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PHENOLOGICAL METHODS IN PERMANENT PLOT RESEARCH

The indicator value of phenological phenomena
A study in limestone grassland in Northern Switzerland

Phänologische Methoden bei Dauerquadratuntersuchungen

Der prognostische Wert phänologischer Phänomene
Eine Untersuchung in Halbtrockenrasen (Mesobrometum) in der Nordschweiz

by Bertil Krüsi

1981

We must try to understand this world and to appreciate the effect of our activities upon it. We have to live within the earth's income, as it were, if we are in the long term to survive at all.

Anthony Huxley

Contents

1. Introduction

Changes in plant communities due to successional development or alterations in the management can be studied by short-term research, communities representing various stages of succession or different management forms being compared; alternatively, a long-term programme dealing with permanent plots can be established. Either of these approaches has its disadvantages: the predictive value of short-term investigations is not always infallible , whereas long-range studies are time-consuming and highly influenced by weather conditions.

Additional information thus being required to predict the future of the vegetation within a given site preferably after only a few years, phenological data seems to be helpful. Modifications of the physical environment due to a successional development or alterations in management may render the site favourable for some species yet disadvantageous for others. In earlier stages of succession, species not adapted to the new conditions most frequently show reduced vegetative vigour, blooming and fruiting (HARPER and OGDEN 1970, HARPER 1977) but they still persist, actual changes in the composition of the vegetation only later being observed. Phenological data is thus expected to reflect environmental changes earlier than the traditional relevés which are used in phytosociology (e.g. those of the Braun-Blanquet type).

Without doubt, man has always payed attention to the phenology of some particularly important species. However, symphenological records comprising the phenology of all or most species within a given plant community date back solely to the beginning of the present century (SALISBURY 1916, 1918, GAMS 1918, ALECHIN 1925, SCHENNIKOW 1927, 1932). Since then, phenological development of whole communities and their individual components has been described by numerous authors both verbally (e.g. BECKER 1941, WALTER 1968, BYKOW 1974) as well as diagrammatically (e.g. ELLENBERG 1939, FÜLLEKRUG 1967, 1969, BALÁTOWÁ-TULÁČKOWÁ 1970b, 1971, DIERSCHKE 1972, 1974, 1977, FALIŃSKA 1972, 1973a, b, 1975, 1976, KRÜSI 1977, 1980). Various ways of recording and presenting phenological data were reviewed by BALÁTOWÁ-TULÁČKOWÁ (1970b) and DIERSCHKE (1972, 1977). The bibliography of symphenological diagrams was compiled by

BALÁTOWÁ-TULÁCKOWÁ (1970a) and later by TüXEN and WOJTERSKA (1977).

It should be noted, however, that phenology is obviously not restricted to merely describing the developmental rhythm of plants or plant communities, but represents an important auxiliary science in various research fields, viz. climatology (e.g. SCHNELLE 1955, ELLENBERG 1956a, SCHREIBER 1968, 1977, HEGG 1967, 1977, LIETH 1974), taxonomy (e.g. MARCET 1956, FALIŃSKA 1974, 1978) or ecosystem analysis (e.g. ELLENBERG 1956b, FALIŃSKA 1978). As far as vegetation science is concerned, phenological observations are useful in delineating phytosociological units (e.g. ZOLLER 1954, HEJNÝ 1978) or revealing some developmental trends (e.g. WELLS 1971). The latter possibility is well known amongst students of vegetation. According to BRAUN-BLANQUET (1964), the direction of development of communities is often first heralded by changes in vigour of particular species. RABOTNOV (1969) considered the decrease in vigour of mature plants and not the actual changes in the number of individuals of a given species as an infallible indicator of its deteriorating life conditions. This aspect has also been emphasized by other authors (e.g. BOTTLÍKOVÁ 1973, FALIŃSKA 1975).

Save for the Russian school (see HARPER and WHITE 1974 as well as GATSUK et al . 1980 for a bibliography), little work has hitherto been undertaken using phenological information to predict developmental trends in plant communities, one of the rare exceptions being the investigation of WELLS (1971). A study was therefore undertaken to examine the possible indicative value of short-term and mid-term phenological observations carried out in limestone grassland ecosystems in northern Switzerland. On one hand, phenological responses of some species towards environmental changes were studied, and on the other hand, phenological behaviour of whole communities was observed in this respect. The present paper deals with the first results obtained in the course of these investigations.

Acknowledgements

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advised on phytosociological problems, Dr O. WILDI (Swiss Federal Institute of Forestry Research SFIFR) helped with the mathematical analysis and Dr H. FUNK (Geological Institute ETH) with geological nomenclature. The advice of Ms C. BROWN, who made many valuable suggestions on style and use of the English language is greatly appreciated. I have had useful discussions on various points with PD Dr A. GIGON. Mr E. SCHäFFER assisted in the field, and Ms A. HONEGGER typed the manuscript; my sincere thanks are addressed to all these persons as well as to numerous colleagues from the Geobotanical Institute who occasionally helped throughout the course of the work.
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2. Description of the study areas

The four study areas are localized in northern Switzerland, within the Jurassic mountains belonging to the community of Merishausen 7.5 km NNW of Schaffhausen (National Grid Reference 688 500 / 291 000, Fig. 1). The substratum consists of Upper Jurassic limestone. The soils are of a mull-like rendzina type; the content of calcium carbonate within the uppermost 5 cm of soil ranging from 29 to 60 per cent, the corresponding pH values vary from 7.6 to 8.0. Climatic conditions are diagrammatically presented in Fig. 2.

The vegetation within all study areas corresponds to grassland of the *Mesobrometum* type. In the region of Schaffhausen this meadow type is usually cut once a year in mid June and very rarely or not at all fertilized. Prior to experimental management, two study areas had been used for hay-making (study areas 1 and 2), two others having been abandoned for ten and twenty years, respectively (study areas 3 and 4). One of the areas used until experimental management was started was drier and poorer in nutrients (study area 1) than the other (study area 2).

The phytosociological classification of the study areas offers some problems as far as nomenclature is concerned. According to ZOLLER (1954), who studied the dry grasslands in this region, our study area 1 should be considered as a *Medicago falcatae-Mesobrometum*, whereas study area 2 should correspond to a *Dauco-Salvio-Mesobrometum*; the study areas 3 and 4 abandoned for ten and 20 years respectively would represent the *Seselio libanotidis-Mesobrometum*.

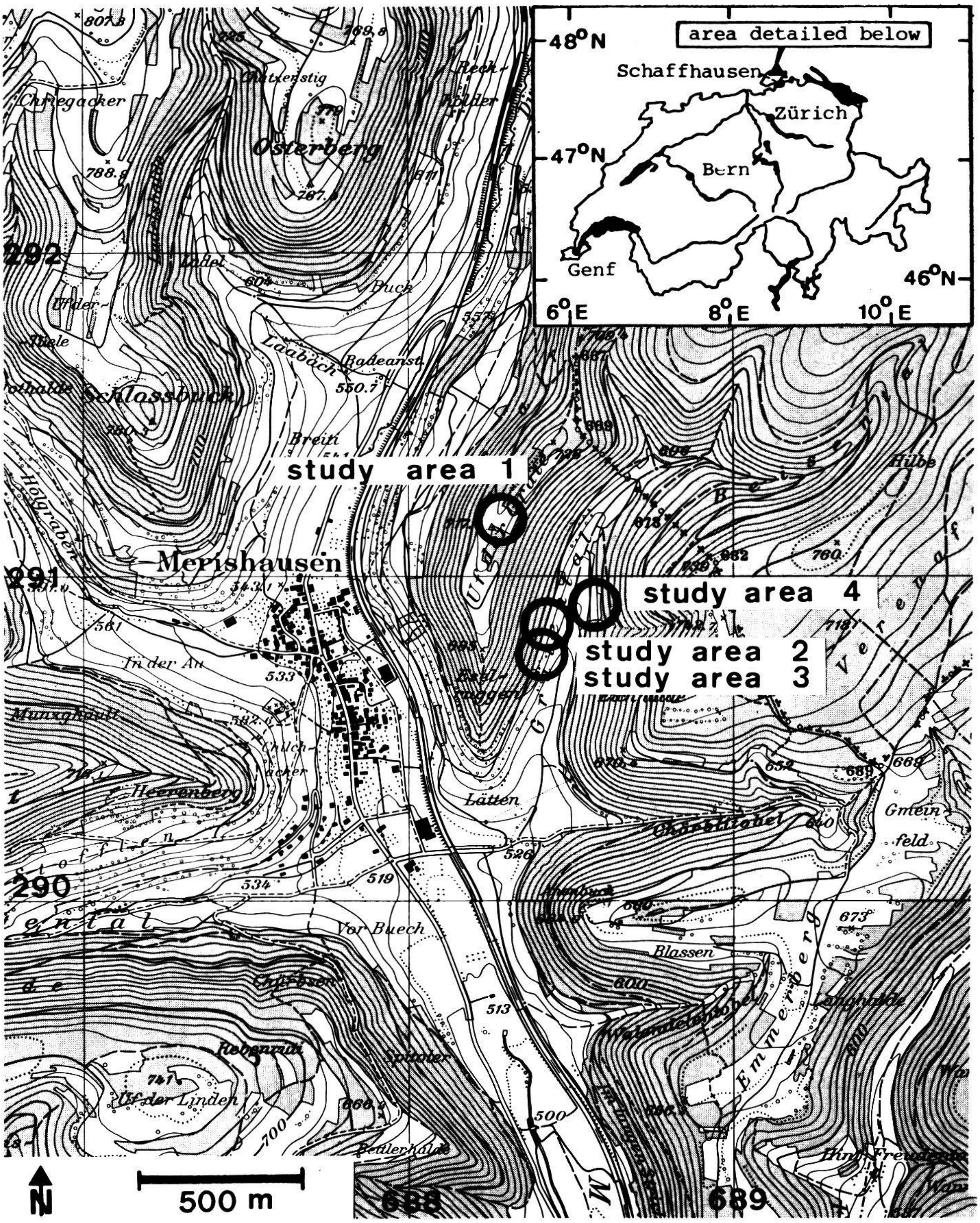


Fig. 1. Location of the four study areas investigated and (inset) their relationship to other places in Switzerland. Scale 1:25000. (Reproduced with permission of the Swiss Federal Office of Topography from May 6, 1981).

The nomenclature proposed by ZOLLER (1954) not being generally recognized, the classification of OBERDORFER (1957, 1978) was followed. According to this author, our study areas 1 and 2 correspond to a *Mesobrometum* Br.-Bl. 1925, the first area being a type with *Trisetum flavescens* and *Medicago falcata* whereas the second, having a soil richer and more humid, represents a type with *Trisetum flavescens* and *Centaurea jacea*. The study areas 3 and 4 correspond to successional stages towards a *Geranion sanguinei*, the former area representing a less advanced stage than the latter.

The floristic composition of the four study areas is shown in a frequency table based upon 18 relevés per area (Table 1); the resemblance of the 72 relevés considered is shown in Figs 3 and 4 representing scatter diagrams constructed by principal component analysis using a cross product matrix. Further characteristics of the four study areas are summarized in Table 2. The study areas will be referred to by their respective numbers in further parts of the present paper.

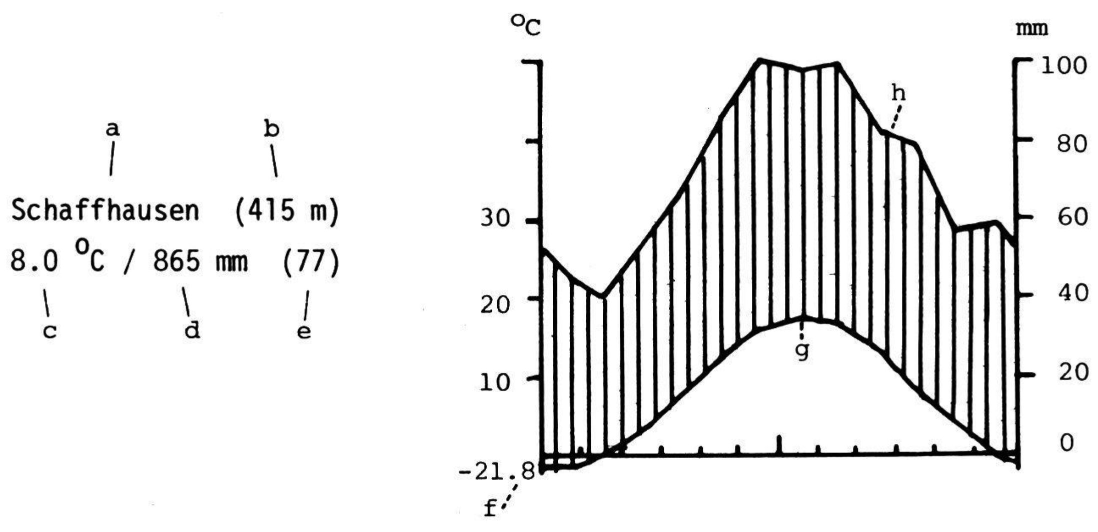


Fig. 2. Climatic diagram of Schaffhausen (from WALTER and LIETH 1960-1967).

a: station
b: hight above sea level
c: mean annual temperature (°C)
d: mean annual precipitation (mm)
e: duration of observations (years)
f: lowest temperature recorded (°C)
g: curve of mean monthly temperature
h: curve of mean monthly precipitation

Ordinate: one division = 10 °C or 20 mm rain
Abscissa: months (January-December)

Table 1. Frequency table representing the floristic composition of the four study areas based upon 18 relevés ($50\ m^2$) per each area (*: value is less than 0.05, 'species value': see page 21).

	Study area 1	Study area 2	Study area 3	Study area 4
Total number of species (herbs/shrubs/cryptogames)	96 (79/3/14)	98 (88/3/7)	120 (103/9/8)	144 (111/21/12)
Mean number of species per $50\ m^2$ (range):	54.8 (48- 62)	54.1 (42- 62)	55.4 (42-68)	62.7 (52- 70)
- herbs	47.4 (43- 53)	51.3 (39- 59)	50.0 (36-62)	54.5 (43- 65)
- shrubs	0.8 (0- 2)	0.6 (0- 2)	2.0 (1- 4)	4.4 (1- 17)
- cryptogames	6.6 (5- 10)	2.2 (1- 5)	3.4 (2- 5)	3.8 (1- 6)
Mean cover-percentage (range)				
- herbs	98% (90-100)	84% (75- 95)	81% (50-95)	80% (60- 95)
- shrubs	<1% (0- <1)	<1% (0- <1)	2% (<1-10)	4% (<1- 20)
- cryptogames	42% (10- 90)	91% (70-100)	81% (50-95)	89% (70-100)

Species	Study area 1 frequency f. (%)	Study area 1 mean cover m.c. (%)	Study area 1 species value s.v.	Study area 2 frequency f. (%)	Study area 2 mean cover m.c. (%)	Study area 2 species value s.v.	Study area 3 frequency f. (%)	Study area 3 mean cover m.c. (%)	Study area 3 species value s.v.	Study area 4 frequency f. (%)	Study area 4 mean cover m.c. (%)	Study area 4 species value s.v.
Prunella grandiflora	95	1.5	1.4	-	-	-	-	-	-	-	-	-
Chrysohypnum chrysophyllum	72	6.2	4.5	6	0.2	*	6	0.1	*	6	0.1	*
Galium verum	72	1.0	0.7	-	-	-	-	-	-	-	-	-
Festuca pratensis	72	0.7	0.5	-	-	-	6	0.1	*	-	-	-
Centaurea scabiosa	44	0.4	0.2	-	-	-	6	0.1	*	-	-	-
Scleropodium purum	44	0.4	0.2	-	-	-	-	-	-	17	0.8	0.1
Anthoxanthum odoratum	39	0.4	0.2	-	-	-	-	-	-	-	-	-
Polygala comosa	33	0.3	0.1	-	-	-	-	-	-	-	-	-
Anacamptis pyramidalis	33	0.3	0.1	-	-	-	-	-	-	-	-	-
Cladonia cf. *rangiferina*	17	0.2	*	-	-	-	-	-	-	-	-	-

Trisetum flavescens	100	1.2	1.2	83	1.0	0.8	-	-	-	6	0.1	*
Trifolium campestre	67	0.7	0.4	100	1.5	1.5	-	-	-	-	-	-
Rhinanthus minor	100	1.3	1.3	39	0.4	0.2	-	-	-	-	-	-
Potentilla heptaphylla	95	1.1	1.1	22	0.2	0.1	6	0.1	*	-	-	-
Achillea millefolium	100	1.1	1.1	83	1.2	1.0	95	4.1	3.9	11	0.2	*
Carex verna	95	1.6	1.5	100	1.2	1.2	50	0.9	0.4	6	0.1	*
Centaurea jacea	39	0.4	0.2	100	7.7	7.7	67	0.7	0.5	6	0.1	*
Camptothecium lutescens	100	20.8	20.8	22	1.2	0.3	78	6.6	5.1	6	0.1	*
Euphorbia cyparissias	95	1.0	1.0	22	0.3	0.1	72	0.8	0.6	22	0.2	*
Inula conyza	-	-	-	6	0.1	*	44	0.4	0.2	-	-	-
Convulvulus arvensis	-	-	-	6	0.1	*	44	0.4	0.2	11	0.1	*
Koeleria cristata	-	-	-	-	-	-	39	0.4	0.2	-	-	-
Medicago sativa	-	-	-	6	0.1	*	27	0.3	0.1	6	6	*
Geranium sanguineum	-	-	-	-	-	-	22	0.4	0.1	-	-	-
Vicia sepium	-	-	-	89	1.0	0.9	95	1.0	1.0	17	0.2	*
Satureja vulgaris	-	-	-	67	0.7	0.4	100	9.7	9.7	17	0.3	0.1
Silene nutans	17	0.2	*	83	1.9	1.6	78	1.1	0.9	6	0.1	*
Sedum sexangulare	-	-	-	95	1.3	1.2	56	0.6	0.3	-	-	-
Pastinaca sativa	-	-	-	39	0.4	0.2	95	1.0	0.9	6	0.1	*
Silene vulgaris	11	0.1	*	33	0.4	0.1	67	0.8	0.5	6	0.1	*
Cerastium caespitosum	17	0.2	*	67	0.7	0.4	17	0.2	*	6	0.1	*
Thlaspi perfoliatum	-	-	-	17	0.2	*	56	0.6	0.3	-	-	-
Geranium pyrenaicum	-	-	-	39	0.4	0.2	33	0.3	0.1	-	-	-
Rumex acetosa	17	0.2	*	44	0.4	0.2	22	0.2	0.1	-	-	-
Trifolium repens	17	0.2	*	44	0.4	0.2	17	0.2	*	-	-	-
Heracleum sphondylium	-	-	-	33	0.3	0.1	17	0.2	*	6	0.1	*
Peltigera canina	6	0.1	*	50	0.5	0.3	-	-	-	-	-	-
Glechoma hederaceum	-	-	-	39	0.4	0.2	-	-	-	11	0.1	*
Mysotis arvensis	6	0.1	*	22	0.2	0.1	-	-	-	-	-	-
Thesium bavarum	-	-	-	17	0.2	*	11	0.1	*	83	1.2	1.0
Quercus petraea (seedlings)	-	-	-	28	0.3	0.1	-	-	-	50	0.5	0.3
Origanum vulgare	-	-	-	28	1.0	0.3	-	-	-	33	0.4	0.1

Table 1 (continued)

Species	Study area 1			Study area 2			Study area 3			Study area 4		
	f.	m.c.	s.v.	f.	m.c.	s.v.	f.	m.c.	s.v.	f.	m.c.	s.v.
Scabiosa columbaria	95	1.1	1.0	83	1.0	0.8	11	0.1	*	100	1.3	1.3
Linum catharticum	100	1.6	1.6	39	0.4	0.2	6	0.1	*	61	0.7	0.4
Onobrychis arenaria	100	1.4	1.4	33	0.3	0.1	6	0.1	*	28	0.3	0.1
Fissidens taxifolius	95	3.2	3.0	-	-	-	-	-	-	17	0.2	*
Pinus silvestris (seedlings)	50	0.5	0.3	-	-	-	-	-	-	22	0.2	0.1
Carex flacca	95	2.8	2.6	-	-	-	28	0.4	0.1	100	2.1	2.1
Rhytidium rugosum	39	0.4	0.2	-	-	-	83	6.5	5.4	89	42.0	37.3
Aster amellus	95	1.0	0.9	-	-	-	11	0.1	*	95	4.7	4.5
Medicago falcata	100	1.6	1.6	-	-	-	22	0.4	0.1	17	0.2	*
Thuidium tamariscifolium	78	3.5	2.7	-	-	-	11	0.1	*	39	1.9	0.8
Gentiana ciliata	56	0.6	0.3	-	-	-	11	0.1	*	50	0.5	0.3
Leontodon hispidus	67	0.7	0.4	11	0.1	*	28	0.3	0.1	72	1.8	1.3
Trifolium medium	100	1.9	1.9	11	0.1	*	28	0.4	0.1	33	0.6	0.2
Ononis repens	95	10.3	9.8	28	0.3	0.1	33	0.5	0.2	83	1.7	1.4
Trifolium pratense	89	1.2	1.1	83	1.0	0.8	17	0.2	*	44	0.4	0.2
Chrysanthemum leucanthemum s.l.	100	1.8	1.8	100	1.7	1.7	39	0.4	0.2	39	0.4	0.2
Salvia pratensis	100	7.0	7.0	100	20.6	20.6	6.1	8.4	5.2	22	0.2	0.1
Plantago media	100	2.3	2.3	100	1.8	1.8	6.1	0.6	0.4	39	0.4	0.2
Primula veris s.l.	95	1.0	0.9	100	2.6	2.6	100	3.3	3.3	100	8.5	8.5
Buphthalmum salicifolium	56	0.6	0.3	100	1.4	1.4	100	5.0	5.0	100	11.4	11.4
Thymus froehlichianus	28	0.3	0.1	89	2.3	2.1	95	2.3	2.2	89	3.3	3.0
Thymus pulegioides	17	0.2	*	100	6.7	6.7	100	4.7	4.7	100	9.9	9.9
Lathyrus heterophyllus	17	0.2	*	67	0.8	0.5	100	4.1	4.1	100	1.2	1.2
Acer pseudoplatanus (seedlings)	17	0.2	*	56	0.6	0.3	61	0.6	0.4	61	0.6	0.4
Lathyrus pratensis	11	0.1	*	100	1.9	1.9	100	1.3	1.3	95	1.0	1.0
Daucus carota	6	0.1	*	100	2.0	2.0	95	1.5	1.4	39	0.4	0.2
Veronica chamaedrys	-	-	-	78	0.9	0.7	50	0.5	0.3	39	0.4	0.2
Fraxinus excelsior (seedlings)	-	-	-	67	0.7	0.4	33	0.3	0.1	22	0.2	0.2
Asperula cynanchica	-	-	-	56	0.6	0.3	78	1.0	0.8	72	1.1	0.8
Viola hirta	-	-	-	39	0.4	0.2	78	1.4	1.2	100	4.7	4.7

Solidago virga-aurea	-	-	-	22	0.2	0.1	33	0.3	0.1	95	1.0	1.0
Seseli libanotis	-	-	-	17	0.2	*	44	0.6	0.3	100	7.1	7.1
Campanula rapunculoides	-	-	-	17	0.2	*	83	1.0	0.8	28	0.3	0.1
Prunus spinosa	-	-	-	17	0.2	*	22	0.9	0.2	28	0.3	0.1
Galium pumilum	6	0.1	*	6	0.1	*	61	0.8	0.5	22	0.2	0.1
Fragaria vesca	-	-	-	-	-	-	78	4.2	3.2	100	2.1	2.1
Cornus sanguinea	-	-	-	-	-	-	39	1.1	0.4	56	2.8	1.5
Tragopogon minor	-	-	-	-	-	-	39	0.4	0.2	50	0.5	0.3
Aegopodium podagraria	-	-	-	-	-	-	33	4.4	1.5	17	0.2	*
Acer campestre	-	-	-	-	-	-	33	0.6	0.2	50	0.5	0.3
Prunus avium	-	-	-	-	-	-	33	0.3	0.1	39	0.4	0.2
Clematis vitalba	-	-	-	-	-	-	22	2.4	0.5	17	0.2	*
Carex ornithopoda	-	-	-	-	-	-	17	0.4	0.1	89	1.6	1.4
Anthericum ramosum	-	-	-	-	-	-	17	0.2	*	83	2.4	2.0
Euphorbia verrucosa	-	-	-	6	0.1	*	17	0.2	*	39	0.4	0.2
Carex montana	-	-	-	-	-	-	-	-	-	95	8.1	7.7
Aquilegia atrata	-	-	-	-	-	-	-	-	-	89	1.6	1.5
Polygala amarella	-	-	-	-	-	-	-	-	-	89	1.0	0.9
Carlina simplex	-	-	-	-	-	-	-	-	-	83	2.3	1.9
Gentiana germanica	-	-	-	-	-	-	-	-	-	83	1.3	1.1
Cephalanthera longifolia	-	-	-	-	-	-	-	-	-	78	0.8	0.6
Orobanche alsatica	-	-	-	-	-	-	6	0.1	*	61	0.6	0.4
Hylocomium splendens	-	-	-	-	-	-	-	-	-	50	10.8	5.4
Phyteuma orbiculare	-	-	-	-	-	-	-	-	-	50	0.6	0.3
Gymnadenia conopea	-	-	-	-	-	-	-	-	-	50	0.5	0.3
Melittis melissophyllum	-	-	-	-	-	-	6	0.1	*	44	0.4	0.2
Teucrium chamaedrys	-	-	-	11	0.1	*	6	0.1	*	39	0.8	0.3
Viburnum lantana	-	-	-	-	-	-	-	-	-	39	0.4	0.2
Rhytidiadelphus triquetrus	-	-	-	-	-	-	-	-	-	33	2.0	0.7
Agrimonia eupatoria	-	-	-	-	-	-	-	-	-	33	0.4	0.1
Carlina vulgaris	-	-	-	-	-	-	-	-	-	33	0.4	0.1
Chrysanthemum corymbosum	-	-	-	-	-	-	-	-	-	22	0.3	0.1
Sorbus aria	-	-	-	-	-	-	-	-	-	22	0.2	0.1
Thalictrum saxatile	-	-	-	-	-	-	-	-	-	17	0.3	0.1
Hepatica triloba	-	-	-	-	-	-	6	0.1	*	17	0.2	*
Hieracium murorum	-	-	-	-	-	-	-	-	-	17	0.2	*
Orchis pallens	-	-	-	-	-	-	-	-	-	17	0.2	*

