SURVIVAL
OF DUTCH
HEATHLANDS

W.H. DIEMONT

FATHER

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CONTENTS

I. INTRODUCTION

History of heathlands

Around 1800, at the time of their maximum extent, heathlands in The Netherlands covered 800,000 ha (fig. 1.1). These heathlands had previously been forests, but probably also developed from mined spagnum peats, which still covered extensive parts of The Netherlands about 1200 years before present (Van der Ven 1993).
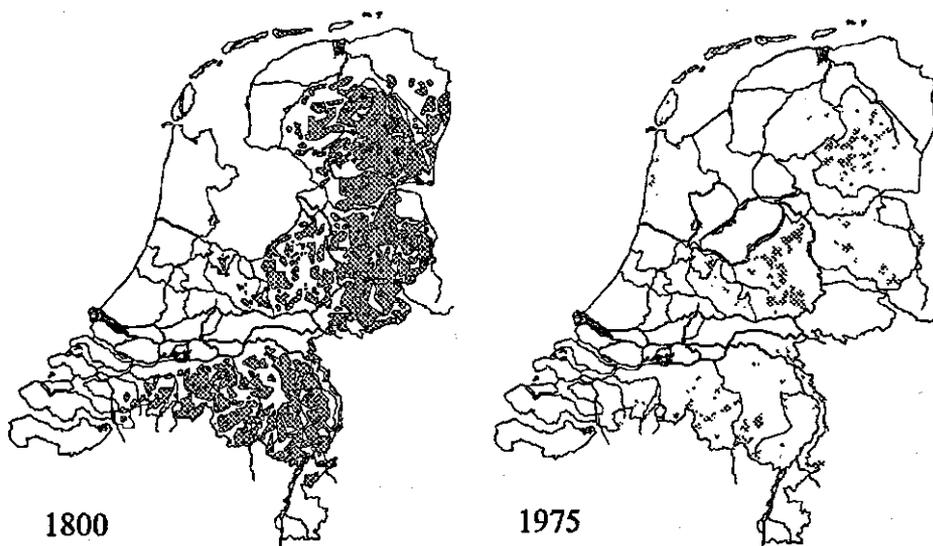

1800

1975

Figure 1.1
Heathlands in The Netherlands in 1800 and in 1975. The map of 1800 is based on Otto (1963); the 1975 map is derived from topographical maps.

Heathlands were used for sheep grazing and collecting *plaggen* (sods, turfs) i.e. heather and the raw humus layer near the surface of the soil. The *plaggen* (and sand) were spread on the floor of the sheds in which livestock were kept at night, and this absorbed the manure. The mixture of manure and *plaggen* fermented in the sheds and after several months was removed, reworked outside the shed and spread on the arable land. Over time, this turf manuring raised the level of the fields, because of the accumulation of the mineral components of the manure.

There are 410,000 ha of these raised arable lands (*Plaggen* soils) in The Netherlands, with an anthropogenic top layer of 40 to 80 cm thick. About 300,000 ha of *plaggen* soils were artificially raised by sands from *plaggen* derived from heathlands as indicated by the black anthropogenic layer, whereas the brownish material in other *plaggen* soils indicates that they originated from *plaggen* from

grasslands (Pape 1970, Diemont et al. 1982).

Historical sources and 14C datings suggest that the use of *plaggen* was already known in the 11th century, but only became widespread in the economic center of the country in the province of Brabant in the 13th century, whereas in the economically peripheral province of Drenthe, turf only became common practice in the 16th and 17th centuries. At that time numbers of sheep flocks were increasing enormously as a result of higher wool prices (Bieleman 1987, Spek 1992, Van Smeerdijk et al. in press).

In 1800 the ratio of area of heathlands (800,000 ha) to area of *Plaggen* soils (300,000 ha) was about 3 to 1, which implies that the heathland was being subjected to intense pressure to provide sufficient *plaggen* manure in the fields. A modest dressing of 20 ton/ha/year (sands not included) is equivalent to the amount of organic matter (biomass and raw humus), which accumulates in heathlands over a period of 10 years (Diemont et al. 1982, Berendse 1990). This implies that about 10 ha of heathlands are needed to secure the manure for 1 ha of arable land. this favourable ratio was indeed found in Drenthe, whereas a ratio of 3 to 1 found in Brabant in the early nineteenth century could only be sustained by intensifying agricultural practices (Gimingham & de Smidt 1983). Fortunately, in Brabant additional sources of manure were available and could be bought by farmers. At that time the province was a centre of economic activity, and night soil from the cities, waste from breweries and wood ash were for sale.

Overexploitation of heathlands eventually led to the widespread formation of drift sands. After 1850 the quality of the *plaggen* manure also became very poor as a result of the high sand content (Salfeld 1890), and yields of rye fell in all heathland areas between 1860 and 1875 (Bieleman 1987; graph 6.15), for reasons which must include the increasing shortage of manure.

After 1800, long before the introduction of chemical fertilizers which occurred at the end of the nineteenth century, heathland was increasingly converted into arable land and forest plantations (table 1.1), intensifying the pressure on the remaining heathland. Over-exploitation of the heath in the nineteenth century is also reflected in the very short heathland shrubs at that time, as can be seen on old photographs. Since 1800, about 600,000 hectares have been converted into agricultural land and 150,000 hectares have been afforested.

Table 1.1

Areas of heathland in The Netherlands since 1800 and heathland invaded by trees (20 to 60% tree cover) in 1964 and 1983 (Anonymous 1988).

HEATHLAND HA (X 1000)		
	total area	invaded by trees
1800	800	
1833	600	
1907	450	
1940	100	
1964	60	15
1983	42	8

In 1964 only 60,000 hectares of heathland were left, including 15,000 ha of heathland invaded by trees (table 1.1). Conversion of heathlands to arable land was prohibited by law in the sixties, but by 1983 another 18,000 of heathland had changed into woodland (over 60 percent tree cover) (Anonymous 1988). At that time only 42,000 hectares of heathlands, including 8,000 ha of heath with a tree cover of 20 tot 60% were left (table 1.1).

Management of heathlands

The low intensity of management of heathlands in the first part of the 20th century is reflected in the increase of areas of spontaneous woodland at the expense of heathlands. Moreover, in Drenthe the overall sheep density (sheep/ha heathland) fell from 1.1 in 1875 to 0.05 in 1950. At that time only 10 flocks were left on heathlands in The netherlands. There are now 20 flocks present, but the grazing intensity in heathlands is still low (figure 1.2). Turf cutting in heathlands was already very rare before 1900, although in some heathlands small areas were still cut for fuel in and after the second world war. Turf cutting died out in the fifties. In 1978 mechanical turf cutting was introduced (Diemont et al. 1982). However, the area treated is less than 300 ha a year (Van Ommeren 1993), whereas some 1200 ha of heathland should be treated each year if a rotation period of 30 years is applied.
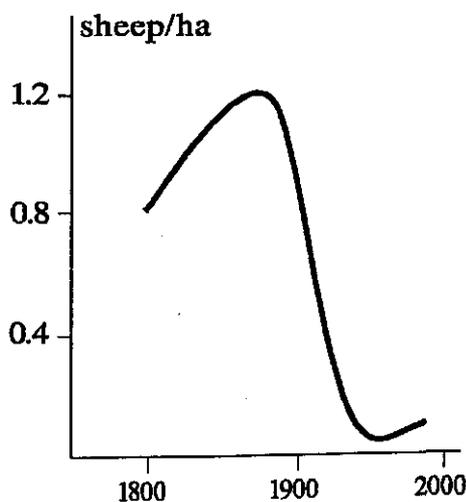
Figure 1.2.
Changes in overall density of sheep grazing in Dutch heathlands. Sources: Verduin 1972 and Diemont unpublished.

The change of heathland to woodland was studied by the 'Studiekring voor de Veluwe" working group in the fifties. In a report titled `Is there still a future for our heathlands ?' it was concluded that there was an urgent need for management i.e. prescribed fire and grazing in heathland so as to avoid further encroachment by forest. However, management by turf cutting was not advised, because the risk of

nutrient depletion was considered too high (Anonymous 1953). In 1978 another problem, the grassing over of heathlands was addressed by the working group "Verwerking en Afzet voor Heideplaggen". In their report the working group suggested in their report that lack of management and also atmospheric pollution and lowering of the water table encourage grasses to take over in Dutch heathlands. Their conclusion was that (mechanical) turf cutting is the most appropriate method to restore a grass heath to a *Calluna* heathland (Diemont et al. 1982). In 1983 ongoing heathland research and management in The Netherlands was evaluated by heathland ecologists from Britain. This party confirmed the rapid and successful establishment of dwarf shrubs from seeds in grass heath, but suggested that 'the effects of *plaggen* to be purely physical and did not need to be attributed to the removal of nutrients contained in the organic matter' (Gimingham et al. 1987). However, basic ecological information on competition between the main contenders for dominance in Dutch heathlands i.e. *Calluna vulgaris* and *Erica tetralix* versus *Deschampsia flexuosa* and *Molinia caerulea* was suggested a worthwhile topic for research in future (Gimingham et al. 1987; see also Gimingham 1987). In 1988 in their report "There is a future for heathlands!", a working group "Heidebehoud en Heidebeheer" of the Ministry of Agriculture, Nature Management and Fisheries confirmed turf cutting to be an effective method to achieve a return to heathlands dominated by dwarf shrubs. Increased nutrient levels, in heathlands, particularly heavier nitrogen inputs through atmospheric pollution, were identified as a risk factor, which for the time being necessitates intensified heathland management (Anonymous 1988).

Mechanisms of heathland succession

Whether the success of the restoration of grassy heath to pure heath by turf cutting can also be explained in physical terms rather than in terms of nutrients has become a matter of scientific investigation in The Netherlands. Fertilizer experiments do indicate that repeated dressings of only 15kg N/ha/year are sufficient to transform a *Calluna* heath (Heil & Diemont 1983) and *Erica* heath (Aerts & Berendse 1988) to a grass heath, although in the case of *Erica*, dressings were applied at a time that atmospheric nutrient deposition had already increased in The Netherlands. So, there is evidence that nutrient levels, in particular N levels, are important. Higher levels of the critical element N in a heathland can be expected from atmospheric pollution. At present, N deposition in The Netherlands ranges from 20 to over 80 kg N/ha/year (Erisman 1992). However, at low levels of nitrogen input any heathland also shows an increase in nitrogen mineralisation over time as a result of organic matter accumulation. Annual levels of nitrogen mineralisation can be up to 130 kg/ha/year in old heath (Berendse 1990). The vegetation changes resulting from changes in nutrient level is assumed to be triggered by changes in the competitive ability of species. Compared to *Calluna* or *Erica* the growth rates of grasses increase much more strongly at higher nutrient levels, whereas at low nutrient levels the dwarf-shrub species are more competitive. The greater competitive ability of heath species at low nutrient levels might be due to their better

ability to conserve nutrients, which is an advantage in nutrient poor environments. However, there appears to be a trade off between nutrient conservation and the ability of a plant species to respond effectively to enhanced nutrient levels (Berendse & Elberse 1990). An explanation for this trade-off might be that N conservation implies a low leaf turnover, whereas plant properties responsible for high growth rates (such as a large specific leaf area), frequently lead to increased leaf turnover rates (Aerts 1990). Although the role of nutrients is important, most studies focus on N and neglect the role of, for instance, P. Moreover, apart from the effect of nutrient levels on competition, other factors such as the shorter life span of heath species such as *Calluna* under higher nutrient levels, have not yet received attention. Nutrients seem to be only part of the explanation of vegetation changes in heathlands. These changes always coincide with perturbations such as management interventions, frost (Berendse et al. 1994), and infestation of *Calluna* by the heather beetle (Berdowski 1987).

Aim of the present study

The focus in the present study is on elucidating the effects of management, soils and to some extent climate on vegetation in heathlands, with the aim to provide improved guidelines for management of Dutch heathlands.

Five hypotheses are advanced and tested. The first hypothesis is that changes from *Calluna* heath to grass heath are part of succession, which can only be reversed by management interventions. A second hypothesis in this thesis is that the critical prerequisite for successful management interventions to restore a *Calluna* heath is for the soil under the grass to be exposed, to allow *Calluna* seed in the seed bank to germinate. The third hypothesis is that, furthermore, nutrient depletion by turf cutting prolongs the life span of *Calluna* and therefore also extends the necessary management rotation period of a heath. When examining this hypothesis I also provide evidence that on podzol soils P limits growth of heather or grasses, whereas on brown podzolic soils N is the growth-limiting factor.

Previous studies suggest that prescribed burning does not deplete nutrients as much as turf cutting, but the actual nutrient losses after a fire have not yet been studied. The fourth hypothesis is that burning does not deplete plant nutrients as much as turf cutting and, furthermore I postulate that the difference in nutrient removal between controlled burning and turf cutting is reflected the productivity of *Calluna* heath, which as suggested above, also affects the life span of *Calluna*.

Finally I provide evidence that turf cutting was not only an economic necessity in the past, but is ecologically necessary today if *Calluna* is to survive in Dutch heathlands.

Outline of this thesis

In chapter 2 the evidence for the increase of grasses in Dutch heathlands is given. The success of various management interventions in grass heaths is explained in terms of their ability to expose the soil under the turf (chapter 3). The effect of

opening up the grass turf on germination of *Calluna* is dealt with in chapter 4. In chapter 5 the negative effect of higher nutrient levels in a heathland on the life span of a *Calluna* heathland is explained and the importance of P as a growth limiting factor is assessed. In chapter 6 the results of prescribed burning experiments on nutrient levels are presented. The effects of management on the productivity of *Calluna* are assessed in chapter 7. The need for turf cutting in Dutch heathlands is discussed in chapter 8 and the overall results and implications of the present study for heathland management are presented in the summary.

2. CHANGES IN DUTCH HEATHLANDS

Summary

Information from sequential aerial photography studies in six Dutch heathland areas indicates that grass heath area has increased in recent decades. Some of these heathlands now have a grass cover of over 80 %. Information from both aerial photographs and permanent plots on the ground indicate that these grasses are a phase in succession from heathland to woodland and not part of a cyclical change. Results are, however, not representative of regularly managed heathlands in The Netherlands.

Introduction

Heathlands are considered one of the cultural landscapes in Europe and conservation of heathlands has become a major issue.

Areas of lowland heathland (Webb & Haskins 1980) have been diminished, which is mainly due to afforestation and agricultural reclamation all over Europe (de Smidt 1979; Webb & Haskins 1978; Veitch et al. 1995). In many cases heathlands dominated by *Calluna vulgaris* (L.) Hull may, in the absence of periodic management, also change i.e. develop into woodland (Marrs et al. 1986).

Succession to woodland may pass a stage where grasses such as Molinia caerulea (L.) Moench or *Deschampsia flexuosa* (L.) Trin. are dominant (Diemont & Heil 1984; Berdowski & Zeilinga 1987). Such grass dominated heathlands may, however, also be considered as a phase in a cyclical process, *Calluna* taking over again spontaneously after some time (Stoutjesdijk 1959; Diemont & Heil 1984; Linneman 1994).

In this paper hypotheses being tested are (1) is *Calluna* heathland stable in the long term, (2) are grasses becoming dominant in Dutch heathlands at the expense of *Calluna* and (3) if grass is becoming dominant is this part of a cyclical or directional succession.

The heathlands selected in this study were included because these heathlands were suspected to be subject to change. Thus, the conclusions of this study may not necessarily apply to all heathlands in The Netherlands. The information on vegetation changes in heathlands was obtained from sequential aerial photography as well as from long-term field observations in permanent plots.

Methods

STUDY AREA

Aerial photographs were available with more or less regular intervals, since 1935 (table 2.1). Heathland sites studied are indicated in figure 2.1. All sites are

lowland heathlands on mineral soil, where there are factors which arrest the natural succession to woodland (Webb & Haskins 1980). The heath vegetation in these heathlands was classified as a Genisto anglicae-Callunetum R. Tüxen 1937, but patches with *Erica tetralix* (L.) may occur (de Smidt 1977). Soils include Haploquods and Haplohumods (Soil Survey Staff 1975).

Table 2.1
Aerial photographs (scale 1:25,000) used in this study. The 1989 data are obtained by satellite imagery.

SITE	DWINGELOO	HOGE VELUWE	HOOG BUURLO	KAMPINA	LEMELERBERG	MEIJNWEG
1935	+			+		
1937		+				
1938			+			
1948				+		
1950	+	+	+		+	+
1954		+				
1955						+
1960				+		
1962	+					
1963		+			+	
1970				+		
1972	+					
1973		+	+		+	
1975						+
1978	+					
1980				+		
1981		+			+	
1989	+					
1992		+				

DATA COLLECTION

Photo interpretations of heathland vegetation were available for Hoog Buurlo (Dijkhuizen et al. 1976), part of the National Park de Hoge Veluwe, Dwingeloo, Kampina, Meijnweg (Diemont et al. 1982; Tol et al. 1993) and Lemelerberg (van Heusden 1982). Surfaces were geometrically corrected and these rectified surfaces were quantified on a ha base. Additional data for the Dwingeloo heathland were available for 1989 from satellite imagery (Moen 1992).

Field checks showed a high reliability of the distinction between dwarf-shrub heath (dwarf-shrub cover > 50 %) and grass heath (grass cover > 50 %). A

check by Kampina (1980) showed that the reliability (from 30 points) of the distinction between these types was nearly 100 %. Surfaces of open water and *Myrica gale* shrubs were, however, also interpreted as dwarf-shrub heath in some cases and corrections were made to account for this. In Dwingeloo (1978) 90 % of all grass heath and heath mapped in the field corresponded with the aerial photo interpretation. In most heathlands, variable surfaces of 'unidentified' area (drifting sands, arable land, clouds etc.) occurred. A field check of the satellite imagery showed that 90 percent of the satellite observations were in agreement with field observations (Moen 1990).
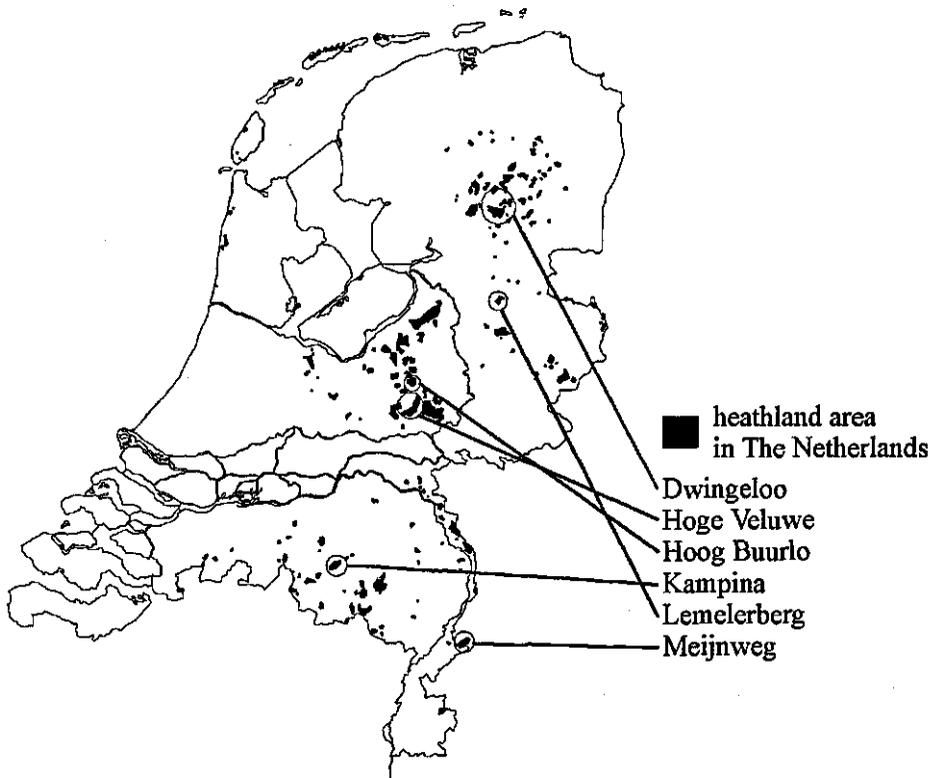
Figure 2.1
Location of six heathland study sites.

Changes in grass heath areas may have been masked by a transition from grass heath to woodland, which occurred in most sites, the exception being Hoog Buurlo. Transitions were assessed using a grid overlay (squares of 1.5 ha each) in the Hoge Veluwe area (1937-1973), Kampina, Dwingeloo (1935-1978), Lemelerberg (1950-1981) and Meijnweg (1950-1975).

On the ground changes in vegetation were monitored in permanent plots (20 by 20 m) at two sites in the Hoog Buurlo area. One site was a Molinia and the other

was a Deschampsia grass heath at the time of establishment in 1976 were established in 1976 (Diemont & Heil 1984). The sites were fenced to prevent rabbit and sheep grazing.

Results

AERIAL PHOTO INTERPRETATION STUDIES

The changes in the area of grass heath, heath and woodland at the six sites are in figure 2.2. In all heathlands except the area of Hoog Buurlo, woodland invades the open area. But, in Hoog Buurlo the surface of heath also decreased dramatically as a result of transition to grass, which had already started in the fifties. It should be noted that wood species invaded the area more recently (see permanent plot section). In Dwingeloo, Hoge Veluwe, Kampina, and Lemelerberg this increase started after 1960.

No increase of grasses was detected in the Meijnweg area. Here, however, an increase in grasses did occur, but this transition was masked by a transition from grasses to woodland during the period of observation (table 2.2). Some 50 ha of grass heath have changed into woodland in the Meijnweg area between 1950-1980 (1 grid point represents 1.5 ha). A similar area of grass heath changed into woodland in the Hoge Veluwe area prior to 1980 (table 2.2). In none of the areas studied have changes from grass heath to heath been observed. Thus, cyclical changes from grass heath to heath did not occur.

Table 2.2
Numbers of grid points which indicated a change from grass heath either to woodland (GW) or to heath (GH) during the indicated period of observation.

	GWGH	TOTAL	GRID POINTS
Dwingeloo (1935-1978)	0	0	751
Hoge Veluwe (1937-1973)	32	0	2069
Kampina (1935-1980)	0	0	495
Meijnweg (1950-1975)	37	0	521
Lemelerberg (1950-1981)	6	0	545

OBSERVATIONS IN PERMANENT PLOTS

In the *Deschampsia* grass heath areas the grass has been present since 1953, whereas in the *Molinia* grass heath, the grasses were present in 1940 (Diemont & Heil 1984). At present no change from grass heath to heath has been observed (table 2.3).

