Observations on north-west European limestone grassland communities. V, a

An experimental approach to the study of species diversity and above-ground biomass in chalk grassland

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SUMMARY

In 1971 a number of permanent plots were established in an abandoned Dutch calcareous grassland, then belonging to the association **Arrhenatheretum elatioris** with some elements of **Mesobrometum erecti** and **Poo-Lolietum**.

A part of the plots was treated with fertilizer of varying N.P.K.-content. Another part was treated with farm yard manure, calcium carbonate, or left untreated. All plots were mown once a year. Each year, species composition, including bryophytes, as well as peak standing crop were determined. After seven years the plots treated with fertilizer are sharply distinct from the others ones, both in species composition and above-ground biomass.

In the fertilized plots the number of species decreased considerably due to dominance of a few species, whilst the above-ground biomass varied from about 550 to 900 g/m^2. In the course of the experiment the species number of the unfertilized plots increased; the above-ground biomass varied from 150 to 350 g/m^2.

Constancy of species composition was highest in the unfertilized plots, especially after a period of extreme drought in 1976.

In 1978 the vegetation of the non-fertilized plots could be reckoned to the **Mesobrometum erecti**; the vegetation of the fertilized plots to an **Arrhenatheretum elatioris** variant poor in species.

The influence of sod removal is discussed in detail. The study will be continued and expanded in the forthcoming years.

1. INTRODUCTION

According to Odum (1969) a number of typical trends may be expected in the development of ecosystems. With regard to the structure of a community, he assumes an increase in species diversity in the course of its development. This species diversity is expected to be correlated with the stability of the community and with a decrease in its net productivity. He pointed out the necessity to

check such hypotheses experimentally. McNaughton (1977) again stressed the necessity for an empirical test of the presumed relation between stability and diversity of ecosystems.

Aiming at the establishment of starting points for optimal management of nature reserves, van Leeuwen (1966) tried to explain this relation by means of cybernetic principles. These theories, elaborated in further studies (van Leeuwen 1970, 1977), were based on observations covering many years in permanent plots in the vegetation.

The relation between species diversity and above-ground biomass is also relevant in Grime's hypotheses (1974) about plant strategies and the triangular model of three determinants in herbaceous vegetation, viz. competition, stress, and disturbance (Al Mufti *et al.* 1977; Grime 1978, 1979), developed from them.

Many investigations about productivity and plant species diversity, especially along gradient ranges, have been carried out by Whittaker (a.o. 1975, 1977).

Recently Stephenson (1973), Reed (1977), and Bakelaar & Odum (1978) carried out experiments to test the relation between diversity, biomass, and stability in herbaceous vegetation.

In order to gain more insight into the development of vegetation and the possible rules governing it, the author and his co-workers started a number of experiments in the frame of a study program of limestone grassland vegetation in North-West Europe (Willems 1973b, 1979). This type of vegetation is particularly suitable for experimental studies, since annual mowing is one of the factors responsible for its existence (Scherrer 1925, Pottier-Alapetite 1943, Müller 1966, Willems 1973a, 1978, Willems & Blanckenborg 1975). This implies that the annual removal of the greater part of the above-ground biomass does not negatively interfere with the development of vegetation. Furthermore, limestone grassland vegetation is as a rule rich in species, and, owing to edaphic conditions, is but little influenced by intense study, as shown by the work in question.

In the present article the results of this study are reported. Special attention is given to two problems:

- Is there a negative correlation between productivity and species diversity?
- What is the relation in time between species diversity and stability?

In the present paper we follow Odum (1969) in defining species diversity as meaning richness in species (variety component) as well as a balanced species distribution (equitability component) in the experimental plots. The term "stability" is applied as to mean constancy (in the sense of Orians 1975). Our index of net productivity is the yearly maximum standing crop.

2. MATERIAL AND METHODS

a. Site details

The study was undertaken in a grassland of about 2 hectares forming a part of the Nature Reserve Gerendal situated in the extreme South of the Dutch province of Limburg. The substrate consists of calcareous sediments of Upper

Senonian (Cretaceous) age, overlain by thick Pleistocene layers of gravel deposited by the River Maas.

During the Late Pleistocene these were again covered by an aeolic deposit (loess). In this landscape the flanks of the valleys are the sites where the calcareous deposits reach the surface, or nearly so, and distinctly influence the vegetation. The Gerendal is a North-South running tributary valley of the valley of the River Geul, itself a tributary of the River Maas.

The area of study can be subdivided into three parts: I. the highest part, sloping weakly (5°) to the North, varying in elevation from 130 to 140 m above N.A.P. (= Dutch Ordnance Level); II. a part of the valley, situated about 15 m lower, also almost level; III. a slope between the two, inclined about 20°, exposed to the North or North-West. These three parts are separated from each other by small, steep escarpments about 1 m high, regarded as cultivation terraces and remnants of former land use.

The bottom of the slope consists of loess and weathering products of the underlying chalk. It may be regarded as a rendzina type of soil. Downward the chalk fragments increase in size and number. At the top of the slope, where the experimental plots are situated, the relatively unweathered chalk is present at a depth of about 40 cm. The pH of the soil varies from 7 to 8. In the uppermost 15 cm of soil the content of calcium carbonate is about 35%; it increases to about 95% at a depth of 50 cm.

Up to the year 1967, when the area was set aside as a nature reserve, it was used for grass production and was heavily fertilized with various kinds of chemical fertilizer and with farm yard manure (F.Y.M.). Between March and October fertilizer was applied about once every six weeks. The area was heavily grazed by cattle and sometimes the grass was also cut. From 1967 to 1970 it was grazed as well as cut but not treated with fertilizer; afterwards it was only used for grass cutting.

As a nature reserve the area is owned by the Ministry of Cultural affairs, Recreation and Social Welfare and is administered by the Department of Nature Preservation of the State Forest Service. Since 1970 experimental work is done by the Department of Plant Ecology and Vegetation Science of the State University of Utrecht.

b. Methods

In 1970 the floristic and vegetational composition of the plant cover in the area were inventarized. Then in three parts permanent plots were established. Only on the slope the vegetation can be assigned to the calcareous grassland type, and here a certain trend in its development can be discerned; only this part is taken into consideration here.

In April, 1971, eleven permanent plots were established in this area (Fig. 1). In the A series the vegetation as well as the uppermost 7–10 cm of the soil were removed ("sod removal"). Subsequently, the plots of the A as well as of the B series were mown once a year, in August or in October, and the material was removed. Besides, a plot of 5 × 2 m was established (C 1) in order to follow the

vegetation succession without "disturbance" by annual cutting; this is not taken into account below. Results concerning this plot will be published in a forthcoming paper.

Starting from 1971, the experimental plots were treated differently twice a year, in April and in October. The treatment consisted of the application of calcium carbonate, F.Y.M., and two artificial fertilizers of different composition. A similar treatment was applied to pairs of plots, one with the top sod removed in 1971, the other without this interference (Fig. 1). The October application of fertilizer, etc., was given after the grass had been cut and the above-ground biomass had been removed. Plots subject to fertilizer treatment received a quantity corresponding to that applied by the farmer-owner before 1967 as different kinds of fertilizer.

