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The effect of nitrogen addition on biomass production and competition in three expansive tall grasses

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ABSTRACT

A large increase of grasses *Calamagrostis epigejos*, *Bromus inermis* and *Brachypodium pinnatum* has often been observed in many regions enriched by higher nitrogen (N) wet deposition inputs. Competitive relationships between these grasses under enhanced N loads have not yet been studied. Therefore an outdoor experiment was established which involved monocultures of *Calamagrostis*, *Bromus* and *Brachypodium* and their 1:1 mixtures in containers under two N treatments, i.e., unfertilized and fertilized (+50 kg N ha^{-1}). In monocultures, the total aboveground biomass of *Calamagrostis*, *Bromus* and *Brachypodium* were 1.1, 3.6 and 2.5 times higher respectively due to enhanced N fertilization. Relative crowding and aggressivity coefficients indicate that *Calamagrostis* and *Bromus* dominate when mixed with *Brachypodium* at both levels of N availability. When mixed with *Bromus*, *Calamagrostis* is the poorer competitor at lower N loads, however, it can be dominating in N fertilized treatments.

1. Introduction

Climate change and airborne N loads in combination with the impacts of land use, will give rise to new opportunities for grassland expansion. Both biological expansions by native plants and invasion of alien plant species are large-scale phenomena of widespread importance and represent one of the major threats to European biodiversity (Lambdon et al., 2008). Similar behaviour is typical for several native European perennial tall grasses such as *Arrhenatherum elatius*, *Brachypodium pinnatum* and *Calamagrostis epigejos*. These expansive tall grasses dramatically change plant diversity in many types of grassland ecosystems (Bobbink and Willems, 1993; Willems et al., 1993; Sedláková and Fiala, 2001; Fiala et al., 2004).

The competitive grasses can arrest succession for a long time forming a dense, compact sward (Prach and Pyšek, 1994). Thus mentioned tall grasses represent plant species of global importance due to their intensive expansion into various ecosystems and to recent spreading in large areas in Europe and North America (e.g., Bobbink and Willems, 1993; Wilson et al., 1995; Ten Harkel and Van der Meulen, 1996; Rebele and Lehmann, 2001; Cully et al., 2003; Fiala et al., 2003; Endresz et al., 2005; Vinton and Goergen, 2006; Dillemuth et al., 2009; Bahm et al., 2011; Fink and Wilson, 2011). We examined the following three grasses (*Calamagrostis epigejos* (L.) Roth, *Bromus inermis* Leysser, *Brachypodium pinnatum* (L.) P.B.) expanding in abandoned field and short dry grass stands disturbed by sheep and forming nearly monospecific secondary successional communities.

The perennial rhizomatous grass *Brachypodium pinnatum* is often the dominant species of chalk grasslands, occurring on mild warm slopes, with middle to deep soils and successfully occupying full sun to shaded sites. *Brachypodium* seems well adapted to high N and low phosphorus conditions (Willems et al., 1993). Addition of N fertilizer leads to increasing dominance of *Brachypodium* in chalk grasslands (Bobbink et al., 1988; Bobbink, 1991). Temporally water stress associated with high radiation load appears to pose a limitation on the ecological distribution of this species in Central Europe (Mojzes et al., 2003).

Bromus inermis is an aggressive and highly competitive species, spreading by both seed and rhizomes and is able to exclude all other species. It can be found along roadsides, on dumps, and on the edges of fields. It has become established by invading disturbed plant communities. *B. inermis* was the species that increased in prairie grasslands with high N deposition (Stevens and Tilman, 2010). In addition, Blankespoor and Larson (1994) reported that *B. inermis* is a drought-resistant plant demanding of nutrients. However, relatively little attention has been paid to *B. inermis* as a plant species that has invaded plant communities even through

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its threatening the diversity of grass communities. Comparison of five native prairie grasses indicated that these grasses, even under the driest conditions, competed poorly with *B. inermis*, a non-native grass (Nernberg and Dale, 1997). Also Corcket et al. (2003) reported that *Bromus* can be more tolerant of drought and disturbance than *Brachypodium* resulting in competition strength. Field studies provide evidence of the negative impact of this grass on native grass ecosystems (Dillemuth et al., 2009).