In fact, the *Molinia* grass heath has already been invaded by trees *i.e. Betula* sp. and *Frangula alnus*, indicating that the grass heath is indeed part of succession. These saplings were removed from the plots, because we are also interested whether
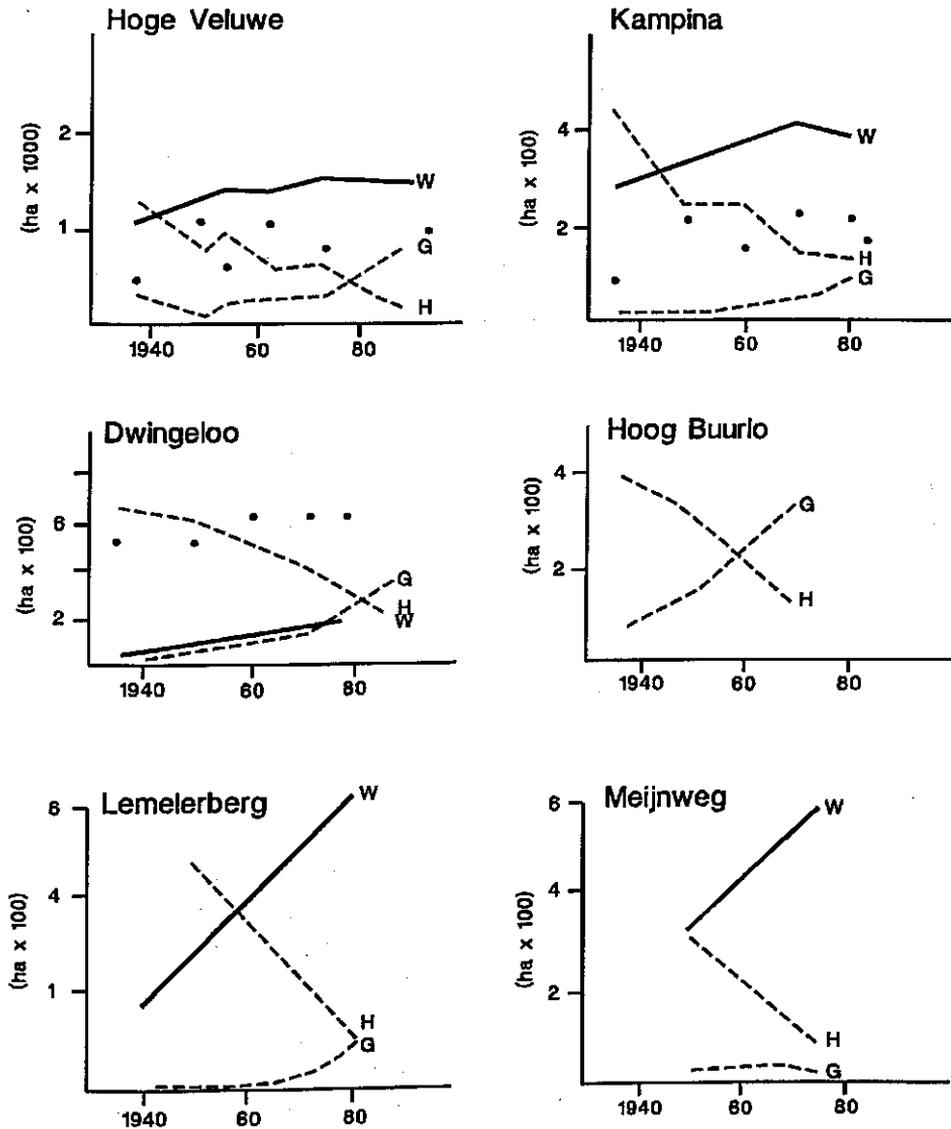

Figure 2.2
Changes of the relative proportions of dwarf-shrub heath (H), grass heath (G), and woodland (W) in six heathlands in The Netherlands. o = unidentified areas (Dwingeloo, Hoge Veluwe, Kampina, Meijnweg). Sources: Diemont et al. 1982, Tol et al. 1993, van Heusden 1982, Moen et al. 1991.

grasses would be replaced by heath species in the absence of trees. But also outside the fenced plots trees invaded the *Molinia* grass heath, because sheep grazing did not occur in the *Molinia*.

In the case of *Deschampsia*, the grass heath died in 1982 as a result of an infestation by *Cerapteryx graminis*. After this event the grass heath recovered and no dwarf shrubs established.

Table 2.3
Composition (% cover) of the vegetation in duplicate permanent plots in grass heath over the period 1976-1994.

	DESCHAMPSIA grass heath			MOLINIA grass heath	
	1976	1982	1994	1976	1994
Deschampsia flexuosa	100	0	90	10	60
Molinia caerulea	—	—	—	90	40
Galium hercinicum	+[2]	—	10	—	—
Rumex acetosa	—	<5[1]	—	—	—
Carex pilulifera	+	—	+[2]	—	—
Rubus sp.	—	—	—	—	10[1]

[1] observed in one plot only, [2] only a few individuals

Discussion

Inquiries (Diemont et al. 1982; Anonymous 1988) indicate that about 8,000 ha of heathland (20 % of the total heathland area) were covered by grasses (over 50 % cover) in the 1980's. The present study indicates a much greater percentage. In Hoog Buurlo, 50 % of the heathland was already grass heath in 1960. Grass heath areas in the other heathlands grass heath areas were much smaller: in these areas only 20 % was dominated by grasses in 1970. Between 1980-1990 the area of grass heaths has increased to about 80 % (Hoge Veluwe and Dwingeloo).

Aerial photography does not allow analysis of fine detail, and for that reason fluctuations such as were found in the Hoge Veluwe area between 1935-1960 (fig. 1) may be due to inaccurate photo interpretation. Some remarks, however, can be made. In the Hoge Veluwe, most of the grass heath present in 1937 (fig. 2.1) is still present as a *Molinia* grass heath in the northern part of this National Park.

The absence of invasion of woods in Hoog Buurlo is remarkable, which may be due to more or less continuous sheep grazing in this area. In Kampina, *Molinia* established in old tracks and roads, i.e. disturbed soil (Beije, pers. comm.). In

Dwingeloo, a lowering of the groundwater table (Bakker et al. 1986) has locally promoted *Molinia*. Where the groundwater was raised, the cover by dwarf shrubs, particularly *Erica tetralix*, increased again at the expense of *Molinia* (Schuiling, pers. comm.).

Overall in The Netherlands these sites are in the worst health as only 20% of all heathland in The Netherlands is dominated by grasses. The heathlands studied in this paper with a higher percentage of grasses are not representative of Dutch heathland. A recent study of the heathlands of Elspeet (449 ha), Westereind (80 ha), and Stakenberg (de Molenaar 1995) indicates that grasses occupied only 10 to 20 percent (Jonkers pers. comm.). The low percentage of grasses in the latter areas may be attributed to management; these heathlands have been used by the Ministry of Defence for training. This regular management in the last 40 years included prescribed burning, mowing and turf cutting (since 1980). It has also been suggested (Heil & Diemont 1983; Berendse 1990) that a higher input of nitrogen in heathlands as a result of atmospheric pollution may have triggered the encroachment of grasses. The sharp increase of grass heath in de Hoge Veluwe and Dwingeloo in the period 1970-1990 (fig. 2.2) coincided with higher levels of atmospheric pollution in The Netherlands.

The observation that grasses encroached on heathlands in the Hoog Buurlo area long before atmospheric pollution occurred indicates that the increase of grasses can not be solely attributed to an increased input of nitrogen in a heathland during the last decades. Transitions of heath into grass heath in Eastern England may also be accelerated by higher atmospheric nitrogen inputs, but these transitions were initiated by endogenous factors, such as changes in management (Marrs 1993).

The conclusion is that in the six heathland areas assessed here grass heath has increased markedly. In the Meijnweg the small increase is masked by a transformation of grass heath to woodland (table 2.2). The observation that grass heath changes to woodland already proves in itself that dominance of grasses in Dutch heathlands at present is part of succession and cannot be considered as a phase in a cyclical process (Stoutjesdijk 1959). Even in the absence of an invasion of trees, grass heath does not spontaneously change again to heath within a period of 40 years. Encroachment of grasses started probably after management of heathland decreased. Local lowering of the groundwater or increased inputs of nitrogen can have accelerated this process. It may also be questioned, however, whether increased nitrogen levels do directly affect vegetation dynamics, because phosphorus and not nitrogen seems to limit growth in many Dutch heathlands (chapter 5). This is probably also the case in lowland heath in South East Anglia (Chapman et al. 1989).

3. RE-ESTABLISHMENT OF DOMINANCE BY DWARF SHRUBS ON GRASS HEATHS

Summary

Experimental fields were established at three sites on different soil types in Dutch heathlands, where grass species have become dominant, in order to find methods for re-establishment of an ericoid dwarf-shrub heath. Treatments including mowing, mowing and cutting for hay, ploughing, milling, sod cutting and burning.

Re-establishment of ericoid dwarf shrubs was only observed after creation of gaps or patches of open soil. The results after nine years for two of the sites and six years for the other site indicate that sod cutting is the most suitable method provided that the mineral top soil is not removed or disturbed. More profound removal of the sod including mineral soil causes a delay in re-establishment of ericoid dwarf shrubs and an increase of grasses.

Factors that may explain different responses to gap creation including availability of seeds, soil moisture, soil fertility and plant survival strategies are briefly discussed.

Introduction

Heath or heathland in Europe can be recognized in the landscape by the virtual absence of trees and the dominance of ericoid dwarf shrubs (Gimingham 1972). The phrase dwarf-shrub heath (Gimingham 1972) is used in this paper to discriminate between the 'true' heath vegetation and a so-called grass heath, with a dominance of grasses, notably *Molinia* or *Deschampsia* (Graebner 1901).

In The Netherlands, interest in grass heath has considerably increased since the mid-seventies. According to circumstantial evidence from heathland managers over a period of 30 yr many areas of dwarf-shrub heath have changed to grass heath. Studies based on the interpretation of sequential aerial photography from heathlands (Dijkhuizen et al. 1976; Diemont et al. 1982; van Gils 1987; Chapter 2) supported this circumstantial evidence. The grass dominance phenomenon in The Netherlands was known earlier, especially after an infestation of *Lochmea suturalis*, but was then interpreted as part of a cyclical change (Stoutjesdijk 1959; de Smidt 1966), instead of a seral change as suggested by the recent aerial photography studies. For the same reason grass heath types as separate units are not included in the classification of heath communities of The Netherlands (de Smidt 1977). At present, vegetation types should be considered as grasslands (J.T. de Smidt, pers. comm.).

Which kinds of grass species are involved in the seral change depends on soil type and geomorphic position (Diemont & Heil 1984). In-depth studies related to plant nutrients involved in these changes can be found in Heil (1984) and

Berendse (1985). Berdowski (1987) studied the impact of *Lochmea suturalis* on the physiology of *Calluna*.

If the objective of heathland management is to maintain a dwarf-shrub heath, a seral change inevitably results in a need for additional management practices to be undertaken (Diemont et al. 1982).

In order to elaborate the most effective method for recovering dwarf shrub from a grass heath, several management practices, including mowing, ploughing and cutting of the sod, were tested in experimental plots from 1976 and 1979 onward. Preliminary results are found in Diemont et al. (1982). The final results are reported in this paper.

STUDY SITES AND METHODS

The three sites form a sequence of a *Deschampsia* grass heath on a well drained soil, through a *Molinia-Deschampsia* grass heath on an imperfectly drained soil to a *Molinia* grass heath on a soil occasionally waterlogged in winter (table 3.1).

Soil types are classified according to Soil Survey Staff (1975). The soils show podzolization i.e. eluviation of iron in podzolic soils (Haplorthod) or eluviation of both iron and organic matter in 'true' podzols (Haplohumod; Haploquod). The latter soil types have developed in sandy parent material and the former ones in loamy sands.

Prior to the treatments the vegetation of the sites was described with the help of relevés. 95 % of the site in Hoog Buurlo was covered by *Deschampsia*, in Kootwijk 90 % of the site was covered by *Molinia* and 5% by *Deschampsia* and in Dwingeloo *Molinia* covered nearly 100 %; the remainder was bare soil.

Following discussions with heathland managers, several management practices were included in the experiments (table 3.2). Sod cutting was simulated by a rotary cultivator adjusted to a prescribed depth. The loosened biomass and soil were manually removed; the soil surface left after removal was not disturbed by the action of the cultivator. Ploughing to a depth of 30 to 40 cm was preceded by a rotary cultivator opening the turf, before ploughing. The milled biomass was ploughed back and the result of the back ploughing was that only mineral soil was left in the top 20 cm. Not included in table 3.2 are 1) prescribed burning in Kootwijk and 2) a sod cutting treatment, including removal of standing crop and only part of the turf, in Dwingeloo.

Table 3.1
Main characteristics of the experimental areas.

GRASS HEATH TYPE	SOIL TYPE	DRAINAGE	SITE LOCATION	ESTABLISHED
Deschampsia	Haplortod	well drained	Hoog Buurlo	1976/1977
Molinia-Deschampsia	Haploquod	imperfect surface drainage	Kootwijk	1976/1977
Molinia	Haplohumod	poorly drained	Dwingeloo	1979

At this point some remarks should be made on the homogeneity of the sites. The *Calluna* and *Erica* data in figure 3.1 for Kootwijk and Dwingeloo show long bars, indicating relatively large differences in cover for the duplicate plots. In Kootwijk *Erica* is absent in replicates of the sod cutting treatments where the Pleistocene aeolian sands have disappeared. In Dwingeloo there is a clear topographical gradient explaining the variation. A wet heath is found in only part of the plots where flooding occurs in winter. Thus, the Dwingeloo site includes a moist and a wet variant. For reasons of clarity only the wet situations of the Dwingeloo duplicates are included in figure 3.2 and table 3.3.

Table 3.2
Treatments in the three experimental sites:
H = Hoog Buurlo, K = Kootwijk and D = Dwingeloo;
+ = treatment included; − = treatment not included.

NR	AREA (M^2)	DESCRIPTION OF THE PRACTICES	H	K	D
I	200	Sod cutting: removal of standing crop, turf and 5 cm mineral soil	+	+	+
II	100	Sod cutting: removal of standing crop, turf and 2 cm mineral soil	+	+	+
III	100	Sod cutting, removal of standing crop and turf to the mineral soil	+	+	+
IV	200	Ploughing to a depth of 30-40 cm	+	+	−
V	200	Milling (rotary cultivator)	+	+	..
VI	100	Annual mowing (June), with removal of standing crop	+	+	+
VII	100	Annual mowing (June); standing crop not removed	+	+	+
VIII	100·	Annual mowing (September), with removal of standing crop	−	−	+
IX	100	Annual mowing (September) standing crop not removed	−	−	+
X	200	No treatment	+	+	+

No prescribed management was practised in the selected plots prior to the treatments. In Hoog Buurlo and Kootwijk, the sites were fenced to exclude sheep grazing, a practise introduced in the area at the time the sites were established. Any trees, e.g. *Pinus sylvestris* which had become established in the experimental site were removed.

From 1980 onwards yearly observations of the vegetation were made in 4 by 4 m square plots using low altitude (4.75 m) vertical stereo aerial photography (Colour section). Special events affecting the vegetation (frost, infestation by *Lochmea suturalis*) were noted.

Results

Figure 3.1 shows the dominant and co-dominant species observed in (duplicate) plots of all treatments in three experimental sites in 1986. The response of the vegetation to sod cutting (treatments I, II and III) in all sites is basically an
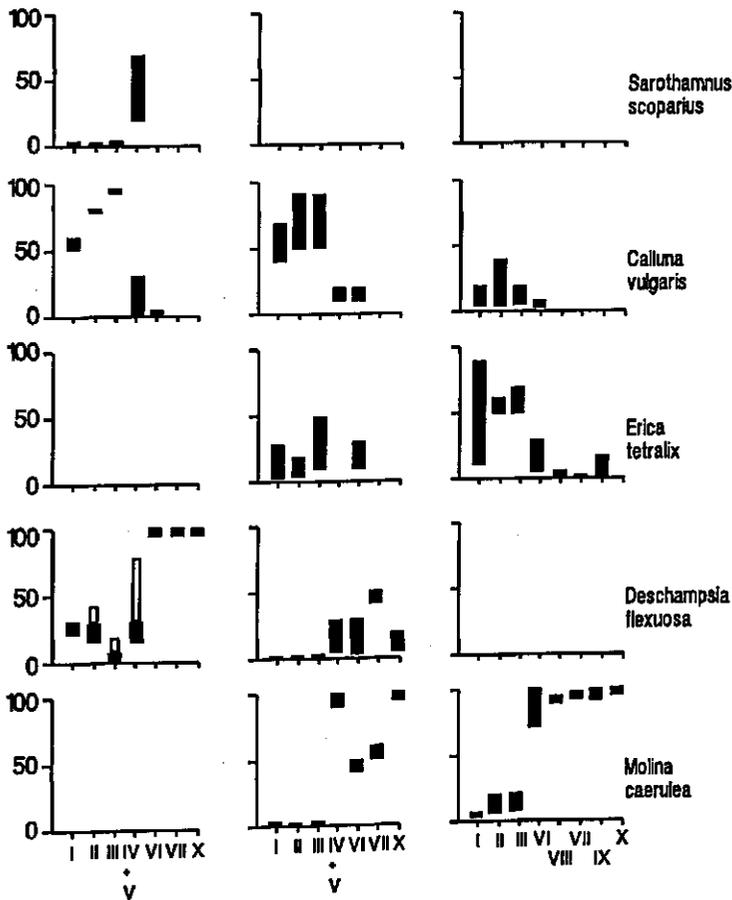

Figure 3.1

Cover percentage in 1986 of dominant and co-dominant species in the experimental sites Hoog Buurlo, Kootwijk and Dwingeloo. The ends of the vertical lines indicate the percentage observed in the duplicate plots for each of the treatments (explanation in table 3.2). The dashed line in Hoog Buurlo indicates the additional cover of *Deschampsia* where it occurs under *Calluna* (treatments II and III) or *Sarothamnus* (treatments IV, V).

almost complete change from a grass heath to a dwarf-shrub heath. The response to ploughing (IV) and milling (V) in Hoog Buurlo and Kootwijk respectively was quite different. The *Deschampsia* grass heath in Hoog Buurlo turned into a mixed vegetation of Sarothamnus with patches of *Deschampsia* and *Calluna. Sarothamnus* was more dominant after ploughing, as compared to milling. In the Kootwijk site both ploughing and milling resulted again in a *Molinia/Deschampsia* grass heath, although also some ericoid dwarf shrubs established.

The mowing treatment without removal of the biomass (VII, IX) did not change the grass heath vegetation in either of the experimental sites. Where the material was removed (VI and VIII) some ericoid dwarf-shrub vegetation established (Kootwijk) in a *Molinia* dominated grass heath, but not in a *Deschampsia* grass heath. In the untreated plots (X) virtually no changes in the vegetation were observed, except for the dying of *Deschampsia* tussocks. This was found to be a temporary phenomenon, typical for an ungrazed *Deschampsia* grass heath (Diemont & Heil 1984). Prescribed burning in the Kootwijk site (September, 1978-1980) did not bring about any change in the dominance of *Molinia*.

The rate of re-establishment of ericoid dwarf shrubs after sod cutting can be derived from figure 3.2. About 90 % of the 'wet' plots in Dwingeloo site was covered by ericoid species within 6 to 7 yr. In the locations Kootwijk and Hoog Buurlo re-establishment has taken at least 9 yr, although a superficial treatment (III) in Hoog Buurlo showed a higher rate as compared to the same treatment in Dwingeloo in the first 5 yr. Compared to superficial sod cutting treatments (III), sod cutting treatments including 2 cm and 5 cm mineral soil (II and I) respectively were retarded in all three locations.
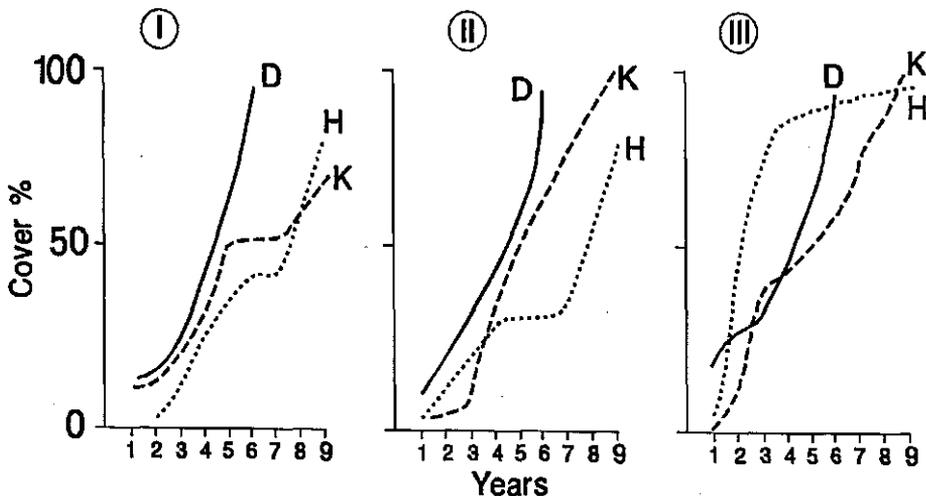

Figure 3.2

Increase in the cover (%) of ericoid species, for the sod cutting treatments (I, II, III see table 3.2) in Dwingeloo (D), Kootwijk (K) and Hoog buurlo (H) from visual cover estimates in the field. The percentages for Hoog Buurlo and Kootwijk are mean values from duplicate plots. In Dwingeloo only one plot value is included.

Table 3.3 shows that (after 9 yr) grasses in Kootwijk (*Molinia*) decreased after sod cutting treatments. In Hoog Buurlo *Deschampsia* increased in time, but at that time (9 yr after the treatment) most of the grass was found underneath a *Calluna* canopy.

Table 3.3

Percentage cover 5 and 9 yr after establishment of three sod cutting treatments in three sites. E = ericoid species, G = grasses; B = bare soil without phanerogams (other abbreviations as in table 3.2).

TREATMENT	LOCATION	COVER %					
		5 yr old			9 yr old		
		E	G	B	E	G	B
I	D	95	5	0			
	K	50	20	40	70	0[1]	30
	H	40	40	20	50	30	20
II	D	90	10	0			
	K	50	20	30	90	10[1]	0
	H	30	40	20	80	20	0
III	D	90	10	0			
	K	50	30	10	100	0[1]	0
	H	90	10	5	95	5	0

[1] A cover of 10-20 % should be added, because in these cases most of the grass (*Deschampsia*) was found underneath a *Calluna* canopy.

Some incidental environmental factors did affect the response of the vegetation to treatments. An infestation by *Lochmea suturalis* in Kootwijk invaded the superficially treated sod cutting plots (I) in October 1978. In these plots *Calluna*, *Erica* and *Molinia* germinated already in 1977 and especially in 1978. As a result of the infestation *Calluna* became, heavily damaged, however, and consequently grasses could increase in 1979. In 1980 most of the *Calluna* plants had recovered and taken over dominance in the upper vegetation layer. In 1981 a light infestation of *Calluna* was recorded in Hoog Buurlo and Kootwijk, but this did not cause any serious damage to the plants. In 1980/1981 *Sarothamnus* (Hoog Buurlo site) was badly damaged by frost at a time when *Calluna* was protected by snow cover. Most of the *Sarothamnus* plants recovered. The severe frost, without snow, in the winter of 1985/1986 caused serious damage to *Calluna* in Hoog Buurlo and Kootwijk. Observations in 1987 show that most of the *Calluna* recovered in Hoog Buurlo and Kootwijk except for the *Calluna* in ploughed and milled plots.

The dominant species in the untreated plots as given in table 3.1, are indicative of the moisture status of the different locations i.e. Hoog Buurlo dry,

Kootwijk moist and Dwingeloo wet grass heath respectively. Also in the treated plots differences in species reflect the moisture status between sites: in Hoog Buurlo *Calluna* is present in the Kootwijk site as well as in the Dwingeloo site (I, II, III, VI), but in Dwingeloo *Erica* is dominant.

Other plant species encountered infrequently and in low numbers confirm the moisture status of the sites. In Hoog Buurlo *Genista pilosa* is a species commonly recognized as a faithful species for dry heath, Genisto anglicae-Callunetum. Other infrequent species in Hoog Buurlo were *Agrostis vinealis*, Rumex acetosella and Carex pilulifera, all found in the sod cutting treatments I, II and III. Moehringia trinerva was present in the treatments VI, VII and X. In the Kootwijk site the only additional species occurring, in treatments III, IV, V and X was *Rubus* sp. This moist heath type is also included in the *Genisto anglicae-Callunetum*.

At Dwingeloo, in the wet part of the site, *Juncus squarrosus* is an additional character species of the wet heath, *Ericetum tetralicis*, but its general position is not clear (de Smidt 1977). Other species encountered especially in treatments I, II and III were Rhynchospora alba, fusca and Drosera rotundifolia. The latter combination is indicative of the *Lycopodio-Rhynchosporetum albo-fuscae*. This community occurs on 'plagged' places and tracks in the Ericetum tetralicis.

Discussion and conclusions

The results of the field trials demonstrate that superficial sod cutting (treatment III) is most appropriate to change a grass heath into a dwarf-shrub heath. The results confirm the effectiveness of sod cutting of grass heath in The Netherlands to re-establish dwarf-shrub heath (Hendriks 1987). In 1982 machinery to treat the grass heath mechanically, and composting techniques have been developed in order to utilize the removed sod material as a valuable compost (Diemont et al. 1982; Riemvis & Diemont 1985). Up to 1986 hundreds of hectares have been successfully treated.

For proper nature management, faunistic aspects should be considered as well and here structural diversity is a key requirement. Guidelines for the optimal spatial pattern of (mechanical) sod cutting are therefore being prepared (Hendriks 1987).

The following discussion concentrates on the similarities and differences in response to treatment at the three sites, and on the underlying mechanisms which may explain the observed phenomena.

