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Plant community responses to climate change

Nielsen, Jane Kongstad

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Jane Kongstad

KØBENHAVNS UNIVERSITET

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ENGLISH SUMMARY

Climate change is expected to affect terrestrial ecosystems across the globe with increased atmospheric CO_2 concentration, higher temperatures and changes in precipitation patterns. These environmental factors are drivers of many important ecosystem processes, and changes in ecosystem function are therefore expected in the future. The aim of this PhD-thesis was to examine the effects of climate change on aboveground plant growth, plant composition and plant phenology in Danish heathland ecosystems. Two sites were investigated in large-scale field experiments: 1) the CLIMAITE site, 'Brandbjerg' and 2) the INCREASE site at Mols. Field manipulations lasted years and included: Warming, summer drought and (CLIMAITE only) elevated CO_2 concentrations. The treatments were applied individually and in all possible combinations. Further, at Brandbjerg, but outside the treatment plots, a study was performed on the effects nitrogen and phosphorus addition on phenolgy, chemistry and growth of the dominant grass *Deschampsia flexuosa* (Wavy Hairgrass).

In general, the aboveground vegetation responded less than expected to changing climatic conditions; even though *Calluna vulgaris* (Heather) increased in biomass over the study period, the biomass was not affected by the manipulations, indicating that *C. vulgaris*, has a strong resistance to changes in climate. Also, the grass biomass (primarily *D. flexuosa*) was not affected and was relatively constant over the period. I argue that the resilience of *D. flexuosa* towards the climatic treatments came from the plants ability to let the tissue die back, and then quickly recover once conditions again became favourable. That gave the plant a high resilience to changes in climatic factors. *Calluna vulgaris*, on the other hand, showed a resistance to changes by constantly maintaining the growth during the whole season, probably because of its evergreen status. Together, the two different strategies made the heathland ecosystem more resilient to the climatic treatments than expected. We also found that the amount of flowering culms of *D. flexuosa* increased in response to increased CO_2, whereas the seed germination success decreased. The bryophyte biomass and the nitrogen content decreased in response to nitrogen addition. Even such apparently minor changes might, given time, affect the plant composition and thereby possibly also the major ecosystem processes. Further, we observed changes in the aboveground plant composition in response to the climate manipulations at the Mols site, where *C. vulgaris* was regenerating after a disturbance. Here a decrease in biomass of the pioneer stage was seen, when subjected to the drought treatment compared to warmed and control treatments. I therefore conclude, that the stage of the *C. vulgaris* population as well as the magnitude and frequency of disturbances determine the effects of future climate change on the plant community in heathland ecosystems.

DANSK RESUMÉ

Fremtidens klimaforandringer vil ændre forholdene for vores økosystemer. Højere atmosfæriske CO_2-koncentrationer, varmere klima og ændrede nedbørsmønstre er alle parametre, der vil påvirke biologiske processer og dermed påvirke vores økosystemer på flere niveauer. Formålet med denne ph.d.-afhandling er at belyse effekterne af klimaforandringer på plantevækst, artssammensætning og fænologi i danske hedeøkosystemer. To lokaliteter blev undersøgt med storskala feltstudier: 1) CLIMAITE-lokaliteten, Brandbjerg og INCREASE-lokaliteten på Mols. Behandlinger i eksperimentet var: forhøjet temperatur, forlænget sommertørke samt (kun på CLIMATE lokaliteten) forhøjet atmosfærisk CO_2-koncentration. Alle behandlinger blev undersøgt enkeltvis og i samtlige mulige kombinationer. Desuden blev der på Brandbjerg, men uden for behandlingsfelterne, udført et gødskningforsøg, der skulle undersøge effekten af øget nitrogen- og fosfortilførsel på fænologi, blad-kemi og vækst af *Deschampsia flexuosa* (Bølget Bunke).

Generelt blev den overjordiske vegetation påvirket i mindre grad af klimabehandlingerne end forventet. Selvom *Calluna vulgaris* (Alm. Hedelyng) forøgede sin biomasse hen over perioden, var der ingen effekt af behandlingerne. Dette indikerede, at *C. vulgaris* var mere modstandsdygtigt over for ændringer i klimaet end forventet. Græsbiomassen af *D. flexuosa* blev heller ikke påvirket af klimabehandlingerne, og biomassen var forholdsvis ens alle årene. Jeg argumenterer for, at *D. flexuosas* modstandsdygtighed skyldes dens evne til at visne ned under en tørkeperiode og hurtigt skyde igen så snart vilkårene igen blev favorable. Denne evne til at visne ned og genskyde gjorde arten overlevelsesdygtig under de ændrede klimaforhold. Lyngen visnede ikke på samme måde ned. Til gengæld kunne arten, formodentligt på grund af at den er stedsegrøn, opretholde en konstant, lav vækst gennem hele sæsonen, uanset klimabehandling. Tilsammen gjorde disse to plantestrategier heden som økosystem langt mere modstandsdygtigt over for forandringer i klimaet end forventet. Antallet af blomsterstande for *D. flexuosa* steg under forhøjet CO_2-koncentration, mens spiringsevnen faldt. Nitrogenkoncentrationer i bryofytterne og bryofyt-biomassen faldt ved nitrogentilførsel. Selv sådan tilsyneladende små forandringer kan, med tiden, påvirke plantesamfundet og dermed muligvis også de væsentlige biologiske processer i økosystemet. Desuden viste eksperimentet på Mols, at regenerationen af *C. vulgaris*, efter et lyngbladbille angreb, blev påvirket af klimabehandlingerne. Her havde unge skud af *C. vulgaris* sværere ved at reetablere sig i felter, der havde været udsat for tørke, end i felter der enten var kontrolfelter eller varmefelter. Jeg konkluderer derfor, at både livs-stadiet af *C. vulgaris*-populationen samt omfanget og frekvensen af forstyrrelser er med til at bestemme effekten af fremtidens klimaforandringer på plantesamfundet i et hedeøkosystem.

PREFACE

This Ph.D. thesis is submitted to the Faculty of Life Sciences, University of Copenhagen, Denmark. The Ph.D. was a part of the Danish climate change experiment "CLIMAITE" (www.climate.dk) and the work was conducted at the Institute of Forest & Landscape Denmark. From September 2007 to March 2008 I visited the Division of Plant Sciences at the University of Tasmania.

The study was financed by the project CLIMAITE (CLIMATE change effects on biological processes In Terrestrial Ecosystems) funded by The Villum Kann Rasmussen Foundation, the EU infrastructure INCREASE and by the research school REFOLANA.

I would like to thank several people, who have all contributed to make this thesis possible. First of all I would like to thank my supervisor Inger Kappel Schmidt, Forest & Landscape Denmark, for support during the whole period both in the field and during the writing process, but also for giving me the chance to teach half a year at the Forest College in Nødebo. Thanks also to Claus Beier for supervision and encouragement during the writing of this thesis.

I would also like to thank the CLIMAITE group for good meetings with high scientific outcome; especially I would like to thank the Ph.D. group for lot of good inspiring meetings, talks and fun. A group like that is unique and I felt very lucky to be part of it.

Thanks to the people at division 3 (now 34) at Forest & Landscape Denmark for six good years and of course a special thanks to my office mates; Marie, Jesper and Shimon and my fellow Ph.D. colleagues Andy and Lisbeth -a lot of things have been easier due to your help and support; practical as well as mental.

Special thanks goes to Mark Hovenden, his wife and two children for your hospitality when Lasse and I were half a year in Tasmania. We had a wonderful time at the university as well as outside.

I would like to thank the Forest College for my half year there. Thanks Trine and Michael for a good time and for a lot of inspiration.

Finally, I am very grateful for having a husband like Lasse who is now an expert on heathland ecosystems. Besides support with the thesis, he has been a fantastic listener and inspirer.

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THE AIM OF THE PROJECT

During the writing of these papers, one question remained in focus again and again. **Will changes in climate alter plant communities over time?** This question may seem simple and easy to answer, but as the following synthesis will hopefully show, simple questions are not always easy to answer – especially not when working with natural ecosystems.

Changes in the climate will affect most biological processes and thereby influence both natural, semi-natural and cultural ecosystems. The challenge of coping with climate changes will increase in the future, and knowledge about the magnitude of the effects on ecosystems is therefore needed.
The aim of the study was to examine the effects of climate changes on aboveground plant growth, plant composition and plant phenology in a Danish heathland.

The thesis consists of data from two projects; the Danish Climate Centre of Excellence, CLIMAITE and the EU infrastructure INCREASE both investigating ecosystem responses to climate in large scale field experiments. Further, four scientific papers are included, all concerned with the relationship between plant growth and climate change. The first paper investigates the effect of climate change on biomass production within a heathland ecosystem. The second paper is about growth and nutrient allocation within the plants in response to nutrient addition. It also deals with the interaction between climate and nutrient addition on the dominant grass species *Deschampsia flexuosa*. The third paper report changes in flower phenology brought about by climate change, based on studies of flowering and seed production of the grass *D. flexuosa.* Finally, the fourth paper is about regeneration of *Calluna vulgaris* after a heather beetle attack under warmer and drier climate conditions.

As stated earlier, my thesis is part of the large climate change experiment CLIMAITE and therefore a part of a network of research covering most biological patterns and processes within the investigated heathland; belowground processes, gas exchanges, plant physiological parameters and plant responses both below- and aboveground. We have all been working at the same study site, with the common key words “climate change” and “heathland ecosystem”. This thesis focuses on the aboveground vegetation, but due to the unique opportunity of knowledge sharing, it is possible to discuss my findings within the findings of others PhD.-students and researchers at the site, and I thereby seek to understand and describe the plant responses in an ecosystem perspective. Finally, the results found in this thesis are discussed in relation to other threats identified for heathland ecosystems including nitrogen deposition, lack of management and land-use changes.

BACKGROUND

Climate change scenarios

Global atmospheric concentrations of greenhouse gasses have increased over the last century, primarily as a result of human activity. The carbon dioxide concentration has increased from a pre-industrial level of 270 ppm to 380 ppm in 2005 (Christensen et al. 2007). This increase mainly owes to fossil fuel burning and land use changes and the CO_2 concentration is expected to increase even further depending on the magnitude of future CO_2 emissions.

Several models have been developed to estimate the magnitude of future changes. Although the models show somewhat different output CO_2 concentrations, there is nevertheless a consensus that the increase in CO_2 will have consequences for other climatic parameters including increased temperature and changes in precipitation patterns with more heavy rain events and longer drought periods. Wind directions and wind speeds are also expected to change with more storms and hurricanes as a result. Most models agree that changes in climate will not be distributed evenly around the world; some areas will be flooded and others may experience severe drought.

In Denmark the temperature is expected to increase with yearly average temperatures 2-3 ^{o}C higher in year 2100 compared to 1990. Night temperatures are expected to increase more than day temperatures and winter temperatures will increase more than summer temperatures (Danish Meteorological Institute http:// www.dmi.dk) (fig 1). Also, precipitation patterns are expected to change in the future. In Denmark, winter precipitation is expected to increase by 20-40 %. In summer, on the other hand, a reduction of 85-90% of current precipitation is expected. Together with a higher frequency of heavy rain falls, the reduction is expected to result in longer drought periods during the growing season (Danish Meteorological Institute http:// www.dmi.dk) (fig. 2).

Dry Heathlands

All studies within this thesis took place in dry inland heathlands. Heathlands are associated with dwarf shrub dominance, in Denmark mainly the evergreen heather; *Calluna vulgaris*. The ecosystem is characterised by a low level of plant-available nutrients and there is often a strong competition for nutrients between plants, fungi and bacteria (Jonasson et al. 1996). Further it is, at least periodically, limited by water. The diversity of higher plants is low, and the vegetation is adapted to cope with stressful conditions. The system depends on continuous management, since nutrients have to be removed to maintain the low levels.

