





DOMINANCE PATTERN CHANGES OF A LICHEN-RICH CORYNEPHORUS GRASSLAND IN THE INLAND OF THE NETHERLANDS

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ABSTRACT - this paper documents the pattern changes of a *Corynephorion*-grassland during the period 1981-2004. All 2-3 years the dominant moss- and lichen microcommunity (mc) types and the dominant grass species were recorded in all 936 square meter subplots of a 26 m x 36 m plot. The study site is situated in the National Park "De Hoge Veluwe", the Netherlands. The area is roamed mainly by deer and wild sheep. Climate is oceanic. Main purpose of the study is long-term monitoring of vegetation dynamics in relation to grazing and climate.

In 1981 the densely vegetated plot was mainly dominated by the *Cladonia glauca – Trapeliopsis granulosa* mc type (5), the *Cladonia glauca* mc type with reindeer lichens (6) and the *Cladonia portentosa* mc type (8) and the grasses *Corynephorus canescens* (C) and *Festuca fili-formis* (F). The subplot dominance of *Corynephorus canescens* appeared positively correlated with that of mc type 5, whereas the subplot dominance of *Festuca filiformis* was correlated with those of mc types 6 and 8. The *Campylopus introflexus* mc type (4) was dominant in one subplot only. During 1981-1984 the subplot dominance frequency of mc types 6 and 8 increased, while that of mc type 5 decreased. These changes are in line with known progressive succession features of the *Spergulo-Corynephoretum*. During 1984-1994 almost all mc types from 1981 disappeared and in 1994 the plot was almost completely dominated by the *Campylopus introflexus* mc type (4) and *Corynephorus canescens*. In the beginning of this period (1985, 1986, 1987) some winter months were very cold and dry (continental). Thereafter the oceanic *Festuca filiformis* and *Cladonia portentosa* (mc type 8) died off. Moreover game density in the National Park increased. The resulting open places with sand and litter were easily occupied by the highly invasive neophytic moss *Campylopus introflexus* (mc type 4).

From 1994 onwards we observe again a development towards the situation of 1981. The dominance frequency of the *Campylopus introflexus* mc type (4) continuously decreased with the oldest moss carpets being overgrown by lichens of the mc types 5, 6 and 8. Subplot dominance frequency of *Festuca filiformis* is increasing; however *Corynephorus canescens* is still the dominant grass species nowadays. The "recovery" of the stand might be due to the rather stable environmental conditions during the last ten years. We postulate that the vegetation structure in terms of square meter subplot dominance of microcommunities and grasses in *Corynephorion* vegetation is regulated by the magnitude of climatic stress and grazing pressure, and by the presence of *Campylopus introflexus*.

KEY WORDS - Campylopus introflexus, climate, dynamics, grazing, microcommunity, monitoring

INTRODUCTION

On poor, dry and sandy deposits in the central part of the Netherlands *Corynephorion* vegetation is still well developed over a few, however extensive areas. This vegetation type is a result of former anthropozoogenic devastation of wood- and heathland and their soils, which changed these landscapes into a bare sandy desert with blown-outs and dunes. In former days such dune areas were covering extensive parts of the Veluwe region and gave the landscape a true desert-like appearance (Fig. 1) with sparse vegetation of pioneer species such as *Corynephorus canescens*, a few other grasses, *Spergula morisonii*, *Polytrichum piliferum* and lichens. From the end of the 19th century most of these infertile lands were planted studies are scant and actually little is known on the dynamics and succession pathways of *Spergulo-Corynephoretum* to woodland (see e.g. van Rheenen et al., 1995; Biermann & Daniëls, 1997, 2001; Jentsch & Beyschlag, 2003; Jentsch, 2004; Hasse & Daniëls, 2006 and Ketner-Oostra, 2006).



Fig.1. The desert-like inland dune area of the Kootwijkerzand in the Netherlands with Corynephorion vegetation in more sheltered sites. Scattered Scots pine trees. Photo FJAD 2006.

with Scots pines or disappeared otherwise for example by land reclamation measures. Small remnants are preserved nowadays in nature reserves. Albeit *Corynephorion* landscapes have a low biodiversity, they have a hot spot status for terricolous lichens and other specialists. As dry oligotrophic enclaves surrounded by moist eutrophic lands they are ecologically very interesting and valuable. Nowadays they are threatened by atmospheric N-deposition.