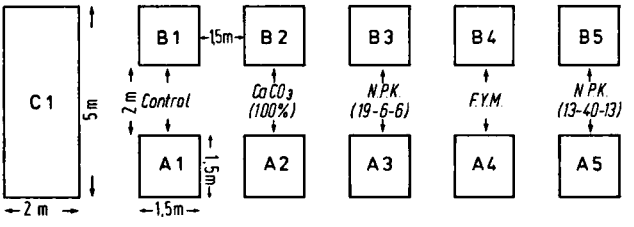


Fig. 1. Situation of the plots. From series A sods were removed in April 1971. Treatments were given twice a year, in April and October. Plot C 1 was left untouched and was not mown annually, like series A and B.

In order to study a possible influence on the vegetation by different percentages of N, P or K in the fertilizer, two fertilizers with different composition were applied. Plots A3 and B3 received an annual quantity of about 170 kg N/ha, 50 kg P/ha, and 50 kg K/ha. The quantity applied to plots A5 and B5 was about 115 kg N/ha, 355 kg P/ha, and 115 kg K/ha. Plots A4 and B4 were treated twice annually with 100 g of dry, ground cow dung, corre sponding to about 2 kg N/ha, 1,5 kg P/ha, and 1,5 kg K/ha per year.

Plots A2 and B2 received an annual amount of chalk equivalent to about 850 kg of calcium carbonate per hectare. This application was chosen because in old times it was an agricultural measure in South Limburg serving to increase the yield during a 3–5 years period; then there was a sharp drop. It was then necessary to let the area lie fallow for some years. By an application of calcium carbonate during more than 3–5 years and by annual removal of the above-ground biomass the nutrient content of the soil in plots A2 and B2 was lowered. The control plots A1 and B1 were left untreated (Fig. 1).

The vegetation of the plots is surveyed once a year, at the end of July or in the beginning of August, on the basis of the method of Braun-Blanquet (1964). Starting from 1975, the estimates of abundance and dominance are made as proposed by Barkman, Doing & Segal (1964).

As shown by a number of relevés made in 1970, the vegetation on the slope had to be assigned to the association **Arrhenatheretum elatioris**. Besides, it

harboured a number of species with an optimum in the **Poo-Lolietum**, a high-yield type of grassland, and also some from the **Mesobrometum erecti**, a species-rich type of grassland (Kruijne *et al.* 1967, Westhoff & den Held 1969) (Table 1).

From 1973 to 1978 (except in 1974) the above-ground plant biomass was determined in the plots. To this end, the plants were clipped about 2 cm above the surface by means of hand shears. This way of harvesting proved to have no lethal effect. The above-ground plant biomasses of some species in the plots were determined separately. The harvesting was done in early August, the vegetation then having reached its peak of biomass, and little material having as yet decayed. The biomass harvested may be regarded as the overall annual above-ground production. Its dry weight was determined after drying the cut plant material for 48 hours at 70–75°C (after Kruijne *et al.* 1967).

Plant nomenclature follows Heukels & van Ooststroom (1975) for phanerogams and Margadant (1959) and van der Wijk *et al.* (1969) for bryophytes, and Westhoff & den Held (1969) and Braun-Blanquet & Moor (1938) for syntaxa.

3. RESULTS

3.1 *Species composition*

As a consequence of the agricultural management starting in 1970, i.e. cuttting and removal of plant material once a year, the species composition of the vegetation started to change. The developmental trends in plots A2 and B2 (calcium carbonate) and plots A4 and B4 (F.Y.M. treatment) corresponds closely to those on the control plots A1 and B1. Consequently these plots are taken together here as one group, the non-fertilized plots. Plots subject to treatment with artificial fertilizer, i.e. A3, B3, A5 and B5, were very similar to one another in their vegetational development but diverged sharply from the first group; they are taken together as fertilized plots. The development of the vegetation in these two groups is described and discussed in special sub-chapters.

a. Non-fertilized plots (B series)

The development of the vegetation in control plot B1 may be regarded as representative for the change in the composition of the vegetation on the entire slope (Table 2). During the first years the vegetation in non-fertilized plots subject to sod removal developed at variance. Its effect is described in a separate sub-chapter. The statements about the vegetation development in non-fertilized plots apply to the A plots only starting from about 1975 (Table 3).

In the first three years after 1970 a number of species disappeared or decreased in frequency and size, e.g. *Cerastium holosteoides, Pimpinella major, Arrhenatherum elatius,* and *Festuca pratensis* in the non-fertilized plots and species like *Heracleum sphondylium, Lolium perenne, Poa trivialis, Cirsium vulgare,* and *Cirsium arvense* on the remaining slope. Taken as a whole, this group of species is typical of grassland on nutrient-rich soil (Kruijne

Table 1. Constancy table, based upon 15 relevés, represents the floristic composition of the grassland community on the slope on which the experimental plots were laid down in April 1971.

CONSTANCY TABLE CALCAREOUS GRASSLAND
Gerendal, Nl. Summer 1970.

Character species Molinio Arrhenatheretea:	
Holcus lanatus	V (+-3)
Centaurea pratensis	V (1-3)
Trifolium pratense	V (1-3)
Plantago lanceolata	V (+-2)
Prunella vulgaris	III (+-1)
Viccia cracca	I (+-1)
Cerastium holosteoides	I (+-3)
Idem Arrhenatherion elatioris:	
Festuca pratensis	V (+-4)
Dactylis glomerata	V (+-3)
Ranunculus acris	V (+-1)
Chrysanthemum leucanthemum	IV (+-2)
Lathyrus pratensis	IV (+-1)
Heracleum sphondylium	I (r-+)
Idem Arrhenatheretum elatioris:	
Knautia arvensis	V (+-3)
Daucus carota	V (+-2)
Pimpinella major	V (+-2)
Trisetum flavescens	V (+-1)
Differential sp. subass. brizetosum:	
Briza media	V (r-4)
Carex flacca	V (+-2)
Linum chatharticum	III (+-1)
Differential species Festuco-Brometea:	
Helictotrichon pubescens	III (+)
Ranunculus bulbosus	+ (r)
Character species Mesobromion:	
Leontodon hispidus	V (1-4)
Plantago media	V (1-3)
Agrimonia eupatoria	II (+-2)
Scabiosa columbaria	I (1-2)
Idem Mesobrometum erecti:	
Brachypodium pinnatum	III (+-3)
Character species Poo-Lolietum:	
Lolium perenne	V (+-1)
Poa trivialis	II (r-+)
Trifolium repens	II (+)
Other species:	
Agrostis stolonifera	V (+-3)
Festuca rubra s.l.	V (+-2)
Achillea millefolium	V (+-2)
Medicago lupulina	V (r-2)
Cynosurus cristatus	V (+-1)
Lotus corniculatus	IV (+-2)
Ononis repens	III (+-2)
Prunus avium (seedling)	III (r-+)
Origanum vulgare	II (+-1)
Vicia sepium	II (+-1)
Campanula rotundifolia	II (+-1)
Cirsium arvense	I (r)
Cirsium vulgare	+ (r)
Veronica chamaedrys	+ (r)
Crataegus monogyna (s.)	+ (r)
Bryophytes:	
Calliergonella cuspidata	V (+-2)
Pseudoscleropodium purum	IV (1-2)
Rhytidiadelphus squarrosus	IV (1-2)
Eurhynchium swartzii	IV (+-2)
Brachythecium rutabulum	IV (+-2)
Mnium rostratum	IV (+-1)
Mnium undulatum	III (+-2)
Cirriphyllum piliferum	III (+-2)
Campylium chrysophyllum	III (1-2)
Ctenidium molluscum	I (2)
Fissidens taxifolius	I (+)
Brachythecium glareosum	I (+-1)

Table 2. Floristic composition of the control plot B 1 during the period 1970–78. Plant species are considered as irregularly present if absent during at least two successive years. Bryophytes were not sampled in 1973. No bryophytes were found in 1976.

