CAMPYLOPUS INTROFLEXUS AS A NITROGEN DEPOSITION DEPENDENT ECOSYSTEM ENGINEER IN INLAND DUNES

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Abstract: In The Netherlands, most of the inland dunes were active dune systems until about 1850. Due to afforestation and disappearance of traditional land management, its area declined to only about 1% of its original size. Around 1960, the introduction of an exotic moss added a new threat to the remaining inland dune vegetation. Also nitrogen deposition from agriculture increased dramatically.

In this study we tested the hypothesis of a positive relation between abundance of the invasive moss *Campylopus introflexus* and increased nitrogen deposition. We compared five succession stages in two sites along a deposition gradient, sampling data on microbial activity and nutrient availability. Additionally, 250 relevées were made and soil samples were taken to assess the variation in edaphic parameters for each species. The data were analyzed using multivariate statistics.

Microbial C/N ratios and ammonium concentrations in the top soil were highly dependent on nitrogen deposition. Nitrogen mineralization and edaphic characters were similar in *Campylopus* mats and vegetations dominated by cup-lichens. Both early and late succession stages are similar in areas with high and low nitrogen deposition: vegetations dominated by *Corynephorus canescens* and *Polytrichum piliferum* (early) and reindeer moss and *Agrostis/Festuca* species (late). However, in high nitrogen deposition areas, moss mats of *Campylopus* invade young *Polytrichum* mats, resulting in a thick, species poor moss carpet, leaving no space for many small cup-lichens. We conclude that vegetation types with small cup-lichens are most affected by nitrogen deposition.

Keywords: eutrophication, invasive species, fragmentation

Introduction

In The Netherlands, most of the inland dunes were active dune systems until about 1850. Due to afforestation and disappearance of traditional land management, its area declined to only about 1% of its original size. Around 1960, the introduction of an exotic moss added a new threat to the remaining inland dune vegetation. Also nitrogen deposition from agriculture increased dramatically (Riksen et al. 2006).

In inland dunes, the succession chronosequence starts with scattered *Corynephorus canescens* plant on open sand with only *c*. 0.3 % organic matter content. In the next stage, the space between the grass is filled with *Polytrichum piliferum* mats. In the subsequent stage, lichen species fill up the space between the *Polytrichum* shoots. In the last stage *Agrostis vinealis*, *Festuca filiformis* and *F. ovina* are becoming gradually dominating, and finally *Pinus sylvestris* settles (Hasse 2005).

Around 1960, the moss *Campylopus introflexus* has been introduced from the Southern Hemisphere. The species appeared to be very successful in dry, acid environments and occurs now everywhere in the European lowlands (Hassel & Söderstöm 2005; Van Tooren & Sparrius 2007), especially in inland dunes and heathlands. In The Netherlands, dominance of *Campylopus introflexus* is restricted to areas with high nitrogen deposition, the central and southern parts of the country. In this study we tested

the hypothesis of a positive relation between abundance of the invasive moss *Campylopus introflexus* and increased nitrogen deposition. We also try to estimate the moment of invasion in the succession series, by comparing edaphic and morphological characters from *Campylopus* and its competitors.

Materials and methods

We compared five succession stages in two sites along a strong deposition gradient: site Aekingerzand receives *c*. 2000 mol N ha^{-1} a^{-1}, site Wekeromse Zand *c.* 3600 mol N ha^{-1} a^{-1}. At both sites, data on microbial activity, nitrogen mineralization and nutrient content was sampled in four habitat types (open sand, *Polytrichum piliferum* mats, *Campylopus introflexus* mats, cup-lichen mats, and grassy vegetations with *Cladina portentosa*) under two circumstances (natural succession starting with open sand, succession starting on top soil rich in organic matter at sites where forest has been removed during the last ten years). Soil samples of 0-5 cm top soil were taken and dried at 60 °C. For *Campylopus introflexus* and cup-lichens, the ectorganic layer was sampled separately, by separating the upper living and non-green lower parts of the lichens and mosses. We sampled four replicates per situation, in total 108 samples.

Total C and N was measured in a CNS analyzer (Fisher EA1110). Nitrate, ammonium and phosphate in water extracts of soil (1:2,5) were measured using an Auto Analyzer III (Bran+Luebbe). Cation concentrations were measured with an inductively coupled plasma analyser (Fisher Iris Intrepid II). To estimate the microbial biomass, a soil sample was fumigated with chloroform. To estimate nitrogen mineralization, soil samples were kept for two months petri dishes in the dark at 14 °C and 90% relative humidity. To estimate microbial activity, CO_2 respiration of the soil biomass was measured at room temperature at 30 min. intervals using gas chromatography.

Additionally, 250 relevées were made together with soil samples, from which the soil profile (A_h depth), pH(H_2O) and concentrations in cations, nitrate, ammonium and phosphate were analyzed using the methods described above. For each species, the variation in these edaphic characters was calculated.