Vegetation ecological studies of *Corynephorion* vegetation are comparatively rare. Permanent plot

The main purpose of this – in reality the first monitoring study is to document the changes in a *Corynephorion* vegetation to gain more insight into its long term dynamics in relation to environmental changes.

The present contribution summarizes the changes for the period 1981-2000 (Biermann & Daniëls, 1997, 2001) and deals with the further development of the vegetation in the subsequent 5 years (2000-2004).

STUDY AREA

The monitoring plot is situated in the Oud-Reemster Zand (about 52°05'N, 5°45'E) in the National Park "De Hoge Veluwe", the Netherlands. Its GPS position in Gauß-Krüger coordinates is GK 24 86 874/57 69 082; GK 24 86 898/57 69 094; GK 24 86 884/57 69 128; GK 24 86 860/57 69 116. Altitude is 26 m a.s.l. The extensive, relatively flat area is wind-exposed and treeless over more than 200 years. The area is roamed by deer, wild sheep and wild boar (Fig. 2). Potential natural vegetation probably is a birch-oak-forest (*Betulo-Quercetum*). The plot consists of a mosaic of lichen-rich dry sand grassland vegetation of the *Spergulo-Corynephoretum* type with locally *Agrostis vinealis* and *Festuca filiformis*. The substrate is



Fig. 2. Corynephorion vegetation in the Oud-Reemster Zand in the National Park "De Hoge Veluwe". The monitoring plot is situated near the group of red deer and wild sheep. Photo FJAD 2005.

	vascular plant-/	рН	conductivity	humus	N-content	C-content	C/N- ratio	K ₂ O	P ₂ O ₅
plot	mc type		[µS/cm]	[%]	[g/100g ds]	[g/100g ds]		[mg/100g ds]	[mg/100g ds]
1	C / mc 8	4,3	9,05	0,81	0,03	0,39	12,9	0,5	16,99
2	F / mc 8	4,2	10,12	1,06	0,08	0,99	12,4	0,62	21,41
3	A / mc 8	4,1	15,86	1,76	0,09	1,14	11,7	1,48	28,88
4	C / mc 4	4,5	7,57	0,37	0,01	0,19	13,0	0,33	31,60
5	sl	4,2	9,96	0,67	0,03	0,32	12,5	0,14	10,19

Tab. 1. Results of some soil analyses (0-10 cm) of 5 subplots near the monitoring plot. Ds means dry soil. Dominant grasses and mc types indicated (for explanation see text).

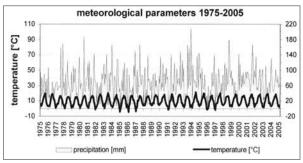


Fig. 3. Monthly precipitation and temperature of the period 1975-2005 measured by the meteorological station Deelen, NL.

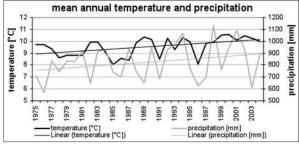


Fig. 4. Survey of mean annual temperature and precipitation of the period 1975-2005 measured by the meteorological station Deelen, NL.

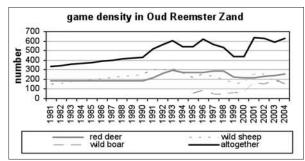


Fig. 5. Game density (1981-2004) in the National Park "De Hoge Veluwe".

of Pleistocene origin and consists of acid very poor sands (van Rheenen et al., 1995; see also Tab. 1). Climate is oceanic (OK-Stufe I according to Jäger, 1968) with moderate cold winters and moist summers. The figures of precipitation and temperatures during the period 1975-2005 are derived from the weather station Deelen, situated 5 km east of the plot (Fig. 3 and 4).