Ericoid species established after gaps or larger patches of open soil had been created by sod removal (treatments I, II, III), ploughing IV), milling (V) or mowing for hay (VI). In case of mowing for hay, ericoid species established only in gaps in between *Molinia* tussocks when the hay was removed (VI) allowing light to enter the soil surface. In case of a *Deschampsia* grass heath, gaps were absent and no establishment of ericoid species was noticed.

The creation of gaps or patches of open soil itself is not always sufficient to establish dominance of ericoid species. For instance, sod cutting including part of the mineral soil was less successful especially in the dry and moist sites. This may indeed be related to soil moisture conditions which become less favourable after sod

cutting resulting in low amounts of organic matter. Also, the availability of seeds and other soil properties may be involved.

After germination and establishment the vegetation may be modified by both competition between plant species and plant specific strategies favouring co-existence. The results in table 3.3 suggest that the balance between co-existence and competition is age-dependent as previously indicated for co-existence of plant species in heathland by Gimingham (1978) and with respect to competition by Heil (1984). In the course of time *Molinia* diminished in Kootwijk (see also Heil 1984). On poor soil (impoverished by a sod cutting treatment) young *Calluna* is a better competitor than *Molinia*. This observation suggest that in case *Molinia* re-establishes after sod cutting additional management to decrease *Molinia* is not necessary.

Deschampsia in Hoog Buurlo increased by adapting its growth form, as to hide under *Calluna* plants. The adaptation strategy of *Deschampsia* may explain why a *Calluna* heath with *Deschampsia* turns into a *Deschampsia* grass heath within 1 or 2 yr, after a severe attack of *Lochmea suturalis* (Berdowski & Zeilinga 1987). Additional grazing after a sod cutting treatment may be beneficial in this case.

The balance between grass species and ericoid dwarf shrubs is also influenced by incidents; *Calluna* populations of the same age may react differently because of differences in soil fertility: all *Calluna* in Hoog Buurlo and Kootwijk was severely affected after 9 yr as a result of frost. The *Calluna* plants were still in the building phase (term used as in Gimingham 1972) in plots where sod cutting was done, but in the ploughed and milled plots the plants were already in the degenerate phase. In 1986 most of the *Calluna* in the building stage regenerated from the basal parts of the stem (exception see below), but the plants in the degenerate phase were dead (observations 1986, 1987). Probably the treatment of ploughing or milling increased soil fertility, resulting in a reduction of carbohydrate reserves and vegetative regeneration of *Calluna* (Berdowski 1987).

The regeneration of *Calluna* in its building phase was largely prohibited when grasses were present close to the *Calluna* plant. This was observed especially in Hoog Buurlo where about 60 % of the *Calluna* plants did not regenerate from the basal part of the stem, because of *Deschampsia* occurring near the stems of *Calluna*. In the Kootwijk site *Molinia* rarely occurred near the stem of *Calluna* plants, and most of the *Calluna* plants in Kootwijk accordingly regenerated from the stem, although *Erica* (which was not injured by frost) already replaced part of the *Calluna*.

It will be concluded from our field observations (Chapter 4) that an explanation of the result of treatments in a grass heath vegetation should also consider the impact of the treatments on the germination of the species involved, as well as soil fertility (Chapter 5).

4. SEEDLING EMERGENCE AFTER SOD CUTTING IN GRASS HEATH

Summary

Experimental plots in grass heath, previously subjected to various sod cutting treatments, contained a seed store of ericoid dwarf shrubs, but seeds of grasses of the former grass heath were not found. The density of emerging dwarf-shrub seedlings in the plots was determined mainly by soil moisture, but with density of seeds stored in the soil and acidity as modifying factors. It is concluded that the restoration of a dwarf-shrub heath by sod cutting is relatively successful, as compared to other measures, because the grass seeds become obsolete.

Introduction

Grassy vegetation in heathlands in The Netherlands, dominated by *Molinia* or *Deschampsia*, is mostly the result of a seral change of a dwarf-shrub heath (Gimingham 1972) into a grass heath, often triggered by an infestation of the heather beetle (*Lochmea suturalis*) or a severe frost (Diemont, Blankenborg & Kampf 1982; Diemont & Heil 1984; Berdowski 1987; Chapter 3).

Sod cutting has been shown to be an appropriate method of recovering a dwarf-shrub heath from a grass heath. It was found, however, that the type of grass heath as well as the depth of soil baring affected the rate of recovery and the species composition of the restored dwarf-shrub heath (Chapter 3). These differences may be caused by the density of seeds stored in the soil as well as by environmental factors, i.e. soil moisture and chemical soil conditions (Gimingham 1972) and in particular soil acidity (Poel 1949), which affects the dormancy of *Calluna* (Helsper & Klerken 1984).

These factors, including spatial and temporal changes in soil moisture and soil acidity (pH) were studied with the aim of understanding better the effects of sod cutting on grass heaths.

Site descriptions

Three common types of grass heath were selected.
1. The site at Hoog Buurlo, HB, represents a *Deschampsia* grass heath on well-drained loamy sands with a podzolic soil profile.
2. The site at Kootwijk, KO, is a *Molinia-Deschampsia* grass heath on sandy, imperfectly drained podzol soil.
3. The Dwingeloo site, DW, is representative for a *Molinia* grass heath on a wet sandy podzol. The experimental plots at HB and KO were established in 1976/1977 and the DW plots in 1979.

The plots received various treatments (Chapter 3). The duplicate treatments discussed in the present paper are:

I. sod cutting, including removal of standing biomass, turf and 5 cm mineral soil (area 100 m²);
II. sod cutting, including removal of standing biomass, turf and 2 cm mineral soil (area 100 m²;
III. sod cutting, including standing crop and turf but excluding mineral soil (area 200 m²);
V. milling of biomass and grass turf by a rotary cultivator (area 200 m²).
    Apart from the experimental sites also two *Calluna* - dominated heathlands near the KO and HB sites were sampled to assess the store.

Field observations

Seedlings were counted annually in the experimental plots subjected to sod cutting, during a period of three years following the establishment of the experimental plots: four replicates (sub-plots of 0.5 m² each) in each plot; only mean figures per plot available.

In early spring 1980 a second experiment was set up at all three sites, previously subjected to various sod cutting treatments, in order to assess the effects of both soil moisture and density of viable seeds on the establishment of *Calluna*, *Erica* and *Molinia* (there were duplicate plots, six sub-plots of 1 m² in each plot). The vegetation, as far as present, was removed. Half of the sub-plots were used to sow separately batches of seeds of *Molinia* (equivalent to 930 seeds/m²); *Calluna* and *Erica* (equivalent to 25,000 seeds/m²). In each plot two subplots were available for adding seeds of a particular species; the other half of the subplots were used as control. The density of sown seeds in the experiment was based on the result of a preliminary study. The viability of the added seeds, tested on filter paper, was 90 % for all seeds under conditioned light. The temperature and moisture regime is given below. Gravimetric soil moisture measurements were carried out three times during the year. Mean values on a dry soil basis are used as a moisture index.

Laboratory observations

The density of seeds stored in the top soil of the experimental plots was assessed for HB and KO in bulk soil samples (about 200 g from six sub-samples) of the top soil up to 1 cm depth. The sampling was done in 1977 about six months after the establishment of the experimental sites. As already mentioned, soil samples were also taken from two *Calluna* heathlands.

Samples were air dried and stored at 5°C. Three replicates of 6 g of the soil (in the case of a milling treatment with a low bulk density of 3 g) were spread on moist filter paper (diameter 5 cm) in a controlled environment. The weights used are equivalent to a surface area of about 5 cm² in the field. For comparison a sample of a medium fine river sand was included in the experiment. The soil was kept moist at field capacity level by a strip of filter paper in contact with demineralized water.

To examine the effect of the soil on the germination of *Calluna* and *Molinia*, 30 seeds of each species were added (separately) to further sets of soil samples in the same experiment.

A variable temperature of 5-30 °C was adopted for maximum germination of *Calluna* (Gimingham 1972; Bekendam 1974) and *Molinia* (Kinzel 1913). Light stimulates both the germination of *Calluna* (Gimingham 1972; Bekendam 1974) and *Molinia* (Kinzel 1913) and therefore white day light was supplied during 8 hours corresponding with the high temperature. Relative humidity was about 80 % at 30oC and 55-70 % at 5 °C. A diluted FeSO4 solution was used to eliminate developing bryophytes. Additional tests were done with *Calluna* seeds pre-treated with a 0.1 % GA3 solution to neutralize dormancy (Mayer & Polijakof-Mayber 1975). Both seeds of *Calluna* and *Molinia* used in the experiment showed a seedling emergence of 80 % on filter paper. The pH of all soil samples was measured after the experiment with a glass electrode in a 1:25 soil to water solution after 24 hours.

Results

The density of dwarf-shrub seedlings in the plots, previously subjected to superficial sod cutting, is relatively high on the wet *Molinia* grass heath at DW, with 500 to over 1000 seedlings/m^2 against 100-300 on the well drained HB and KW sites. However, in plots which received a sod cutting treatment including removal of the top mineral soil, numbers of seedlings were lower than 100/m^2 and did not differ significantly between sites. These results may, at least partly, be explained by the seed bank in the soil. The density of germinative seeds in the soil, as assessed for KO and HB was unexpectedly low in plots which received a superficial sod cutting treatment, as compared with cuttings including mineral soil (table 4.1). The milling grass treatment produced a significantly higher dwarf-shrub seed density (P<0.05), but the highest densities, 26 000 to 80 000/m^2, were recorded in *Calluna* heaths (not included in the table). No viable seed banks of either *Deschampsia* or *Molinia* seeds were found. The pH measurements (table 4.1) suggest that the lower density found with a more shallow soil baring may be caused by the lower pH.

The effect of pH was studied in more detail by adding seeds to additional batches of soil. The emergence of added *Molinia* seedlings to soil samples is about the same (80 %) as on filter paper; no significant differences were found between sites or between sod cutting treatments (fig. 4.1). For *Calluna*, however, differences between sites and between most of the treatments within a site are significant (P < 0.05). These differences are not found after pre-treatment of *Calluna* seeds with GA3. Figure 4.2 suggests that pH in the absence of a GA3 pre-treatment may explain the effect of the soil on *Calluna* seedling emergence.

As compared with seedling emergence under the optimum moisture conditions in the controlled environmental (usually 80-90 %), emergence in the field is very low, less than

20 % (table 4.2). Increased germination from added seeds of *Calluna*, *Erica* and *Molinia* occurred when the moisture index was relatively high.

As different from the seed store experiment, *Molinia* seedlings were found in the field experiment at DW (table 4.2). The density of emerged *Molinia* seedlings

calculated for DW (table 4.2), is ca. 40 times lower than that of ericoid seeds.

Table 4.1
Mean number of germinative *Calluna* and *Erica* seeds in top soils (numbers per m² soil surface; n=3; CV < 10 %) after sod cutting treatments in a *Deschampsia* grass heath (Hoog Buurlo) and a *Molinia-Deschampsia* grass heath (Kootwijk). Corresponding soil pH values in brackets.

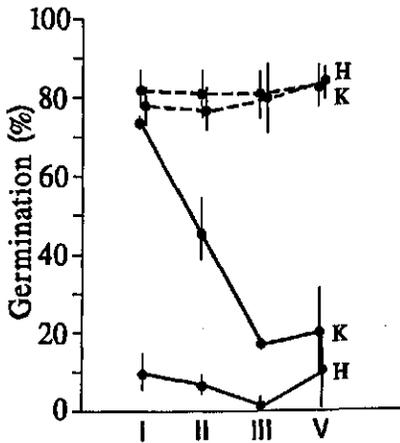| | TREATMENT | HOOG BUURLO | | KOOTWIJK | |
		NR.	pH	NR.	pH
I	Sod cutting: turf + 5 cm soil	3400	(4.3)	2200	(4.7)
II	Sod cutting: turf + 2 cm soil	4200	(4.1)	4400	(4.8)
III	Sod cutting: turf	1600	(4.0)	3000	(4.4)
V	Milling: Rotary cultivation	10000	(4.2)	8000	(4.3)

Figure 4.2
Emergence of *Calluna* seeds added to different top soils from Hoog Buurlo (HO) and Kootwijk (K) after sod cutting treatments I, II and III and the milling treatment V (see table 4.1).
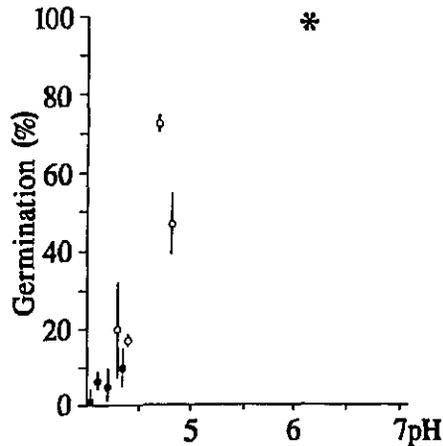---- = pre-treatment of the seeds with GA3;
—— = no pre-treatment.

Figure 4.2
Effect of soil pH (after sod cutting) on the emergence of added *Calluna* seeds;
○=top soil from plots in Hoog Buurlo;
●=top soil from Kootwijk;
*=fine river sand.

Table 4.2
Emergence of *Molinia* (M), *Calluna* (C) and *Erica* (E) seedlings in three grass heath sites previously subjected to three different sod cutting treatments, I, II and III, see site descriptions in the text). Site DW=Dwingeloo; KO=Kootwijk; HB=Hoog Buurlo. A=seeds added; B=no seeds added; X=mean; CV=Coefficient of variation; EM=Emergence of added seeds (%); Moist.=moisture index; Sp.=plant species.

SITE	TR.	SP.	NUMBER OF SEEDS PER M²				EM.	MOIST.
			A		B			
			X	CV	X	CV	%	INDEX
Dw	III	M	222	31	140	63	9	
		C	4250	51	2500	33	7	68
		E	3400	27	1900	25	6	
	II	M	226	18	70	37	17	
		C	3250	32	1600	37	7	68
		E	5000	12	1700	40	13	
	I	M	112	73	28	85	9	
		C	178	55	8	100	1	19
		E	24	75	4	100	0	
KO	III	M	160	40	116	41	5	
		C	270	19	52	58	1	23
		E	48	96	22	136	1	
	II	M	14	100	12	33	0	
		C	88	50	14	100	0	15
		E	1	100	0		0	
	I	M	6	167	6	100	0	
		C	26	138	8	75	0	11
		E	6	166	12	92	0	
HB	III	M	0		0		0	
		C	12	50	6	66	0	23
		E	2	100	0		0	
	II	M	0		0		0	
		C	20	120	0		0	16
		E	0		0		0	
	I	M	1	0	0		0	
		C	3	200	0		0	16
		E	0		0		0	

Discussion and conclusions

The emergence of seedlings in undisturbed *Calluna* heathland is usually poor compared to the emergence of seedlings on bared soil (Miles 1973). In a grass heath the creation of gaps - or larger patches of open soil - is a prerequisite for seedling

emergence, but the results depend on the method used to create a bared soil: a superficially sod cutting method caused dwarf shrubs to become dominant species, but ploughing and milling resulted in either a grassy or a mixed vegetation (Chapter 3). The results presented here suggest that the success of sod cutting in restoring a dwarf-shrub heath should be attributed in the first place to the absence of grass seeds and in the second place to the presence of dwarf-shrub seeds in the mineral soil.

Even in a undisturbed natural pasture with 70 % *Molinia* cover, few *Molinia* seeds were found and only in the upper 2 cm of the soil, but viable seeds from dwarf shrubs were numerous down to a depth of 9 cm in the soil (Chippendale & Milton 1934). *Molinia* seeds on the other hand, may survive in the soil for several years (Pons 1989). The absence of any seeds of either *Molinia* or *Deschampsia* in the seed store experiment may be explained by the fact that grass seeds are only present in top soil which was previously removed by the sod cutting treatment. Whether the smaller seeds of *Deschampsia* may enter the soil or not, is probably not relevant as these seeds are not persistent (Heil 1984; Pons 1989).

Despite these limitations, grasses appeared in due course in all plots previously subjected to sod cutting (Chapter 3; see also table 4.2). These grasses must have been imported earlier from the surrounding grass heath, at only 2 m distance.

Both soil moisture and the relative air humidity appear to be important for seedling emergence. Sod cutting including removal of mineral soil, caused lower soil moisture levels (probably because of a decrease in soil organic matter (Diemont unpublished) and consequently a low recovery of added seeds of both ericoid dwarf shrubs and grasses.

If the soil moisture content is high enough for seedling emergence, seed density in the soil as well as pH (in the case of *Calluna*) may also affect the seedling emergence. Under optimal moisture conditions in the laboratory a lower pH of the soil lowered seedling emergence of *Calluna* and consequently affected the assessment of the seed store of dwarf- shrub seeds. In the field, the pH of the soil increases with depth, as a result of leaching of bi-carbonates and the production of acids by decomposition and uptake of ammonia by plants in the upper part of the soil (Rowell 1988). The beneficial effect of a higher pH for seedling emergence of *Calluna* (as a result of sod cutting with removal of mineral soil) is overruled by the decrease of viable seeds and less favourable moisture conditions in the field.

In conclusion, superficial sod cutting may be a good method of recovering a dwarf-shrub heath. Soil moisture may become very critical after sod cutting including removal of mineral soil, in particular in dry years, and for that reason only a shallow baring of the soil, only including standing biomass turf, is recommended.

5. EFFECTS OF REMOVAL OF ORGANIC MATTER ON THE PRODUCTIVITY OF HEATHLANDS

Summary

Effects of milling, mowing and sod cutting on productivity in a *Deschampsia* grass heath and a *Molinia-Deschampsia* grass heath were studied from 1977 to 1986. The sum of above-ground biomass, litter and accumulated humified matter (TOM) in both types was ca. 70 ton/ha and the primary productivity 3 - 5 ton ha-1y-1, respectively. Mulching did not affect the annual production. Sod cutting reduced the productivity to 1 - 2 ton ha^{-1}y^{-1}; on the *Molinia-Deschampsia* site this reduction lasted for at least a decade, while the *Deschampsia* heath started to recover from sod cutting soon and increased in productivity again. Annual mowing both with and without removal of hay reduced the production as well, particularly on the *Molinia-Deschampsia* heath. Lower production was either the result of phosphorus depletion -*Molinia-Deschampsia* site - or nitrogen depletion - (*Deschampsia* site). In the mowing treatments there was also a depletion of carbohydrate reserves.

Introduction

In so-called grass heath, i.e. heathland where grasses have replaced dwarf shrubs, a dwarf-shrub heath can be restored by sod cutting (Chapter 3). The success of sod cutting has been explained by depletion of viable grass seeds and improved light conditions for germination of dwarf-shrub seeds from reserves in the soil (Chapter 4). However, *Calluna* which re-established after sod cutting in a relatively fertile *Deschampsia* heath, had a shorter life span as compared to a low-fertile *Molinia-Deschampsia* heath. Also, effects of treatments on nutrient availability are reflected in the life span of *Calluna*. For instance, the life span of (low-abundant) *Calluna* was shorter where the grasses and the turf layer were milled with a rotary cultivator, but not removed until after sod cutting. On the basis of these observations it is suggested (Chapter 3) that a lower nutrient availability resulted in a lower production of the vegetation, but is accompanied by a longer life span of *Calluna* which retards the formation of suitable gaps for the establishment of grasses. Data regarding the productivity and nutrient availability were not presented in that study.

The present study provides data which support the hypothesis that a higher productivity of *Calluna* induces an early replacement by grasses. Further, this study may also contribute to the general understanding of the role of biomass for maintaining productivity on nutrient-poor soils.

Site description

Experimental plots were laid out in 1976 on a *Deschampsia flexuosa* grass heath on a brown podzolic soil at Hoog Buurlo (HB) and in a *Molinia* caerulea-*Deschampsia flexuosa* grass heath on a well-drained podzol soil in Kootwijk (KO), The Netherlands (52o 9' N, 5o 35' E). Chemical characteristics of the soils - which reflect differences in soil morphology - are presented in table 5.2. The treatments (table 5.1) were applied in duplicate plots of 100 and 200 m^2. All treatments were applied once in 1977, except for mowing, which was repeated each year.

Table 5.1
Survey of treatments in the experimental sites Hoog Buurlo and Kootwijk and abbreviations used in the text

CODE	DESCRIPTION OF THE PRACTICES
SR$_5$	Sod cutting; removal of standing crop, turf and 5 cm mineral soil
SR$_2$	Sod cutting, removal of standing crop, turf and 2 cm mineral soil
SR$_0$	Sod cutting; removal of standing crop and turf to the mineral soil
Pl	Ploughing to a depth of 30-40 cm
Mi	Milling of the above-ground biomass and the turf (rotary cultivator); no removal of the milled material
M$^-$	Annual mowing, with removal of the standing crop (mowing for hay) during nine years
M	Annual mowing, standing crop not removed during nine years
Ct	No treatment (control)

Table 5.2
Values for soil variables indicating fertility in the mineral soil - six bulk samples (two replicates in 1977, 1982 and 1986) - for different treatments (see table 5.1). Coefficient of variation < 15 %, for treatment SR$_0$ < 25 %.

	TREATMENT	OM %	P g/k	K g/kg	C/N
Hoog Buurlo	Ct, M, M$^-$, P	9.8	0.5	0.8	18
	Mi	5.5	0.5	0.6	22
	SR$_0$	9.6	0.4	0.7	23
	SR$_2$	6.4	0.5	0.7	22
	SR$_5$	6.4	0.5	0,7	24
Kootwijk	Ct, M, M$^-$, P	5.8	0.2	0.8	30
	Mi		0.1	0.4	26
	SR$_0$		0.2	0.4	24
	SR$_2$		0.1	0.4	26
	SR$_5$		0.1	0.3	38

Procedures

Total above-ground organic matter (TOM), comprises living standing biomass and organic matter in the soil, which includes a litter layer (L), a partly humified layer (F), and humified organic matter (H). The mineral soil sampled was arbitrarily taken from the upper 5 cm of the (mineral) soil profile. Samples of TOM and the mineral soil were taken from all plots after treatment in 1977. Bulk samples from each plot, were composed of eight volumetric subsamples of 0.0625 m^2. Sampling was repeated in 1982 and 1986 with only four subsamples from a larger area of 0.25 m2, this because the above-ground spatial variation observed in these years was larger. The ploughed and mulched plots were not sampled again in 1986, as it appeared that these treatments were not appropriate for restoring a dwarf-shrub heath (Diemont & Linthorst Homan 1988).

Bulk samples were air dried, sieved (2 mm) and ground prior to chemical analysis. Analyses included organic matter (OM; loss on ignition at 375 °C), total nitrogen (N-Kjehldahl; % dry weight), total phosphorus (P; g/kg dry weight) measured colorimetrically after digestion in a 1:1 mixture of H2SO4 (96 %): HNO3 (65 %). Total potassium (K; g/kg dry weight) was measured in the same extract by Atomic Absorption Spectrometry. Carbon (% dry weight) was estimated arbitrarily from the equation C = 1.8*OM (Howard 1965).

Separate samples of TOM and the mineral subsoil could easily be taken, because of the sharp boundary between them in the field.

Annual above-ground production of the grasses *Molinia* and *Deschampsia* was assessed by harvesting and measuring the above-ground biomass at the time of peak standing crop (September/October). This procedure may lead to underestimation of the annual production of *Deschampsia* as the turnover of leaves within a growing season is not taken into account (Bülow-Olsen 1980), but the underestimation is probably less than 10 % (Wallis de Vries 1989). Annual above-ground production of *Calluna* is usually assessed by summing up the annual litter fall and the annual increment of the standing crop (Chapman et al. 1975). An indirect annual production estimate can be derived from standing crop measurements in *Calluna* stands of a known age using the equation (Chapter 7)

$$\frac{\text{Standing crop}}{\text{Annual production}} = 1.8 + 0.23 \cdot \text{Age} \qquad (1).$$

Heathlands can have a nutrient deficiency for either N or P (Groves 1981). N is mainly included in carbon fixing enzymes, which determine plant production, while P is essential for the formation and maintenance of these proteins. The ratio of P to N in plants is therefore constant (Penning de Vries & Djiteye 1982; van Wijngaarden 1985; Olivaris & Medina 1992). In the case of a P-deficiency, however, the P/N ratio will be low (0.04), whereas in the case of N-deficiency a high ratio (0.4) is found (Mohren et al. 1986). Thus, also in this study, we use the P/N ratio to assess N- or P-deficiencies.

