SIMULATED CLIMATE CHANGE ALTERED DOMINANCE HIERARCHIES AND DIVERSITY OF AN ALPINE BIODIVERSITY HOTSPOT

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Abstract. Alpine and arctic ecosystems may be particularly vulnerable to climate change. We know little about alpine plant community responses to the predicted abiotic changes, or to possible changes in the biotic environment caused by climate change. Four years of experimental warming and nutrient addition altered dominance hierarchies, community structure, and diversity of an alpine biodiversity hotspot in south Norway. The previously dominant dwarf shrub Dryas octopetala was replaced by graminoids and forbs under nutrient addition and warming with nutrients. Community diversity declined due to decreased bryophyte and lichen richness and abundances, and dwarf shrub abundances. In controls and in plots with only warming, where Dryas maintained dominance, the relationships between changes in Dryas cover and changes in community parameters were negative, suggesting that Dryas controls community processes. Under nutrient addition, bryophyte and lichen diversity decreased with decreasing Dryas cover, probably due to increased competition from graminoids and forbs. The shift in dominance hierarchies changed community structure and dynamics through increased biomass, vegetation height, and competition for light. Community diversity dropped primarily because changes in the abiotic environment modified biotic interactions, highlighting that species interaction must be considered in climate change experiments and in models predicting climate change effects.

Key words: alpine tundra; competition; dominant species; Dryas octopetala; functional groups; nutrient addition; open top chambers; plant community diversity; south Norway; species interactions; warming.

INTRODUCTION

Changes in the abiotic environment caused by global warming, such as increased growing season length, permafrost melting, and nutrient availability due to higher mobilization of resources in warmer soils (Intergovernmental Panel on Climate Change [IPCC] 2001), are predicted to impose large effects on alpine and arctic plant species (e.g., Callaghan and Jonasson 1995, Körner 1999). However, associated changes in the biotic environment may have even greater effects on plant community composition and diversity (Mooney 1991, Kingsolver 1993). Alpine and arctic climate change experiments show that most plants increase their vegetative growth and reproductive effort and success after short-term increases in temperature (e.g., Arft et al. 1999) and/or nutrient availability (e.g., Dormann and Woodin 2002). However, the speed and amplitude of responses to abiotic environmental change may differ substantially between species and functional groups (e.g., Arft et al. 1999, Dormann and Woodin 2002). Thus, longer-term changes in the biotic environment (e.g., biomass, canopy height) experienced by individual species may occur within a community. Furthermore, individual species or functional groups may vary in their competitive abilities and may respond differently to the presence of other species (Wilson and Whittaker 1995), which may again affect plant community dynamics and diversity.

Dominant species, i.e., the most prevalent species in a community, may strongly influence the biotic conditions experienced by other species and are often important drivers of ecosystem function and community dynamics (Grime 1998). A dominant species may have negative (competition) or positive (facilitation) impacts on other species (e.g., Callaway 1995, Baer et al. 2004, Klanderud and Totland 2004). Thus, the changes in abundance of a dominant species may influence community dynamics and diversity because of altered interactions (both direction and magnitude) between this species and others.

Few studies have examined climate change effects at the community level (but see, e.g., Chapin et al. 1995, Molau and Alatalo 1998, Press et al. 1998, Robinson et al. 1998, Shaver and Jonasson 1999). Furthermore, although both alpine and arctic ecosystems are predicted to be particularly vulnerable to climate change (e.g., Callaghan and Jonasson 1995, Körner 1999), we know of only one experimental study on alpine plant community responses to increased nutrient availability (Theodore and Bowman 1997) and one on
the possible effects of warming (Klein et al. 2004). Furthermore, the relationship between possible changes in the cover of a dominant species and changes in community diversity has received little attention. Climate change effects on the interactions among species may modify direct responses of abiotic environmental change (Shevtsova et al. 1997, Dormann et al. 2004, Klanderud 2005), but biotic interactions are still mostly ignored in experiments and in models predicting climate change effects (Mooney 1991, Davies et al. 1998, Dormann and Woodin 2002).

The dwarf shrub *Dryas octopetala* L. is a circumpolar “wintergreen” (Welker et al. 1997) species that may dominate plant communities in alpine, subarctic, and arctic habitats (Hultén 1959). The northern European *Dryas* heaths may be characterized as biodiversity hotspots relative to other alpine plant communities in this region. *Dryas* may be a key species with both negative and positive impacts on ecosystem carbon gain (Welker et al. 1997), population dynamics of other species (Klanderud 2005), community diversity (Klanderud and Totland 2004), and establishment of other species (*Dryas drummondii* Richard; Chapin et al. 1994). Previous studies have found both increased (Welker et al. 1997) and decreased (Henry et al. 1986, Robinson et al. 1998) abundance of *Dryas* after climate-change simulations.