MATERIAL AND METHODS

We used a so called microcommunity (mc) type mapping method (MCMM). Microcommunities are understood as structural parts of plant communities with a specific floristically composition and microhabitat. They often consist of species groups of the same stratum with uniform growth-/life form, periodicity and habitat exploitation. They are floristically typified and can be syntaxonomically classified as plant communities (cf. Barkman, 1973). The mapping base is a self made typology of 1980 for the *Corynephorion* microcommunities of the entire National Park. The following mc types are of relevance for this study.

1. Cetraria aculeata - green algae mc type

2. Cetraria aculeata - green algae mc type with Polytrichum piliferum

3. *Polytrichum piliferum* mc type with stalk and cup bearing lichens

- 4. Campylopus introflexus mc type
- 5. Cladonia glauca Trapeliopsis granulosa mc type
- 6. Cladonia glauca mc type
- 7. Cladonia glauca mc type with Cladonia arbuscula
- 8. Cladonia portentosa mc type

Types 6 and 7 are floristically rather similar and for practical reasons considered as one mc type, indicated as 6. Mc types 1, 4, 5, 6, and 8 are the most prominent. They are floristically characterized and can be physiognomically easily identified. Mc type 1 is a very open vegetation with Cetraria aculeata and green algae; 4 is characterized by the strong dominance of the neophytic moss *Campylopus introflexus*; mc type 5 by the dominance of stalk and/or cup bearing lichens (surface lichens), mc type 6 by surface (stalk and cup bearing lichens) and reindeer lichens (volume lichens) (Cladonia arbuscula, C. portentosa) and mc type 8 by the strong dominance of the volume lichen Cladonia portentosa. The numbering is the same as in Biermann & Daniëls (1997, 2001), not so the nomenclature. For detailed information the reader is referred to Biermann & Daniëls

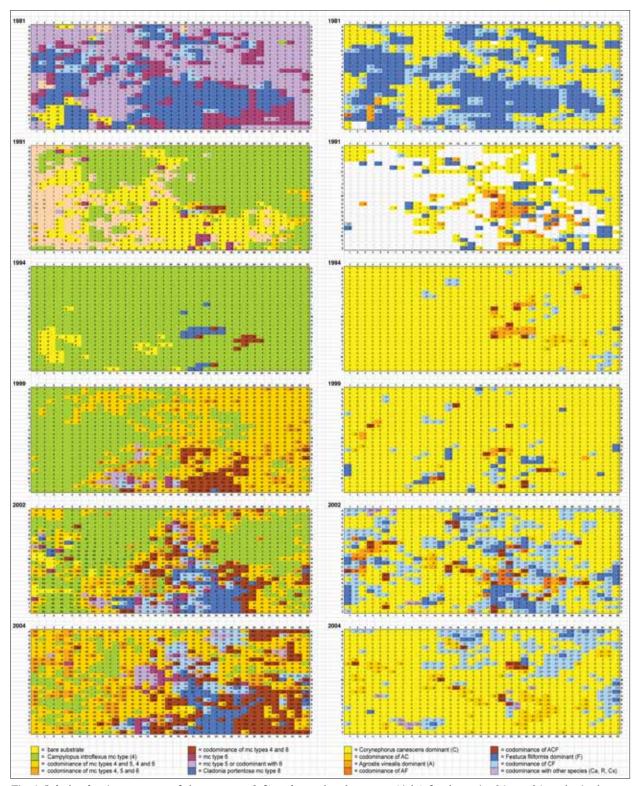


Fig. 6. Subplot dominance maps of the mc types (left) and vascular plant types (right) for the entire 26 m x 36 m plot in the years 1981, 1991, 1994, 1999, 2002 and 2004. (Ca=Calluna vulgaris, R= Rumex acetosella and Cx= Carex arenaria).

(1997, 2001). The characteristical species composition and structure of the mc types did not change during the entire monitoring period.

