Interspecific variations in responses of *Festuca rubra* and *Trifolium pratense* to a severe clipping under environmental changes

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Abstract: Understanding and predicting possible responses of grassland species to global change is of important meaning for adapting grassland management to a changed and changing environment. A laboratory clipping experiment was conducted to examine the interspecific responses in an ecological context of competition and environmental changes. *Festuca rubra* and *Trifolium pratense*, either in monoculture or two- and three-species mixtures, were grown in three environmental combinations (ambient and increased temperature, repetitive N supply, and simulated acid rain), respectively. After a growth time of three months, plants were clipped at the height of 1.0 cm above soil surface. Plant height and aboveground biomass prior clipping, and survival rate and regrowth (height and biomass) after clipping were analyzed. *F. rubra* and *T. pratense* responded differently in compensatory growth and competition intensity to environmental change and co-existing species. The differences in their physiological and ecological traits may account for species-dependent responses. The present study emphasizes that predicting the plant assemblage response in the face of global change requires in understanding the integrating effects of abiotic and biotic factors.

Key words: climate change; compensatory growth; defoliation; grassland ecosystem; interspecific competition; species-specific response

Abbreviations: MonoF/MonoT, Monoculture of *Festuca rubra* or *Trifolium pratense*; MixFT, Mixed culture of *F. rubra* and *T. pratense*; MixFTO, Mixed culture of *F. rubra*, *T. pratense*, and *Oenothera biennis*; MixFTH, Mixed culture of *F. rubra*, *T. pratense* and *Hieracium pilosella*; T₀N₀W_{6.0}, ambient temperature + no additional N applied + watering at pH6.0; T₊N₊W_{6.0}, increased temperature + N-addition + watering at pH6.0; T₊N₊W_{4.0}, increased temperature + N-addition + watering at pH 4.0.

Introduction

Grazing/mowing is a major impact factor on plant persistence and grassland ecosystems (McNaughton 1983; Belsky 1986). Selective defoliation by grazing/mowing not only affects the growth and survival of individual plants, also modifies species composition and species interactions (Crawley 1997; Augustine & McNaughton 1998). A single severe defoliation can lead to an immediate decrease in photosynthesis (Parsons et al. 1983) and N uptake (Lestienne et al. 2006), resulting in reductions in root carbohydrate reserves (Gonzalez et al. 1989; Morvan-Bertrand et al. 1999), and even to root and tiller senescence (Jarvis & Macduff 1989). However, defoliation does not always impose deleterious effects. Many plants possess substantial compensatory mechanisms following defoliation damage, through increasing relative growth rate (Staalduinen & Anten 2005), intensifying nutrient uptake capacity (Chapin &

McNaughton 1989), or stimulating photosynthesis rate (Painter & Detling 1981).

The regrowth potential following defoliation may be affected by the presence or absence of co-existing species (Lee & Bazzaz 1980). In the literature, two mechanisms of interspecific competition in influencing plant regrowth are extensively discussed. The first, and most studied, focuses on the shading effects of taller neighbouring species. By removal of the canopy, it may therefore moderate competition by increasing light to small co-occurring species (McNaughton 1992). The second mechanism is related to the neighbour identity, which associated with species-specific ability to acquire resources (Hartley & Amos 1999) and to suppress the potential competitors (Louda et al. 1990; Bullock et al. 2001). Species which are more able to regrow, or regrow more rapidly after defoliation, are able to dominate after grazing (Augustine & McNaughton 1998; Bullock et al. 2001).