Control plot B1. CALCAREOUS GRASSLAND, GERENDAL, The Netherlands.									
Date	1970 15/7	1971 13/8	1972 6/7	1973 4/8	1974 17/7	1975 17/7	1976 2/8	1977 20/7	1978 8/8
Cover % phanerogams	95	100	100	95	100	90	80	85	85
Number of phanerogams	28	30	28	27	28	27	32	31	38
Number of cryptogams	7	9	8	.	8	7	0	12	7
Disappeared:									
Cerastium holosteoides	+								
Pimpinella major	+	+							
Bellis perennis		r							
Arrhenatherum elatius			+	+					
Permanently present:									
A. Graminoids:									
Cynosurus cristatus	1	+	+	+	+	+p	+r	+p	1p
Festuca pratensis	2	1	2	1	+	+b	+p	+p	+a
Agrostis stolonifera	+	1	+	+	1	+p	+p	1p	2m
Festuca rubra	1	1	1	2	1	2m	2m	1p	2m
Holcus lanatus	1	+	+	+	+	1b	+b	+p	+p
Trisetum flavescens	1	1	2	1	+	1b	+p	1p	2a
Briza media	2	1	2	2	3	3b	3a	2b	2a
Helictotrichon pubescens	+	1	+	+	+	+b	+p	1p	2m
Dactylis glomerata	+	1	+	+	+	+b	+a	+p	2m
Poa pratensis		+		+	+	+p	+p	+p	+p
Carex flacca	2	+	1	1	1	1b	1p	1p	2m
B. Forbs:									
Lotus corniculatus	2	1	2	+	1	1a	1b	1b	2a
Chrysanthemum leucanthemum	+	r	r	+	+	+r	1a	+p	2m
Knautia arvensis	1	+	2	+	+	+p	+b	+p	+p
Medicago lupulina	+	+	1	+	1	1p	+a	1b	+p
Leontodon hispidus	2	3	3	2	2	2b	3a	2b	2a
Linum catharticum	1	+	+	r	+	1p	+p	+p	+p
Ranunculus acris	1	+	+	+	+	+p	+p	+p	+p
Centaurea pratensis	1	1	+	+	1	1b	1a	1b	1a
Daucus carota	1	+	+	+	1	+p	+b	+p	+a
Plantago media	1	2	1	2	2	2a	2a	2a	1b
Plantago lanceolata	1	+	+	+	+	+p	1b	+p	+p
Achillea millefolium	1	+	+	+	+	+p	+b	+p	2m
Trifolium pratense	1	+	+	+	+	1b	1p	1a	+p
Lathytus pratensis		+	r	+	+		+p		+r
Irregularly present:									
Prunella vulgaris	+	+	+			+b	1b	1p	1p
Veronica chamaedrys	+				r		+r	+p	+p
Listera ovata		r	r				+r		r
Ranunculus bulbosus		+	+				+p	+p	+p
Trifolium repens	+								+r
New:									
Pimpinella saxifraga				+	+	+b	+p	+p	1p
Brachypodium pinnatum					+	+a	+p	1a	1p
Senecio jacobaea							+r		r
Ononis repens								+r	+r
Taraxacum sect. vulgaria								+r	+p
Luzula campestris									+p
Betonica officinalis									r
Anthoxanthum odoratum									r
Bryophytes:									
Eurhynchium swartzii	x	x	x						
Mnium rostratum	x	x	x		x	x		x	
Calliergonella cuspidata	x	x	x		x	x		x	x
Pseudoscleropodium purum	x	x	x		x	x		x	x
Rhytidiadelphus squarrosus	x	x	x		x	x		x	x
Brachythecium rutabulum	x	x	x		x	x		x	x
Mnium undulatum		x	x	not recorded	x	x		x	x
Fissidens taxifolius		x	x		x	x		x	x
Campylium chrysophyllum	x							x	
Cirriphyllum piliferum		x					absent	x	
Bryum rubens								x	
Phascum cuspidatum					x			x	
Ctenidium molluscum								x	x

Table 3. Floristic composition of plot A 1 during the period 1971–78. In 1972 the inventarisation of the bryophytes took place in February (wintertime). Bryophytes were not sampled in 1973. No bryophytes were found in 1976.

Plot A1. CALCAREOUS GRASSLAND, GERENDAL, The Netherlands.								
Date	1971 13/8	1972 6/7	1973 4/8	1974 2/8	1975 22/7	1976 2/8	1977 20/7	1978 27/7
Cover % phanerogams	75	90	95	80	80	80	85	85
Number of phanerogams	32	33	32	27	32	31	33	33
Number of cryptogams	6	15	.	8	9	0	6	7
Disappeared:								
Mercurialis annua	r							
Plantago major	+							
Pimpinella major	+							
Euphorbia helioscopia	r	r						
Cerastium holosteoides	r	r						
Cirsium arvense	+	r	r					
Elytrigia repens	+	2	+	r	+p			
Permanently present:								
A. Graminoids:								
Holcus lanatus	r	+	+	1	1p	+p	+p	+a
Festuca pratensis	1	2	+	+	2m	1b	+p	+r
Trisetum flavescens	r	+	+	+	1p	+p	+p	1a
Festuca rubra	2	+	2	2	2a	1b	2a	2m
Agrostis stolonifera	1	+	+	+	2m	+p	+p	1p
Brachypodium pinnatum		r	+	+	1a	2a	2b	2a
Cynosurus cristatus		+	+	+	1p	+b	+p	+a
Dactylis glomerata		+	+	+	1a	+p	+p	1p
Briza media		+	+	+	+p	2a	2m	2m
Carex flacca	r	1	2	1	1p	+b	2m	2a
B. Forbs:								
Plantago lanceolata	2	3	+	+	+r	+p	+p	+a
Lathyrus pratensis	1	+	+		+p		+p	
Lotus corniculatus	1	+	1	1	1a	1b	1a	2m
Achillea millefolium	+	+	+	+	1p	+p	1p	1p
Knautia arvensis	1	2	+	+	+p	1b	+a	+a
Plantago media	2	2	2	2	2a	2a	2a	2a
Daucus carota	+	1	+	1	1p	+a	1p	+p
Pimpinella saxifraga	+	+	+	+	+p	+p	1p	+p
Trifolium pratense	1	+	+	+	1p	+b	+p	+p
Ononis repens	+	+	+	1	+p	+a	1a	+a
Chrysanthemum leucanthemum	1	1	+	1	1a	1b	1p	1a
Medicago lupulina	1	1	+	1	1p	1a	+p	1p
Taraxacum sect. vulgaria	r	+	r		+p	+r	+p	+r
Prunella vulgaris	r	+	+	+	+p	1p	+p	1a
Centaurea pratensis	1	+	1	1	1p	+a	1a	1a
Ranunculus bulbosus	+	+		+	+r	+p	1p	+p
Ranunculus acris		r	+		+p		+p	+p
Leontodon hispidus	1	1	1	3	2a	3a	2b	2b
Irregularly present:								
Senecio jacobaea	+							+r
Bellis perennis	+	+			1a		+p	
Trifolium repens						1a		
Origanum vulgare						+r		
Fraxinus excelsior (s.)						r		
Scabiosa columbaria			r				+p	
New:								
Helictotrichon pubescens			+	+	1a	+b	1p	2m
Linum catharticum			r		+p	+p	+p	1p
Poa pratensis							+p	1p
Prunus avium								r
Listera ovata								r
Bryophytes:								
Anisothecium schreberianum		x						
Barbula convoluta		x						
Bryum klinggraeffii		x						
B. microerytrocarpum		x						
B. rubens		x						
Pottia davalliana		x						
Eurhynchium swartzii	x	x						
Phascum cuspidatum		x		x				
Mnium rostratum	x	x			x			
Cirriphyllum piliferum		x			x			
Mnium affine				x	x			
Pseudoscleropodium purum	x	x		x	x		x	x
Brachythecium rutabulum	x	x		x			x	x
Calliergonella cuspidata	x	x		x	x		x	x
Rhytidiadelphus squarrosus	x	x		x	x		x	x
Mnium undulatum		x		x	x		x	x
Fissidens taxifolius				x	x		x	x
Campylium chrysophyllum					x			x