Results

LOSSES OF ORGANIC MATTER AND NUTRIENTS

Sod cutting (treatments SR_0, SR_2, SR_5) in a grass heath implies that all biomass and organic matter, organic and associated nutrients are removed, which causes a substantial drain of organic matter and potential nutrients (table 5.3). Recovery in the sod cutting treatments after a period of five yr (1982) was still very limited in comparison to the controls (fig. 5.1). Levels in milling and mowing treatments (Mi, M-,M) did not yet (see below) significantly differ (P < 0.01) from levels in the controls. Recovery after ploughing (P) was modest in HB and was intermediate in KO (fig. 5.1).

In 1987, 9 yr after treatment the accumulated TOM and associated nutrients were assessed again for sod-cutting treatments, mowing treatments and controls. In the sod-cutting treatments the levels of TOM and associated nutrients had only increased by about 20 % compared to 1982. Significant changes over the period 1977 to 1987 occurred in the mowing treatments and controls (fig. 5.2). The decrease after 1977 in the control plots (Ct) in HB was caused by the death of *Deschampsia* in 1981/1982. No explanation can be given for the lower TOM in KO in 1982. In the mowing treatments, TOM and associated nutrients decreased gradually. Losses were highest (fig. 5.2) in mowing treatments with removal of hay (M-).

Nutrient losses caused by the removal of hay over a period of 9 yr (treatment M-) were moderate compared to indirect losses induced by mowing (table 5.3), which also occurred in mowing treatments where hay was replaced (treatment M).

Table 5.3
Total losses of organic matter (TOM) and associated nutrients (N, P, K) in sod cutting (SR_0, SR_2, SR_5) and mowing treatments. Losses comprise actively removed material (by a single sod cutting treatment or by annual mowing for hay for 9 yr) and indirect losses induced by mowing. The actively removed OM and N, P, K with hay (treatment M-) is indicated between brackets. Coefficient of variation ca. 25 %.

	TREATMENT	TOM ton/ha	N ton/ha	P kg/ha	K kg/ha
Hoog Buurlo	Ct	66.7	1.4	85	110
	SR_0, Sr_2, SR_5	66.7	1.4	85	110
	M-	39.2	1.2	60	107
		(10.8)	(0.1)	(17)	(59)
	M	32.7	1.0	35	60
	Ct	72.8	1.5	66	110
Kootwijk	SR_0, SR_2, SR_5	72.8	1.5	66	110
	M-	47.4	1.3	45	102
		(12.4)	(0.2)	(9)	(71)
	M	14.4	1.0	14	56

The indirect losses in mowing treatments are probably induced by losses of carbohydrate reserves (see Discussion). Total losses in mowing treatments with removal of hay after 9 yr were nearly as high as nutrient losses from a single sod-cutting treatment (table 5.3). Additional removal of mineral soil (treatment SR_2, SR_5) or bringing mineral soil to the surface by deep ploughing (treatment Pl) resulted in the decrease of organic matter and N-levels decreasing proportionally with the depth of ploughing or removal (table 5.2), although such differences are not significant ($P < 0.05$). A higher total amount of P and K and a lower C/N ration are found in the brown podzolic soil in HB as compared to the podzol in KO, which reflects the higher soil fertility of the brown podzolic soil.
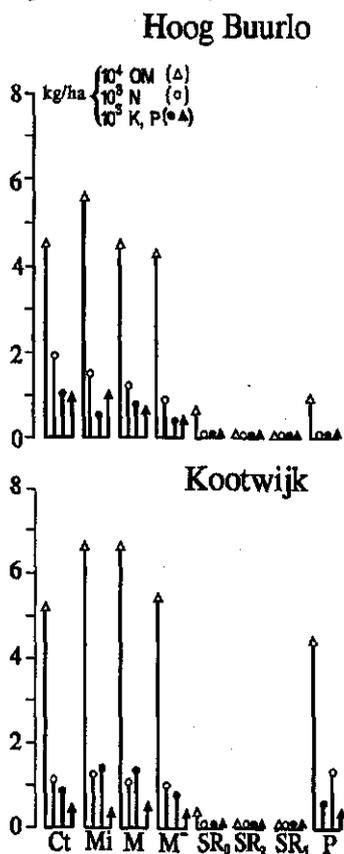
Figure 5.1
Organic matter and nutrients in above-ground biomass, litter and humified litter (TOM) in all treatments at Hoog Buurlo and Kootwijk in 1982, 5 yr after sod cutting, milling and ploughing and the start of annual mowing. For treatments, see table 5.1.
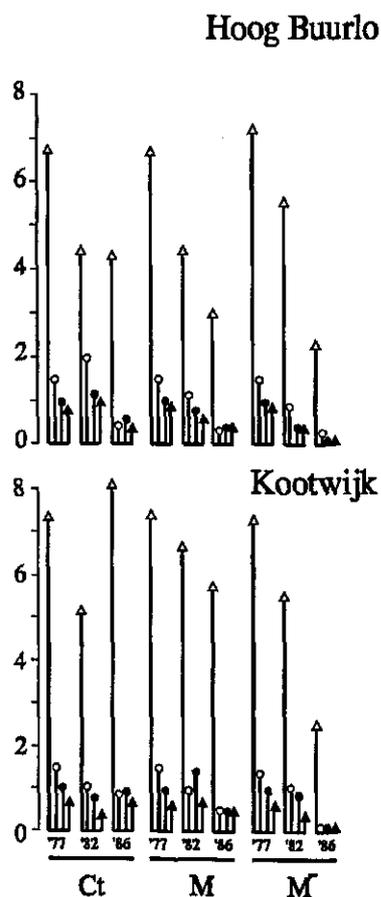
Figure 5.2
Organic matter and nutrients in the aboveground biomass litter and humified matter (TOM) in control plots (Ct), mown plots with (M-) and without (M) removal of hay, in 1977, in 1982 and in 1986. The figures for 1982 are derived from figure 5.1. For treaments, see table 5.1.

CHANGES IN PRODUCTIVITY

The production in cleared plots (treatments SR_0, SR_2, SR_5) in HB (1982) and KO (1982, 1986) was significantly lower ($P < 0.05$) than in the control plots (table 5.4). Exposure of the top soil and mowing did not produce significant differences (table 5.4). Exposure of deeper soil layers in one of the replicate plots (table 5.4; KO 1982) showed a lower production. This was because coarse sands with a low soil-moisture-holding capacity became exposed. Mowing and removal of hay also resulted in lower production than where hay was not removed (fig. 5.3). The production in ploughed and milled treatments (P, Mi) was somewhat lower than in the control plots. In HB the values were 3.2 and 2.4 ton/ha, and in KO 4.5 and 5.1 ton/ha, both in 1982 (not shown in table 5.4). The higher soil fertility in HB (table 5.2) is not reflected in the production figures in 1982 (table 5.4). The data for 1986 indicate that production in the HB site on relatively fertile brown podzolic soil recovered better from sod cutting and mowing than in KO on the nutrient-poor podzol.

LIMITING NUTRIENTS

The mean concentrations of nutrients in the hay of the mowing treatments are not significantly different from plots where the hay was either removed (treatment M-) or not removed (treatment M) (table 5.5). A significant difference exists between the brown podzolic soil in HB and the podzol in KO. The P/N ratio in KO is much lower, which suggests a P deficiency, while the higher P/N ratio in HB suggests that N may be a more limiting nutrient on that site. The P/N ratio is not extremely high, suggesting that N deficiency is probably not very great (see Procedures section).

Table 5.4
Estimates of the above-ground annual production (kg ha^{-1}yr^{-1}) at Hoog Buurlo and Kootwijk in 1982 and 1986. Coefficient of variation for total production < 15 %; <10 % for treatment M; for the production of individual species < 25 %

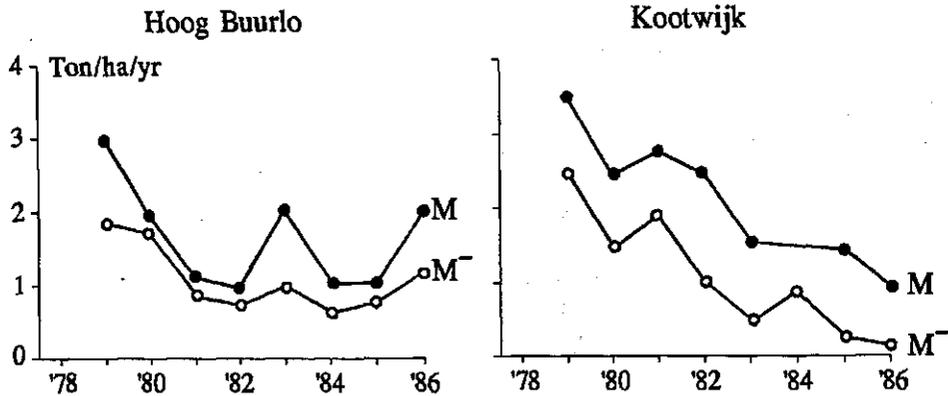| TREAT-MENT	HOOG BUURLO								KOOTWIJK			
	DESCHAMPSIA		CALLUNA		TOTAL		MOLINIA		CALLUNA*		TOTAL	
	1982	1986	1982	1986	1982	1986	1982	1986	1982	1986	1982	1986
Ct	5.0	2.0			5.0	2.0	5.6	3.3			5.6	3.3
M	0.9	3.0			0.9	3.0	2.5	1.4			2.5	1.4
M⁻	0.7	2.3			0.7	2.3	1.1	0.8			1.1	0.8
SR₀		0.6	2.5	2.0	2.5	2.6	1.2		1.4	1.5	2.6	1.5
SR₂	0.3	1.1	0.5	1.4	0.8	2.5	1.4**		1.6	1.1	1.6-2.7	1.1
SR₅	0.5	0.8	0.7	2.0	1.2	2.8	0.7**		1.8	0.7	1.8-1.4	0.7

*including some *Erica*; **present in one replicate only

Figure 5.3
Yields by annual mowing (in October or July) for hay with removal (M-) and without removal of the hay (M) at Hoog Buurlo and Kootwijk in the period 1978 to 1986.

Table 5.5
Mean percentages of nitrogen (N), phosphate (P) and Potassium (K) and P/N ratios in hay annually removed (treatment M-) or not removed (treatment M) in grass heath at Hoog Buurlo (HB) and Kootwijk (KO) in the period 1979 -1987. Coefficient of variation 25 %.

TREATMENT	N		P		K		P/N	
	HB	KO	HB	KO	HB	KO	HB	KO
M⁻	1.5	1.7	0.17	0.08	0.63	0.64	0.11	0.05
M	1.6	1.7	0.16	0.09	0.77	0.77	0.10	0.05

Discussion and conclusions

EFFECT OF BIOMASS REMOVAL ON PRODUCTIVITY

Removal of organic matter by sod cutting nearly halved the production for at least a decade, although on the relatively fertile brown podzolic soil the recovery of the production was somewhat faster. These results agree with the general hypothesis that the productivity on nutrient-poor soils can only be maintained by (tight) cycling of nutrients in the biomass, as suggested for tropical forest (Went & Stark 1968), heathlands (Gimingham 1972) and grassland (Floate 1970).

Evidence for a lower productivity after removal of biomass is limited to a

few studies. On nutrient-poor oxisols clear cutting of virgin tropical forest resulted in very low growth increments of a plantation forest (Jordan 1985). The negative effect of sod cutting on growth of a temperate plantation forest on podzols was shown (van Goor & Tiemens 1963). The removal of hay (Jones 1934 in Klapp 1971; Wolton 1963) was shown to result also in a lower productivity of grassland. But contrary to our results, in particularly with *Molinia*, the production stabilized where hay was not removed. As nutrient losses in our mowing experiments were large, even if the hay was not removed (table 5.3) some other factor must be involved. Possibly the depletion of carbohydrate reserves, as a result of a severe cutting regime may be the explanation. Such a factor would inhibit both the development of new shoots and the uptake of nutrients (Klapp 1971; Torvell et al. 1988), while enhancing nutrient losses.

Both production and TOM in the milling treatments (Mi) fully recovered. Thus, the vegetation which established after milling (mainly grasses, but also dwarf shrubs) was able to take up nutrients from littered biomass. In the ploughed plots (treatment Pl) the recovery was less in the *Deschampsia* site, probably because part of the ploughed-in organic matter could not be reached by the developing root system. Higher production figures were found in ploughed plots in the *Molinia-Deschampsia* site, where the soil profile showed that ploughing-in of organic matter was rather superficial.

P AND N AS LIMITING NUTRIENTS

The low P/N ratios suggest that P is the primary limiting nutrient on the Kootwijk site, a factor which is reflected in the low total P (0.01 % P) of the topsoil. The limiting nutrient in the brown podzolic at Hoog Buurlo soil may well be N, but the P/N ratio in the plant material is not very high, and a N-concentration of 1.5 in the soil does not seem problematic. However, in another Dutch heathland on brown podzolic soil (Westerheide, Gooisch Natuurreservaat near Hilversum), also with a relatively high concentration of total P of 0.05 % P (Diemont unpublished), N was the most limiting nutrient in a fertilization experiment (ter Braak 1982; Heil & Diemont 1983). In heathland soils in Scotland with a relatively high total P (0.03 to 0.2 %; Gimingham et al. 1979: table 14.4) N is probably the most limiting nutrient too (Miller 1976). In heathland soils low in phosphorus in Dorset and Devon, P is probably the most limiting nutrient (Chapman et al. 1989). In a fertilization study on phosphorus depleted podzols in The Netherlands with a total P less than 0.01 % (Diemont unpublished) no growth response of nitrogen was found (Prins et al. 1991) and a low P/N ratio (<0.05) in *Calluna* indicates that phosphorus is the most limiting factor. Low P/N ratios can also be calculated from other fertilizer experiments in heathlands with a podzol soil (Aerts & Berendse 1989, Aerts 1989a, b). P-deficient Australian heathlands with a total-P level in the soil as low as 0.002 % P (Groves 1981) - which is similar to a heathland podzol (table 5.2) - invariably show a response to P-fertilization only. Thus, an early suggestion that P is the limiting factor in Dutch heathlands (Aerts & Berendse 1988) should only be considered for heathlands on podzol. In general, N may be the most limiting nutrient in heathland soils, high in P, whereas in P-deficient soils P is limiting the growth.

P-deficiency may be induced in The Netherlands by increased atmospheric

nitrogen as a result of air pollution over the last two decades. This has been shown for stands of Douglas fir on a soil with 0.02 % total-P, but (in the same study) P-deficient soils (< 0.01 % total-P) already showed a low P/N ratio and no growth response to N-fertilizer ca. 30 yr ago - however, then levels of airborne N-pollution were much lower (Mohren et al. 1986). Podzols in Dutch heathland are probably very low in P and therefore P must always have been the growth-limiting nutrient in heathlands on podzol in The Netherlands.

REPLACEMENT OF CALLUNA BY GRASSES

Ploughing (treatment Pl) and in particular milling (treatment Mi) did not seriously decrease the productivity in the two grass heaths. Thus, the results confirm the idea that *Calluna* reached a degenerate phase in milled and ploughed plots within a few years as a result of a higher growth rate. This in turn made *Calluna* more susceptible to frost, causing an early death, and replacement by grasses. The higher production found in the plots cut for sods on the brown podzolic soil in HB probably limited the life-span of *Calluna*. Thus, on soils with a higher productivity grasses may replace *Calluna* at an early age.

6. EFFECTS OF BURNING ON NUTRIENTS IN HEATHLANDS

Summary

Nutrient losses due to burning were assessed for three *Calluna* heathlands in The Netherlands. Losses of both the standing biomass and humus layers were measured to be about 560 kg N/ha, 63 kg K/ha, and 23 kg P/ha. These losses, in particularly from the soil humus layers, are much higher than found in the literature. The extractable quantities of P and K were observed to be strongly increased immediately after a fire. Further, it is suggested that in heathland where growth is P-limited a nutrient pulse of P after a fire may induce a shorter life-span of *Calluna* due to a higher growth rate of *Calluna*.

Introduction

Fires may result in significant nutrient losses from both natural and cultural ecosystems (MacLean, Woodley, Weber & Wein 1983), but the information about nutrient losses is mainly based on combustion of the standing biomass in simulated fires, which does not consider potential losses from the (fermentated) organic matter layers (Allen 1964; Chapman 1967; Evans, Grimshaw & Allen 1971). The latter losses may indeed be disregarded for controlled spring fires in heathland, in case temperatures near the litter layer were below 100 °C (Gimingham 1972). Even, where higher temperatures near the litter layer have been recorded, it is postulated that combustion of organic litter layers is not likely, because the period of heating above 100 oC in the litter layer might be too short (Hobbs & Gimingham 1984). Field observations in Dutch heathlands, however, suggest that burning of the litter layer and humus layers is not exceptional. In this regard the present study was undertaken to assess the magnitude of total N, P and K losses in Dutch heathlands as well as the levels of 'plant available' N, P and K after a fire, which may affect productivity of a heath vegetation. Such information is also useful for simulation models which assess the impact of fire. So far these models did not consider the possible losses from nutrients in the litter and humus layers (de Jong & Klinkhamer 1983; Chapman, Rose & Clarke 1989).

Field description

Three sites of man-made *Calluna** dominant heathland in The Netherlands were sampled in spring 1) one month prior to burning, 2) immediately (within one hour) after the fire and 3) about 6 months later. The sites are referred to as Dwingeloo (52°50'N, 6°20'E), Asseltse heide (52°14'N, 5°49'E), and Strabrecht (51°25'N,

5°45'E).

Annual rainfall among the sites ranges from 720 mm to 820 mm. The mean annual air temperature ranges from 8.8 °C to 9.3 °C in the south. The vegetation is classified as a Genisto anglicae-Callunetum R. Tüxen 1937, but in the plots in Dwingeloo *Erica* tetralix Schwick, 1933 also occurs (de Smidt 1977). The soils in these sites are developed on Pleistocene aeolian sands. According the German classification soils are iron podzols and drained gley podzols (Schachtschabel et al. 1984). These types correspond to Haploquods and drained Haplohumods, respectively in the U.S. system (Soil Survey Staff 1975). Soil chemical characteristics of the mineral topsoil are listed in table 6.1.

Table 6.1
Percentage (dry weight) of organic matter (OM) and total N, P and K concentrations in the mineral topsoil (0-5 cm) in Dwingeloo, Asselt and Strabrecht.

LOCATION	pH_{H_2O}	pH_{KCl}	OM	N	P	K
					%	
Dwingeloo	3.9	2.9	15	0.23	0.012	0.033
Asselt	3.9	2.9	11	0.15	0.010	0.034
Strabrecht	4.1	3.0	18	0.12	0.010	0.023

Methods

TOTAL NUTRIENTS

Prescribed burning was done in the period March to April 1980. Data of moisture conditions in the field, wind speed (2 m height), fire spread, total organic material, including biomass and (humified) litter, and temperatures during the fires in different compartments are listed in table 6.2. These compartments refer to the standing crop, litter layer (L horizon), the (partly) humified organic layers (F- and H-horizon).

In particular the distinction between humified litter (F- and H- horizon) and mineral sub-soil is pivotal for calculation of changes in the carbon and nutrient stock before and after the fire. Fortunately, the transition between these soil compartments is sharp in the field also after a fire, as a result of lack of mixing between organic layers and mineral soil. After fire the L layer may include also charred remnants of the standing biomass and/ or charred remnants of the F and H horizon. In Dwingeloo the H horizon was absent in the samples after the fire, which is attributed to the large spatial variation of this layer. In Asselt and Strabrecht the H horizon was still visible after the fire.

In each site, 4 randomly chosen plots of 16 m², were marked by (iron) pins. In

each of the plots 12 randomly sub-plots of each 0.25 m² were sampled, before treatment as well as after a fire; the sub-plots samples were combined prior to further chemical treatment. volumetric bulk samples of the standing crop, L, F and H horizon were collected in each plot from 12 randomly taken sub-plots (0.25 m²). Thus, after completion of sampling in each site 4 samples of each compartment (standing crop, L-, F- and H- horizon) were available foR further chemical analyses before as well after a fire. Samples were air dried, sieved to exclude gravel (2 mm), but subsequently the sieved out organic matter was added again to the sample and also ground. Analyses included organic matter (loss on ignition at 600 °C), total nitrogen(N-Kjeldahl), total phosphorus (P) measured spectrophotometrically after digestion in a 1:1 mixture of H_2SO_4 (96 %): HNO3 (65 %); potassium (K) was measured in the digest by AAS.

Average total losses of carbon, N, P and K and 95 % confidence intervals were calculated per site. An analysis of variance was done to assess average total losses for all 3 sites, which followed closely the experimental design with in each site 4 randomly chosen plots, which is measured twice i.e. before and after a fire. This design leads to an ANOVA with three strata (sites, plots within sites, and time within plot) and one treatment factor fire. To meet the homogeneity of variances and normality requirements of an ANOVA, data were first logarithmically transformed. Homoscedasticity (Genstat 1987) was satisfactory, as judged visually from residual versus fitted values.

Table 6.2
Moisture content, combusted organic matter, wind speed, fire spread rate, organic material and temperatures reached during the fire.
Legend: Moist.= moisture (% dry weight base) before the fire; St.= standing crop;
L= Litter; F= humified litter (F and H horizon). W.S. = wind speed; RS = rate of spreading of the fire; B = total combusted biomass; TB, TL; TH = temperature at a height of 15 cm above ground, in the litter, and in the F+H horizon, respectively.

| | St. | L. | F. | WS | RS | B | TB | TL | TH |
	moist. %			m/s		kg/m²	°C		
Dwingeloo	82	153	231	3	0.5	2.0	800	500	40-100
Asselt	88	110	209	2	5	1.0	800	500	40-100
Strabrecht	77	137	106	5	5	1.5	--	--	40-100

EXCHANGEABLE NUTRIENT LEVELS

Exchangeable nutrients were determined before, immediately after the fire and also 6 month later in both the L and F horizon for each plot. Exchangeable P and K were extracted with 1 N ammonium acetate (pH 4.65). NH_4 was extracted with 2 N KCl, NO_3 was determined from the same extract after removal of ammonia and

addition of Devarda alloy according to Allen (1974).

Results

The concentrations of organic matter, total nitrogen and ash minerals in the litter and (partly) humified litter layers are of a same magnitude before and after a fire; the post-fire pH is somewhat lower for all three locations (table 6.3).

The amounts of organic matter and total nutrients on a surface base in each site before and one hour after a fire are given in figure 6.1 and 6.2. Most of the losses originate

from the organic F and H layers. The overall average losses for the 3 sites were calculated from an ANOVA with sites and replicates per site as random variables (see methods). After back-transformation of the logarithmic transformed data mean losses over the three sites are 56 gN/m^2, 6.3 gK/m^2 and 2.3 gP/m^2. Corresponding confidence intervals (95 %) after back-transformation are 14 to 61 gN/m^2, 1.9 to 5.2 gK/m^2 and 0.3 to 2.9 gP/m^2. The width of these intervals reflects a high variability, which is mainly explained (r=0.8) by the availability of organic matter in the standing biomass and in the L, F and H horizons (fig. 6.3).

Extracted amounts of P and K in the sites on a surface base (table 6.4) show a maximum immediately after the fire in the litter layer (L), but levels have decreased to pre-fire levels or less within 6 months. The mean site differences are significant (P < 0.05). Data for extracted ammonia and nitrate are only available for Dwingeloo, suggesting that post fire ammonia and nitrate levels are lower (table 6.5).

