Growth Performance and Species Interaction of *Festuca rupicola* Heuff. and *Dianthus carthusianorum* L. Subjected to Temperature Increase and Nitrogen Addition

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Abstract

Global processes, such as warming and eutrophication, affect plant-plant interactions. The positive (facilitation) and negative (competition) interactions depend on environmental conditions and species' characteristics and play a key role in regulating the composition, productivity, structure and dynamics of communities and ecosystems. Recently, biodiversity in former species-rich, semi-dry grasslands has decreased due to the abandonment of traditional land use, under which grass species expanded and dicots declined. The hypothesis that this phenomenon will intensify with warming and eutrophication is tested on the expanding grass *Festuca rupicola* (F) and the dicot *Dianthus carthusianorum* (D). A competition experiment were conducted with conditions simulating current average summer temperatures (20 ℃ during day/10 ℃ during night) and predicted warmer conditions (22/15 ℃) in growth-chambers, both under nutrient-poor (simulated natural habitat conditions) and nutrient-rich conditions (simulated annual N deposition). The plants were placed in pots with constant densities (five individuals per pot) but under varying mixture ratio (F5, D5, D4/F1, D3/F2, D2/F3, D1/F4). The measured plant parameters (biomass, leaf number and leaf length) and the interactions varied species-dependent: under nutrient poor conditions the performance of both species was low and the interactions were weak. After nutrient addition, growth parameters of both species developed between twofold and tenfold better and the species interacted more markedly. Under both nutrient levels, *D. carthusianorum* was significantly promoted by warming. But, warmed conditions did not affect the biomass and leaf length of *F. rupicola*, whereas leaf number significantly decreased under both nutrient levels. As such, the dicot became competed against and the grass facilitated under current conditions, while under warmed conditions the competitive ability of the grass declined and that of the dicot increased, indicating that interactions between both species reverses with warming climate. This suggests, that under predicted climate conditions, the expanding grass will decline, while the dicot will be promoted, which can have positive effects on biodiversity of semi-dry grasslands.

Keywords: global warming, global eutrophication, competition, facilitation, semi-dry grasslands

1. Introduction

Ongoing global change is characterized by different processes including warming and eutrophication. Over the past 100 years, the global average temperature has increased by approximately 0.6 ℃, and a rise of between 1.1 and 6.4 ℃ (depending on the scenario) is forecast for 2100 (Intergovernmental Panel on Climate Change [IPCC], 2007). A meta-analysis of 143 studies including several plant and animal species showed that a significant impact of global warming is already discernible, and affects the connectedness, evenness and turnover up to the rearrangement of biotic communities and extinction events (Root et al., 2003). In addition to the effects of increasing temperatures, agriculture, combustion of fossil fuels and other human activities have substantially altered the global cycle of nitrogen (N), leading to increases in availability and mobility of N over large global regions, which have environmental consequences that can be serious and long lasting (Vitousek et al., 1997). The critical N load of semi-dry grasslands lies between 14 and 25 kg ha^{-1} a^{-1} (De Jong, Fangmeier, & Jäger, 1998), but the annual deposition in the dry region of central Germany during the nineties of the last century was between 46 and 51 kg ha^{-1} a^{-1} (Körschens & Mahn, 1995). Such long-term N enrichment leads to competitive exclusion of characteristic species by more nitrophilic plants, especially under oligo- to mesotrophic conditions (Bobbink, Hornung, & Roelofs, 1998), and is implicated in floristic changes in semi-dry grasslands (Horswill et

al., 2008; Stevens, Thompson, Grime, Long, & Gowing, 2010). Thus, such increases in yield and changes in the species composition have promoted grass species (Willems & Bobbink, 1990; Bornkamm, 2006; Dupré et al., 2010).

In order to predict biotic responses to climate change, it is necessary to investigate plant-plant interactions as important elements of population dynamics (Davis, Jenkinson, Lawton, Shorrocks, & Wood, 1998), which play a key role in regulating the composition, productivity, structure and dynamic of communities and ecosystems (Fowler, 1986; Callaway, 1995; Whitford, 2002; Brooker, 2006; Cheng, Wang, Chen, & Wie, 2006; Thorpe, Aschehoug, Atwater, & Callaway, 2011). They depend on environmental conditions and species' characteristics and are manifold between the constituent species (Holmgren, Scheffer, & Huston, 1997; Callaway & Walker, 1997; Callaway, 2007; Soliveres, De Soto, Maestre, & Olano, 2010). The interactions can be estimated as "intensity", which describes the effect of one plant on another ignoring the influence of other environmental factors and as "importance where the other environmental factors are including (Welden & Slauson, 1986; Brooker et al., 2005; Zhang, Cheng, Yu, Kräuchi, & Li, 2008). Interactions are mostly identified as being negative in terms of competition for light, nutrients, space, pollinators or water, and positive in terms of facilitation, where plants protect each other from the impacts of competitors, climate extremes or herbivores as well as resources through canopy leaching, microbial and mycorrhizal networks and hydraulic lift (del-Val & Crawley, 2005; Gao, Wang, Han, Patton, & Nyren, 2005; Kuijper, Dubbeld, & Bakker, 2005; Weigelt et al., 2007; Brooker et al., 2008). Whereas competition is widely dominant in benign environments (Grime, 1973; Huston, 1979), facilitation is equally common in stressful ecosystems (Bruno, Stachowicz, & Bertness, 2003), such as savannas, deserts, shrublands or salt-marshes (Belsky, 1994; Pugnaire & Luque, 2001; Callaway et al., 2002; Maestre, Bautista, & Cortina, 2003; Maestre & Cortina, 2004). A number of studies have demonstrated that plant-plant interactions are affected by climate conditions, which change between years (Greenlee & Callaway, 1996; Herben, Krahulec, Hadincová, Pecháčková, & Wildová, 2003; Veblen, 2008; Soliveres et al., 2010), within a single growing season (Bertness & Ewanchuk, 2002), or along a climate gradient with increasing altitude (Choler, Michalet, & Callaway, 2001; Kikvidze, Khetsuriani, Kikodze, & Callaway, 2006), where competition can switch to facilitation and vice versa. In general, increasing environmental severity leads to a shift from negative to positive interactions and suggests that the global shift toward increasingly drier Mediterranean-type ecosystems will result in greater facilitation between species (Brooker, 2006).