not recorded

absent

et al. 1967, Ellenberg 1967). Some other species disappeared or decreased in frequency during the first years of study but reappeared later, like *Trifolium repens, Senecio jacobaea*, and *Taraxacum* species. Some other species appeared as new settlers or increased in coverage. Most of these are typical of non-fertilized, calcareous soils, like *Brachypodium pinnatum, Pimpinella saxifraga, Betonica officinalis, Origanum vulgare*, and *Scabiosa columbaria* (Braun-Blanquet & Moor 1938, Ellenberg 1974). Outside the plots *Carex carryophyllea* appeared and increased in coverage. This species is characteristic of **Mesobromion** communities (Braun-Blanquet & Moor 1938). *Gymnadenia conopsea* and *Orchis militaris* flowered for the first time on the slope in 1977. In South Limburg these orchids must also be regarded as typical of moderately dry calcareous grassland (Westhoff & den Held 1969).

Bryophytes occurring in the non-fertilized plots were mostly pleurocarpic or large acrocarpic mosses, like *Calliergonella cuspidata, Pseudoscleropodium purum, Rhytidiadelphus squarrosus, Brachythecium rutabulum, Fissidens taxifolius, Mnium affine*, and *Mnium undulatum. Eurhynchium swartzii* disappeared entirely, whereas, in 1975 *Ctenidium molluscum* appeared newly in plot B2, and *Campylium chrysophyllum* expanded.

Sometimes small acrocarpic mosses from the general *Bryum* and *Phascum* established themselves in the plots. This phenomenon will be discussed more fully in connexion with the effects of sod removal, as it depended on the appearance of gaps in the sward.

b. Fertilized plots (B series)

During the first years of the experiment a number of species disappeared from the fertilized plots. The first to disappear were species typical of moderately dry chalk grassland, like *Leontodon hispidus* and, to a lesser degree, *Plantago media* (Braun-Blanquet & Moor 1938), as well as species typical of a low trophic level of the soil, like *Briza media, Carex flacca*, and *Linum catharticum* (Ellenberg 1974).

A number of species which can be regarded as typical of a high trophic level of the soil, disappeared too, viz. *Festuca pratensis, Poa pratensis* (plot B3), *Trifolium pratense*, and *Pimpinella major* (plot A3). The casual establishing of species like *Brachypodium pinnatum, Pimpinella saxifraga*, and *Helictotrichon pubescens* which can be considered as typical of a nutrient-poor soil (Ellenberg 1974) in the fertilized plots, is striking.

Only a few species in the fertilized plots belong to the category "permanently present", see table 4 and 5. This in contrast with the situation in the non-fertilized plots.

Within the fertilized plots some differences can be noticed between the plots A3 and B3 (treated with N.P.K. 19.6.6.) on the one hand and the plots A5 of B5 (treated with N.P.K. 13.40.13) on the other. The above-ground biomass of the plots A5 and B5 exceeded that of the plots A3 and B3 in the years 1973 and 1975. The reverse was noticed later on in the study, viz. in 1977 and 1978.

Another difference between both pairs of plots in the percentage of dry

Table 4. Floristic composition of plot B 3 during the period 1971–78. Artificial fertilizer treatment was applied twice a year. Bryophytes were not sampled in 1973.

Plot B3. CALCAREOUS GRASSLAND, GERENDAL, The Netherlands.

Date	1971 23/6	1972 7/7	1973 5/8	1974 7/8	1975 24/7	1976 2/8	1977 20/7	1978 7/8
Cover % phanerogams	90	90	90	90	85	85	90	90
Number of phanerogams	26	23	17	17	17	8	16	17
Number of cryptogams	7	8	.	3	3	0	4	4
Disappeared:								
Cerastium holosteoides	r							
Linum catharticum	+							
Briza media	+	r						
Medicago lupulina	1	+						
Carex flacca	3	+						
Leontodon hispidus	3	+						
Poa trivialis	r	+	+					
Agrostis stolonifera	+	+	+	r				
Plantago media	2	1	r	r	+r			
Festuca pratensis	2	1	1	1	1p	+b		
Permanently present:								
A. Graminoids:								
Holcus lanatus	2	1	+	2	1p		+p	2a
Helictotrichon pubescens	+	+	+	+	1p		+p	
Trisetum flavescens	1	1	1	1	1p		+p	+p
Dactylis glomerata	3	3	3	3	2b	+b	2a	2a
Festuca rubra	+	2	2	3	3a	4a	5a	3a
B. Forbs:								
Daucus carota	+	+	+	r	+p		+r	
Plantago lanceolata	+	r		r	+r		+r	+r
Ononis repens	2	1	+	r	+p	+p	+p	+p
Centaurea pratensis	2	2	2	3	2a	1b	2a	1a
Achillea millefolium	+	+	1	2	+p		1a	1p
Irregularly present:								
Ranunculus acris	+	+	+	r				+r
Chrysanthemum leucanthemum	+	+	+				+p	+p
Knautia arvensis	+	+	+	r			+r	
Pimpinella saxifraga	r				+p	+r	+p	+p
Trifolium pratense	+	+						+p
Lotus corniculatus	1	+						+r
Pimpinella major				r	+p			
Brachypodium pinnatum			+					
Fraxinus excelsior (s.)					+r			
New:								
Poa pratensis				1	2a	1b	2a	2m
Heracleum sphondylium					+p	2a	2a	2a
Lathyrus pratensis							+p	+p
Prunus avium (seedling)								+r
Bryophytes:								
Eurhynchium swartzii	x	x						
Rhytidiadelphus squarrosus	x	x						
Bryum microerytrocarpum		x						
Phascum cuspidatum		x						
Mnium rostratum					x			
Bryum rubens			not recorded		x		x	
Fissidens taxifolius	x	x					x	
Calliergonella cuspidata	x			x				x
Pseudoscleropodium purum	x	x		x		absent		x
Mnium undulatum	x	x			x		x	x
Brachythecium rutabulum	x	x		x			x	x

Table 5. Floristic composition of plot A 3 during the period 1971–78. Artificial fertilizer treatment was applied twice a year. Sods were cut in April 1971. In 1972 the Bryophytes are studied in February. Bryophytes were not sampled in 1973 and 1977.