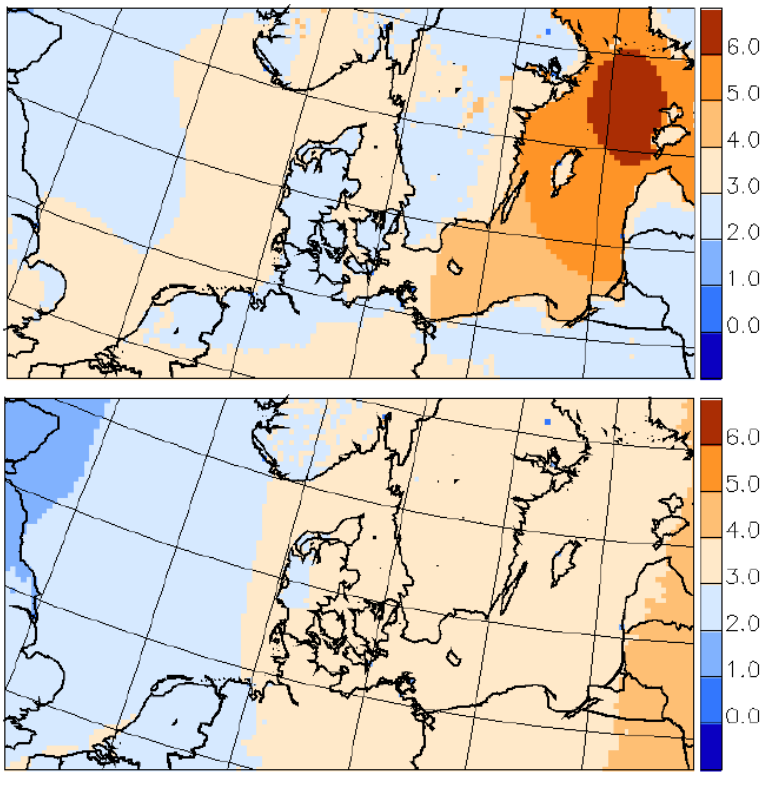


Figure 1 *Predicted changes in temperature (°C) in winter (top) and summer (bottom) in the period 2071-2100 compared to the period 1961-1990 in Denmark (from www.DMI.dk).*

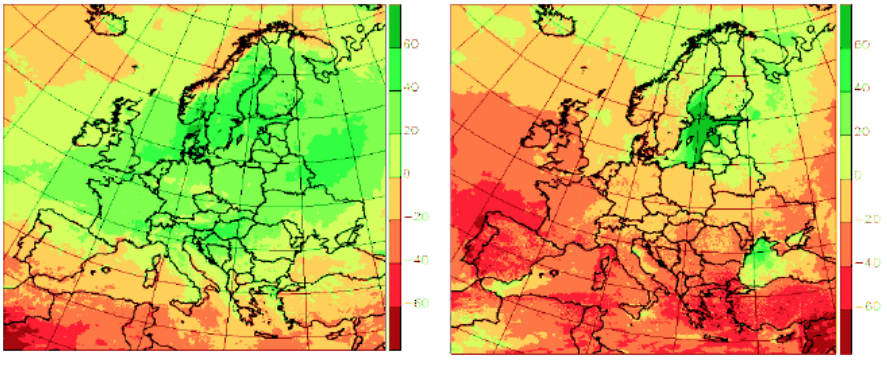


Figure 2 *Predicted changes (%) in winter (left) and summer (right) precipitation in the period 2071-2100 compared to the period 1961-1990 (from www.DMI.dk).*

The need for management has increased progressively with the industrialization since the nutrient load into the system has increased markedly during this period. The increased nutrient load together with the lack of management has brought about changes in the plant species composition of heathlands. First of all by invasion of grasses, but also by invasion of trees and bushes, all resulting in higher decomposition rates, changes in soil structure and exclusion of previously present species (Terry et al. 2004). Climate changes could enhance these changes further by speeding up the processes.

Deschampsia flexuosa *Calluna vulgaris*

Climate change effects on aboveground vegetation

Increased CO_2 directly stimulate plant growth due to a higher CO_2 assimilation rate (de Graaff et al. 2006) and it has also been shown to increase the number of flowers or seeds per plant (Jablonski et al. 2002; Thurig et al. 2003). Further, increased carbon assimilation may lead to higher rhizodeposition (Zak et al. 1993) and thereby stimulate belowground activity and the mineralization rate. However, nutrient and water limitation has been shown to quench the CO_2-induced biomass increase, resulting in a more limited response in natural ecosystems compared to agricultural systems (Leakey et al. 2009). Studies on natural ecosystems that have reported increased biomass production under elevated CO_2, concluded that this increase mainly was due to an indirect effect on the hydrological cycle, because elevated CO_2 decreases the stomatal conductance, leading to improved water use efficiency (WUE) (Ainsworth and Long 2005).

Increased CO_2 has, on the other hand, been shown to increase C/N and C/P ratios in litter, which may decrease the mineralization rate (van Heerwaarden et al. 2005; Hovenden et al. 2008). A decreased mineralization rate could result in an increased immobilization of N and P, and thus a reduction in the plant-available N/P pools. However, since CO_2 is expected to

increase the plant biomass production and thereby also the litter production this could compensate for the lower litter quality.

Since *C. vulgaris* is abundant from the North of Norway down to Spain and Portugal, a direct effect of warming should probably not be expected within the short time scale of this study. However, warming may influence the abundance of *C. vulgaris* indirectly, for instance by influencing the number of heather beetles, since they are stimulated by a warm and dry spring (Penuelas et al. 2004). Further, warming has been demonstrated to stimulate N-mineralization and thereby increase N-availability (Aerts et al. 2006; Emmett et al. 2004; Rustad et al. 2001). Thus, warming may therefore increase the aboveground biomass of especially the grass, since it is a weaker competitor for nutrients compared to the heather under nutrient deficient conditions.

Lately, monitoring of the Danish heathlands has shown that the cover of the grass *D. flexuosa* is now relatively high in many of the Danish heathlands (Andersen et al. 2005). Grass invasion on heathlands has been linked to the relatively high levels of N-deposition (Barker et al. 2004; Terry et al. 2004). If future warming increase the N-availability at the site, the grass could increase in cover at the expense of the slow growing *C. vulgaris*. The study site is at the 55°53' N, and at this latitude, warming also prolongs the growing season (Cleland et al. 2006; Mikkelsen et al. 2008) and thereby increases the biomass production in spring and autumn. Also, spring phenology, such as leaf appearance and flowering time, has been shown to shift forward in response to a warmer climate, due to an earlier start of the growth season (Hovenden et al. 2008; Menzel et al. 2006).

Drought has been shown to decrease plant biomass due to a slow down of most biological processes including photosynthesis (Gordon et al. 1999; Penuelas et al. 2007) mineralization, nutrient cycling and biomass production (Emmett et al. 2004; Schmidt et al. 2004; Larsen et al. 2011). The fraction of biomass found as litter has been shown to increase in response to severe drought (Kongstad et al. 2011), whereas actual litter production may decrease due to lower biomass production (Penuelas et al. 2004). Further, it has been reported that repeated droughts can change soil compactness and water holding capacity even in wet ecosystems (Sowerby et al. 2008). In semi-natural and nutrient poor ecosystems such as heathlands, such alterations can change the plant production and as a result also change plant-plant interactions (Damgaard 1999; Penuelas et al. 2007). However, heathland ecosystems are characterised by a low level of plant-available nutrients and the ecosystem is, at least periodically, limited by water. The vegetation is therefore adapted to cope with stressful conditions, and studies with heathlands similar to ours have recently shown an unexpected resistance towards changes in climate conditions including prolonged drought periods (Grime et al. 2008; Hudson and Henry 2010).

The climate change factors will interact. Recent studies on plant growth, phenology and plant composition have shown that changes in the main climate drivers, individually as well as interactions between increased CO_2 and precipitation and temperature, have a significant impact on ecosystem functions (Shaw et al. 2002; Beier 2004; Norby and Luo 2004; Luo et al. 2008). A higher CO_2-assimilation rate theoretically increases WUE and CO_2 enrichment was thus expected to counterbalance any drought effects by stimulating plant growth and thus also plant nutrient demands (Ainsworth and Long 2005). Drought may, as described above, decrease the biomass production in mid-summer and thereby counteract the increased biomass production expected from increased CO_2 concentration and from warming. Further, since this ecosystem periodically was limited by water, warming might add to the effect of drought, during drought periods in mid-summer (Beierkuhnlein et al. 2011; Penuelas et al. 2007).

Changes in species composition

The distribution of the North Western heathlands is highly linked to the distribution of the key species *C. vulgaris*. Heathlands are also native habitats for the grass *D. flexuosa* and the two species typically co-occurr with high cover of the grass after disturbances such as fire or clearances resulting in nutrient releases. Lately, *D. flexuosa* has increased in both cover and area of distribution in Denmark (Nielsen et al. 2011). The increase is assumed to be associated with previously high levels of nitrogen deposition and to the lack of management in nutrient poor areas. *D. flexuosa* and *C. vulgaris* belong to two different functional groups, graminoid and dwarf shrub respectively, and have highly different life strategies, with the grass being faster growing, more productive and having a lower nutrient turn-over time. *Deschampsia flexuosa* has AM- mycorrhiza which facilitates the uptake of especially phosphorus (Smith and Read 2008). *Calluna vulgaris* is, on the other hand, evergreen with a long leaf life span, it has a high content of complex compounds in tissue that make the decomposition rate of the litter low. It has the ericoid mycorrhiza that provides nutrient uptake in organic form (Cornelissen et al. 2001). *Calluna vulgaris* has the so-called 's-strategy' (Grime 2002); it is adapted to nutrient and water limitation, but on the other hand fails to compete when changes lead to a more productive ecosystem (Friedrich et al. 2011).

If warming increases mineralisation and increased CO_2 concentrations increases root exudation, altered climate conditions may induce changes in the plant community similar to nitrogen deposition. For instance, changes in climate conditions may, as seen in the case of increased nitrogen availability, speed up the life cycle of *C. vulgaris*. Invasion by grasses often occur in openings of the *C. vulgaris* canopy, where *D. flexuosa* capture the water and

quickly create a close litter layer that prevents *C. vulgaris* seedlings to establish (Aerts 1993). Changes in climate therefore may result in an even faster spreading of *D. flexuosa* into heathlands.

Grasses have been shown to respond more quickly to changes compared to heather (Aerts 1995; Chapin and Shaver 1996; Arft et al. 1999; Michelsen et al. 1999; Graglia et al. 2001) and the positive effect on biomass production in response to elevated CO_2 may therefore be more pronounced for the grass than for the heather. On the other hand, heather may be more tolerant than the grass towards drought and would suffer less from the higher C/N ratio in litter, due to the ericoid mycorrhiza that provides nutrient uptake in organic form (Cornelissen et al. 2001).

Hypothesises

Based on the above-mentioned I hypothesized that:

- Elevated CO_2 and warming would stimulate aboveground biomass production, but drought would decrease biomass.
- Drought would increase the fraction of litter, but due to the lower production of biomass, the litter pool would decrease in response to drought.
- The amount of flowering culms would increase under elevated CO_2, whereas drought would lead to higher mortality before reaching the state of flowering.
- The main climate drivers were expected to interact. Drought was expected to counterbalance the stimulation of both biomass and flowering culms by elevated CO_2.
- During drought episodes, warming was expected to enhance the intensity of the drought.
- Within the time scale of this thesis, I further expected the grass, *D. flexuosa* to be more responsive to the climate drivers and the nitrogen addition than the heather, *C. vulgaris* due to differences in life growth forms.

