Effects of moss-encroachment by *Campylopus introflexus* on soil-entomofauna of dry-dune grasslands *(Violo-corynephoretum)*

Joost Vogels[1], Marijn Nijssen[2], Wilco Verberk[2] & Hans Esselink[1,2]
[1]Department of Animal Ecology and Ecophysiology, Radboud University of Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands;[2] Bargerveen Foundation, Department of Environmental Studies, Radboud University of Nijmegen, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands

Due to acidification and eutrophication, extensive areas of sandy, dry and lichen-rich dune grasslands (*Violo-corynephoretum*) are overgrown by the invasive moss species *Campylopus introflexus*. Species assemblages of spiders, carabid beetles, Sciaridae and Empidoidea differed between a *Violo-corynephoretum* reference site and moss-encroached sites. Sciaridae emerged in relatively high numbers from thick moss layers, Empidoidea showed a preference for moss-encroached sites. This suggests that moss-encroachment induces changes in soil fauna composition. Total activity of both carabid beetles and spiders was significantly lower in the moss-encroached sites, suggesting lower food density in moss-encroached dry dune grasslands. Night-active carabid and spider species showed equal or higher activity in the moss-encroached sites, whereas day-active species had a lower activity in moss-encroached sites. This indicates that moss-encroached sites have a more extreme microclimate, or that specific vegetation structures used by xerophylous species disappear by moss-encroachment.

Keywords: dune grassland, soil entomofauna, spiders, carabid beetles, Sciaridae, Empidoidea

Lime-poor dunes are often acidic and highly N-limited (Westhoff & Van Oosten 1991). As a result, these dunes inhabit different vegetation types compared to dunes with a higher Calcium content of the soil. In these lime-poor dunes, dry dune grassland *(Violo-corynephoretum)* used to be a commonly found vegetation type (Westhoff & Van Oosten 1991). This vegetation is typically common on east and south-exposed slopes, which inhabit a dryer and warmer microclimate due to the increased input of solar radiation. Most characteristic for this plant community is the high richness and abundance of lichens. As lichens have no well developed root system, sand fixation is poor and as a result of aeolian dynamics vegetation succession is frequently set back to earlier succession stages (cyclic succession). This results in a mosaic of open sandy patches and patches covered with short vegetation and lichens.

As a result of the increased atmospheric nitrogen and acid deposition in the Netherlands, the lime poor dunes are no longer N-limited and decomposition of organic matter is inhibited. Tall grass and sedge species *Ammophila arenaria* and

Carex arenaria gain a selective advantage under these nutrient-rich and acidic conditions, resulting in grass-encroachment (Kooijman *et al.*, in press). In addition, moss-encroachment by *Campylopus introflexus* takes place. In a former dry dune grassland on the island of Terschelling, a comparison to the historical reference situation in 1966 and the situation in 1991 revealed that 10 out of 14 lichen species had disappeared, the cover of lichens had declined from 50% to 3% and the cover of *A. arenaria* and *Calamagrostis epigejos* had increased from 30% to 90%. In addition, a dominance of *C. introflexus* was found (Ketner-Oostra 1993) On deeply decalcified soils, encroachment by the exotic moss species *C. introflexus* often occurs. This moss is a pioneer species and has a preference for disturbed highly acidic soils (Biermann 1997, 1999). Acidification of the soil by increased acidic deposition enhances the distribution of this species (Van der Meulen *et al.* 1987). Possibly, eutrophication due to the increased nitrogen deposition plays an important role as well. By means of vegetative reproduction, this species is able to cover large areas in a short time span. As a result, characteristic plant and lichen species decline or disappear. High sand fixation by *C. introflexus* could lower the frequency of cyclic succession as well. Finally, moss-encroachment could lead to an increased formation speed of a humus-layer in the soil (Westhoff & Van Oosten 1991).

