	1	22.16	***
NC	1	8.66	**	1	5.54	*	1	0.10	ns	1	2.13	ns	1	8.67	**
SC	2	0.67	ns	2	0.21	ns	2	0.45	ns	2	5.44	**	2	1.98	ns
CT × NC	1	2.39	ns	1	0.90	ns	1	3.92	ns	1	0.69	ns	1	46.77	***
CT × SC	2	0.69	ns	2	1.10	ns	2	0.75	ns	2	0.48	ns	2	0.87	ns
NC × SC	2	0.01	ns	2	0.13	ns	2	0.59	ns	2	0.79	ns	2	0.21	ns
CT × NC × SC	2	0.43	ns	2	0.18	ns	2	1.48	ns	2	1.24	ns	2	1.07	ns
E	84			84			83			83			84		
B. pinnatum															
CT	1	36.18	***	1	9.75	**	1	0.44	ns	1	1.81	ns	1	50.37	***
NC	1	12.36	***	1	42.38	***	1	3.16	ns	1	2.06	ns	1	61.21	***
SC	2	14.53	***	2	7.82	***	2	3.06	ns	2	2.21	ns	2	11.71	***
CT × NC	1	0.33	ns	1	0.45	ns	1	1.05	ns	1	0.92	ns	1	35.62	***
CT × SC	2	1.81	ns	2	2.66	ns	2	0.47	ns	2	0.27	ns	2	3.57	*
NC × SC	2	1.40	ns	2	1.28	ns	2	0.31	ns	2	0.76	ns	2	4.40	*
CT × NC × SC	2	1.00	ns	2	0.02	ns	2	3.20	*	2	3.52	*	2	2.40	ns
E	83			83			82			82			83		
2. *B. erectus* in combination with *S. capillata*															
B. erectus															
CT	1	13.81	***	1	2.42	ns	1	1.24	ns	1	2.17	ns	1	97.94	***
NC	1	21.43	***	1	1.74	ns	1	0.98	ns	1	0.04	ns	1	12.38	***
SC	2	78.53	***	2	15.27	***	2	1.42	ns	2	0.16	ns	2	65.70	***
CT × NC	1	0.36	ns	1	0.12	ns	1	1.32	ns	1	0.00	ns	1	40.05	***
CT × SC	2	1.41	ns	2	0.91	ns	2	1.12	ns	2	0.65	ns	2	2.18	ns
NC × SC	2	0.13	ns	2	0.25	ns	2	1.17	ns	2	0.07	ns	2	0.80	ns
CT × NC × SC	2	0.56	ns	2	0.69	ns	2	2.62	ns	2	4.13	*	2	2.14	ns
E	84			84			83			83			84		
S. capillata															
CT	1	11.06	**	1	14.93	***	1	0.44	ns	1	2.30	ns	1	21.84	***
NC	1	0.73	ns	1	6.45	**	1	0.21	ns	1	2.62	ns	1	5.77	**
SC	2	8.61	***	2	6.11	***	2	1.25	ns	2	4.56	*	2	8.25	***
CT × NC	1	3.32	ns	1	0.87	ns	1	0.37	ns	1	0.82	ns	1	2.26	ns