*Dryas* covers ~35% of the ground of our study site in alpine Norway, and had primarily a competitive role on the performance of other plant species here (Klanderud and Totland 2004, Klanderud 2005). Thus, with continued global warming (IPCC 2001), three possible scenarios may occur: (1) If *Dryas* cover increases as a result of environmental changes (Welker et al. 1997), community diversity may decrease because of increased competition from *Dryas*. (2) If *Dryas* cover decreases (Henry et al. 1986, Robinson et al. 1998), *Dryas* heath diversity might increase due to competitive release experienced by other species. (3) Other species than *Dryas* may become dominant as a result of environmental changes and thereby affect community diversity. To better understand how biotic interactions influence community response to climate change, we experimentally manipulated the environmental conditions in an alpine *Dryas* heath. The specific objectives of our study were to determine (1) how warming and increased nutrient availability affect the cover of the dominant *Dryas octopetala* and the diversity of different functional groups (graminoids, forbs, dwarf shrubs, bryophytes, lichens); (2) whether there are any effects of changes in *Dryas* cover on community diversity; and (3) whether dominance hierarchies change as a result of environmental change, and if so, what the consequences are for community structure.

**Study System and Methods**

This study was conducted on a southwest exposed slope of a *Dryas octopetala* heath at ~1500 m elevation on Sandalsnuten, Finse, in the northern part of Harangervidda (~60° N, 7° E), the alpine region of southwest Norway (see Plate 1). Mean monthly temperature during June, July, and August at 1200 m elevation at Finse is 6.3°C (Aune 1993), and mean monthly precipitation during the same months is 89 mm (Førland 1993). See Klanderud and Totland (2004) for species composition on Sandalsnuten, and Welker et al. (1997) for growth characteristics of *Dryas octopetala*. The experiment started in early July 2000 and lasted until the end of the growing season (late August) in 2003. To examine if environmental changes may affect *Dryas* cover and plant community diversity, we randomly positioned 10 blocks in the *Dryas* heath. Temperature treatment (T), nutrient addition (N), temperature and nutrient addition (TN), and controls (C, no treatment) were randomly allocated to four randomly positioned 1 × 1 m plots (~1 m apart from each other) within each block. We used open top chambers (OTCs) with an inside diameter of ~1 m, and with qualities as described in Marion et al. (1997) to increase temperature. OTCs are commonly used in climate change experiments to raise the temperature while minimizing secondary experimental effects, such as changes in atmospheric gas concentrations and ambient precipitation (e.g., Marion et al. 1997, Hollister and Webber 2000). The chambers did not affect the duration of snow cover and we therefore left them in place during the whole experimental period. To increase nutrient availability, we added slow-released granular NPK fertilizer (~10 g N, 2 g P, and 8 g K per m² per growing season) immediately after snowmelt in the beginning of each growing season. These amounts are in line with other climate change experiments (e.g., Chapin et al. 1995, Press et al. 1998, Shaver and Jonasson 1999).

To determine changes in *Dryas* cover and plant species diversity, we established two 60 × 30 cm permanent squares in the center of each plot separated by a 10 cm wide row. Furthermore, we divided each square into 18, 10 × 10 cm subplots and recorded percent cover of live and dead *Dryas*, and presence of species (graminoids, forbs, dwarf shrubs, bryophytes, lichens) in all the subplots during two weeks of the approximate peak of the growing season in August 2000 and 2003. We used subplot frequencies averaged over the two squares in each plot as a measure of abundance of each species in the analyses. To assess possible changes in community structure, we measured the height of the vegetation in the center of five randomly selected subplots per square, and sampled aboveground biomass (only green parts of the woody plants) in two randomly chosen subplots in each square during one day at the end of the last growing season (late August 2003). We dried the biomass at 75°C for 48 h and weighed them immediately thereafter. Average values per plot are used for all parameters in all analyses.

We measured mean air (~5 cm aboveground) and soil (~5 cm belowground) temperature with Tinytag
12 Plus G data loggers (Intab Interface-Teknik AB, Stenkullen, Sweden) inside and outside four of the OTCs from early June to early September 2003. We measured leaf surface temperature of *Dryas* inside and outside ten OTCs by using an infrared thermometer (FLUKE 65, Fluke Corporation, Everett, Washington, USA). To assess the effect of community structure on light levels, we measured the photosynthetically active radiation (PAR) with a Li-Cor Quantum Sensor (Li-Cor, Lincoln, Nebraska, USA) on the ground at five randomly chosen positions in each 30 × 60 cm square (10 measurements per plot) on a clear day in August 2003.