Effects of moss-encroachment will probably not be limited to the vegetation and will also affect fauna assemblages, but studies on this subject are lacking. This paper deals with the effects of moss-encroachment on the fauna community of dry dune grasslands. Intact dry dune grasslands are characterized by an extreme dry and warm microclimate, both in the soil as on the surface. The presence of a dense moss-carpet in encroached situations could have a buffering effect on microclimate, both in the soil as on the surface. As a result, a change in species assemblage is expected from a dominance of xero- and/or thermophylous species to a dominance of mesophylous species. Increased humus formation is expected to cause a rapid colonization of moss-encroached areas by detritivorous soil-inhabiting species. Finally, differences in fauna density are expected between moss-encroached vegetations and to intact vegetations.

MATERIALS AND METHODS

This study was carried out on Terschelling, in an area known as 'The Groenplak', an old, deeply decalcified area, in which both severely moss-encroached vegetation as well as relatively intact vegetations could be found. In this area, three vegetation types were sampled: an intact, late succession stage of a dry dune grassland, dominated by *Corynephorus canescens* and *Cladina portentosa*, a moss encroached vegetation in early succession and a moss encroached vegetation in late succession, both dominated by *C. introflexus*. Soil-inhabiting fauna was sampled using emergence traps (n=5, sampling surface 0.25 m^2), surface active fauna was sampled using pitfall-traps (n=5). Of each vegetation type,

Table 1. Soil characteristics, cover and vegetation cover of the sampling locations. n=5. M: Moss, P: Vascular plant, L: Lichen.

	Vegetation	Reference vegetation	Moss-encroached, early succession	Moss-encroached, late succession
Mean thickness/ height (cm)	Organic layer	1.24	0.16	0.28
	Humus layer	0.94	0.76	1.66
	Moss layer	1.34	0.66	0.76
	Lichen layer	3.32	0	0.08
	vegetation layer	5.7	3.52	3.16
Mean cover (%)	Vegetation	97.16	97.32	97.24
	Litter	2.24	1.16	2.76
	Bare sand	0.6	1.52	0
Mean total surface (m^2)		14.8	20.8	420.0
Mean vegetation cover	*Campylopus introflexus* (M)	0.80	80.84	94.88
	Dicranum scoparium (M)	22.60	11.92	0.20
	Corynephorus canescens (P)	4.28	4.88	4.96
	Carex arenaria (P)	2.12	0.44	0.32
	Ammophila arenaria (P)	0.40	0.08	0.04
	Luzula campestris (P)	0.40	0.00	0.00
	Rumex acetosella (P)	1.20	0.16	0.36
	Hypochaeris radicata (P)	0.00	0.12	0.04
	Coelocaulon aculeatum (L)	0.00	1.32	0.28
	Cladina portentosa (L)	72.20	1.60	1.08
	Cladonia sp. (L)	0.00	0.56	0.00

thickness of moss, humus and vegetation and vegetation composition was determined (n=5). Sampling was performed between April 3rd and June 12th 2002, divided in four sampling periods. Of the soil-inhabiting fauna Diptera, the (super)families Sciaridae and Empidoidea were analyzed, of the surface-active fauna, carabid beetles (Carabidae) and spiders (Araneae) were analyzed. Statistical analysis was performed using SPSS 11.5.1 (SPSS inc. 2002). Tests used for analyses were one-way ANOVA when data was distributed normally, otherwise a Kruskal-Wallis test or a Mann-Whitney U test were used. In order to correct for inflated significance values when using a Mann-Whitney U test, significance value was set to 0.01 instead of 0.05.

Carabid beetles and spiders were classified into habitat preference and climatic preference (after Turin 2000 and Martin 1991). Carabid beetles were also classified in day- or night-activity (after Turin 2000). There was no ecological information on day- and/or night-activity of the sampled spider fauna obtainable from literature. Therefore, two functional species groups were distinguished.

Both species groups consisted out of surface active, running spiders. The family Gnaphosidae largely consists of night-active species, the family Lycosidae largely consists of day-active species.

RESULTS

Vegetation

The reference vegetation could be characterized as a late succession stage of a dry dune grassland (Westhoff & Van Oosten 1991). *Cladina portentosa* was the dominant lichen. The moss *Dicranum scoparium* reached highest cover percentages here.