Table 1 (continued)

Species	Study area 1			Study area 2			Study area 3			Study area 4		
	f.	m.c.	s.v.	f.	m.c.	s.v.	f.	m.c.	s.v.	f.	m.c.	s.v.
Bromus erectus	100	55.5	55.5	100	35.6	35.6	100	15.4	15.4	100	15.1	15.1
Sanguisorba minor	100	1.0	1.0	100	2.3	2.3	100	3.0	3.0	95	1.7	1.6
Knautia arvensis	100	1.2	1.2	100	2.3	2.3	95	2.8	2.7	100	1.7	1.7
Medicago lupulina	100	1.2	1.2	100	1.0	1.0	83	0.8	0.7	100	1.1	1.1
Festuca ovina	100	1.1	1.1	100	21.5	21.5	83	4.9	4.1	95	3.2	3.0
Pimpinella saxifraga	72	0.7	0.7	100	2.0	2.0	100	1.0	1.0	100	1.1	1.1
Plantago lanceolata	100	1.6	1.6	95	1.5	1.4	89	0.9	0.8	83	0.9	0.7
Campanula rotundifolia	89	1.0	0.9	100	1.0	1.0	95	1.4	1.3	83	0.8	0.7
Lotus corniculatus	78	0.8	0.6	100	1.6	1.6	95	1.0	1.0	89	1.3	1.2
Thuidium abietinum	83	4.0	3.3	100	93.3	93.3	100	56.2	56.2	78	16.0	12.4
Galium album	61	0.7	0.4	100	5.6	5.6	100	7.4	7.4	89	1.3	1.2
Arrhenatherum elatius	95	1.0	0.9	100	8.5	8.5	100	12.6	12.6	50	0.7	0.3
Picris hieracioides	95	1.7	1.6	100	2.9	2.9	89	0.9	0.8	61	1.0	0.6
Briza media	100	1.2	1.2	83	0.9	0.7	67	0.7	0.4	95	1.0	1.0
Brachypodium pinnatum	100	4.1	4.1	67	0.7	0.4	89	1.8	1.6	100	9.4	9.4
Hippocrepis comosa	100	1.1	1.1	95	1.2	1.2	33	0.4	0.1	100	3.9	3.9
Anthyllis vulgaris s.l.	100	1.6	1.6	72	0.8	0.6	67	1.7	1.2	95	2.6	2.5
Dactylis glomerata	95	1.0	0.9	100	1.1	1.1	78	0.8	0.6	56	0.6	0.3
Poa angustifolia	50	0.5	0.3	100	1.9	1.9	100	2.5	2.5	72	1.1	0.8
Ranunculus bulbosus	95	1.0	0.9	100	1.0	1.0	39	0.4	0.2	89	0.9	0.8
Hieracium pilosella	50	0.5	0.3	78	0.8	0.7	89	1.1	1.0	89	0.9	0.8
Arabis hirsuta	83	0.8	0.7	100	1.0	1.0	83	0.8	0.7	33	0.3	0.1
Helictotrichon pubescens	56	0.6	0.3	95	1.3	1.2	89	1.7	1.5	33	0.3	0.1
Hypericum perforatum	50	0.5	0.3	72	0.7	0.5	78	0.9	0.7	56	0.6	0.3
Taraxacum officinale s.l.	61	0.6	0.4	83	0.8	0.7	11	0.1	*	50	0.5	0.3
Vicia cracca	33	0.3	0.1	78	1.0	0.8	50	0.7	0.4	39	0.4	0.2
Weisia viridula	50	0.5	0.3	39	0.4	0.2	6	0.1	*	33	0.3	0.1
Entodon orthocarpus	33	1.2	0.4	17	0.7	0.1	56	3.4	1.9	17	0.2	*
Fagus silvatica	11	0.1	*	6	0.1	*	6	0.1	*	22	0.2	0.1
Festuca rubra	17	0.2	*	17	0.2	*	-	-	-	6	0.1	*
Allium sp.	-	-	-	11	0.1	*	22	0.2	0.1	6	0.1	*

Brachyhecium rutabulum	6	0.1	*	11	0.1	*	6	0.1	*	11	0.1	*
Potentilla reptans	-	-	-	-	-	-	11	0.1	*	22	0.2	0.1
Mnium rostratum	17	0.2	*	11	0.1	*	-	-	-	-	-	-
Rosa canina	-	-	-	-	-	-	17	0.2	*	6	0.1	*
Geum urbanum	-	-	-	-	-	-	17	0.2	*	6	0.1	*
Pirus malus	-	-	-	-	-	-	6	0.1	*	17	0.2	*
Tragopogon orientalis	17	0.2	*	-	-	-	-	-	-	6	0.1	*
Ligustrum vulgare	-	-	-	-	-	-	11	0.3	*	6	0.1	*
Ophrys insectifera	6	0.1	*	-	-	-	-	-	-	11	0.1	*

Species only found in one or two relevés

Study area 1: *Ctenidium molluscum (2x), Dianthus carthusianorum (2x), Agrostis stolonifera (lx), Bellis perennis (lx), Brachythecium laetum (lx), Campanula patula (lx), Euphrasia rostkoviana (lx), Nostoc communis (lx), Peucedanum cervaria (lx).*

Study area 2: *Campanula patula (lx), Festuca arundinacea (lx), Malva moschata (lx), Orobanche vulgaris (lx), Valerianella locusta (lx).*

Study area 3: *Sedum maximum (2x), Stachys recta (2x), Epipactis latifolia (lx), Erigeron acer (lx), Linaria vulgaris (lx), Melandrium diurnum (lx), Melilotus officinalis (lx), Senecio erucifolius (lx), Veronica hedericifolia (lx), Tortella tortuosa (lx).*

Study area 4: *Corylus avellana (2x), Crataegus oxyacantha (2x), Rhamnus cathartica (2x), Carex digitata (lx), Campanula persicifolia (lx), Cephalanthera damasonium (lx), Cephalanthera rubra (lx), Coronilla coronata (lx), Evonymus latifolius (lx), Festuca duriuscula (lx), Hedera helix (lx), Juniperus communis (lx), Lactuca perennis (lx), Lonicera alpigena (lx), Melampyrum pratense (lx), Platanthera bifolia (lx), Picea abies (lx).*

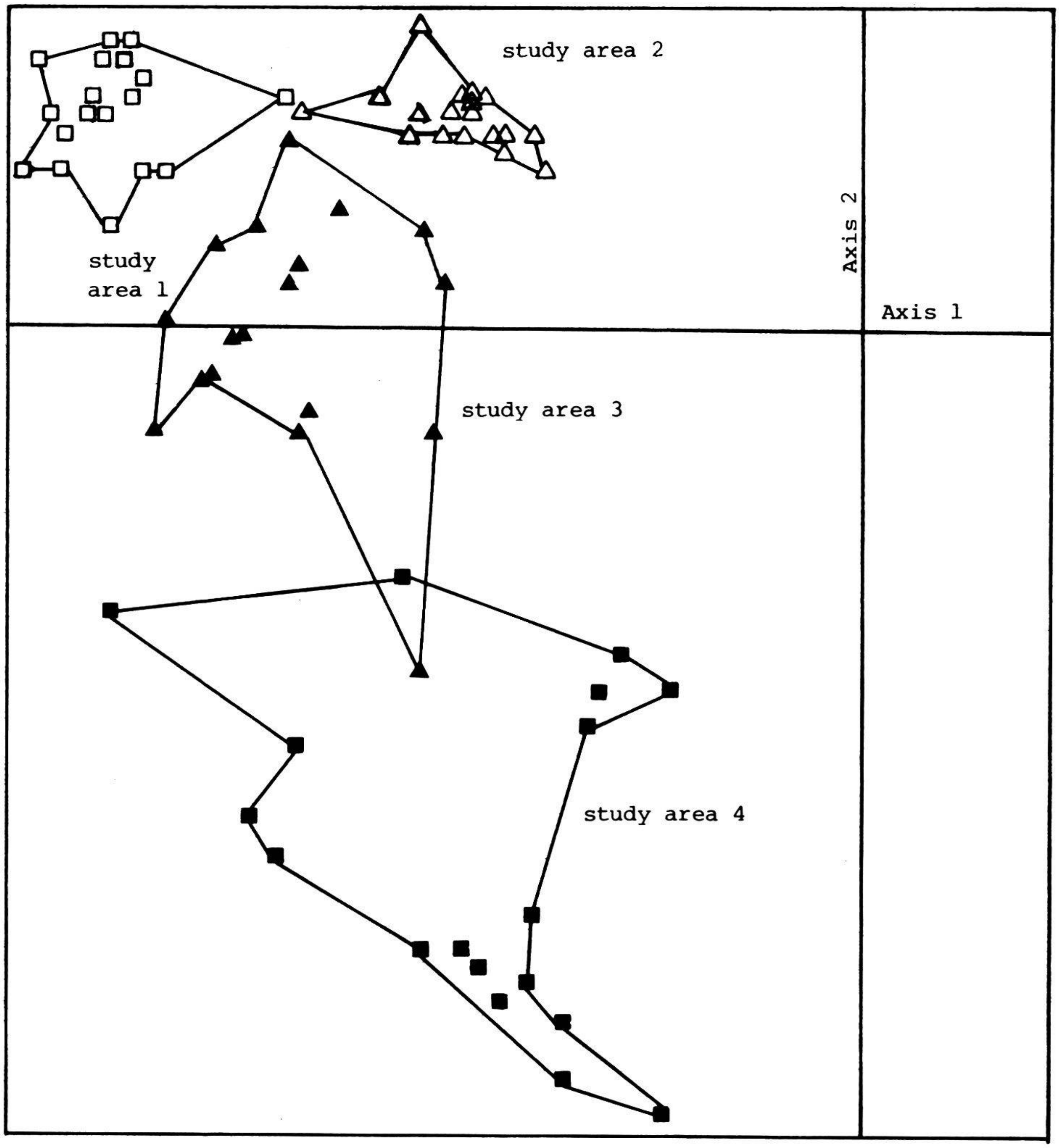


Fig. 3. Ordination by principal component analysis of 72 relevés (50 m^2) within the four study areas (18 relevés per each area).
Axis 1 and 2 are presented.
Axis 1: percentage of variation accounted for: 45.81%
range of co-ordinates: - 15.48 to 3.14
Axis 2: percentage of variation accounted for: 12.99%
range of co-ordinates: - 13.64 to 4.98

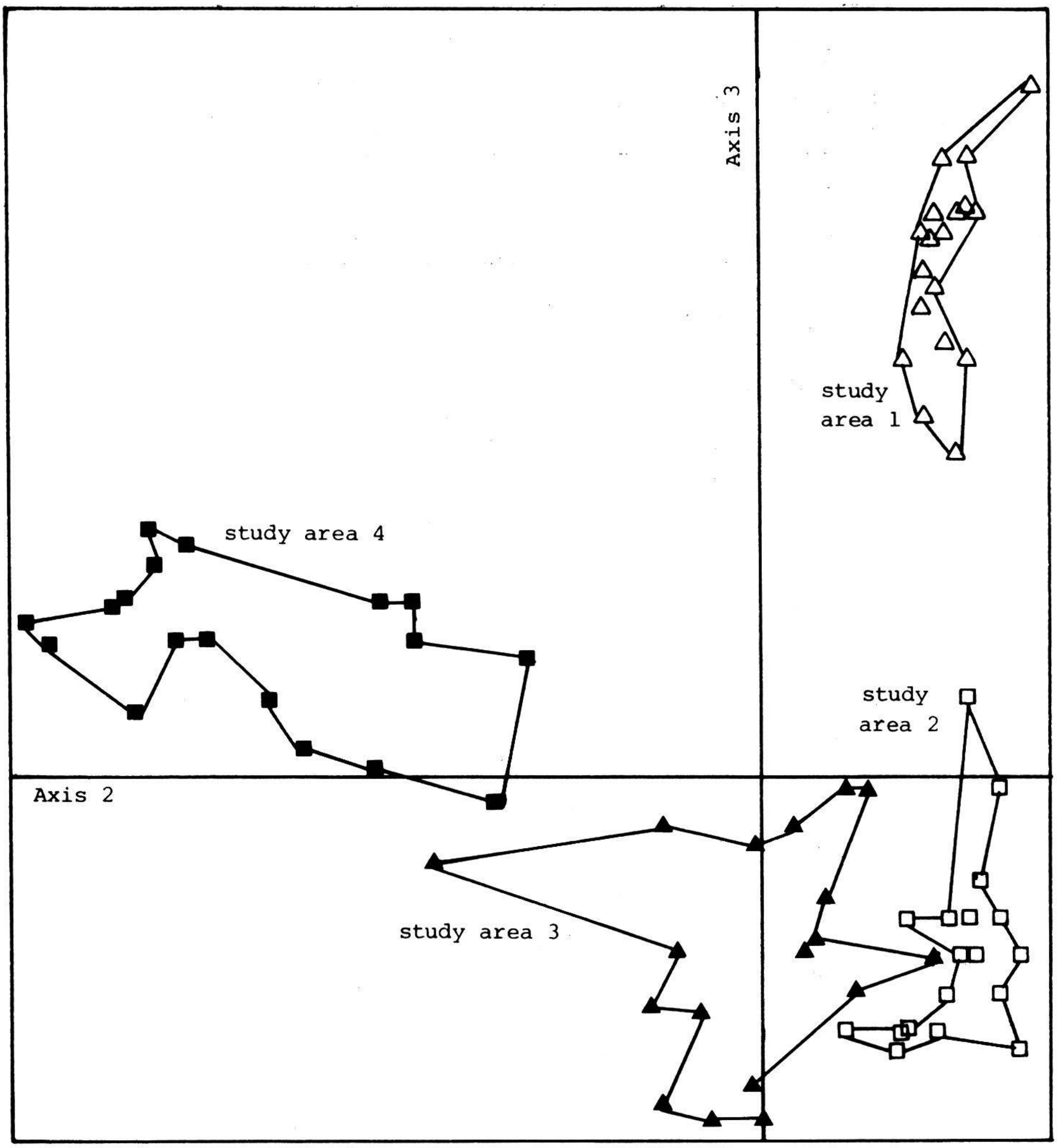


Fig. 4. Ordination by principal component analysis of 72 relevés (50 m^2) within the four study areas (18 relevés per area).
Axis 2 and 3 are presented.
Axis 2: percentage of variation accounted for: 12.99%
range of co-ordinates: - 13.64 to 4.98
Axis 3: percentage of variation accounted for: 11.10%
range of co-ordinates: - 6.07 to 12.55

Table 2. Characteristics of the four studied areas

Study area	Grassland type according to ZOLLER (1954)	Grassland form	Treatment prior to experimental management	Experimentally managed since	Geology	Aspect (°)	Slope (%)	Altitude a.s.l.
1	*Medicago falcatae-Mesobrometum*	dry	annually cut in mid June	1978*	Gamma-Marl	124 (SE)	27	710 m
2	*Dauco-Salvio-Mesobrometum*	dry-fresh	annually cut in mid June	1977**	talus of Beta-limestone	111 (SE)	45	565 m
3	*Seselio libanotidis-Mesobrometum*	dry	abandoned for 10 years	1977**		114 (SE)	47	570 m
4	*Seselio libanotidis-Mesobrometum*	dry	abandoned for 20 years	1977**		265 (NW)	43	588 m

* burnt for the first time in 1979

** burnt for the first time in 1978

3. Methods

3.1. *Experimental design and treatments*

Within each of the four study areas, 18 plots were delineated, each mesuring 5 m x 10 m. The following six treatments were carried out:

A) cutting in mid June every year

B) cutting in mid June every second year

C) cutting in mid June every fifth year

D) cutting in early October

E) burning in March

F) no management at all.

The study having been carried out for a rather limited period of time, treatment C and F to date yielded the same results; thus the effects of these two treatments are not discussed apart. Treatment B was very similar to treatment A and sometimes provided no additional information; therefore, the effects of treatment B are not always separately presented.

Taking into account possible gradients occurring in the study areas, three replicas were laid out for each treatment - bar two surfaces within study area 4 that had been burnt in March (Figs 5, 6). To examine small scale changes within a given stand, a 1 m^2 plot was marked in each 50 m^2 surface.

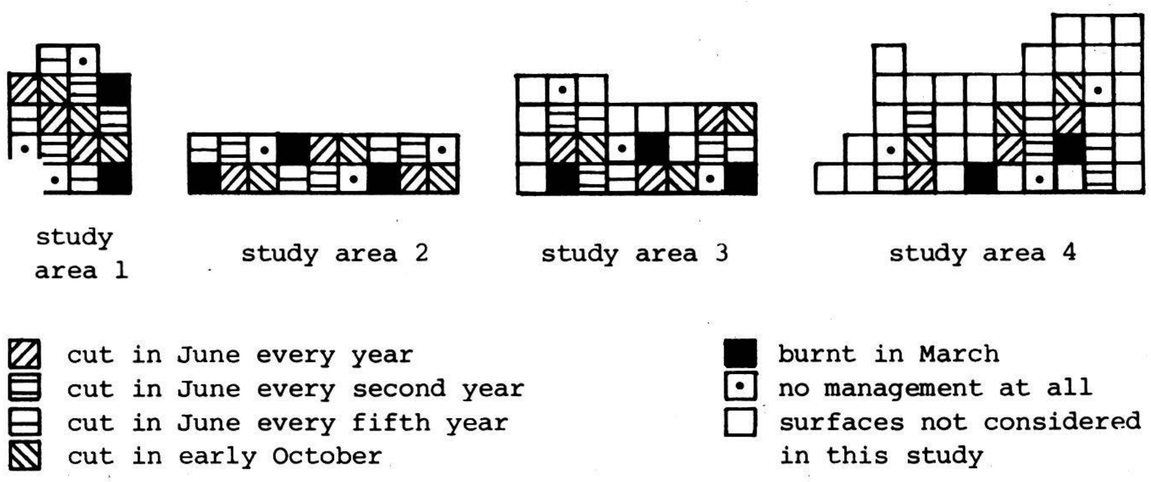


Fig. 5. Management of the four study areas.

Fig. 6. The study area 2 just after burning.

3.2. *Distribution maps, relevés and 'species value'*

The distribution maps are based upon the 50 m^2 relevés taken in 1977 when the study areas 2, 3 and 4 were experimentally managed for the first time. The relevés in study area 1 only data back to 1978, when experimental management was started in this area. Due to technical factors, the rectangular 50 m^2 plots are indicated in the distribution maps by squares. The different cover values are marked as shown in Table 3.

Phytosociological relevés were taken once a year, for plots cut in mid June this occurred just prior to cutting, for all other plots relevés were taken in August. In 1977, the vegetation in the 1 m^2 as well as in the 50 m^2 plots was recorded according to the BRAUN-BLANQUET method (e.g. BRAUN-BLANQUET 1964, MUELLER-DOMBOIS and ELLENBERG 1974). From 1978 onwards, the finer scale of LONDO (1975) was used; LONDO's values can easily be transformed into BRAUN-BLANQUET's cover-abundance values. Plant nomenclature follows HESS, LANDOLT and HIRZEL (1967, 1970, 1972) for phanerogams and BERTSCH (1966) for bryophytes.

Table 3. Code replacement for the mathematical analysis of the phytosociological data.

a) BRAUN-BLANQUET's scale

Code	Mean cover (%)	Frequency table (Ordinal scale)	Trend analysis		Signature in distribution maps
			qualitative (Signum-transformation)	quantitative	
(blank)	0	0	0	0	
+/r	1.0	1	1	10	•
1	2.5	2	1	25	•
2	15.0	5	1	150	●
3	37.5	7	1	375	●
4	62.5	8	1	625	●
5	87.5	9	1	875	■

b) LONDO's scale

(blank)	0	0	0	0	
0.1	1.0	1	1	10	•
0.2	2.0	2	1	20	•
0.4	4.0	3	1	40	
1	10.0	4	1	100	●
2	20.0	6	1	200	
3	30.0	6	1	300	●
4	40.0	7	1	400	
5	50.0	8	1	500	
6	60.0	8	1	600	●
7	70.0	8	1	700	
8	80.0	9	1	800	
9	90.0	9	1	900	■
10	97.5	9	1	1000	

'Species value'. According to the group value of TÜXEN and ELLENBERG (1937) the importance of a species in a community can be expressed as:

'species value' = frequency (%) x mean cover degree (%) / 100

The species value rises with increasing frequency and/or mean cover degree and can maximally be equal to 100. For computing the mean cover degree, BRAUN-BLANQUET's and LONDO's sale respectively were converted to cover-percentages as indicated in Table 3.

3.3. *Mathematical processing of the phytosociological data*

Phytosociological data was processed to obtain a frequency table; in addition, possible developmental trends appearing throughout the experiment within the vegetation (relevés) were considered to be better assessed with the help of mathematical methods.

The frequency table (Table 1) is based upon 72 relevés of 50 m^2 each; 18 relevés per study area were considered, for the study areas 2, 3 and 4 those taken in 1977, for the study area 1 those taken in 1978. Rare species occurring only once or twice have not been included in the mathematical processing. For the analysis the FORTRAN-IV programme package described by WILDI and ORLÓCI (1980) has been applied; the programme names referred to are those used by these authors. As a first step, the raw data consisting of BRAUN-BLANQUET (1964) or LONDO (1975) codes had to be transferred to numerical data. For this, the ordinal scale proposed by VAN DER MAAREL (1979) with no further transformation was chosen (Table 3). The ordination co-ordinates of the relevés were computed by principal component analysis (programme PCAB) based upon the cross product matrix but not on the correlation matrix as is usual (ORLÓCI 1978). The scatter diagrams of the relevés were printed by programme ORDB. In order to find a group structure within the set of species, the cross product matrix (programme RESE) was subjected to cluster analysis (minimum variance clustering, programme CLTR) yielding a dendrogram. Finally the frequency table (Table 1) was printed by programme TABS.

In an attempt to assess developmental trends appearing in the vegetation throughout the experiment, the 1 m^2 relevés were used, because they provide more reliable cover estimations than the 50 m^2 relevés. Within a given study area, the relevés of all surfaces and of all years were processed together.

The phytosociological data was analysed in a twofold way. To reveal possible *qualitative* alterations of the vegetation resulting from the different treatments, the quantitative raw data was transformed to presence-absence data (signum transformation). To reveal possible *quantitative* alterations of the vegetation the BRAUN-BLANQUET and the LONDO scale were replaced by numerical values approximating reasonably well to the original cover percentages (Table 3). In both cases, the pathway of the analysis was the same as that indicated for the relevés by the construction of the frequency table yielding scatter diagrams of the relevés. For each surface, the points representing the relevés taken in subsequent years were connected by arrows. This method proposed by VAN DER MAAREL (1969) aims at revealing developmental trends in a data set as a whole. In order to make the diagrams easy to survey, the arrows were presented for each treatment in a separate graph.

3.4. *Phenological records*

Phenological observations were carried out weekly from March to early November. They were assigned to three categories:

a) quantitative observations of all phases in the four study areas leading to complete-quantitative-analytical-total diagrams (for terminology see DIERSCHKE 1972, 1977);
b) especially detailed records of the flowering phase in all 1 m^2 plots and of the number of species in blossom per 1 m^2 and per 50 m^2, respectively, throughout the year;
c) estimation of the percentage of surface covered by the flowers of different colours in the 50 m^2 plots, presented in the form of synthetic colour diagrams.

a) *Quantitative-analytical-total diagrams.* Various phenological phases were recorded of all species within the four study areas (Table 4). Observations refer to the whole study areas and were carried out in 1977, 1978 and 1979 and comprised vegetative as well as generative phases. The percentage of individuals of a given species at a particular phase was estimated according to a six-degree-scale (Table 5). In the diagrams,each species is represented

Table 4. Key to phenological records

Vegetative phases:

- ground leaves
- shoots
- yellowing

Generative phases:

- flower buds
- bloom
- fading
- fruit
- seed dispersal

Table 5. Scale for the estimation of the percentage of individuals at a given phenological phase

Code	Percentage of individuals at a given phenological phase
+	0% < and < 5%
1	5% < and < 20%
2	20% < and < 40%
3	40% < and < 60%
4	60% < and < 80%
5	80% < and < 100%

Table 6. Scale for the estimation of the surface covered by flowers of a given colour

Code	Mean cover (%) of the flowers of a given colour
+	< 0.1%
0.1	0.1%
0.2	0.2%
0.4	0.4%
0.4-1	0.7%
1	1.0%
1-2	1.5%
2	2.0%
2-3	2.5%
3	3.0%
4	4.0%
5	5.0%
6	6.0%
⋮	⋮

by two horizontal stripes, the upper one corresponding to generative phases and the lower one representing the vegetative development. Developmental phases and their percentage are differently marked (Table 4). The width of all stripes is equal. The significance of a species within the study areas is indicated by the species value.

b) *Flowering intensity and number of species in blossom per 1 m^2 and per 50 m^2*. In each 1 m^2 plot studied, the flowering units depending on the morphology of different species (e.g. 1 flower, 1 flower head, 1 inflorescence, 1 umbel and so on) were counted every week for all species in blossom within the plot. If a given species did not flower in the 1 m^2 surface but only in the adjacent 50 m^2 plot, a note was taken but the flowering intensity was not specified. The flowering units of some species (e.g. *Primula veris, Orchis pallens, Ranunculus bulbosus, Buphthalmum salicifolium, Aster amellus*) were also counted in the 50 m^2 surfaces. As far as grasses were concerned, further information was gathered: in addition to the above mentioned observations, the total number of inflorescences was recorded for the different grasses within the 1 m^2 plot cut in mid June just before cutting whilst those in the other 1 m^2 plots were recorded in early July.

For the presentation of the response of the flowering intensity to the different treatments, the highest recorded values or the total number of inflorescences (*Gramineae*) were taken into consideration. Most of the diagrams are based upon three replicas of 50 m^2 each, otherwise the number of samples and the plot size is specified in the explanation of figures in the text.

In some cases the data gathered was incomplete. For instance, cutting in June almost completely prevented the flowering of *Buphthalmum salicifolium* and *Aster amellus* within study area 4 from the very beginning of the experimental management in 1977. 1976 values being unknown, the flowering intensity on surfaces subject to this treatment prior to the beginning of experiment had to be inferred from the corresponding values of the surrounding, otherwise treated plots. Connections between the supposed starting points and the first recorded values are indicated by dashed lines.

c) *Synthetic colour diagrams*. The percentage of surface covered by flowers grouped according to the flower colours (i) yellow, (ii) white, (iii) blue and violet and (iv) red was estimated weekly in all 50 m^2 plots studied (Table 6). These estimates were verified from time to time by counting the flowering units of species most contributing to the effect of a given colour within some 50 m^2 surfaces; it was thus possible to compute quite reliably the real cover. The cover percentages of the four flower colours throughout the year are presented in synthetic colour diagrams one above the other, all values being the average of three replicas.