Results

Microbial C/N and N/P (Fig. 1) ratios, nitrogen mineralisation and the ammonium concentrations in the top soil were highly dependent on nitrogen deposition. This suggests leaching of N at the high-deposition site, and accumulation of nitrogen in the microbial biomass. Respiration efficiently and P mineralization did not differ. P mineralization was extremely high in the lichen ectorganic layer (*c*. 5 x higher than in the *Campylopus* ectorganic layer).

Within each site, edaphic characters (pH, soil profile, cation concentrations) for *Campylopus* mats and vegetations dominated by cup-lichens were of the same magnitude. Both were different from grassy vegetation and early succession stages. This support the hypothesis that *Campylopus introflexus* is especially invasive in cup-lichen vegetations. There was no difference in soil nitrogen content in the logged areas at both

sites. In both cases nitrogen is high. This is probably caused by the ongoing mineralization of litter, saturation and leaching of excess nitrogen.

At both sites, both early (sand and young *Polytrichum* mats) and late (grassy vegetations) succession stages are similar in microbial activity.

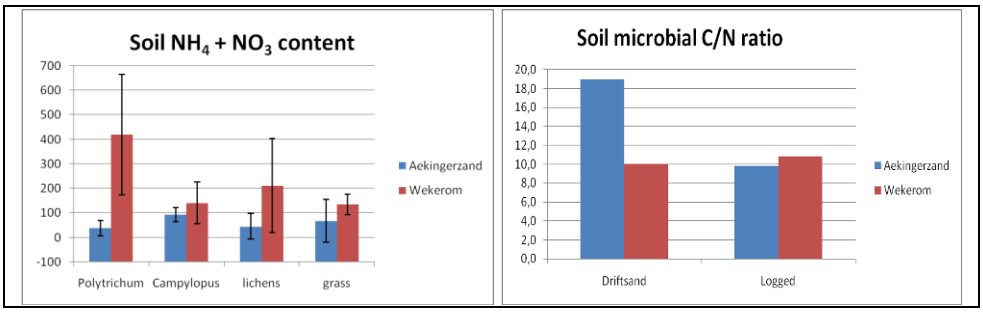

Figure 1. Water extractable inorganic nitrogen in the mineral topsoil different successional stages at both sites (left); difference soil C/N ratio between drift sand and logging sites (right).

Discussion

By comparing morphology of the vegetation, the success of *Campylopus* can be explained: cup-lichens develop on mats of *Polytrichum piliferum*. These mats consist of circa 50% open sand with numerous, slender, *c*. 2 cm tall *Polytrichum* plants at regular intervals (Fig 2). The moss plants are connected below-ground with fast-growing rhizoids, the primary soil-forming factor is this succession stage. While soil formation continues, the nutrient availability and substrate humidity increase. At a certain point *Campylopus* enters the vegetation using spores and/or leave fragments and forms a tight mat, filling up the open space between the *Polytrichum* plants and lichens. *Campylopus* develops a poorly degradable above-ground ectorganic layer (Fig 2). Nitrogen formed by mineralization of the ectorganic layer can be directly taken up by the living parts of the moss plant. The *Campylopus* mats are often 1 to 4 cm higher than the original cup-lichen vegetation.

Cup-lichen mats can become very old, probably over 50 years, accumulating species over time. Soil formation continues and make a rough dating of the vegetation possible. In the low-deposition areas of the Netherlands, the average A_h is 4.9 ± 2.0 cm thick, in the high-deposition areas 8.4 ± 3.8 cm. This is evidence for a relic status of cup-lichen vegetations in the high-deposition areas: older cup-lichen vegetations are densily filled with lichens, leaving no opening for *Campylopus* to colonize. Younger cup-lichen vegetations have already been invaded by *Campylopus* and new cup-lichen mats cannot develop anymore. Alternatively, increased nitrogen could speed up the soil formation, but it is unlikely that this explains this significant difference.

Conclusions

We conclude that vegetation types with small cup-lichens are most affected by nitrogen deposition, through competition with *Campylopus introflexus*. *Campylopus introflexus*

Figure 2. A typical *Polytrichum* mat before lichen colonization (left) and a vertical section through a *Campylopus* mat (right). Both species can build monotonous vegetations of several hectares.

dominance however, appears to be dependent on additional nitrogen.

The success of *Campylopus introflexus* can be explained partly from its anatomy, and partly from the ability to absorb nutrients formed by mineralization of its ectorganic layer, features absent in its main competitor *Polytrichum piliferum*. *Campylopus* mats could be regarded as a dry version of a *Sphagnum* bog.

The mineralization experiment yielded new evidence on the N and P efficiency of *Cladonia* lichens. An earlier study (Hyvärinen & Crittenden 1998) demonstrated a fast uptake of phosphate by lichens. The high P mineralization found in this study suggests that there is a rapid P cycle in a growing lichen mat.

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