Table 6.3
Percentages organic matter (OM), total nitrogen (N), total phosphorus (P) total potassium (K) before (I) and immediately after (II) a fire in the litter soil horizon (L) and humified organic soil layers (F and H horizon).

|	LOCATION	OM I	OM II	N I	N II	P I	P II	K I	K II	pH_{H_2O} I	pH_{H_2O} II	pH_{KCl} I	pH_{KCl} II
L	Dwingeloo	90	81	1.8	2.0	0.08	0.09	0.09	0.11	4.4	4.3	3.6	3.4
	Asselt	76	73	2.1	1.8	0.09	0.09	0.09	0.11	4.5	4.3	3.6	3.3
	Strabrecht	90	84	1.9	1.7	0.08	0.07	0.09	0.09	4.7	4.3	3.5	3.3
L	Dwingeloo	68	73	1.5	1.7	0.06	0.06	0.15	0.08	4.3	3.8	3.4	2.8
	Asselt	65	55	0.7	0.7	0.03	0.04	0.07	0.07	4.0	3.8	2.9	2.8
	Strabrecht	—	—	—	—	—	—	—	—	—	—	—	—
L	Dwingeloo	29	53	0.6	1.1	0.02	0.04	0.07	0.07	3.9	3.9	2.9	2.9
	Asselt	34	38	0.7	0.7	0.03	0.03	0.07	0.07	3.8	2.8	3.8	2.7
	Strabrecht	37	35	0.8	0.8	0.04	0.04	0.06	0.07	4.2	4.1	3.1	3.0
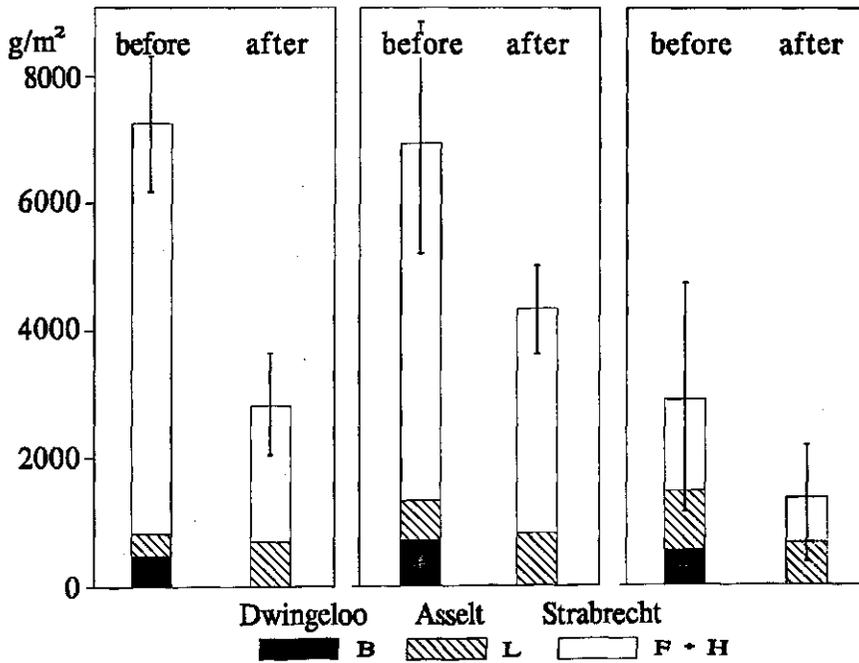
Figure 6.1
Pre-fire and post-fire organic matter quantities in three sites (95 % confidence intervals are indicated).
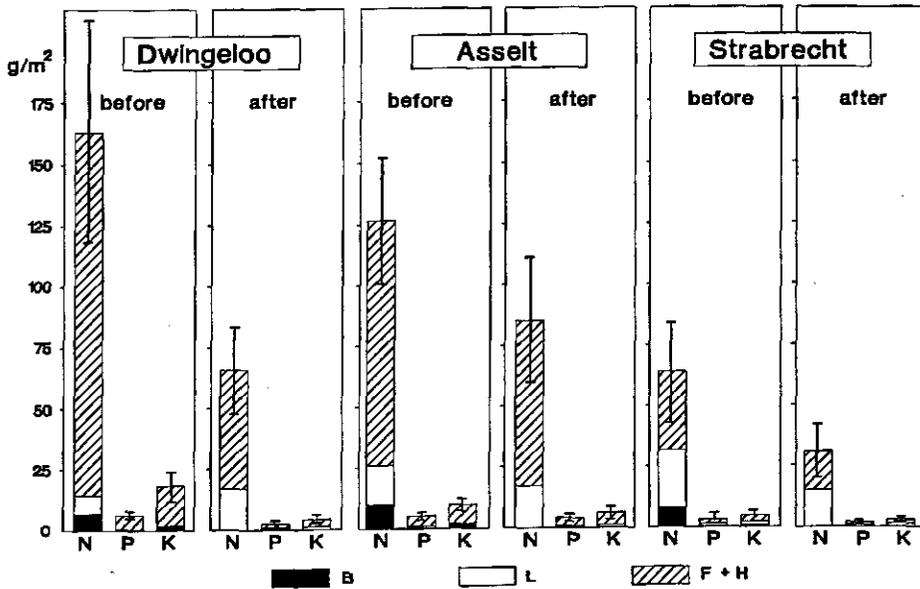

Figure 6.2
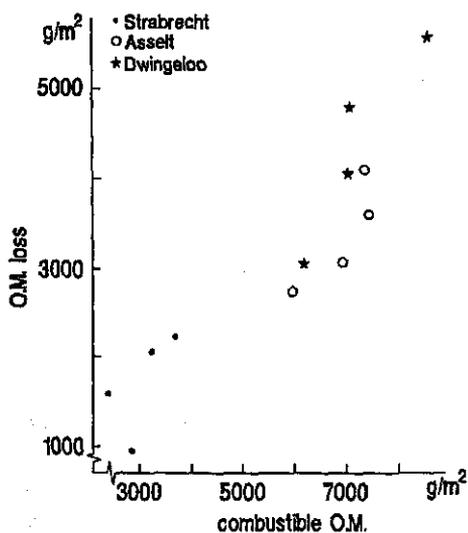Pre-fire and post-fire quantities of N, P, K in three sites (95 % confidence intervals indicated).

Figure 6.3
Post-fire losses of organic matter as a function of the available pre-fire combustible material (r = 0.81).

Table 6.4
Extractable potassium (K) and phosphorus (P) in the L and F horizon before(I) immediately after a fire (II) and 6 months later (III).

	LOCATION	P			K		
		I	I	III	I	II	III
				mg/m³			
	Dwingeloo	46	256	41	451	1108	88
L	Asselt	65	178	49	586	1241	201
	Strabrecht	47	145	61	830	1547	209
	Dwingeloo	311	120	114	n.a.	1099	474
F	Asselt	125	119	70	729	986	686
	Strabrecht	126	69	50	728	686	379

Table 6.5
Extractable ammonium and nitrate nitrogen in the litter layer (L) before burning (I) and immediately after burning (II) in Dwingeloo.

LOCATION	NO_3-N		NH_4-N	
	I	II	I	II
		mg/m³		
Dwingeloo	58	7	517	433

Discussion and conclusions

Average total losses of N in the present study are as high as 560 kg/ha N. Such losses are comparable with losses reported for fires in forests (MacLean, Woodley, Weber & Wein 1983) and much higher than a previous reported loss of 170 kg N/ha for *Calluna* heathlands (Chapman 1967). Losses of K and P (63 kg/ha K and 23 kg/ha P) in the present study are also high compared to estimates given by Chapman (2 and 9 kg/ha). The much higher losses of nutrients for heathlands indicated in the present study must be attributed to the fact that part of the organic layers (L, F and H) were also combusted. However, the nutrient losses differ for various sites. The highly variable effect of a fire is due to differences in the amount combustible material, the intensity and frequency of fires and soil properties (Hobbs & Gimingham 1984; Chapman, Rose & Basanta 1989). In the present study the amount of combustible material i.e. standing biomass and organic matter in the L, F and H horizon explains most of the variability in nutrient losses.

An important issue for management of heathlands is the effect of fire on plant nutrients levels and its consequences for plant growth. With respect to nutrient losses from fire, sources of nutrient replenishment should be known i.e. the inputs in the system by dry and wet deposition, inputs by N fixation, efficiencies of uptake of nutrient from various input sources, internal inputs from soil weathering, and losses of nutrients by leaching and erosion (Chapman, Rose & Clarke 1989). With exception of deposition figures for nitrogen, which has increased in result of pollution from a few kg per ha to some 50 kg ha^{-1} y^{-1} in The Netherlands (van Aalst 1984), the information on replenishment of nutrients cannot yet be answered. Despite the lack of pertinent information, it has been suggested that replenishment of N and P may become critical in heathlands (Chapman 1967; Gimingham 1972).

For the time being, we limit ourselves here to the possible effect of 'plant available' nutrients on growth of *Calluna* in heathland. Fire may induce a nutrient 'pulse', i.e. liberates nutrients tied up in biomass and litter (MacLean et al. 1983). Such a pulse may temporarily enhance the productivity and in the long run help to maintain the average level of productivity in grassland (Vogl 1974; Lamotte 1983), in fynbos (Stock & Lewis 1986) and in Black spruce forests (Viereck 1983). Nutrient pulses have also been described for heathland (Allen 1964; Allen, Evans & Grimshaw 1969), and the data in the present study confirm a nutrient pulse for P and K. It has been shown that P can limit plant growth in heathlands on podzols (Chapter 5) and therefore an increase of 'available' P may increase the productivity of *Calluna*. Indeed, productivity in burned *Calluna* heath was higher as compared to the productivity in previously mowed heath on podzols in the Lüneburger Heide in Germany (Muhle & Röhrig 1979). A higher productivity in a site due to increased nutrient levels may induce a lower life-span of *Calluna* (Heil & Diemont 1983; Chapter 5). As a result the management rotation cycle in a heathland may become shorter, implying a need for more intensive heathland management.

7. EFFECTS OF CLIMATE AND MANAGEMENT ON THE PRODUCTIVITY OF DUTCH HEATHLANDS

Summary

Effects of burning and turf cutting treatments on the productivity of *Calluna vulgaris* heathlands were studied for a climatologically dry site (Strabrecht) as well as for relatively wet sites (Dwingeloo/Hoge Veluwe) on podzol soils in The Netherlands. Productivity for specific site-treatment combinations was assessed from age-sequences (chronosequences) of the above-ground biomass in *Calluna* stands of different age-classes, and from indirect as well as direct estimates of the above-ground annual production.

A two parameter Mitscherlich curve $y=c(1-e^{-at})$ with $c=y_{max}$ is used to describe the relation between above-ground biomass (y) and age (t) for various site-treatment combinations. The relation is used to examine the effect of management and site on biomass. After correcting for age differences, biomass for plots subjected to turf cutting was a factor of 0.57 lower than in burned stands. The biomass in Strabrecht was lower by a factor of 0.81 than in Dwingeloo/Hoge Veluwe. Maximum indirect estimates of the annual production of burned heathland at Dwingeloo/Hoge Veluwe and at Strabrecht were 257 and 209 g m^{-2} $year^{-1}$, respectively and, for stands subjected to turf cutting, 147 and 119 g m^{-2} $year^{-1}$, respectively. Direct annual production estimates for various site-treatment combinations confirmed differences between site-treatment combinations obtained from indirect production estimates. The assumptions underlying the productivity estimates are discussed and possible causes of differences in productivity are indicated.

Introduction

Information on productivity in heathlands is available for lowland heath in England and upland heath in Scotland (Gimingham, Chapman & Webb 1979), but information is lacking for Continental heathlands.

Some estimates of the annual production of heather are available for Dutch heathlands (Berdowski 1987; Aerts 1989), but these estimates may have been biased by the method used, which does not account for the high spatial variability detectable even within a distance of 1 meter (Diemont, unpublished). Moreover, no attempt has been made so far to relate productivity of heather in The Netherlands to management practice (burning and turf cutting; in Dutch plaggen) and climatic conditions.

Productivity in heathlands can be assessed from biomass measurements in stands of different ages i.e. chronosequences (Gimingham et al. 1979). We selected

heathland sites on similar soil types where both burning and turf cutting had been practised, under different climatic conditions. This procedure allowed us to asses the effect of both treatment and climatic conditions on productivity, whereas soil conditions which may also affect productivity, are assumed constant. We further hypothesize that the humus left over after the last treatment reflects both climatic conditions (more humus accumulates in a wet climate) and treatment (turf cutting leaves less humus in the soil than burning). Because the nutrients in left-over humus may be an important resource and humus also improves soil moisture conditions, the amount of humus left probably affects the productivity on these nutrient poor podzols. It may therefore, be possible to replace climate and treatment, as explanatory variables for productivity by one factor i.e. the amount of humus in the F and H horizon.

The productivity of various site-treatment combinations in this paper are also assessed from annual production estimates. An indirect method was used to obtain an estimate for a long-term average above-ground production (g m^{-2} yr^{-1}). Furthermore, some direct annual production measurements were obtained, which can usefully be compared with indirect estimates.

The aims of this paper therefore can be summarized as follows: (i) to relate productivity in terms of biomass to management practice (burning or turf cutting) and climatic conditions (potential moisture deficits in summer) in The Netherlands; (ii) to test the possibility that instead of two explanatory variables (management and climatic conditions), the mass of organic matter in the F and H horizon could be used as a single variable of productivity in terms of biomass; (iii) to present an indirect method estimating long-term average above-ground annual production for various site-treatment combinations; (iv) to compare differences between indirect annual production estimates and differences in direct measurements; (v) to relate these estimates of the productivity from burned heathlands on podzols measured to estimates from the United Kingdom and to assess whether the data support the hypothesis that differences are due to both direct and indirect effects of climatic conditions.

Methods

FIELD DESCRIPTION

Sites were located in the north of The Netherlands near Dwingeloo (52°48'N, 6°20'E; Dwingeloose heide), in the central part of the country at Hoenderloo (52°9'N, 5°35'E; Hoge Veluwe) and in the south of the country near Heeze (51°23'N, 5°35'E; Strabrechtse heide). These sites were selected on the following criteria: (i) availability of sufficient age-classes of stands previously subjected to burning or to turf cutting in *Calluna* heathland; (ii) locations with relatively high and low potential moisture deficits in summer, which reflect the range of climatic conditions in The Netherlands; (iii) similar soil i.e. a podzol (not affected by ground water), to avoid confounding soil effects with climate or management effects; (iv) pure stands of *Calluna vulgaris* (L) Hull.

Heathlands with both burned and plaggen stands of different age on the

same soil (podzols) were only found at Dwingeloo, Hoge Veluwe and Strabrecht. Climatic conditions at Dwingeloo and Hoge Veluwe are relatively wet as shown by the potential moisture deficit, which is calculated on a monthly basis for the periods when potential evapotranspiration is in excess over precipitation (Green 1964), whereas temperatures are not much different (table 7.1). Unfortunately, stands subjected to turf cutting were all younger than 13 years. The reason for this is that turf cutting was abandoned in most heathlands in The Netherlands for decades, the work being too cumbersome and labour-intensive (Gimingham & de Smidt 1983). Only recently has this practice been re-introduced using mechanical equipment (Riem Vis & Diemont 1985).

All stands at Strabrecht and Hoge Veluwe were pure *Calluna*. At Dwingeloo *Erica* (*Erica tetralix* L.) mixed with *Calluna* was accepted up to a limit of 20 % of total ground cover in the stand as well as the presence of *Molinia caerulea* (L.) Moench, but biomass samples were taken from pockets with pure *Calluna*. The effect of grazing on biomass was negligible as grazing intensity by sheep or deer was less than 0.1 animal ha^{-1}.

The heath vegetation in the three heathlands is classified as a Genisto anglicae-Callunetum R. Tüxen 1937, but some of the plots in Dwingeloo with *Erica tetralix* show some affinity to Ericetum tetralicis Schwick, 1933 (de Smidt 1977). The soils in these sites developed on Pleistocene aeolian sands were podzols. According the German classification soils were iron podzols and drained gley podzols (Schachtschabel et al. 1984). These types correspond with Haploquods and drained Haplohumods, respectively (Soil Survey Staff 1975). The water table lay beneath the rooting zone.

Table 7.1
Climatic data for the heathland locations. (MAT = mean annual temperature; MT = mean temperature MAP = mean annual precipitation WD = average potential water deficit in months where the potential evapotranspiration exceeds precipitation (KNMI 1972).

LOCATION	MAT °C	MT JANUARY °C	MT JULY °C	MAP mm	WD mm
Dwingeloo	8.8	1.3	16.3	820	90
Hoge Veluwe	9.3	1.3	17.3	800	90
Strabrecht	9.3	1.7	17.3	720	125

DATA COLLECTION

The above-ground biomass data were obtained from the turf cutting and burning treatments of various age-classes at Strabrecht, Dwingeloo and Hoge Veluwe (fig. 7.1). The age-classes in figure 7.1 were derived from management maps of burned and plaggen treatments. Above-ground biomass and humus horizons were sampled at Strabrecht and Dwingeloo in 1979, and at Hoge Veluwe in 1980. Using a

pair of scissors each of a total of 70 plots was sampled from eight sub-plots of 0.25 m², in four out of eight sub-plots, samples of 0.0625 m² were taken from the F and H soil horizons.

Biomass and soil samples were air-dried and sub-samples of about 0.2 kg (wet weight) were oven-dried at 70 °C for 24 hours. Soil organic matter was measured by loss-on-ignition (375 oC) for 24 hours. Mean values and standard deviations for the standing crop (g m²) and for the mass of organic matter in the F (partly fermented litter) and H (humus) horizons (kg m⁻²) were calculated.

MODELLING ABOVE-GROUND BIOMASS

In order to examine the effects of management and site on above-ground biomass in stands of different ages, one must be able to correct for age differences. To achieve this one needs a satisfactory description of the relationship between above-ground biomass (y; g m⁻²) and age (t; year). Chapman, Hibble & Rafarel (1975) and Miller (1979) used a Gompertz curve to describe this relationship. However, since our data do not relate to any old stands subjected to turf cutting, and since furthermore young burned stands were lacking at Hoge Veluwe, this 3-parameter curve would have lead to over parameterization. It appeared out that our data, and those in the literature (Chapman, et al. 1975) can be satisfactorily described by a Mitscherlich curve:

$$y = c(1-e^{-at}) \quad (1)$$
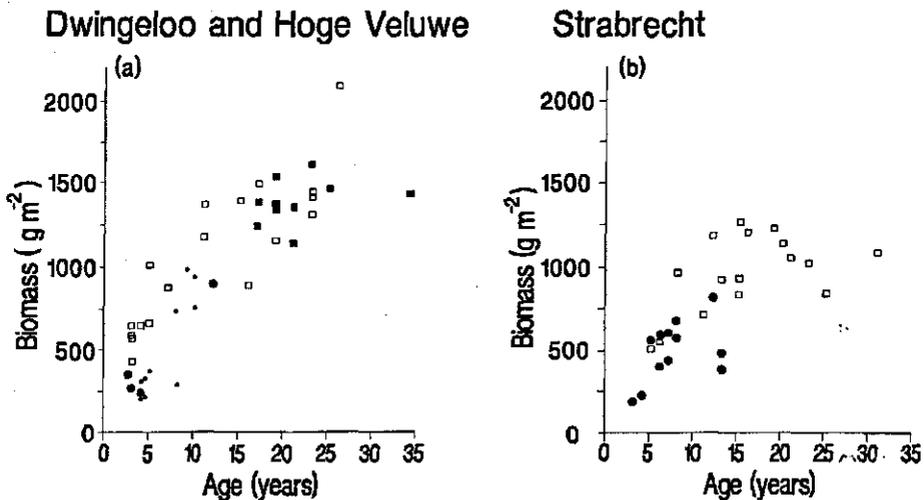
Figure 7.1

Biomass plotted in relation to age (year) for burned and stands subjected to turf cutting at (a) Dwingeloo □, ● and Hoge Veluwe ■, •; (b) at Strabrecht. Treatments: burning □; turf cutting ●.

Here c equals the value of the horizontal asymptote, which is the maximum biomass (y_{max}). The value of the parameter a determines at what age y_{max} is approached. If for instance a=0.15 then ymax is approached after 20-25 years.

In principle, the values of both a and c may depend on site and management, but for our data the parameter a can only be estimated for burned stands. Because parameter a was almost constant, sharing no statistically significant difference for burned stands at Strabrecht and Hoenderloo/Dwingeloo, parameter a could be considered equal for all burned sites. It had to be assumed that the value of a for burned sites was also applicable for turf cutting treatments.

Furthermore equation 1 should include a component which reflects stochastic variability. This residual variation increases as the biomass increases, implying a constant coefficient of variation. A model with constant residual variance, which allows a simple testing of management and site effects, is obtained by rewriting the model for the logarithm of y (Slob 1986). Hence, the following regression model was analyzed.

$$lny = ln(1-e^{-at}) + s + m + m_s + \varepsilon \quad (2)$$

where s = site effect, m = management effect, m_s = management site interaction and ε = a random error with constant variance.

For this regression model with one nonlinear parameter a, the effects of management x site interaction were tested by successive inclusion of these terms in the model. Because the effects of management and site may be partly confounded by the unbalanced sample design, we also tested the reverse order of inclusion. Back-transformation of equation 2 to 1 gives the effects of management and site reflected in parameter c. In the case when there is no management site interaction, the effects are additive on the log scale and thus proportional on the original scale.

We also examined to what extent the effects of management and site can be explained by one single variable i.e. the amount of humified litter (A; kg m^{-2}), which includes the quantity of organic matter (kg m^{-2}) both in the fermentated litter horizon (F) and in the humified litter horizon (H). To this end the effects of management and site were tested after first including A in the model.

The nonlinear regressions were performed with the computer program Genstat (Genstat Committee 1987).

ANNUAL PRODUCTION ESTIMATES

An indirect estimate of the total net above-ground annual production can be obtained from a linear relationship between biomass:annual production ratios and age for burned heathlands in the British Isles in stands younger than 25 years. The data are derived from different heathlands which comprise a wide range of environmental conditions (Gimingham et al. 1979; table 14.8).

A direct estimate in 1983 was obtained by measurement of the net above-ground annual production (g m^{-2}) of the green parts and flowers in plots previously used for biomass measurements. At that time only 49 of the original 70 stands used previously for biomass measurements could be sampled. Measurements included

current year's flowers, flower buds and long and short shoots (Miller 1979). Measurements were taken in November and may have therefore somewhat underestimated the contribution of flowers (Miller 1979). A mean figure for each plot was obtained from a bulk sample, comprising green parts and flowers in four subplots of 0.25 m^2. To minimize differences due to age between different site-management combinations measurements were (visually) corrected for the percentage of ground covered by *Calluna*, which is regarded as a major source of spatial variability in the annual production of green parts by this community (Miller 1979). For each site-treatment combination the mean and standard deviation are given.

Results

ABOVE-GROUND BIOMASS

The biomass data are displayed in figure 7.1. In the chosen regression model for ln(biomass), both management and site explain a significant part of the variation (table 7.2). The order of inclusion of these explanatory factors did not affect the significance. The interaction between management and site was not significant. The absence of a significant interaction between those two factors implies that the proportional effects of management were the same for all three locations and, conversely, the effect of location was the same

for different management types. Data from Dwingeloo and Hoge Veluwe (with similar climatic conditions) can be pooled, since no significant differences between these sites were found.

After back transformation the resulting model can be written

$$y = s\, m\, (1-e^{-0.12t}) \qquad (3)$$

where y = biomass (g m-2); the variable s assumes the value 1500 for Dwingeloo and Hoge Veluwe and 1215 for Strabrecht; the variable m assumes the value 1 for burning and 0.57 for turf cutting; and t = age (year).

This model is displayed in figure 7.2. The individual plots show a coefficient of variation of 28 % around the predicted value (since the residual standard deviation is 0.28 on the log scale). The model shows that plaggen as compared with burning nearly halved the biomass. The biomass at Strabrecht was also significantly lower than in the other two locations.