Plot A3. CALCAREOUS GRASSLAND, GERENDAL, The Netherlands.

Date	1971 13/8	1972 6/7	1973 4/8	1974 7/8	1975 23/7	1976 2/8	1977 20/7	1978 7/8
Cover % phanerogams	70	95	95	95	95	80	85	90
Number of phanerogams	32	27	19	19	18	12	19	20
Number of cryptogams	7	11	.	1	2	0	2	1
Disappeared:								
Mercurialis annua	+							
Euphorbia helioscopia	+							
Carex flacca	+							
Senecio jacobaea	+							
Leontodon hispidus	+							
Anagallis arvensis	+	r						
Trifolium pratense	+	r						
Medicago lupulina		+						
Prunella vulgaris	+	+						
Cerastium holosteoides	r	+	r					
Agrostis stolonifera	+	+	+					
Elytrigia repens	+	+	1					
Cynosurus cristatus	1	2	+					
Plantago lanceolata	1	+	+	r				
Plantago media	1	2	2	+				
Vicia cracca	+	+	+	r	1p			
Pimpinella major	+	+		r	+p	+r		
Permanently present:								
A. Graminoids:								
Poa pratensis	+	2	+	1	2m	+b	2a	+p
Trisetum flavescens	r	2		+	1p	+p	+p	+p
Dactylis glomerata	+	3	2	4	2b	3a	2b	3a
Festuca rubra	+	2	2	3	2a	2b	4b	2a
B. Forbs:								
Achillea millefolium	r	+	+	r	+p		+p	
Ranunculus acris	+	r		r	+r		+p	
Ononis repens	+	2	+	r	+r		+p	+p
Cirsium arvense	r	r	+	+		1b	+b	+a
Chrysanthemum leucanthemum	1	3	+	+	+r	+r	1a	+r
Centaurea pratensis	+	+	1	2	1a	1b	1b	+p
Knautia arvensis	+	3	+	+	+r	+b	+p	+r
Irregularly present:								
Holcus lanatus	r	2	2	2	1p			1p
Lotus corniculatus	+	+		r			+b	+p
Pimpinella saxifraga	+	+	+				+p	+r
Daucus carota	+	+			+p			
Festuca pratensis	+							+p
Cirsium vulgare				+	2a			
Helictotrichon pubescens			+				+p	
New:								
Heracleum sphondylium				+	3a	2b	3a	2b
Hypericum perforatum					+r	+r	+p	+r
Festuca arundinacea					1p	2a	+p	+p
Lathyrus pratensis							+p	+a
Vicia sativa							+r	+r
Taraxacum sect. vulgaria								+r
Brachypodium pinnatum								+r
Bryophytes:								
Rhytidiadelphus squarrosus	x							
Fissidens taxifolius	x							
Pseudoscleropodium purum	x							
Calliergonella cuspidata	x	x						
Mnium rostratum	x	x						
Bryum rubens		x						
B. klinggraeffii		x						
B. microerytrocarpum		x						
B. bicolor		x						
Anisothecium schreberianum		x	not recorded			absent		
Veratodon purpureus		x						
Pottia davalliana		x						
Phascum cuspidatum		x						
Mnium undulatum	x				x			
Brachythecium rutabulum	x	x		x	x			x

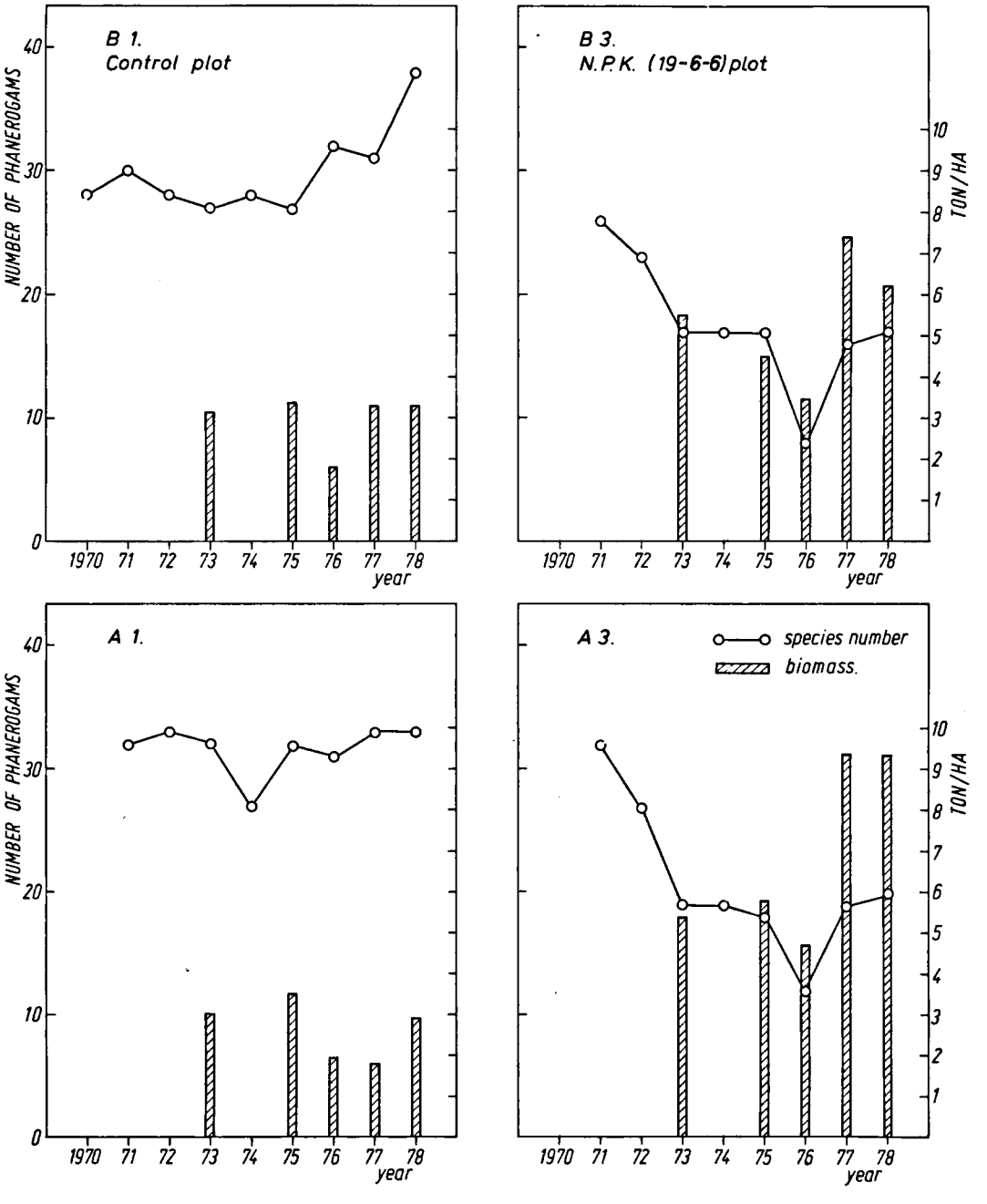


Fig. 2. Relation between number of phanerogam species and above-ground plant biomass in two control plots (A 1 and B 1) and two plots (A 3 and B 3) with a complete yearly fertilizer treatment. One ton/hectare = 100 g/m^2.

weight of *Papilionaceae*. This is considerable higher in the plots A5 and B5. According to Smith *et al.* (1971) this might be due to a high percentage of potassium in the fertilizer.