While there is a justifiable interest in the impacts of global change on rare or endangered species (Maschinski, Baggs, Quintana-Ascencio, & Menges, 2006), the fate of widespread species is of greater relevance, because a reduction in abundance of a dominant species can have consequences in terms of habitat quality and ecosystem functioning (Hovenden et al., 2008). In this study, the interactions between two semi-dry grassland species adapted to nutrient poor soils and warm, dry climate conditions are assessed. They belong to the steppe-like ecosystem in the dry region of central Germany (Meusel, 1940; Mahn, 1965). A vegetation analyse over 40 years showed, that the abandonment of grazing over the last twenty years has led to grass species becoming more dominant while dicots have declined and become endangered (Partzsch, 2000; 2001) and the negative effect of traditional land use change on biodiversity was also detected in experimental way (Partzsch, 2011b; Partzsch & Bachmann, 2011). This phenomenon is expected to intensify as a result of predicted global change (Dupré et al., 2010).

The expanding grass *Festuca rupicola* and the rare dicot *Dianthus carthusianorum* were chosen with the aim to test the hypothesis that the performance of these species will improve under global climate change, with interactions becoming stronger in such a way that the dicot suffers for stronger competition from the grass. In order to simulate the effect of eutrophication, the performance of the species was tested under nutrient poor and nutrient rich conditions. To simulate climate conditions, two different temperature-light regimes were tested (current conditions during summer: 20/10 ºC Max and Min daily temperatures, respectively; predicted conditions: 22/15 ºC Max and Min daily temperatures, respectively; i.e. an increased temperature of approximately 3.5 ºC). The specific regimes were chosen because it is predicted that night-time radiant emittance will be much less than it is today in central Germany (Easterling et al., 1997). Competition experiments with a replacement design (after De Wit, 1960) were conducted with the following questions being investigated: 1) How do the two species perform in terms of biomass, number of leaves and leaf length under nutrient poor and nutrient rich conditions and under current and predicted climate conditions? and 2) Is there a change in biotic interactions (positive or negative and intensity and importance) between the two species after nutrient addition and warming?

2. Material and Methods

2.1 Study Species and Collection

Dianthus carthusianorum L. (Clusterhead; Caryophyllaceae) is a perennial, 15-45 cm high hemicryptophyte and *Festuca rupicola* Heuff. (Gramineae) is a perennial, 15-80 cm high tussock grass. Both species are distributed in submeridional to southern temperate Europe (Jäger, 2011) and mainly occur together in the communities of Festuco-Brometea. Whereas the rare dicot is protected by law in Germany (Korneck, Schnittler, & Vollmer, 1996), the grass is common and has spread extensively over the last 20 years and currently often dominates grassland communities subject to the abandonment of traditional land uses (Partzsch, 2000; 2001). Both species are very similar in germination biology: the seeds are not dormant and germinate very quickly after dispersal (Partzsch, 2010; 2011a). Mature seeds of the species were collected from semi-dry grasslands in the surroundings of Halle (Saale) (51.48 N, 11.97 E) at the end of June 2008. The local climate is characterized by a mean annual temperature of 9.2 ºC and a mean annual precipitation of 473 mm (Döring, 2004).

2.2 Competition Experiment

To detect interactions between the two species, a competition experiment with replacement design (De Wit, 1960) was conducted in September 2008. The proportion of both species within mixtures was varied, maintaining a constant density throughout in the pots. Treatments included a combined total of five individuals of *D. carthusianorum* (D) and *F. rupicola* (F) (adapted to the pot size: 10 cm width x 10 cm length x 11 cm height, soil substrate mass (dry): 250 g), with the proportion of each species being varied: D4/F1, D3/F2, D2/F3, D1/F4. Additional monocultures of both species (D5, F5) were prepared and all treatments were applied with eight replications. Simultaneously the treatments were tested under two nutrient-levels: pots (48) with nutrient poor soil substrate (pH 5.9; N 80 mg/l, P_2O_5 80 mg/l, K_2O 80 mg/l) simulating current field conditions and pots (48) with nutrient rich soil substrate simulating eutrophication by the use of an NPK-granule fertilizer (Basacote Plus 9M, 15 % N; produced by COMPO GmbH & KG, Münster, Germany). One gram of this fertilizer was added to each pot in order to simulate an annual N deposition of ca. 50 kg ha^{-1} a^{-1}.