Adding the amount of humus A to the model showed that ln (A) gave a better fit than the untransformed A. After addition of ln (A) to the regression model the differences between sites became no longer significant; but there remained a significant effect of management, although the contribution of the latter had become less significant (table 7.3). After back-transformation the resulting model was:

$$y = e^{0.15+0.21\ln(A)}\, m^{(1-e-0.13t)} \quad (4)$$

where y = biomass (g m-2); A = humus (kg m-2); the variable m assumes the value 1 for burning and 0.74 for turf cutting; t = age of a stand (year). Individual plots show a coefficient of variation of 25 % around the predicted value. The model is

Table 7.2
Accumulated analysis of variance for successive inclusion of age, management, site and their interactions in the nonlinear regression model for ln(biomass). The results of a reverse order of inclusion for management and site are given in parentheses. df = degrees of freedom; SS = sums of squares; MS = mean squares

	dF	SS	MS	F		(F)
+age	1	17.97	17.97	238		
+management	1	4.09	3.31	54.1	(+site	15.6)
+site	2	0.81	0.41	5.4	(+management	35.5)
+management site	2	0.15	0.08	1.1		
-interaction residual	63	4.76	0.08			

Pooling Dwingeloo and Hoge Veluwe in the additive model: F=1.0
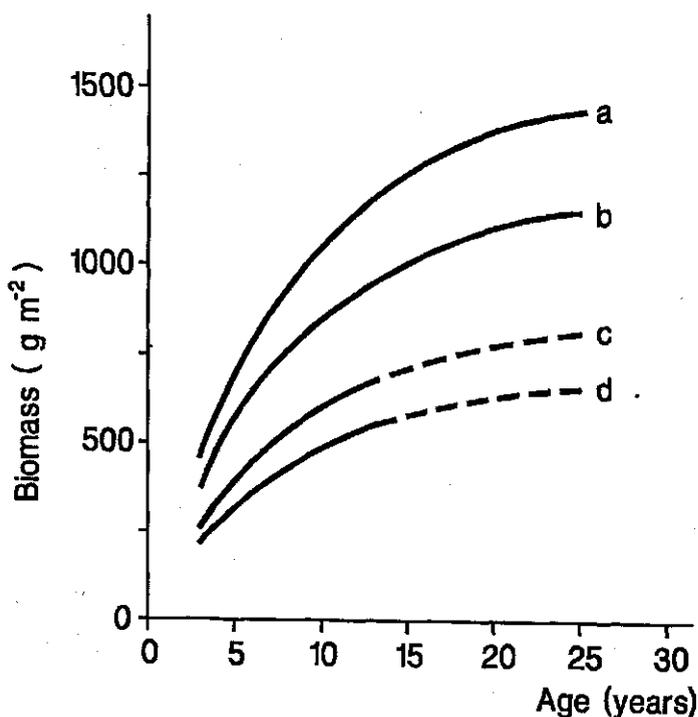
Figure 7.2
Time sequence of estimated standing biomass as a function of location and management. The coefficient of variation of the estimated biomass is 28 %. No observations available for broken lines. (a) and (c) burning and plaggen respectively at Dwingeloo and Hoge Veluwe; (b) and (d), burning and sod cutting respectively at Strabrecht.

Table 7.3
Accumulated analysis of variance for successive inclusion of age, the amount of humus ln(A), management and site in the nonlinear regression model for ln(biomass). The results of a reverse order of inclusion of management and site are given between brackets.

	dF	SS	MS	F		(F)
+ age	1	17.97	17.97	238		
+ ln (A)	1	5.62	5.62	89.2		
+ management	1	0.64	0.64	10.1	(+site	0.4)
+ site	2	0.14	0.07	1.1	(+management	11.6)
residual	64	4.05	0.063			
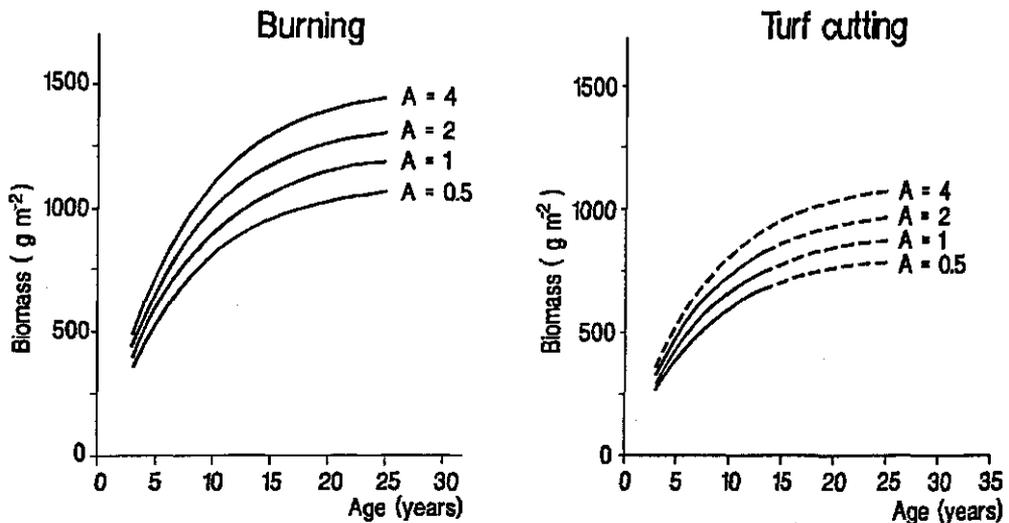
Figure 7.3
Time sequences of estimated standing biomass in relation to humus accumulation A (kg m^{-2}) in heathland previously subjected to   burning and turf cutting. The coefficient of variation of the estimated biomass is 25 %. For the pecked lines no observations are available.

displayed in figure 7.3. It can therefore be concluded that A explains differences between locations totally, but management effects are only partly explained by A.

NET ABOVE-GROUND ANNUAL PRODUCTION

The biomass: annual production ratio k calculated from the original data in the British Isles (Gimingham et al. 1979) increase linearly with age t (*year*) for *t*< 25 years. The following relationship was found: $k = 1.8 + 0.23\ t$; r=0.98 (fig. 7.4). After substituting the model equation for biomass, the following relationship between annual production p and age t was found:

$$p = \frac{s\ m(1 - e^{-0.12t})}{1.8 + 0.25t} \qquad (5)$$

This indirectly estimated production *p with variables s and m* (see equation 3) is maximal at an age of 9 years and is nearly constant between 6 and 15 years (fig. 7.5). The nearly constant production after 5 years probably reflects probably a full ground cover at later ages (Miller 1979). The maximal annual production i.e. the nearly constant production after 5 years in burned and plaggen stands at Dwingeloo/Hoge Veluwe was 257 and 147 g m^{-2} year^{-1} respectively; and at Strabrecht 209 and 119 g m^{-2} year^{-1}, respectively.

Direct measurements on productivity corrected for ground cover are shown in table 7.4. These figures are lower than the above indirect estimates for the maximal annual production in a closed stand, but show consistent differences for the four management-site combinations.
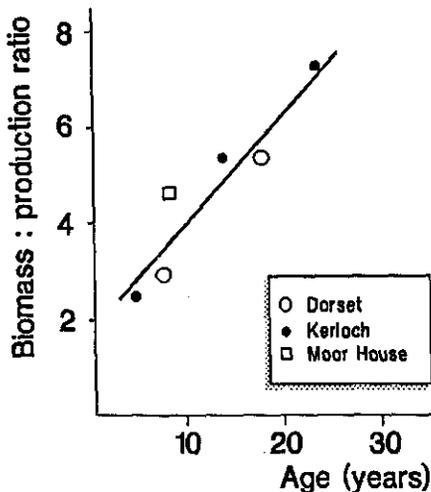
Figure 7.4
Relationship between biomass: production ratios and age (< 25 years) of burned heathlands in the British Isles.
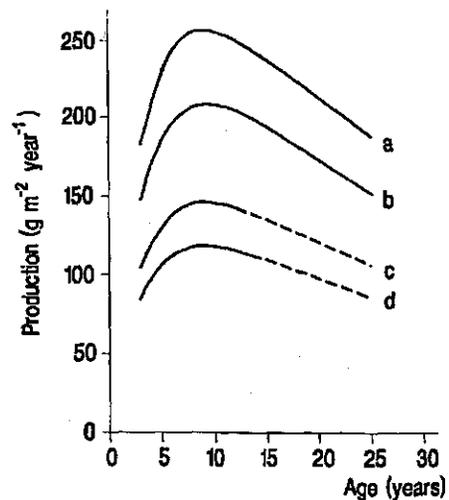
Figure 7.5
Indirect estimates of the annual production (g m^{2} year^{1}) for the site-treatment combinations specified in fig. 7.2. No data are available for broken lines.

Table 7.4
Annual production of green parts and flowers of *Calluna* (g m^{-2} year^{-1}) in 1983, corrected for percentage cover.

LOCATION	MANA-GEMENT	MEAN G M^{-2}	STANDARD DEVIATION G M^{-2}	n
Dwingeloo / Hoge Veluwe	Burning	158	81	21
	Turf cutting	87	32	7
Strabrecht	Burning	116	42	11
	Turf cutting	88	32	10

Discussion

The assumption of a constant value of parameter a for all management site combinations is somewhat restrictive for our conclusions on biomass. In fact we assessed management effects only for stands younger than 13 years, because older stands subjected to turf cutting were absent. For older stands the management effects can be extrapolated using the model, but the extrapolation depends on the assumption that parameter a is the same for turf cutting treatments as for burned stands. If future research reveals that parameter a depends on the kind of treatment, then the observed biomass ratio between plots subjected to turf cutting and burned plots (0.57) is still valid for plots younger than 13 years, but not for older plots. Circumstantial evidence in Dutch heathlands suggests (Chapters 3 and 5) that on relatively more fertile podzolic soils a (higher) y_{max} is reached earlier than on podzols with a lower y_{max}. This may hold for less productive stands subjected to turf cutting when compared with burned stands, implying a value somewhat lower than 0.12 for parameter a in turf cutting treatments, and hence the biomass ratio between plots subjected to turf cutting and burning exceeds 0.57 for stands older than 13 years. Further research is needed.

All variation in biomass which is explained by site, and most of the variation explained by treatment, was accounted for by the humus factor A. So it is possible to predict the biomass-age curve from an estimate of the amount of humus, provided that the previous treatment is known. This relation may be used in heathland management to predict the amount of future above-ground biomass in any heathland on a podzol in The Netherlands.

The chronosequence curves indicate a lower biomass in burned heathlands in The Netherlands than in the British Isles. The maximum biomass in Strabrecht and Dwingeloo was estimated as 1215 and 1500 g m^{-2}, respectively. These figures compare with 2000 g m^{-2} in Dorset/ Kincardineshire (Kerloch) and 3000 g m^{-2} in Devon (Dartmoor) (Chapman 1967; Chapman et al. 1975; Gimingham et al. 1979; Miller 1979). Comparison of the biomass curves in Dorset and Devon, which have a similar climate, showed that the productivity was higher on mineral-rich soils in

Devon than on mineral-poor soils in Dorset. At Kerloch the biomass was the same as in Dorset, the effect of relatively mineral rich soil at Kerloch being compensated by adverse climatic conditions (Gimingham et al. 1979; Miller 1979; Chapman & Clarke 1980). Differences in productivity between burned heathlands in Dorset, at Dwingeloo/Hoge Veluwe, and at Strabrecht are probably due to climatic differences (see below).

The maximum biomass in turf cutting treatments in Dwingeloo/ Hoge Veluwe and Strabrecht is 855 and 629 g m^{-2}, respectively. The lower productivity in heathland subjected to turf cutting is probably due to the more effective removal of litter, humus and associated nutrients by the latter technique (Gimingham & de Smidt 1983). Nevertheless, burning practices in The Netherlands may remove nearly as much nitrogen as turf cutting (Chapter 5). Thus, it is difficult at first sight to deduce how the productivity in heathlands subjected to turf cutting comes to be lower than in burned heathlands. The answer to this question is that phosphorus, which is less depleted by fire, rather than nitrogen, limits the productivity on podzols (Prins et al. 1991; Chapter 6). For the same reason higher levels of atmospheric nitrogen do not increase the productivity in Dutch heathlands on podzols, although they may do so on more fertile heathland soils, where nitrogen is the growth limiting factor (Heil & Diemont 1983; Aerts 1989; Chapter 5).

It is also important to consider, whether the linear relationship between biomass: annual production and the age of a stand in British heathlands (fig. 7.4) can be used to estimate the annual production from biomass in Dutch heathlands, since a lower biomass increment may be compensated by a higher litter fall (Chapman & Clarke 1980). We are confident that it is reasonable to use this relationship. Although the litter fall in The Netherlands is probably higher, following more frequent calamities such as infestation by the heather beetle, frost and summer drought, it is reasonable to assume that the reduction in biomass which results grow a higher litter fall has a proportional effect on the annual production in subsequent years, because most of the reduction in biomass reflects the loss of leaves; that is of photosynthetic apparatus. This would imply that indirect estimates of the annual production in Dutch heathlands can be compared with production measurements in the British Isles.

It should therefore be possible to assess possible climatic causes for differences between burned sites on podzol at Strabrecht, Dwingeloo/Hoge Veluwe and in Dorset. Mean annual temperatures for the three sites are rather similar. The sites differ however in moisture deficit. The average moisture deficit for months when potential evapo-transpiration is higher than rainfall is only 70 mm in southeast Dorset (Green 1964), but 90 mm for Dwingeloo/Hoge Veluwe and 120 mm for Strabrecht (table 7.1). Higher moisture deficits may depress the annual production, which may explain how the (maximum) annual production of 300 g m^{-2} year^{-1} in Dorset (Chapman et al. 1975) is highest, followed by an intermediate production in Dwingeloo/Hoge Veluwe (257 g m^{-2} year^{-1}) and a low production in Strabrecht (209 g m^{-2} year^{-1}). However, an alternative explanation is the higher frequency of outbreaks of the heather beetle, which is also controlled by climatic conditions, especially humidity (Cameron et al. 1944; Blankwaardt 1977; de Smidt 1977).

Dutch heathlands are not only lower in productivity, but the annual production is also more variable than at the British heathland sites mentioned in this

study. Annual production higher than has been reported from heathlands in the British Isles was found in two other Dutch studies (Berdowski 1987; Aerts 1989). On the other hand the production can be very low, even zero, due to calamities in Dutch heathlands. After severe frost a production (green parts and flowers) as low as 10 g m^{-2} $year^{-1}$ was measured (Diemont unpublished). Thus, although the high estimates may be biased (see Introduction), it is evident that annual production in Dutch heathlands may be very variable, which may explain the lower annual production in 1983 (table 7.4), whereas annual production in the British Isles is rather stable (Miller 1979).

8. SOME CONSIDERATIONS ON MANAGEMENT AND THE GEOGRAPHIC POSITION OF HEATHLANDS

Summary

The position of *Calluna vulgaris* at the margin of its geographic range margin is reflected by its shorter life, productivity, competitive power, and its narrower eco-edaphic range. We suggest that adverse climatic conditions in the geographic margin can be compensated for by lower nutrient levels. The implication of this hypothesis is that, towards its geographic range margin, heathland management should be more directed towards nutrient removal than it need to be in the centre of its range.

Introduction

In this paper, we relate the geographic position of *Calluna vulgaris* in lowland heathland in the British Isles and The Netherlands with several ecological traits, considering the nutrient depletion needed to maintain *Calluna* dominance, to be a function of this position. *Calluna* heathlands in Europe are found in the climatically oceanic region (Koppen's Cfb climate) and on rather nutrient-poor soils. To avoid succession, these heathlands are managed by controlled fires, grazing, mowing, or by removal of the biomass and the organic topsoil (called sod cutting in English, and 'plaggen' in Dutch).

Although the principles of heathland management are clear (Gimingham et al. 1972; Berendse 1990), the level of nutrient depletion necessary to maintain heaths is still debated (Gimingham 1987). Earlier recommendations in both the British Isles and in The Netherlands to use fire for management of *Calluna* heathland emphasized the need to limit nutrient losses (Anonymous 1953; Anonymous 1977; Gimingham 1992). This is why in the fifties the previously widespread habit of 'plaggen' in Dutch heathlands was no longer recommended (Anonymous 1953).

So far, nutrient levels required for heathland survival have not explicitly been related to the geographic position of a *Calluna* heathland. In this paper, we summarize the available information on ecological traits i.e. on longevity, productivity, competetivity and eco-edaphic range as expressions of (cf. Hengeveld 1990) the geographic position of *Calluna* in lowland heath in the British Isles and The Netherlands. The available information is rather circumstantial, but supports the hypothesis that towards the geographic range margin of *Calluna*, adverse climatic conditions such as drought, frost and the damage from the heather beetle,

may to some extent be counteracted by maintaining low nutrient levels in heathlands.

Circumstantial evidence

ECO-EDAPHIC RANGE

Calluna heathlands are usually confined to soils with low nutrient content (Gimingham et al. 1979), but in the British Isles they are found in a wide array of geological formations, ranging from Eocene sands, peat, coastal sand dunes, granites, and meta-basic igneous till (Gimingham et al. 1979) to calcareous substrates (Grubb et al. 1969). These British formations therefore represent a wide range of soil fertility, whereas in The Netherlands, heathlands occur on a narrow range of substrates, i.e. on Pleistocene aeolian quartz sands, loamy fluvio-glacial deposits, and deposits of pushed moraine and shallow loess (de Smidt 1966; Diemont & Heil 1984). A wider eco-edaphic range is indicative of a central position within its geographic ranges (Hengeveld 1990). However, comparisons in this respect are biased because the full range of geological substrates in the British Isles does not occur in The Netherlands. Nevertheless, most Dutch heathlands are found on nutrient-poor podzol soils, whereas only a few occur on more fertile brown podzolic soils.

PRODUCTIVITY

Differences in the net above-ground production of *Calluna* in different stands may reflect differences in age of the stand, differences in soil type, climatic conditions and previous management. The many factors affecting the primary production pose as many problems to make comparisons between the productivity of different stands and sites. Age sequences of the standing biomass in combination with information on soil type, management such and the close correlation between biomass and above ground productivity provide however the means to compare the single effects of soil, management and climate on the productivity of *Calluna*. Effects of soil and management and climate on productivity is already discussed in Chapter 7 and the information there is summarized for the present discussion. Net above-ground annual production for similar soil conditions as a measure of productivity in lowland *Calluna* heathlands subjected to controlled burning is higher in the British Isles than in The Netherlands. The maximum annual production in burned heathlands in Dorset in southern England is ca. 3 tonnes $ha^{-1}yr^{-1}$ (Chapman et al. 1975). This result was also obtained in Grampian (Miller 1979), where a higher soil fertility is probably offset by adverse climatic conditions (Chapman & Clarke 1980). In The Netherlands, but on similar soils as in Dorset, the maximum annual production in burned heathland in Dwingeloo in the North and Strabrecht in the South is 2.5 and 2.0 tonnes $ha^{-1}yr^{-1}$, respectively (Chapter 7). The differences between Dorset, Dwingeloo and Strabrecht, despite similar management and soil conditions, can be attributed to difference in climate, i.e. to evaporation in the absence of other climatic differences such as temperature (Chapter 7). Higher levels of evapo-transpiration can incur damage of *Calluna*. These higher levels are either

due to summer drought, or to outbreaks of the heather beetle *Lochmaea suturalis*) which damages the photosynthetic apparatus. The lower productivity of *Calluna* in The Netherlands and its larger annual variability in productivity, resulting from adverse climatic conditions, are indicative for a marginal geographic position (Hengeveld 1990) of *Calluna*, which is most pronounced at the climatologically marginal southern parts of the country.

LONGEVITY

In British heathlands, *Calluna* can become more than 40 years old (Chapman et al. 1975; Miller 1979), whereas in The Netherlands it rarely reaches 25 years (Beijerinck 1940; Stoutjesdijk 1953). This reduced lifespan is probably caused by a higher damage incidence from frost, summer drought, and climate-induced infestation by the heather beetle (Blankwaardt 1977; de Smidt 1977), expressing *Calluna*'s geographically marginal position in The Netherlands. However, the above information is rather circumstantial and for instance biomass age sequences (fig. 7.1) suggest that *Calluna* may reach an age of 30 years (see also Berendse 1990). For instance, figure 7.1 suggests that also burned stands in The Netherlands may reach an age of 30 year.

Longevity, just as other ecological traits, can further be modified by factors such as soil fertility and management intensity. Shorter life-spans were found after soil fertilization, and can be attributed to a higher growth rate under these conditions (Heil & Diemont 1983). Higher nutrient levels triggered by ploughing and mulching has a similar effect as fertilization. Life-span is also shorter on relatively nutrient-rich, brown podzolics than on nutrient-poor podzol soils. Nutrient depletion by, for instance, sod cutting has a positive effect on longevity (Chapters 3 and 5).

COMPETITIVENESS

Calluna can be stable on exposed cliffs and in maritime heaths, where, without management interventions, climatic conditions both prevent invasion by trees and shrubs, and allow re-juvenation from seed or from adventitious trailing roots (runners). Yet, in most habitats, probably also in Dutch maritime heath (Huisman, Berendse & Olff 1995), management is necessary for preventing trees and shrubs to invade (Gimingham et al. 1979; Gimingham 1992).

Factors affecting the rate of succession of a heath into woodland, for example, the dispersion of tree seeds, are not well studied. As information with respect of encroachment of trees is lacking, the discussion on competitiveness and geographic position is focused on succession of *Calluna* heathland into grass heath. In the Pennines, changes from *Calluna* heath into a *Molinia* grass heath some 75 years ago (Jefferies 1915) probably resulted from a too frequent burning in combination with intensive grazing (Grant et al. 1963; King & Nicholson 1958; Gimingham 1970). More recent changes reported from Dutch heathlands (Dijkhuizen et al. 1976; Diemont et al. 1982; Diemont & Heil 1984; Chapter 6) are however attributed to higher nutrient levels through litter accumulation in the absence of management (Berendse 1990). The latter successional changes in Dutch heathlands can even be accelerated by a higher nitrogen input through precipitation. Higher

nitrogen input has been shown to affect the rate of transition of a *Calluna* heath into grass heath (Heil & Diemont 1983) on relatively fertile brown podzolics, but not on less fertile podzols where growth is limited by phosphorus (Chapter 6). Although in former cases higher nitrogen promotes a higher incidence of gaps in Dutch heathlands (Chapter 3), it should be noted that one of the main causes of a transition from *Calluna* heath into grass heath is the limited lifespan of *Calluna* plants and the impossibility for *Calluna* seeds to germinate unless accumulated litter is removed (Pons 1989; Chapter 4).

The crucial role of suitable gaps for the germination of *Calluna* seeds is also indicated there where changes are temporary rather than successional, that is when succession is cyclic (Watt 1947). Although the existence of cyclic changes has been questioned (Marrs 1986, Marrs et al. 1986), cyclic changes with a temporary replacement of *Calluna* by *Molinia caerulea* or by *Deschampsia flexuosa* have been observed in Dutch heathlands after gaps were formed (Stoutjesdijk 1953; Beijerinck 1940, plate XXV; Stoutjesdijk 1959; de Smidt 1966). Cyclic changes in unmanaged heathland, without a temporary replacement of *Calluna* have also been found in Dutch heathlands after *Calluna* died off (Diemont & Heil 1984, Diemont unpublished). Moreover, where gaps are formed after a fire, grasses can also become a temporarily dominant (Stoutjesdijk 1953; Malmer 1965; Clement & Touffet 1981; Gimingham 1972). Severe fires, however, burn most of the accumulated litter and destroy all grasses and short-lived grass seeds, as was observed in the National Park 'De Hoge Veluwe', The Netherlands (Boers pers.com.).

Climate is the main factor determining the frequency with which the vegetation is opened and with which gaps suitable for competitors are formed. Climatic agents in The Netherlands for an untimely replacement of *Calluna* by, for instance, grasses include frost, summer drought, as well as a climatically induced higher outbreak frequency of the heather beetle (Blankwaardt 1977; de Smidt 1977). Such catastrophic climatic events reduce the longevity of *Calluna*. Direct evidence exists for an early replacement of *Calluna* by grasses after heather beetle gaps in Dutch heaths (Berdowski & Zeilinga 1987; Aerts et al. 1990).

Thus, adverse climatic conditions, leading to a higher incidence of calamities, are the main cause of the untimely formation of gaps, which are unfavourable for *Calluna*. This process can even be speeded up by increased nutrient levels, which shorten the life span of *Calluna* through increasing its growth rate. Alternatively, higher nutrient levels may also cause the outcrowding of *Calluna* by grasses. Early experiments indeed suggest that growth rates of *Molinia caerulea* increase relative to those of *Calluna* (Heil & Bruggink 1987), but further experimentation suggests that outcrowding of *Calluna* by *Molinia* at increased nutrient levels is not likely (Aerts 1990).

In the absence of management, adverse climatic and increased nutrient levels events speed up the transformation of *Calluna* heaths into grass heaths. A decrease of the competitive power of *Calluna* corresponds with its occurrence in its geographical range margin.