3.5. *Profile diagrams (photographs)*

In 1980, six cuttings of 0.5 x 0.5 m were taken for each of the differently treated surfaces within the study area 1. For those plots cut in mid June samples were taken on June 19th just before cutting, for plots under other treatments samples were taken on July 1st. Prior to photographing, each sample was aligned at a distance of 0.5 m.

4. Results

4.1. *Phenological responses of individual species to environmental changes*

4.1.1. *Short-term observations*

Under certain circumstances, phenological records collected during a single vegetation season have some predictive value. Using analytical total diagrams (for terminology see DIERSCHKE 1972, 1977) it should be possible to predict the effect of a given treatment upon the sexual reproduction of plants (WELLS 1971) as well as the reproductive success of animals; in particular, insects frequently depend for part of their life-cycle on flowers or fruits (BONESS 1953, MORRIS 1967, 1969, 1973a, b, 1978, 1979, MORRIS and LAKHANI 1979). For this reason, short-term phenological observations were carried out in the course of the present study. After comparing the expected and the actual effects, the obtained results were assigned to one of the two categories respectively comprising a) effects as expected and b) effects contrary to expectation.

a) *Effects as expected.* This category is exemplified by an incomplete-analytical-quantitative-total diagram of a *Mesobrometum* meadow community (Figs 7, 8); the grassland was abandoned for almost 20 years (study area 4), but no shrubs have occurred there to date. In mid June, when such surfaces were usually cut by the farmers, various developmental stages are observed in different species. For instance, *Polygala amarella* and *Fragaria vesca* have already produced fruit but not yet dispersed the seeds, whereas *Thesium bavarum* and *Aquilegia atrata* are still in full bloom. On the other hand, *Anthericum ramosum* is only at the bud stage and *Solidago virga-aurea* exhibits well developed shoots but no flower buds have appeared yet. Cutting in mid June is thus likely to prevent the sexual reproduction of these species and may accordingly be considered as unfavourable for them in the long term. Conforming to our expectation, the aforementioned species were not observed in regularly cut surfaces or when present they were definitely less abundant than in unmanaged areas (Fig. 8).

Cutting in mid June thus proved to have a damaging influence upon species that reproduced sexually at this time. However, the performance of taxa with a generative cycle either completed or not yet started at the time of cutting should not be influenced by this treatment. This assumption was indeed confirmed: for instance *Taraxacum officinale* s.l. which has its seeds completely dispersed by June as well as *Pimpinella saxifraga, Scabiosa columbaria, Daucus carota* and *Sedum sexangulare* that have not yet developed flower buds by the time of cutting manifested an undiminished occurrence in areas subject to this treatment (Figs 9, 10).

b) *Effects contrary to expectations.* This category was exemplified by the incomplete-analytical-quantitative-total diagrams of two *Mesobrometum* meadow communities; the study area 2 was regularly cut in mid June prior to experimental management starting in 1977 (Figs 11, 12), whereas study area 4 had been abandoned for almost 20 years until 1977 (Figs 13, 14).

The species occurring within study area 2 exhibit fairly different stages of sexual reproduction at the time of cutting. For example, *Arabis hirsuta* and

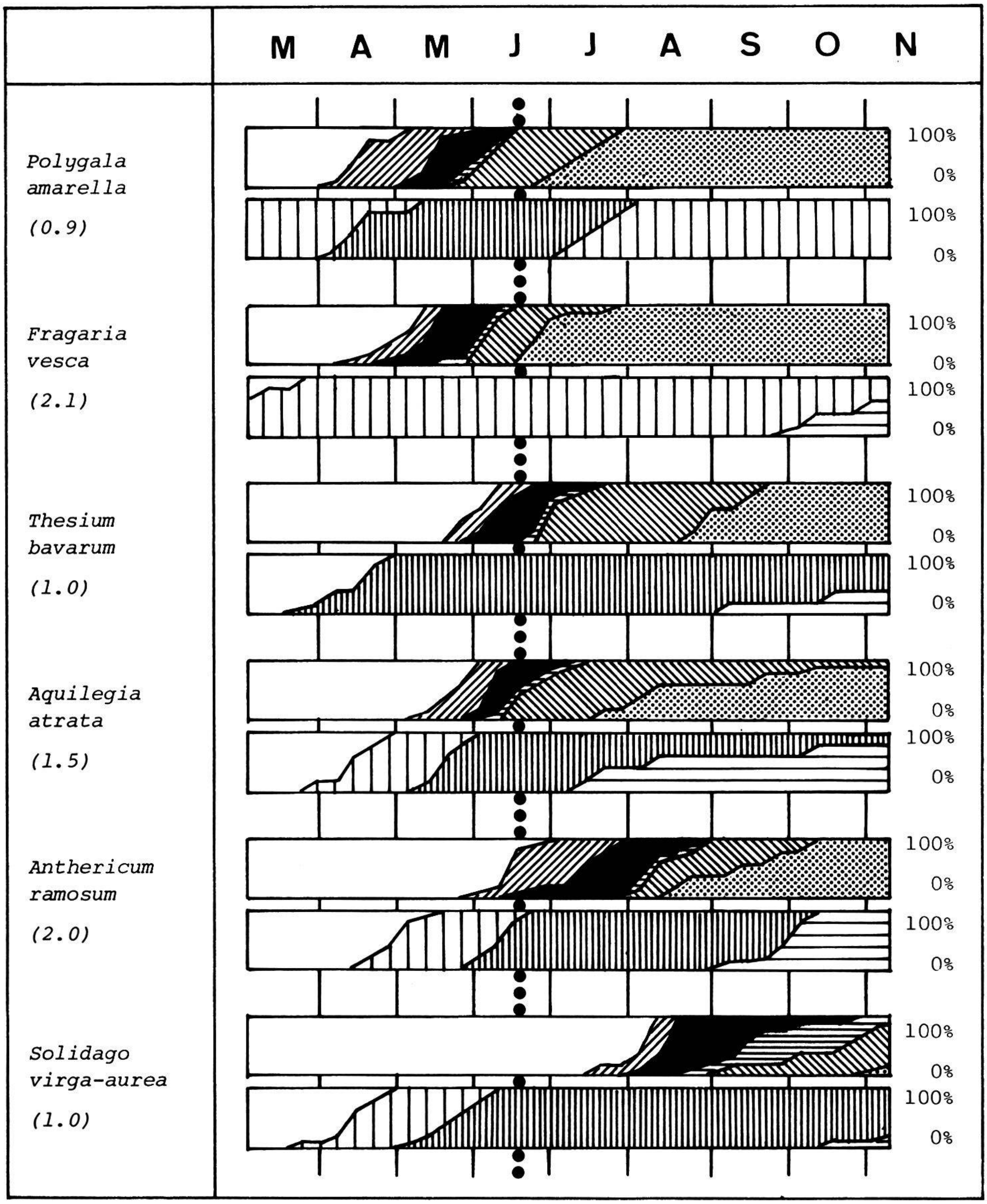


Fig. 7. Incomplete-analytical-quantitative-total diagram of study area 4.

Vegetative phases: ground leaves, shoots, yellowing

Generative phases: flower buds, bloom, fading, fruit, seed dispersal

●●●● time of cutting

(...) species value (see page 21)

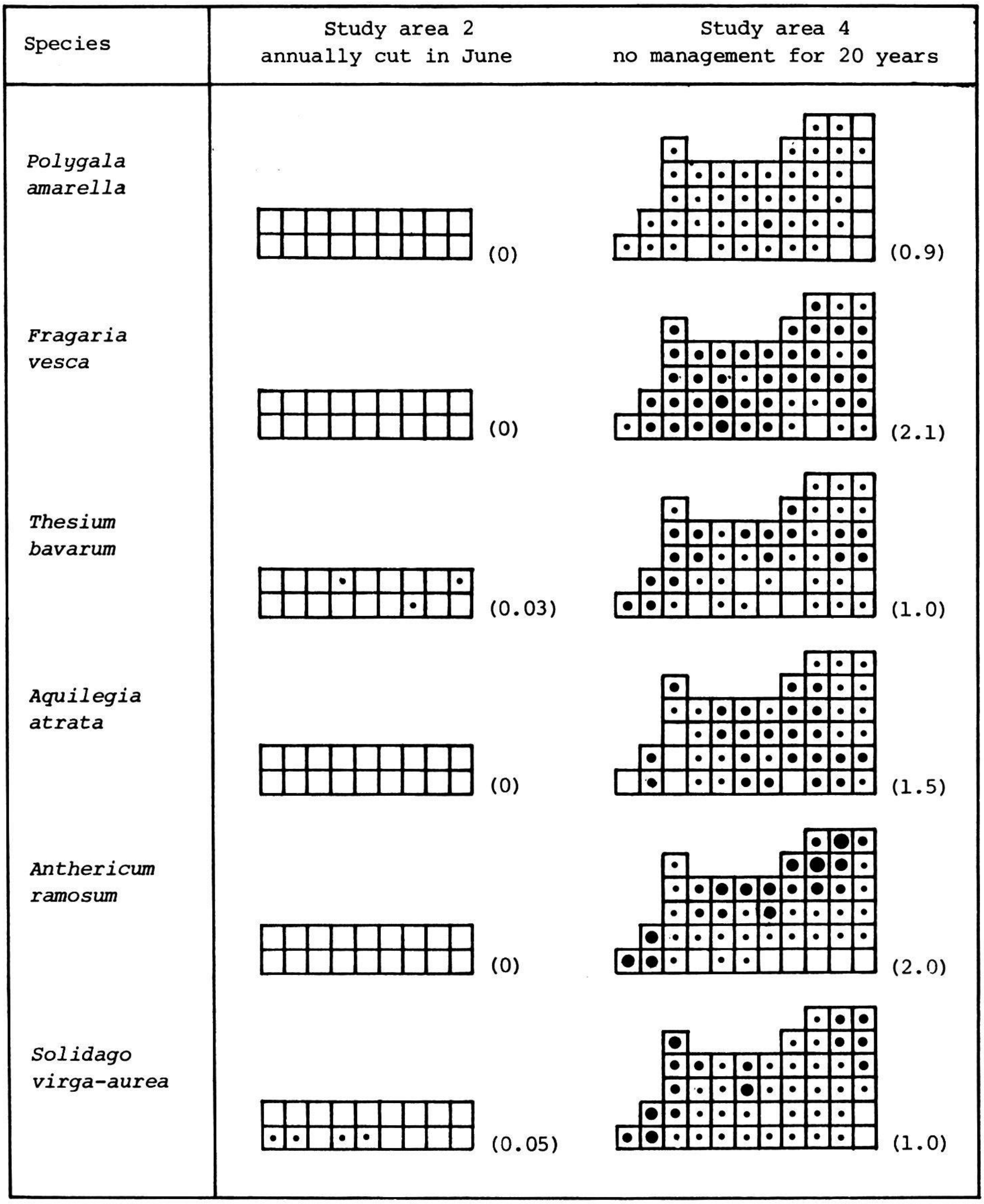


Fig. 8. Distribution pattern of the species represented in Fig. 7 within two successional stages of *Mesobrometum* grassland.

The cover-abundance values of the BRAUN-BLANQUET scale are marked as follows:
+/r: • ; 1: • ; 2: ● ; 3: ● ; 4: ● ; 5: ■ .

(...): species value (see page 21)

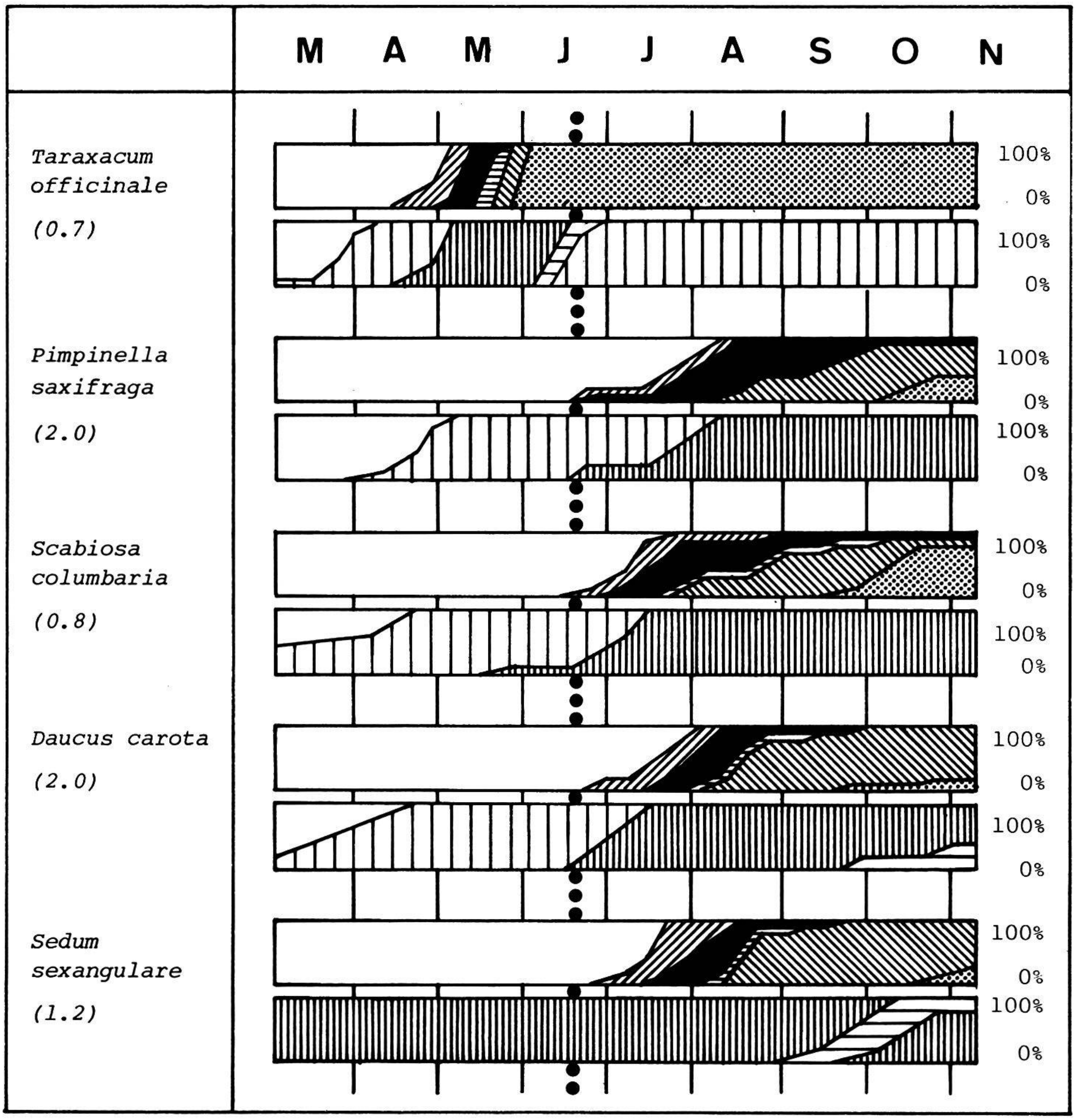


Fig. 9. Incomplete-analytical-quantitative-total diagram of study area 2.

Vegetative phases:
- ground leaves
- shoots
- yellowing

Generative phases:
- flower buds
- bloom
- fading
- fruit
- seed dispersal

●●●● time of cutting

(...) species value (see page 21)

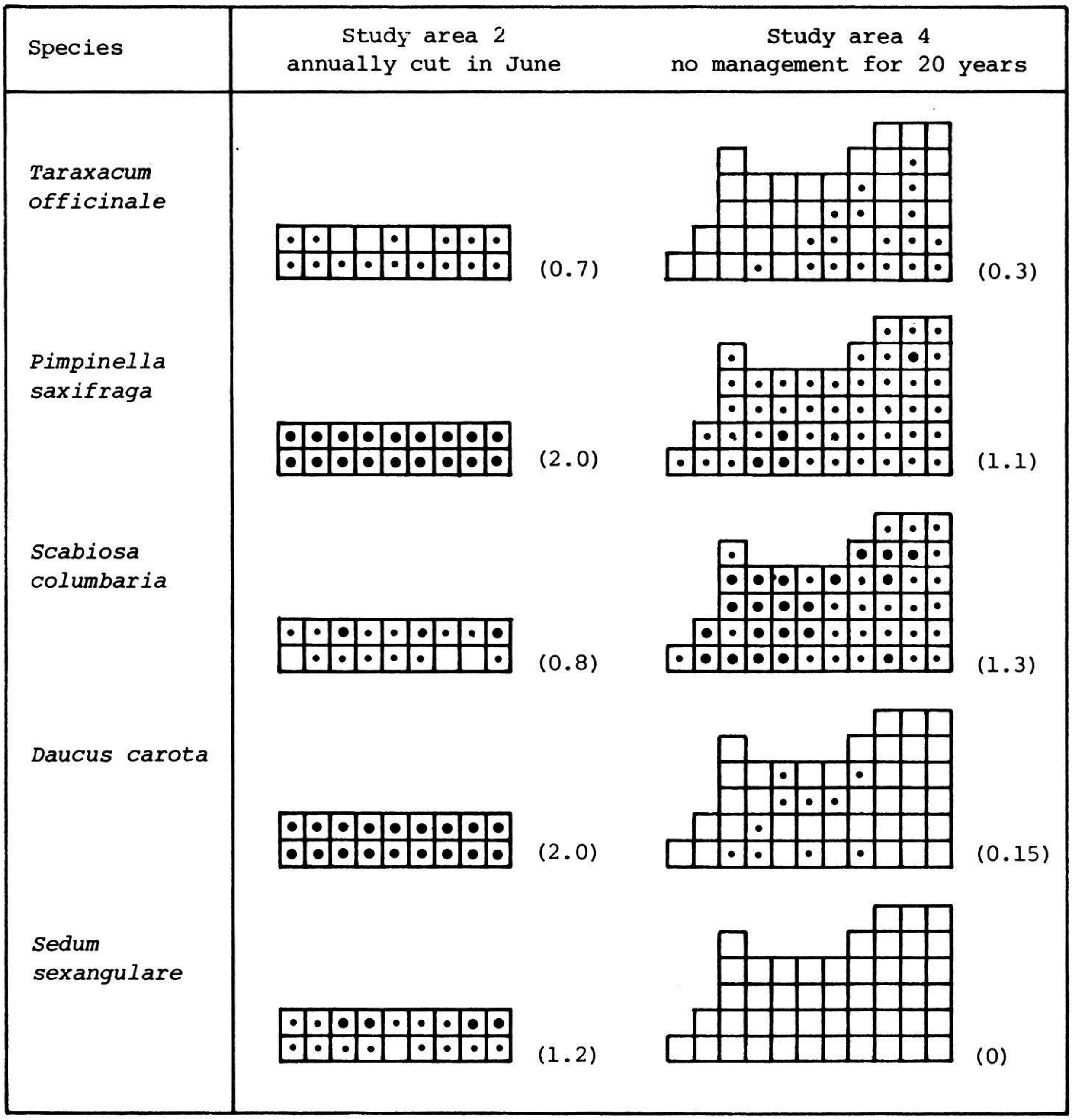


Fig. 10. Distribution pattern of the species represented in Fig. 9 within two successional stages of *Mesobrometum* grassland.

The cover-abundance values of the BRAUN-BLANQUET scale are marked as follows:
+/r: • ; 1: • ; 2: ● ; 3: ● ; 4: ● ; 5: ■ .

(...): species value (see page 21)

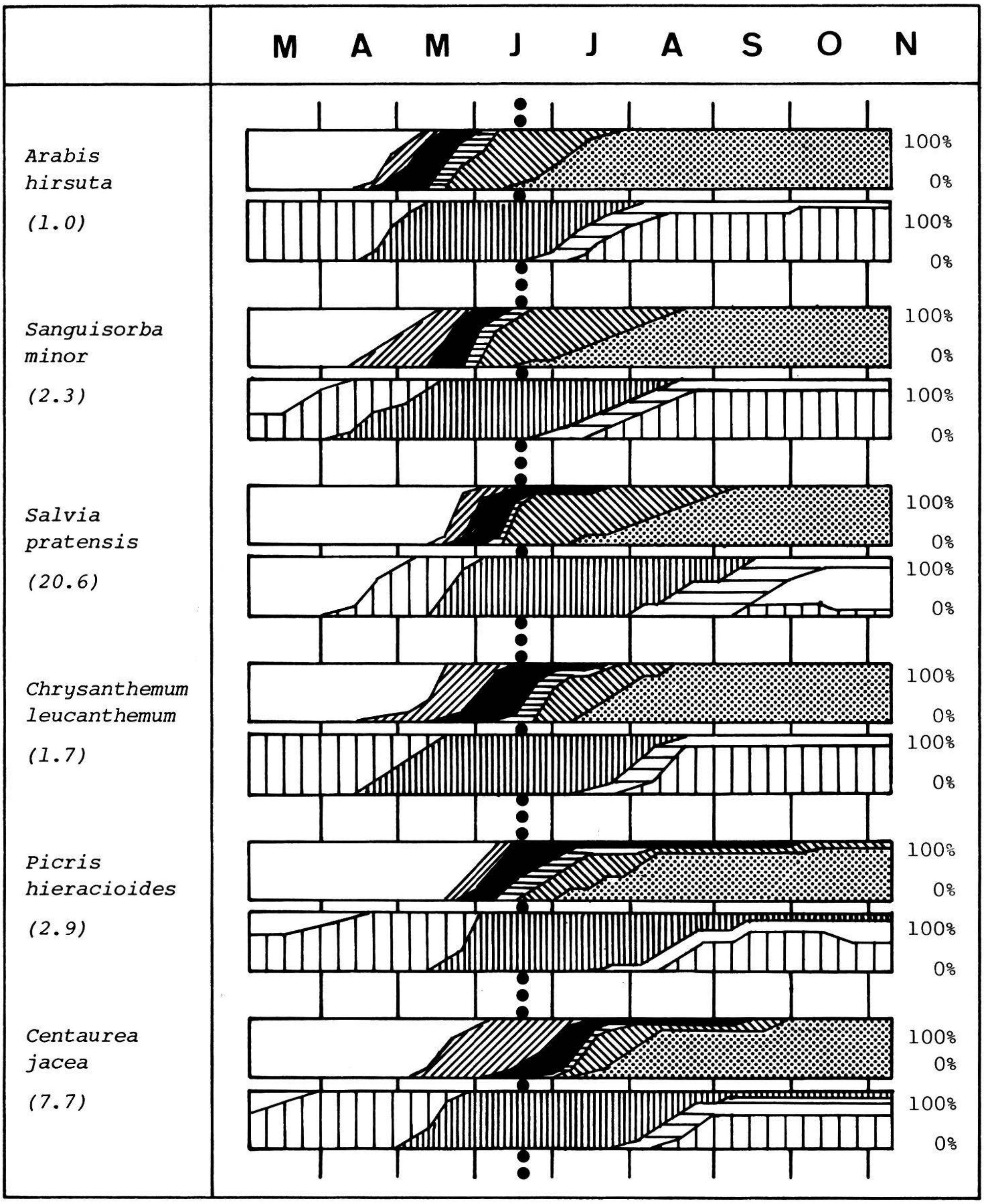


Fig. 11. Incomplete-analytical-quantitative-total diagram of study area 2.

Vegetative phases: ground leaves, shoots, yellowing

Generative phases: flower buds, bloom, fading, fruit, seed dispersal

●●●● time of cutting

(...) species value (see page 21)

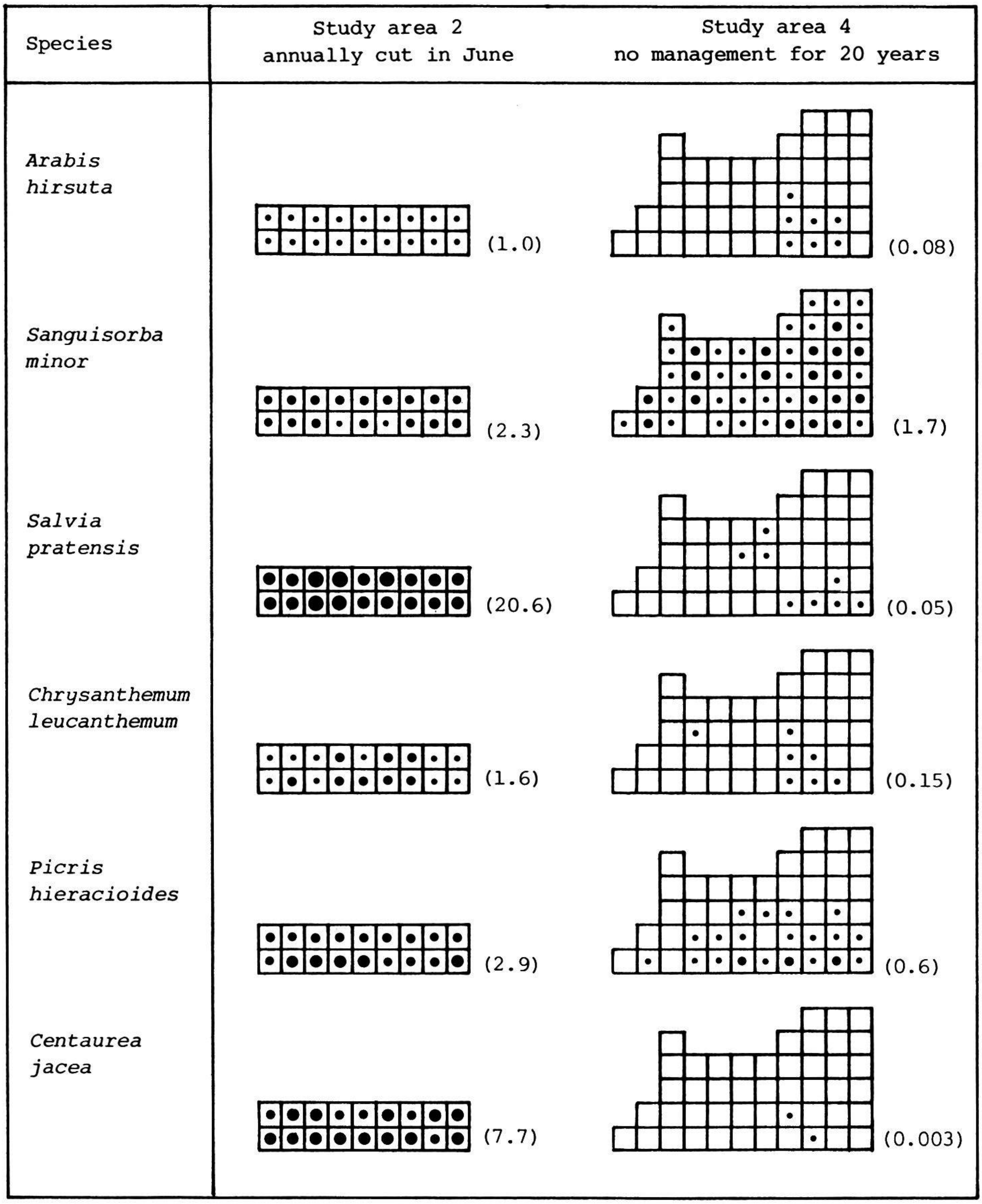


Fig. 12. Distribution pattern of the species represented in Fig. 11 within two successional stages of *Mesobrometum* grassland.