METHODS

Study site

CLIMAITE

The experimental site for paper I-III is situated at Brandbjerg, Denmark (55º53'N; 11º58'E) on a hilly, nutrient poor, sandy moraine from the Weichsel glaciation surrounded by areas of elevated sea bed. The site is a heathland/grassland community co-dominated by the perennial grass *Deschampsia flexuosa* and the evergreen dwarf shrub *Calluna vulgaris*. The soil consists of 70 % sand, 20 % coarse sand, 6 % silt and 2 % clay. The pH_{CaCl_2} is around 4.2 in the organic layer and 3.5 in the upper 10 cm of the mineral soil. The vegetation comprises 17 species of vascular plants, 10 mosses and 9 lichens. Plant species are listed in table 1. Pretreatment analyses in 2004 showed an aboveground biomass of approximately 700 g DW m^{-2}, where *C. vulgaris* accounted for 40 %, *D. flexuosa* 32 %, mosses 26 % and herbs and other grasses only comprised 2 %. At the same time *D. flexuosa* covered 76%, *C. vulgaris* 41 %, mosses 7%, herbs 1% and lichens < 1%. The vegetation can be classified as high light demanding, with relatively little need for nutrients (Ellenberg 1991). The annual bulk nitrogen deposition in 2006-2007 was ~13 kg N ha^{-1} $year^{-1}$ measured at the location (Larsen et al. 2011). The study site was fenced to exclude larger herbivores.

Table 1 *Species list and cover of species (%) in ambient plots in the study period of 5 years at the CLIMAITE site.*

	2004	2006	2007	2008	2009	2010
C. vulgaris	41	55	67	58	63	65
D. flexuosa	76	56	66	42	42	38
F. ovina	0.7	0.1	3	1	2	0
S. decumbens	2	2	2	0.3	0	0.3
A. stricta	0.6	0	0	0	0.3	0
C. arenaria	3	2	1	0.3	0	0
R. acetosella	0.3	0	0	0	0	0
H. cupressiforme	1	2	3	2	2	-
P. schreberi	5	8	6	13	13	-
D. scoparium	0.6	0.3	0.3	1	1	-
Brachythecium sp	0	0	0.3	0	0	-

MOLS

The experimental site for paper IV is located at Mols, Denmark (56º23′ N, 10º57′E) and is generally similar to the Brandbjerg site. It is part of the inter-European research projects VULCAN "Vulnerability assessment of shrubland ecosystems in Europe under climatic changes" (Beier 2004) and the European network of large scale climate change experimental sites IN-

CREASE (www.increase-infrastructure.eu). The site is a semi-natural heathland/grassland ecosystem subjected to low-intensity grazing until 1992 and with no further management activities prior to the start of the experiment in 1999. The soil at Mols is a sandy podzol with a shallow organic layer. Also here is the vegetation co-dominated by the evergreen ericaceous shrub *C. vulgaris* (45 %) and the perennial grass *D. flexuosa* (45 %) with low abundances of other grasses, herbs and mosses associated with acidic heathland/grassland. When the experiment was initiated in 1999 the aboveground biomass was approx. 1050 g DW m^{-2}.

Experimental setup

CLIMAITE - A CLIMATE CHANGE EXPERIMENT

The CLIMAITE experiment was set up to study the **climate change effects on biological processes in terrestrial ecosystems.** It was initiated in 2004 and the experimental treatment was initiated one year later. The manipulations were chosen to match the climate scenarios for Denmark in the year 2075; Increased CO_2 concentration, warmer climate, and changes in precipitation patterns. However, we had one important exception: precipitation is predicted to change with prolonged summer drought and increased winter precipitation. The CLIMAITE experiment focused on the summer drought only, because eventual responses would be difficult to interpret in a combined summer removal and winter addition scenario. Fig. 3 shows a schematic view of the plots. The treatments were: Untreated control (A), CO_2-enriched with a target concentration of 510 ppm (CO2), increased temperature of 1°C (T) and prolonged drought period of 4-6 weeks during spring/summer (D). Drought treatment was alleviated if soil water content was about 5% in the top 20 cm soil (Table 2). The treatments were applied alone and in all possible combinations: temperature×drought (TD), temperature×CO_2 (TCO2), drought×CO_2 (DCO2), and temperature×drought×CO_2 (TDCO2) replicated in 6 blocks. In each block, the 4 treatments with or without CO_2 were grouped in an octagon in a split-plot design. Each plot was 9.1 m^2. CO_2 was enriched by FACE (free air carbon enrichment) as described by others (Miglietta et al. 2001). Passive night-time warming increased the air temperature 1 °C by covering the vegetation from dusk to dawn with reflective curtains all year around except during rain events. In the drought period curtains automatically covered the vegetation during rain events. The curtains were activated by a rain sensor and retracted again as soon as the rain stopped. The drought treatment removed 95% of the precipitation during drought period (Table 2). The rest of the year, the curtains were inactive and the plots exposed to control conditions. Soil water contents were measured by TDR probes, air temperature and precipitation were

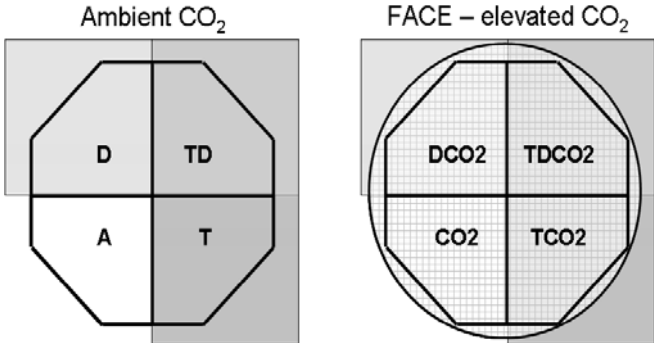


Figure 3 *Schematic presentation of a block at the CLIMAITE site with two separate octagons, ambient CO_2 and receiving CO_2 respectively, together hosting all eight treatment combinations with CO_2 (CO2), warming (T) drought (D) and untreated control (A) (Redrawn from Mikkelsen (2008))*

measured by two weather stations located at the site (Table 2). For further technical details see (Mikkelsen et al. 2008).

Within each plot, two permanently marked vegetation subplots were placed with the size of 0.5 x 0.5 m. All CLIMAITE data collected in this thesis took place in these subplots. The vegetation plots remained untouched over the whole study period, and only non-destructive analyses were performed here.

FERTILIZER EXPERIMENT

To examine the nutrient status of the heathland and to investigate the plant responses to increased nitrogen and phosphorus addition, a fertilizer experiment was setup outside the CLIMAITE plots. Fertiliser was applied in plots of 1.2 × 1.2 m as three levels of nitrogen, 0, 25 (N) and 75 (NN) kg N $ha^{-1}yr^{-1}$ and two levels of phosphorus, 0 and 10 (P) kg P $ha^{-1}yr^{-1}$ as well as two combinations of nitrogen and phosphorus (NP) and (NNP) in a 6 × 6 factorial block design with six replicates. The nutrients were dissolved in 2 l distilled water and added monthly from April to June 2005 as NH_4Cl and $NaH_2PO_4 * 2H_2O$. The plots without nitrogen and phosphorus addition were control (C) plots, to which 2 l of distilled water were added.

THE MOLS EXPERIMENT

The field scale climate treatments were initiated in 1999 after one pre-treatment year in order to identify variability between plots (Beier et al. 2004). Three replicated blocks with field-scale night-time warming and extended summer drought treatments and an un-treated control were installed in 1998 and treatments were initiated spring 1999. A light-weight scaffold-

Table 2 *Soil minimum and maximum temperatures for April and July are measured in the depth of 5 cm. Precipitation (mm) is an average of two weather stations in 2 m height at the site. Water excluded by the drought in mm and in % of annual precipitation is based on data from the two weather stations. SWC in volume % measured by TDR probes in 0-20 cm depth. See Mikkelsen et al. (2008) for technical details. Data from 2010 was not availably from the site and was therefore acquired from the Danish Meteorological Institute measured in the region (www.DMI.dk).*

	A	D	T	TD	CO2	DCO2	TCO2	TDCO2
2006								
Drought period: 3/7- 21/7 and 26/7- 8/8								
Min temp Apr (°C)	4.5	4.5	5.0	4.8	4.6	4.6	5.1	5.0
Max temp Apr (°C)	7.1	7.1	8.0	7.9	7.3	7.0	7.1	7.2
Min temp July (°C)	15.4	15.2	16.2	15.7	15.4	15.2	15.7	15.6
Max temp July (°C)	20.7	20.6	21.7	22.1	21.0	21.0	20.2	20.8
Precipitation (mm yr^{-1})	629	577	629	577	629	577	629	577
Precipitation excluded (mm)	-	5 and 47	-	5 and 47	-	5 and 47	-	5 and 47
Precipitation excluded (% of annual)	-	1 and 7	-	1 and 7	-	1 and 7	-	1 and 7
Annual mean SWC in depth (Vol%)	15.73	14.54	14.55	13.57	15.19	15.65	14.44	13.99
2007								
Drought period: 21/5- 22/6								
Min temp Apr (°C)	6.4	6.4	7.3	7.0	6.4	6.6	7.1	7.1
Max temp Apr (°C)	9.8	9.6	10.7	10.8	10.3	9.8	10.1	10.2
Min temp July (°C)	15.2	14.8	15.3	15.1	15.2	15.0	15.3	15.1
Max temp July (°C)	17.5	17.7	19.4	17.8	18.2	17.9	17.4	17.5
Precipitation (mm yr^{-1})	852	758	852	758	852	758	852	758
Precipitation excluded (mm)	-	94	-	94	-	94	-	94
Precipitation excluded (% of annual)	-	11	-	11	-	11	-	11
Annual mean SWC in depth (Vol%)	17.31	15.63	15.96	14.88	16.37	16.81	15.72	14.96