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Today's plant communities are the result of long-term adaptation to their site factors, including climatic and anthropogenic impacts. Changed and changing environment conditions will lead to changes in availability of resources (nutrients, light and water) and interactions between co-existing species (Hilbert et al. 1981; Li et al. 2006). The rapid environmental changes that humans are currently causing in the natural world will certainly play both direct and indirect roles in plant response to defoliation. Over the past 100 years, the earth is rising by $0.74 \pm 0.18^\circ\text{C}$ in mean surface temperatures (IPCC 2007). Deposition of human-derived soluble nitrogen has reached unprecedented levels, and now exceeds natural nitro-fixation by the globe's biota (Vitousek et al. 1997). Nitrogen deposition increases N mineralisation, but it may also accelerate soil acidification by increased ammonium oxidation (Vitousek et al. 1997). Simultaneously, increased atmospheric carbon dioxide and sulphuric compound contribute to an additional acid deposition regionally, causing changes in species compositions (Houdijk et al. 1993; Roem & Berendse 2000). Understanding and predicting possible responses of grassland species to global change is of important meaning for adapting grassland management to a changed and changing environment.

Many studies have investigated the responses of a single plant species (without co-existing species) to just one factor (e.g. CO_2 , elevated temperature, N-deposition) contributing to major global changes (Shaw et al. 2002). The combined effects of co-occurring environmental changes on plant communities or ecosystems are, however, still poorly understood (Zavaleta et al. 2003). The effects of multiple environmental changes may be synergistic or antagonistic (Sala et al. 2000). To understand the combined effects of multiple environmental changes and defoliation on grassland ecosystem, we, therefore, grown *Festuca rubra* L. and *Trifolium pratense* L., either in monoculture, or in two- and three-species mixtures with *Oenothera biennis* S. and *Hieracium pilosella* L., under different combinations of environmental factors (increased air temperature, nitrogen supply, and simulated acid rain). We addressed following questions: i) Species-specific regrowth response to interaction between competition and abiotic conditions following clipping; ii) Clipping effects on competition intensity for both species; iii) Plant traits determining potential species-dependent compensatory growth.

Material and methods

Plant materials

The target species were *F. rubra*, and *T. pratense*, two of the most important components of meadows and pastures in Central Europe. The selected co-existing species were *O. biennis* and *H. pilosella*. Seeds of the four experimental species were obtained from the company of Fanoca Saemereienzentrum (Winterthur, Switzerland). Seeds were sown on May 24, 2004. Seedlings were transplanted at the 2-leaf stage, when *O. biennis* was ~ 2 cm and the others were ~ 6 cm in height, into plastic pots (14 cm in diameter and 14 cm in

Fig. 1. Experimental layout: a – Monoculture of 6 *Festuca rubra* or 6 *Trifolium pratense* plants (MonoF/MonoT); b – Mixtures of 3 *F. rubra* and 3 *T. pratense* plants (MixFT); and c – Mixtures of 2 *F. rubra* + 2 *T. pratense* + 2 *Oenothera biennis* plants and/or 2 *F. rubra* + 2 *T. pratense* + 2 *Hieracium pilosella* plants (MixFTO/MixFTH).

height) on June 11, 2004. The potting soil was a 1:1 (v/v) mixture of sand and peat. Each pot contained 1700 g potting soil (pH ~ 5) with 3.06 g slow-release fertilizer (15% N, 9% P_2O_5 , 9% K_2O and 3% MgO). Six seedlings were arranged and planted per pot in monocultures and mixtures (Fig. 1). There were totally five culture treatments.

Each culture treatment was subjected to one of three environmental treatments: i) ambient temperature, basal N supply and watering with water at pH6.0 ($T_0N_0W_{6.0}$); ii) increased temperature, N-addition, and watering with water at pH6.0 ($T_+N_+W_{6.0}$); and iii) increased temperature, N-addition, and watering with simulated acid rain at pH4.0 ($T_+N_+W_{4.0}$). Each culture treatment was repeated six times ($n = 6$).