The experiment was carried out simultaneously in two growth-chambers (type VB 1514, Vötsch Industrietechnik, Germany; with 96 pots per each chamber) to simulate the summertime conditions in the dry region of central Germany. A light regime (illumination 185 µmol s^{-1} m^{-2}) of 10 hours light and 10 hours dark was used, while the light phase started and ended with a twilight period (illumination 80 µmol s^{-1} m^{-2}) of two hours. The temperature regime in the first chamber simulated the approximate current summertime conditions, with 20 ºC during the day and 10 ºC during the night, while the second chamber simulated the temperature conditions under global warming, with 22 ºC during the day and 15 ºC during the night. During the twilight phases, the temperature was gradually increased or decreased and relative humidity was kept at 65% during the day and 80% at night. The pots were rearranged and randomly placed every week to mitigate effects of location in the chambers (The chambers were brand-new with guaranteed identical conditions). The pots were watered as required and the whole experiment lasted nine month.

The parameters 'number of leaves', 'length of the longest leaf' and 'above-ground biomass per individual' were measured at the end of the experiments; biomass was weighed after drying at 80 ºC for eight hours.

2.3 Data Analysis

In order to determine competition intensity, the Relative Interaction Indices (Armas, Ordiales, & Pugnaire, 2004) were calculated by

$$RII = P+N – P-N/P+N + P-N,$$

where P+N is the performance of the target plant in the presence of neighbours and P-N is the performance of the target plant in the absence of neighbours. Competition importance was calculated using the index of Interaction Importance by Seifan, Seifan, Ariza and Tielbörger (2010). The calculation follows

$$I_{imp} = N_{imp}/|N_{imp}| + |E_{imp}|,$$

whereas $N_{imp} = P+N – P-N$, and $E_{imp} = P-N – P_{max\pm N}$. ($E_{imp}$ = environmental contribution to plant performance; N_{imp} = neighbour contribution to plant performance; $P_{max\pm N}$ = maximum value of plant performance in the studied system, regardless of neighbours). Both values range from -1 to 1, are symmetrical around zero, with positive values indicating facilitation and negative values indicating competition.

All collected data of plant parameters were checked for normality of distribution and were log-transformed to meet the assumption of the analysis of variance (ANOVA). A parametric one-way ANOVA with HSD Tukey's post hoc test ($p < 0.05$) was used to compare the differences within the mixture ratio (D4/F1, D3/F2, D2/F3, D1/F4, D5, F5). To compare the performance of the plant parameters of the two species under all environmental factors, a three-way ANOVA was conducted with nutrient level, temperature and treatment as fixed factors. For the calculation of biomass, leaf number and leaf length values for the mixtures and the monocultures were

included, while only the values of the mixtures were included for the calculation of the three-way ANOVA for RII and I_{imp}. Statistical analyses were performed using SPSS 19.0 (2011).