Calamagrostis epigejos, a rhizomatous perennial grass, most often tolerates dry sites on soils with very low organic matter content and low to very low contents of N; however both the growth and reproduction are enhanced under open, moist and nutrient (especially N) rich conditions (e.g., Rebele and Lehmann, 2001; Fiala et al., 2003). *C. epigejos* exhibits extremely broad ecological amplitude, growing from littoral zones of aquatic habitats to dry steppe sites. It can be considered as the most expansive species in the landscape of the Czech Republic. Nowadays, *C. epigejos* is dominant in the majority of disturbed habitats from lowland to the submontane zone. A conspicuous increased expansion of this species is expected (Prach and Wade, 1992).

Plant species composition is to a large extent influenced by nutrient availability. N is often considered to be the most limiting element for plant growth in natural ecosystems. Increased N availability is obviously of major importance in European grasslands and is indicated by enhanced growth of some tall grasses (Bobbink and Roelofs, 1995). *Calamagrostis epigejos* and *Brachypodium pinnatum* mostly strongly increased as a result of enhanced nutrients availability, especially of N (e.g., Oomes and Mooi, 1981; Bobbink, 1991; Berendse et al., 1992; Fiala et al., 2003, 2004; Van den Berg et al., 2005; Liancourt et al., 2009). However, the effect of increased N availability on growth and biomass production of *Bromus inermis* has often not been examined (Dillemuth et al., 2009; Fink and Wilson, 2011).

Long term N enrichment has gradually increased the availability of N in several vegetation types, leading to competitive exclusion of characteristic species by more nitrophilic plants, especially under oligo- to meso-trophic soil conditions (Bobbink et al., 1998). Our earlier studies of the competitive ability of tall grasses suggested that the ability of *Calamagrostis* relative to *Arrhenatherum* declined in the heterogeneous soil environment when compared to homogeneous treatments (Tůma et al., 2009). Thus nutrient heterogeneity can enhance the competitive ability of *Arrhenatherum* relative to *Calamagrostis*. In addition, the greatest significant increases in relative yield of *Arrhenatherum* growing in mixtures with *Calamagrostis* occurred in both unfertilized and fertilized unclipped treatments (Tůma et al., 2005).

The aim of this study was to determine and compare the effect of higher inputs of N (1) on growth and formation of aboveground biomass of *C. epigejos, B. inermis* and *B. pinnatum* growing in monoculture and (2) to test their competitive ability in the mixture of two plant species. Therefore garden experiment was established, involving monocultures of these grasses and their mixtures (1:1) in containers of unfertilized and fertilized (+50 kg N ha^{-1}) treatments.

The following hypotheses were tested:

1) In monocultures, the most intensive growth and aboveground biomass formation will be recorded in *Calamagrostis epigejos* and *Brachypodium pinnatum* in response to N fertilization because biomass of these both grasses responds dramatically to a high soil fertility treatment (e.g., Bobbink et al., 1988; Brünn, 1999).
2) In mixtures, *Calamagrostis epigejos* can suppress *Brachypodium pinnatum* and *Bromus inermis* at both N availability levels, as *C. epigejos*, one of the most expansive grasses, will increase in N loads, due to an extensive growth of below-ground organs which can take up and use nutrients more easily and effectively (Rebele, 2000; Fiala et al., 2003, 2004).