Environmental treatments

The experiment was conducted at Swiss Federal Institute for Forest, Snow and Landscape Research (WSL). Two controlled environment glasshouse compartments were used to impose the temperature treatments. The average temperature achieved by air warming (T_+) were $24.7 \pm 0.9^\circ\text{C}$ in daytime and $19.0 \pm 1.2^\circ\text{C}$ at night, while for ambient treatment (T_0), the temperature was averaged $22.7 \pm 0.8^\circ\text{C}$ during the day and $18.4 \pm 1.4^\circ\text{C}$ at night, i.e. warming treatment increased air temperature by ~ 1.7 – 2.1°C in daytime and ~ 0.3 – 0.9°C at night. Plants were watered using 10 L water for 30 pots on a weekly basis. Pots in $W_{6.0}$ treatments received water (pH 6.0) weekly, while pots in $W_{4.0}$ treatment were watered once a week alternately using water (pH 6.0) and simulated acid rain (pH 4.0). For plants treated with N-addition (N_+), the additional N (Harnstoff, 46% N; Lonza, Valais, Switzerland) was applied in combination with watering (10 g Harnstoff dissolved in 10 L water) every other week, from July 12 to October 29 on a total of 8 occasions. All pots were randomly placed in the glasshouse and then randomly moved to different positions every week during the experimental period to avoid edge effects on plant growth.

On September 6, 2004, after recording individual height, plants were clipped to 1.0 cm above the soil surface. The clippings were collected and sorted into each species for determining pre-clipping aboveground biomass. After 3-month's regrowth, plants were harvested on December 4, 2004. The number of individual plants surviving and regrowth heights were recorded. Pots were then immersed in water and roots, washed free from soil. Plants were sorted into species where the cultures were mixed. Plant biomass was separated into above- and belowground parts, and weighed to nearest 0.001 g after oven-drying at 70°C for 72 hours.

Data analysis

The survival rate for both *F. rubra* and *T. pratense* at the end of the experiment was averaged by each of the replications. Data were ranked transformed before running a standard two-way ANOVA (Conover & Iman 1981), using environmental and culture treatments as fixed factors. To test clipping effects on plant growth, repeated-measures ANOVA was performed, using environmental and culture treatments as fixed factors, plant height and aboveground biomass per plant using as dependent variables, separately, time of measurement (pre- or post-clipping) as a repeated factor. A significant two- or three-way interaction between clipping and environmental and/or culture treatment would indicate there was a shift or reversal in growth hierarch following clipping. Total biomass (i.e. pre- and post-clipping aboveground biomass plus belowground biomass) was analyzed in another two-way ANOVA, separately, using environmental and culture treatments as fixed factors. In cases where there was significant treatment effect(s), multiple comparisons were further examined using Turkey's HSD. Species were separately analyzed.

To determine competition intensity, random pair-wise comparisons were made between aboveground biomass (either pre- or postclipping) of individual plants grown in monoculture and mixtures in a given environmental treatment (i^{th}). Competition intensity (C_{int}) was calculated using relative neighbour effect (Markham & Chanway 1996):

$$C_{\text{int}} = (XP_i - XM_i)/x_i$$

where XP is the aboveground biomass per plant of a species grown in monoculture, and XM is the total biomass per plant of the same species grown in mixture. x is the greater value of $[XP_i, XM_i]$. C_{int} values ranging between 0 and 1 indicate competition and values between -1 and 0 indicate facilitation.

A second repeated-measures ANOVA was performed, using environmental and culture treatments as fixed factors, ranked transformed C_{int} as dependent variables (Conover & Iman 1981), time of measurement (pre- or post-clipping) as a repeated factor. All data analyses were performed using SPSS 14.0. Unless otherwise noted, the 0.05 level of probability was used for significance tests.