The cover-abundance values of the **BRAUN-BLANQUET** scale are marked as follows:

+/r: • ; 1: • ; 2: ● ; 3: ● ; 4: ● ; 5: ■ .

(...): species value (see page 21)

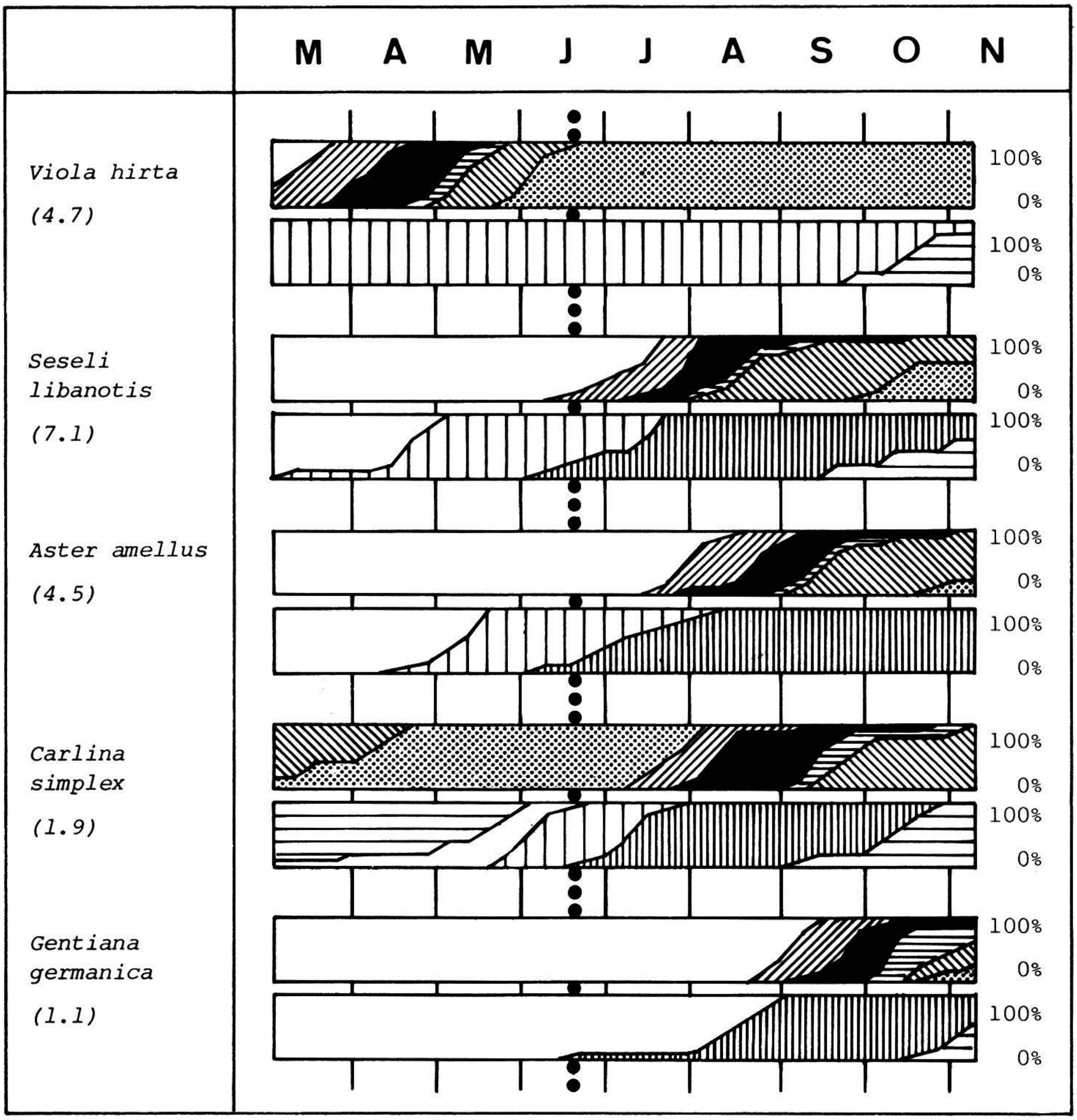


Fig. 13. Incomplete-analytical-quantitative-total diagram of study area 4.

Vegetative phases: ground leaves, shoots, yellowing

Generative phases: flower buds, bloom, fading, fruit, seed dispersal

●●●● time of cutting

(...) species value (see page 21)

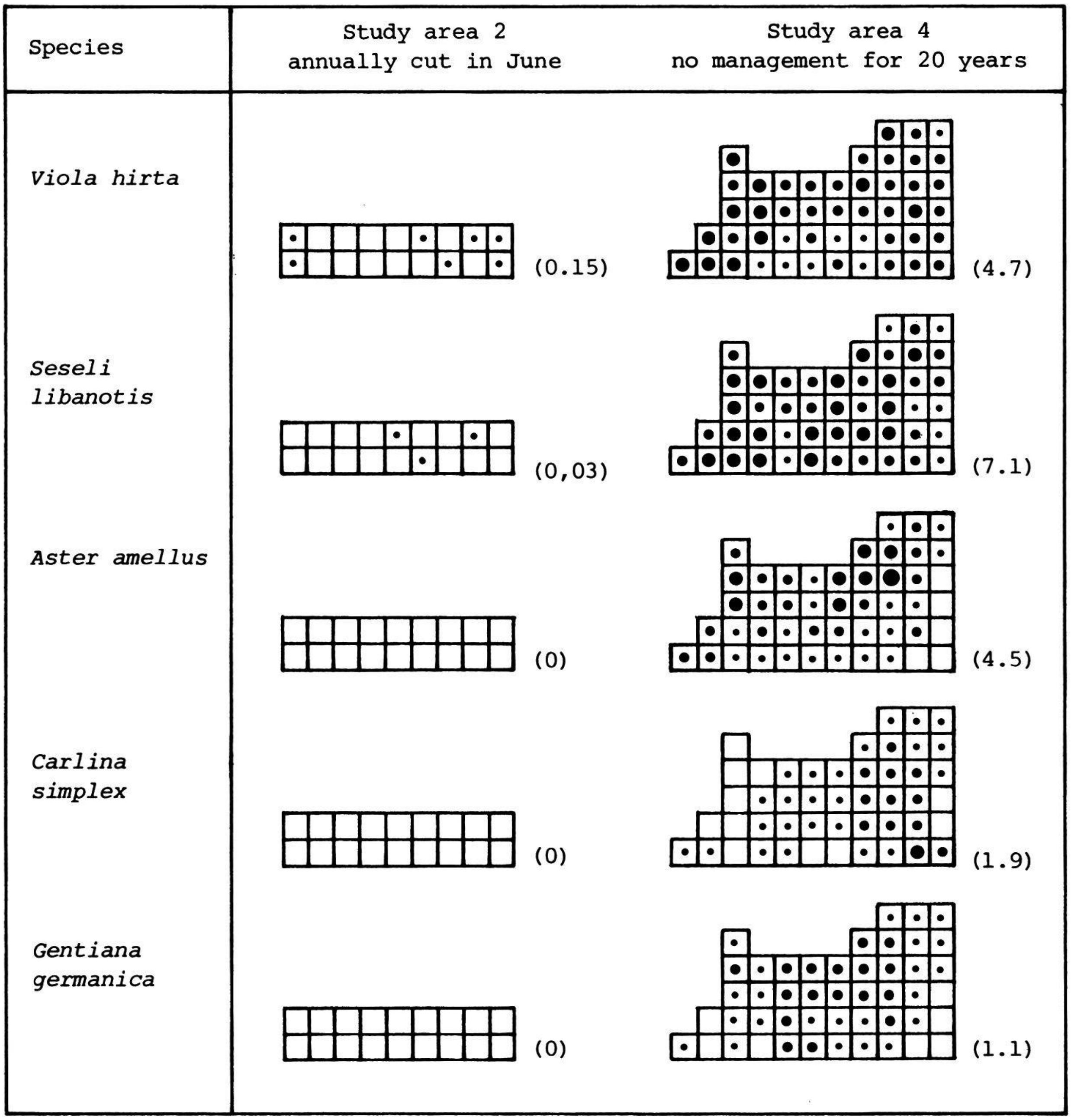


Fig. 14. Distribution pattern of the species represented in Fig. 13 within two successional stages of *Mesobrometum* grassland.

The cover-abundance values of the BRAUN-BLANQUET scale are marked as follows:
+/r: • ; 1: • ; 2: ● ; 3: ● ; 4: ● ; 5: ■ .

(...): species value (see page 21)

Sanguisorba minor have already produced fruit but have not yet dispersed their seeds, whereas *Salvia pratensis*, *Chrysanthemum leucanthemum* and *Picris hieracioides* are still in full bloom. On the other hand, *Centaurea jacea* is only at the bud stage. One might therefore expect that cutting in mid June should severely damage these species by preventing their sexual reproduction. Our observations on communities representing various successional stages, however, proved the contrary (Fig. 12).

Some species occurring within study area 4 either have already completed their sexual reproduction by the time of cutting (e.g. *Viola hirta*) or have not yet reached the generative phase at that time (e.g. *Seseli libanotis*, *Aster amellus*, *Carlina simplex*, *Gentiana germanica*; Fig. 13). Accordingly cutting in mid June should not affect these species, but it apparently did; in regularly cut surfaces the aforementioned species were exceptionally rare or did not occur at all (Fig. 14).

The results obtained indicate that predictions concerning the future development of particular species under a given treatment that are based upon analytical diagrams may sometimes be reliable; however, they are not foolproof and the effects of a given treatment may as well prove the contrary.

4.1.2. *Mid-term phenological observations and cover data*

Phenological data gathered over a period of several years turned out to be a rather useful indicator of transformations occurring in the environment. The behaviour of the species described below is a good illustration of this opinion.

Out of more than 150 species investigated only seven have been selected for presentation. The rather arbitrary choice was mainly influenced by the need for species to be sufficiently abundant as well as reasonably homogeneously distributed, at least within one of the four studied areas; high values are by far less sensitive towards random errors than small ones. Owing to insufficient abundance or homogeneity of distribution, the effects of the different treatments on a given species usually could not be presented for all four areas. As often as possible, however, the effects of the different treatments were presented for one of the study areas used until experimental management

Table 7. Indicator values of the seven investigated species according to LANDOLT (1977)

W = growth form
F = humidity value
R = reaction value
N = nutrient value
H = humus value
D = dispersion value
L = light value
T = temperature value
K = continentality value

1 represents the lowest, 5 the highest value
Growth form : h = hemicryptophyte, g = geophyte
Humidity value: w = indicators of changeable dry-wet soils

Species	Indicator value								
	W	F	R	N	H	D	L	T	K
Primula veris	h	2w	4	2	4	5	4	3	3
Primula columnae	h	2	4	3	4	3	3	4	4
Orchis pallens	g	3	4	3	4	4	3	4	4
Bromus erectus	h	2	4	2	3	4	4	4	3
Ranunculus bulbosus	h	2	4	2	3	4	4	3	3
Aster amellus	h	2	4	2	3	4	3	4	4
Buphthalmum salicifolium	h	2w	4	2	3	5	3	3	4
Brachypodium pinnatum	h	2	4	3	3	4	3	3	3

was started as well as for one of the areas abandoned prior to the beginning of the experiment.

The ecological requirements of the seven species are summed up in Table 7 according to the indicator values of LANDOLT (1977). All taxa usually occur in relatively continental and dry parts of the colline or montaine zone. They are chiefly found on dry, alkaline, fine sandy, dusty and more or less well ventilated soils that are poor in nutrients and have a medium humus content. *Primula veris* s.str., *Bromus erectus* and *Ranunculus bulbosus* primarily occur in full light (light value 4) whereas the other species often grow in half-shade (light value 3). *Primula veris* s.str. and *Buphthalmum silicifolium* are in addition indicators of changeable dry-wet soils.

1. *Primula veris* s.l. (Figs 15-26)

Primula veris s.l. is a perennial, medium-sized, scapose hemicryptophyte with a short vertical rhizome. The leaves are arranged in a semi-rosette. In the

Fig. 15. *Primula veris* s.l. within study area 4 on May 10, 1980: the flowering intensity on the surface cut in June from 1977 on (middleground) was very low compared to that on the surfaces cut in October (background) or not managed at all (foreground).

study areas, the *Primula veris* group was represented not only by typical individuals but also by those corresponding rather to *P. columnae* or intermediate types. No distinction between particular units has been made for presentation of our results. *P. veris* s.str. is a plant typical of grasslands growing on soils poor in nutrients, whereas *P. columnae* grows in the surrounding forests. According to OBERDORFER (1979) *P. veris* s.str. is mainly associated with *Mesobromion*, and *P. columnae* with *Quercion pubescentis* communities.

In the experimentally managed study areas, the flowering intensity of *Primula veris* was in 1980 lower by far within the surfaces annually cut in mid June than in the adjacent differently treated plots (Fig. 15). In the study areas 2, 3 and 4, a decrease in the flowering intensity of *Primula veris* was observed from 1978 onwards in the surfaces annually cut in mid June but not in the surfaces subject to other treatments (Figs 16, 18, 20). A distinct increase in the flowering intensity of this species observed in some surfaces within

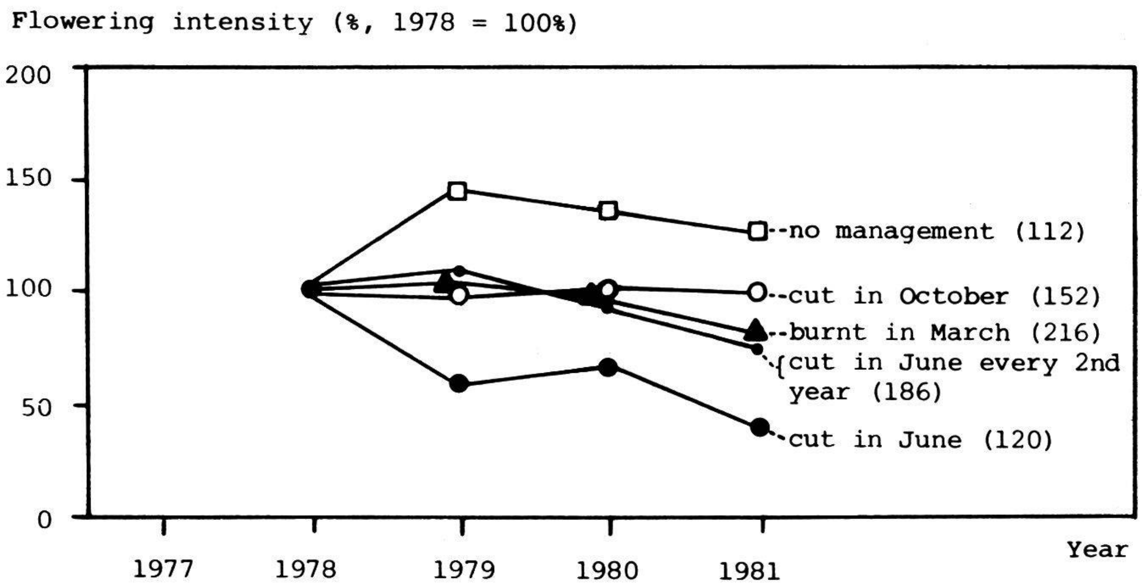


Fig. 16. *Primula veris* s.l. within study area 2: development of the flowering intensity under different treatments for the period 1978-1981; data expressed as percentages of the corresponding values of 1978; absolute magnitudes recorded in 1978 in parentheses following the treatment indications. (Three samples of 50 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 50 m^2 each were evaluated).

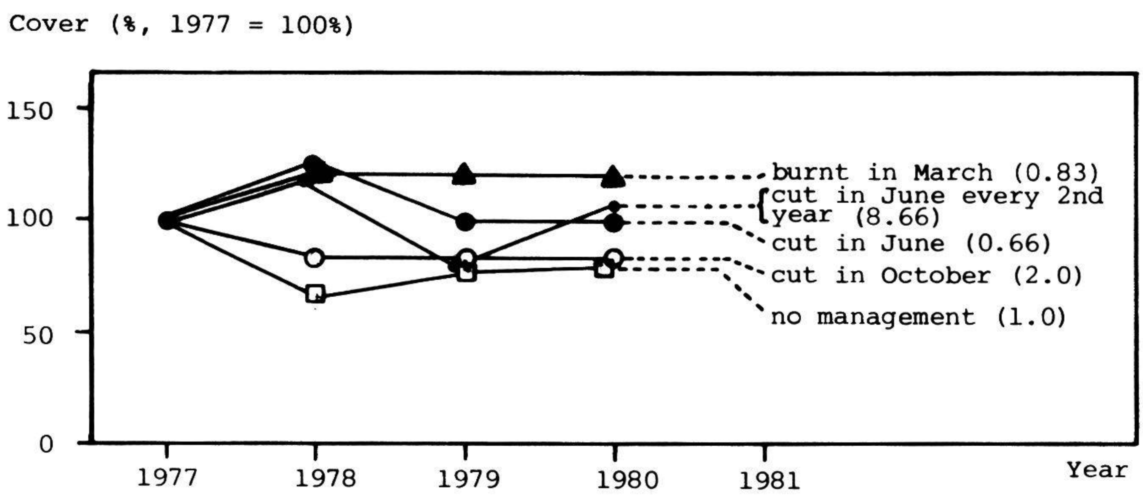


Fig. 17. *Primula veris* s.l. within study area 2: development of the cover under different treatments for the period 1977-1980; data expressed as percentages of the corresponding values of 1977; absolute magnitudes recorded in 1977 in parentheses following the treatment indications. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

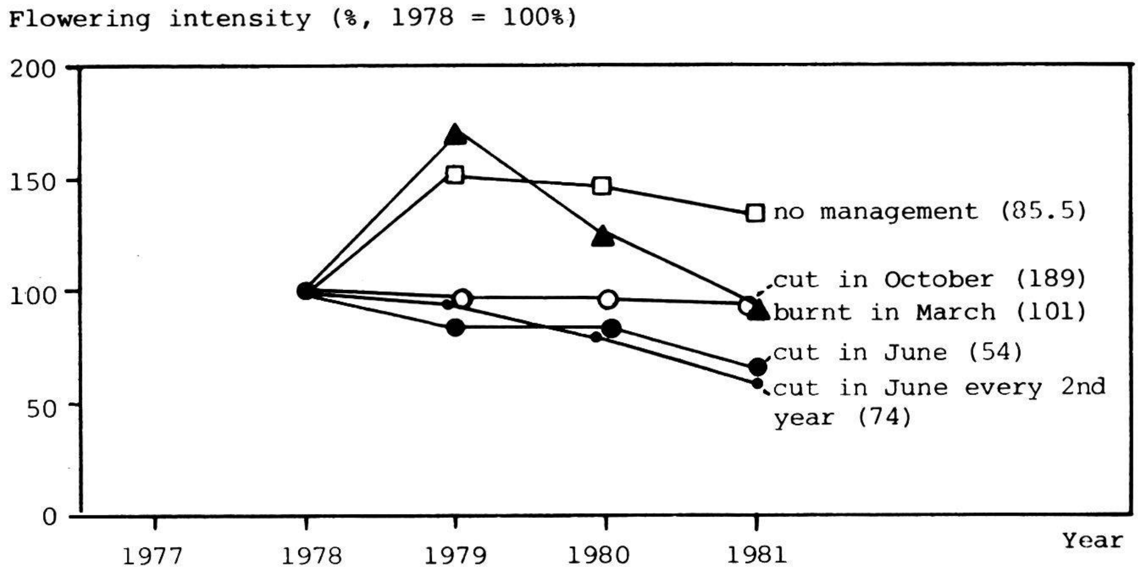


Fig. 18. *Primula veris* s.l. within study area 3: development of the flowering intensity under different treatments for the period 1978-1981; data expressed as percentages of the corresponding values of 1978; absolute magnitudes recorded in 1978 in parentheses following the treatment indications. (Three samples of 50 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 50 m^2 each were evaluated).

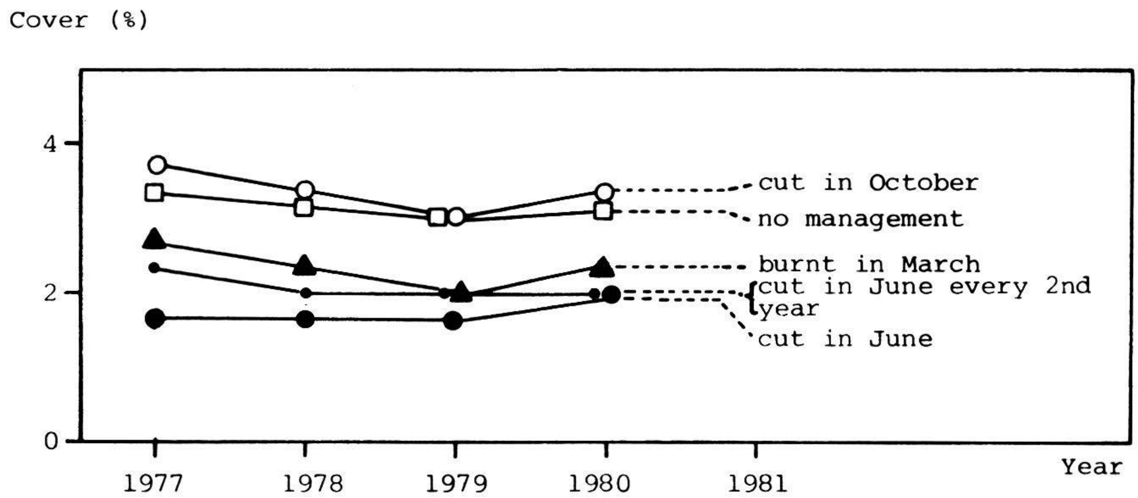


Fig. 19. *Primula veris* s.l. within study area 3: development of the cover under different treatments for the period 1977-1980. (Three relevés of 50 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 50 m^2 each were evaluated).

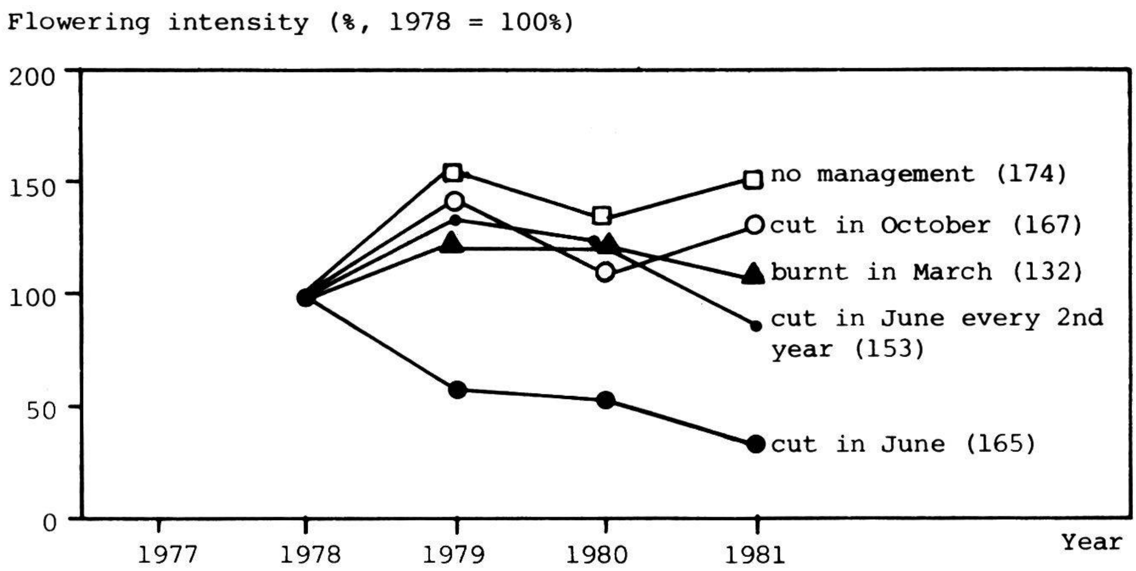


Fig. 20. *Primula veris* s.l. within study area 4: development of the flowering intensity under different treatments for the period 1978-1981; data expressed as percentages of the corresponding values for 1978; absolute magnitudes recorded in 1978 in parentheses following the treatment indications. (Three samples of 50 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 50 m^2 each were evaluated).

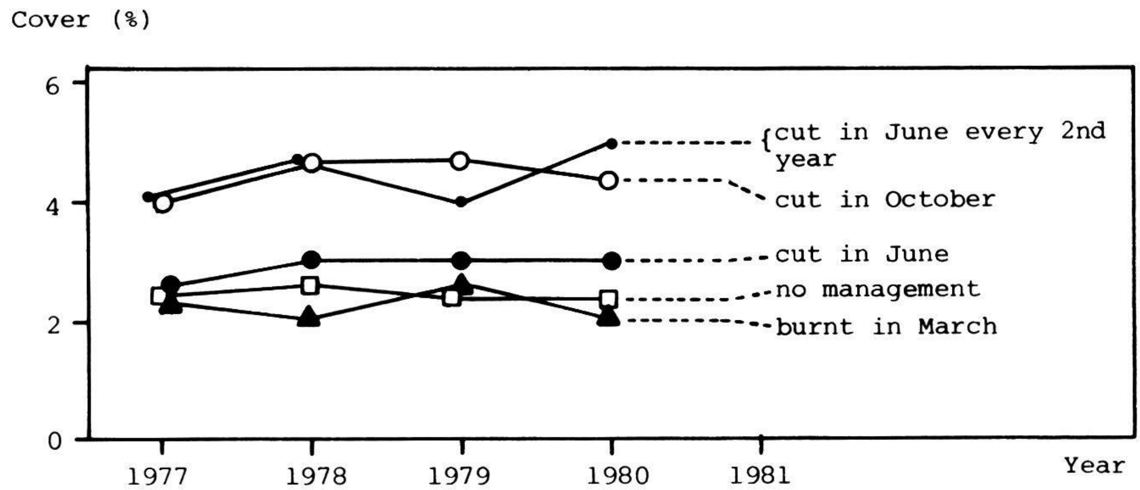


Fig. 21. *Primula veris* s.l. within study area 4: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 were evaluated).