CT × SC	2	0.67	ns	2	0.40	ns	2	0.20	ns	2	1.13	ns	2	0.19	ns
NC × SC	2	0.05	ns	2	1.28	ns	2	1.12	ns	2	0.18	ns	2	0.55	ns
CT × NC × SC	2	0.24	ns	2	0.11	ns	2	0.66	ns	2	2.05	ns	2	0.58	ns
E	75			75			75			71			75		
3. *B. erectus* in combination with *S. tirsa*															
B. erectus															
CT	1	30.93	***	1	3.18	ns	1	8.29	**	1	0.05	ns	1	42.54	***
NC	1	5.54	*	1	0.53	ns	1	1.86	ns	1	1.92	ns	1	22.86	***
SC	2	74.16	***	2	14.10	***	2	0.37	ns	2	2.31	ns	2	56.67	***
CT × NC	1	0.77	ns	1	0.00	ns	1	2.69	ns	1	0.32	ns	1	23.78	***
CT × SC	2	1.55	ns	2	2.76	ns	2	0.84	ns	2	1.59	ns	2	4.99	**
NC × SC	2	4.47	*	2	2.79	ns	2	1.42	ns	2	0.57	ns	2	2.68	ns
CT × NC × SC	2	1.14	ns	2	1.04	ns	2	0.95	ns	2	4.35	*	2	0.07	ns
E	84			84			83			83			84		
S. tirsa															
CT	1	18.93	***	1	11.05	**	1	0.35	ns	1	5.13	*	1	4.67	*
NC	1	11.87	***	1	7.26	**	1	2.35	ns	1	15.77	***	1	660.91	***
SC	2	100.68	***	2	48.64	***	2	3.15	*	2	1.88	ns	2	308.83	***
CT × NC	1	1.06	ns	1	0.58	ns	1	0.12	ns	1	0.01	ns	1	0.00	ns
CT × SC	2	1.64	ns	2	1.06	ns	2	0.52	ns	2	1.04	ns	2	0.57	ns
NC × SC	2	2.29	ns	2	0.03	ns	2	2.39	ns	2	3.91	*	2	124.89	***
CT × NC × SC	2	0.68	ns	2	4.18	**	2	0.10	ns	2	7.59	**	2	1.65	ns
E	73			73			73			73			71		
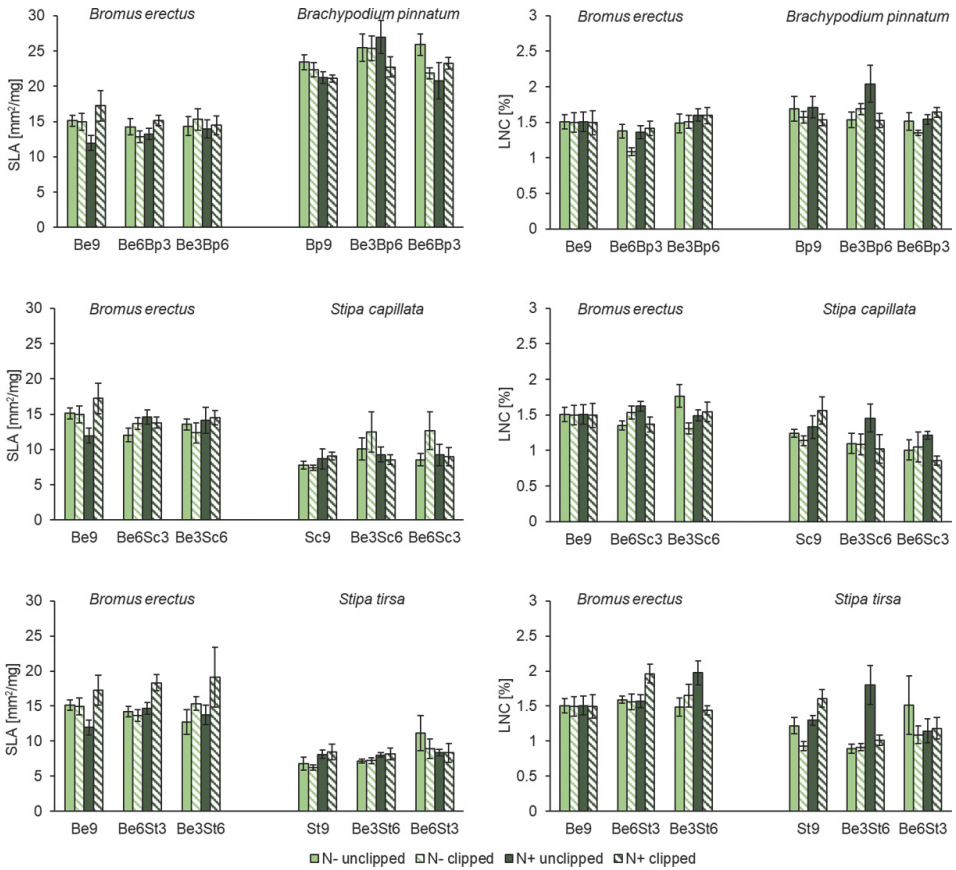
Fig. 2. Second-year performance in terms of SLA (left) and LNC (right) per individual of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). The different coloured bars (mean+SE) represent the species compositions (9, 6:3, 3:6) in the different combinations of nutrient conditions and clipping treatments. Using three-way ANOVA for testing mean differences (see Table 1).