Results

Survival to clipping

Clipping combined with $T_+N_+W_{6.0}$ or $T_+N_+W_{4.0}$ significantly reduced survival of *F. rubra* relative to clipping in $T_0N_0W_{6.0}$ ($F_{2,72} = 33.215$, $P < 0.001$; Fig. 2). Clipping combined with co-existing species (i.e. in mixtures) generally suppressed survival of *F. rubra* compared to clipping in monoculture ($F_{3,72} = 4.212$, $P = 0.009$). No significant interaction between environmental and culture treatments was detected. Compared to monoculture, interspecific competition reduced survival of *F. rubra* by 50~67% in $T_+N_+W_{6.0}$ and by 61~83% in $T_+N_+W_{4.0}$ (Fig. 2).

Clipping combined with $T_+N_+W_{4.0}$ suppressed *T. pratense* survival (-28%) profoundly ($F_{2,72} = 14.108$, $P < 0.001$; Fig. 2), compared to $T_0N_0W_{6.0}$ or $T_+N_+W_{6.0}$. The survival rate of *T. pratense* in MixFT was significantly ($F_{3,72} = 3.816$, $P = 0.014$) facilitated (+17%), compared to that in MonoT. No significant

Fig. 2. Survival rate after clipping (mean values $\pm$ SE; $n = 6$) for *Festuca rubra* and *Trifolium pratense* under different treatments at the end of the experiment. Treatment codes are listed in "Abbreviations".

interaction between environmental treatment and culture treatment was detected.

Primary and compensatory growth

Repeated-measures ANOVA revealed that *F. rubra* grown in $T_0N_0W_{6.0}$ was relatively taller than in $T_+N_+W_{6.0}$ or $T_+N_+W_{4.0}$ ($F_{2,55} = 71.916$, $P < 0.001$; Fig. 3). Co-existing species generally suppressed *F. rubra* height ($F_{3,55} = 26.773$, $P < 0.001$), and the inter-specific suppression was more profound in $T_+N_+W_{6.0}$ and $T_+N_+W_{4.0}$ ($F_{6,55} = 3.555$, $P = 0.006$), compared to $T_0N_0W_{6.0}$. Clipping combined with $T_+N_+W_{6.0}$ or $T_+N_+W_{4.0}$ reduced regrowth height of *F. rubra* more profoundly than in $T_0N_0W_{6.0}$ ($F_{2,55} = 5.544$, $P = 0.007$). There was significant interaction of clipping $\times$ environmental treatment $\times$ culture treatment ($F_{6,55} = 2.914$, $P = 0.018$), where the reduction was profound in mixtures growing in $T_+N_+W_{6.0}$ or $T_+N_+W_{4.0}$. However, no significant effects of co-existing species on regrowth height in *F. rubra* was detected.

Trifolium pratense growing in $T_+N_+W_{6.0}$ was relatively taller than in $T_0N_0W_{6.0}$ and $T_+N_+W_{4.0}$ ($F_{2,69} = 8.093$, $P = 0.001$; Fig. 3). Height in *T. pratense* did not respond to culture treatment. No significant interaction between environmental and culture treatments was detected. Clipping combined with $T_+N_+W_{4.0}$ or $T_+N_+W_{6.0}$ significantly suppressed regrowth height in *T. pratense* than clipping with $T_0N_0W_{6.0}$ ($F_{2,69} = 4.067$, $P = 0.022$; Fig. 3). There was neither significant interaction of clipping $\times$ culture treatment nor clipping $\times$ environmental treatment $\times$ culture treatment on height of *T. pratense*.

Aboveground biomass in *F. rubra* was significantly higher in $T_0N_0W_{6.0}$ than in $T_+N_+W_{6.0}$ or $T_+N_+W_{4.0}$ ($F_{2,55} = 40.663$, $P < 0.001$; Fig. 4). Co-existing species

Fig. 3. Treatment effects on plant height (mean values $\pm$ SE; $n = 6$) in *Festuca rubra* and *Trifolium pratense*. Treatment codes are listed in "Abbreviations".