3. Results

3.1 Performance of Plant Parameters

Under nutrient poor conditions, the produced biomass and the number of leaves of *D. carthusianorum* did not significantly differ under unwarmed conditions, but leaf length decreased significantly with increasing *D. carthusianorum* individuals in the pots (Figure 1). Under warmed conditions, the parameters of biomass and leaf length showed no significant differences, but the number of leaves did. After nutrient addition, biomass and number of leaves strongly increased (almost tenfold) and leaf length nearly doubled. Under unwarmed conditions, biomass increased significantly with an increased number of *D. carthusianorum* individuals being recorded for each pot; however, leaf number and length did not significantly differ. Under warmed conditions, biomass and leaf number significantly decreased with increased number of dicot individuals, but leaf length did not.
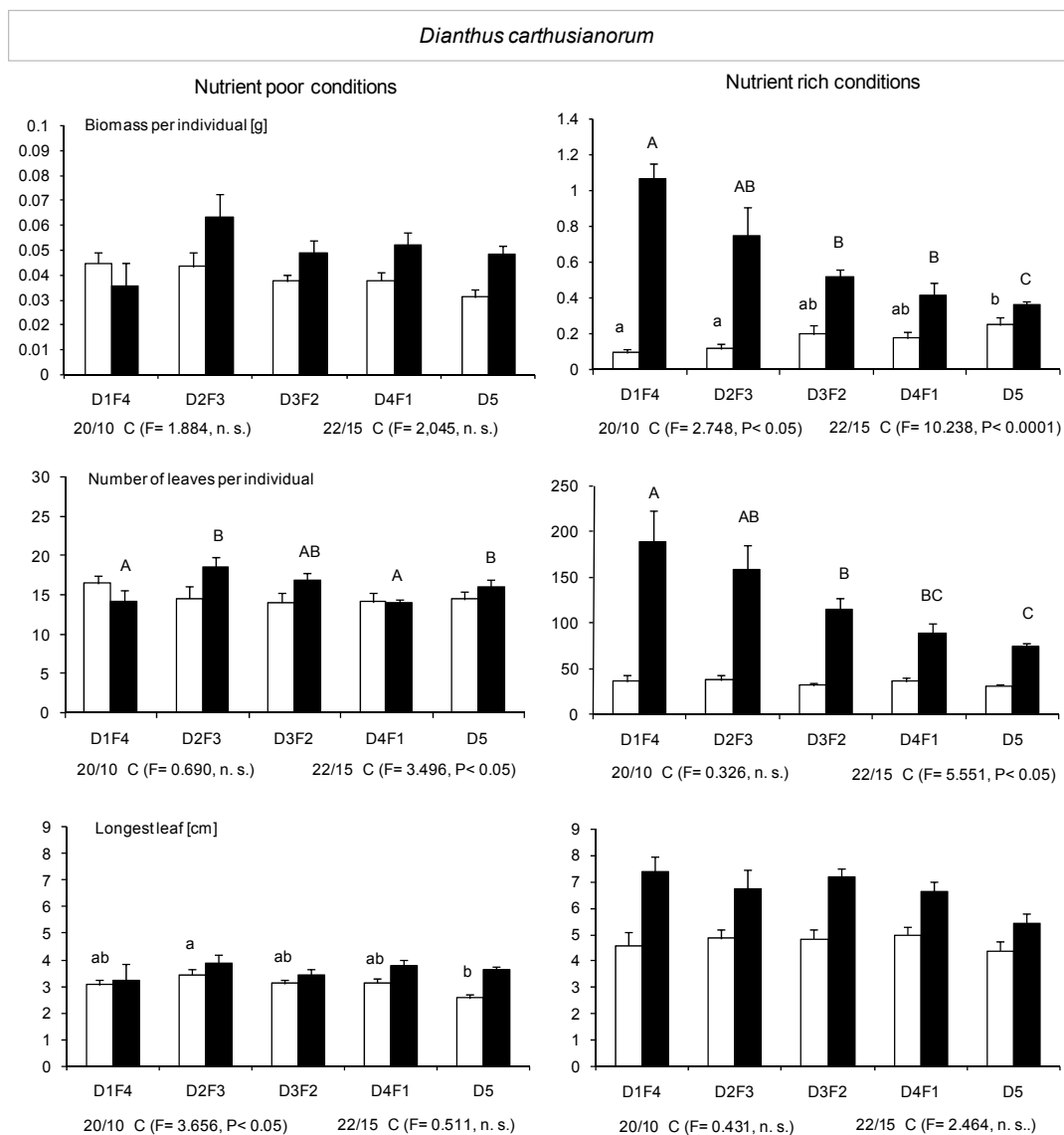

Figure 1. Performance of *Dianthus carthusianorum* in mixtures (D1F4, D2F3, D3F2, D4F1) and monocultures (D5) with constant density (with increasing number of *D. carthusianorum* from left to right) under nutrient poor (left) and nutrient rich (right) conditions at current (20/10 ºC; white bars) and predicted (22/15 ºC; black bars) conditions (means with standard error). The results of the one-way ANOVA are shown (F- and P-values; letters show significant groups: small letters: 20/10 ºC; large letters: 22/15 ºC)