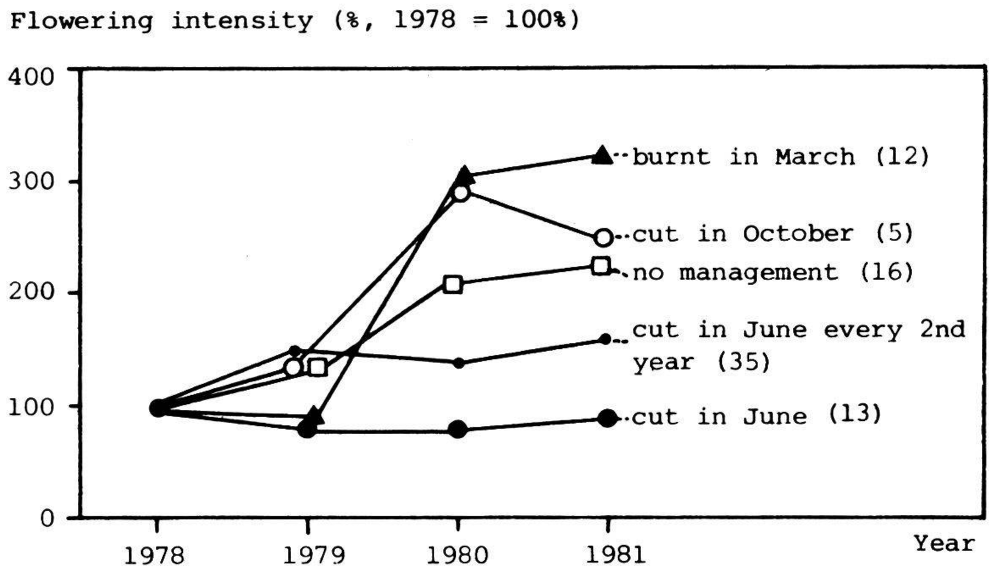


Fig. 22. *Primula veris* s.l. within study area 1: development of the flowering intensity under different treatments for the period 1978-1981; data expressed as percentages of the corresponding values of 1978; absolute magnitudes recorded in 1978 in parentheses following the treatment indications. (Three samples of 50 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 50 m^2 each were evaluated).

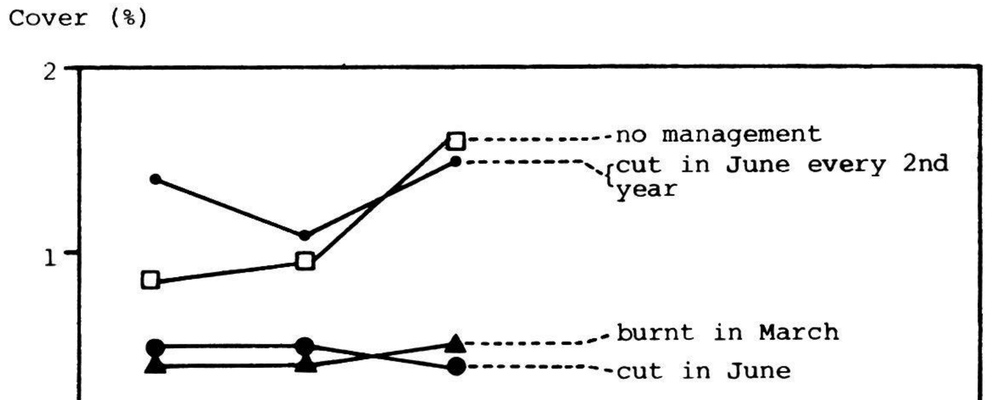


Fig. 23. *Primula veris* s.l. within study area 1: development of the cover under different treatments for the period 1978-1981. (Ten relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m^2 each were evaluated).

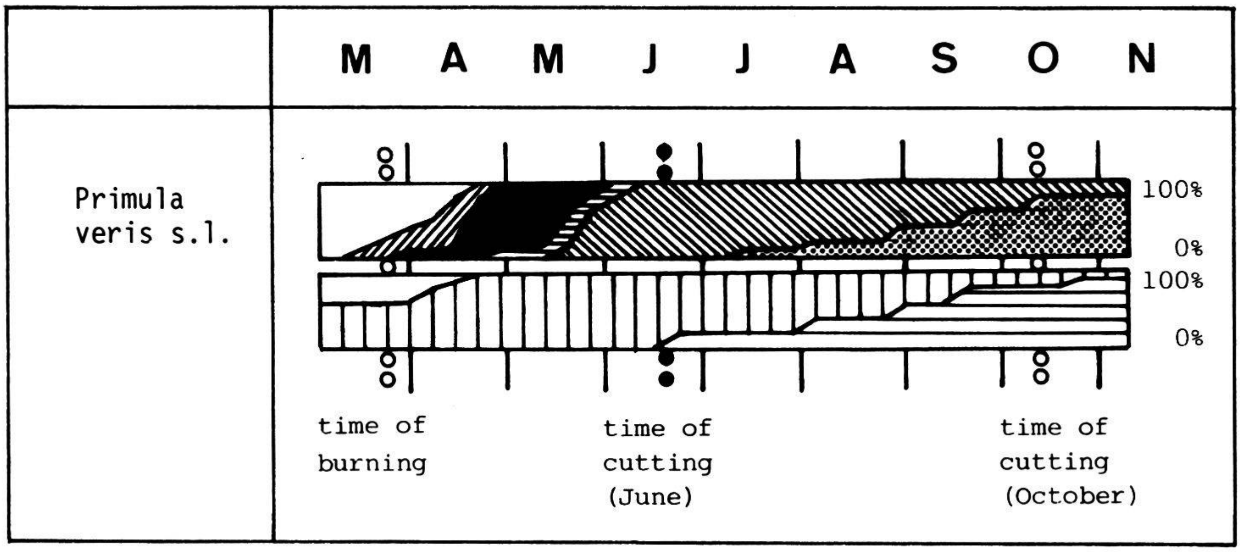
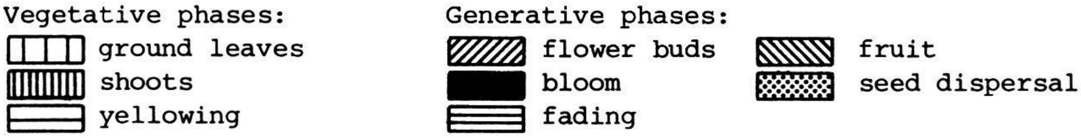


Fig. 24. *Primula veris s.l.*: analytical diagram of the phenological development within study area 4.



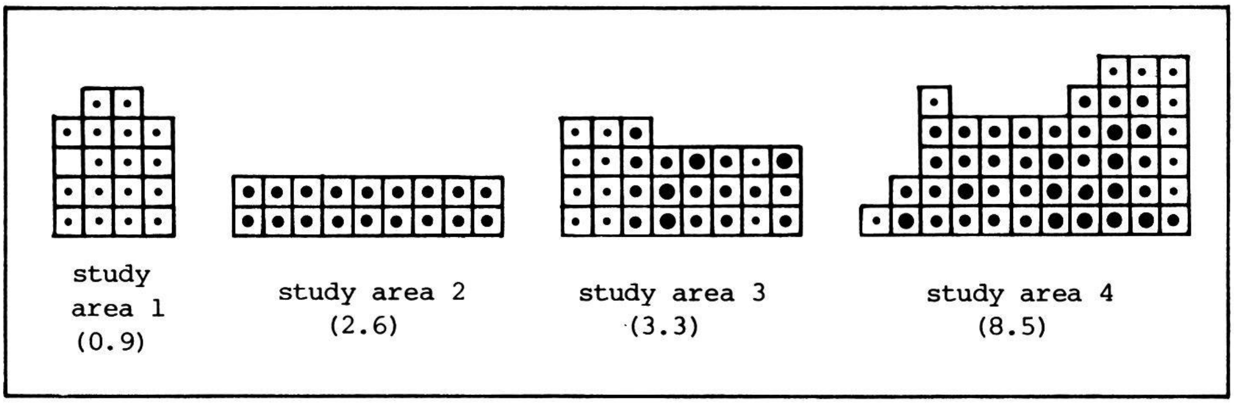


Fig. 25. *Primula veris s.l.*: distribution pattern within four successional stages of *Mesobrometum* grassland (study areas 1, 2, 3, 4).

The cover-abundance values of the BRAUN-BLANQUET scale are marked as follows:

+/r: • ; 1: ● ; 2: ● ; 3: ● ; 4: ● ; 5: ■ .

(...): species value (see page 21)

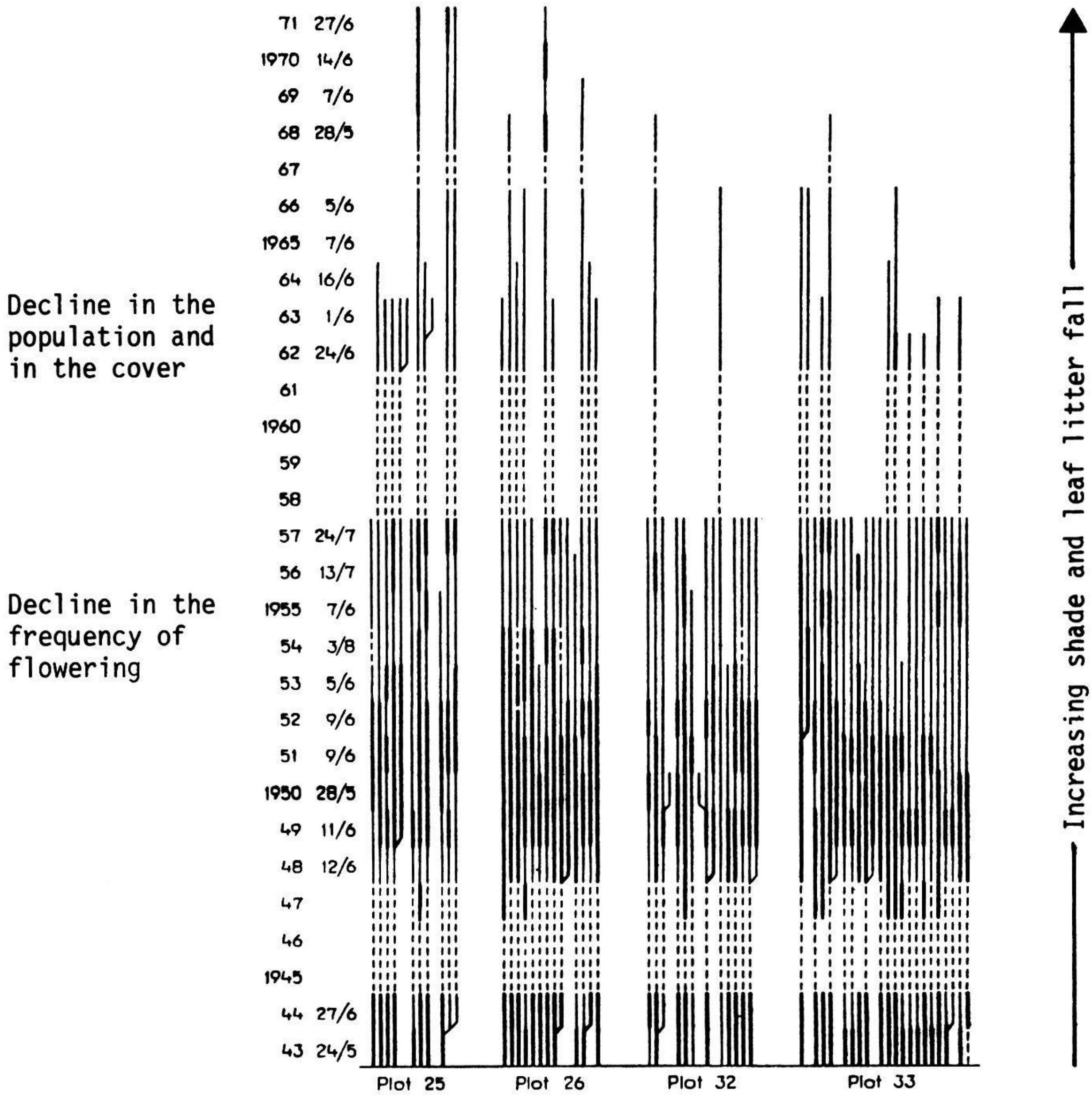


Fig. 26. The behaviour of *Primula veris* within a meadow subjected to increasing shade and leaf litter fall in the course of time. (From TAMM 1972; reproduced from OIKOS with permission of the editor).

——— flowering individuals
——— non-flowering individuals
- - - - - no observation

study area 1 (Fig. 22) further suggested that cutting in mid June was unfavourable for *Primula veris*.

The observations on the flowering intensity of *Primula veris* within differently treated surfaces only partly corresponded to the phenological rhythm of this species (Fig. 24). Cutting in mid June that causes removal of fruit of *P. veris* was accordingly unfavourable. On the other hand, burning in March i.e. at the early bud stage was not found to cause any remarkable damage (Figs 16, 18, 20, 22).

While the phenological behaviour of *Primula veris* s.l. responded rapidly and quite markedly to the different treatments, the cover of this species did not change within the first three or four years of experimental management (Figs 17, 19, 21, 23); only within study area 1 did the cover data suggest 'no management' as a preferential treatment. However, mid-term phenological data as well as the analytical diagram (Fig. 24) and the observations on various successional stages of this grassland type (Fig. 25) suggest that the cover of *Primula veris* s.l. should decrease in the long term within surfaces subjected to cutting in mid June.

This conclusion is supported by long-range studies of TAMM (1972) dealing with a site where conditions changed from 1943 to 1971 causing increasing shade and leaf litter fall (Fig. 26). During the 1950's TAMM observed at this site a sharply declining frequency of flowering in *Primula veris*, whereas the actual cover and population size of this species diminished only about ten years later. The observations of TAMM suggest that environmental conditions changing in a direction disadvantageous for *P. veris* are detectable with the help of phenological observations much earlier than by traditional monitoring of the cover.

2. *Orchis pallens* Figs 27, 28)

Orchis pallens is a perennial, spring green, medium-sized, bulbous geophyte with the leaves mainly arranged in a semi-rosette. According to OBERDORFER (1979), *Orchis pallens* is primarily associated with *Fagion* and *Tilio-Acerion* communities.

Orchis pallens was investigated within study area 4 that had been abandoned

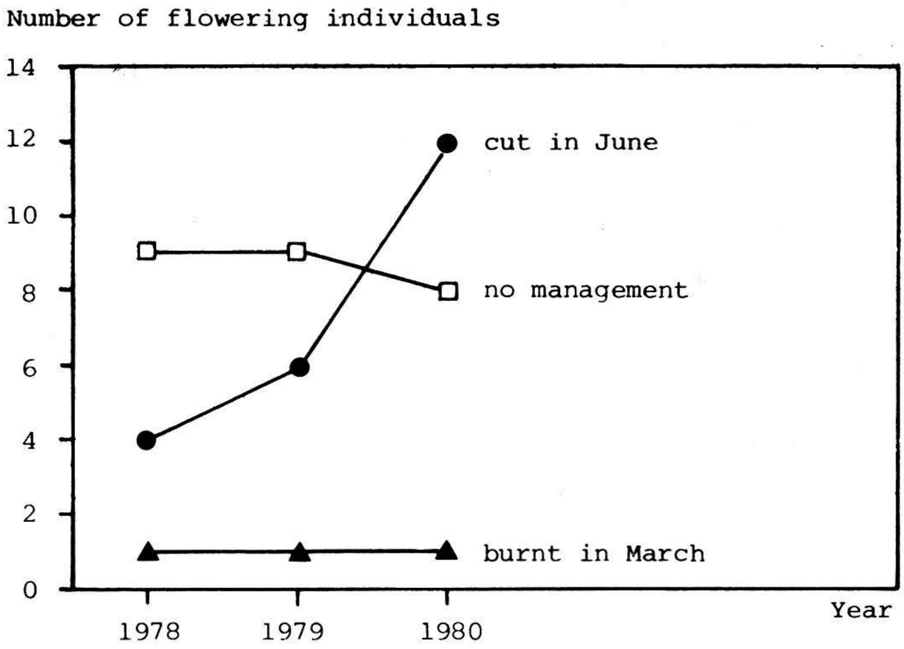


Fig. 27. *Orchis pallens* within study area 4: development of the number of flowering individuals under different treatments for the period 1978-1980.

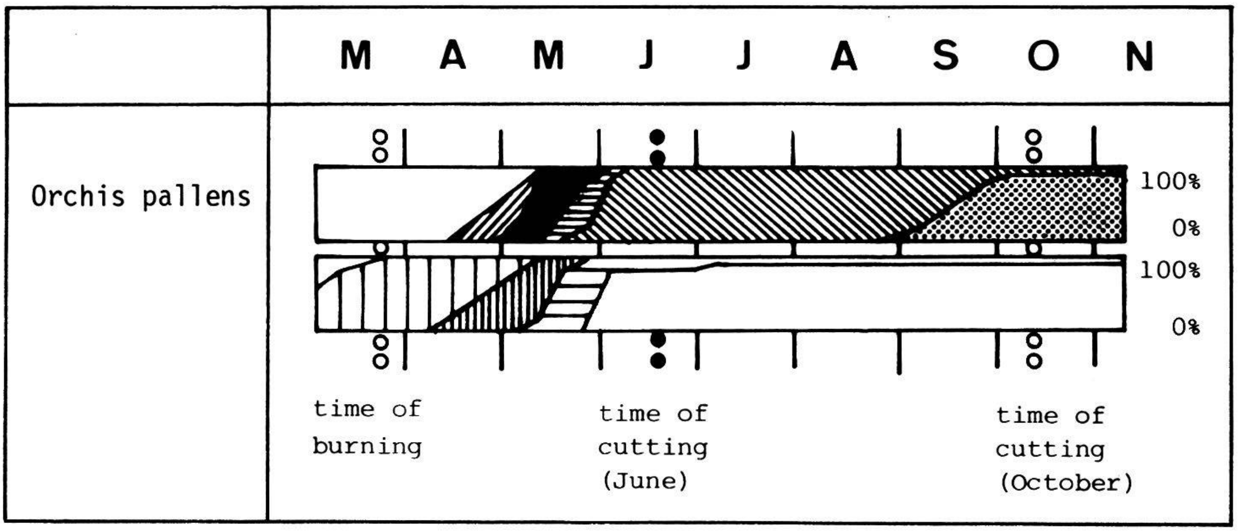


Fig. 28. *Orchis pallens*: analytical diagram of the phenological development within study area 4.

Vegetative phases: ground leaves, shoots, yellowing

Generative phases: flower buds, bloom, fading, fruit, seed dispersal for almost 20 years prior to the beginning of experimental management in 1977. The number of flowering plants of *Orchis pallens* was observed to increase in surfaces cut annually in June, whereas it remained more or less stable in adjacent plots subject to burning in March or to no management at all (Fig. 27). The species was not seen within surfaces cut in October; therefore the effect of this treatment is unknown. Cutting in mid June removed the fruit of *O. pallens* (Fig. 28), but this treatment seemed to be the most favourable for this species, probably because it provided the most suitable microclimatic conditions. It can also be supposed that the fruit which fall onto the ground may eventually ripen and yield viable seeds.

3. *Bromus erectus* (Figs 29-33)

Bromus erectus is a perennial, caespitose, tall hemicryptophyte forming dense tussocks and sometimes short underground runners. The leaves are mainly arranged between 5 and 25 cm above ground. After the first cut of the year the species produces little new material and almost no new inflorescences. According to OBERDORFER (1979), *Bromus erectus* is mainly associated with *Brometalia* communities.

Study area 1 was cut once a year but not fertilized until 1977 and was experimentally managed from 1978 onwards. In 1980, the number of inflorescences of *Bromus erectus* per unit area was great in the plots cut in June, moderate in the plots burnt in March, small in those cut in October and exceedingly small in the unmanaged surfaces (Fig. 29, top). Contrary to expectations based upon the analytical diagram (Fig. 32), the phenological data indicated that cutting in June, although preventing sexual reproduction, was likely to be the most favourable treatment for *Bromus erectus*. The results obtained within study area 1 were corroborated by observations in the other areas. Within study areas 3 and 4 that had been abandoned prior to the beginning of experimental management, a distinct increase in the flowering intensity of *Bromus erectus* was only observed in the surfaces cut in June as exemplified by Fig. 30.

It should be pointed out that the cover data suggested 'no management' as a preferential treatment for this species (Figs 29 bottom, 31, 75); however, observations on communities representing various successional stages suggested

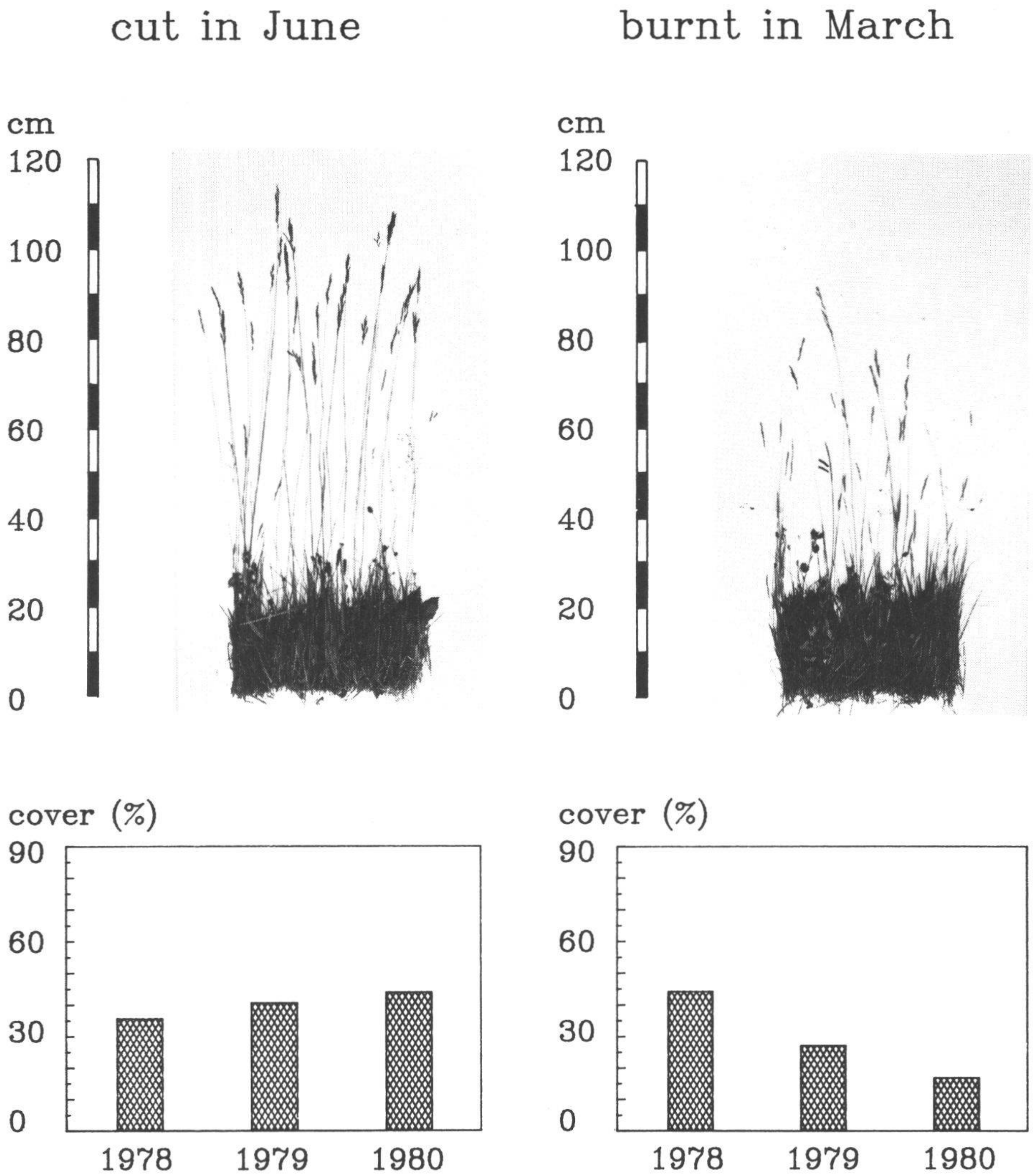


Fig. 29. *Bromus erectus* within study area 1.

Top: flowering intensity in late June/early July 1980 in surfaces under four different treatments since 1978, represented by 0.25 m^2 cuttings aligned on a distance of 0.5 m.