significantly suppressed *F. rubra* on its aboveground biomass ($F_{3,55} = 20.057$, $P < 0.001$). There was no significant interaction between environmental and culture treatments). Clipping effect on aboveground biomass in *F. rubra* was relatively severer in $T_+N_+W_{6.0}$ compared to that in $T_0N_0W_{6.0}$ and $T_+N_+W_{4.0}$ ($F_{1,55} = 3.166$, $P = 0.050$). However, there was neither significant interaction of clipping $\times$ culture treatment nor interaction of clipping $\times$ environmental treatment $\times$ culture treatment. Belowground biomass of *F. rubra* showed a decreased trend from $T_0N_0W_{6.0}$ to $T_+N_+W_{6.0}$ and further to $T_+N_+W_{4.0}$ ($F_{2,55} = 29.031$, $P < 0.001$; Fig. 4). Total biomass of *F. rubra* followed a similar response pattern with aboveground biomass ($F_{2,55} = 42.861$, $P < 0.001$ for environmental treatment; $F_{3,55} = 23.846$, $P < 0.001$ for culture treatment; there was no significant interaction between environmental treatment $\times$ culture treatment (Fig. 4).

Aboveground biomass of *T. pratense* was significantly higher in $T_0N_0W_{6.0}$ and $T_+N_+W_{6.0}$ than in $T_+N_+W_{4.0}$ ($F_{2,69} = 5.326$, $P = 0.008$; Fig. 4). Aboveground biomass of *T. pratense* was significantly higher in MixFTH than in MonoT ($F_{3,69} = 3.339$, $P = 0.025$). There was no significant interaction between environmental treatment and culture treatment. Clipping effects on aboveground biomass in *T. pratense* did not vary among environmental treatments nor culture treatments. No significant interaction between environmental treatment and culture treatment was detected. Total biomass of *T. pratense* followed a similar response pattern with its aboveground biomass ($F_{2,69} = 7.231$, $P = 0.002$ for environmental treatment; $F_{2,69} = 3.048$, $P = 0.036$ for culture treatment; and no significant interaction between environmental $\times$ culture treatments (Fig. 4).

Fig. 4. Treatment effects on plant biomass (mean values $\pm$ SE; $n = 6$) in *Festuca rubra* and *Trifolium pratense*. Treatment codes are listed in "Abbreviations".

Competition variations

Competition for *F. rubra* was less intensive in $T_0N_0W_{6.0}$ and increased in $T_+N_+W_{6.0}$ and $T_+N_+W_{4.0}$ ($F_{2,36} = 6.748$, $P = 0.004$; Fig. 5). Competition for *F. rubra* did not significantly differ among culture treatments. There was no interaction between environmental treatment and culture treatment. Clipping significantly intensified competition for *F. rubra* ($F_{1,36} = 5.105$, $P = 0.032$) along either environmental treatments or culture treatments.

Competition intensity for *T. pratense* did not significantly respond to either environmental treatment or culture treatment. However, there was significant interaction between environmental and culture treatments ($F_{1,51} = 2.710$, $P = 0.043$; Fig. 5). Clipping did not affect competition intensity for *T. pratense* in any environmental treatment or culture treatment.

Discussion

Species-specific response

The two target species, *F. rubra* and *T. pratense*, responded differently to manipulated environmental and culture treatments. Altered environments ($T_+N_+W_{6.0}$ and $T_+N_+W_{4.0}$) markedly suppressed *F. rubra* in its height, aboveground biomass, and survival following

Fig. 5. Competition intensity (mean values $\pm$ SE; $n = 6$) for *Festuca rubra* and *Trifolium pratense* in relation to clipping under different treatments. Treatment codes are listed in "Abbreviations".

clipping when grown in mixtures. The greater the abiotic stress, the more significant the neighbour effects for *F. rubra*. On the contrary, *T. pratense* remained a similar growth responses across experimental conditions (i.e. environmental and culture treatments).