Festuca rupicola showed no significant variation in biomass and leaf length under unwarmed and warmed conditions at nutrient poor levels; and only the number of leaves significantly differed under unwarmed conditions (Figure 2). Nutrient addition caused an approximate tenfold increase in biomass, a threefold increase in leaf number and a twofold increase in leaf length. Under unwarmed conditions, biomass, leaf number and length decreased significantly with increasing number of *F. rupicola* individuals in the pots. Under warmed conditions, biomass and leaf number did not differ significantly, but leaf length did.
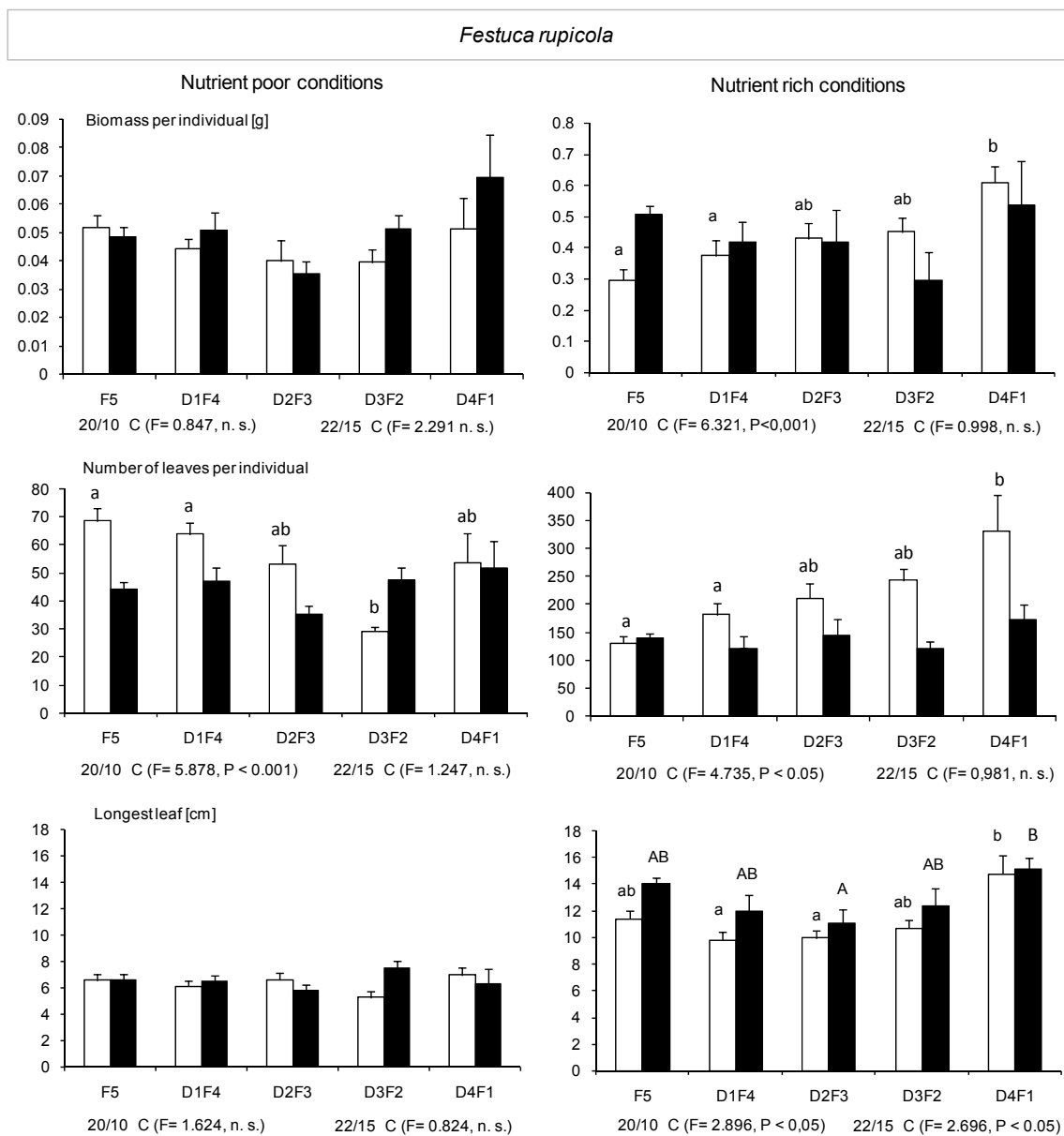

Figure 2. Performance of *Festuca rupicola* in mixtures (D1F4, D2F3, D3F2, D4F1) and monocultures (F5) with constant density (with decreasing number of *F. rupicola* from left to right) under nutrient poor (left) and nutrient rich (right) conditions at current climate (20/10 ºC; white bars) and predicted climate (22/15 ºC: black bars) conditions (means with standard error). The results of the one-way ANOVA are shown (F- and P-values; letters show significant groups: small letters: 20/10 ºC; large letters: 22/15 ºC)

Results of the three-way ANOVA showed that nutrient addition significantly promoted all plant parameters in both species (Table 1). The increase in temperature significantly enhanced above-ground biomass, leaf number and length of *D. carthusianorum* while treatments showed significant effects only on leaf number and length.

Nutrient*temperature interaction had significant effects on all parameters but temperature*mixture ratio interaction significantly affected only biomass. Also, the interaction of all three environmental factors significantly enhanced biomass in the dicot. Surprisingly, *F. rupicola* biomass did neither significantly differ with temperature or mixture ratio nor with their interactions; only the interaction nutrient*temperature*mixture ratio showed significant effects. Leaf number was however significantly reduced by warming and was significantly affected by all interactions that included nutrient as a factor. Leaf length was only significantly affected by treatment and the nutrient*mixture ratio interaction.

Table 1. Results of the three-way ANOVA on the plant parameters of *Dianthus carthusianorum* and *Festuca rupicola* in all treatments under nutrient poor and nutrient rich conditions and under current and predicted climate conditions