Corynephorus canescens was the dominant higher plant species in all three vegetation types. *Rumex acetosella* and *Carex arenaria* were also abundant in the reference vegetation and a humus and organic layer was present (Table 1).

The moss-encroached vegetation in early and late succession was characterized by the dominant presence of *C. introflexus*. The organic, humus and moss layer were relatively thin in early succession, although relatively thick in late succession. However, the organic layer was thin compared to the reference vegetation (Table 1).

Soil fauna

Sciaridae

In total, 296 individuals, belonging to 17 species were sampled. Mean emergence activity differed significantly between the reference vegetation and the moss encroached vegetation in early succession (one-way ANOVA, p=0.004) (Fig. 1).

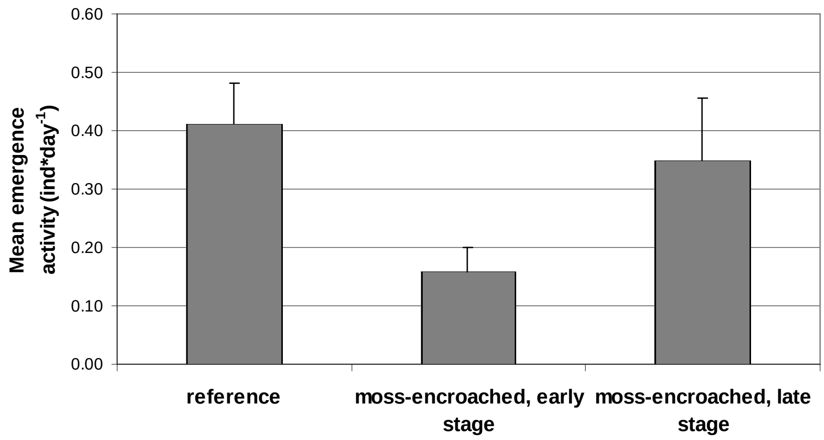

Figure 1. Emergence activity of Sciaridae. SE error bars shown. Siginifcant difference was found between the reference vegetation and moss-encroached vegetation in early succession (ANOVA, Games-Howell-test: p=0.004).

Empidoidae

In total, 53 individuals belonging to 6 were sampled. Mean emergence activity differed significantly between the vegetations (Kruskal-Wallis: p=0.020) (Fig. 2). *Tachypeza nubila* was most abundant (35 individuals) and the pattern of its emergence activity activity was consistent with the pattern of all Empidoidea (Fig. 2).

Surface-active fauna

Carabid beetles (Carabidae)

In total, 233 individuals were sampled, belonging to 17 species. In the first three sampling periods mean activity was significantly higher in the reference vegetation (ANOVA, Tukey test; $p<0.05$) than in both moss-encroached vegetations. In the fourth sampling period, mean activity in the reference vegetation only differed significantly from the moss-encroached vegetation in early succession (ANOVA, Games-Howell test: $p<0.05$) (Fig. 3).

No changes in species assemblage in terms of habitat preference were found. In all three vegetation types, species assemblage consisted for 85-90% of eurytopic species with a preference for heath land habitats (data not shown). No difference in species assemblage in terms of moisture preference was found. In all three vegetation types, species assemblage consisted for 80-90% out of xerophylic species (data not shown). The species composition in moss-encroached vegetation in late succession was dominated by night-active species (60% of total). In contrast, the species composition in the reference and moss-encroached vegetation in early succession was dominated by day-active species (60% of total in both cases) (Fig. 5).