2008								
Drought period 5/5- 27/5 and 16/9- 2/10								
Min temp Apr (°C)	5.4	5.4	6.1	5.9	5.5	5.6	6.1	6.1
Max temp Apr (°C)	8.0	7.8	8.8	8.8	8.3	8.0	8.2	8.5
Min temp July (°C)	14.2	14.1	14.9	14.6	14.2	14.1	14.4	14.4
Max temp July (°C)	18.0	17.7	18.8	19.2	18.0	17.6	17.4	17.7
Precipitation (mm yr^{-1})	632	597	632	597	632	597	632	597
Precipitation excluded (mm)	-	12 and 23	-	12 and 23	-	12 and 23	-	12 and 23
Precipitation excluded (% of annual)	-	2 and 4	-	2 and 4	-	2 and 4	-	2 and 4
Annual mean SWC in depth (Vol%)	16.56	14.83	14.44	13.87	15.12	15.77	14.28	14.16
2009								
Drought period:18/5 -25/5 and 25/6 – 13/7								
Min temp Apr (°C)	5.5	5.6	6.3	6.0	5.4	5.5	6.0	6.0
Max temp Apr (°C)	8.8	8.6	9.7	10.0	8.5	8.4	8.49	8.8
Min temp July (°C)	14.8	14.6	15.3	14.9	14.6	14.4	14.7	14.7
Max temp July (°C)	17.8	17.5	19.2	18.9	17.4	17.3	17.0	17.3
Precipitation (mm yr^{-1})	668	625	668	625	668	625	668	625
Precipitation excluded (mm)	-	18 and 25	-	18 and 25	-	18 and 25	-	18 and 25
Precipitation excluded (% of annual)	-	3 and 4	-	3 and 4	-	3 and 4	-	3 and 4
Annual mean SWC in depth (Vol%)	15.47	13.86	13.71	12.90	14.02	14.41	13.87	13.29
2010								
Drought period: 4/5- 3/6								
Min temp Apr (°C)	4.4	4.6	5.1	4.9	4.6	4.7	5.1	4.9
Max temp Apr (°C)	7.6	7.8	9.2	8.3	7.4	7.3	7.4	8.0
Min temp July (°C)	14.5	14.5	15.3	15.1	14.6	14.5	14.8	14.9
Max temp July (°C)	19.1	19.9	22.3	20.9	18.7	19.2	19.0	19.9
Precipitation (mm yr^{-1})	844	771	844	771	844	771	844	771
Precipitation excluded (mm)	-	73	-	73	-	73	-	73
Precipitation excluded (% of annual)	-	9	-	9	-	9	-	9
Annual mean SWC in depth (Vol%)	17.43	14.82	15.55	14.61	15.38	17.40	16.29	16.25

ing was placed on each 4 x 5 m plot to carry the roof. The drought plots were subjected to a 1-2 months drought period in the spring/summer from 1999 to 2010 by covering the vegetation with transparent PVC roofs but only during rain events to avoid influences on wind, temperature and light conditions. As at the CLIMAITE the site the roofs were retracted again as soon as the rain stopped. The curtains removed up to 95 % of incoming rain during the drought which equals 20 % (11-29%) of the annual precipitation. The temperature treatment was designed to mimic an increased minimum temperature (night-time warming) rather than a general temperature increase. The warming plots were covered with a reflective aluminium curtain approximately 20 cm above the vegetation. The curtains reflect the major part of the infrared (IR) radiation (Beier et al. 2004). The curtains were controlled by a light sensor and automatically drawn over the vegetation to reduce the loss of IR radiation at dusk, and at sunrise the curtains were retracted to leave the plots open during the day. Further, a rain sensor over-ruled the night-time warming and the curtains were retracted during rain events to avoid major impact on the hydrological cycle. The curtains increased the mean temperature by 0.4°C in the air and by 1.2°C in the soil. The moderate increase in mean temperature increased the growing degree days by 112 % and decreased the number of days with frost by 44%. For further information on the field site and the experimental design, see (Beier et al. 2004).

Vegetation analyses

All the applied methods are described in detail in each paper, but in the following section I outline some of the considerations regarding the use of some of the different methods. Not all the methods that were applied during the work presented in this thesis are included, and those that are included are not described in detail – only some considerations and the rationale for choosing the methods that we did.

PIN-POINT METHOD

To measure plant cover, vegetation height and compactness we used the non-destructive pin-point analysis (Jonasson 1988), as described in more detail in paper I and paper IV. The pin-point method allows conversion of the data into biomass estimates. When using such a model there will always be advantages and disadvantages. The advantages are first of all that the method is a non-destructive method. This was a necessity in this study, since the aim was to follow the vegetation responses to climate change over a period of 1-5 years and the plots were far too small to do actual harvesting. Secondly, the method is relatively time-saving in the field, and to cover all 48 plots at

the site took about 2-3 weeks. However, data processing also takes time, and all together time will also be a disadvantage of the pin-point method since it only allows 1-3 analyses within a year, and therefore can only provide snapshots. Further 2-3 weeks is too long time when recording phenological patterns such as leaf appearance and flowering. The most important disadvantage, however, is the uncertainty of the model; the estimates are based on measurements from outside the CLIMAITE plots, and the model does not take into account differences between treatments that are not related to changes in cover or density. This could be thicker leaves, longer or thicker stems etc. Further, the method is useful in this ecosystem with only a few dominant species. It would be difficult to use in an ecosystem with a higher plant biodiversity. However, I do consider this method not only to be the best available option, but also overall a good tool for consistently estimating plant biomasses in this heathland ecosystem, with only a few dominant species.

PLANT PHENOLOGY

All measurements and observations related to plant phenology are time consuming. Counting flowers, observing flowering stages, collecting seeds and germination experiments all take time. Further, there is a discrepancy between the fact that flowering observations optimally should be performed every day or every second day and of the size of our experimental site (8 treatments, 6 replicates and 2 sub-plots), which resulted in a labour intensive period during flowering. Additionally, the phenological pattern turned out to be very different from one year to the next, and this made it difficult to plan before the flowering started. These difficulties caused some compromises, including the fact that flowering in 2008 should ideally have been followed more closely, since the poor temporal resolution in the end blurred any differences in flowering time between the treatments. Also, the study of flowering development was only done in one season, and the same was true for seed weight and seed germination studies. Thus, despite the shortcomings of the data, I do believe we managed to cover at least some of the phenological patterns of *D. flexuosa*. As a supplement to the pin-point method I, each year (2007-2009) in September, harvested 3-5 *C. vulgaris* shoots in a 10 cm buffer zone around the permanent vegetation plots. I fractioned the material into leaves, flowers and wood and weighted the fractions to identify any changes in allocation of resources into flowering-, leaf- or woody tissue.

NDVI

NDVI (Normalized Difference Vegetation Index) measurements were done using a spectrometer with four sensors for simultaneous measurements of both intrinsic and reflected light within the PAR and NIR bands. The method was applied because we expected to identify phenological patterns such as leaf appearance, flowering time, and biomass peaks. The method is simple

and a good supplement to the time consuming observation method mentioned above. The NDVI turned out to be most efficient during spring when green grass vegetation did not fully cover the area. At that time, I could measure clear differences in leaf appearance (*D. flexuosa*) between warmed and non-warmed plots (Fig 4). Later during the season I observed a point of saturation and the method could not handle the dense vegetation cover. In order to apply the method to determine flowering time and leaf senescence, the method therefore has to be developed or automated cameras for daily image collection could be applied. Further, the phenology measurements have to be performed very often and access to both the instrument and to the field site should be easy.

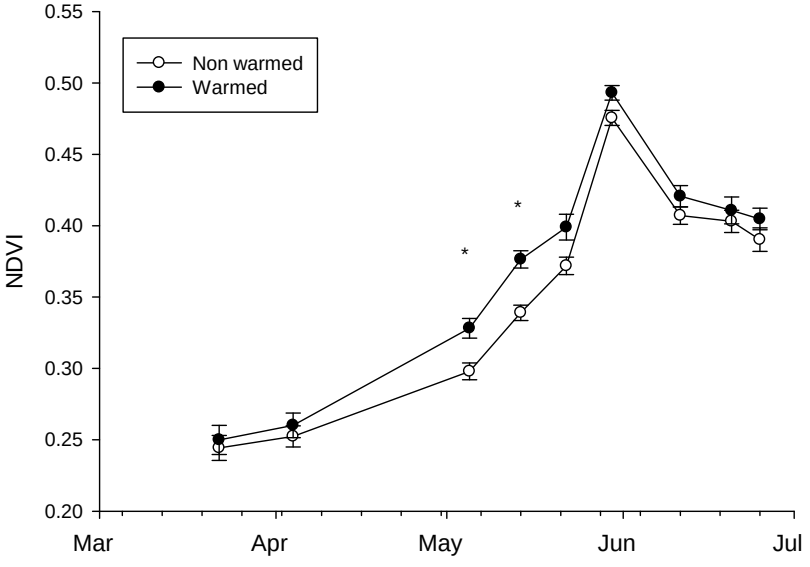
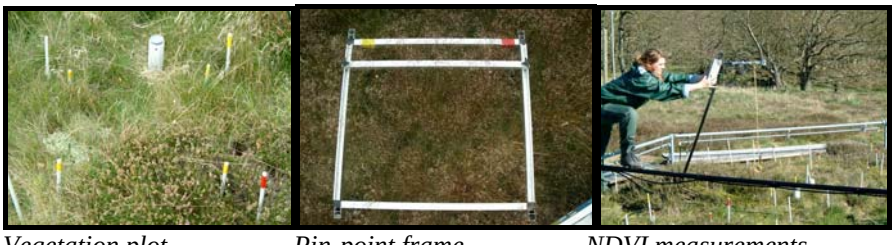


Figure 4 *Difference in NDVI (Normalized Difference Vegetations Index) in warmed plots (1 °C) compared to ambient plots at the CLIMIATE site. Measured in spring 2007. *= p < 0.05.*



Vegetation plot *Pin-point frame* *NDVI measurements*

RESULTS AND DISCUSSION

Why climate change experiments?

Models are a useful tool in ecology; they can predict changes in future climate conditions and predict future responses in ecosystems due to changes in climate. But all models need input (data), and that is (one reason) why we need experiments. Experiments, besides providing knowledge about ecosystem processes and functions, feed models (Beier 2004). Experiments, both in laboratories and in the field, with effects of single climate factors on ecosystems have been carried out for the last decades. However, interactions between the main drivers of climate change are not necessarily simply additive (Shaw et al. 2002). Interactions can also be synergistic or antagonistic (Larsen et al. 2011), implying that conclusions based on single factor experiments could be insufficient, when trying to predict responses to climate change. Interactions are very difficult, if not impossible, to predict to some degree of certainty unless we have multi-factorial experiments to demonstrate any synergies or antagonisms. Multifactorial experiments have of course many disadvantages; they are often costly and time consuming, and in a global context they will always be case studies (Norby and Luo 2004). However, multi-factorial experiments are crucial in our attempt to understand ecosystem responses to a changing climate. They are needed to unravel the complexity of interactions between the main climate components, and to understand the responses on species level as well as on ecosystems level. Further, they are much needed if we are to identify site- and inter-annual variations, when attempting to extrapolate and upscale. To meet these requirements we first of all need experiments around the world and further we need the experiments to last for more than a couple of years.

Effects of climate change on vegetation at CLIMAITE

In general the aboveground vegetation responded less than I had expected; even though *C. vulgaris* increased in biomass over the study period, the biomass was not affected by the manipulations indicating that *C. vulgaris*, have a strong resistance to changes in climate determined by its evergreen status. Also, the grass biomass was not affected and was relatively constant over the period. The lack of response for *D. flexuosa* to the climatic treatments came from the plants ability to let the tissue dieback and then quickly recover once conditions again become favourable. It therefore showed a high resilience to changes in climate factors. Together the two strategies made the heathland ecosystem more resistant to the climatic treatments than I had expected.

In the following sections I describe the effects found in this thesis, and consider them in context with some of the many other findings from the study site.

ENHANCED CO_2

The photosynthetic rate measured at the site increased for both species in response to enhanced CO_2 concentration (Albert et al. 2011a; 2011c). However, this increase in carbon assimilation was not converted into aboveground biomass (paper I), since I saw no treatment response in biomass for neither *C. vulgaris* nor *D. flexuosa* (fig 5) except for a increased biomass production (green biomass and litter) in 2008 for *D. flexuosa*.

The question was therefore; where was the extra carbon then allocated to? Some of it was apparently allocated into grass reproduction since I saw an increase in the amount of flowering culms in response to increased CO_2 (paper III) (fig 6). But will this increase in flowering result in changes in the species composition? Since flowering is important for spreading and maintenance of the population, I consider an increased reproduction success as an indicator of future growth. However, we saw a negative effect on the germination success, indicating a lower seed quality under elevated CO_2 concentrations which has also been shown in other plants by (Andalo et al. 1996). It has been hypothesised that seed nitrogen content rather than seed weight determines germination success (Hara and Toriyama 1998; Miyagi et al. 2007; Hikosaka et al. 2011) and since there is abundant evidence that nitrogen concentrations of seeds decreases due CO_2 fertilisation (Jablonski et al. 2002; Thurig et al. 2003) this may be the reason for the lower germination in this study. Further the large inter annual variations in flowering, as described below, must also be taken into account before making conclusion on future spreading from seeds.