Source of variation	df	Biomass per individual [g]		Number of leaves per individual		Longest leaf [cm]	
		F	P	F	P	F	P
Dianthus carthusianorum							
Nutrient	1	543.337	**<0.0001**	612.566	**<0.0001**	207.795	**<0.0001**
Temperature	1	100.51	**<0.0001**	140.092	**<0.0001**	42.065	**<0.0001**
Mixture ratio	4	0.411	0.8	3.304	**0.013**	2.573	**0.04**
Nutrient * Temperature	1	61.784	**<0.0001**	112.795	**<0.0001**	8.91	**0.003**
Nutrient * Mix. ratio	4	1.474	0.213	1.81	0.13	1.226	0.303
Temperature * Mix. ratio	4	2.824	**0.027**	1.622	0.172	0.186	0.945
Nutr. * Temp. * Mix. ratio	4	12.04	**<0.0001**	2.414	0.052	2.139	0.079
Error	140						
Festuca rupicola							
Nutrient	1	379.807	**<0.0001**	367.245	**<0.0001**	271.948	**<0.0001**
Temperature	1	0.67	0.414	20.181	**<0.0001**	3.602	0.06
Mixture ratio	4	1.954	0.105	2.037	0.092	3.192	**0.015**
Nutrient * Temperature	1	3.401	0.067	6.3	**0.013**	1.978	0.162
Nutrient * Mix. ratio	4	0.981	0.42	4.587	**0.002**	2.68	**0.034**
Temperature * Mix. ratio	4	1.323	0.264	1	0.41	2.043	0.092
Nutr. * Temp. * Mix. ratio	4	2.77	**0.03**	4.758	**0.001**	1.353	0.253
Error	140						

3.2 Plant-Plant Interactions

The results indicated that the positive and negative interactions between the two species are generally minor under nutrient poor conditions (Figures 3 and 4). Whereas *D. carthusianorum* became slightly facilitated and *F. rupicola* competed against under unwarmed conditions, the interactions were more or less neutral under warmed conditions. After nutrient addition, *D. carthusianorum* suffered from competition, but it did not significantly differ between treatments. After warming, *D. carthusianorum* switched to facilitation, which significantly increased with increasing number of grass individuals in the pots, and *F. rupicola* was facilitated under unwarmed conditions (Figure 4). The positive interactions significantly increased with increasing number of *D. carthusianorum* in the pots. However, after warming, the grass suffered from competition by the dicot. The competition intensity and importance were very similar for both species (Figures 3 and 4), however the intensity is higher than the importance in *D. carthusianorum* and visa-versa in *F. rupicola*.
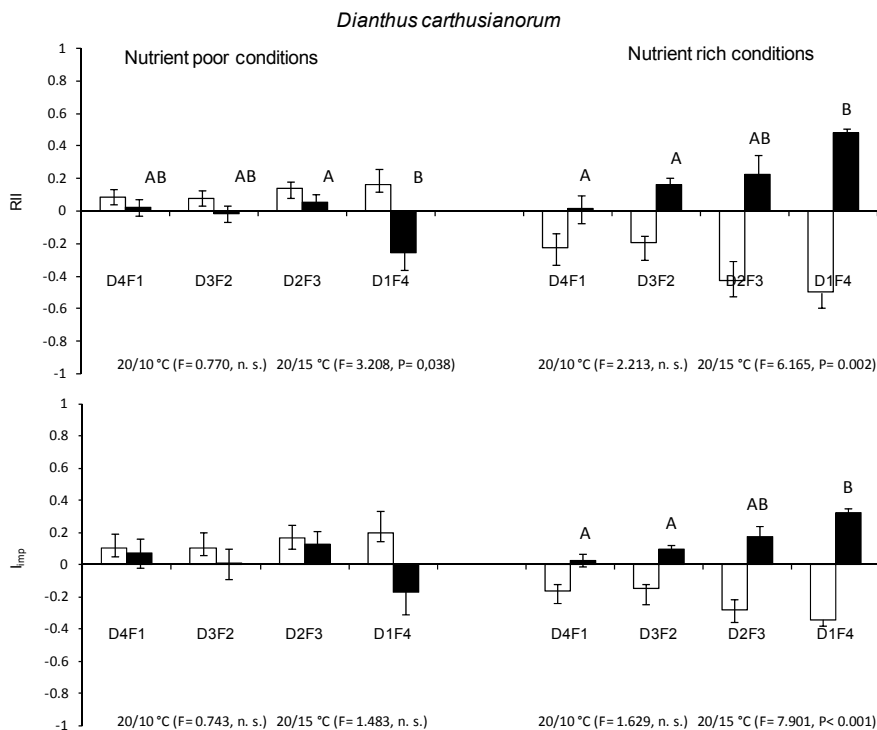
Dianthus carthusianorum

