Heathland ecosystem functioning under climate change

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General introduction

Heathland history
Heathlands are characteristic ecosystems in Europe. They fulfill an important role in the preservation of species diversity, provision of drinking water, conservation of a cultural landscape and recreation (Haaland, 2004). Most of them are man-made and exist because of clear cutting of the original forest stand, hundreds of years ago, to obtain fuel, graze livestock and improve arable land. This was achieved by sod-cutting and mowing of the vegetation and herding of sheep and other cattle on the heathlands. Their waste products were collected in stables at night and applied to the arable land together with the sods and vegetative remains (Webb, 1998). Through this ongoing practice the heathland soil became more and more impoverished and a typical vegetation developed, dominated by plants like *Calluna vulgaris* (L.) Hull., *Vaccinium myrtillus* (L.), *Empetrum nigrum* (L.), *Erica tetralix* (L.), *Molinia caerulea* (L.) Moench. and *Dechampsia flexuosa* (L.) Trin.. In the last decades traditional management has nearly disappeared and heathlands are invaded by trees, bracken or other vegetation with less ecological value. Nowadays, the remaining patches of this unique semi-natural nutrient poor ecosystem are preserved by nature management such as grazing, mowing and burning for their value as cultural landscapes, their historical associations and their characteristic biodiversity.

Nutrient cycling in heathlands
These semi-natural heathland ecosystems are characterized by low levels of plant available nutrients and low turnover time of nutrients in plant and soil (Aerts and Chapin, 2000). Plant nutrient demand is mostly met by nutrient resorption from senescing leaves and mineralization of decomposing organic matter (Aerts, 1995). The adaptation of the vegetation to the low nutrient availability makes these ecosystems vulnerable to changes in nutrient availability (Jonasson et al., 1999b). The recycling of nutrients through organic matter decomposition in the ectorganic soil horizons (LFH) is an important process in these ecosystems as the mineral soil is often highly impoverished. Decomposition of organic matter is primary driven by microbial activity and involves the succession and interaction of many different species of microorganisms. Microorganisms produce intra and extra cellular enzymes that catalyze specific biological reactions in degrading organic substances. As a result
the presence and activity of different enzymes changes during litter decomposition and is often inversely related to the availability of the degrading substance (Linkins et al., 1990). Enzymes that are of primary interest in litter decomposition are those involved in the degradation of the main litter components cellulose, hemicellulose and lignin and those that are involved in the cycling of essential nutrients as nitrogen (N) and phosphorus (P).

Microorganisms
In nutrient poor ecosystems soil microbial biomass is considered as an important nutrient pool (Jonasson et al., 1999b; Schmidt et al., 2002). In a sub arctic heath in North Scandinavia two third of the total ecosystem P pool was immobilized in microbial biomass (Jonasson et al., 1999b). Microbial biomass can act as source and/or sink for available plant nutrients. In nutrient-poor arctic heathlands microbial biomass has been found to be a strong sink for nutrients added through fertilization (Jonasson et al., 1996). For instance, addition of 5 g m$^{-2}$ of N and 5 g m$^{-2}$ of P, equaling approximately 3-5 times the annual incorporation of N into vegetation and 20-40 times the annual uptake of P, gave small responses in plant growth, and low nutrient recovery in vegetation, but high recovery in soil (Marion et al., 1982; Jonasson and Chapin, 1991). However, after addition of considerably larger amounts of up to 25 g m$^{-2}$ N and 25 g m$^{-2}$ P, a substantial fertilizer effect on the vegetation was found (Shaver and Chapin, 1980; Shaver et al., 1986). The limited effect of plant growth to fertilization has been ascribed to microbial immobilization of nutrients. Microbial nutrient transformations can therefore play an important role in the regulation of nutrient availability for plant growth in the nutrient-deficient ecosystems (Harte and Kinzig, 1993; Jonasson et al., 1996b).