Allocation to reproduction also increased for *C. vulgaris,* the fraction of biomass from flowers was higher under elevated CO_2 compared to ambient CO_2. This was mainly at the expense of a decrease in the fraction of leaf biomass at that time. However, this pattern was only seen in one year (fig 7). *D. flexuosa* may also increase in cover by vegetative growth, and overall I therefore concluded that changes to the flowering pattern alone are not enough to positively identify changes in future interactions between *D. flexuosa* and *C. vulgaris*.

Apart from reproductive tissue, the excess carbon was also allocated belowground since increases in root biomass (Arndal et al submitted), microbial biomass (von Oheimb et al. 2009) and enchytraeids biomass was reported from the site in response to higher CO_2 concentration (Maraldo and Holmstrup 2009a; Andresen et al. 2010b). This indicated that carbon from

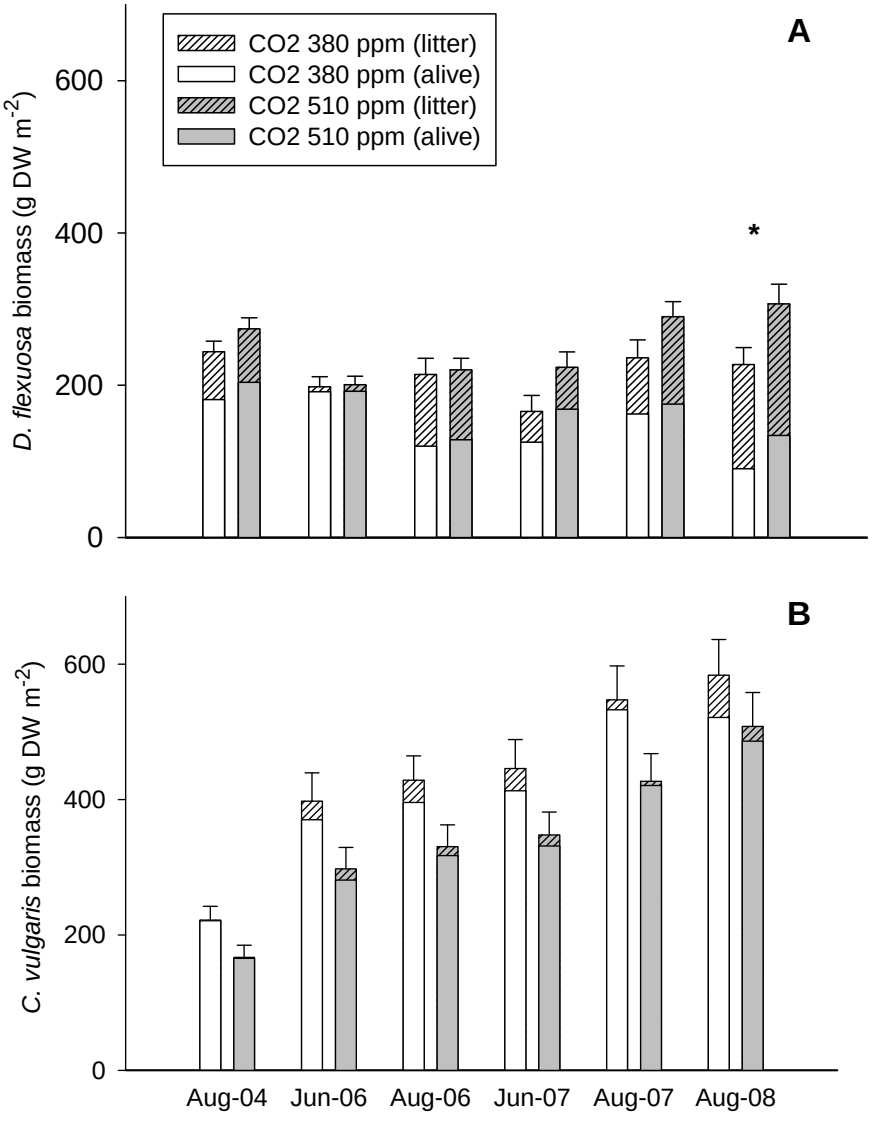


Figure 5 *A) Biomass of* D. flexuosa *(g m^{-2}, mean±SE), B) biomass of* C. vulgaris *(g m^{-2}, mean±SE) Ambient CO_2 (White) and elevated CO_2, 510 ppm (grey). Litter (hatched) and alive (unhatched) material. * =p<0.05.*

the increased photosynthetic assimilation was transported from the leaves and excreted as root exudates to stimulate the microbial activity. It was thus quickly incorporated into belowground biomass or the food web. This was further supported by both an increased microbial activity seen under elevated CO_2 concentrations (Selsted et al. 2012) and by an isotope study done by Andresen et al. (2011) that showed traceable labeled C and N in the detritivores within a year from labeling in CO_2 plots. The large allocation of carbon to belowground processes may reflect nutrient limitation of the plants and may explain why I did not observe any responses in biomass to the CO_2 fumigation (paper I). If the increased microbial activity released nutrients, I would expect a stimulation of plant growth with time, but immobilization of nutrients by microbes may prevent such a release at least in the short-term (Michelsen et al. 1999).

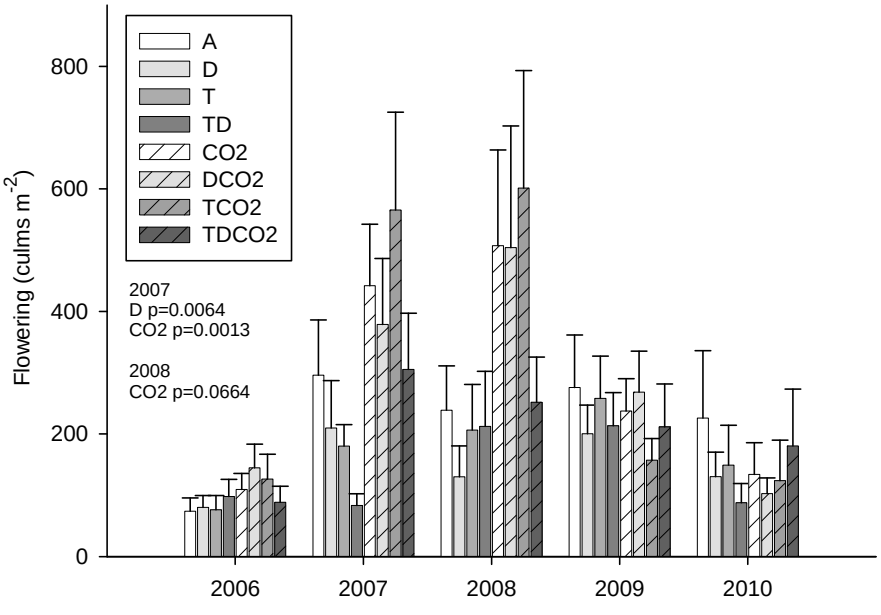


Figure 6 *Number of* D. flexuosa *flowering culms (mean±SE) from 2006 to 2010 at the CLIMAITE site. There was an overall CO_2 effect p=0.036; repeated measurement. Treatments were: A-ambient, D-summer drought , T-warming 1-2°C, CO2- enriched CO_2 concentration of 510 ppm, and all treatment combinations.*

Some nutrients used for flowering were lost to the litter pool after flowering (paper III). Since grass has a less complex structure and a faster decomposition rate compared to *C. vulgaris* (Aerts 1995), an increased production of flowering culms in *D. flexuosa,* and thus of litter, could increase the rate of nutrient turn-over even further. However, the C:N ratio of both leaf tissue and of roots was found to increase in response to CO_2 fumigation (Albert 2011a; Arndal (submitted)). This was also reflected in litter chemistry (Larsen et al. 2011), and with time, this may result in a decreased mineralization rate, increased nutrient immobilization by microbes and thus in a decreased amount of plant-available nutrients.

I would expect the increase in C:N ratio, as described by Albert et al. (2011a; 2011b) and Larsen (2011), to be caused by an increase in plant biomass in response to CO_2 and thus a dilution of N, nevertheless I did not see an increase in the aboveground biomass within this experiment. But Arndal (pers. comm.) found an increase in belowground biomass and it is therefore plausible that nitrogen was allocated from the above ground part to belowground. The results could perhaps also be explained by an increase in carbon-based secondary metabolites or low molecular mass sugar compounds that increased the biomass, but was undetectable with the pin-point method used for biomass estimates. Unfortunately, presently, we have no data to document whether or not this was indeed the case.

So, to answer the question whether the plant community will change over time: The results from the CO_2 manipulation suggested that the system was a lot more resilient towards changes than expected.

DROUGHT

Drought influenced the aboveground vegetation directly by causing a decrease in biomass during midsummer (paper I) (Fig 8) and by increasing the amount of flower abortions (paper III) (Fig 9). However, the drought effect on plant biomass only lasted for a short period of time; just two months after the drought period, we observed a full recovery of both grass and heather biomass. On the other hand, drought decreased the rate of most biological processes studied at the site, at least periodically. This included photosynthesis, litter decomposition and gross mineralization (Albert et al. 2011a; Albert et al. 2011c; Larsen et al. 2011). Also, the enchytraid biomass (Maraldo et al. 2010a) and the C:N ratio of plant tissue decreased (Albert et al. 2011b) in response to the drought treatment, and I therefore consider drought to be an important factor in changing the plant community in the future. Nevertheless, drought effects often last for a short period of time, and in many cases CO_2 counteracted the effects. For instance, the photosynthetic rate, enchytraeid biomass and the C:N ratio all responded oppositely, when drought was combined with elevated CO_2, indicating that short term drought periods may not be as important to these biological processes as previously

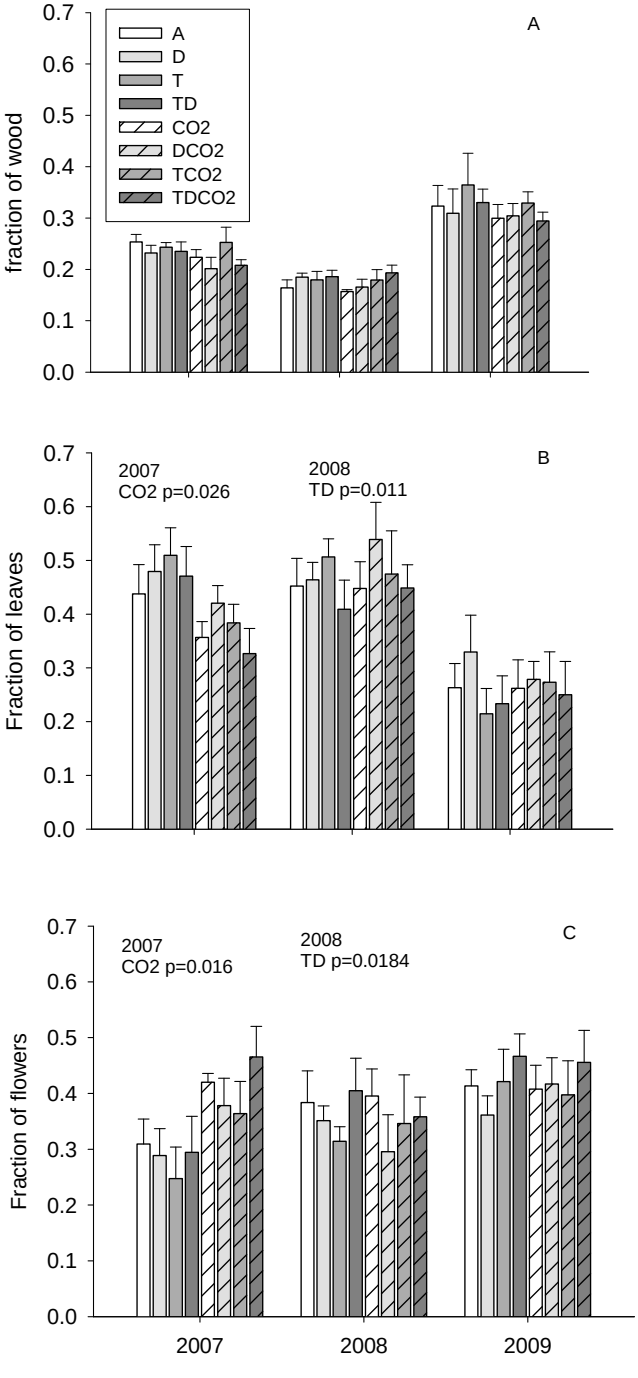


Figure 7 *Weight fraction of* Calluna vulgaris *in year 2007-2009. Fractions were: wood (A), leaves (B) and flowers (C). Treatments were: A-ambient, D-summer drought , T-warming 1-2°C, CO2- enriched CO_2 concentration of 510 ppm and all treatment combinations.*