To separate natural changes in *Dryas* cover and community diversity parameters from treatment-induced changes when comparing treatment effects with controls, we used the changes in the vegetation data (i.e., sampling in 2003 minus sampling in 2000) as response variables in the analyses (see Robinson et al. 1998). All measured variables had equal variances. To assess the effects of warming, nutrient addition, and the combined effects of these manipulations on *Dryas* cover, total biomass, height of vegetation, species richness, abundances, and diversity (Shannon’s index; $H = - \sum p_i \ln(p_i)$, where $p_i$ is the proportion of a particular species in the sample, Ludwig and Reynolds 1988) of each of the functional groups (graminoids, forbs, dwarf shrubs, bryophytes, lichens), we used a randomized block design, with treatment as the fixed factor and block as the random factor in multifactorial General Linear Models (GLMs). To examine significant differences between treatment means, we used the Tukey hsd post-hoc test. To separate possible diversity changes in changes in species richness from changes in abundances, we used Shannon’s diversity index, species richness, and abundances as response variables in the analyses.

To assess if there was a relationship between the changes in *Dryas* cover and the changes in community parameters, we used the change in *Dryas* cover as a predictor in simple linear regressions, with diversity, richness, and abundances of all species, graminoids, forbs, dwarf shrubs, bryophytes, and lichens as dependent factors. Because of heterogeneity of slopes, the regressions were done separately within each treatment. Simple linear regressions were also used to assess possible relationships between biomass (predictor) and PAR (dependent factor). All analyses were done in SYSTAT 10 (Systat Software, Inc., Point Richmond, California, USA).

**RESULTS**

*Environmental factors*

The OTCs increased mean *Dryas* leaf surface temperature from 12.1 ± 0.1°C (controls) to 13.6 ± 0.2°C, air temperature from 9.8 ± 0.1°C (controls) to 11.3 ± 0.1°C, and soil temperature from 9.0 ± 0.1°C (controls) to 10.0 ± 0.1°C (all values are mean ± SE). Photosynthetically active radiation (PAR) measured on the ground at the end of the experiment differed significantly between all treatments (Tukey hsd; GLM treatment effect, $F_{3,27} = 126.01$, $P < 0.001$; block effect, $F_{9,27} = 3.17$, $P = 0.001$), with 1653.2 ± 43.5, 1457.2 ± 53.3, 797.0 ± 97.5, and 394.0 ± 49.4 μmol·m⁻²·s⁻¹ measured in the control, warming, nutrient addition, and warming combined with nutrient addition plots, respectively.

*Dryas cover and community structure*

Four years of experimental warming alone had no effect on the cover of *Dryas octopetala*. On the other hand, the cover of both live and dead *Dryas* leaves decreased in plots with nutrient addition and in plots with warming combined with nutrient addition from 2000 to 2003 (change significantly different from zero), although only the decrease of dead leaves differed significantly from the control plots (Tukey hsd, Fig. 1A and B; Appendix A).
Community biomass measured at the end of the experiment was 56.3% higher in plots with nutrient addition and 77.4% higher in plots with warming combined with nutrient addition compared to the control plots (Fig. 1C; GLM treatment effect, $F_{3,27} = 7.13, P = 0.001$; block effect, $F_{9,27} = 0.64, P = 0.756$). Biomass in plots with only warming did not differ significantly from the controls (Tukey’s hsd, Fig. 1C). Compared to controls, the vegetation was 393.2% taller in plots with only nutrient addition and 835.0% taller in plots with warming combined with nutrient addition. Vegetation height in plots with only warming did not differ significantly from the controls (Fig. 1D; GLM treatment effect, $F_{3,27} = 57.25, P = < 0.001$; block effect, $F_{9,27} = 1.46, P = 0.213$). PAR measured on the ground decreased significantly with increasing biomass (linear regression, coefficient $= -0.58, P < 0.001$).