significant differences were only recorded for *S. tirsa* in the nutrient and clipping treatments (Fig. 2, Table 1). Moreover, *B. erectus* and *B. pinnatum* had higher leaf areas and leaf dry masses than *S. capillata* and *S. tirsa* (Supplementary Fig. S1). Nevertheless, both species of *Stipa* had a higher LDMC and C/N ratio than *B. erectus* (Supplementary Fig. S2). For these grasses, significant differences in the C/N ratio between the monocultures and mixtures were detected (Supplementary Table S2). There were no pronounced differences in the effects of species composition and nitrogen addition recorded in the first and second year, so the results for the first year are shown in the supplement (Supplementary Fig. S3–S6, Supplementary Table S3, S4).

Generative performance of plants

Bromus erectus produced flowers in the second year, but the other three grasses did not. In general, the seed mass of *B. erectus* was highest in the monocultures in the clipped
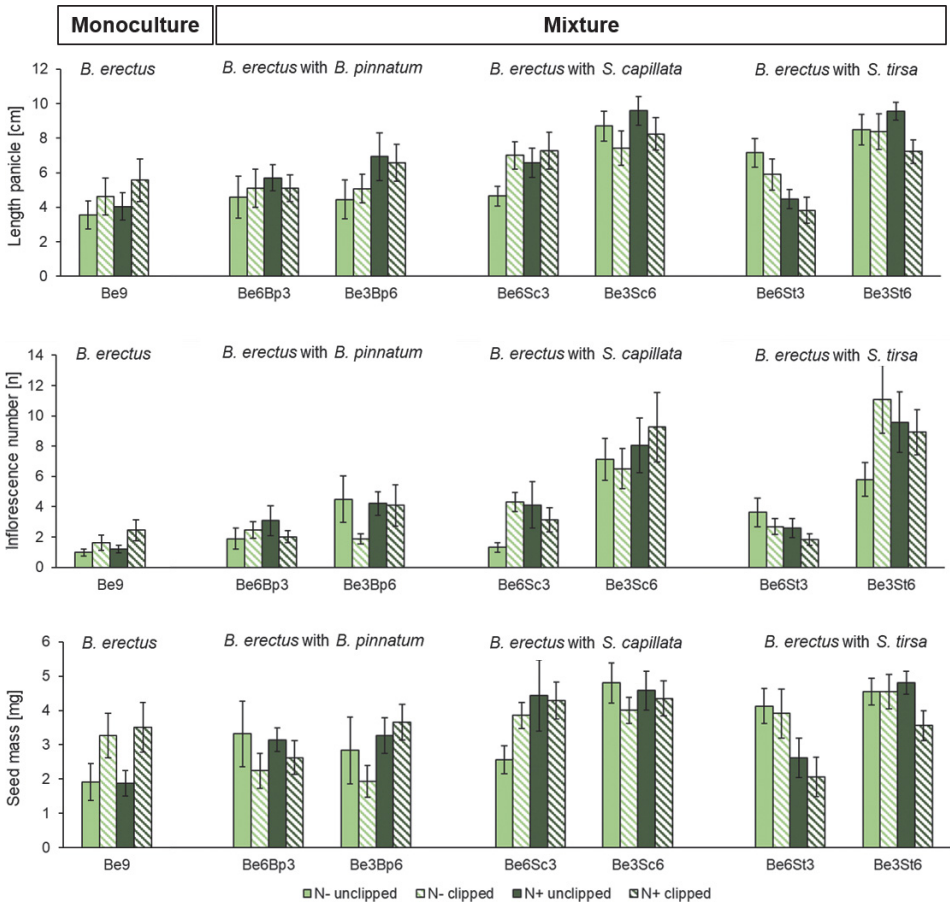
Fig. 3. Second-year performance in terms of panicle length (above), number of inflorescences (middle) and seed mass (below) per individual for the monoculture of *Bromus erectus* and in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*. The different coloured bars represent the species compositions (9, 6:3, 3:6) in the different combinations of nutrient conditions and clipping treatments (mean+SE). Using three-way ANOVA for testing mean differences (see Table 2).

treatment, while the number of inflorescences increased significantly with decrease in the number of individuals of *B. erectus* in the pots (Fig. 3, Table 2). In the mixture with *B. pinnatum*, the only significant differences in the nutrient conditions were panicle length and seed mass associated with the interaction between clipping and species composition treatments. In contrast to the monoculture, panicle length and seed mass significantly increased in the mixtures Be3Sc6 and B3St6. Seed mass decreased significantly under nutrient addition in the mixture Be6St3 (interaction nutrient condition × species composition), especially when there were higher numbers of individuals of *B. erectus*.

Plant-plant interactions

The value of RII was significantly the lowest for the monoculture of *B. erectus* in the first year and nutrient addition resulted in a reduction in RII (Fig. 4, Supplementary Table S3).

Table 2. Results of the three-way ANOVA of the panicle length, number inflorescence and seed mass for *Bromus erectus* in the competition experiment: *B. erectus* in combination with (1) *Brachypodium pinnatum*, (2) *Stipa capillata* and (3) *S. tirsa* in the second year (clipping treatment: unclipped/clipped; nutrient condition: nutrient poor/ nutrient rich; species composition: 9, 6:3, 3:6). Degrees of freedom (df), F-values and error probabilities (* $P < 0.05$, ** $P < 0.1$, *** $P < 0.001$) are given. Abbreviations: CT = clipping treatment; NC = nutrient condition; SC = species composition; E = error; ns = not significant.

Source of variation	Panicle length [cm]			Inflorescence number [n]			Seed mass [mg]		
	df	F	P	df	F	P	df	F	P
1. *B. erectus* in combination with *B. pinnatum*									
CT	1	0.87	ns	1	0.07	ns	1	0.89	ns
NC	1	4.23	*	1	2.10	ns	1	3.14	ns
SC	2	2.02	ns	2	6.48	**	2	0.81	ns
CT × NC	1	0.71	ns	1	0.37	ns	1	0.00	ns
CT × SC	2	0.19	ns	2	1.11	ns	2	3.37	*
NC × SC	2	0.17	ns	2	0.04	ns	2	0.72	ns
CT × NC × SC	2	0.11	ns	2	0.90	ns	2	0.33	ns
E	84			84			74		
2. *B. erectus* in combination with *S. capillata*									
CT	1	0.75	ns	1	2.71	ns	1	5.09	*
NC	1	2.03	ns	1	1.17	ns	1	0.94	ns
SC	2	17.70	***	2	32.00	***	2	13.68	***
CT × NC	1	0.36	ns	1	1.12	ns	1	0.56	ns
CT × SC	2	1.48	ns	2	1.43	ns	2	3.07	ns
NC × SC	2	0.05	ns	2	0.06	ns	2	0.58	ns
CT × NC × SC	2	0.19	ns	2	1.18	ns	2	0.46	ns
E	84			84			81		
3. *B. erectus* in combination with *S. tirsa*									
CT	1	0.31	ns	1	0.55	ns	1	0.11	ns
NC	1	0.59	ns	1	0.02	ns	1	3.58	ns
SC	2	18.54	***	2	40.48	***	2	11.46	***
CT × NC	1	0.28	ns	1	0.57	ns	1	1.17	ns
CT × SC	2	1.71	ns	2	1.08	ns	2	5.27	**
NC × SC	2	3.35	*	2	1.22	ns	2	3.29	*
CT × NC × SC	2	0.10	ns	2	0.17	ns	2	0.02	ns
E	84			84			82		