The monitoring plot is 26 m x 36 m large and 1981 situated in well developed dense *Corynephorion* vegetation (Fig. 2). The plot is subdivided into 936 subplots of 1 m² and for each square meter, covered at least for 10% by a mc type, the dominant mc type (e.g. 4, indicated as 4) or codominant mc types (e.g. 4 and 8, indicated as 48) or intermediate mc types (e.g. between 4 and 8, indicated as 48) were recorded. Dominant means coverage at least 50% of the total cover of the mc type(s) in the subplot. The dominance (or codominance) of vascular plants in the subplots was recorded as well on the same way. They include *Corynephorus canescens* (indicated as C), *Festuca filiformis* Pourr (F), *Agrostis vinealis* (A), *Calluna vulgaris* (Ca), *Rumex acetosella* (R) and *Carex arenaria* (Cx).

Subplots without dominance are indicated nd. Moreover subplots with dominance of sand and/or litter were indicates as sl.

The plot was cautiously recorded in 1981, 1984, 1987, 1991, 1994, 1997, 1999, 2002 and 2004, always in autumn during moist weather conditions. The field mapping takes three days.

Subplot dominance frequency (SDF) of mc types, combinations, vascular plants and combinations was calculated in % (total number of square meter subplots with dominance of a type or combination x 100, divided by 936; see Tab. 2 and 3). Subplot dominance of mc types and vascular plants was mapped as well (Fig. 6).

Moreover subplot dominance transition frequency (SDTF) of subplots between all 8 subsequent pairs of years (1981-1984, 1984-1987, 1987-1991, 1991-1994, 1994-1997, 1997-1999, 1999-2002, 2002-2004) was calculated as well. This value expresses the rate of change (in percentage) of a mc type or vascular plant type into another type. If a subplot with codominance of two mc types, e.g. mc 1 and mc 4 (indicated as 14), in the next recording year is codominated by e.g. mc type 5 and mc type 8 (indicated as 58) 4 possible combinations (1 to 5, 1 to 8, 4 to 5, 4 to 8; indicated as 15, 18, 45, 48) were taken into the calculation; and so on. Thus SDTF= $(x/y) \ge 100$, x = sum of transitions of a mc type into another, y = sum of all transitions of this mc type. The average SDTF (ASDTF) of the mc types and vascular plant species is based on the sum of the 8 values divided by 8 and is presented in Fig. 7. The ASDTF enables the interpretation of the changes in terms of succession.

Plot similarity (Barkman, 1958) between pair of years was calculated on the basis of the SDF values of all mc types and vascular plant species. Mc types and vascular plant species occurring only 5 times during the whole recording period have been omitted from the tables. Correlations between of mc types and vascular plants were calculated after Cole (1949). For the methodology of soil analyses the reader is referred to Minarski (2005).

This recording approach allows a rather quick, but solid analysis of the vegetation structure of such an extensive, dry grassland stand rich in lichens without disturbing the vulnerable lichens too much. Moreover, due to the size of the plot with 936 subplots, it enables a generalisation of vascular plant and mc dominance transitions, which can be interpreted with some reservation in terms of succession.

Nomenclature of syntaxa follows Pott (1995), lichens Wirth (1995), bryophytes Frahm & Frey (1987) and vascular plants Wisskirchen & Haeupler (1998).

RESULTS

In 1981 the densely vegetated plot was mainly dominated by the *Cladonia glauca* – *Trapeliopsis granulosa* mc type (5), the *Cladonia glauca* mc type with reindeer lichens (6) and the *Cladonia portentosa* mc type (8) and the grasses *Corynephorus canescens* (C) and *Festuca filiformis* (F). They have the highest SDF values. The *Campylopus introflexus* mc type (4) was dominant in one subplot only (Tab. 2). In 1991 half of the plot

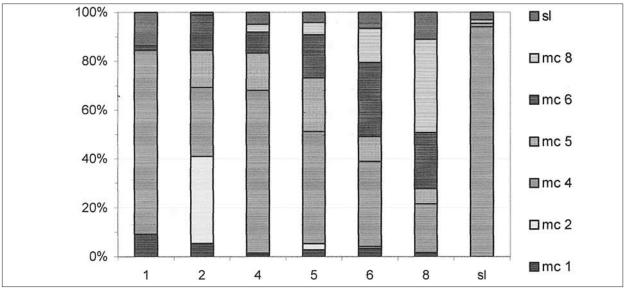


Fig. 7. Average subplot dominance transition frequency of the mc types. For explanation see text.