Community diversity

Community diversity index (Shannon) decreased from 2000 to 2003 due to species loss and decreased species abundances, in particular in plots with nutrient addition combined with warming (Fig. 2A–C; Appendix A; see Plate 1). Graminoid diversity increased in plots with only nutrient addition and in plots with warming combined with nutrient addition due to increases in species richness and abundances (change significantly different from zero, Fig. 2D–F; Appendix A), although these changes did not differ significantly from the changes in the control plots due to large variation in the changes among plots within each of the treatments (Tukey’s hsd, Fig. 2D–F). Forb diversity increased in plots with only nutrient addition, primarily due to increased species abundances (Fig. 2G–I; Appendix A). Dwarf shrub diversity decreased in plots with only nutrient addition and warming combined with nutrient addition, primarily due to decreased species abundances, although these decreases did not differ significantly from the controls due to large variation in the changes among plots within each of the treatments (Tukey’s hsd, Fig. 2J–L; Appendix A). Bryophyte and lichen diversity decreased significantly in plots with warming combined with nutrient addition due to significant species loss and decreased species abundances (Fig. 2M–R). Moreover, abundances of bryophytes decreased significantly in plots with only warming and only nutrient addition, whereas the number and abundances of lichen species decreased significantly in plots with only nutrient addition (Tukey’s hsd, Fig. 2M, O, P, R; Appendix A).

Relationship between Dryas cover and changes in community diversity

The percent cover of Dryas decreased over the four years, both in the control plots and in plots with only nutrient addition and warming combined with nutrient addition (Fig. 1A; Appendix A). However, the persisting high Dryas cover (Appendix A) and the lack of increased diversity or abundance in functional groups in the controls and in plots with only warming (Figs. 1C–D, 2A–R) suggests that Dryas maintained dominance here. On the other hand, in plots with only nutrient addition and warming combined with nutrient addition, Dryas cover decreased (Fig. 1A; Appendix A), biomass and vegetation height increased due to increased richness and abundances of graminoids and
forbs (Figs. 1C–D, 2D–I), and diversity of all other functional groups decreased (Fig. 2J–R). These changes suggest that *Dryas* was replaced as the dominant species by graminoids and forbs in plots with only nutrient addition and mainly by graminoids in plots with warming combined with nutrient addition.

There were few significant relationships between the changes in *Dryas* cover and changes in community parameters, which may be due to small variations in the changes within treatments. However, the sign of the relationship between *Dryas* cover and community parameters differed between the treatments. In plots where *Dryas* maintained dominance (control plots and plots with only warming), significant or close to significant relationships between changes in *Dryas* cover and changes in community parameters were negative.
(Appendix B, C). When *Dryas* cover decreased, lichen diversity increased in the controls, and total diversity, forb diversity, total species richness, bryophyte richness, and forb abundances increased in plots with only warming (Appendix B, C). In plots with only nutrient addition on the other hand, where graminoids and forbs had increased in abundances at the expense of *Dryas*, the significant or close to significant relationships were always positive. Lichen diversity, total, bryophyte and lichen richness, and bryophyte abundances decreased with decreasing *Dryas* cover (Appendix B, C). In plots with warming combined with nutrient addition, forb abundances increased with decreased *Dryas* cover (Appendix B, C).

**DISCUSSION**

Four years of environmental manipulations altered dominance hierarchies and community structure of an alpine *Dryas* heath community. In particular, graminoids and forbs increased in abundances in plots previously dominated by the dwarf shrub *Dryas octopetala* and community diversity decreased, primarily because of a sharp decline in the number and abundances of bryophyte and lichen species.

The decreased cover of the key species *Dryas* after nutrient addition and warming combined with nutrient addition was unexpected based on the results of Welker et al. (1997). They found increased *Dryas* cover after 1–3 yr of climate change simulations (warming, watering, fertilizing, or combinations of these) in one alpine and three arctic sites. On the other hand, negative effects of nutrient addition on *Dryas* abundance was found in some arctic sites, but these decreases were most likely caused by delayed winter hardening (Robinson et al. 1998) or direct damage on *Dryas* leaves caused by the fertilizer (Henry et al. 1986). One important difference between alpine and arctic habitats is that vegetation cover in the alpine is more closed and consists of more species (e.g., Klanderud and Totland 2004). In the arctic, graminoid species are very rare in *Dryas* heaths (Wookey et al. 1993), suggesting limited possibilities for competitive interactions here, at least in the short-term (Wookey et al. 1995). This is in sharp contrast to alpine Finse, where the faster and greater amplitude of the responses of graminoids and forbs to the increased nutrient availability and warming combined with nutrients altered the dominance relationship. *Dryas* commonly dominates severe habitats with low soil nitrogen levels, and may be a stress tolerator more than a competitor (Chapin et al. 1994). The increased dominance of nutrient-demanding competitors, such as graminoids and some forbs, at the expense of *Dryas* when nutrient availability increased at Finse, supports this. Our results are in line with studies from Alaskan fell fields, where *Dryas* cover decreased due to increased competition from graminoids after fertilization (McGraw 1985, Fox 1992), and they are in line with Chapin et al. (1995), who found increased biomass of graminoids and a decrease of evergreen shrubs and forbs after three years of warming and fertilizing in the Alaskan tussock tundra. After nine years, however, deciduous shrubs dominated the plots, which may indicate that we still know little about the long-term responses of arctic and alpine plant communities to climate change. The warming induced by the OTCs corresponded with the predicted increase in summer temperature of ~1.5°C over the next 75 years in southern Norway (IPCC 2001). However, four years of warming alone had only minor effect on community parameters at Finse. This is in line with climate change experiments from the arctic, where nutrients appear to limit plant growth more than temperature, but that synergistic effect of warming and nutrients may occur (e.g., Robinson et al. 1998, Dormann and Woodin 2002).