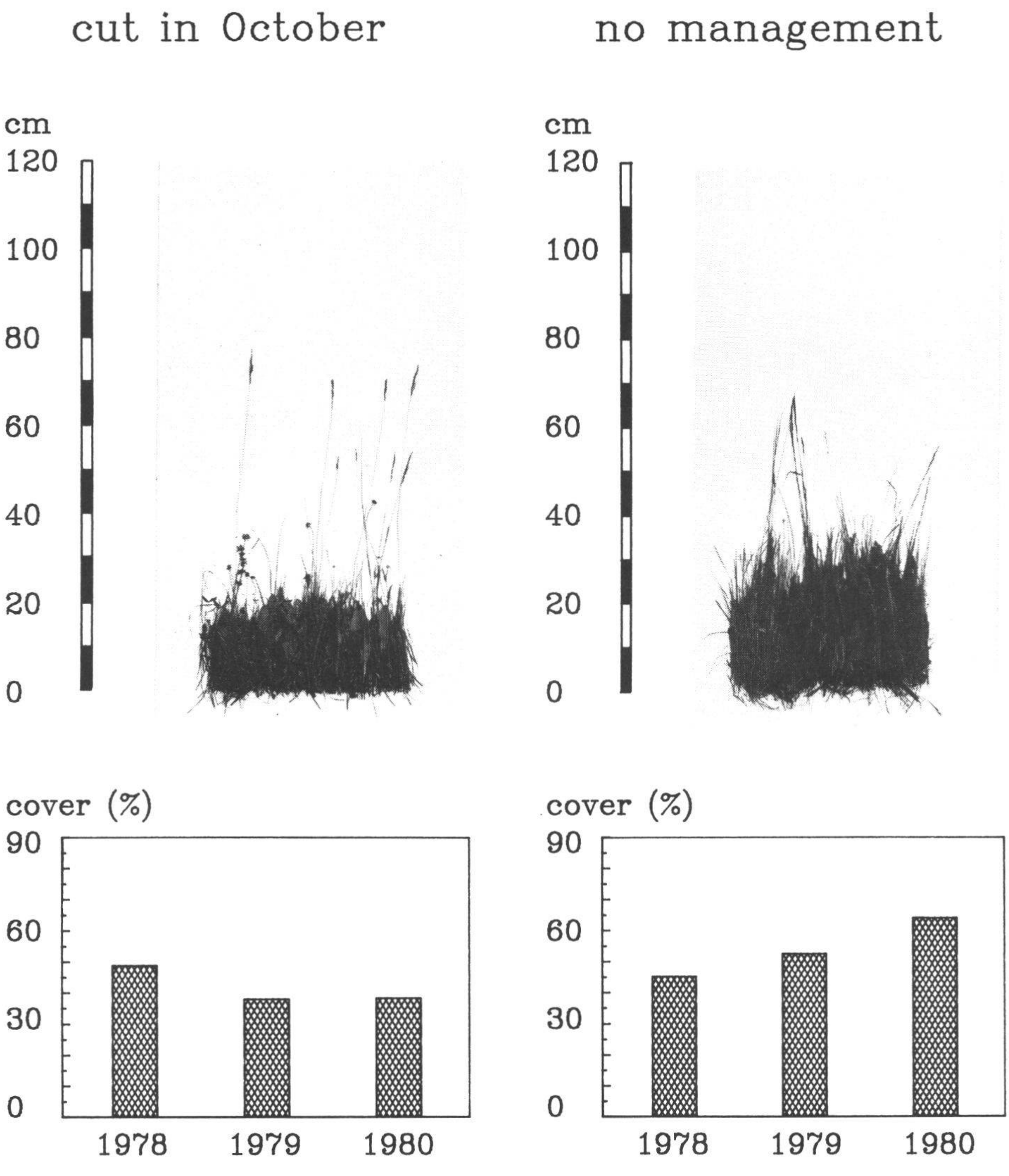


Fig. 29 (continued). *Bromus erectus* within study area 1.

Bottom: development of the cover under four different treatments from 1978 to 1980. (Ten relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m^2 each were evaluated).

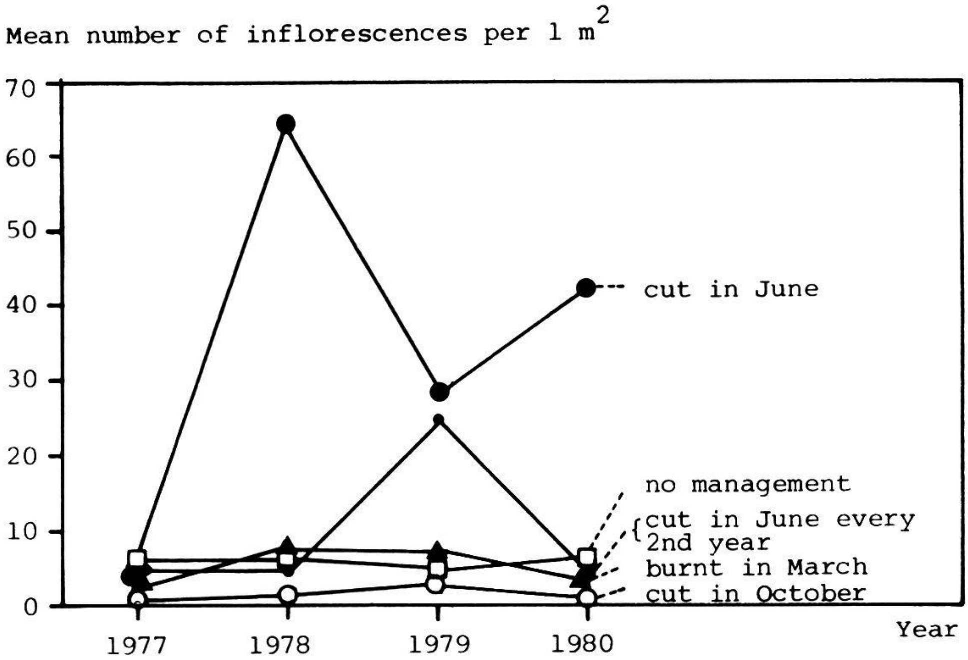


Fig. 30. *Bromus erectus* within study area 4: development of the flowering intensity under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

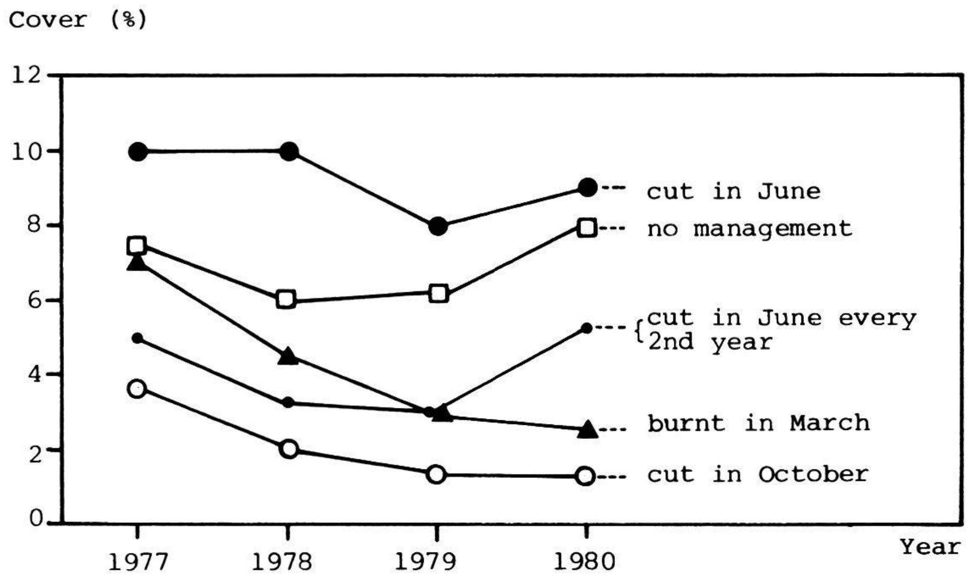


Fig. 31. *Bromus erectus* within study area 4: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management where six samples of 1 m^2 each were evaluated).

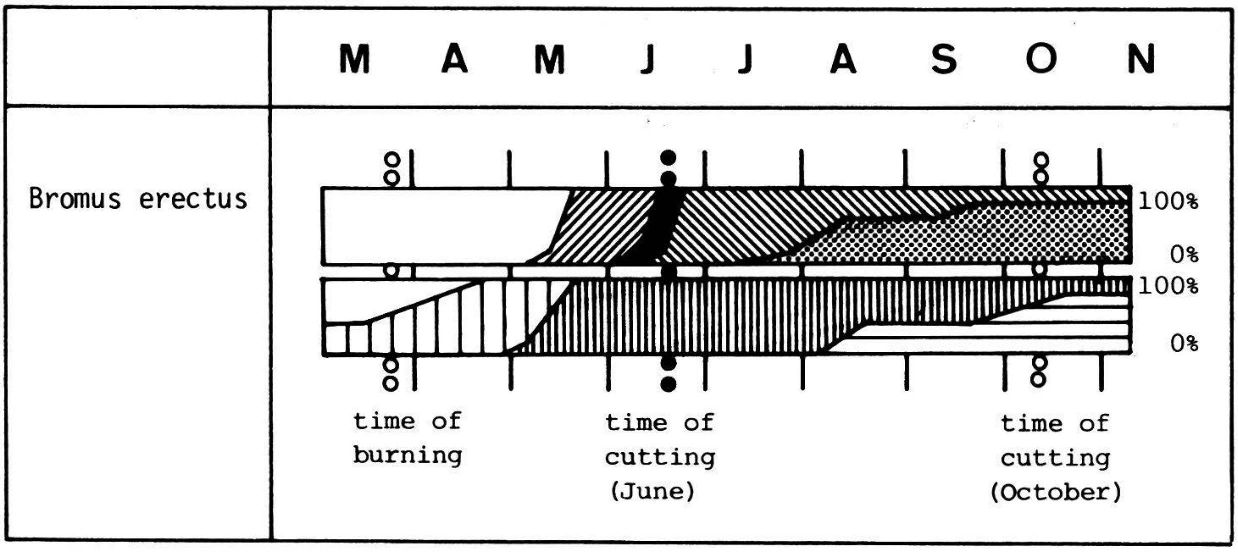


Fig. 32. *Bromus erectus*: analytical diagram of the phenological development within study area 1.

Vegetative phases: ground leaves; shoots; yellowing

Generative phases: flower buds; bloom; fading; fruit; seed dispersal

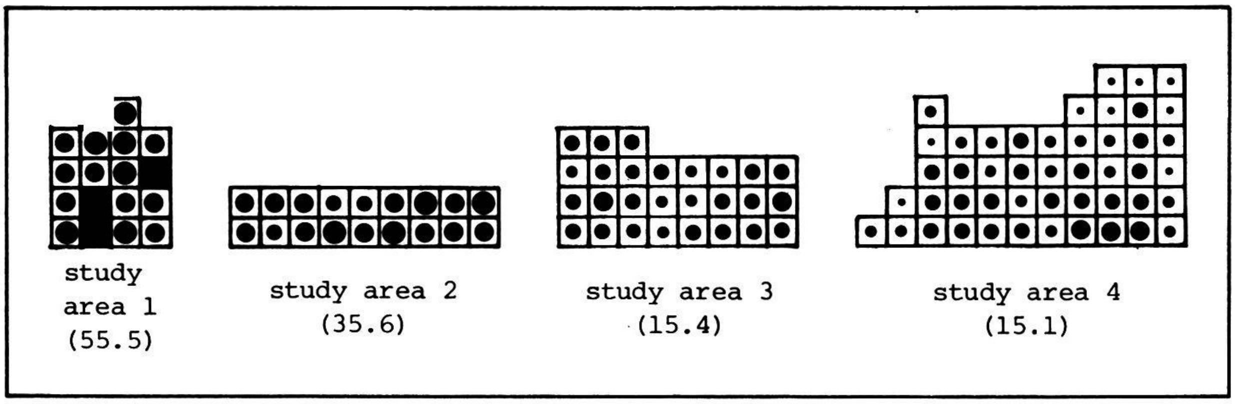


Fig. 33. *Bromus erectus*: distribution pattern within four successional stages of *Mesobrometum* grassland (study areas 1, 2, 3, 4).

The cover-abundance values of the BRAUN-BLANQUET scale are marked as follows:

+/r: • ; 1: • ; 2: ● ; 3: ● ; 4: ● ; 5: ■ .

(...): species value (see page 21)

that a temporary increase in the cover of *Bromus erectus* will be followed in the long term by a positive decline (Fig. 33). The field data thus corroborates the conclusions inferred from the phenological observations.

4. *Ranunculus bulbosus* (Figs 34, 35)

Ranunculus bulbosus is a perennial, scapose, medium-sized hemicryptophyte with a short rhizome and a bulbous, swollen stem-base. The leaves are mainly arranged in a semi-rosette. According to OBERDORFER (1979), *Ranunculus bulbosus* is primarily associated with *Mesobromion* communities but occurs also within dry *Arrhenatherum* meadows.

Ranunculus bulbosus occurred only in small quantities within the study areas, usually covering less than 1% of the surface. Using traditional relevés, it was rather difficult to decide whether this species was affected by a given treatment or not and, should this be the case, to what extent and in which direction. Phenological methods, on the other hand, proved to be helpful (Fig. 34). Until 1977, when the experimental management was started, the site (study area 2) was always cut once a year. During the period 1977-1980, the flowering of *Ranunculus bulbosus* observed in the plots annually cut in June was always significantly higher than in plots managed in a different way, whereas the cover of this species did not change remarkably. It can thus be inferred that annual cutting in June, although removing the fruit and therefore preventing sexual reproduction (Fig. 35), is the most favourable treatment for *R. bulbosus*. This conclusion, supported by the fact that *Ranunculus bulbosus* occurs to a far lesser extent in later successional stages of this community, could not be drawn either from analytical diagrams (Fig. 35) or cover estimations.

The example of *Ranunculus bulbosus* also points out the importance of control plots when phenological methods are being used in permanent plot research; it should be mentioned that year to year fluctuations in flowering intensity were observed even when the management was unchanged (Fig. 34, surfaces cut in June).

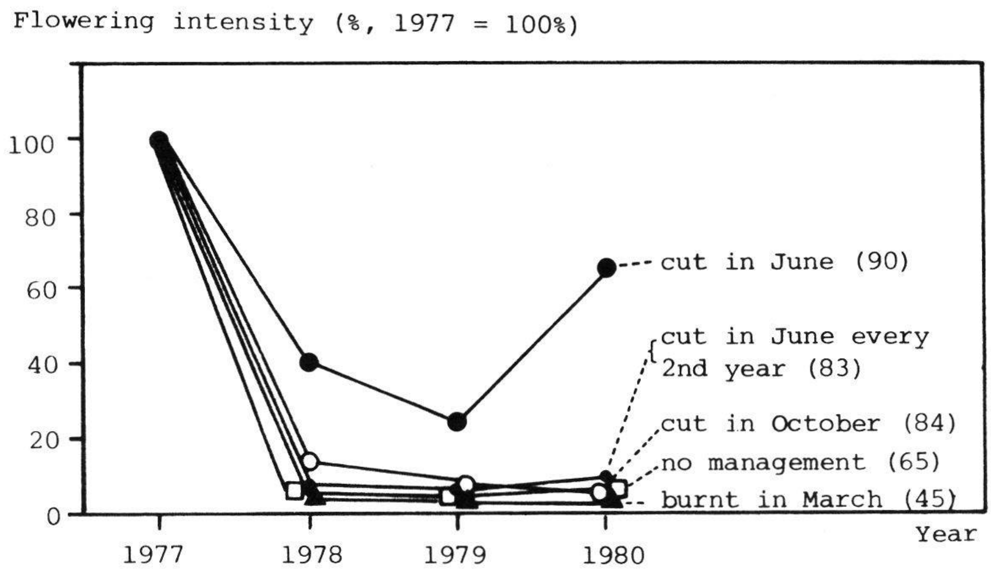


Fig. 34. *Ranunculus bulbosus* within study area 2: development of the flowering intensity under different treatments for the period 1977-1980; data expressed as percentages of the corresponding values of 1977; absolute magnitudes recorded in 1977 in parentheses following the treatment indications. (Three samples of 50 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 50 m^2 each were evaluated).

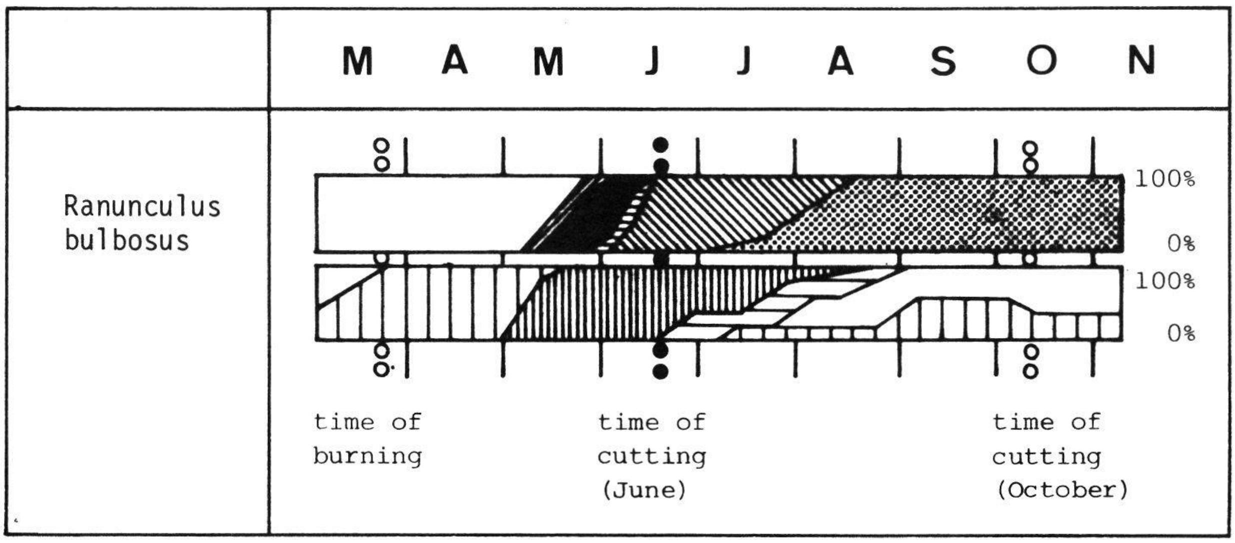


Fig. 35. *Ranunculus bulbosus*: analytical diagram of the phenological development within study area 2.

Vegetative phases: ground leaves, shoots, yellowing

Generative phases: flower buds, bloom, fading, fruit, seed dispersal

5. *Aster amellus* (Figs 36-41)

Aster amellus is a perennial, scapose, tall hemicryptophyte with a thin rhizome. A semi-rosette as well as leaves on the stalk form the main assimilating surfaces. According to OBERDORFER (1979), *Aster amellus* is primarily associated with communities of the alliances *Cytiso-Pinion*, *Erico-Pinion* and *Geranion sanguinei* but also with those of the class *Festuco-Brometea*; it is a characteristic species of the *Geranio-Peucedanetum* and today occurs mostly within communities of this type.

From the analytical diagram (Fig. 40), one might expect that cutting in October removing flowers and fruit of *Aster amellus* would have a severely damaging effect while cutting in June should have little or no effect on this species. However, mid-term phenological observations revealed that cutting in June resulted in an immediate sharp decrease of the flowering intensity, whereas burning in March turned out to be the most favourable treatment for *Aster amellus* (Fig. 36). The results obtained within study area 4 were confirmed by observations in study area 1 (Fig. 38). Phenological behaviour of *Aster amellus* changed rapidly in response to different treatments, but to date cover data mostly suggested no preferential management for this species (Figs 37, 39); only in burnt surfaces within study area 1 did the cover of *Aster amellus* increase significantly until 1980. On the other hand, observations of communities representing various successional stages corroborated the conclusions inferred from the phenological records, for *Aster amellus* was primarily found in later successional stages (Fig. 41).

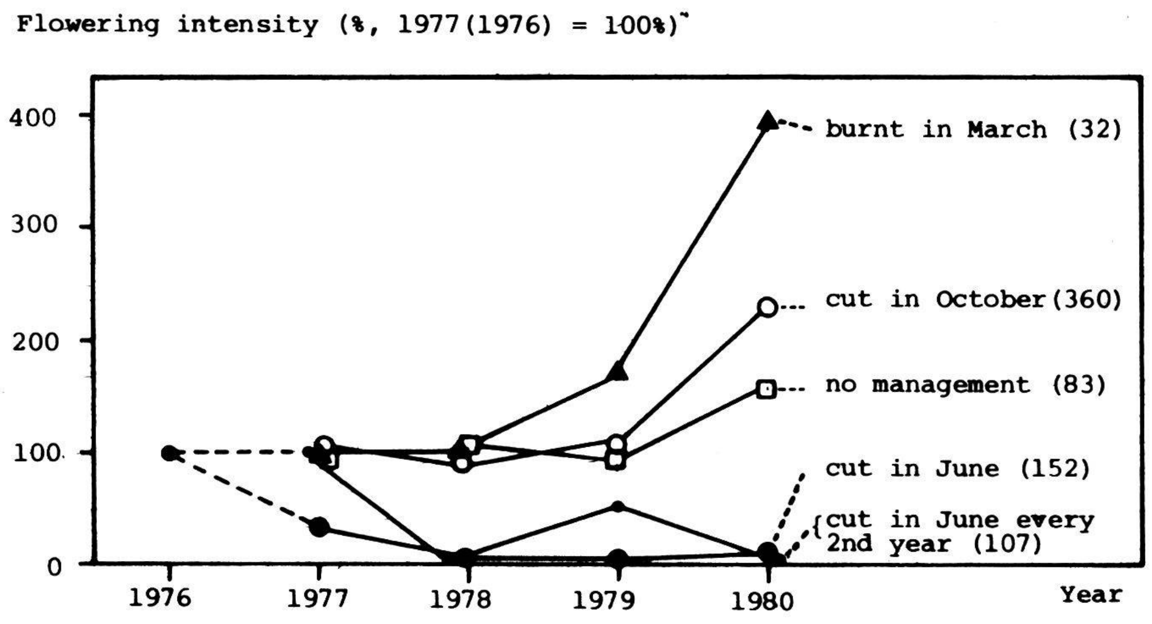


Fig. 36. *Aster amellus* within study area 4: development of the flowering intensity under different treatments for the period 1977(1976)-1980; data expressed as percentages of the corresponding values of 1977 (1976); absolute magnitudes recorded in 1977(1976) in parentheses following the treatment indications. (Three samples of 50 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 50 m^2 each were evaluated).

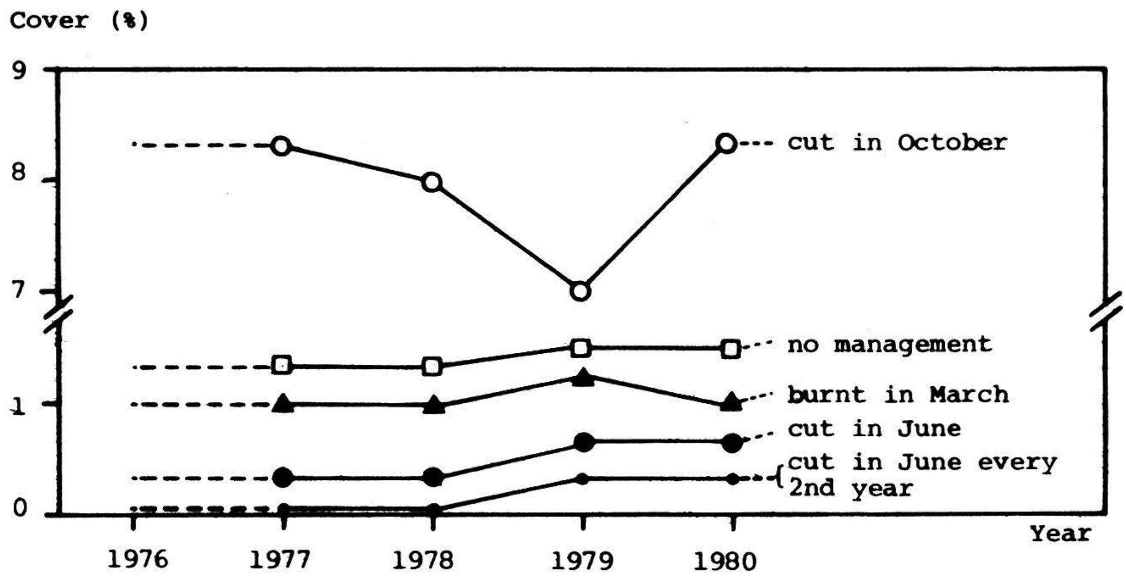


Fig. 37. *Aster amellus* within study area 4: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

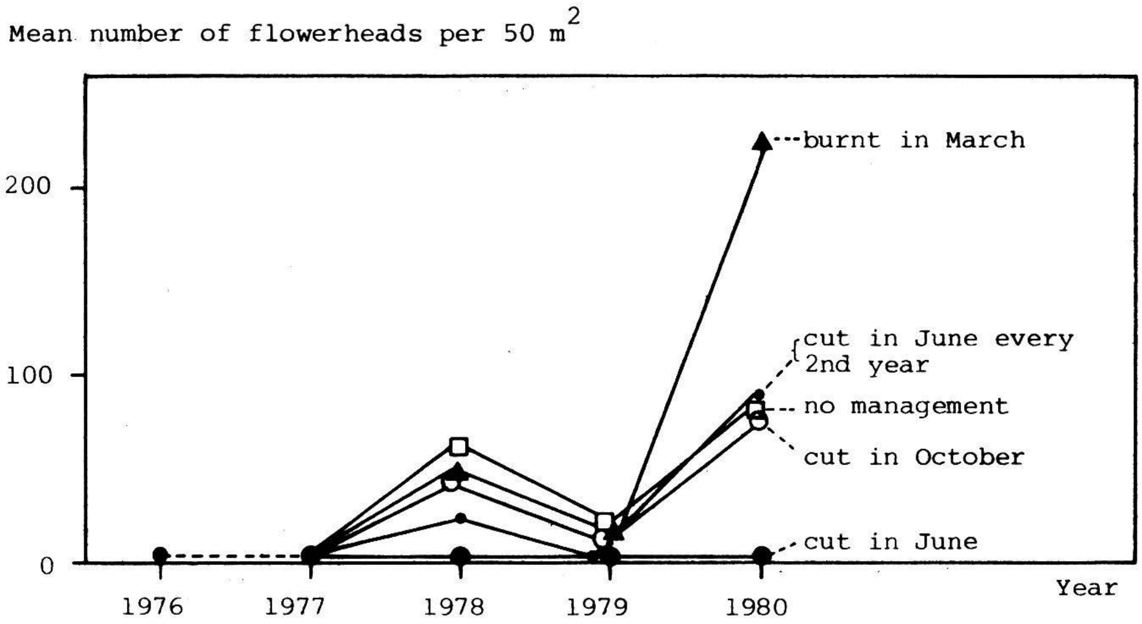


Fig. 38. *Aster amellus* within study area 1: development of the flowering intensity under different treatments for the period 1977-1980. (Three samples of 50 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 50 m^2 each were evaluated).

