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Some Long-Term Observations on Cyclical and Seral Processes in Dutch Heathlands

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ABSTRACT

Changes over a period of 10–30 years in the vegetation of some Dutch heathlands were studied, using aerial photographs and information derived from observations and permanent plots. The sites studied are situated in (formerly) Calluna vulgaris*-dominated heathlands, known to be infested in the past by the heather beetle* Lochmaea suturalis, *Thoms., followed by a* Calluna *die-off. No interference by management practices had interrupted the natural changes in the vegetation following the infestation. Evidence for both seral and cyclical changes is presented. It is concluded that abiotic factors, i.e. physiographically controlled minor differences in the soil type, determine whether a cyclical or seral change will occur.*

INTRODUCTION

Most of the ericaceous vegetation in Europe is situated in man-made heathlands. These heathlands are maintained by management practices, such as burning, mowing or cutting sods, which remove the standing crop and in the last case also the organic matter accumulated in the A_0-horizon (Gimingham, 1972). These practices lead to the development of even-aged

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stands. It is appropriate, then, to refer to the 'regeneration of stands' (Miles, 1979).

Ericaceous vegetation also occurs where tree growth is prevented by environmental conditions, and may then be regarded as 'climax' (Gimingham, 1972). Attention has been drawn (Watt, 1947) to the occurrence of cyclical processes in such vegetation, where the regeneration of *Calluna* in a particular patch may be delayed by a temporary colonization of *Arctostaphylos uva-ursi*, although in time it is again occupied by *Calluna*.

There is evidence, however, that cyclical processes may also occur in man-made heathlands when management practices are infrequent or have been abandoned, and colonization by trees is for any reason slow or absent. Watt (1955) describes cyclical change in heathlands, where *Pteridium aquilinum* temporarily replaces *Calluna* on blown sand overlying a podzol. Evidence from uneven-aged stands of *Calluna* in Dutch heathlands on stabilized drifting sands, on podzolic soils, and on brown podzol soils also suggests cyclical changes including stages with mosses, *Deschampsia flexuosa* or *Molinia caerulea*, respectively (Stoutjesdijk, 1959). Mosses, *Empetrum nigrum*, *Vaccinium myrtillus* and *V. vitis-idaea* have been described as part of a cycle on a shallow peat overlying glacial till (Barclay-Estrup & Gimingham, 1969). The evidence for cyclical changes, however, is scant as so far it is derived from spatial patterns coinciding with different growth phases of *Calluna*, e.g. as described by Watt (1955). 'Temporal patterns' resulting from long-term observations covering the lifespan of one or more cycles are needed to provide direct proof. In this paper data are presented on changes over a period of 10–30 years in three (formerly) *Calluna*-dominated heathlands in The Netherlands following infestation by the heather beetle *Lochmaea suturalis*. Nomenclature follows Tutin *et al.* (1964–1980).

METHODS

In 1976 we looked for sites in (formerly) *Calluna*-dominated heathlands, known to have been infested in the past by *Lochmaea*, followed by a *Calluna* die-off, and where no interference by management practices had interrupted the natural changes in the vegetation following the infestation. Few were found and three sites were selected on the basis of

their rather different vegetation development after infestation by the heather beetle:

1. Kampina (province Noord-Brabant). According to the local manager the site was infested by the heather beetle in about 1970. Prior to and after the infestation *Calluna* was, and has remained, the only vascular species.
2. Kootwijk (province Gelderland). According to the local manager the heathland at the site was *Calluna*-dominated vegetation with some *Erica tetralix* and *Molinia caerulea* about 40 years ago. After infestation by the heather beetle the vegetation changed to a grass heath of mainly *Molinia caerulea*.
3. Hoog Buurlo (province Gelderland). Nowadays this site is covered by a grass heath of *Deschampsia flexuosa*. In 1950 it was, according to Stoutjesdijk (1953) a *Calluna* heath rich in *Deschampsia flexuosa*. The site is known to have been infested by the heather beetle in 1970 and no management has been practised since.

Kootwijk and Hoog Buurlo were fenced to prevent grazing by sheep, red deer and rabbits in 1976. Descriptions of the soil profiles (in sand) of the sites are given in Table 1. The preglacial deposits in Hoog Buurlo, however, contain slightly more silt than the Pleistocene eolian deposits of the other sites.