Environmental pressure
Nutrient poor semi-natural heathland ecosystems are known to be sensitive to environmental pressure. Shifts from shrub to grass dominated systems have been reported and have been associated with increased N availability through atmospheric N deposition and overgrazing (Heil and Bobbink, 1993). In addition, size reduction or fragmentation can lead to the loss of the ecosystem. The impact of climate change could further threat heathland ecosystem functioning. Mean temperatures are predicted to increase with 1.4- 5.8°C over the next century and also changes in precipitation patterns are forecasted. Although changes in precipitation are more difficult to forecast and there is a large variation among regions, many models predict increased summer drought for central European regions (Houghton et al., 2001). Changes in temperature and moisture conditions affect practically all ecosystem processes such as plant growth, plant net photosynthetic and transpiration rate, plant nutrient uptake (Llorens et al., 2004; Peñuelas et al., 2004), microbial activity, litter decomposition and consequent mineralization and
immobilization of nutrients (van Gestel et al., 1991; Grierson et al., 1998; Kieft et al., 1987; Pulleman and Tietema, 1999; Jonasson et al., 1999a; Rustad et al., 2001; Emmett et al., 2004). As the microbial pool can contain such a large amount of the ecosystem nutrients, this suggest that small changes in microbial biomass can have a large effect on nutrient availability in soil and thereby on the nutrient availability to plants. In nutrient poor ecosystems, plants and microorganisms compete for the same nutrients.

Figure 1 Research location: □

Figure 2 The ‘Oldebroekse heide’ with scaffolding structure

Geology and chemistry
Climate manipulation was carried out at the Dutch heathland area the ‘Oldebroekse heide’ in the center of the Netherlands (52°24' N; 5°55' E) (Fig. 1). The parent material in the area are fluvioglacial deposits consisting of gravelly white quartz rich sands originally deposited by eastern rivers and pushed by the glaciers in the Saalien. These sands are mineralogical very poor. On top of the fluvioglacial deposits a coversand is present dispersed by the wind from these deposits during the Weichselien. On top of this coversand, locally a thin layer (ca. 30 cm thickness) of drift sand is present probably dating from the Middle ages. The soil is a well-drained, acid sandy Haplic Podzol (FAO, 1988) with a mormoder humus form (Green et al., 1993). A complete description and chemical characterization of the soil profile is given in the Appendix (Table 2, 3 and 4). Average long term annual precipitation amounts to 793 mm with a precipitation surplus of 250 mm. Long term mean minimum and maximum temperatures are respectively 5.7°C and 13.7°C. The ecosystem is N saturated, as atmospheric N deposition in the Netherlands has exceeded critical loads of 15-20 kg N ha⁻¹ year⁻¹ for half a century (Heil and Bobbink, 1993) and N leaching is high at the site (Schmidt et al., 2004), indicating that N is not limiting vegetation growth. Besides N, potassium (K) and P are important
nutrients that can exert control on vegetation growth. In highly weathered sandy soils the K availability for plants is mainly dependent on (i) atmospheric deposition of K and (ii) K mineralization of (fresh) litter, because K exchange from the mineral soil is negligible due to the lack of large amounts of primary K bearing minerals and clay minerals such as illites and/or vermiculites. Wet atmospheric K deposition at the site is 2.0 kg ha\(^{-1}\) year\(^{-1}\), while K leaching from the mineral soil (at 30 cm depth) is 8.1 kg ha\(^{-1}\) year\(^{-1}\) (Schmidt et al., 2004). This large increase is probably due to interception deposition by the vegetation, leaching from senesced plant parts and/or canopy exchange of K after foliar uptake of NH\(_4\) (Bobbink et al., 1990). The relatively high K leaching in relation to K input indicates that plant growth at the site is not limited by too low K availability. Wet atmospheric P deposition is very low as well as P leaching. The dominating dwarf shrub, Calluna vulgaris, produces P poor litter with an N/P (g/g) ratio of >16, indicating that P is the most important nutrient limiting vegetation growth (Koerselman and Meuleman, 1996). Detailed inspection into the factors that are important in determining P availability in the mineral soil revealed that the soil solution chemistry was always undersaturated with respect to Al- and Fe-phosphates like variscite and strengite (data not presented). Consequently, equilibrium with these Al- and Fe-phosphates does not govern the P concentrations in the soil solution in these oxidative soils with a low pH level. In addition, the amorphous Al and Fe content of all soil horizons is relatively high and the P/(Al + Fe) and S/(Al + Fe) molar ratios are very low, respectively 0.01-0.05 and 0.01-0.03 (Appendix –Table 4). This means that the binding capacity for P in this soil is very high (Van der Zee, 1988), resulting in very low P concentration levels in the soil solution and consequently a limited P availability.

