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Heathland ecosystem functioning under climate change
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Summary

Heathland ecosystems are semi-natural ecosystems valued for their cultural historical associations, their characteristic biodiversity and their recreational function. They are characterized by low levels of plant available nutrients and low turnover time of nutrients in plant and soil (Aerts and Chapin, 2000). The recycling of nutrients through organic matter decomposition in the ectorganic soil horizons 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, but microbial biomass itself is also considered as an important nutrient pool (Jonasson et al., 1999; Schmidt et al., 2002). Microbial nutrient transformations can therefore play an important role in the regulation of nutrient availability for plant growth in these nutrient-deficient ecosystems (Harte and Kinzig, 1993; Jonasson et al., 1999a). Climate change affects 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 (Kieft et al., 1987; van Gestel et al., 1991; Grierson et al., 1998; 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.

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. Although the role of microbial community in organic matter decomposition and nutrient transformations 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 could possibly play an important role in the response of this ecosystem to climate change. Long term field experiments were conducted at the Dutch heathland area ‘Oldebroekse heide’ to assess the impact of climate change on ecosystem functioning. Climate conditions were manipulated since May 1999. The manipulation involved night time warming (on average 0.7°C increase) or summer drought in 20 m² plots (Beier et al., 2004). Nitrogen (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). The highly weathered acid sandy soil is mineralogicaly very poor with very low inorganic phosphorus (P) concentrations. The dominating dwarf shrub, Calluna vulgaris, produces P poor litter with an N/P (g/g) ratio of >16:1, indicating that P is the most important limiting nutrient for vegetation growth (Koerselman and Meuleman, 1996). Because in field experiments, processes are dependent on the ruling climate conditions, in addition laboratory experiments were performed to investigate the impact of climate conditions more mechanistic. To integrate several results and make predictions beyond the field measurement period mathematical modeling was used.

In chapter 1 the relationship between microbial dynamics, phosphorus availability and microbial acid phosphatase activity in decomposing phosphorus poor litter was studied by means of a laboratory incubation experiment. The litter originated from the dry heathland ecosystem ‘Oldebroekse heide’. The highly weathered acid sandy soil had low available P concentrations and as a result plant productivity at the site was limited by the availability of phosphorus. Phosphatase activity did not play a role in the low P availability in the litter of this P poor heathland, because phosphatase activity was very high throughout the experiment and therefore did not restrict P mineralization. Instead low P availability in litter was caused by rapid microbial P immobilization. Within 48 days 85% of total P present in the decomposing litter was incorporated in microbial biomass. Of the remaining P, 7% was present as inorganic P, while 9% remained in the litter. The distribution of P over the P pools changed only slightly over the duration of the experiment, despite the high acid phosphatase activity measured throughout the experiment.

In chapter 2 the hypothesis was tested that P availability affects the temperature and moisture response of microbial nutrient transformations during litter decomposition. Fresh C. vulgaris litter was incubated at 5°, 10°, 15° and 20°C and at 50%, 100% and 200% humidity. The litter originated from the dry heathland area ‘Oldebroekse heide’. Microbial nutrient transformations were studied during two periods, an
Initial decomposition period of 48 days in which P was not limiting microbial activity and a second period from 48 to 206 days in which P was limiting microbial activity. Microbial nutrient transformation rates depended both on temperature and humidity. Under non-P limited conditions microbial C and N immobilization rates, net P mineralization, net N mineralization and net nitrification were controlled predominantly by temperature conditions; whilst microbial P immobilization was controlled by humidity. Under P limiting conditions, in the second incubation period, microbial immobilization and net nutrient mineralization rates decreased significantly, while CO2 respiration and the metabolic quotient increased. The effect of temperature and humidity on process rates under P limitation was smaller, absent or opposite to the effect of temperature and humidity under non P limiting conditions. Although further microbial growth was limited by low P availability, microorganisms remained active and the metabolic quotient increased with temperature. This increase indicated decreased C utilization efficiency of the microbial community and was probably caused by stress induced by either or both increased temperature and increased P limitation.