In all mixtures, the RII values of *B. erectus* were (significantly) slightly lower in the nutrient addition treatment. Nutrient addition resulted in the strongest reduction in RII in the monocultures and the mixtures with *B. pinnatum*, but weakest for *S. capillata* in mixtures with *B. erectus*. Interestingly, the monoculture of *S. capillata* had positive RII values in the nutrient addition treatment. The monoculture of *S. tirsa* had negative RII values similar to their mixtures, but nutrient addition resulted in an increase in RII.

In terms of RII, similar to the first year, in the second year high negative interactions between all species of grass were recorded, with significant differences in clipping, nutrient and species composition treatments (Fig. 4, Table 1). In particular, the RII recorded for the monoculture of *B. erectus* was more negative and varied less than those recorded in the mixtures. In contrast to *B. pinnatum*, the RII values were generally lower for *B. erectus* under the nutrient addition and unclipped treatments and there were strong negative interactions between *B. erectus* and both species of *Stipa*. *Stipa capillata* had the significantly lowest RII in the nutrient addition and clipped treatments, but in the monocultures with and without the nutrient addition and clipped treatments, the RII values were positive. *Stipa tirsa* had the significantly lowest RII values in the without nutrient addition treatment in both the monocultures and the mixtures, whereas in the monoculture, positive RII values were recorded in the nutrient addition treatment.
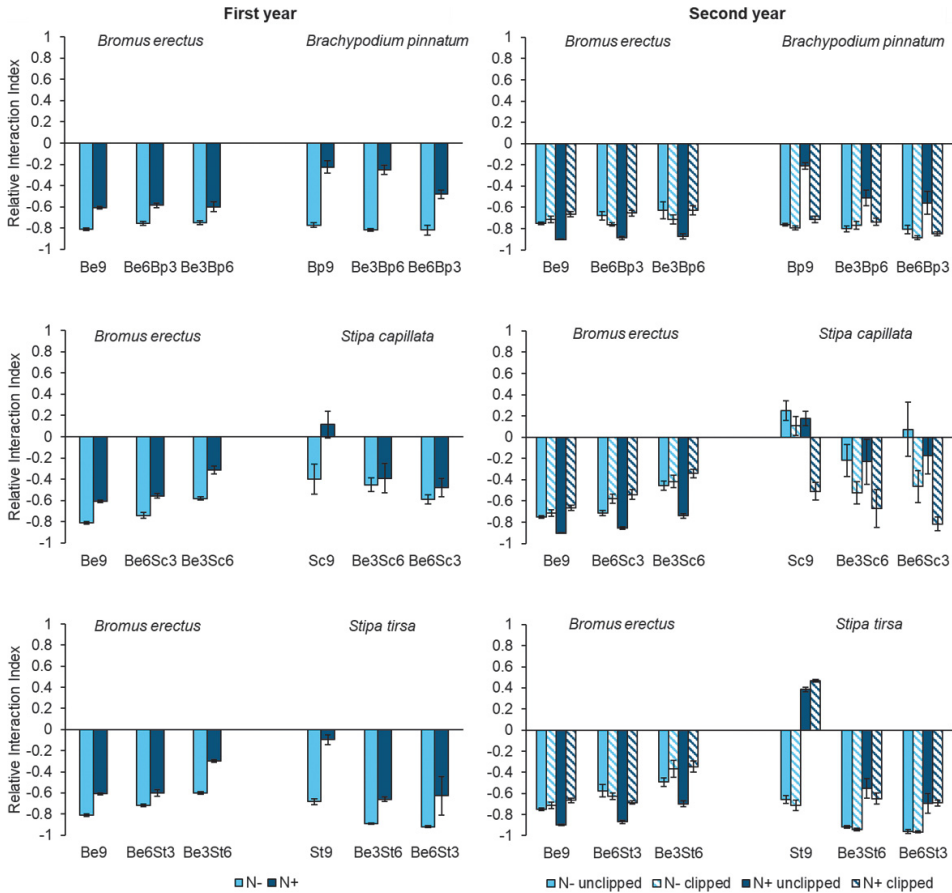
Fig. 4. First-year performance (left) and second-year performance (right) in terms of the Relative Interaction Index (calculated using above-ground biomass) of *Bromus erectus* in combination with *Brachypodium pinnatum* (above), *Stipa capillata* (middle) and *S. tirsa* (below). Positive values correspond to facilitation and negative values to competition. The different coloured bars (mean+SE) represent the species compositions (9, 6:3, 3:6) in the different combinations of nutrient conditions (left) and the combination of different nutrient conditions and clipping treatments (right). Two-way ANOVA (first-year performance) and three-way ANOVA (second-year performance) were used to test mean differences (see Table 1, Supplementary Table S2).