The *Dryas* heath diversity decreased due to decreased abundances of dwarf shrubs, bryophytes, and lichens, and a significant loss of bryophyte and lichen species. These results are in line with arctic and sub arctic climate change experiments, which have found decreased community diversity, most likely due to increased cover of vascular at the expense of the number of non-vascular species (e.g., Chapin et al. 1995, Molau and Alatalo 1998, Press et al. 1998). Although the decrease of some species may be due to direct effects of warming and nutrient addition at alpine Finse, the main causes to the decreased community diversity was most likely caused by the change in community structure caused by the shift in dominance hierarchies. When the community changed from heaths dominated by the low stature *Dryas*, to meadows of tall graminoids and forbs, community biomass and height of vegetation increased significantly. Moreover, the role of biotic interactions, such as competition for light, likely increased considerably. The most dramatic diversity decrease occurred when warming was combined with nutrient addition. In these plots, graminoid diversity increased at the expense of all other functional groups, attaining higher biomass and taller vegetation compared to the other plots. Graminoids are expected to respond faster to environmental changes than other functional groups because of their modular organization and high tissue turnover (Shaver et al. 1997). The role of competition in alpine and arctic habitats is still debated, but changes in nutrient regimes caused by higher soil temperature and increased nitrogen mineralization is predicted to increase the role of species interactions, and alter the competition hierarchies in alpine and arctic plant communities (Chapin et al. 1995, Shaver and Jonassen 1999, Dormann and Woodin 2002), as we have found here. Moreover, decreased diversity after nutrient addition is commonly observed, and is often explained by competitive displacements of species of low stature because of light limitation (Shevtsova et al. 1997, Theodose and Bowman 1997, Baer et al. 2004).
The negative relationship between changes in Dryas cover and changes in forb, bryophyte, and lichen community parameters in the control plots and in plots with only warming, where Dryas maintained dominance, may suggest that competition from Dryas control community processes of these groups. This is in line with previous studies predicting negative impacts of Dryas on community diversity at Finse (Klanderud and Totland 2004). The positive relationship between Dryas cover and bryophyte and lichen community parameters in plots with only nutrient addition, on the other hand, is most likely explained by the increased diversity of graminoids and forbs here. Because these functional groups may be stronger competitors than Dryas when nutrient availability increases, they may have negative effects on both Dryas and bryophytes and lichens. Thus, this may result in a negative relationship between changes in Dryas cover and changes in bryophyte and lichen community parameters. Furthermore, the increased abundances of forbs with decreasing Dryas cover in plots with warming combined with nutrient addition, may also suggest a shift in the competitive hierarchies, with forbs becoming more competitive than Dryas when resources increase.

Environmental manipulations led to considerable community changes in the alpine Dryas heath at Finse. From being a diversity-hotspot, it became a graminoid and forb meadow, with substantially lower diversity. The drop in diversity was primarily caused by changes in the community structure. Thus, this study highlights that the complexity of biotic interactions and their responses to environmental changes may modify the direct effects of changes in the abiotic conditions, and that species interactions must be considered in climate change experiments and in models predicting climate change effects.

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APPENDIX A

APPENDIX B
A figure showing the relationships between change in Dryas octopetala cover and change in community diversity parameters from 2000 to 2003 in climate change simulation plots in alpine Norway is available in ESA’s Electronic Data Archive: Ecological Archives E086-105-A2.

APPENDIX C
A table of simple linear regressions between change in Dryas octopetala cover and changes in community diversity parameters in climate change simulation plots from 2000 to 2003 in alpine Norway is available in ESA’s Electronic Data Archive: Ecological Archives E086-105-A3.