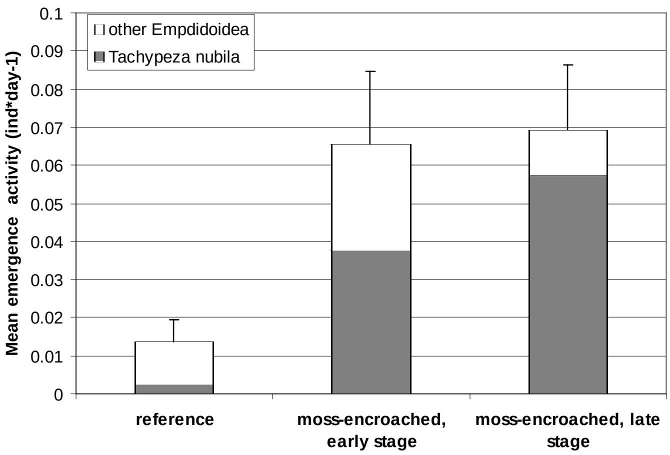

Figure 2. Emergence activity of *Tachypeza nubila* and of total Empidoidae. SE error bars of total emergence activty shown. Siginifcant difference was found between the vegetations (Kruskal-Wallis test: p=0.020).

Spiders (Araneae)

In total, 1912 individuals were sampled, belonging to 55 species. In all sampling periods mean activity was significantly higher in the reference vegetation than in both moss-encroached vegetations (ANOVA, Tukey test: $p<0.01$) (Fig. 4).

No changes in species assemblage in terms of habitat preference were found. In all three vegetation types, species assemblage consisted for 90% of species with a preference for sparsely vegetated habitats (data not shown). No difference in species assemblage in terms of moisture preference was found. In all three vegetation types, species assemblage consisted for 90% of xerophylic species (data not shown).

For night-active Gnaphosidae, no significant difference in activity between the vegetations was found (Fig. 6). Day-active Lycosidae had a significantly higher activity in the reference vegetation than in both moss-encroached vegetations (Mann-Whitney U test: $p<0.001$; Fig. 6)

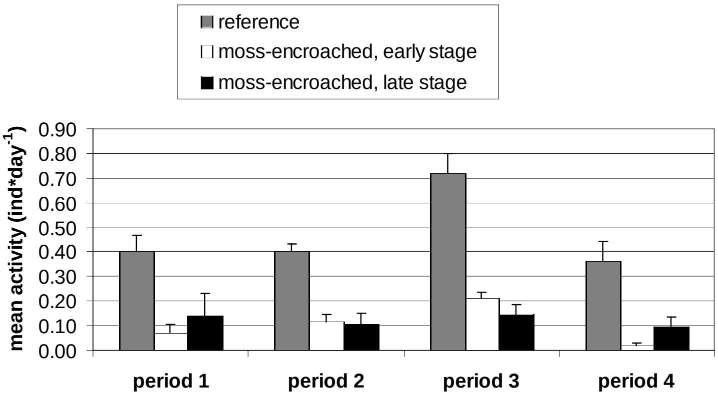

Figure 3. Mean activity of Carabidae per sample period. Activity was significantly higher in the reference vegetation (ANOVA, Tukey test: $p<0.05$; Games-Howell test: $p<0.05$).

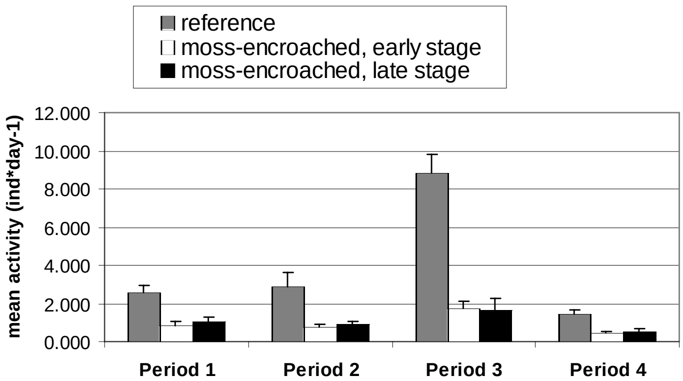

Figure 4. Mean activity of Araneae per sample period. Activity was significantly higher in the reference vegetation (ANOVA, Tukey test: $p<0.05$).