In general, the biomass of single individuals and interactions between the four grasses differed significantly in the different nutrient conditions (Fig. 5, Table 3). Nutrient addition resulted in a significant increase in biomass of *B. erectus* when grown alone and affected both its intra- and interspecific competitive ability, with the former interaction being more negative. On the other hand, a different pattern was identified for *B. pinnatum* and *S. tirsa*: the biomass of single individuals was significantly higher in the without nutrient addition treatment, and both intra- and interspecific competition was significantly higher than in the nutrient addition treatment. Moreover, for *S. tirsa* there was a slight intraspecific facilitation in the nutrient addition treatment. For the biomass of single individuals of *S. capillata* only a small significant increase in the nutrient addition
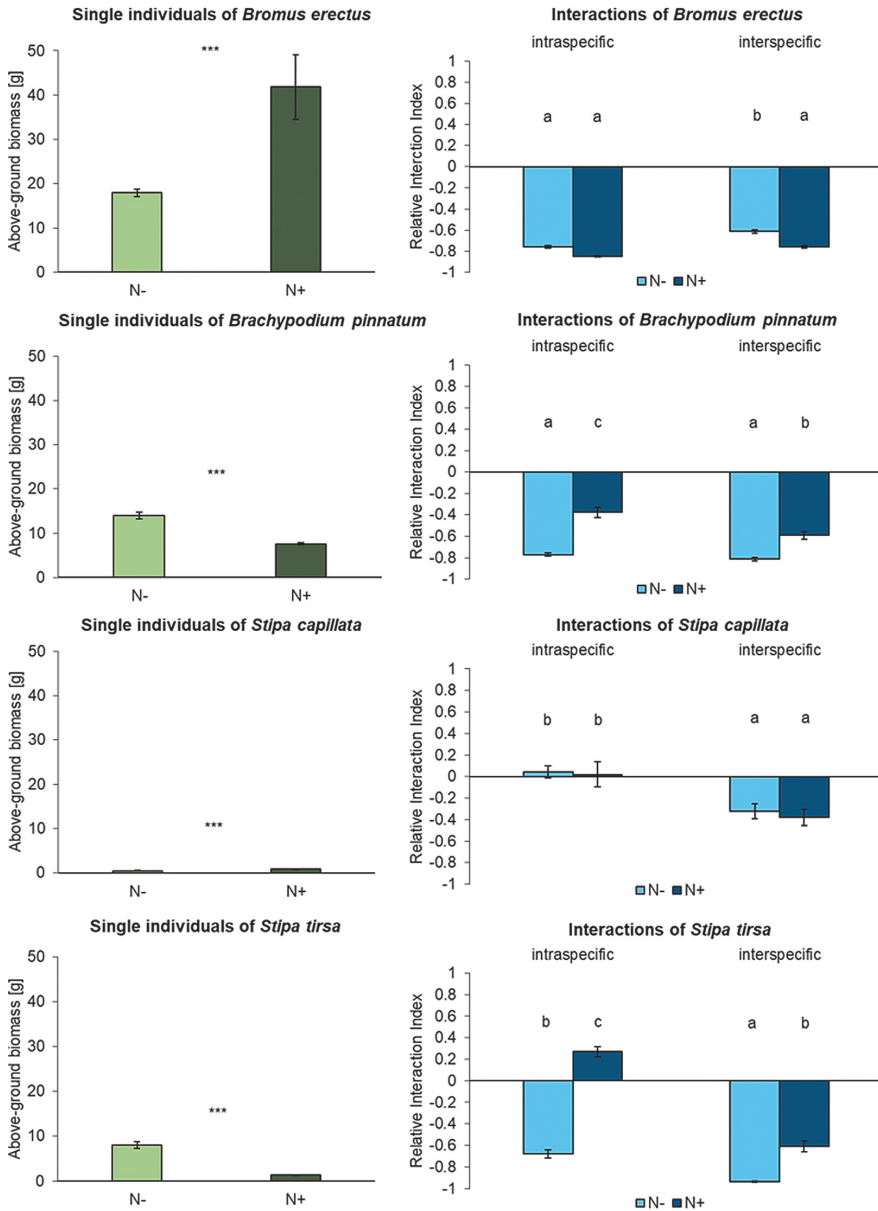
Fig. 5. General comparison of the above-ground biomass produced by single individuals (left) and plant interactions (intraspecific = species composition in monocultures (9); interspecific = species composition in mixtures (6:3, 3:6)) calculated using the Relative Interaction Index (right) of the four grasses in terms of the above-ground biomass. Relation based on the Relative Interaction Index: positive values correspond to facilitation and negative values to competition. The different coloured bars (mean+SE) represent the different nutrient conditions. The data for the first- and second-year performances in terms of above-ground biomass were pooled (no differentiation between clipped and unclipped treatments in the second year; for interspecific interaction, the species compositions (6:3, 3:6) were pooled). Results of the t-test (single individuals): *** $P < 0.001$. Results of the two-way ANOVA (see also Table 3) and calculated Tukey's post hoc-test (plant interactions): different letters indicate significant differences at $P < 0.05$.