believed. However, results in this thesis indicate that the severity of the drought is very important. In order to avoid a major tissue dieback, the drought treatment was alleviated whenever the SWC fell below 5%, and we may therefore not see the full effect of the predicted future drought patterns. I expect the ecosystem would show long-lasting responses if future drought pushes heathland plants beyond their drought threshold and causes major tissue death. Further, as seen for both enchytraeid biomass and photosynthetic activity of *D. flexuosa*, the magnitude of the rewetting after drought also has a large impact on the organisms' opportunity to recover (Maraldo and Holmstrup 2009b; Albert et al. 2011c).

At Brandbjerg, where *C. vulgaris* was in the building/mature stage (Gimingham 1972), we observed an increase in *C. vulgaris* biomass over the study period (paper I) but no response to the drought treatment. At the Mols site, on the other hand, where *C. vulgaris* was regenerating after a disturbance, we observed a decrease in biomass of the pioneer stage, when subjected to drought treatment compared to warmed and control treatments (paper IV) (fig 10). This drought-induced decrease in *C. vulgaris* was associated with an increase in grass biomass. We consider this a key finding to answer some of the unanswered questions regarding the CLIMAITE site, Brandbjerg. With this finding from Mols in mind, I expect *C. vulgaris* to be much more susceptible to drought damage after an intense disturbance event such as heather beetle attacks, but potentially also frost damage and severe drought. This is important to keep in mind, since heather beetle attacks are expected to increase in the future due to higher N-deposition (Sheppard et al. 2008;Heil & Bobbink 1993). Also, frost damage events will properly be more frequent because of more frequent freeze-thaw cycles due to increased temperature and earlier snow melt (Walther et al. 2002). Furthermore, frost damage/winter desiccation will induce openings in the heather canopy and thus allow invasion of *D. flexuosa* (Bobbink et al. 1998).

TEMPERATURE

I did not observe any changes in aboveground vegetation in response to increased temperature. *Calluna vulgaris* has a natural distribution from the North of Norway down to Portugal, and *D. flexuosa* is common in most of Europe. Both species are therefore able to compete successfully within a large temperature amplitude which may explain the lack of response to warming. However, observations of an earlier leaf appearance (NDVI measurement) (fig 5) (paper I) and earlier appearance of inflorescences when subjected to increased temperatures (paper III) were reported in this study. Warming also resulted in higher photosynthetic rates at the site (Albert et al. 2011a), and together these changes are evidence of an earlier onset of the growing season in response to warming. Even so, these changes were neither transformed into increased biomass later during the season nor into more

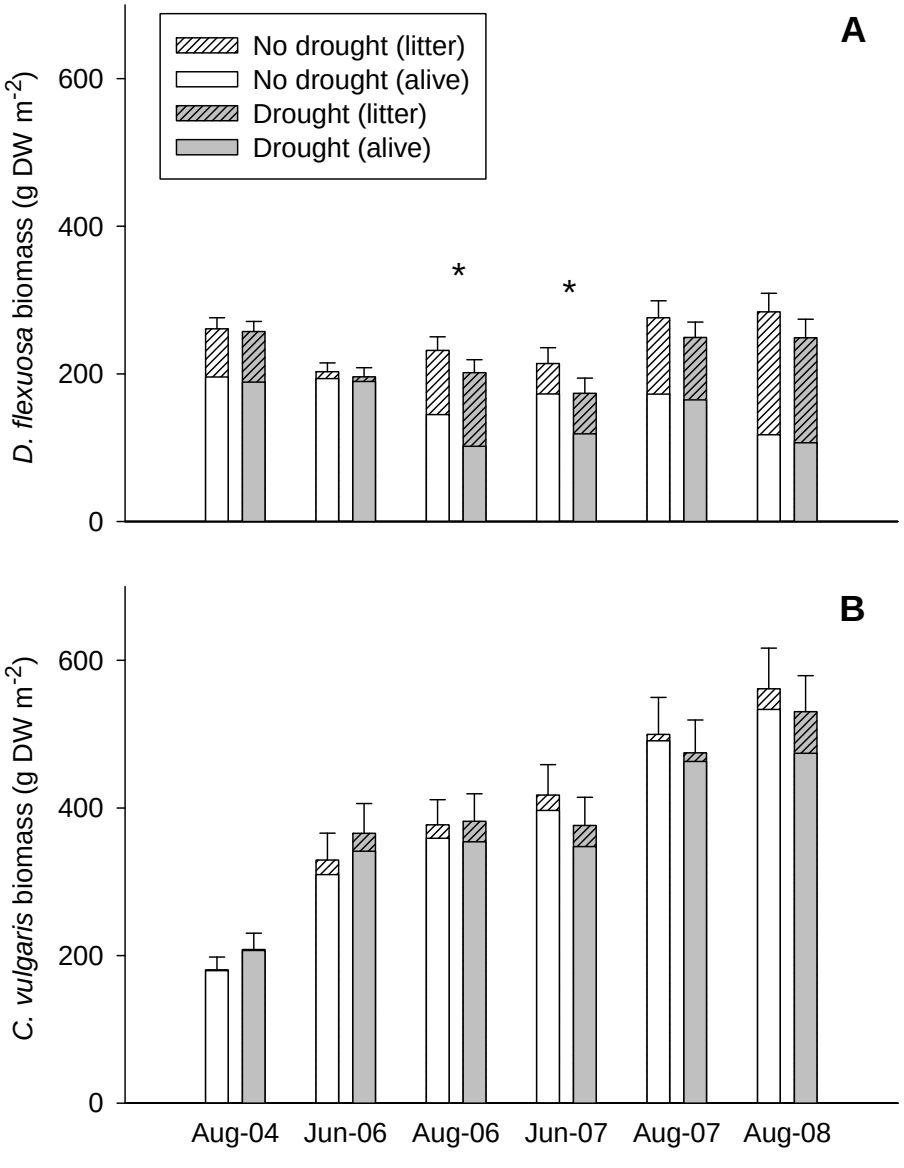


Figure 8 *A) Biomass of* D. flexuosa *(g m^{-2}, mean±SE), B) biomass of* C. vulgaris *(g m^{-2}, mean±SE). Ambient (White) and drought treatment (grey). Litter (hatched) and alive (unhatched) material. *=p<0.05.*

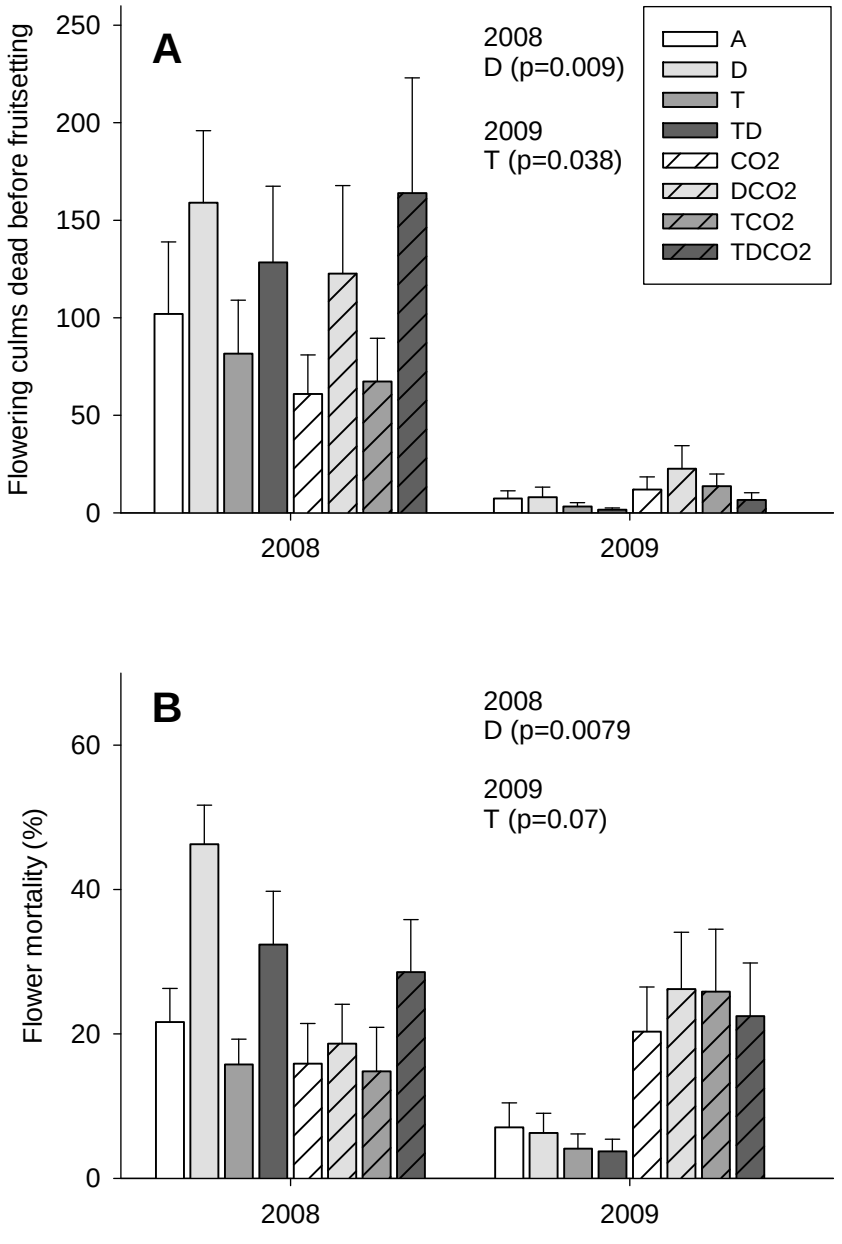


Figure 9 *Flowering in* Deschampsia flexuosa*. A) Flowers dead before flowering and fruit setting in 2008 and 2009. Treatments: A-ambient, D-summer drought for about 4-5 weeks, T-warming of 1-2°C, CO2- enriched CO_2 concentration of 510 ppm and all combinations. Means±SE.*

flowers. Thus, the changes should probably be seen only as a transient event, with limited ecological repercussions.

Warming was also hypothesized to accelerate most biological processes and thereby have an indirect effect on the plant community. An increase in the mineralization rate and N-turnover were reported by Andresen et al. (2010a) and Larsen et al. (2011), but within the time frame of this thesis I did not observe any secondary effects on the aboveground biomass. How, and whether, the plant community will change under a future warmer climate depends on the outcome of those interactions, but it seems fair to expect that changes in belowground processes will result in effects on the aboveground plant community – at least given a longer time scale than our five year study period.