TABLE 1

Characteristics of the Soil of the Study Sites in Hoog Buurlo, Kootwijk and Kampina

Site:	*Hoog Buurlo*		*Kootwijk*		*Kampina*	
Classification:	*Haplotord*		*Haploquod*		*Haploquod*	
	Soil profile layer	*Depth (cm)*	*Soil profile layer*	*Depth (cm)*	*Soil profile layer*	*Depth (cm)*
	A_0	+3-0	A_0	+8-0	A_0	+3-0
	A_{11}	0-20	A_1	0-7	A_1	0-8
	A_{12}	20-36	A_2	7-20	A_2	8-14
	A_2	36-58	B_2h	20-32	B_2h	14-20
	B_3	58-70	B_2ir	32-37	B_2ir	present
	C	70-120	C	37-120	C	20-120

TABLE 2
Dominant Species (% canopy cover) in Three Dutch Heathlands Before Infestation of the Heather Beetle in 1970 (Kampina), 1952 (Kootwijk) and 1970 (Hoog Buurlo) and the Dominant Species in 1982

		Calluna vulgaris	Molinia caerulea	Deschampsia flexuosa
Kampina	1970	100	0	0
	1982	20	0	0
Kootwijk	1952	80	10	?
	1982	0	90	10
Hoog Buurlo	1970	80	0	40
	1982	0	0	100

Black and white aerial photographs scale 1:20 000 (obtained from the Topographic Service in The Netherlands) were used to determine the year of infestation by the heather beetle for Kampina and Kootwijk.

RESULTS

Table 2 summarizes the percentage canopy cover of the dominant species present in the study sites, prior to the infestation by the heather beetle, and the dominant species 10–30 years later, in 1982. Percentage canopy cover is estimated to the nearest 10%. The year of infestation mentioned in Table 2 is known exactly in the case of Hoog Buurlo (1970). Aerial photographs from the Kootwijk site taken in 1951 show that the site was covered with *Calluna*, but imagery from 1960 reveals a grass heath. The year of infestation in Kootwijk must have been 1951 or 1952. The year of infestation in the Kampina site (1970) could be confirmed by counting annual rings of *Calluna* stems that had regenerated since the massive die-off.

Table 2 shows that in 1982 in Kampina *Calluna* is still the dominant species: no other vascular plant species has invaded the site and in 1982, about 10 years after infestation and die-off of *Calluna*, most of the site is still bare soil. Apart from vegetative regrowth, from 1980 onwards we observed seedlings of *Calluna* in places where the mineral soil was not covered by litter (A_0-horizon). In Hoog Buurlo all the *Calluna* has been replaced by grasses after the infestation; some *Potentilla erecta* and *Galium hercynicum* also occurred. Remnants of *Calluna* stems were found in the *Deschampsia* turf. In the absence of grazing, *Deschampsia* forms

tussocks. From 1981 onwards a gradual die-off of *Deschampsia* has been observed, starting at the fringes of the tussocks. No die-off of *Deschampsia* has so far been observed outside the fenced site.

DISCUSSION

Cyclical changes in vegetation types are special cases of a process of regeneration (Miles, 1979). A cyclical change is by definition (Gimingham, 1972) limited to changes induced and governed by (natural) events in the vegetation. The definition includes changes in *Calluna* dominated heathlands brought about by the heather beetle, even though these changes occur in large even-aged stands which result from former management. *Molinia* and *Deschampsia* now dominant in Kootwijk and Hoog Buurlo respectively were already present before infestation by the beetle. The fact that no new species have yet entered the vegetation has sometimes been used as a criterion for deciding whether the change involved is seral or cyclical (Gimingham, 1972). Using this criterion the grass heath in Kootwijk and Hoog Buurlo can be part of a cyclical change. The presence of a monoculture of *Calluna* in Kampina, the presence of *Calluna* and *Molinia* in Kootwijk, and *Calluna* and *Deschampsia* in Hoog Buurlo may be related to edaphic differences. We found a brown forest soil under the *Deschampsia* grass heath in Hoog Buurlo and a podsol in the *Molinia* grass heath; the latter soil type is also found in the pure *Calluna* vegetation in Kampina. Co-occurrence of pure *Calluna* heath and *Calluna-Molinia* heath on the same soil type is a regular feature of Dutch heathlands. The differences seem related to physiographically controlled differences in water relations at various sites in the landscape: the *Calluna-Molinia* vegetation is confined to flat areas and depressions, while the *Calluna* type is found on sloping land.