Table 3. Results of the two-way ANOVA of the combined effects of the nutrient poor/ nutrient rich and interspecific/ intraspecific treatments for the four grasses in terms of above-ground biomass. The data for the first year and second year above-ground biomasses were pooled (see chapter: data analysis). Degrees of freedom (df), F-values and error probabilities (** $P < 0.1$, *** $P < 0.001$) are given. Abbreviations: NC = nutrient condition; PI = plant interaction; E = error; ns = not significant.

Source of variation	*B. erectus*			*B. pinnatum*			*S. capillata*			*S. tirsa*		
	df	F	P	df	F	P	df	F	P	df	F	P
NC	1	62.26	***	1	80.90	***	1	0.17	ns	1	195.38	***
PI	1	21.91	***	1	15.55	***	1	18.84	***	1	174.91	***
NC × PI	1	1.18	ns	1	7.13	**	1	0.04	ns	1	53.99	***
E	220			91			87			83		

treatment was recorded, but it had no significant effect on the interactions between plants. Unfortunately, the effects on the generative traits of *B. erectus* could not be studied as only a few individuals produced flowers so it was not possible to calculate its RII.

Discussion

The four species of xerothermic grass responded differently to nitrogen addition and above-ground biomass removal. Compared to the other three grasses, the growth of *B. erectus* in terms of its vegetative traits was the greatest. The greater growth and competitive ability of *B. erectus* affected *S. capillata* and *S. tirsa* more negatively than *B. pinnatum*. *Bromus erectus* was often dominant in the nutrient addition treatment, but less so in the clipping treatment, which had the strongest effect on its intraspecific competition and slightly weaker effect on its interspecific competitive ability. It is likely that in the future *B. erectus* will become increasingly dominant in xerothermic grasslands in central Germany and displace both species of *Stipa*.

Vegetative performance of the four xerothermic grasses

In the first and second year, species-specific responses in growth performance in the monocultures and mixtures and nutrient conditions and clipping treatments were detected for the four species of grass, with *B. erectus* being most frequently dominant. In general, there was a clear significant effect of the presence of neighbouring plants in the different species compositions on above-ground biomass, whereas there were only slight (none significant) effects on other vegetative traits. The vegetative traits of *B. erectus* (highest biomass production and tallest) and *B. pinnatum* (highest SLA) increased significantly better than those of *S. capillata* and *S. tirsa*.

There were few interactive effects between nutrient addition, clipping and species composition for all the grasses studied. Grasses are strongly nitrogen-limited (Ellenberg et al. 2001), which was particularly evident as the growth of *B. erectus* and *B. pinnatum* in the first year was enhanced by the addition of nitrogen; although LNC also increased in all grasses under the same conditions. Nitrogen addition can lead to increased LNC in grasses, as a richly branched root system enable the rapid uptake of nutrients from soil (You et al. 2017).

Bromus erectus was the tallest and produced the most biomass of all the species, even in the second year, with lower numbers of individuals in the mixtures with both species of *Stipa* in the nutrient addition and unclipped treatments. This indicates a trend towards overcompensation in the production of above-ground biomass (Stevens & Gowing 2014), as in the second year, nitrogen addition resulted in the above-ground growth of *B. erectus* being even higher, as competitive species can quickly obtain additional resources (Hautier et al. 2009). Meier et al. (2021) report that leaves of large tussocks of *B. erectus* are partially grazed in summer and rapidly resprout in autumn. Nitrogen inputs and abandonment can favour an increase in the dominance of *B. erectus* (Bornkamm 2008) such that this species becomes a major contributor to the above-ground biomass in plant communities (Steinger et al. 2007). Nevertheless, *B. pinnatum* had a higher SLA than *B. erectus*, indicating a presumably higher mass-based light-saturated photosynthetic rate (Wright et al. 2004).

Differences in growth are also associated with the morphology of the species. Taller, more broad-leaved grasses generally outcompete more medium-sized, fine-leaved grasses (Bohner et al. 2019), which was verified by the results for the mixtures of *B. erectus* (higher SLA) and *S. capillata* or *S. tirsa* (lower SLA). In this context, light plays a crucial role, as plants that use light more efficiently and position their leaves between neighbouring plants have a greater or faster growth rate (Farrer & Goldberg 2011, Craine & Dybzinski 2013). Thus, the increased biomass accumulation of *B. erectus* growing in pots may reduce the light available to both species of *Stipa* and consequently inhibit their growth.