In the fertilized plots the bryophytes dropped sharply in species number. In 1978 only a single species was still present in all fertilized plots, viz. *Brachythecium rutabulum. Mnium undulatum, Pseudoscleropodium purum, Calliergonella cuspidata*, and *Fissidens taxifolius* were to be met with only rarely during the last years of study.

3.2. Above-ground plant biomass

Only in the second year (1972) a distinct difference in height between the vegetation on non-fertilized and that on fertilized plots could be observed. In 1973 the above-ground biomass of the phanerogams in all plots was measured and its dry weight in the non-fertilized A and B plots amounted to about 300 g/m^2. On the fertilized B plots this was 550 g/m^2 (B3), and on the fertilized A plots 540 g/m^2 (A3) and 680 g/m^2 (A5) (Fig. 3).

Over the years the difference in above-ground biomass of fertilized and non-fertilized plots increased. In the former an increase in biomass could be observed, whereas in the latter it remained approximately stable (Fig. 2). Calculated as the average of all years of observation, the biomass of the non-fertilized plots is less than half of that of the fertilized ones.

The part of the total biomass contributed by grasses and sedges, and by forbs, is indicated separately in fig. 4. Clearly, the gasses take a much greater part in the biomass of the fertilized plots than do the forbs. Only in a single fertilized plot, viz. A5 (during the period from 1975 to 1977) the biomass of the forbs surpassed that of the grasses. This was caused by a single plant of *Heracleum sphondylium*, established in 1971 and, after a few years, grown to a size of over 1.5 m. Thereafter the part of *Heracleum sphondylium* in the biomass dropped sharply, and in 1978 the grasses again exceeded the forbs in the biomass. This is in contrast with the situation in the non-fertilized plots. Up to 1976 the greater part of the biomass in these non-fertilized plots consisted of forbs while in 1978 there was a balance in the part of grasses and forbs (Fig. 4).

The grass *Dactylis glomerata* and the forb *Centaurea pratensis* occurred each year in the fertilized as well as in the non-fertilized plots; their parts in the biomass are shown in fig. 4. In the fertilized plots *Dactylis glomerata* constituted a considerable part of the biomass while its part in the non-fertilized plots was minor and still decreased since 1973, but it did not completely disappear from the plots. In plot B1 the number of individuals even increased from a few in 1973 to over 100 in 1978. The coverage, however, in 1978 was less than 5% of the surface. The part played by *Centaurea pratensis* is small, both in the fertilized and in the non-fertilized plots. The fertilized plots usually showed a few but tall individuals of this species, whereas the non-fertilized nearly always contained several dozen low plants (Table 2).

In 1976 a long, dry spell substantially affected the vegetation, and the production of all plants decreased to a minimum (Figs. 2 and 3). In the spring

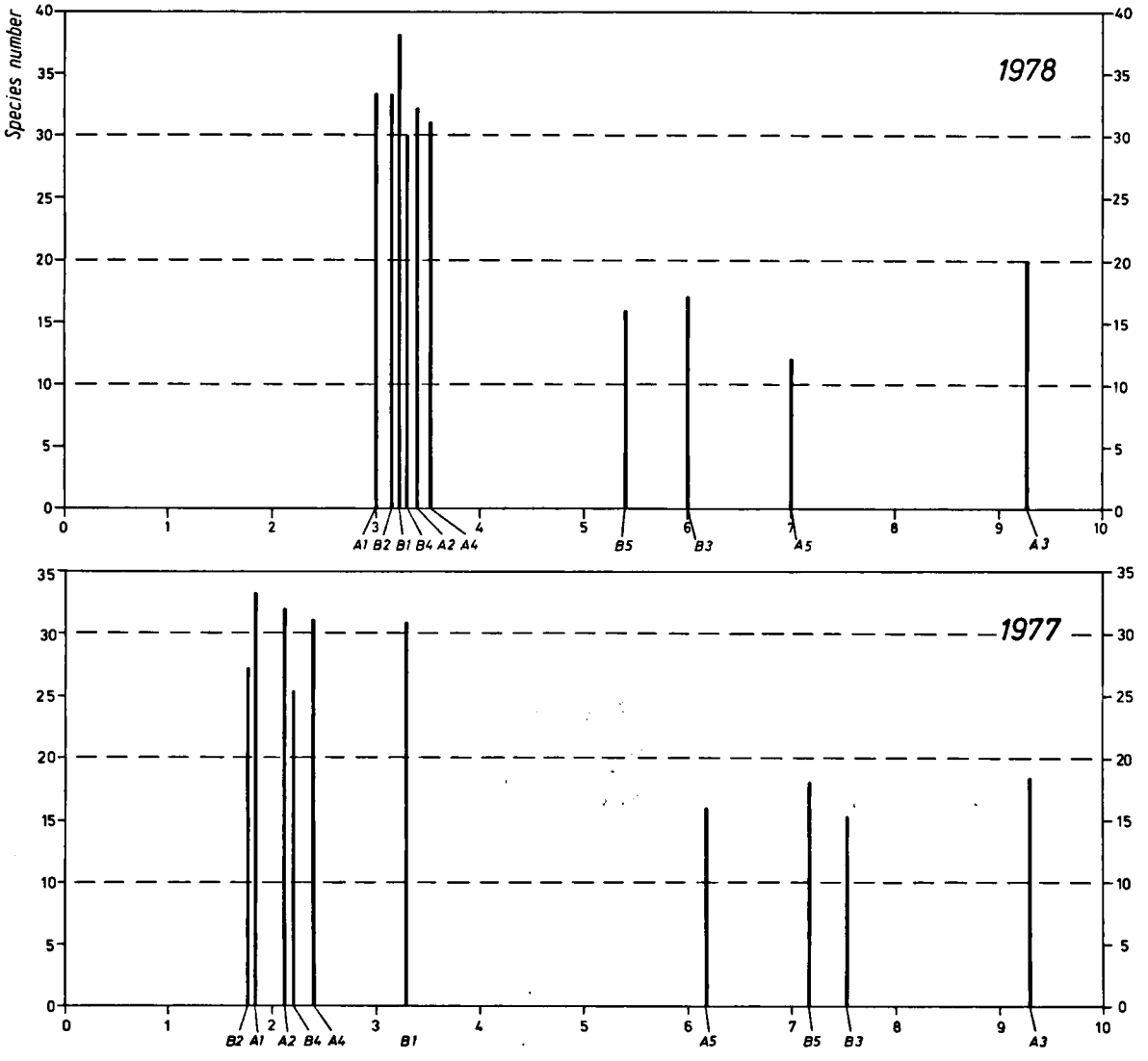
and summer of that year only one half of the amount of precipitation (as measured over the 30 preceding years) was recorded (Table 6). Except for plot A1, the production rose after the drought was over. In certain fertilizer-treated (e.g., B5, B3, and A3) and untreated plots (B2) the yield of 1977 was even about twice that in 1976.