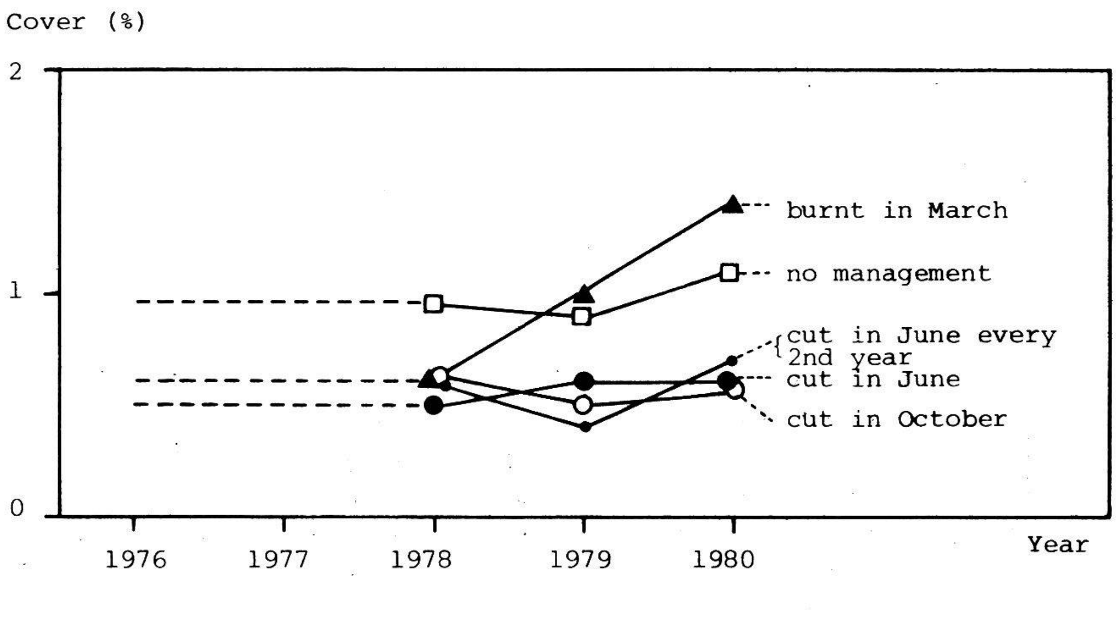


Fig. 39. *Aster amellus* within study area 1: development of the cover under different treatments for the period 1978-1980. (Ten relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m^2 each were evaluated).

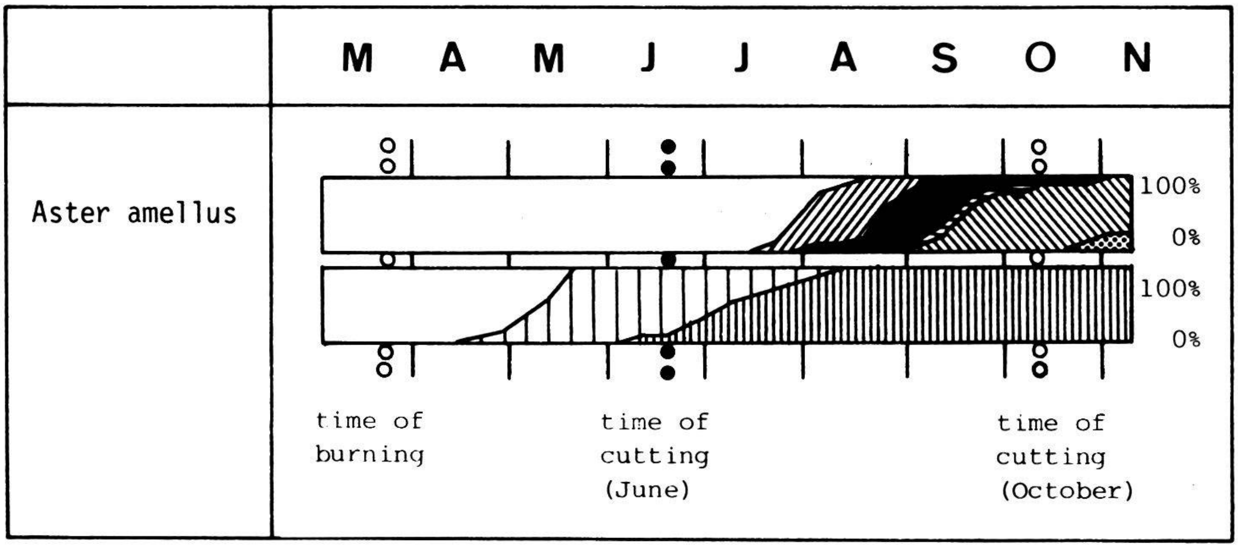


Fig. 40. *Aster amellus*: analytical diagram of the phenological development within study area 4.

Vegetative phases: ground leaves; shoots; yellowing

Generative phases: flower buds; bloom; fading; fruit; seed dispersal

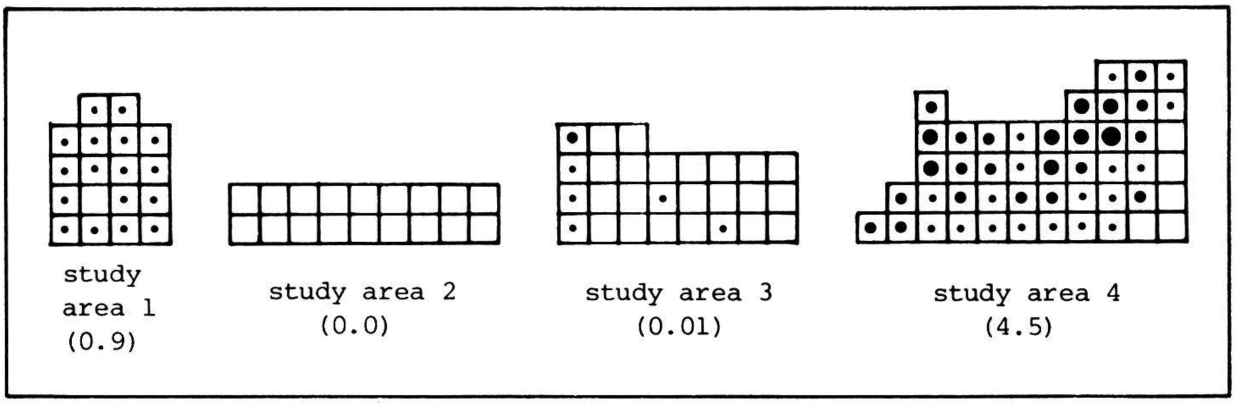


Fig. 41. *Aster amellus*: distribution pattern within four successional stages of *Mesobrometum* grassland (study areas 1, 2, 3, 4).

The cover-abundance values of the BRAUN-BLANQUET scale are marked as follows:
+/r: • ; 1: ● ; 2: ● ; 3: ● ; 4: ● ; 5: ■ .

(...): species value (see page 21)

6. *Buphthalmum salicifolium* (Figs 42-47)

Buphthalmum salicifolium is a perennial, scapose, tall hemicryptophyte with a knotty rhizome. A semi-rosette as well as leaves on the stalk form the main assimilating surfaces. According to OBERDORFER (1979), *Buphthalmum salicifolium* is primarily associated with communities of the alliances *Erico-Pinion, Geranion sanguinei, Molinion, Mesobromion* and also *Xerobromion*; today it occurs primarily in communities belonging to the *Geranion sanguinei*.

Mid-term phenological observations carried out within study area 4 showed that cutting in mid June is exceedingly disadvantageous for this species (Fig. 42); this treatment almost completely prevents the sexual reproduction of *Buphthalmum salicifolium* (Fig. 46). Cutting in October also resulted in a significant but lesser decrease in the flowering intensity of *Buphthalmum salicifolium* from 1977 onwards, whereas burning in March and in particular no management at all seemed to be more favourable (Fig. 42). The observations within study area 2 were generally in accordance with these results (Fig. 44); the higher flowering intensity of *Buphthalmum salicifolium* on surfaces subjected to burning in March or to cutting in October compared with that on unmanaged plots might primarily result from successful seedling establishment. However, in the long term, these treatments seem to be apparently less favourable than no management at all for *Buphthalmum salicifolium*.

The conclusions based upon the analytical diagram (Fig. 46) conformed to these observations. Cutting in June was likely to completely prevent sexual reproduction of *Buphthalmum salicifolium* by removing the flower buds and cutting in October occurred at a time when seed dispersal had only just started and was still very incomplete; the aforementioned treatments were thus supposed to be unfavourable for *Buphthalmum salicifolium*. On the other hand, burning in March did not affect the sexual reproduction in that only some ground leaves were damaged. This management as well as no management at all could therefore be considered as favourable.

It should be pointed out once more that the cover of *Buphthalmum salicifolium* exhibited no significant response to the different treatments whereas the phenological response proved to be remarkably distinct (Figs 42, 43, 44, 45). However, observations on communities representing various successional stages

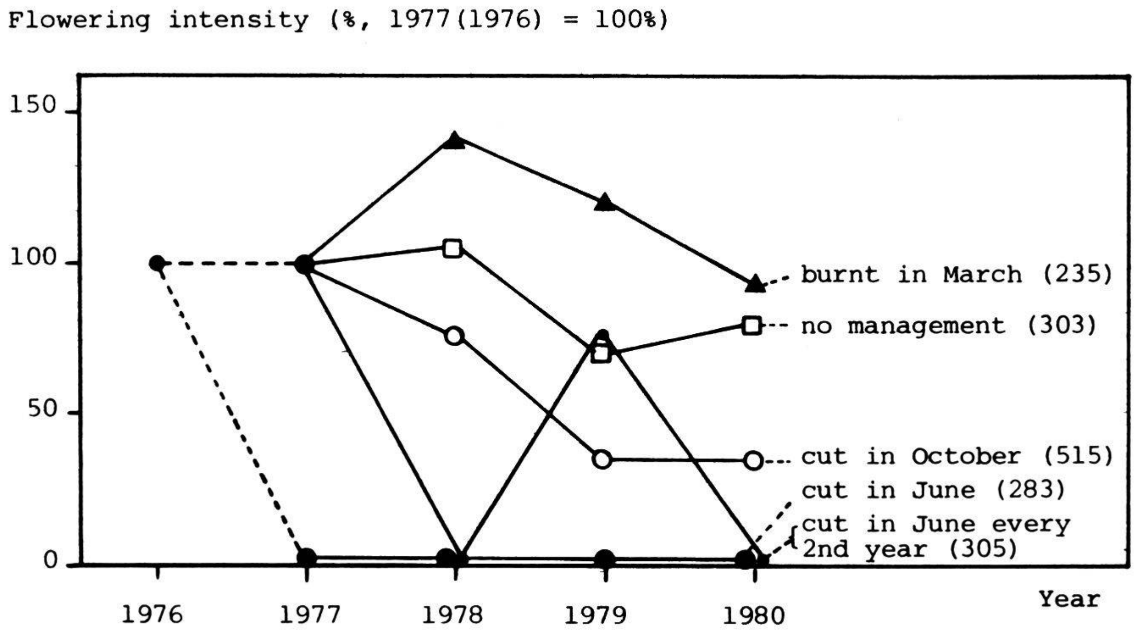


Fig. 42. *Buphthalmum salicifolium* within study area 4: development of the flowering intensity under different treatments for the period 1977 (1976)-1980; data expressed as percentages of the corresponding values of 1977(1976); absolute magnitudes recorded in 1977(1976) in parentheses following the treatment indications. (Three samples of 50 m^2 each were considered per treatment save for the condition 'no management' where six samples of 50 m^2 each were evaluated).

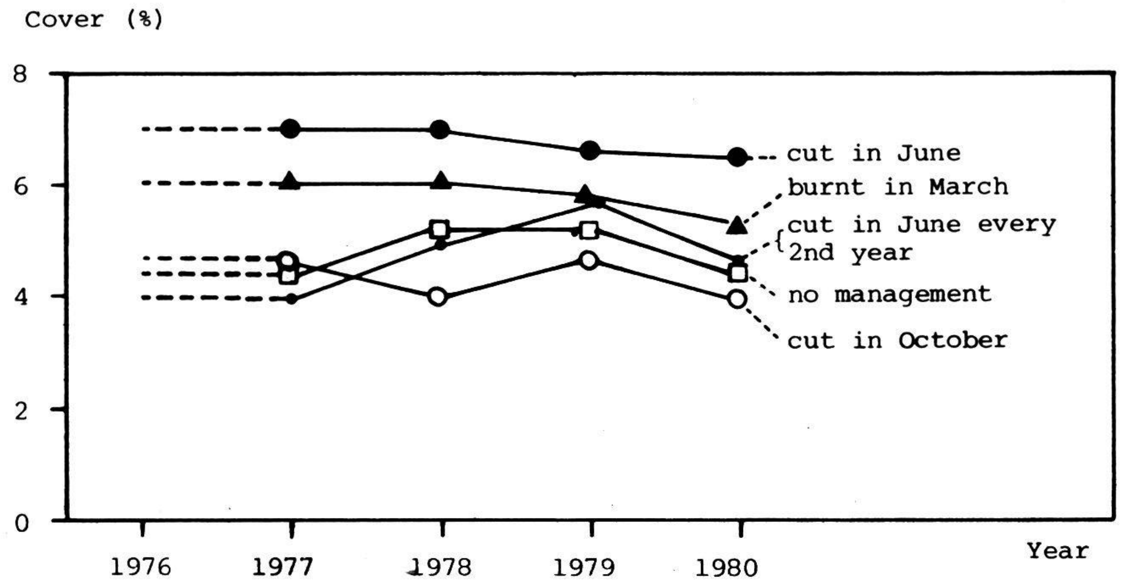


Fig. 43. *Buphthalmum salicifolium* within study area 4: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

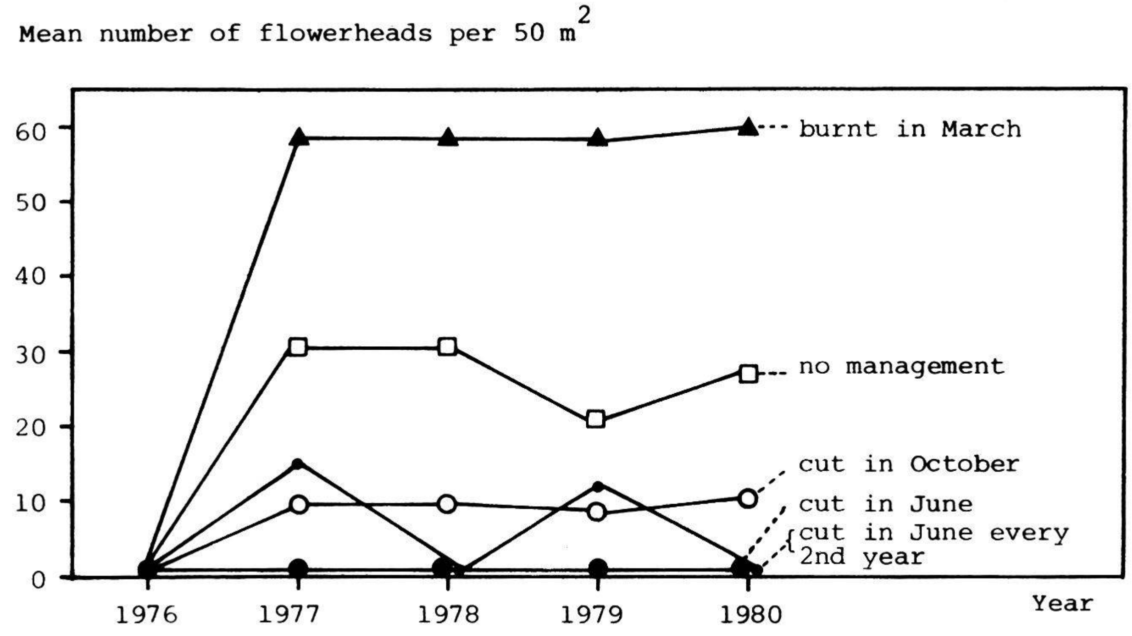


Fig. 44. *Buphthalmum salicifolium* within study area 2: development of the flowering intensity under different treatments for the period 1976-1980. (Three samples of 50 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 50 m^2 each were evaluated).

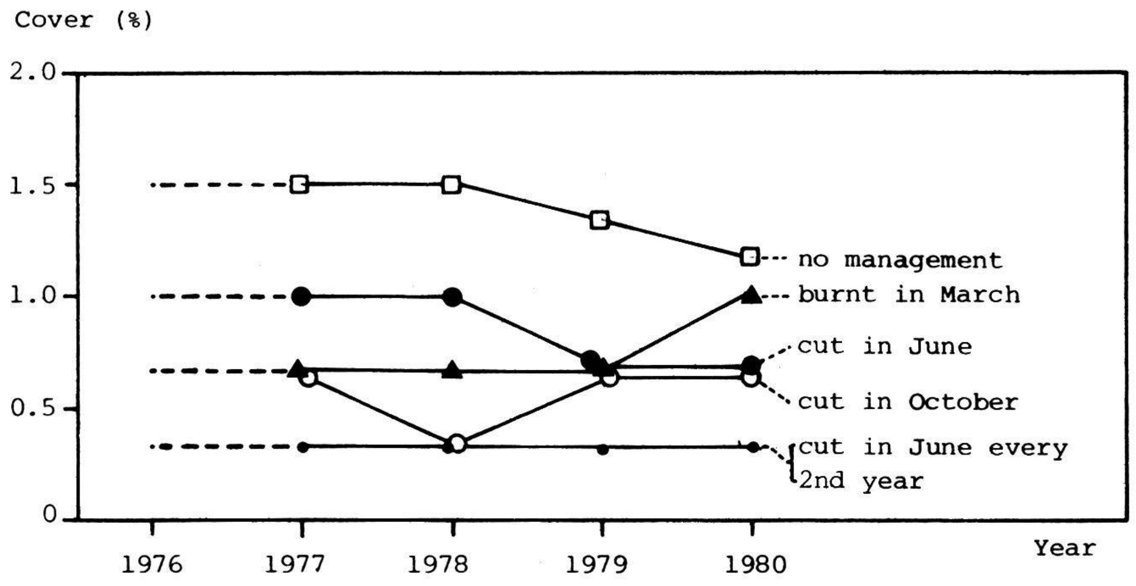


Fig. 45. *Buphthalmum salicifolium* within study area 2: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

of *Mesobrometum* grassland corroborated the conclusions based upon mid-term phenological records. *Buphthalmum salicifolium* occurred in much lower abundance in areas regularly cut in mid June than in unmanaged areas (Fig. 47).

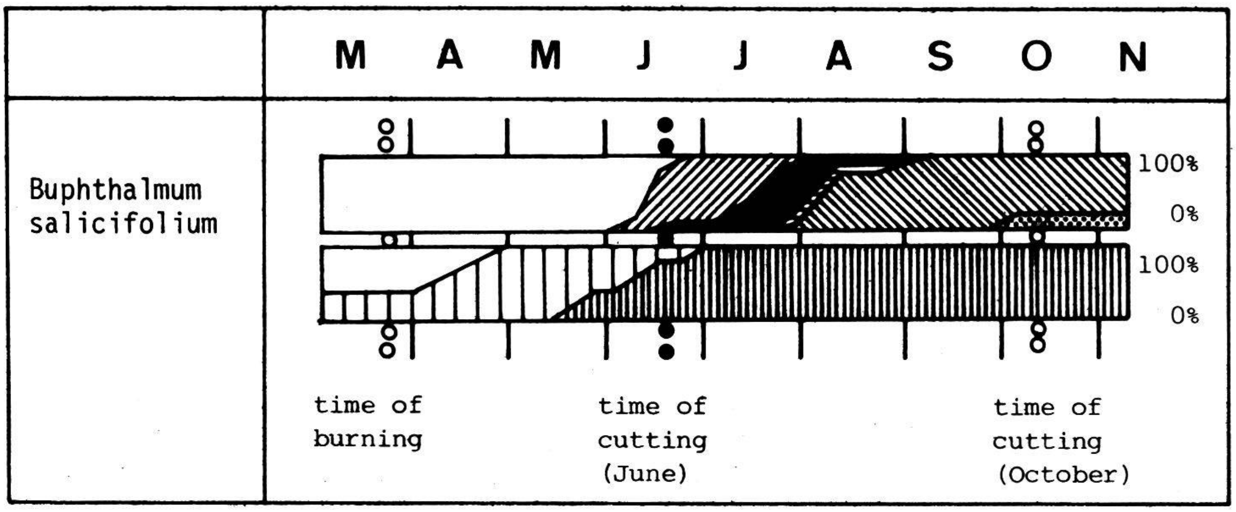


Fig. 46. *Buphthalmum salicifolium*: analytical diagram of the phenological development within study area 4.

Vegetative phases: ground leaves, shoots, yellowing
Generative phases: flower buds, bloom, fading, fruit, seed dispersal

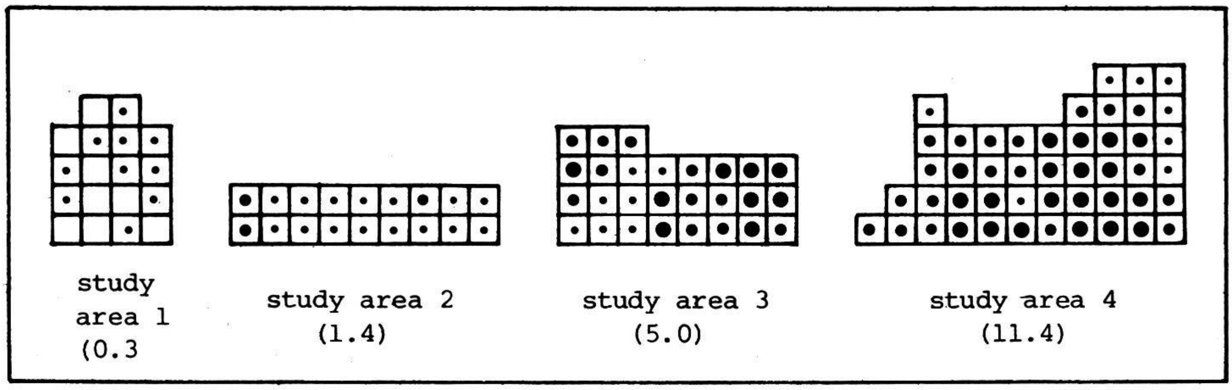


Fig. 47. *Buphthalmum salicifolium*: distribution pattern within four successional stages of *Mesobrometum* grassland (study areas 1, 2, 3, 4).

The cover-abundance values of the BRAUN-BLANQUET scale are marked as follows:
+/r: • ; 1: • ; 2: ● ; 3: ● ; 4: ● ; 5: ■ .

(...): species value (see page 21)

7. *Brachypodium pinnatum* (Figs 48-57)

Brachypodium pinnatum represents a perennial, reptant, tall hemicryptophyte forming long underground runners. The leaves are mainly arranged between 5 and 25 cm above ground. According to OBERDORFER (1979), *Brachypodium pinnatum* is primarily associated with communities belonging to the *Cephalanthero-Fagion*, *Erico-Pinion*, *Geranion sanguinei*, *Mesobromion* and *Cirsio-Brachypodion*; today it occurs mainly in communities of the two last named alliances.

Brachypodium pinnatum was investigated in all study areas. The number of inflorescences was observed to greatly increase within the burnt surfaces whereas it remained relatively stable in adjacent plots subject to cutting in June, cutting in October or in plots not managed at all (Figs 48, 50, 52, 54).

On the other hand, the cover of *Brachypodium pinnatum* generally exhibited no significant response to the different treatments (Figs 49, 51, 53, 55). Within the study areas 1 and 4 the cover of this species remained stable until 1979 and increased until 1980, save for those plots cut in June where it changed very little during this period of time (Figs 49, 55). However, the present data was insufficient to decide whether the increase would continue in future or not, possibly being merely a fluctuation due to weather conditions. In *Mesobrometum* grassland the cover of *Brachypodium pinnatum* was observed to respond to a marked degree to meteorological conditions (BORNKAMM 1961). Observations on communities representing various successional stages, however, suggested an increase in the cover of *Brachypodium pinnatum* during the course of succession (Fig. 57).

On the whole, cutting in June almost completely prevented sexual reproduction by removing the flower buds (Fig. 56) and conforming to expectation proved to be the most disadvantageous treatment, whereas the mid-term phenological data suggested burning to be the most favourable (Figs 48, 50, 52, 54); the latter management was thus expected to lead in the long term towards an increase in the cover of *Brachypodium pinnatum*. On the other hand, there were no signs so far to indicate a marked change in the cover of this species in the near future when under the influence of no management or cutting in October (Figs 49, 51, 53, 55). However, taking into account the analytical diagram (Fig. 56) and the observations of various successional stages of the investigated grassland type (Fig. 57) there is a reasonable chance of cover increase in the long term within unmanaged surfaces.

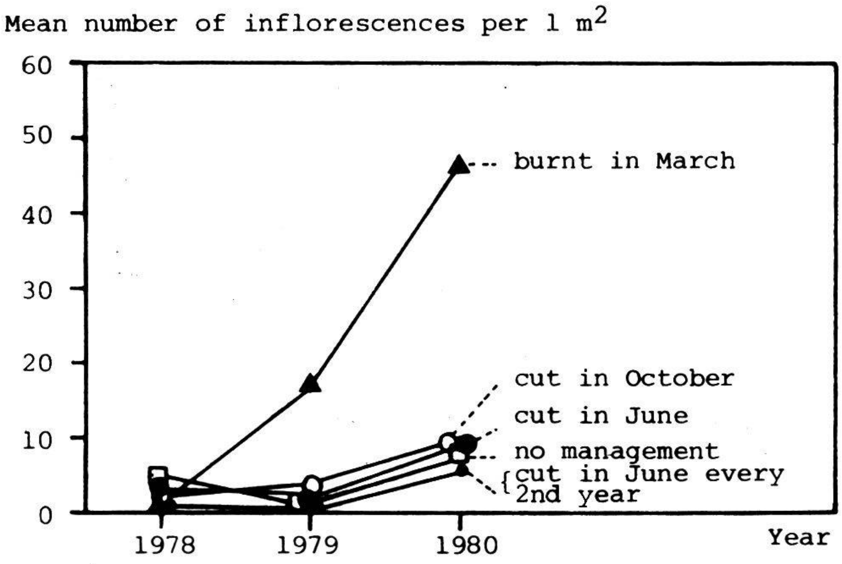


Fig. 48. *Brachypodium pinnatum* within study area 1: development of the flowering intensity under different treatments for the period 1978-1980. (Ten samples of 1 m^2 each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m^2 each were evaluated).

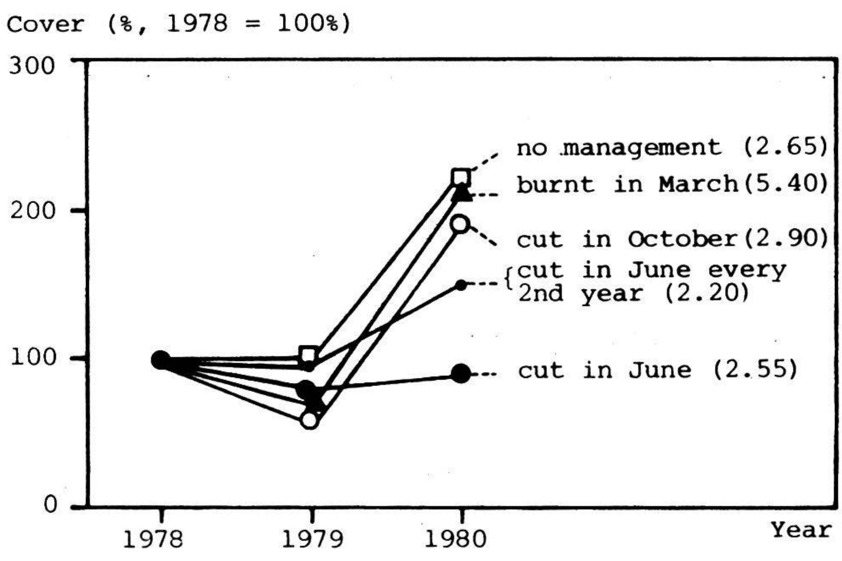


Fig. 49. *Brachypodium pinnatum* within study area 1: development of the cover under different treatments for the period 1978-1980; data expressed as percentages of the corresponding values of 1978; absolute magnitudes recorded in 1978 in parentheses following the treatment indications. (Ten relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m^2 each were evaluated).