Generative performance of Bromus erectus

The likelihood of *B. erectus* flowering in the second year was significantly enhanced by decreasing numbers of individuals in the pots at all three species composition levels. This indicates intraspecific competition in the mixtures. In the clipping treatment, seed mass significantly increased in the monoculture. The production of heavier and larger seeds can be beneficial for seedling establishment and survival (Leishman & Westoby 1994, Moles & Westoby 2006) and clipping may have a positive effect on the fitness of *B. erectus*. Lemmer et al. (2021) experimentally demonstrate that under current climatic conditions, population growth of *B. erectus* is higher in mowed than in grazed plots, while under future climatic conditions, population growth rates are similar in both types of management. Thus, population growth rates of *B. erectus* can respond quickly to environmental conditions and their interactions (Compagnoni & Adler 2014, Prevéy & Seastedt 2015), but this may be considered to be problematic for conservation as it could enable this grass to become more abundant in the future compared to other xerothermic grassland species.

Plant-plant interactions of the four xerothermic grasses

We revealed very strong intraspecific competition for *B. erectus*, as the significantly lowest RII values were recorded for the monoculture of this species in the nutrient addition treatment (see Splith et al. 2021) and intraspecific competition was evident for *B. pinnatum* in nutrient poor conditions. Similar results are well documented experimentally for *Festuca rupicola*, in that this species is more negatively affected by high intraspecific competition and, consequently, it suppresses itself (Schulze et al. 2014, Faulhaber & Partzsch

2018, Partzsch 2019). As such, increased self-limitation may occur with increase in numbers of individuals of the same species in pots (see e.g. Blank 2010, Müller et al. 2016), which was also confirmed for *B. erectus* (Splith et al. 2021). Such self-limitation induced by intraspecific competition is consistent with the theory of species coexistence, which assumes that competition inevitably results in a decline in biodiversity (Aschehoug & Callaway 2015). Hence, the effect of intraspecific competition should be stronger than that of interspecific competition in order to provide a stabilizing mechanism for regulating species abundance and coexistence (Chesson 2000, Silvertown 2004).

Conversely, in the second year, both species of *Stipa* showed facilitative effects in the monocultures, but with different responses to the respective nutrient conditions and clipping treatments. Here, the biomass of *S. capillata* was higher under nutrient-poor conditions (although the general comparison based on the pooled data revealed no differences between the nutrient conditions for the plant interactions), while that of *S. tirsa* was promoted under nutrient-rich conditions. This indicates the best conditions for both species, with *S. capillata* occurring mainly in continental dry and *S. tirsa* in continental semi-dry grassland communities, which have higher nutrient and water supply (Schubert et al. 1995, Meier & Partzsch 2018). Moreover, intraspecific competition was recorded for *S. capillata* in nutrient addition and clipping treatments. It is generally known that this species is intolerant of mowing (mowing tolerance 2; Klotz et al. 2002) and, probably based on our simulated above-ground removal, only single individuals of the monoculture were able to resprout in the second year.

Then again, strong interspecific competition occurred in mixtures, which favoured *B. erectus*. Neighbouring species compete for essential resources from a common finite pool (Aschehoug et al. 2016), which was simulated by the limited amount space in the pots in our experiment. While *B. erectus* is more sensitive than *B. pinnatum* to competition, it is more stress tolerant with regard to drought and disturbance (Corcket et al. 2003, Liancourt et al. 2005). Furthermore, *B. erectus* develops very extensive root systems of up to at least 90 cm (Kutschera & Lichtenegger 1982), which outcompete *B. pinnatum* with its shallow rooting system and elongated rhizomes (Bornkamm 2006). Plants with deeper root systems are also able to obtain water from deeper soil layers and thus reduce the water available for competitors (Violle et al. 2009). However, site-specific aspects cannot be neglected in the field, where the cover of *B. erectus* may decrease due to being shaded by surrounding shrubs (Dierschke 2006) and the cover of *B. pinnatum* may increase (Baier & Tischew 2004).

The lowest RII values were recorded for the functionally similar species *S. capillata* and *S. tirsa* in the presence of *B. erectus* in the clipping treatment. In accordance with the results of Meier et al. (2019), this could lead to the competitive exclusion of both species of *Stipa* in the field if abiotic conditions change in the future (e.g. global warming and/or eutrophication) and *B. erectus* becomes increasingly more competitive. Indeed, *B. erectus* is spreading more and more into *Stipa* grasslands, which is considered to be consequence of succession (Bieringer & Sauberer 2001, Meier & Partzsch 2018, Meier et al. 2021). Functionally similar dominant species of grass play an equivalent role in ecosystem function (Joner et al. 2011) and are key drivers of plant community dynamics (Smith & Knapp 2003, Smith et al. 2020).