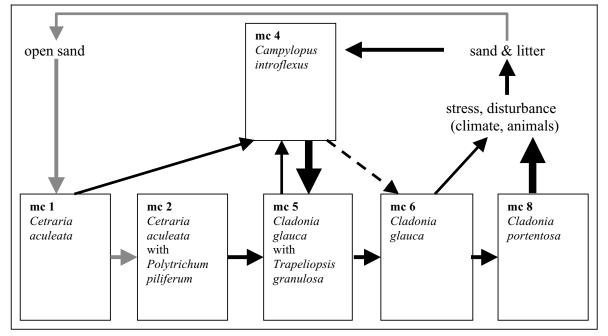


Fig. 8. Succession scheme of the mc types of the plot in relation to stress and disturbance events.

was dominated by the *Campylopus introflexus* mc type (4). Mc types 1 and 14 were represented as well, just as sand/litter subplots with a high SDF value of 26%. In 1994 nearly the entire plot was dominated by the *Campylopus introflexus* mc type (4) and

Corynephorus canescens (Tab. 2 and 3, Fig. 6). In 1994 almost all initial mc types from 1981 had disappeared. From 1994 onwards we observe again a certain development towards the situation of 1981. The SDF of the *Campylopus introflexus* mc type (4) continuously decreased (from 92, via 39 and 29 to 12), while the oldest moss carpets are getting overgrown by lichens of the mc types 5, 6 and 8. In general codominant mc types of mc type 4 with mc types 5, 6 and 8 became more common. We might speak of a "relichenisation" of the plot after a period of "bryophytification". SDF of *Festuca filiformis* increases, however *Corynephorus canescens* is still the dominant grass species in 2004. Plot similarity between the years 1981/1991, 1991/1994, 1994/1999,

1999/2002, and 2002/2004 calculated with the mc types gradually increases from 0,024 to 0,193 (Tab. 2) and calculated with the vascular plants as well (Tab.3).

The subplot dominance distribution pattern of the mc and the vascular plant types in the plot over the last part of the monitoring period are depicted in Fig. 6. This figure also shows the diversification of the plot pattern during the first years of the monitoring.

year		1981		1991		1994	199		200		200	
	absol.	%	absol.	%	absol.	%	absol.	%	absol.	%	absol.	%
mc												
1	•		123	13,1	•			•	•			
14	:	. :	60	6,4	•	•		•	•	•	•	
25	6	0,6										
4	1	0,1	446	47,6	868	92,7	365	39,0	272	29,1	115	12,3
45	•	•	9	1,0	•	•	301	32,2	39	4,2	105	11,2
456	•	•	1	0,1	•	•	58	6,2	46	4,9	92	9,8
458 451	•	•	•	-	•	•	11	1,2	20 12	2,1	36	3,8
	•	•	•	•	•	•	•	•		1,3	•	
45s 45sl	•	•	•	•	•	•	•	•	7 9	0,7 1,0	•	
4551	•	· ·	•	•	•	•	•	•	9 15	1,0	•	-
401 46s	•	•	•	•	•	•	•	•	15	1,0	•	•
40s 46sl	•	•	•	•	•	•	•	•	17	1,0	•	•
481	•	•	•	•	•	•	•	•	6	0,6	•	
40	•	•	•	•	•	•	•	•	40	4,3	•	•
4s	•		•	•	•	•	•	•	23	2,5	•	
4sl			•	•	•	•	•	•	70	7,5		
46	•		18	1,9	•	•	128	13,7	111	11,9	247	26,4
468				1,0			26	2,8	6	0,6	34	3,6
48			4	0,4	11	1,2	19	2,0	46	4,9	100	10,7
5	341	36,4	1	0,1		• ,	7	0,7		.,-	1	0,1
56	52	5,6					9	1,0	12	1,3	32	3,4
568	2	0,2					3	0,3	5	0,5		· ·
58									3	0,3	32	3,4
6	180	19,2	16	1,7			6	0,6	5	0,5	24	2,6
6s									8	0,9		
6sl	•			-		-			6	0,6		
68	54	5,8	3	0,3	•		2	0,2	20	2,1	39	4,2
68s			•		•				6	0,6	· _	
8	268	28,6	1	0,1	19	2,0	1	0,1	42	4,5	53	5,7
8s			•	-	•	-	•	•	20	2,1		
8sl	•		•	•	•	•	· ·	•	2	0,2	15	1,6
s	•	·						•	10	1,1	:	
sl			244	26,1	38	4,1		•	13	1,4	4	0,4
nd	27	2,9	•	•		•					· ·	
imilarity 981 with				0,024		0,022		0,030		0,097		0,193