Figure 3. Competition intensity (RII) and competition importance (I_{imp}) of *Dianthus carthusianorum* in mixtures under nutrient poor (left) and nutrient rich (right) conditions and under current climate conditions (white bars) and predicted climate conditions (black bars). Positive values show facilitation and negative values show competition (means with standard error)
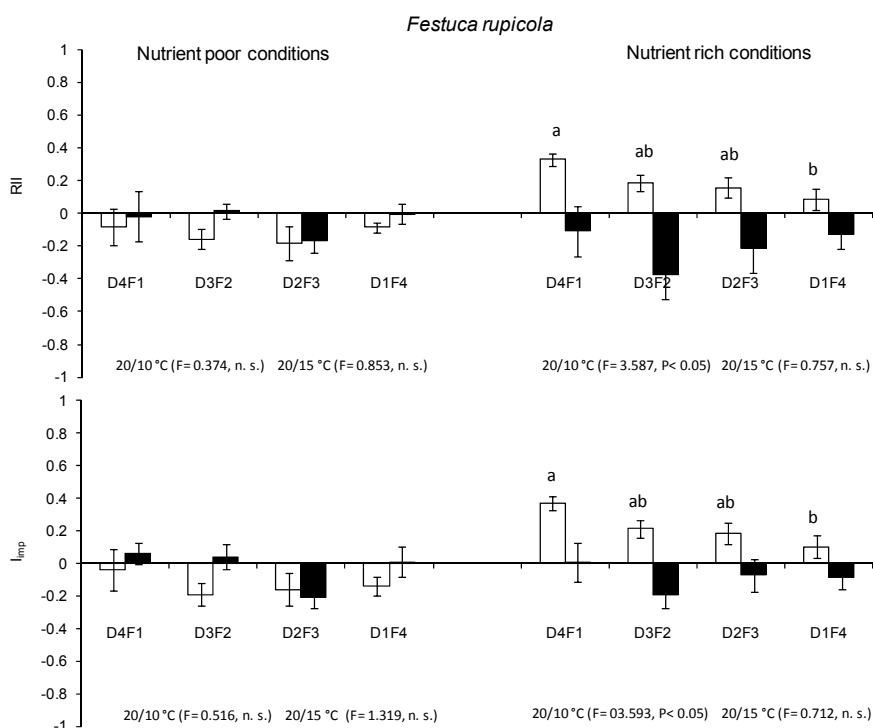
Festuca rupicola

Figure 4. Competition intensity (RII) and competition importance (I_{imp}) of *Festuca rupicola* in mixtures under nutrient poor (left) and nutrient rich (right) conditions and under current (white bars) and predicted climate conditions (black bars). Positive values show facilitation and negative values show competition (means with standard error)

Results of the three-way-ANOVA (Table 2) showed that RII and I_{imp} of *D. carthusianorum* was significantly affected by nutrient addition and temperature and the interactions nutrient*temperature and nutrient*temperature*mixture ratio. However, nutrient addition significantly enhanced only I_{imp} of *F. rupicola*. Temperature and nutrient*temperature interaction had significant effects on both "importance" and "intensity" of interaction of the grass.

Table 2. Results of the three-way ANOVA on competition intensity (RII) and importance (I_{imp}) of *Dianthus carthusianorum* and *Festuca rupicola* in the mixtures under nutrient poor and nutrient rich conditions and under current und predicted climate conditions

Source of variation	df	Competition intensity (RII)		Competition importance (I_{imp})	
		F	P	F	P
Dianthus carthusianorum					
Nutrient	1	5.268	**0.024**	9.772	**0.002**
Temperature	1	24.389	**<0.0001**	11.929	**<0.001**
Mixture ratio	3	0.220	0.883	0.238	0.870
Nutrient * Temperature	1	82.987	**<0.0001**	50.901	**<0.0001**
Nutrient. * Mixture ratio	3	1.810	0.149	1.196	0.315
Temperature * Mixture ratio	3	1.655	0.181	0.811	0.490
Nutr. * Temp. * Mixture ratio	3	9.586	**<0.0001**	5.966	**<0.001**
Error	112				
Festuca rupicola					
Nutrient	1	2.489	0.117	9.856	**0.002**
Temperature	1	10.553	**0.002**	4.533	**0.035**
Mixture ratio	3	1.487	0.222	2.558	0.059
Nutrient * Temperature	1	24.527	**<0.0001**	20.716	**<0.0001**
Nutrient. * Mixture ratio	3	0.896	0.446	0.737	0.532
Temperature * Mixture ratio	3	0.390	0.760	0.405	0.750
Nutr. * Temp. * Mixture ratio	3	0.957	0.416	1.023	0.385
Error	112				

4. Discussion

4.1 Performance of the Plant Parameters

The semi-dry grassland species, *D. carthusianorum* and *F. rupicola*, responded differently to the manipulated environmental factors. While eutrophication showed strong positive effects on the growth of both species, they responded differently to warming. However, the biomass of both species was not affected by coexisting species under nutrient poor conditions, both under unwarmed and warmed conditions. After nutrient addition significant effects were detected, which showed that the species reached the developing stage much earlier than they do under natural nutrient poor conditions. As such, a few individuals of *D. carthusianorum* started to flower after four months (data not shown) and the species interacted in the same way as they do in the adult stages. After warming, all parameters of *D. carthusianorum* became significantly increased, but *F. rupicola* was not positively affected in biomass, and the number of leaves per individual was significantly reduced, which was similar under both nutrient levels under warming. Similar species-specific responses were detected by Zhang et al. (2008), where the biomass and height of *Festuca rubra* decreased, whilst *Trifolium pratense* parameters remained unchanged with increased temperature and nutrient addition. This is in line with results reported from arctic and alpine ecosystems: whereas *Ledum palustre* and *Empetrum nigrum* tended to increase shoot height and biomass production, *Vaccinium uliginosum*, *V. vitis-idaea* and *Arctous alpinus* did not (Kuodo & Suzuki, 2003); or in

Mediterranean shrubland, where *Erica multiflora* became promoted and *Globularia alypum* inhibited by warming (Llorens, Penuelas, Estiarte, & Bruna, 2004). Otherwise, Hovenden et al. (2008) found that seedlings of a temperate grass (*Austrodanthonia caespitosa*) descendent from "warmed plants" were 20% smaller than those from "unwarmed plants", suggesting that global warming will most likely reduce population growth or distribution of this dominant grass.