Discussion

The reduced longevity, productivity and competitiveness of *Calluna* in Dutch heathlands as compared to that in British lowland heaths indicate in The Netherlands *Calluna* is geographically in a more marginal position. This marginality can be attributed to adverse climatic conditions. However, differences in soil fertility as well as differences in management between sites can bias a straightforward interpretation of the available information. In particular, the interpretation of productivity in terms of the geographic position is difficult. Damage to the photosynthetic apparatus of *Calluna* by infestation of the heather beetle or by climatic actors, such as by frosts or by summer droughts, lower *Calluna*'s longevity and competitivity, which reduce the average annual production (Chapter 7). However, a decrease in productivity due to nutrient limitation may diminish negative effects of adverse climatic conditions. This occurs when *Calluna* shifts to poorer soils or to soils where nutrients are removed through intensive management. The physiological mechanism is that growth limiting nutrient levels will induce higher reserves of non-structural carbohydrate (Matson 1980; Chapin 1980). The explanation of this inverse relationship between nutrient levels of the soil and carbohydrate reserves in the plants is that the conversion of primary non-structural photosynthates to structural plant material is more inhibited than CO^2 assimilation under conditions of growth-limiting low nutrient levels (van Keulen et al. 1989). This inverse relation between growth and carbohydrate reserves on the one hand and the positive effect of higher carbohydrates on restoration of the photosynthetic ability of *Calluna* after damage has indeed been found (Berdowski & Siepel 1988). This implies that the relationship between low nutrient levels and the occurrence of *Calluna* heathlands is tighter in the climatically induced geographic margin than in the range centre.

Although the evidence on the eco-edaphic width in the British Isles and in The Netherlands is still inconclusive, differences in nutrient removal between these countries are rather clear. In the past, nutrient removal by sod cutting was far more intense in Dutch than in British heathlands, although burning (Chapter 6) and probably also sheep grazing removes nutrients, but to a lesser extent. In The Netherlands, the sods from about 800,000 ha heathland mixed with the droppings of sheep were used to manure 300,000 ha of arable land, resulting in so called 'plaggen' soils. Because of the annual addition of this manure these soils are 50 to 100 cm higher than the surrounding area.

As mentioned above burning also causes nutrient losses. At least under Dutch conditions nitrogen losses due to burning can be as high as those for sod cutting. This does not hold for the removal of phosphorus (Chapter 6). Phosphorus appears to be the main growth limiting factor in heathlands on true podzol soils, as these contain little phosphorus (Gimingham 1972; Chapman et al. 1989; Chapter 5). Therefore, in Dutch heathlands extensive nutrient removal, in particular phosphorus, is probably crucial on the majority of phosphorus-limited soils. On podzol soils, but probably not on brown podzolic soils, the life-span of *Calluna* is longer after a sod cutting treatment than after prescribed burning. In the case of brown podzolic soils, where growth is nitrogen-limited, the longevity of *Calluna* in sites subjected to sod cutting will not differ very much from sites subjected to prescribed burning, because nitrogen losses due to either management interventions are more or less similar.

SUMMARY

OBJECTIVES OF THE THESIS

Heathlands in The Netherlands are vanishing due to the invasion of trees. The transition from heathland to woodland in Dutch heathlands may either proceed directly or is preceded by the development of an intermediate grass heath. These changes are due to natural succession in the absence of management. In addition to the absence of management atmospheric pollution i.e. increased inputs of nitrogen has accelerated the replacement of heather heath by grass heath.

The main hypothesis in this thesis is that the encroachment of grasses in heathlands as well as the response of the vegetation to management and environmental change depend on soil type, climatic conditions, and previous management. This thesis deals in particular with the performance of heather (*Calluna vulgaris*) and grasses (*Molinia caerulea*, *Deschampsia flexuosa*) on dry lowland heath as a function of environmental conditions in a site, with the purpose of matching management options with site conditions (Chapter 1).

CHANGES IN DUTCH HEATHLANDS

Evidence for replacement of heather by grasses in The Netherlands was obtained from sequential air photographs of heathlands. It is shown that apart from the transition of heathland to woodland, even before atmospheric pollution started in the seventies, heather was already being replaced by grasses in sites where there was no periodic management. However, in most sites the increase of grasses has been accelerated appreciably during the last decade (Chapter 2).

RESTORATION OF HEATH

The results of long term field experiments (since 1976) show that a heathland taken over by grasses can be restored by turf cutting. Other treatments i.e. burning, ploughing or mowing treatments had no result, or in the case of mowing (including removal of the biomass), the result was short lived (Chapter 3).

The good result of turf cutting may be due to physical environmental changes or changes in nutrients. It is shown that the establishment of heather after turf cutting has partly a physical explanation i.e. can be attributed to exposure of the bare soil, which enables heather seeds in the seed bank to germinate, while the short-lived grass seeds are absent (Chapter 4). These results also suggest that direct succession of heath to woodland (without a grassy stage) is due to the absence of grass seeds.

SOIL TYPE AND LIFE SPAN OF HEATHER

Although the establishment of heather after turf cutting has a physical explanation, the removal of nutrients by turf cutting does increase the life span of

Calluna and reduces the competitive ability of the grasses. The effect of turf cutting lasts longer on poor soils. A heathland subjected to turf cutting appears to be more enduring on podzol soils than on more fertile brown podzolic soils, where the lifespan of heather plants is shorter. The advantage of a longer life span of heather is that the formation of suitable gaps for the establishment of grasses or other species is retarded (Chapter 5). Furthermore, in this chapter it is shown that the accelerated encroachment of grasses in heathland due to atmospheric pollution (Chapter 2) is likely to occur only in heathlands on brown podzolic soils. On such soils growth is limited by nitrogen, whereas on podzol soils, where growth is limited by phosphorus, nitrogen does not affect growth (Chapter 5).

MANAGEMENT AND LIFE SPAN OF HEATHER

The nutrient status of a site depends not only on the soil present, but also on the management, and therefore growth rates and the life span of heather probably also depend on these. An analysis of the effects of burning on nutrient levels reveals that as much nitrogen may be depleted by fire as by turf cutting, particularly if the shorter rotation period of prescribed burning is taken into account (Chapter 6). Thus, it seems likely that the nitrogen-depleting effects of turf cutting and burning are more or less equal on brown podzolic soils, where nitrogen is the growth-limiting factor. Turf cutting, however, depletes phosphorus more effectively than burning and the phosphorus available to plants may even increase after a fire (Chapter 6). This implies that growth rates on podzol soils will be higher on burnt heath than on heath subjected to turf cutting. A comparison of growth of *Calluna* in Dutch heathlands confirms this (Chapter 7).

CLIMATE AND LIFE SPAN OF HEATHER

Finally, the effect of climatic conditions on the performance of heather is assessed. It is shown that the climate in The Netherlands - especially in the south of the countries sub-optimal for heather (Chapter 7). Periodic drought and frost frequently damage heather in Dutch heathlands and make it more susceptible to attack and damage from the heather beetle (Chapter 8).

THE NEED FOR SITE SPECIFIC MANAGEMENT

It is hypothesized that heather plants in The Netherlands have a shorter life span because the climatic conditions are adverse for them. These adverse conditions can, however, be compensated to some extent by low nutrient levels, which induce higher carbohydrate levels in the heather plants. Plants with enhanced carbohydrate contents are less susceptible to plant damage and enable the plant to regrow after dying back. It is concluded that under climatic conditions that are sub-optimal for heather, as occur in The Netherlands (particularly in the South) heather can only for longer periods survive if nutrient levels are low. Turf cutting as practised in The Netherlands in the past was therefore not only an economic necessity, but seems also to be ecologically necessary if Dutch heathlands are to be kept purple (Chapter 8).

SAMENVATTING

DOEL VAN HET ONDERZOEK

Heidevelden in Nederland verdwijnen, waarvoor al dan niet na een grasstadium bos in de plaats komt als gevolg van een natuurlijke successie. De successie kan worden onderbroken door de heide te beheren. Er zijn aanwijzingen dat de successie van hei naar grashei versneld kan worden door een toename van de stikstofdepositie.

De hypothese in dit proefschrift is dat zowel de toename van grassen in heidevelden als de reactie van een heidevegetatie op beheer en luchtverontreiniging afhangen van de lokale bodemgesteldheid en de klimaatomstandigheden.

Met name wordt ingegaan op de reactie van struikheide en de twee meest voorkomende grassen pijpestrootje en bochtige smele, met als uiteindelijk doel om beheersadviezen te formuleren die zijn toegesneden op de specifieke milieuomstandigheden (Hoofdstuk 1).

VERANDERINGEN IN NEDERLANDS HEIDEVELDEN

In hoofdstuk 2 is nagegaan aan de hand van luchtfoto's wat er in de periode 1930-1990 is veranderd in de heide. Aangetoond wordt dat de heide in velden met weinig of geen beheer op veel plaatsen is vervangen door bos en door grassen, waarbij de indruk bestaat dat de vergrassing sinds 1970 versneld is ten gevolge van luchtverontreiniging.

HERSTEL VAN DE HEIDE

Resultaten van langdurige experimenten in de vergraste heidevelden vanaf 1976 in hoofdstuk 3 tonen aan dat de heide hersteld kan worden door de vergraste heide af te plaggen, waarbij aanwijzingen zijn gevonden dat het succes van afplaggen mogelijk is te verklaren door zowel veranderingen in het fysieke milieu als door veranderingen in de beschikbare nutriënten.

KIEMING VAN STRUIKHEIDE

De fysieke verandering door het plaggen bestaat hierin dat kiemkrachtig heidezaad in de bodem aan de oppervlakte komt en in het licht kan kiemen, terwijl graszaden met een korte levensduur niet langer aanwezig zijn. Deze resultaten suggereren dat het soms ontbreken van een grasstadium in de successie van heide naar bos verklaard kan worden door de afwezigheid van graszaden (Hoofdstuk 4).

BODEMTYPE EN LEVENSDUUR VAN HEIDE

Hoewel de vestiging van Struikheide na plaggen geheel verklaard wordt uit veranderingen in het fysische milieu ten gevolge van afplaggen, zijn het de verande-

ringen in het nutriëntenaanbod door plaggen die een belangrijk effect kunnen heb-
ben op zowel de concurrentiekracht van de grassen als de levensduur van struikhei-
de en daarmee ook bepalen hoe lang het duurt voor de heide weer vergrast. Uit
hoofdstuk 5 blijkt dat het effect van plaggen het langste in stand blijft op de armste
bodem. Een heideveld blijft langer door struikheide gedomineerd op voedselarme
humuspodzolgronden, waar de plant langzamer groeit, waardoor de levensduur lan-
ger is dan op de wat voedselrijkere moderpodzolgronden. Een langere levensduur
van struikheide heeft het voordeel dat het langer duurt voordat er weer een geschik-
te groeiplaats ontstaat voor grassen en andere soorten. Ook wordt in dit hoofdstuk
aangetoond dat een toename van vergrassing door verhoogde stikstofdepositie in de
jaren '70, waarschijnlijk alleen plaats heeft gevonden op de rijkere moderpodzolen,
waar stikstof de groeibeperkende factor is, maar niet op armere humuspodzolen
waar fosfaat de beperkende groeifactor is.

BEHEER EN LEVENSDUUR VAN STRUIKHEIDE

Niet alleen het bodemtype, maar ook het beheer kan van invloed zijn op de
beschikbaarheid van nutriënten en daarmee op de groei èn de levensduur van struik-
heide. Ruwweg komen op heidevelden twee bodemtypen voor: voedselarme humus-
podzolgronden en de wat voedselrijkere moderpodzolgronden. In hoofdstuk 6 wordt
aangetoond dat met branden minder fosfor wordt afgevoerd dan met plaggen, wat
zou betekenen dat op humuspodzolgronden de groei van struikheide na branden
hoger is dan na plaggen, omdat op deze bodem fosfaat immers de groei beperkt. Maar
voor voedselrijkere moderpodzolen, waar stikstof de groei beperkt, is het verschil
tussen branden en plaggen niet groot, omdat de stikstofafvoer door branden in
dezelfde orde van grootte ligt als de verliezen die optreden door plaggen. In hoofd-
stuk 7 wordt inderdaad waargenomen dat de groei van struikheide op humus-
podzolgronden na branden veel lager is dan op geplagde heide. Het ligt daarom voor
de hand (en de kortere rotatieperiode in gebrande heide wijst daar ook op) dat de
levensduur van *Calluna* in gebrande heide dan ook korter is dan in geplagde heide,
althans voor humuspodzolen. Harde gegevens daarover ontbreken echter nog.

KLIMAAT EN LEVENSDUUR VAN HEIDE

Tenslotte is in hoofdstuk 8 aandacht besteed aan de effecten van het klimaat
op de groei en levensduur van struikheide (Hfdst. 8). De hypothese is dat in
Nederland het klimaat minder goed is voor struikheide dan wel gedacht wordt.
Periodiek komen droogte en vorst voor en het is ook waarschijnlijk dat de schade aan
struikheide door het heidehaantje op de eerste plaats is terug te voeren op het kli-
maat. Het suboptimale klimaat in Nederland (vorst, droogte en sterfte door heide-
haantje) betekent ook dat de levensduur van struikheide hier korter is. Deze veron-
derstelling wordt ondersteund door een vergelijking van de leeftijd die struikheide
in Nederland in Engeland bereikt, maar ook hier ontbreken nog harde gegevens.

DE NOODZAAK VAN GEBIED-SPECIFIEK HEIDEBEHEER

In hoofdstuk 8 wordt eveneens aandacht besteed aan de consequenties van een suboptimaal klimaat voor het beheer van heide. Het lijkt erop dat de suboptimale klimaatomstandigheden in zekere mate gecompenseerd kunnen worden door de nutriëntenbeschikbaarheid laag te houden, waardoor namelijk hogere koolhydraat-reserves in de plant aanwezig blijven. Als de plant wordt beschadigd ten gevolge van droogteschade, vorst of heidehaantje, kunnen deze reserves gebruikt worden om de schade te herstellen. Dit betekent dat het plaggen niet alleen historisch noodzakelijk was voor de bemesting van akkers, maar ook nu nog een ecologische noodzaak om de heide paars te houden.

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ACKNOWLEDGEMENTS

CURRICULUM VITAE

Willem Herbert Diemont (11-12-1944) was born in Maastricht. He graduated in Soil Science (MSc) at the Wageningen Agricultural University in 1975. Since then he is attached to what is now the Institute for Forestry and Nature Research (IBN-DLO) in Wageningen. His scientific field of interest covers plant-soil relationships in heathlands, mangroves and acid sulphate soils, tropical peat forests, and dipterocarp rain forest. From 1987 to 1990 he was attached to the Ministry of Forestry in Indonesia, working on watershed management and erosion. At present he coordinates international land-use studies in IBN-DLO and is involved in the Land and Water Research Group (LAWOO), which is a consortium of five research institutes under the authority of the Netherlands Ministry of Agriculture, Nature Management and Fisheries. At present his main activities are related to land-use planning and sustainable forestry and conservation in mangrove forests in Vietnam and dipterocarp rain forest and peat forests in Malaysia and Indonesia.

Stellingen bij het proefschrift van W.H.Diemont: Survival of Dutch Heathlands

1. Over het heidebeheer moet men geen gras laten groeien.

Dit proefschrift

2. De noodzaak van heidebeheer neemt toe van Zuid-Engeland via Noord-Nederland naar Zuid-Nederland.

Dit proefschrift

3. Een verhoogde stikstofdepositie heeft geen invloed op vergrassing van heide op humuspodzolgronden.

dit proefschrift

4. Dat vader gelijk heeft, maar het niet altijd krijgt kan toegelicht worden aan de climaxtheorie.

R.Tüxen und W.H.Diemont 1937. Klimaxgruppe und Klimaxschwarm, ein Beitrag zur Klimaxtheorie. Jahresbericht der Naturhistorischen Gesellschaft zu Hannover: 73-87.

5. Erosie op Java wordt niet langer veroorzaakt door ontbossing van berghellingen, maar door uitbreiding van de sawahs in de dalen.

W.H.Diemont, F.Smiet & Nurdin 1991. Re-thinking erosion on Java. Netherlands Journal of Agricultural Science 39: 213-224

6. Voor het behoud van bosvenen in de tropen is bescherming van volledige stroomgebieden een vereiste.

LAWOO/DID 1996. Draft Final Report Western Johore integrated agricultural development project consultancy services on peat soil management.

7. In droge jaren staat het bos in Oost-Kalimantan stil.

Oldeman, Eijk-Bos en Diemont. in prep. Water stress in dipterocarp forest in East Kalimantan.

8. Voor bosbescherming in de tropen is een nationale landgebruiksplanning een eerste vereiste.

Report of the Second meeting of the Ad-hoc Technical Working Group Malaysia-The Netherlands, 1996.

9. Dat klimaat het al of niet aanwezig zijn van bos bepaald, sluit niet uit dat het bos bepalend is voor het klimaat.

J. Namias 1989. Nature, 338:15-16.
G.L. Potter, H.W.Ellsaesser, M. C. MacCracken & J.S Ellis.Nature 1981. 291:47-49.

10. Natuurconcessies als alternatief voor houtconcessies zijn cruciaal voor het natuurbehoud in Indonesië.

H.D.Rijksen en M. Griffiths. 1995. Development programme Leuser. Integrated Conservation and Development Project for Lowland Rainforest in Aceh.

11. De ontijzerde bodems van Pulau Petak op Kalimantan zijn geen ontijzerde kattekleien, maar gleygronden.

C.J.M. Konsten, N. van Breemen, Supardi Suping, I.B. Aribawa & J.E. Groenenberg 1994. Effects of flooding on pH of rice-producing, Acid Sulfate Soils in Indonesia. Soil Science Society of America Journal 58 (3):871-883.

12. De uitdrukking "het is helder" dient voor de duidelijkheid beperkt te blijven tot opmerkingen over het weer of een glas bier.

Colour section
Effects of management on Deschampsia and Molinia dominant heathland

W. H. Diemont & H. D. M. Linthorst Homan
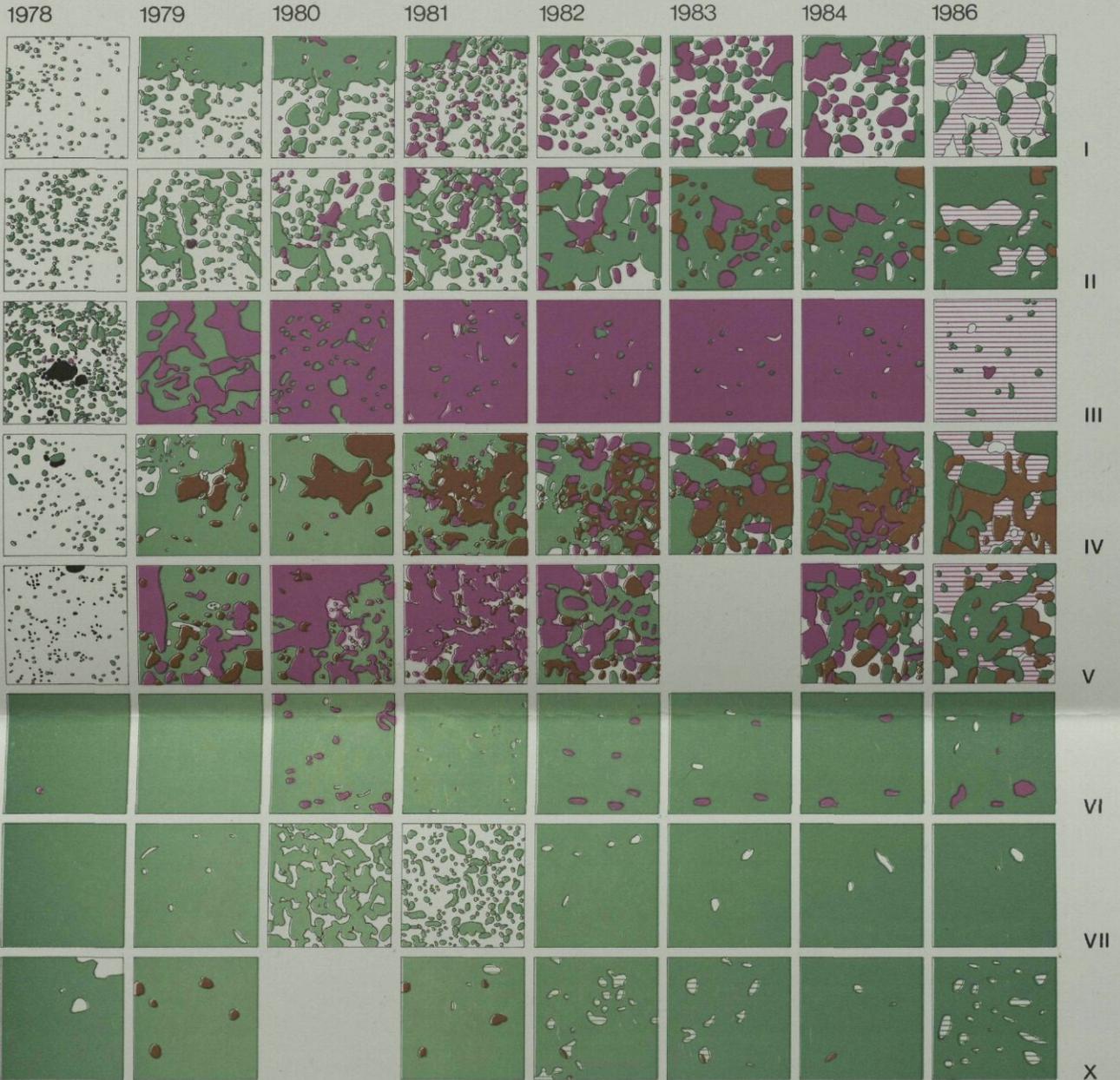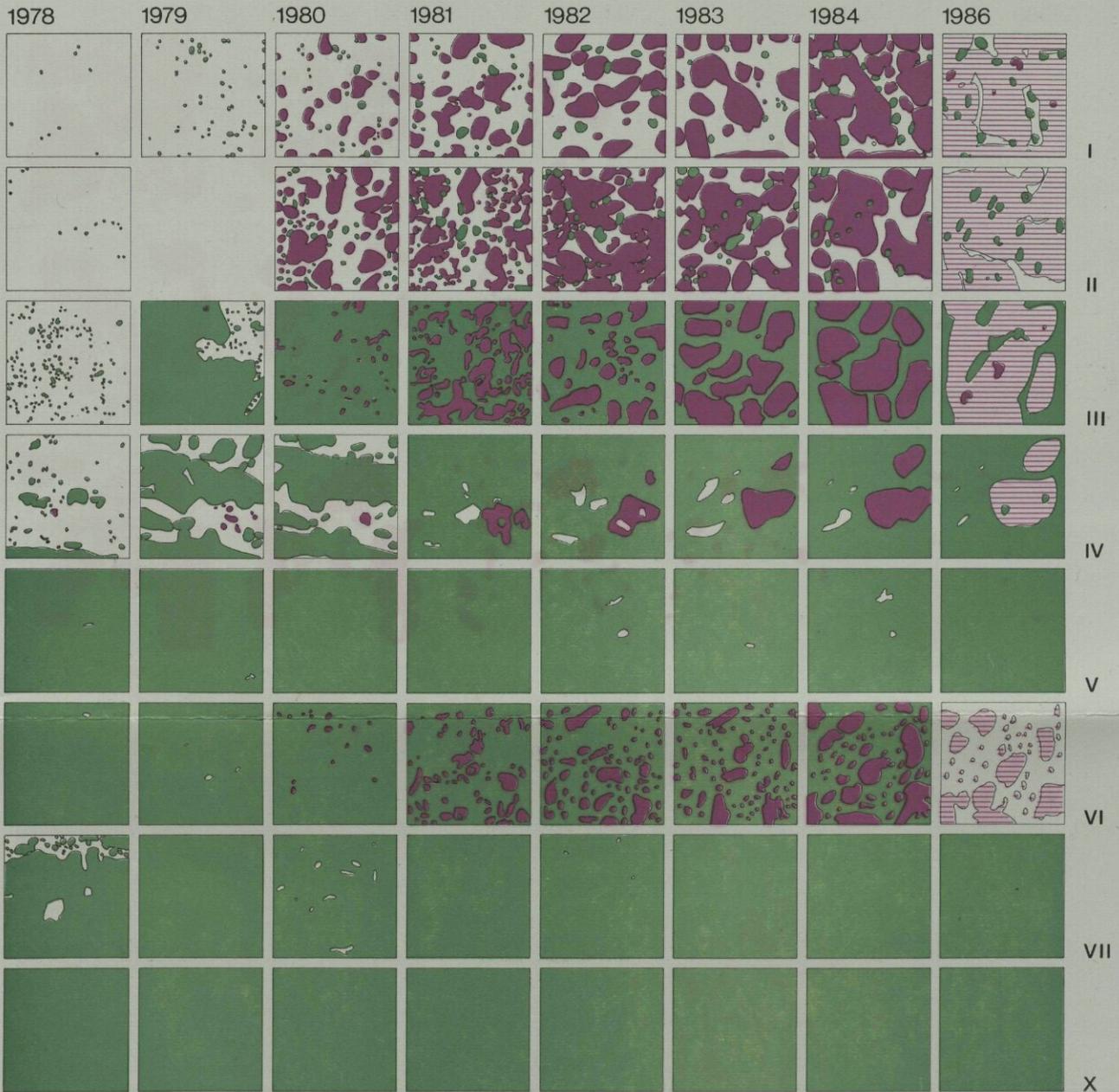*Rijksinstituut voor Natuurbeheer, Kasteel Broekhuizen, 3956 ZR Leersum, The Netherlands*

Fig. 1. Effects of treatment in 1977 of a *Deschampsia Flexuosa* stand, Hoog Buurlo, the Netherlands during the period 1978–1986. A and B: duplicate plots.