INTERACTIONS

In general I did not see many statistically significant interactions between the climate parameters. This indicates that interactions did not influence the effects of single manipulations on the aboveground vegetation. However, the experiment has so far lasted only five years, and effects of interactions

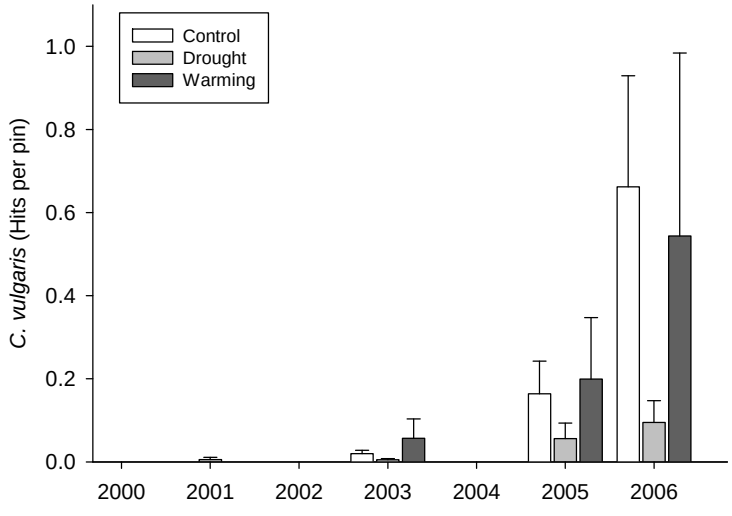


Figure 10 *Recruitment of new* Calluna vulgaris *plants after the heather beetle attack in 1999 registered as hits per pin. Treatments: Control, Summer drought for about 4-5 weeks and Warming of 1-2°C. Values and bars are means ± SE.*

between single factors may appear only after a longer period of climate manipulation. I had expected some of the single-factor effects to be either leveled out or enhanced by interactions between climatic factors similar to the way reported by Larsen et al. (2011). They reported most interactions to be antagonistic and therefore the system to be more robust when more than one factor was changed. For instance C/N ratio in mosses increased in response to drought and to CO_2, but not when these factors were combined.

SEASONAL VARIATIONS

We observed that several effects of the treatment were dependent on the seasonal variation in natural climate –mainly the amount and timing of precipitation within a year. Photosynthesis measured at the site was high in spring and autumn (Albert et al. 2011a), whereas a combination of tissue dieback in *D. flexuosa*, as shown in paper I and paper II, and a lower photosynthetic capacity resulted in lower carbon assimilation during midsummer (Albert et al 2011 submitted). However, this dieback and reduction in carbon assimilation did not reduce the overall biomass – quite the contrary: Albert et al. (2011b) showed a higher photosynthetic rate following the prolonged drought period, and I observed that grass biomass had already recovered one month after the severe drought event (Paper I). Seasonal variations in microbial biomass may be essential for plants, since a microbial dieback could release nutrients and thus temporarily increase the N-availability. The fast recovery could have been due to such a nutrient release during re-wetting following the drought period (van Meeteren et al. 2008).

There are many reports on nutrient immobilization by microbes (Jonasson et al. 1996; Schmidt et al. 1999). Andreasen et al. (2010a) concluded, based on a study from the same site, that microbes acquire glycine faster than plants, and therefore may be better competitors for nutrients. Immobilization of the nutrients and a nutrient limitation may therefore constitute at least some of the reason for the absent response of the plant biomass (paper I) to the climate change manipulations, despite the higher photosynthetic rate after re-wetting (Albert et al. 2011b). However, nutrients immobilized by microbes may periodically be released, and in general the microbial biomass is kept at the same level by the availability of carbon and by grazers. This was also seen at the site where enchytraeid biomass increased in response to elevated CO_2 depending on season, with the largest response during summer (Maraldo et al. 2010a). Further, Nielsen et al 2009 showed that there was a good correlation between nutrient availability and SWC at the site and this may reflect that microbial activity is controlled by the soil moisture (Nielsen et al. 2009). This indicates that the amount of nutrients that were available for the plants differed within the season, and that a potential microbe-plant interaction may explain the plant biomass to a higher degree than expected. This is of course important in order to understand the ecosystem, but it also

highlights the importance of incorporating such seasonal variations when planning studies and fieldwork. One sampling only provides a snapshot, and to understand the ecosystem processes, it is important not to make conclusion about ecosystem responses, based upon short time drought effects during e.g. midsummer.

INTER-ANNUAL VARIATIONS

Climate change is ongoing; in the period of 5 years where the study took place we observed large inter-annual variations in the climate. In addition to the climate manipulations within the two climate experiments, we can use this inter-annual variation in climate to describe and test the effects of climate change on the plant growth and phenology.

Especially the precipitation pattern showed inter-annual variations. There were, for instance, large differences between years in the amount of rain falling from September to November (Table 2), and since autumn SWC was positively correlated with the number of inflorescences, this could potentially explain the large inter-annual variation found in flowering (paper III).

The growing season in 2007 was very wet compared to the last 30 years average in Denmark. The following season in 2008 was, on the other hand, very dry compared to normal. This inter-annual variation in precipitation resulted in variations in the amount of precipitation that was excluded under the drought treatments (see table 2). Furthermore, we recorded months with precipitation far above average indicating heavy rain falls (July 2007 and June 2009).

In all years from 2006 to 2009 the temperature in the warmest month was 4-6 °C above the 30 year average for that month, and the coldest months were also mostly warmer than average, but with a larger variation, with some years close to average and others 5°C above average. By comparison, the warming curtains increased the temperature with 1°C in the soil surface all year round, and thus the increase caused by the temperature treatment was less than the natural variation between years. All this caused inter-annual variations in many biological processes that out-scaled those seen in response to the treatments. The large climatic inter-annual variations also resulted in different responses to the manipulations from year to year. For instance, we saw an increase in the number of *D. flexuosa* inflorescences in response to enhanced CO_2, but only in 2 out of 5 years. Maraldo et al. (2010b) also reported that the observed drought effect on enchytraeid biomass was dependent on the amount of precipitation within that year, i.e. the drought treatment had a more pronounced impact on enchytraeids during the year with a dry summer and autumn (2006) compared to the wet year (2007). Further, leaching and thus loss of nitrogen from the system was shown to vary between years, with 0.13 ±0.06 g N m^{-2} yr^{-2} in 2006 and 0.56 ±0.20 g N m^{-2} yr^{-2} in 2007 (Larsen et al. 2011). These findings signify the importance of

long term studies, and emphasise that conclusions based on only one or two seasons should be drawn with outmost caution.

Resilience to disturbances

Results from this thesis showed that the vulnerability of the heathland ecosystems depends on the phase of *C. vulgaris*. The ecosystem in the aggregading to mature phase was a lot more resilient towards changes in climate than expected. So to the question whether the plant community will change due to climate change, the answer may be 'yes, but not so much as we thought'. So, the next question followed: Why? In the following I will try to give some answers to this question.

1) This study showed that *D. flexuosa* has a high resilience to changes in climatic factors determined by its ability to let the tissue dieback and then quickly recover once conditions again become favourable, whereas *C. vulgaris* shows a strong resistance determined by its evergreen status, at least when it is established. Overall this led to a general lack of response for this heathland ecosystem to the climatic treatments. The plant biomass recovered rapidly after drought events, and was not affected by an earlier onset of the growing season (paper I). Thus the manipulation did not directly affect the plant biomass production. However, other studies at the site have shown that changes do occur; photosynthesis, mineralization, litter quality and flowering were all affected by the climate manipulations. Thus, it is possible that some of the observed changes in other ecosystem processes with time will affect the aboveground plant biomass, and this way the manipulations may still affect plant biomass, however in a more indirect way.

2) The manipulations caused smaller variations than the natural climate conditions. The plants are thus adapted to changes in climate exceeding the manipulations applied. Further, they are adapted to nutrient- and water limited conditions, and the capability of the plants to use both nutrients and water when available and then survive long periods without, may help to keep the ecosystem in balance.

3) In general, the drought treatment affected most biological processes, but it was also the climate driver for which effects were most dependent upon the inter-annual natural variation; i.e. the drought treatment was only statistically significant if supplementing a naturally occurring drought. In CLIMAITE it was decided not to push the plants beyond the drought threshold, in order to avoid a full dieback of any of the two species. This may explain the high resilience of the aboveground biomass. A stronger water limitation could possibly also have shed light on the differences between the two life form strategies in their responses to drought.

4) Results from this thesis indicate that the heather at Brandbjerg was in a state where it was very resistant towards changes. Although a number of es-

pecially soil parameters responded to the treatment, the plant community responded neither to direct nor to indirect effects. Together with results from the regeneration of *C. vulgaris* at the Mols site (paper IV), this leads us to conclude that both the state of the *C. vulgaris* population and the magnitude and frequency of disturbances determine the effects of future climate change on the plant community.

Carbon sequestration

Changes in climate can not only influence plant species but may also change the ecosystem structure and ecosystem functioning (Aerts et al. 2006; Beier et al. 2009). Terrestrial ecosystems play an important role in regulating the atmospheric carbon concentration. Based on this thesis, the plant composition at Brandbjerg did not change, meaning that aboveground vegetation did not contribute to changes in the carbon pools. However, we expect changes in the plant community on a longer time scale, either due to indirect effects slowly altering the relations between the two species or due to sudden major events negatively affecting the heather vegetation and providing the grass with an opportunity to increase in cover (Aerts et al. 1990;Heil & Diemont 1983;Heil & Bruggink 1987). If the vegetation changes from heather to grass, it would lead to a loss of organically bound carbon, simply because the standing biomass of a *C. vulgaris* vegetation is larger than that of a *D. flexuosa* vegetation (Kongstad et al. 2011). Since litter from *D. flexuosa* is more easily remineralized than *C. vulgaris* litter (Aerts 1995), a change towards grass-dominance, would probably also cause the system to release more CO_2, and thus increase the 'source effect' of the system compared to the 'sink effect'. Whether coupled to changes in plant species composition or not, results from the site have indeed shown an increase in the release of CO_2 from the ecosystem due to increased microbial activity under full treatment combination ($T \times D \times CO_2$) compared to ambient plots (Selsted et al. 2012). If carbon sequestration of the ecosystem is to remain unchanged in the future, this increased loss would have to be mirrored by an equal increase in photosynthetic assimilation.

The future carbon sequestration will however depend on the level of future management. Since heathlands are semi natural ecosystems lack of management will lead to invasions by bushes and trees and thus increase the vegetation carbon pool and change the source- and sink processes.

HEATHLANDS IN A FUTURE CLIMATE

Several conditions have changed and will change heathland ecosystems in the future. In the following section I describe some of the expected interactions between changes in climate conditions and other threats affecting heathland ecosystems, including land-use, nitrogen deposition and management. It is an attempt to see the results from this thesis in a larger context and answer the question whether plant communities will change in the future. Since most of the threats were not studied within this thesis, this part relies mostly on the literature.

Land-use and fragmentation

Lately, heathland research has focused on climate changes in order to understand changes in functions and services of the ecosystem and to prepare for incorporation into management plans. But to venture into the future, we must first go back in time. Most heathlands are a result of human activity and land-use. Nutrients were removed from the heathlands by domesticated grassing animals or by harvesting of the heather for later use as winter fodder. The organic layer was used as fuel and the heather was burned to keep some areas in early succession phase and thereby ensure a high nutrient quality of the fodder. All together the ecosystem was kept in a nutrient poor state, where only species adapted to this condition would grow.