In chapter 3 the effect of a modest temperature increase and repeated summer droughts on litter decomposition rate and microbial biomass dynamics was studied at the climate manipulated P deficient dry heathland. The continuous heating treatment positively affected decomposition rate temporarily during the first half year of litter decomposition, whereas the decomposition rate of the more recalcitrant litter fraction was not affected. The two summer drought treatments retarded litter decomposition rate permanently, indicating that both the labile and recalcitrant fraction were affected. Microbial C, N and P immobilization was affected by the heating as well as by the drought treatment. Enhanced temperature increased microbial biomass C during the first half year of incubation, while the first drought treatment significantly retarded microbial N and P immobilization. The delayed microbial N and P immobilization in the drought plots prevented a period of net N and P mineralization that was observed in the control plots. After one year of incubation microbial biomass C, N and P was significantly higher in the drought plots, probably as a result of availability of new substrate caused by the drying and rewetting process. Although microbial biomass was higher in the drought plots, the microbial C/N ratio was equal to the control, indicating that longer-term microbial composition was not affected by the drought. In conclusion, climate change shifted microbial biomass dynamics and the timing of P mineralization, which might affect plant growth in this already P deficient ecosystem.

In chapter 4 the effect of repeated summer droughts on plant growth and microbial dynamics at a P poor Dutch heathland ecosystem was investigated at the climate manipulated heathland area. The dominating dwarf shrub C. vulgaris was directly and indirectly affected by the repeated summer drought treatments. Direct effects were (a) a reduced ability to recover from a heather beetle attack (b) a decreased
elongation of the main shoots during a drought and (c) a decreased amount of buds that developed to flowers. An indirect effect was a reduction in foliar P and N concentration, which indicated a reduced P and N uptake from the soil. During peak drought, the size of the microbial biomass P in litterbags was reduced with 79%. This microbial induced P flush comprised 65% of yearly plant P uptake. Plants could however not benefit from the P flush as was indicated by the reduced foliar P concentrations, which suggests that *C. vulgaris* was a weak competitor for nutrients compared with microorganisms after drought.

In chapter 5 the effects of changes in plant biomass, in annual plant litter production, in litter decomposition rates and in net phosphorus (P) mineralization in the litter layer as a result of the climate manipulations on ecosystem C and P cycling was studied. Plant biomass dynamics were monitored and a simple model was developed to simulate the decay of daily litterfall cohorts during a short (1 year) and long term (5 years) period for the different climate conditions. Monte Carlo simulations were used to evaluate the statistical significance of the model outcome. On the short term, the heating treatment decreased soil C storage, however plant C biomass increased, which resulted in increased ecosystem C storage. On the long term increased litterfall as a consequence of increased plant biomass increased soil C storage. Soil C storage in the drought treatment decreased on the short and long term. Together with decreased plant C biomass this resulted in decreased ecosystem C storage. In both treatments less P was mineralized and P cycling rates decreased which could limit plant growth in the heating treatment and further limit plant growth in the drought treatment.

In the synthesis a more complete picture of Dutch heathland ecosystem functioning under climate change is drawn by synthesizing the results from the previous chapters and incorporating these with other results collected at the site within the CLIMOOR and VULCAN project. This is done on the basis of the research questions posed in the introduction. In conclusion: the modest temperature increase and summer droughts affected ecosystem functioning in various related ways. Increased temperature positively affected plant growth, although foliar P concentrations decreased due to relatively higher C uptake than P. Increased temperature did not increase P mineralization or affect the size and dynamics of the largest P pool in fresh organic matter: the microbial community. On the contrary P mineralization and P cycling rates were even reduced due to decreased litter production. Drought affected plant growth negatively and foliar P concentrations decreased. Drought and subsequent rewetting induced microbial cell lysis. However plants could not benefit from the resulting P flush. Decreased litterfall and decreased P mineralization reduced P cycling rates. C storage in plants and fresh organic matter increased in response to warming, but decreased in response to drought.