DISCUSSION

The investigated vegetation types differed most strongly in the cover of lichens and the thickness of the humus and organic layer. The reference vegetation was mostly covered by a layer of *C. portentosa* and had a high 3D-structural complexity as a result of the open structure of this lichen species. In contrast, the moss-encroached vegetations, had a two-dimensional vegetation structure. The moss-encroached vegetation in early succession was relatively young (<5 years) and had a thin humus and organic layer compared to the other vegetation types. The reference vegetation was estimated to be several decades old since earlier succession stages of intact dry dune grasslands often lack a humus layer. The moss-encroached vegetation in late succession was estimated to be less than 10 years old, but had a thicker humus-layer compared to the reference vegetation. Thus, moss-encroachment increases the humus formation.

The emergence activity pattern of Sciaridae was related to the thickness of the humus-layer. The explanation is that a thinner humus-layer enhances the risk of desiccation and larvae of Sciaridae are relatively sensitive for desiccation (Heller, pers. comm.). Hövemeyer (1999) also found a positive correlation between larval densities of Sciaridae and the thickness of the humus layer. This does not explain the emergence activity of Empidoidea. This group showed a preference for moss-encroached vegetations. When comparing the overall survival strategy of both groups, the Sciaridae are generally r-strategists. Adults are short-living and often do not feed in their adult stage. Females generally mate directly after emerging and subsequently start ovipositing. The larvae are generally a-selective detritus feeders (Van Zuijlen *et al.* 1996; Heller, pers. comm.) and ovipositing of Sciaridae is probably a-selective. Local abiotic conditions therefore determine the emergence activity. Empidoidae on the other hand, are generally K-strategists. To complete their life-cycle, Empidoidae do feed in adult stage and use different habitats (Van Zuijlen *et al.* 1996, Dekoninck *et al.* 2000, Delettre *et al.* 1992). Females have to fly from their foraging habitat to their

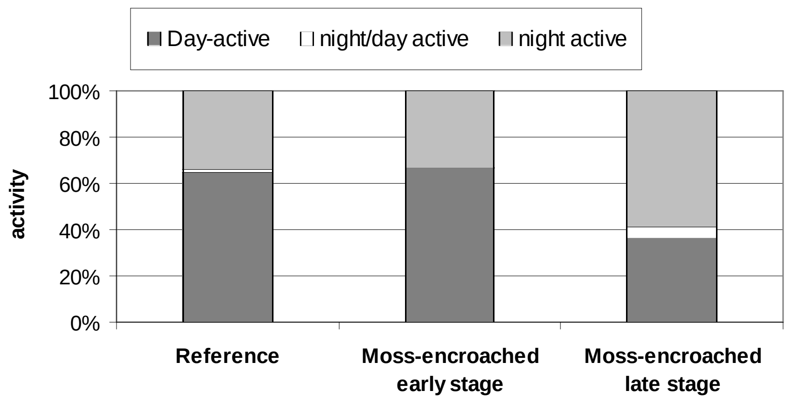

Figure 5. Relative amount of day-active and/or night active species of Carabidae.

reproduction habitat in order to lay eggs. It is therefore plausible that females of Empidoidae are selective ovipositionists and in that case emergence activity is primarily determined by the female habitat choice. The most abundant empidoid species, *T. nubila*, is known to prefer vegetation poor, humus rich substrates (Dekoninck *et al.* 2000). Most likely, this species has selectively oviposited in the moss-encroached sites, explaining the low emergence activity in the reference vegetation.

The activity of carabid beetles and spiders was much lower in the moss-encroached vegetation types. This probably reflects lower densities of both groups in the moss-encroached vegetation types. Pit trap catches are biased towards species with higher activity. As the physical resistance from the vegetation in the reference vegetation was higher compared to the moss-encroached vegetation types, actual densities are even more different than suggested by the differences in activity pattern (Greenslade 1964). Densities of both spiders and