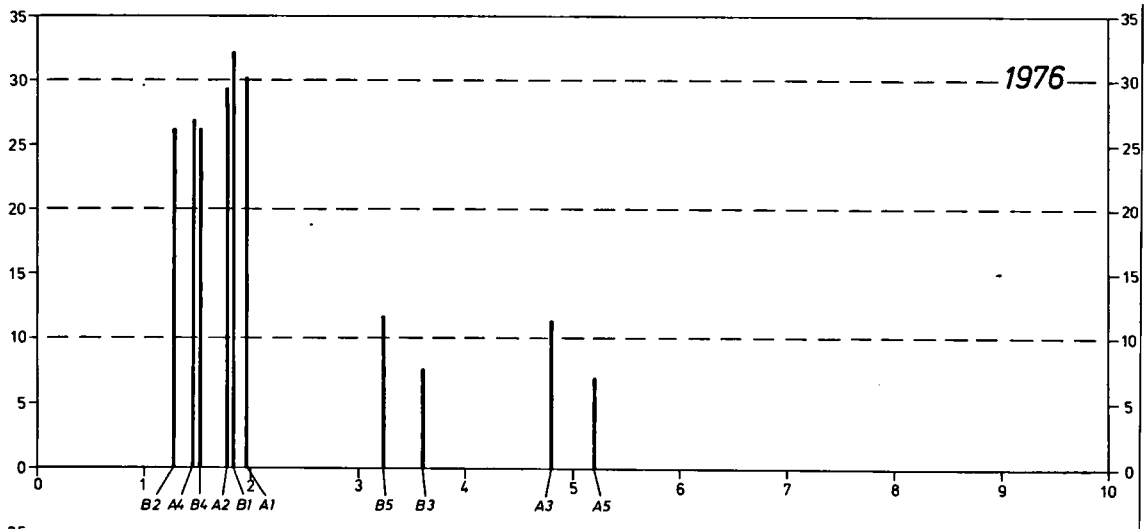
3.3. Species diversity

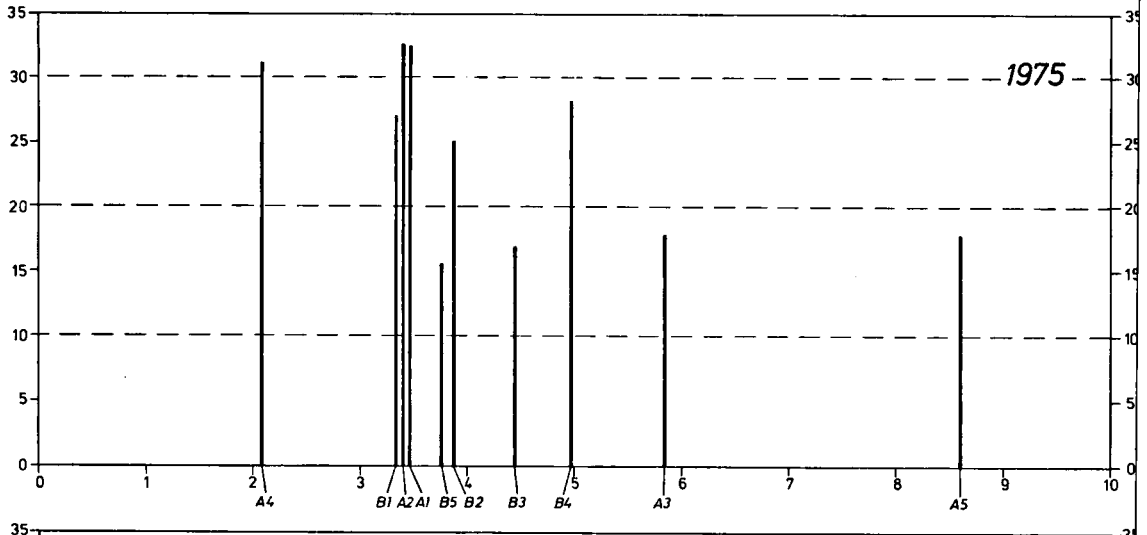
a. Variety component

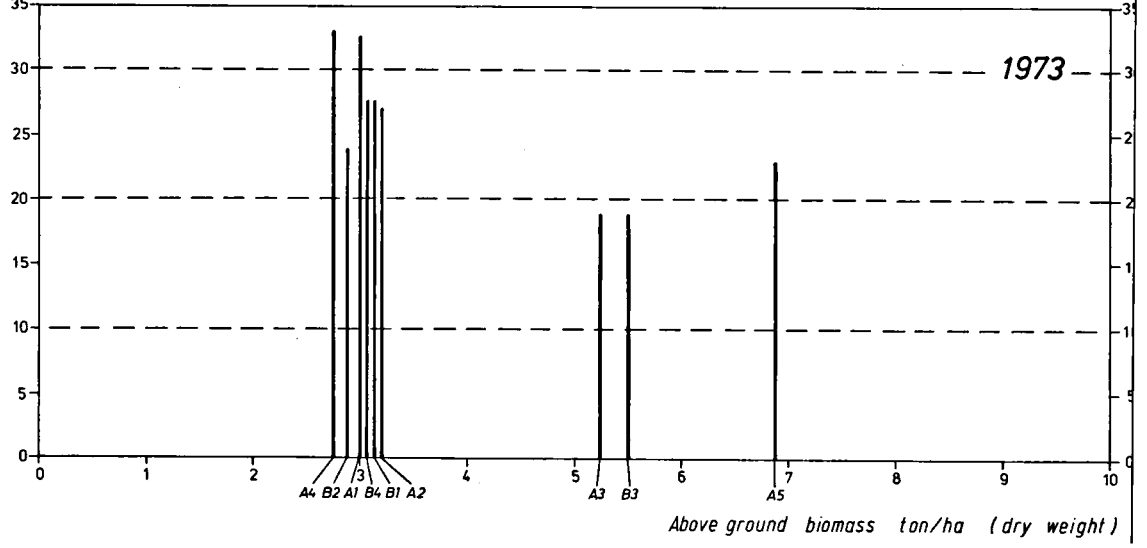
The average number of phanerogamic plant species in plots B1, 2, and 4 was 22 in 1971; it fluctuated from 17 (B2) to 30 (B1). Seven years later the average

Fig. 3. Relation between number of phanerogam species and above-ground biomass on the experimental plots with different treatments during the period 1973–78.









Above ground biomass ton/ha (dry weight)