Tab. 2. SDF values of the mc types and combinations, which occur in at least 6 subplots during the entire period of recording (1981-2004). For the explanation of similarity see text.

The dominancy history of the subplots can be derived from the ASDTF values, based on the SDTF of the mc types (Fig. 7 and 8). It shows that subplots with sand/litter (sl) are almost always changed in subplots with dominance of the mc type 4, the Campylopus introflexus mc type. Mc type 1, the Cetraria aculeata type, mainly develops into this mc type as well. Mc type 2, the Cetraria aculeata type with Polytrichum piliferum, preponderantly develops into mc types 4, 5 and 6. The ASDTF value of the Campylopus introflexus type (4) is rather low. Most of the subplots (>60%) did not change at all. If they did, they developed into mc types 6 and 8, and in a lesser degree into mc type 5. ASDTF of mc type 6, with surface and volume lichens, is rather high (over 60 %). This mc type mostly changes into mc types 4, 5, 8 and sl. The Cladonia portentosa mc type (8) is more constant, however over 50 % of the subplots changed into dominances of mc types 4 and 6, and sl.

DISCUSSION

As said before in 1981 the densely vegetated plot was mainly dominated by the Cladonia glauca - Trapeliopsis granulosa mc type (5), the Cladonia glauca mc type with reindeer lichens (6) and the Cladonia portentosa mc type (8) and the grasses Corynephorus canescens (C) and Festuca filiformis (C). The subplot dominance of Corynephorus canescens appeared positively correlated with the subplot dominance of mc type 5, whereas the subplot dominance of Festuca filiformis was correlated with those of mc types 6 and 8. The Campylopus introflexus mc type (4) was dominant in one subplot only. During 1981-1984 the number of subplots with dominance of mc types 6 and 8 increased, while that of mc type 5 decreased (Biermann & Daniëls, 1997). These changes are in line with known progressive succession features of the Spergulo-Corynephoretum (cf. Biermann & Daniëls, 1997; Hasse, 2005).

During 1984-1994 almost all initial mc types from 1981 disappeared and in 1994 the entire plot was almost completely dominated by the *Campylopus in*- troflexus mc type (4) and Corynephorus canescens. In the beginning of this period (1985, 1986 and 1987) some winter months appeared to be very cold and dry (continental) (Fig. 3). These environmental conditions very likely have caused the dying off of Festuca filiformis, followed somewhat later by that of Cladonia portentosa mc type (8). Both are oceanic species with comparatively low indicator values for continentality ((2 for Festuca filiformis (Ellenberg et al. 2001), 3 for Cladonia portentosa (Bültmann 2006)), as can derived from Tab. 4. However the disappearance of Cladonia portentosa might also be influenced by the disappearance of Festuca filiformis, the main micro habitat of the Cladonia portentosa mc type (8). Additionally grazing increased (Fig. 2). This all resulted in a strong increase of non-vegetated surfaces with bare sand and litter, indicated in 1991 by the relatively high SDF value (26) for sand and litter (sl) and for the open mc types 1 and 14 (together almost 20). These subplots were easily occupied by the highly invasive neophytic moss Campylopus introflexus with its highly effective vegetative and generative propagation strategy. This moss (mc type 4) covered nearly the whole plot in 1994 (cf. Fig. 6, also Biermann & Daniëls, 2001).