**Climate manipulation**
The site is one of the locations of the European projects: Climate driven changes in the functioning of heath and moorland ecosystems (CLIMOOR) that ran from 1997 to 2001 and Vulnerability assessment of shrubland ecosystems in Europe under climate change (VULCAN) that ran from 2001 to 2005. During this period the site was intensively studied in various related disciplines to study the impact of climate change on plants, soil processes, soil water and fauna (Beier et al., 2004; Emmett et al., 2004; Gorissen et al., 2004; Llorens et al., 2004; Peñuelas et al., 2004; Schmidt et al., 2004; Wessel et al., 2004) and the podzolization process (Jansen et al., 2004). The climate manipulation involved nighttime warming or summer drought in 20 m\(^2\) plots (Beier et al., 2004) (Fig. 2 and 3). Nine experimental plots of 5 m * 4 m each were established in relatively homogeneous areas within the site. Each plot was randomly assigned a treatment: control (C), heating (H) and prolonged drought (D) during the growing season, so that three replicate plots per treatment were present. Around each plot, a light scaffolding structure was built of galvanized steel tubes
covered by thin plastic sleeves to prevent contaminants leaching into the plot. In the heating plots, this frame supported a retractable, reflective curtain made of strips of infrared reflective material bound into a high-density polyethylene mesh. A small motor activated by a light sensor drew this curtain over the vegetation at night, to reduce the loss of infrared radiation, and removed it again at daytime. A tipping bucket rain sensor activated the removal of the curtain at night to enable rain to enter the plot. Over the drought plots, the retractable curtain was made of transparent polyethylene plastic. During two months in the growing season (generally June and July), the rain sensor activated the motor to extend this cover over the plots once rain was detected and removed the cover when the rain had stopped. Further details on the method can be found in Beier et al. (2004).

Monitoring of the plots started in December 1998 (pre-treatment period) and the treatments started in May 1999. The average effect of the nighttime warming was continuously on average 0.5°C in the topsoil. In the air (20 cm above the soil) an average temperature increase of 0.7°C during the night (04:00 hour) was observed, which decreased gradually during the day to 0°C at 16:00 hour (Beier et al., 2004) (Fig. 4). This was a relatively small increase not exceeding the natural year-to-year differences at the site. But it is realistic in relation to the predicted future temperature increase (Houghton et al., 2001). It also reflects the pattern of increased minimum temperatures in the air rather than a general diurnal increase (IPCC, 1995). The two-month summer drought treatment reduced precipitation in the growing season (May to September) with 45% compared to control in 1999, 51% in 2000, 43% in 2001, 43% in 2002, 70% in 2003 and 42% in 2004 (Table 1). As a result of the reduced precipitation soil moisture content decreased significantly during the treatments (Fig. 5).

Figure 3 Overview of climate treatment plots at the ‘Oldebroekse heide’.
Table 1 Precipitation from May to September in the control and drought plots (mm).

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<td>control (mm)</td>
<td>269</td>
<td>274</td>
<td>244</td>
<td>220</td>
<td>211</td>
<td>293</td>
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<tr>
<td>drought (mm)</td>
<td>148</td>
<td>134</td>
<td>139</td>
<td>125</td>
<td>63</td>
<td>170</td>
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<td>reduction (%)</td>
<td>45</td>
<td>51</td>
<td>43</td>
<td>43</td>
<td>70</td>
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Figure 4 Mean temperature in the control and heated plots during 24 hours at -10 cm, -5 cm and 0 cm soil depth and at 20 cm above the soil surface.