Heathlands no longer provide services for human existence. Many heathlands were taken into formal agricultural use in the middle of the last century, or were disturbed by infrastructural and urban expansion – a process that is still going on today.

This results in a decrease in the total heathland area but also in a high fragmentation of heathlands. Fragmentation decrease genetic variation of both heathland plants and animals within an area, due to a prevented or delayed spreading and pollination from other populations (Assmann and Janssen 1999; Vergeer et al. 2003). This could, with time, make the vegetation less resistant to changes, both due to less genetic variation and due to a decrease in biodiversity - both of which may derease the stability of ecosystems. Climate change will alter growth conditions further, and may result in suppression of some species and the introduction of others. Alien species are often characterised by high spreading ability and new growth conditions may lead them to germinate in sensitive habitats such as heathlands (Penuelas et al. 2010). Biodiversity is also threatened within heathland ecosystems. Heathlands are characterized by a low plant biodiversity, dominated by dwarf shrubs co-existing with a few graminoids and herbs. Disturbance of growth conditions by climate change or land-use may initially increase the plant biodiversity due to an introduction of new species (Bobbink et al.

1998). However, with time heathland species will disappear and plant biodiversity will decrease, and land-use changes is predicted to be the most severe driver of changes in biodiversity in grassland ecosystems (Sala et al. 2000).

Distribution regimes

Plant distribution is among other things determined by species-specific physiological thresholds of temperature and water requirements (Woodward and Williams 1987). *Calluna vulgaris* has a wide distribution in Europe. It is a drought tolerant species with xeromorphic leaves (Aerts 1995) and low, but constant, photosynthesis even under dry conditions (Albert et al. 2011c). Higher temperature and changes in precipitation may alter the plant distribution and may accelerate the transformation of heathland/grassland into temperate forest.

Crawford (2008) predicted the biomes of *C. vulgaris* to move either northward if summer temperature increases more than winter temperature, or eastward if winter temperature increases more than summer temperature. Fosaa et al. (2004) found *C. vulgaris* to be positively correlated to increased temperature whereas *D. flexuosa* was found to be negatively correlated. Further, reports from Spain have shown that a replacement of *C. vulgaris* by oak (*Quercus* spp.) has already occurred due to a warmer climate and land use changes (Penuelas and Boada 2003).

These findings indicate that increased temperature may change the plant community at our site with time. *Calluna vulgaris* seedlings are, however, susceptible to drought and require maintenance of high soil moisture levels and high air humidity (Miller and Cummins 1987) and the species is therefore often found near the coastline because of the higher amount of precipitation here compared to continental climate. Results from paper IV indicate that a decrease in summer precipitation will have consequences for the spreading of *C. vulgaris* due to water limitation in the pioneer phase, and future changes in precipitation may therefore be more important for the future distribution regime of this species than increased temperature.

Besides changes in temperature and precipitation, competition with other present and new-coming species also has to be taken into account. Further, the genetic variation in the *C. vulgaris* population from this site may be very different from that of the *C. vulgaris* population in the boreal and subarctic region, where growing seasons are shorter and the climate is cooler, or from the Southern European populations where drought tolerance is a key element to survive. Changes due to climate change may therefore be different from site to site.

Nitrogen deposition

Changing climatic conditions may interact with effects of the present high nitrogen deposition. Some changes will enhance the effects of the increased nitrogen load whereas others will counteract.

Brandbjerg heathland was, as mentioned before, very resilient towards changes in climate and also towards nitrogen and phosphorus addition (paper II). There was no response in biomass when adding fertilizer, and already one year after the fertilizer addition, leaf nutrient concentrations were back to previous levels. This could be an effect of nutrient poor adapted plants being less efficient in translating an enhanced nutrient supply into a biomass increase – a strategy that could be important if the source is only temporarily available. In that case it would be advantageous to save the excess nutrients in storage organs or invest it in seed production (Falk et al. 2010). Further, other studies from the CLIMAITE experiment have indicated that the ecosystem seasonally was limited by water (Albert et al. 2012 in press; paper II) and since nutrient availability are correlated with SWC (Nielsen et al. 2009), the lack of response to nutrient addition may be caused by water limitation. However, the bryophytes responded negatively to nutrient addition by a decrease in biomass which may results in a decrease in biodiversity since 10 species were mosses compared to 17 vascular plants and 9 lichens (the latter were not included in this study).

Higher nitrogen availability has also been shown to increase *C. vulgaris* sensitivity towards drought (Gordon et al. 1999; Sheppard et al. 2008), and increased nitrogen deposition may therefore decrease the drought threshold and enhance the damage induced by future severe drought events. An increase in nitrogen availability either due to increased mineralization or increased nitrogen deposition may also accelerate the life cycle of *C. vulgaris* (Gimingham 1972). Since grasses are competitively superior in the early phase of heathland development, especially after exposure to drought as shown in paper IV, shortening of the *C. vulgaris* life cycle or more frequent heather beetle attacks or severe drought events may result in further dominance of grasses. Heather beetle attacks are expected to be more frequent in a milder climate, where both larval and adult survival may be higher (Power et al. 1998) and where warming may increase nutrient levels in the leaves (Penuelas et al. 2004). All this indicate a shift from heather to grass in the future. On the other hand, Albert et al. (2011a) and Larsen et al. (2011) reported an increased C:N ratio in leaf tissue in response to an enhanced CO_2 concentration and thereby a decrease in the nutrient quality of the leaves. That is opposed to the general effect of increased nitrogen deposition in heathlands which results in lower tissue C:N ratio and thus a better food quality for herbivores (Berdowski 1994). The increased C:N ratio in litter in response to increased CO_2 consequently counterbalance the N induced in-

crease in mineralization rate, and Larsen et al. (2011) concluded that the outcome would be a decrease in nitrogen cycling. Warming is also expected to increase the mineralisation rate and thereby enhance the nitrogen effect making more nutrients available for plants. However, the third environmental factor, precipitation, also plays a role in shaping the N-cycle: As seen in Larsen et al. (2011), leaching of nitrogen was dependent on the precipitation pattern – a higher frequency of heavy rain falls is expected to increase nitrogen leaching and thereby the nitrogen output from the site.

Finally, increased N deposition can have an impact on the carbon sequestration within the ecosystem (Wamelink et al. 2009). If plant growth is limited by nitrogen, increased nitrogen availability will increase growth and thereby the amount of carbon incorporated into plant biomass. However, De graff et al. (2006) concluded that increased C sequestration will only occur if nutrients are supplied. We assume the yearly nitrogen supply at Brandbjerg will not increase further, since it is used for military activities, but the current level may already be too high to maintain the current vegetation composition. Time will show whether increased nitrogen availability will change vegetation composition from dwarf shrub dominance with a high, all year around, standing carbon pool to grass dominance with higher productivity but lower standing biomass, and thus less carbon storage in aboveground vegetation.

CONCLUSION

In conclusion, and to answer the question: **Will changes in climate alter plant communities over time?**

This heathland ecosystem in the aggregating/mature phase was a lot more resilient towards changes in climate than expected. None of the applied manipulations resulted in long lasting changes in the aboveground biomass. The resilience was probably due to:

- *Calluna vulgaris* had a strong resistance to changes in climate determined by its evergreen status, maintaining the growth constantly over the season.

- The lack of response for *D. flexuosa* to the climatic treatments came from the plants ability to let the tissue dieback and then quickly recover once conditions again became favourable. It therefore showed a high resilience to changes in climate factors.

I conclude that this plant community was resilient to changes in climate – at least on a short time scale of a few years. On the other hand, the Mols study, where *C. vulgaris* was regenerating after a disturbance, showed a decrease in biomass of the pioneer stage, when subjected to drought treatment compared to warmed and control treatments. I therefore conclude that the vulnerability of the heathland ecosystems may depend on the growth phase of *C. vulgaris*, indicating that, in the long run, we may see effects at Brandbjerg as well.

The increase in flowering culms in response to elevated CO_2, the higher fraction of flower abortions in response to drought and the decrease in moss biomass in response to nitrogen addition indicate that changes do occur. This, together with findings from other studies at the Brandbjerg site, indicated that the biomass production and plant composition may not be the first parameter to mirror effects of climate changes on the ecosystem. Thus, it is possible that some of the observed changes in other ecosystem processes with time will also affect the aboveground plant biomass, and this way the manipulations may still affect plant biomass but in a more indirect way. This confirms that studies on climate change and ecosystems should cover the entire ecosystem. Further, it signifies the importance of longer term studies, and emphasises that conclusions based on only one or two seasons should be drawn with outmost caution.

In general I did not see many statistically significant interactions between the climate parameters. This indicates that interactions did not influence the effects of single manipulations on the aboveground vegetation. However, we do have to keep in mind that the experiment has so far only lasted five years, and that effects of interactions between single factors may appear only after a longer period of climate manipulation. Further, we deliberately did not push the system above a certain drought threshold in order to avoid a full tissue dieback, and we therefore may not see the full effects of the future drought patterns. I expect the ecosystem would show long-lasting responses if the drought period exceeds such a threshold.

Together with results from the regeneration of *C. vulgaris* at the Mols site, this leads us to conclude that both the state of the *C. vulgaris* population and the magnitude and frequency of disturbances determine the effects of future climate change on the plant community.

FURTHER RESEARCH

This thesis deals with the effects of climate change on the aboveground vegetation in a Danish heathland. However, the studies presented only lasted for 1- 5 years, which is a very short time in a climate change perspective. All results in this thesis are therefore short term responses and preliminary conclusions. Longer term studies are needed to overcome some of the differences between seasons and to survey a possible tipping point. Further, the

age of the vegetation was shown to be important and more time is needed to study responses and recovery from a disturbance in all stages of the *C. vulgaris* life cycle.

Changes in biodiversity, both new species and species that disappear, also need a longer time scale than 5 years before they become apparent. Furthermore, potentially invasive species are not dealt with in this thesis, but could, on a longer time scale, be extremely relevant to both the species composition and ecosystem functioning.

Studies on flowering pattern, seed production and seed quality for both species all needs to be studied closer. For instance, a germination experiment within the climate manipulation should be implemented. Also methods (for instance NDVI) for observing phenological patterns has to be developed. Further, this thesis does not cover any genetic variation, acclimation or adaption.

Finally, possible interactions between climate change and other parameters, including nitrogen deposition and management, are presently only assumptions, and since this type of ecosystem is only maintained by management actions, studies with a management perspective are needed.

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LIST OF PAPERS

I. Jane Kongstad, Inger K. Schmidt, Torben Riis-Nielsen, Marie F. Arndal, Teis N. Mikkelsen and Claus Beier. **High Resilience in Heathland Plants to Changes in Temperature, Drought and CO_2 in Combination**: Results from the CLIMAITE Experiment. Ecosystems (2011) DOI: 10.1007/s10021-011-9508-9.

II. Jane Kongstad, Sven Jonasson, Inger K. Schmidt, Pia L. Nielsen and Anders Michelsen. **Changes from heathland to grassland; a study on the impact of fertilizer on phenology, chemistry and growth of the heathland grass *Deschampsia flexuosa.*** Submittet to Oecologia, Jan 2012.

III. Jane Kongstad, Inger K. Schmidt and Johannes Ransijn J. **Altered flower phenology and allocation of resources to reproductive structures in response to drought, warming and CO2 enrichment.** Manuscript to be submitted to Plant Ecology

IV. Inger K. Schmidt, Torben Riis-Nielsen T, Jane Kongstad, Johannes Ransijn, Christian Damgaard, Claus Beier. **Vulnerability of Calluna vulgaris in response to long-term climate manipulation and ecosystem disturbances**. Early draft of manuscript to be submitted to Journal of Ecology

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