Generally, nutrient addition led to increases in growth of semi-dry grassland species reported by several authors (Willems & Bobbink, 1990; Bobbink et al., 1998; Dupré et al., 2010). Otherwise, biomass loss by warming is caused by the temperature-sensitive respiration process (Yoshida, 1981; Amthor, 2000), which reduces the amount of assimilates available for growth and yield (Monteith, 1981). The faster increase in night-time temperatures recorded for the past century (Easterling et al., 1997) led to a negative effect on the yield of agricultural products such as maize, wheat, sorghum and soybean (Brown & Rosenberg, 1997). Peng et al. (2004) found a decrease in the biomass of rice by ca. 10% for every 1 ℃ of warming. In contrast, nocturnal warming led to a 36.3% increase in respiration for two dominant grass species in a temperate steppe ecosystem in northern China, and enhanced consumption of carbohydrates in the leaves, which stimulated plant photosynthesis by 19.8% in the subsequent days (Wan, Xia, Liu, & Niu, 2009). Such species-specific responses to warming lead to a shift in competitive priority along environmental gradients (Zhang et al., 2008), consistently with the results from the present study.

4.2 Performance of Plant-Plant Interactions

Under nutrient poor conditions, the interactions between the two species were more or less neutral, probably in relation to the reduced plant performance. At an early stage of development, the plants did not interact, whereas interactions increased with increasing plant growth. As such, plant size or development stage can be good predictors of plant performance for several ecological conditions, including responses to neighbours (Miriti, 2006). Rafferty and Young (2002) found in a competition experiment that the desert needlegrass seedlings *(Achnatherum speciosum)* in comparison to cheatgrass (*Bromus tectorum*) started to significantly differ in growth height and interactions after the 5th week following emergence. In another study, competition tended to be greatest during the establishment stage of pine seedlings in the bunchgrass understorey (Kolb & Robberecht, 1996). However, the differences in physiological and morphological traits of the species led to different levels of plant performance and interaction (Zhang et al., 2008).

After nutrient addition, both species interacted more intensively. Under warmed conditions, the competitive ability of the dicot increased, but the competitive ability of the grass decreased, which caused not only a change in the interspecific interaction but also the intraspecific interaction. As such, biomass and leaf number of *D. carthusianorum* significantly decreased with increasing dicot individuals in the pots. However, the interaction of *D. carthusianorum* switched from competition to facilitation and was further bolstered with increasing numbers of *F. rupicola* individuals, as a result of reduced plant performance of the grass. Kuodo and Suzuki (2003) pointed out that competition accelerated under warmed conditions (between 1.5-2.3 ℃ higher), and the less competitive *Vaccinium vitis-idaea* was suppressed by other plant species. A shift between facilitation and competition due to changing climate conditions was also described by Greenlee and Callaway (1996), Choler et al. (2001), Bertness and Ewanchuk (2002) and Kikvidze et al. (2006), which is further confirmed by the present results.

The plant traits life history and strategy type (Grime, 1977) of the co-existing species, as well as the characteristic of the stress factors which are distinguished between resource (e.g. water, nutrients, light) and non-resource stress factors (e.g. temperature, wind, salinity, soil structure), determine the interplay between facilitation and competition (Chen et al., 2009; Maestre, Callaway, Valladares, & Lortie, 2009). Therefore, *D. carthusianorum* exhibits an intermediate strategy type (CSR-strategist) that is more stress-tolerant, whereas *F. rupicola* is a stress tolerant competitor (CS-strategist) with greater competitive ability (Frank & Klotz, 1990). The combination of both stress factors (nutrient and temperature) led to a reduction in competitive ability for the grass and increased competitiveness for the dicot. It agrees with the finding of Sala et al. (2000), that multiple environmental changes induce synergistic or antagonistic effects.

According to what has been proposed by Brooker et al. (2005), biotic interactions should be evaluated for "intensity" and "importance" in order to identify both physiological factors as well as ecological ones. However, the present results showed a very high similarity for both indices, which is also confirmed by Zhang et al. (2008). In contrast, Gaucherand, Liancourt and Lavorel (2006) found a different pattern in competition intensity and importance along a fertility gradient, while the importance depended on the species individual tolerance to low nutrient availability. However, both species in the present study showed similar behaviour to nutrient availability.

In general, the results of the present study suggest that environmental change in terms of eutrophication and warming may lead to a change in plant species composition in such a way that *F. rupicola*, the grass which currently dominates the semi-dry grassland communities of central Germany, will decline as the rare dicot *D. carthusianorum* is promoted. From a nature conservation perspective, this may represent a positive effect in terms of biodiversity enhancement of such steppe-like ecosystems. However, the interactions between grasses and dicots need further investigation in order to provide a wider and more robust understanding of their dynamics under different environmental conditions.

Acknowledgement

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