Figure 5 Soil moisture content in the upper 10 cm of the soil in the control and drought plots from 1 Feb. 2000 to 31 Jan. 2001. The drought treatment was from 25 May to 25 July.
Rationale, objectives and approach
Most studies related to nutrient-poor ecosystems have been focused on climate and nutrient driven changes in the arctic and sub-artic regions, mainly because the mean surface temperature is predicted to increase more in northern latitudes than in other climate zones (Houghton et al., 2001). This geographic bias resulted in a lack of knowledge about the response of mid and southern latitude ecosystems to climate change (Rustad et al., 2001). While climate change is likely to affect ecosystem functioning at mid latitudes as well through changes in the soil nutrient pool, which could affect plant growth on top of the direct effects of climate change on plant growth. As a result of the very low P availability in the mineral soil horizon, which acts as a strong sink for P, the most important P source for plants is the ectorganic soil horizon. Although the role of microbial community in organic matter decomposition and nutrient transformation is widely recognized, less is known about the effect of P limitation on microbial dynamics under climate change. The limited P availability in this ecosystem could probably determine the response of ecosystem processes to the climate manipulation. Considering the importance of P for both plants and microorganisms in this ecosystem more detailed insight on the P dynamics between the ecosystem P pools is needed.

The main objective of this research was to improve the understanding of heathland ecosystem functioning under climate change and the role of microbial nutrient transformations in decomposing litter herein. Special focus was given to the most limiting nutrient P as P was expected to play an important role in the response of this ecosystem to climate change. To accomplish this objective this study mainly concentrated on three research questions:

- What is the effect of climate change on microbial nutrient transformations, especially P transformations during litter decomposition?
- What is the effect of climate change on plant growth?
- What are the short and long term effects of climate change on the interaction between plant growth and litter decomposition and subsequent C and P cycling?

Research into the effects of climate change on ecosystem functioning is complicated as climate conditions gradually change and its effect is often hard to assess among the effects of other disturbances. Experiments are therefore essential to study the effects of climate change in isolation. In this PhD research, field and lab experiments were combined with simulation modeling. Long term field experiments were conducted to assess the impact of climate change on ecosystem functioning as ecosystems are already adapted to a large short-term inter-annual variability in climate. Because in field experiments, processes are dependent on the ruling climate
conditions, additional laboratory experiments were performed to investigate certain processes in isolation for more mechanistic research. Simulation modeling was used to integrate several results and make predictions beyond the field measurement period.

**Outline of this thesis**

As the mineral soil in the study area is P poor, P mineralized from decomposing litter is an important source of P to plants. Microorganisms are the first to access senesced litter and microbial P transformation could be an important factor determining P availability to plants. Microorganisms produce the enzyme acid phosphatase that mineralizes organic P to inorganic P, which is available for plant uptake. In chapter 1 the relation between microbial dynamics, phosphatase activity and inorganic P is studied in a laboratory experiment to determine whether phosphatase activity restricts P mineralization and to determine the importance of microbial biomass in the mineralization of P. Temperature and moisture conditions affect microbial activity and the immobilization and mineralization of C, N and P. The P availability might affect the rates of these processes. Therefore, in chapter 2 the effect of P limitation on the temperature and moisture response of microbial nutrient transformations is studied in a laboratory experiment. Chapter 3 deals with the effect of a simulated climate change on litter decomposition and microbial nutrient transformations in a large scale field experiment conducted at the dry heathland ecosystem.

In chapter 4 the effect of a summer drought on microbial dynamics and plant growth is studied as from previous work the role of moisture conditions had become evident. The direct effect of drought on the interaction between plants and microorganisms was evaluated at the ecosystem level.

In chapter 5 plant litterfall at the site is monitored together with plant biomass. A model calculation is made to unravel the effect of changes in litterfall and litter decomposition rate on fresh organic matter storage. Together with plant and litterfall data, ecosystem C and P cycling is quantified on the short and longer term. Finally in the synthesis, a more complete picture of Dutch heathland ecosystem functioning under climate change is drawn by integrating the results from the previous chapters and combining these with other results collected within the CLIMOOR and VULCAN projects.