Treatment: I sod cutting: removal of standing crop, turf and 5 cm mineral soil. II sod cutting: removal of standing crop, turf and 2 cm mineral soil. III sod cutting: removal of standing crop and turf to the mineral soil. IV ploughing to a depth of 30 cm. V milling (rotary cultivator). VI annual mowing (June), standing crop removed. VII annual mowing (June), standing crop not removed. X no treatment.

Kootwijk B

| 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1986 |

Rows labeled: I, II, III, IV, V, VI, VII, X

4m

Plant species.

☐ No vasculars

🟩 *Molinia caerulea/Deschampsia flexuosa*

🟪 *Calluna vulgaris/Erica tetralix*

🟥 *Calluna vulgaris†/Erica tetralix†*

⬛ *Rumex acetosella*
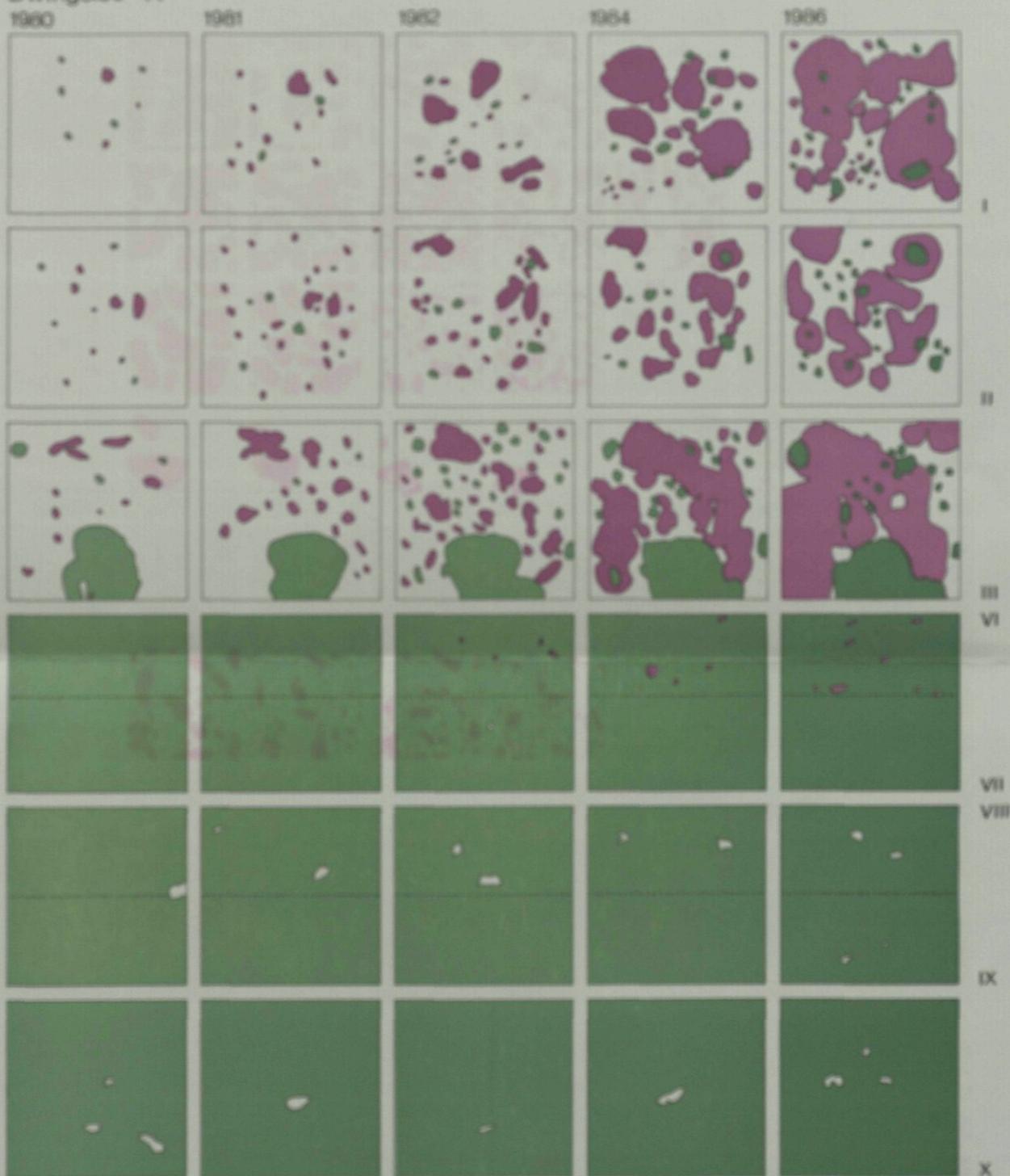
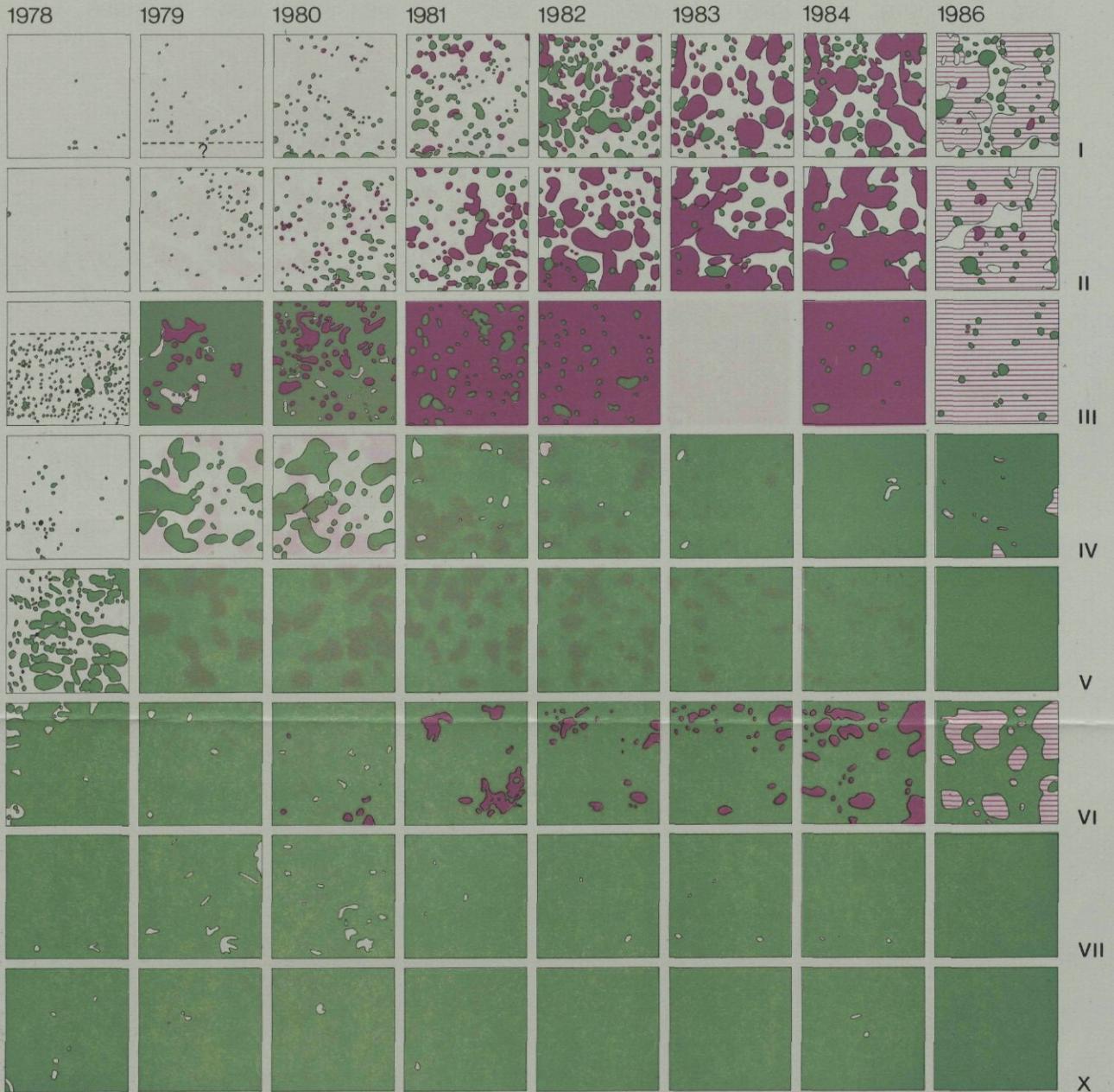*Fig. 3.* Effects of treatment in 1979 of a *Molinia caerulea* stand, Dwingeloo, the Netherlands during the period 1980–1986. A and B: duplicate plots.

Treatment: I sod cutting: removal of standing crop, turf and 5 cm mineral soil. II sod cutting: removal of standing crop, turf and 2 cm mineral soil. III sod cutting: removal of standing crop and turf to the mineral soil. VI annual mowing (June), standing crop removed. VII annual mowing (June), standing crop not removed. VIII annual mowing (September), standing crop removed. IX annual mowing (September), standing crop not removed. X no treatment.
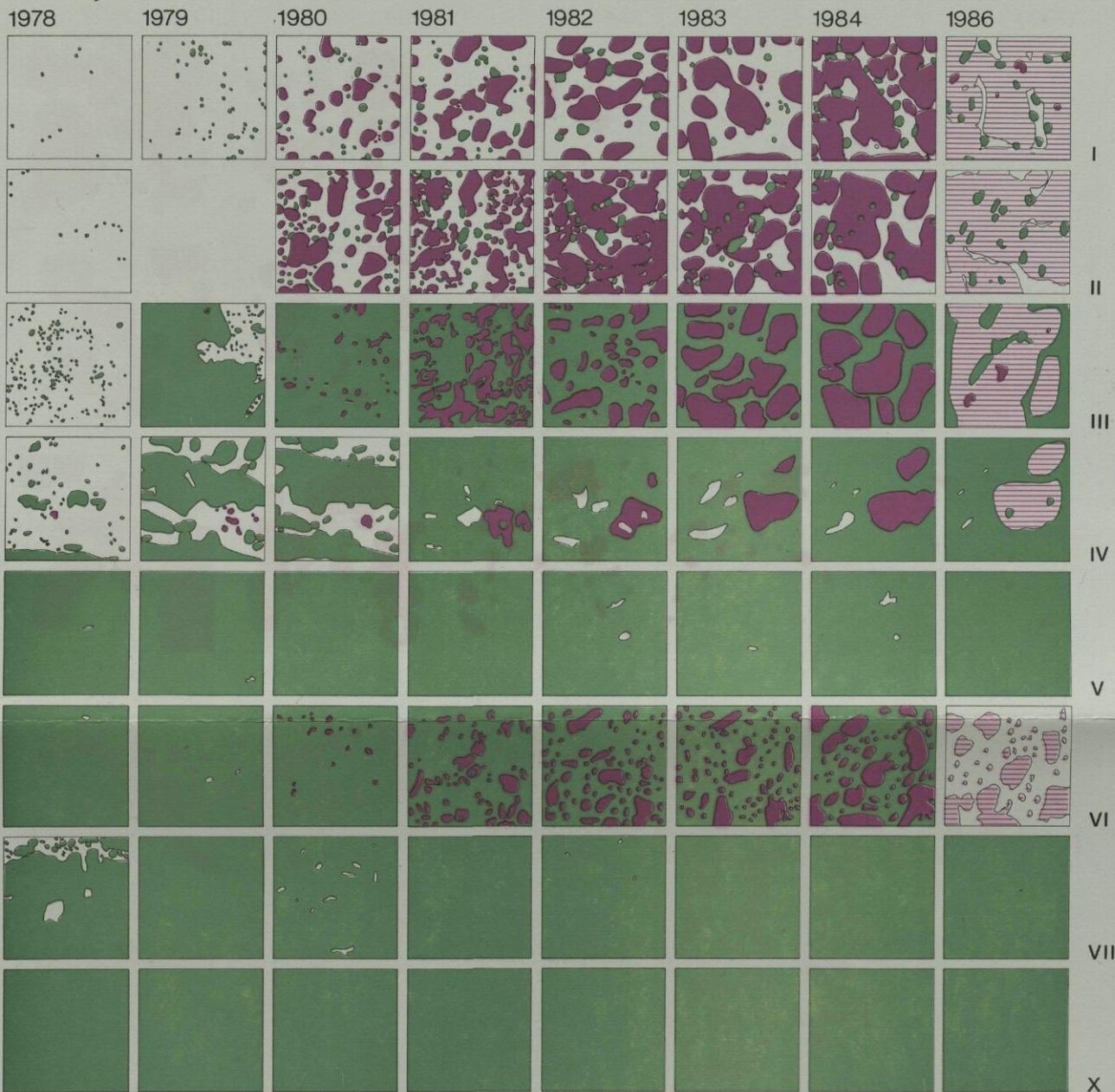
Kootwijk B

1978 1979 1980 1981 1982 1983 1984 1986

I
II
III
IV
V
VI
VII
X

Plant species.

☐ No vasculars

🟩 *Molinia caerulea/Deschampsia flexuosa*

🟪 *Calluna vulgaris/Erica tetralix*   🟪 *Calluna vulgaris†/Erica tetralix†*
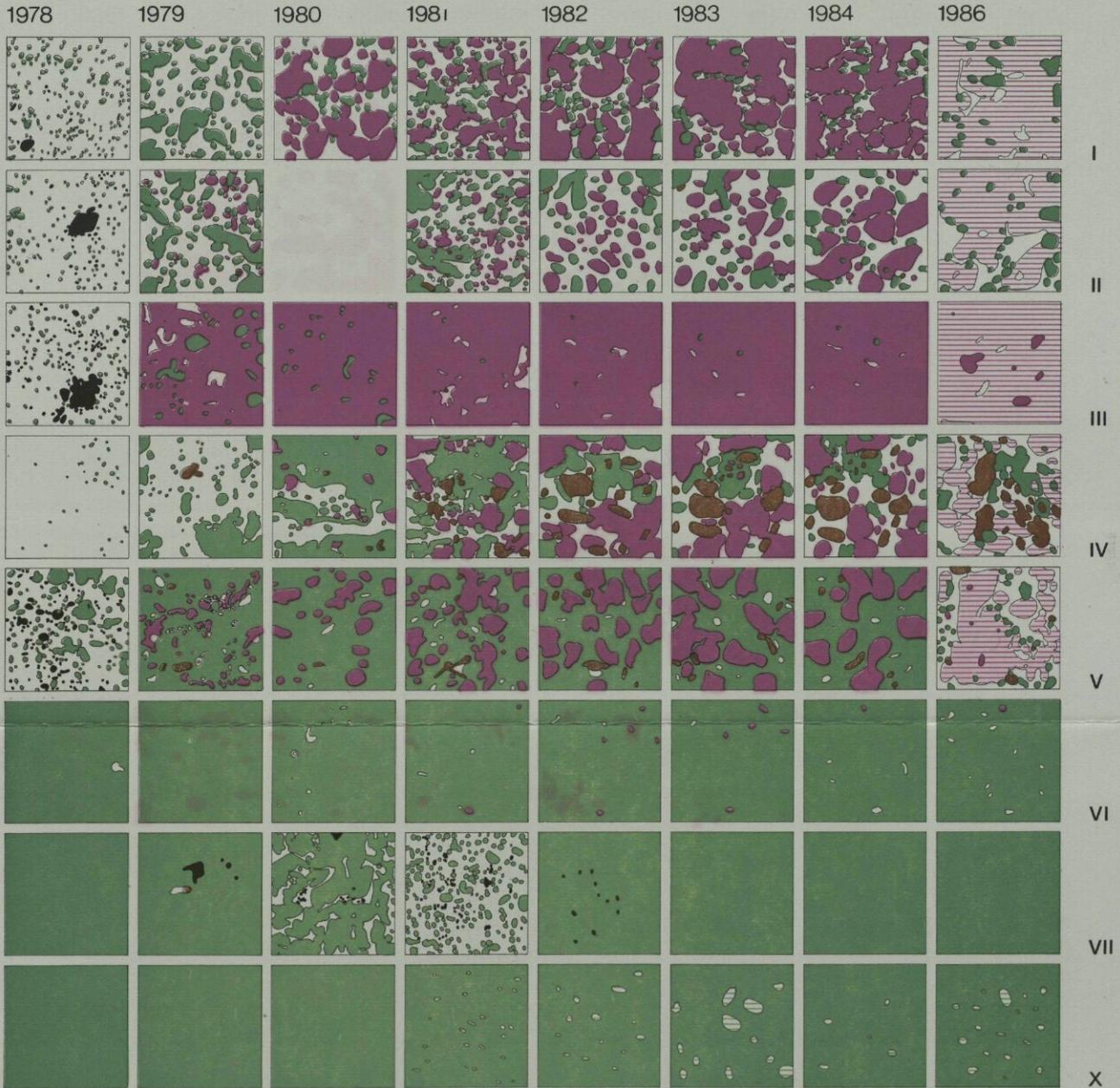
⬛ *Rumex acetosella*

4m

Fig. 2. Effects of treatment in 1977 of a *Molinia Caerulea/Deschampsia flexuosa* stand, Kootwijk, the Netherlands during the period 1978–1986. A and B: duplicate plots.

Treatment: I sod cutting: removal of standing crop, turf and 5 cm mineral soil. II sod cutting: removal of standing crop, turf and 2 cm mineral soil. III sod cutting: removal of standing crop and turf to the mineral soil. IV ploughing to a depth of 30 cm. V milling (rotary cultivator). VI annual mowing (June), standing crop removed. VII annual mowing (June), standing crop not removed. X no treatment.

Hoog Buurlo B

1978	1979	1980	1981	1982	1983	1984	1986	

Plant species.

☐ No vasculars

🟩 *Deschampsia flexuosa*   ▤ *Deschampsia flexuosa†*

🟪 *Calluna vulgaris*   ▤ *Calluna vulgaris†*
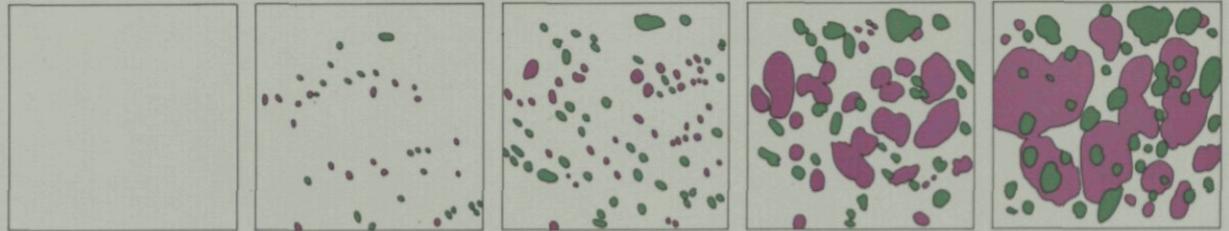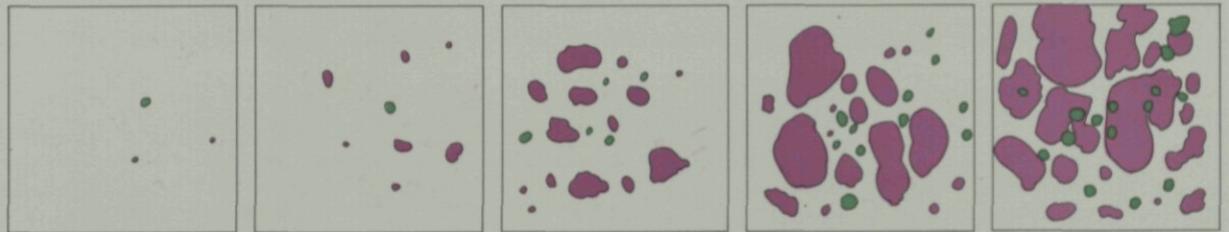
⬛ *Rumex acetosella*

🟫 *Sarothamnus scoparius*

4m

Dwingeloo B

1980   1981   1982   1984   1986

I
II
III
VI
VII
VIII
IX
X

4 m
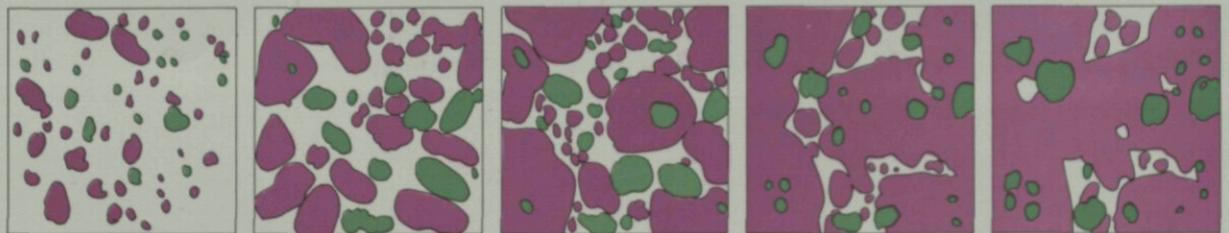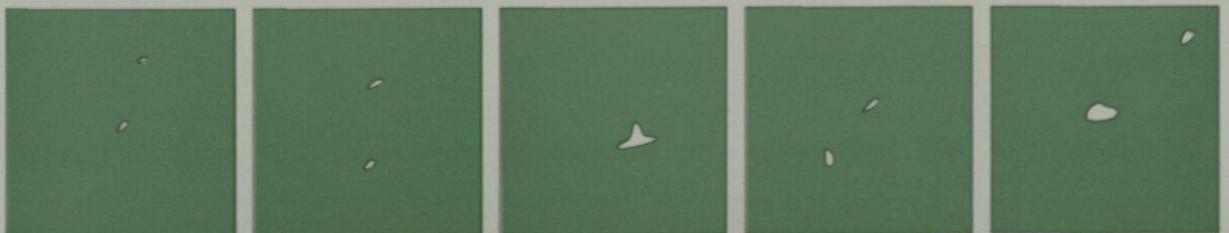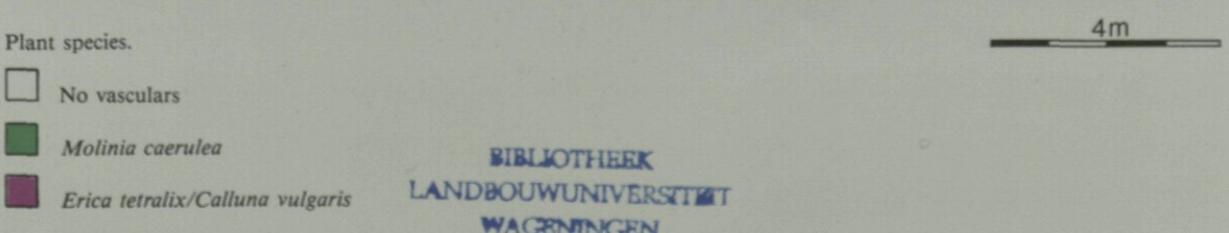
Plant species.

☐ No vasculars

🟩 *Molinia caerulea*

🟪 *Erica tetralix/Calluna vulgaris*