We consider the period after 1994 as a period of moderate environmental stability allowing a progressive succession process with an obvious increase of reindeer lichens and their mc types. The influence of the game density on changes in the period 1994-2004 is difficult to assess, since the game density figures concern the entire National Park (Fig. 5). And detailed information about the plot area does not exist. However game density clearly decreased from 1994-2000, but increased again since 2001. Nevertheless increased impact of grazing and trampling in the monitoring plot during the last 10 years could not be observed. Mean annual precipitation and temperature gradually increased (Fig. 4), but no extreme events in terms of very cold and dry winters as in the eighties occurred during this time.

The mean subplot dominance transition fre-

year	198	31	199	91	199	94	199	99	200)2	20
	absol.	%	absol.	%	absol.	%	absol.	%	absol.	%	absol.
C	377	40,3	340	36,3	856	91,5	843	90,1	477	51,0	658
CF	191	20,4	16	1,7	34	3,6	37	4,0	269	28,7	162
CCa	.								1	0,1	6
F	352	37,6	59	6,3	2	0,2	26	2,8	86	9,2	17
Α	6	0,6	41	4,4	13	1,4	8	0,9	14	1,5	
AC			4	0,4	21	2,2	10	1,1	29	3,1	77
AF	1	0,1	10	1,1	4	0,4		0,1	24	2,6	1
ACF			1	0,1	6	0,6	11	1,2	31	3,3	11
nd	6	0,6	465	49,7							
similarity											
1981 with	1			0,724		0,816		0,917		2,439	

Tab. 3. SDF values of the vascular plant species and combinations, which occur in at least 6 subplots during the entire period of recording (1981-2004). For the explanation of similarity see text.

quencies of the mc types (Fig. 7 and 8) allows an interpretation in terms of microsuccession. The few subplots with dominance with the open mc types 1 and 2 develop either into mc type 4 (Campylopus introflexus) or 5 (Cladonia glauca, surface lichens). Under stable moderate environmental conditions mc type 5 is succeeded by mc type 8 (Cladonia portentosa) via mc type 6. This type is rather stable and might be considered as a final stadium of the microcommunity succession within a Corynephorion vegetation. When climatic stress and/or severe disturbance events occur the Cladonia portentosa mc type (8) dies off and on the resulting sand and litter surfaces Campylopus introflexus mc type (4) develops. The latter mc type is able to develop from all subplots in particular with mc type 5. The Campylopus introflexus mc type might

be succeeded again by the lichen mc types and finally by the *Cladonia portentosa* mc type (8) when environmental conditions keep rather stable. This succession might take at least 15-20 years.

The changes in the period 1999-2004 are in line with the model outlined by Biermann & Daniëls (1997, 2001).

Finally we might postulate that the long term presence of the invasive neophytic *Campylopus introflexus* in *Corynephorion* vegetation seems to be not that dramatic. Although the ecological role of this species is still insufficiently studied (Hasse & Daniëls, 2005; Hasse, 2007) we might state that the dominance of this species influences negatively the biodiversity of lichens and their microcommunities

Ellenberg indicator values	Light	Temp.	Conti-	Moisture	pН	Ν
			nentality			
Corynephorus canescens	8	6	5	2	3	2
Festuca filiformis	7	6	2	4	3	2
Agrostis vinealis	9	7	3	2	2	1
Cladonia portentosa	7	6	3	3	Х	2
Cladonia macilenta	7/8	х	6	3	2/3	2
Campylopus introflexus	8	6	3	2	2	
Polytrichum piliferum	9	Х	5	2	2	

Tab. 4. Ellenberg indicator values for several species derived from Ellenberg et al. (2001). Those for the lichens are by Bültmann (2006).

only locally and temporarily.

CONCLUDING REMARKS

The results of this monitoring study show that the mc type composition of the *Corynephorion* plot keeps rather stable over at least 25 years, however their dominance expression and distribution varies considerable due to stress and disturbance events. A three years experimental study of small plots in *Spergulo-Corynephoretum* vegetation by Hasse & Daniëls (2006) showed that species composition was constant, however species quantities were influenced by the application of moisture, litter, N-enrichment and disturbance. Our studies show that the *Corynephorion* vegetation of the National Park "De Hoge Veluwe" is a rather stable plant community complex without signs of succession towards heath- or woodland. However internal dynamics can be rather high.

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