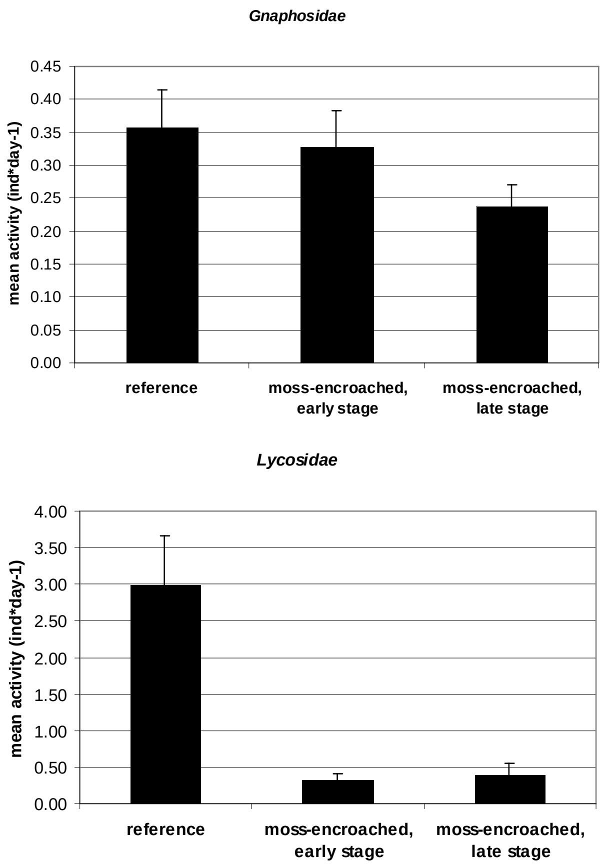

Figure 6. Mean activity pattern of Gnaphosidae and Lycosidae. SE error bars are shown. No significant difference between sites was found for Gnaphosidae, Lycosidae showed a significant difference in activity between the reference vegetation and both moss-encroached vegetations (Mann-Whitney U test: $p<0.001$).

carabid beetles are primarily limited by food abundance (Chen & Wise 1999, Turin 2000). This suggests that the food abundance in the moss-encroached dry dune grasslands is much lower than in an intact dry dune grassland.

Comparison of species assemblage with respect to habitat preference (Turin 2000, Martin 1991) suggested that there was no difference in microclimatic conditions between intact and moss-encroached dry dune grasslands. However, in the moss-encroached vegetation, night-active carabid beetles were more abundant compared to the reference vegetation. The spider community showed the same shift from day-activity to night-activity, as the day-active Lycosidae showed a strong preference for the intact vegetation, whereas the night-active Gnaphosidae showed no difference in activity between intact or moss-encroached dry dune grasslands. This suggests a relation with the extremity of the microclimate. Night-active species are able to avoid the most extreme conditions during the day by means of hiding, while day-active species have to be adapted to the most extreme conditions during the day, for instance with metallic colours to reflect heath. When conditions become too extreme, even the tolerant day-active species can no longer cope and are in a disadvantage compared to the night-active species. Therefore, the results suggest a more extreme warm and dry microclimate in the moss-encroached dry dune grasslands. An additional factor is the lack of a three-dimensional vegetation structure in the moss-encroached vegetation. This deprives day-active species the opportunity to temporarily take shelter during foraging.

In conclusion, moss-encroachment of dry dune grasslands rapidly leads to the formation of a humus layer, resulting in a buffering of the microclimatic conditions in the soil, thereby facilitating the settlement of soil-inhabiting larvae. On the surface, moss-encroachment leads to a more homogeneous and possibly more extreme microclimate, resulting in a shift form day-active dominated to a night-active dominated species composition. The extreme low activity of the predaceous spiders and carabid beetles suggest a very low food abundance in the moss-encroached vegetation. Summarizing, moss-encroachment by *C. introflexus* has a large impact on fauna species assemblages both above and below the ground. This paper stresses the importance for nature management to counteract the effects of moss-encroachment on characteristic fauna species. As ecological characteristics of species known from literature do not provide sufficient thresholds for testing the hypotheses in this research, a deeper understanding of the different adaptations that species posses (life history tactic) to survive in their preferred habitat is important to: 1) obtain knowledge on the underlying causal mechanisms that affect characteristic species assemblages, and 2) design sound management strategies to counteract the effects of moss-encroachment of dry dune grasslands on both plant and fauna communities.

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