A single application of nitrogen stimulates *Calluna*, thereby hastening the development of the typical vegetation (Helsper *et al.*, 1983). Heil & Diemont (1983) found, in a fertilizing experiment, that four years' application of an equivalent of about 28 kg N ha^{-1} $year^{-1}$ turned a *Calluna*-dominated heathland into a grass heath of *Festuca ovina*. The amount of nitrogen from dead plant material in a *Calluna* stand after die-off due to the heather beetle was calculated to be of the same magnitude. It was therefore suggested that the mineralization of nitrogen after die-off of *Calluna* may be the reason why grasses take over as the dominant species.

Data from the pure *Calluna* stand in Kampina show however that grasses do not take over in every case after *Calluna* has died. The reason for this is not clear but there might be lack of viable seed in pure *Calluna* stands (see Table 2), since there is no grass within a radius of 50 m and seeds of these heathland grasses have shown a very limited dispersal capability (own unpublished results; J. M. M. Berdowski & R. Zeilinga, pers. comm.). However, the occurrence of seedlings of *Calluna* in the Kampina site in places where litter is absent suggests that here a natural regeneration of *Calluna* takes place. The process is probably cyclical in the sense of Gimingham (1972), as we also observed *Cladonia* species in places where litter was still present.

In the *Deschampsia* grass heath of Hoog Buurlo Stoutjesdijk (1959) found in 1952: (1) degenerating *Calluna* plants, and considerable amounts of *Cladonia* species; (2) places where *Deschampsia flexuosa* entered gaps in a degenerating *Calluna* plant by vegetative propagation; (3) *Deschampsia* in closed mats with remnants of *Calluna* present; and (4) places where *Deschampsia* had decayed and *Calluna* seedlings were present. From these observations he concluded that there was a cyclical process. At this site information from local managers and remnants of *Calluna* found in the turf in 1976 allowed us to presume that stages 1 and 2 were present. Stage 3 described by Stoutjesdijk was identified in 1976 and in 1981 the *Deschampsia* started to decay (stage 4). No *Calluna* has yet been found. However, decay of *Deschampsia* grass heath was observed all over the country in 1981 in places where the grass was not grazed by sheep, red deer or rabbits. Management of the grazing regime, even in the absence of reseeding, can cause far-reaching changes in botanical composition. *Calluna* heath can be converted to grass heath by grazing and the reverse process can take place after protection from grazing (Jones, 1967; Gimingham, 1972). However, grazing by sheep, red deer or rabbits is not the cause of the changes described in this paper. The Hoog Buurlo and Kootwijk sites are fenced and have remained as grass heath; the Kampina site is not fenced and is still a *Calluna*-dominated heath.

Stoutjesdijk (1959) also suggested the possibility of a cyclical change with *Calluna* and *Molinia*. However, we have so far not observed any decay of the *Molinia* grass heath in the Kootwijk site.

For the time being we conclude that a natural regeneration in man-made heathland occurs in a pure *Calluna* heath as shown in our Kampina site. Though *Cladonia* species suggest a cyclical change, the regeneration seems a very slow process. Future observations may confirm a cyclical

change in Hoog Buurlo and Kootwijk. If this occurs we think that such an expected change of *Deschampsia* grass heath into a *Calluna*-dominated vegetation will require at least 15 years and in the case of a *Molinia* grass heath more than 25 years. The discussion whether a grass heath is a stage of a cyclical or seral change is of theoretical interest only. As far as heathland management is concerned it has been demonstrated (Diemont *et al.*, 1982) that removal of the grasses including the sod brings back a *Calluna*- or *Erica*-dominated heath within two years. Part of the grass heath areas now found in The Netherlands which were also covered by *Calluna* or *Erica* are now being regenerated by this management practice. However, the observations in Hoog Buurlo and Kootwijk will be continued to check the hypothesis whether (in the absence of colonization by trees) the grass heath of *Deschampsia* or *Molinia* is part of a special case of natural regeneration, i.e. a cyclic succession.

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