Plant compensatory growth following clipping was species-dependent and environment-dependent. For example, clipped *F. rubra* plants exhibited a compensation growth of $\sim 80\%$ of pre-clipping aboveground biomass in T₀N₀W_{6.0} and T+N+W_{4.0}, and only of $\sim 39\%$ in T+N+W_{6.0}. However, compensatory growth in *T. pratense* did not markedly differ among three environmental treatments. This result may be explained by species differences in optimal growth environments and tolerance to a particular abiotic stress (Hartley & Mitchell 2005). Co-existing species with different physiological and ecological properties may modify and amplify a particular plant's environmental response (Dunnett & Grime 1999). On the other hand, canopy removal through defoliation or clipping will alter the availability of resource, leading to changed interaction between plant and environment (McNaughton 1992). For example, Magda et al. (2006) observed that grazing created a dense grass sward structure which leads to a high level of light competition. Therefore, a fast-growing species, e.g. *T. pratense*, is advantageous for new growth following defoliation. Moreover, defoliation may alter competition balance between co-existing species (Louda et al. 1990), leading to different responses in survival and growth to defoliation (van Der Wal et al. 2000; Magda et al. 2006).

Both total biomass per plant (i.e. *F. rubra* and *T. pratense*) and total pot biomass were significantly

different among three environmental treatments, with the lowest in T+N+W_{4.0}, we may say the productivities significantly differed among the three environments. We observed that both species showed a much stronger compensatory growth, in terms of aboveground biomass, in T+N+W_{4.0} than in T₀N₀W_{6.0} or T+N+W_{6.0} (c.85% for *F. rubra* and c.68% for *T. pratense*). This finding is supported by the conceptual model developed by Hilbert et al. (1981). Their model predicts that plants in stress environment with growth rate far below their maximum penitential are more likely to respond positively to clipping than plants growing in optimal conditions. Experimental studies (review in Ferraro & Oesterheld 2002) also reported that plants growing at low nutrient or water availability exhibited stronger compensatory growth than those under more favorable conditions.

Clipping effects on competition

As *T. pratense* retained the same competitive superiority following clipping, competition intensity for *F. rubra*, measured on aboveground biomass, generally increased after clipping. These different competitive responses to clipping may be mainly resulted from an unbalanced loss of aboveground tissue and reserves through clipping, since the aboveground biomass of *T. pratense* was two- to three-time higher than the aboveground biomass of *F. rubra* before clipping. Compared to *F. rubra*, the fast-growing species *T. pratense* may more rely on carbohydrate reserves stored in roots for regrowth due to loss of foliage. On other words, a dramatic decrease in carbohydrate reserves in *T. pratense* may lead to an insufficient carbon supply to support a fast regrowth following a severe defoliation (Coley et al. 1985). However, the N-fixation ability of *T. pratense* will have a greater capacity for regrowth and competition when new leaves occurred. Carlsson & Huss-Danell (2003) found that the N-fixation ability of *T. pratense* allows legume to survive and compete with grass through a critical period when legume roots and grass roots must compete for soil nutrients. In high soil fertility, grasses and legumes compete predominantly for light (Schwinning & Parsons 1996). The broad-, flat-leaved *T. pratense* would be advantageous in intercepting incoming light, compared with narrow-leaved *F. rubra* (Fynn et al. 2005). Consequently, the former will shade out the latter or competing neighbours. However, as asymmetry competition may occur when there are pronounced variations in plant size within a community (Goldberg & Werner 1983). Otherwise, the regulatory mechanisms of species coexistence may be due to some parameters other than shoot size, such as species-specific competitive ability, or growth form of the neighbouring species (Hara 1993).

In conclusion, *F. rubra* and *T. pratense* responded differently in compensatory growth to environmental change and co-existing species. Interspecies competition was modified and amplified in the complex interaction between clipping and environmental change. Species-dependent responses are associated with the differences

in their physiological and ecological traits. The present study emphasizes that predicting the plant assemblage response in the face of global change requires in understanding the integrating effects of abiotic and biotic factors.

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