2. Material and methods

The study was carried out as an outdoor experiment. The experimental garden is located in the SW part of Brno (49°12′N, 16°34′E) at 190 m a.s.l. Mean annual temperature in Brno is 9.4 °C and long-term mean annual precipitation is 595 mm. In May 2004, large containers (650 × 480 × 240 mm) were filled with an artificially prepared substrate of river sand and peat (pH H_2O = 6.1, pH KCl = 5.8, organic matter = 3.48%, P = 30 mg kg^{-1}, K = 38 mg kg^{-1}, Ca = 970 mg kg^{-1}, Mg = 145 mg kg^{-1}, N–NO_3 = 4.0 mg kg^{-1}, N–NH_4 = 5.6 mg kg^{-1}). In order to facilitate drainage a 30-mm layer of gravel-sand was placed in the bottom of each container. The soil moisture content in each container was maintained with irrigation wicks. On very dry summer days, the soil in each container was also watered daily. Nitrogen (solution of ammonium nitrate) was applied in fortnight intervals and represented 50 kg N ha^{-1} during the entire growing season.

Plants used in this study were propagated vegetatively from the field material. Original mother plants of three grasses (*Calamagrostis epigejos*, *Bromus inermis* and *Brachypodium pinnatum*, further *Calamagrostis, Bromus, Brachypodium*) were dug from grass stands in the Dunajovické kopce hills with xerothermic vegetation, situated near the village of Dolní Dunajovice in southern Moravia of the Czech Republic (ca 7 km SW of the town Mikulov) (see Buček et al., 2006) and transported to the experimental garden. Plants, young tillers of a similar size (with 3–5 tillers of each plant) were inserted in sand in autumn 2003. In the spring of the next year 2004, sprouting plants of a similar size were transplanted to large containers and used in the experiment. Containers were planted to contain 20 plants (92 plants per m^2). Individual plants of each species were planted in a regular pattern in a standard replacement design either as a monoculture of one of the three species or in a 1:1 ratio of potentially competing species. Each combination was replicated 4 times. At the end of the second growing season (September 2005), plants were clipped at the soil surface and separated into sterile and fertile shoots if present. Numbers of shoots were counted. Plant samples were dried (at 70 °C) to the constant dry weight, weighed and dry mass of sterile and fertile shoots was determined. Data on shoot densities and their dry mass were evaluated and compared.

In this study we used two competition indices, i.e. relative crowding coefficient (RCC) and aggressivity (A) (see Hu and Jones, 2001; Rauber et al., 2001; Nassab et al., 2011). RCC is a measure of relative dominance of one biomass component over another in a competitive system. Calculations were conducted for the individual plant species studied. The second competition index that was used was aggressivity (A) which is measure of how much the relative yield of one component of biomass production is greater than that of the other. If the aggressivity of species 1 is positive, then the species 1 is dominant, if species 1 is negative, then species 2 is the dominant species. If the absolute value of A is large, there is a large difference in the competitive abilities of the two species.

Obtained data were evaluated by means of the multifactorial analysis of variance, using the statistical package STATISTICA 7.0. A *t*-test was performed to compare mean differences between control and N fertilized treatments within individual grass species. Two-way ANOVA analysis was used to test the effect of species and of N supply as independent variables on the biomass production and shoot density of studied grasses as dependent variables. F-value and resulting P level were determined. Transformation of the data was not necessary.

3. Results

3.1. Responses of three tall grasses to additional N input when grown in monoculture

The analysis of variance (ANOVA) of grasses grown in monoculture showed a significant effect on the aboveground biomass of sterile and fertile shoots (Table 1). In all species studied, a significant effect of N treatment was found only in the biomass of sterile and total shoot biomass. Significant effect of N fertilization on monocultures of individual grass species was found in *Brachypodium* and *Bromus* but not in *Calamagrostis* (Table 1). The greater availability of N resulted in conspicuous increases of 262 and 147% in the total aboveground biomass of *Bromus* and *Brachypodium* monocultures, respectively (Table 1). N fertilization did not result in a marked increase of *Calamagrostis* aboveground biomass in monoculture. In comparison with unfertilized stands, sterile shoots accounted for most of the increase of dry mass of grasses representing 0.8, 2.5 and 3.2 fold increases in *Calamagrostis*, *Brachypodium* and *Bromus* monoculture, respectively.