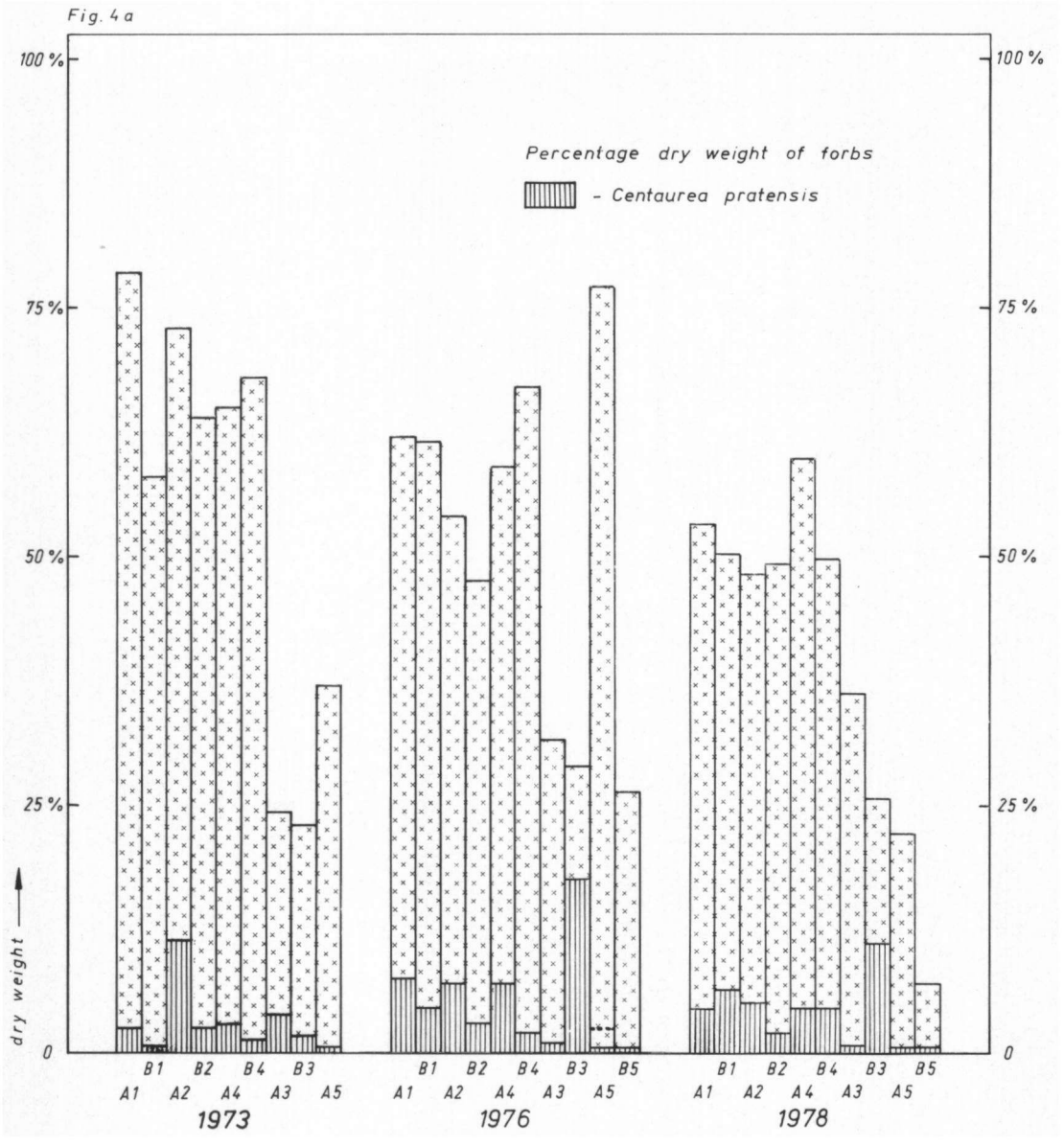
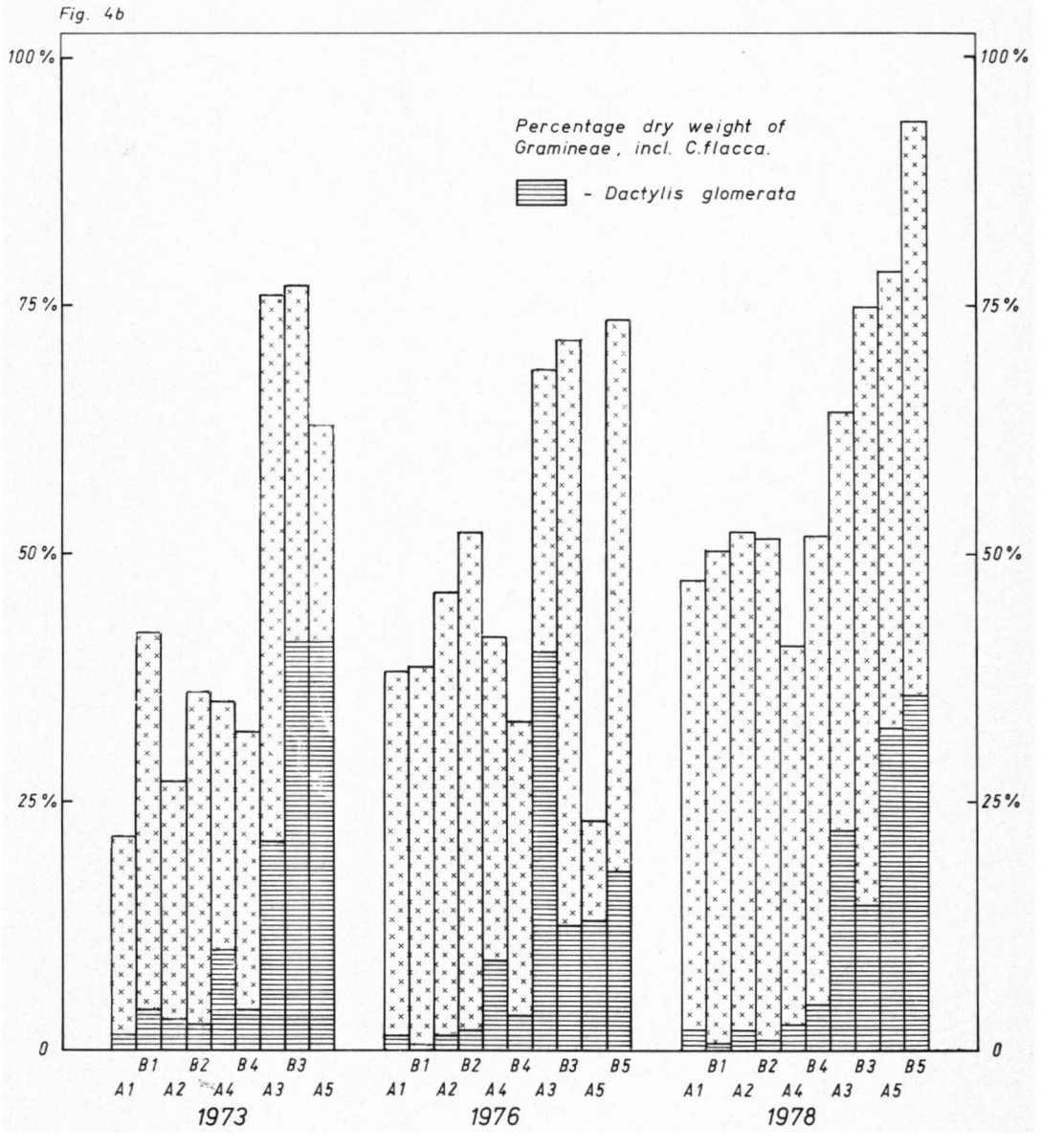


Fig. 4. Percentage of the total biomass of forbs (a) and grasses (b), respectively, during several years. The percentage of forbs in 1976 in plot A 5 above the dotted line is due to a single plant of Heracleum sphondylium.

number was 34, with extremes 30 (B4) and 38 (B1). This means that the species number increased considerably in these plots and the extremes came closer to the mean; the increase was not rectilinear. (Fig. 2 and Table 2). This fluctuation was also evident in the number of bryophyte species, but without a tendency towards increase or decrease.

Fig. 4b



In the fertilized plots B3 and B5 the number of phanerogamic species in 1971 was on the average 22, varying from 26 (B3) to 18 (B5). Seven years later the average had decreased to 16, with 17 as a maximum (B3) and 15 as a minimum (B5). The same holds for the bryophyte species; in 1978 there were about half as many as in 1971.

(To be continued)