Conclusions

Based on our results, the growth and competitive ability of *B. erectus* affected *S. capillata* and *S. tirsa* more negatively than *B. pinnatum*. In particular, the growth of *B. erectus* was greater in the nutrient addition treatment, but slightly less in above-ground removal treatment. This species is taller and benefits from both nitrogen deposition and climate warming (Meier et al. 2022), and is favoured by low levels of management (Lemmer et al. 2021). We also found the same pattern, when *B. erectus* grew alone as its biomass production was boosted by the addition of nitrogen. *Bromus erectus* is spreading in xerothermic grassland and is therefore classified as a neophyte in the federal states of Thuringia and Saxony-Anhalt in Germany (Heinrich 2010, Frank & Schnitter 2016). Currently, the average cover values for *B. erectus* are between 30% and 40% in xerothermic grasslands in central Germany, but its competitive potential may not yet be fully achieved (Meier et al. 2021). In the future, tall-growing species like *B. erectus* may become more dominant, affecting the community through high competition and structural changes, resulting in a lower species diversity (Meier et al. 2021, 2022). Zhang & van Kleunen (2019) report that high intrinsic growth rates are the main drivers of the highly competitive ability of common alien plants with strong intraspecific competition and thus play an essential role in the invasion success of a species, which indicates the superiority of *B. erectus*.

Compared to clipping or annual mowing, grazing had a more positive effect in the conservation of grasslands by promoting gradual but continuous biomass removal as well as more openness throughout the growing season, which reduces competition between species (Tälle et al. 2016). In practice, additional intensive spring grazing may be required to suppress highly competitive grasses (Elias et al. 2018), as mowing late in the season can promote the spread of grasses (Nowak & Schulz 2002, Briemle 2004).

Supplementary materials

Fig. S1. – Second-year performance in terms of leaf area and leaf dry mass of *Bromus erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Fig. S2. – Second-year performance in terms of LDMC and C/N ratio of *Bromus erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Fig. S3. – First-year performance in terms of above-ground biomass and plant height of *Bromus erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Fig. S4. – First-year performance in terms of of SLA and LNC of *Bromus erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Fig. S5. – First-year performance in terms of the leaf area and leaf dry mass of *Bromus erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Fig. S6. – First-year performance in terms of LDMC and C/N ratio of *B. erectus* in combination with *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa*.

Table S1. – First-year and second-year performance in terms of above-ground biomass of *Bromus erectus*, *Brachypodium pinnatum*, *Stipa capillata* and *S. tirsa* in the different nutrient conditions and clipping treatments.

Table S2. – Results of the three-way ANOVA of leaf area, leaf dry mass, LDMC, C/N ratio and RII in the competition experiment.

Table S3. – Results of the two-way ANOVA of above-ground biomass, plant height, SLA, LNC and RII in the competition experiments.

Table S4. – Results of the two-way ANOVA of leaf area, leaf dry mass, LDMC, C/N ratio and RII in the competition experiment.

Supplementary materials are available at www.preslia.cz

Acknowledgements

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Vliv přidání živin a odstranění nadzemní biomasy na interakce mezi druhy xerotermních trav

Aspekty globální změny, jako jsou zvyšující se atmosférická depozice dusíku a změny ve využívání půdy, podporují nárůst dominance trav v xerotermních travních porostech. Předpokládá se, že zvýšený obsah živin a změny ve využívání krajiny ovlivňují interakce mezi expandujícím sveřepem vzpřímeným (*Bromus erectus*) a dalšími xerotermními druhy trav ve středním Německu. Interakce mezi rostlinami jsou klíčovým faktorem regulace druhového složení, produktivity, struktury a dynamiky rostlinných společenstev i fungování ekosystémů. Provedli jsme kompetiční pokus s *B. erectus* a dalšími druhy trav (*Brachypodium pinnatum*, *Stipa capillata* a *S. tirsa*). Abychom zjistili vliv *B. erectus* na ostatní trávy, pěstovali jsme všechny druhy ve dvou hustotách (9 jedinců nebo 1 jedinec na květináč) a ve třech různých druhových složeních devíti rostlin v monokultuře a směsi (6:3, 3:6). Ošetření zahrnovala přídavek živin (prostředí chudé vs. bohaté na živiny) a odstranění nadzemní biomasy (nestříhané vs. stříhané). Během dvou po sobě následujících let byl růst každého druhu dokumentován měřením vegetativních (nadzemní biomasa, výška rostlin, specifická listová plocha – SLA, koncentrace dusíku v listech – LNC) a generativních znaků (délka lat, počet květenství, hmotnost semen). Interakce mezi rostlinami byly hodnoceny pomocí relativního interakčního indexu (RII). *Bromus erectus* prospíval na úkor ostatních tří druhů, při přidání živin měl nejvyšší produkci biomasy. Vliv vnitrodruhové kompetice na *B. erectus* byl intenzivnější než vliv kompetice mezidruhové. *Bromus erectus* měl při mezidruhové kompetici větší negativní vliv na *Stipa capillata* a *S. tirsa* než na *B. pinnatum*, takže v budoucnosti předpokládaná rostoucí dominance *B. erectus* v důsledku zvýšeného obohacování dusíkem může vést k vytlačení obou vzácných druhů rodu *Stipa*.