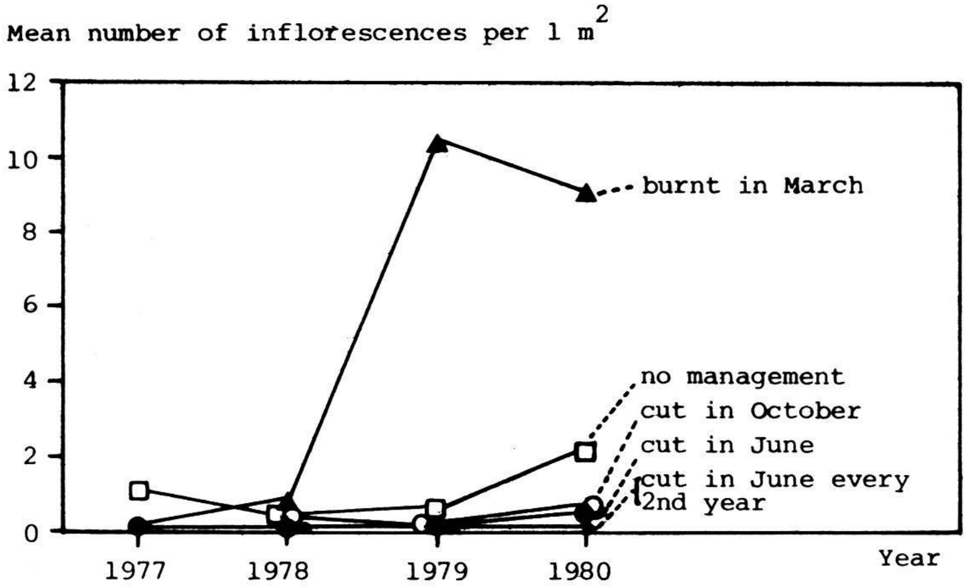


Fig. 50. *Brachypodium pinnatum* within study area 2: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

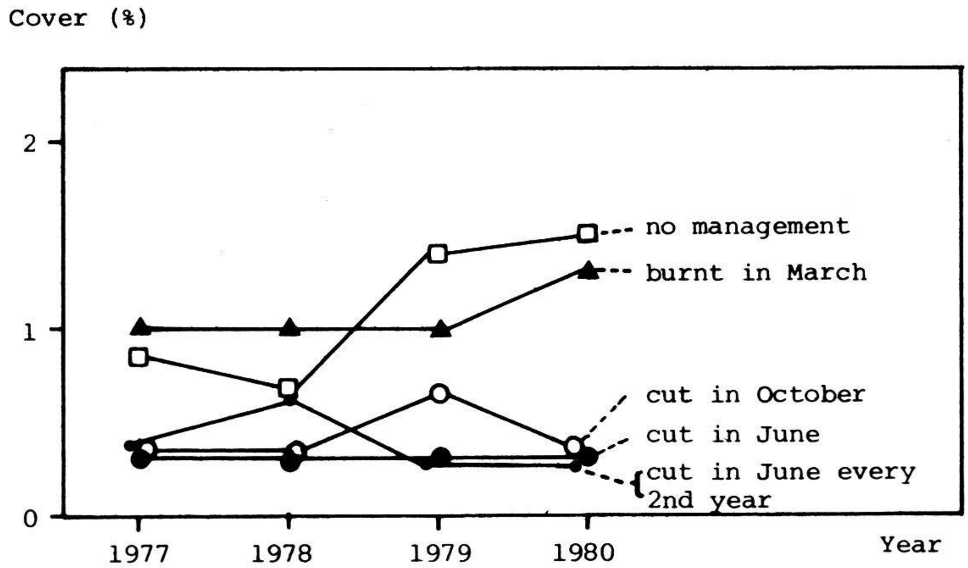


Fig. 51. *Brachypodium pinnatum* within study area 2: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

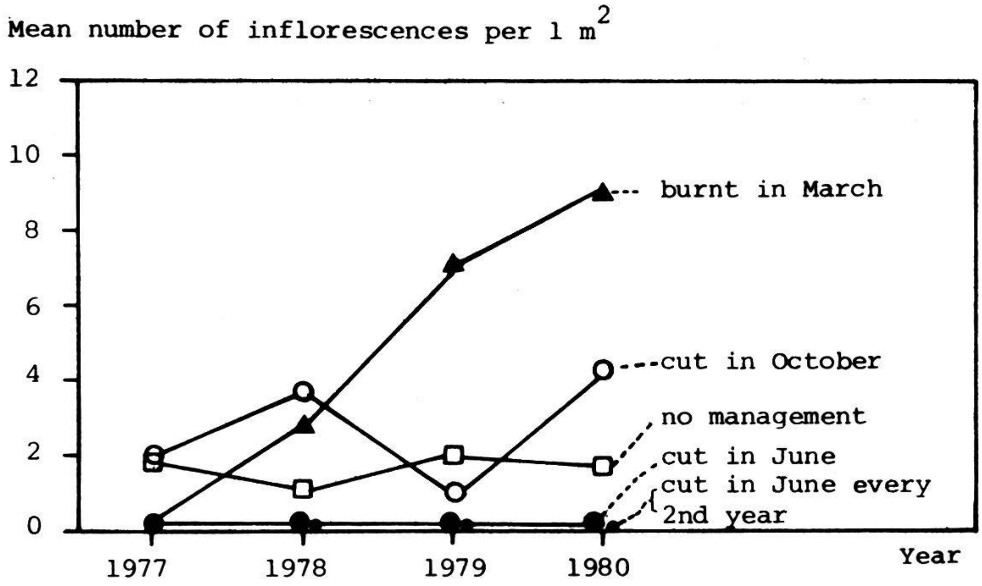


Fig. 52. *Brachypodium pinnatum* within study area 3: development of the flowering intensity under different treatment for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

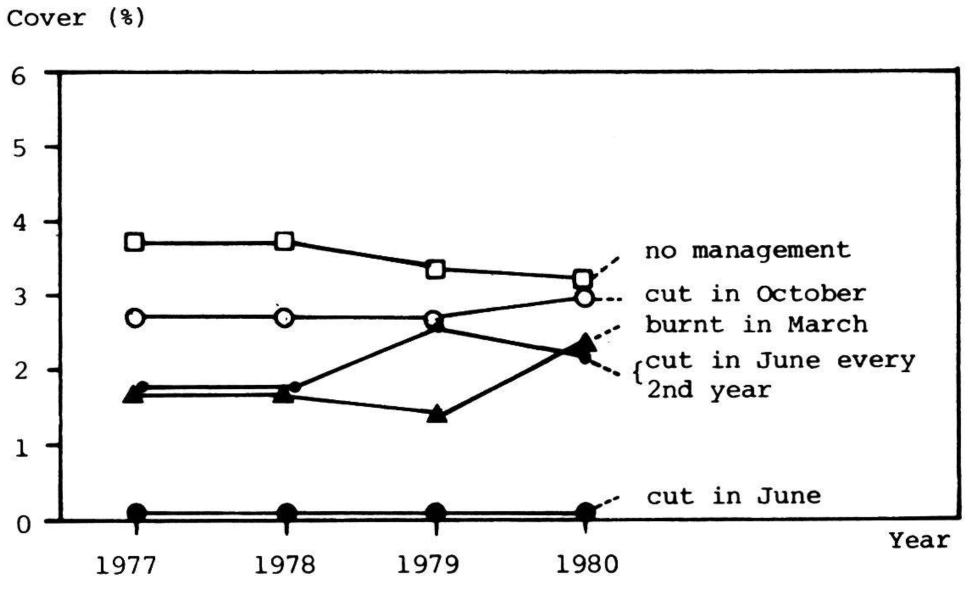


Fig. 53. *Brachypodium pinnatum* within study area 3: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considred per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

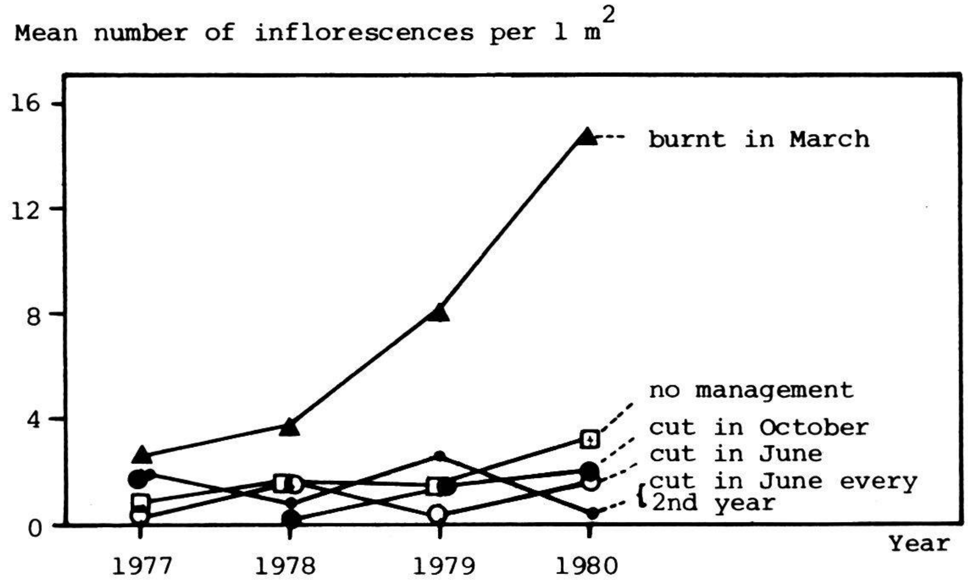


Fig. 54. *Brachypodium pinnatum* within study area 4: development of the flowering intensity under different treatments for the period 1977-1980. (Three samples of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

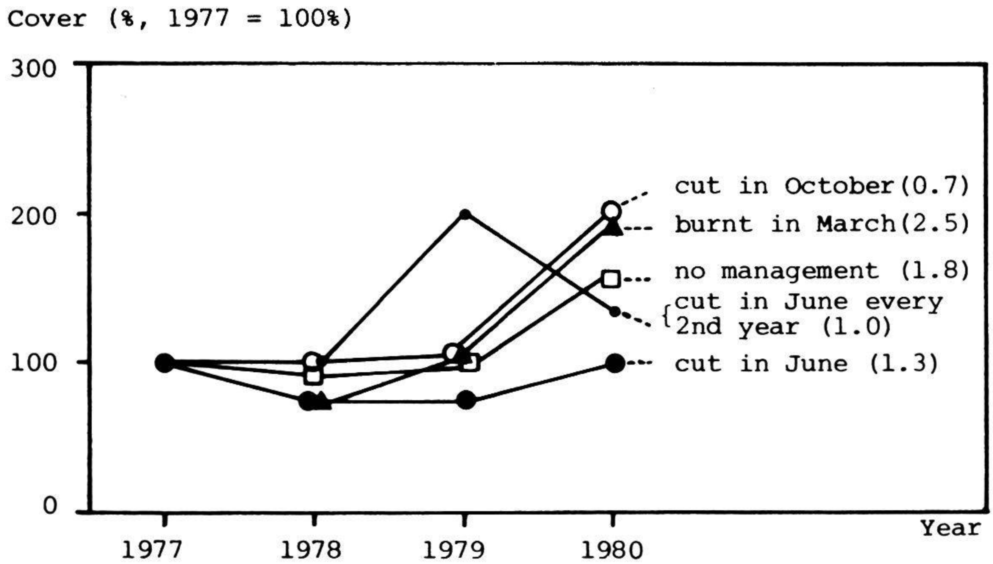


Fig. 55. *Brachypodium pinnatum* within study area 4: development of the cover under different treatments for the period 1977-1980; data expressed as percentages of the corresponding values of 1977; absolute magnitudes recorded in 1978 in parentheses following the treatment indications. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

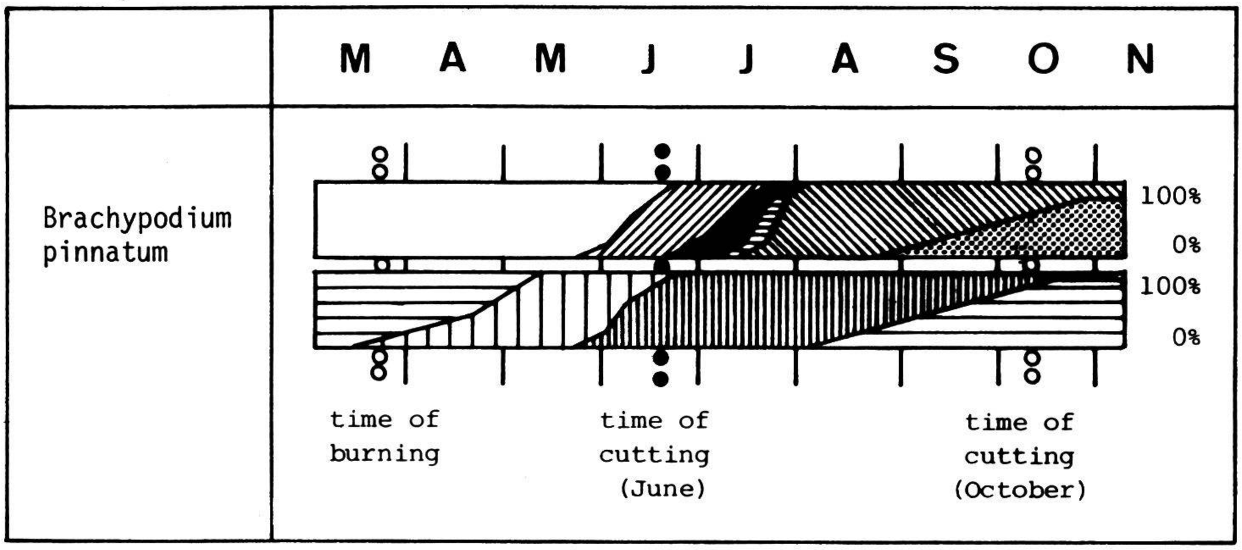


Fig. 56. *Brachypodium pinnatum*: analytical diagram of the phenological development within study area 1.

Vegetative phases: ground leaves; shoots; yellowing

Generative phases: flower buds; bloom; fading; fruit; seed dispersal

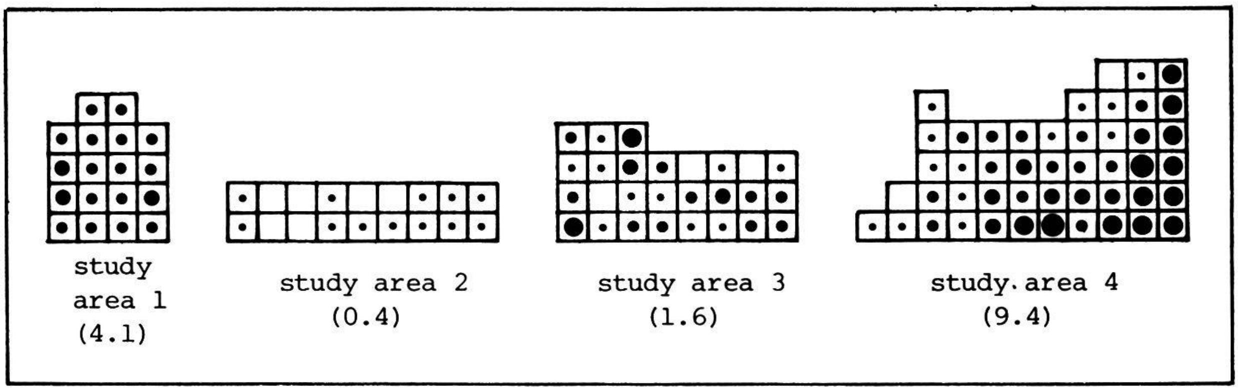


Fig. 57. *Brachypodium pinnatum*: distribution pattern within four successional stages of *Mesobrometum* grassland (study areas 1, 2, 3, 4).

The cover-abundance values of the BRAUN-BLANQUET scale are marked as follows:
+/r: • ; 1: • ; 2: ● ; 3: ● ; 4: ● . ; 5: ■ .

(...): species value (see page 21)

4.2. *Responses of whole communities to environmental changes*

4.2.1. *Phenological data*

The phenological behaviour of particular components within a given community obviously contributes to its global phenological rhythm. Two approaches are helpful in phenological studies on whole communities: a) plotting the number of species in blossom per unit area against time (e.g. FALIŃSKA 1968, 1972a, 1972b, BOTTLÍKOVÁ 1973), and b) synthetic colour diagrams first suggested in 1962 by TüXEN and then used by several authors (e.g. FüLLEKRUG 1967, 1969, BALÁTOVÁ-TULÁČKOVÁ 1971, FALIŃSKA 1976, NEUHäUSL and NEUHäUSLOVA 1977, KRüSI 1980). Both these approaches were used in the described investigations. Four sites were studied, the study areas 1 and 2 being regularly used for hay making prior to experimental management and the study areas 3 and 4 representing the same grassland type but abandoned for about ten and 20 years respectively until the experiment was started.

Number of species in blossom per unit area vs. time

In study area 2 the largest number of species in blossom both per 1 m^2 and 50 m^2 was observed in mid June i.e. just before cutting (Fig. 58 top). On the other hand, in study area 4 the intense blooming lasted much longer i.e. from June to September (Fig. 58 bottom).

Within study area 1, the number of species in blossom per 1 m^2 and 50 m^2 respectively was recorded in plots treated differently, over a period of three years. The shape of the curves and, in particular, the magnitude of the June peak remained unchanged within plots regularly cut in mid June i.e. subject to the control treatment (Fig. 59). In contrast, within plots unmanaged from 1978 onwards, the 1 m^2 curve and especially the June peak value of 1980 were remarkably different to those of 1978, no peak value differences being found in this respect within the 50 m^2 plots (Fig. 59). It can be inferred that, owing to succession, the small-scale homogeneity of the stand will decline. This conclusion was supported by comparative investigations on homogeneity carried out within the four areas 1, 2, 3 and 4 representing various successional stages (Fig. 60). In Fig. 60 the point dispersion increases as

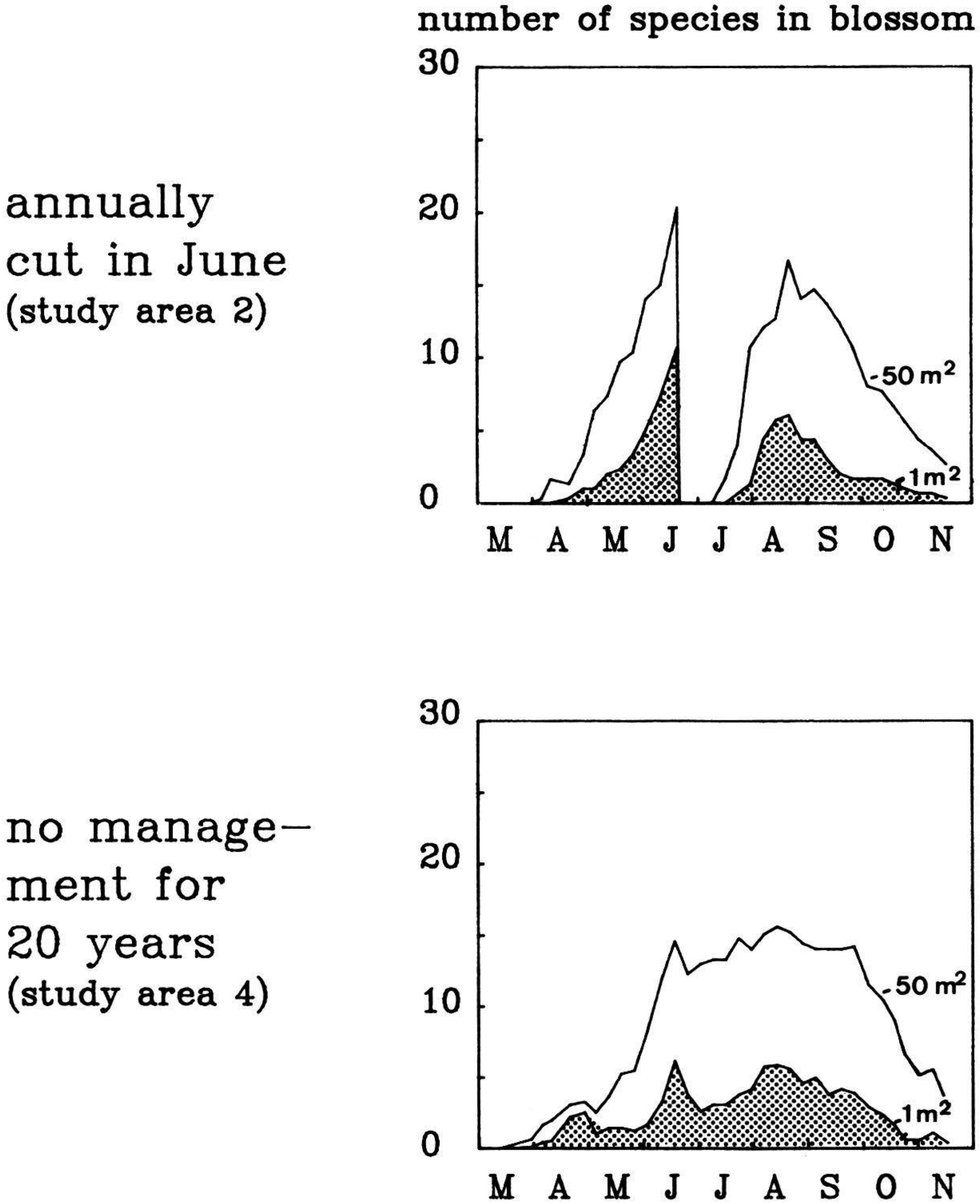


Fig. 58. Number of species in blossom per 50 m^2 (upper curve) and per 1 m^2 (lower curve) recorded weekly throughout 1978 within two successional stages of *Mesobrometum* grassland. Three samples per location were considered.

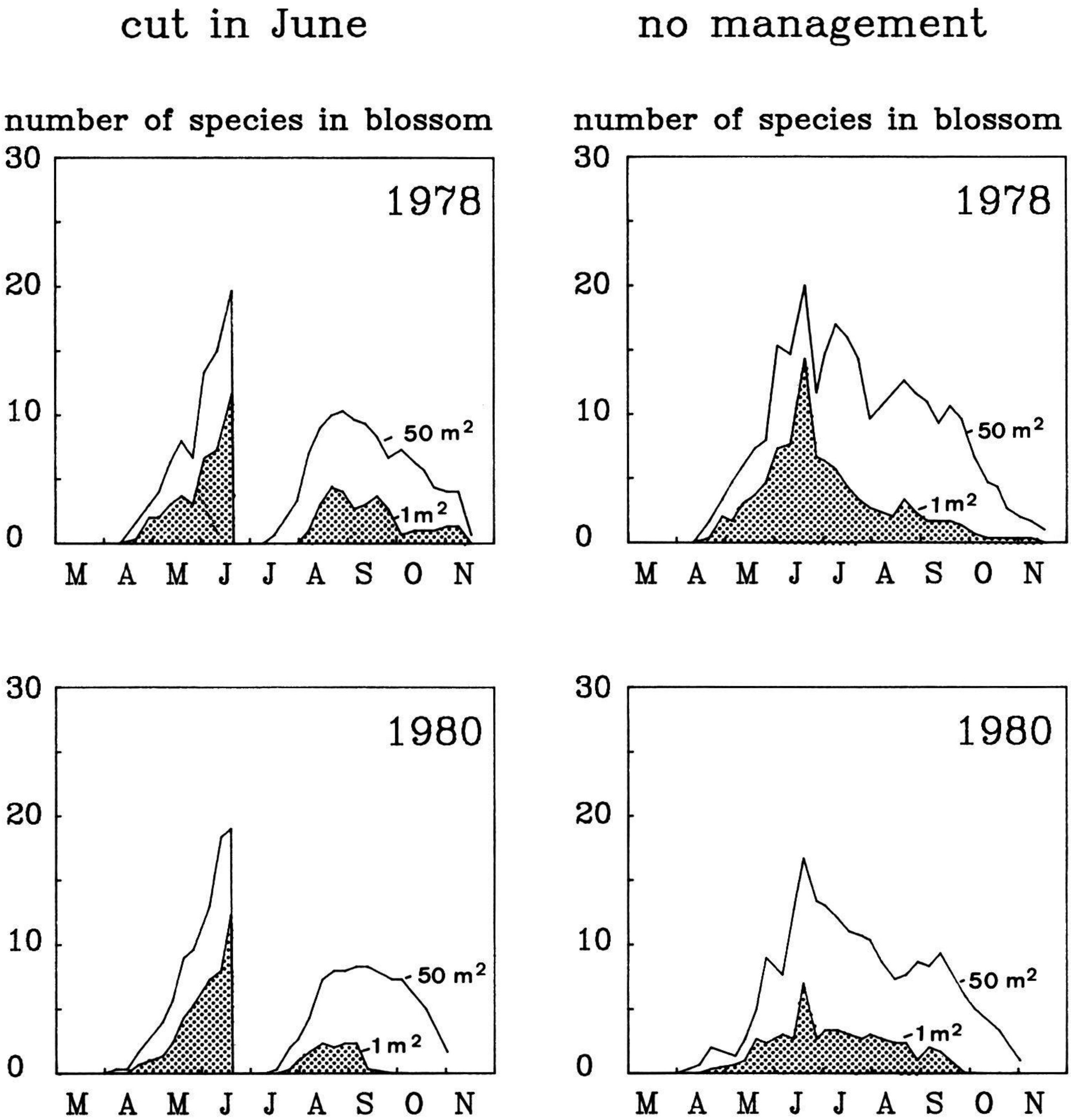


Fig. 59. Study area 1: development of the number of species in blossom per 50 m^2 (upper curve) and per 1 m^2 (lower curve) in surfaces under different treatments. Years represented: 1978, 1980. (Three samples per treatment were considered).

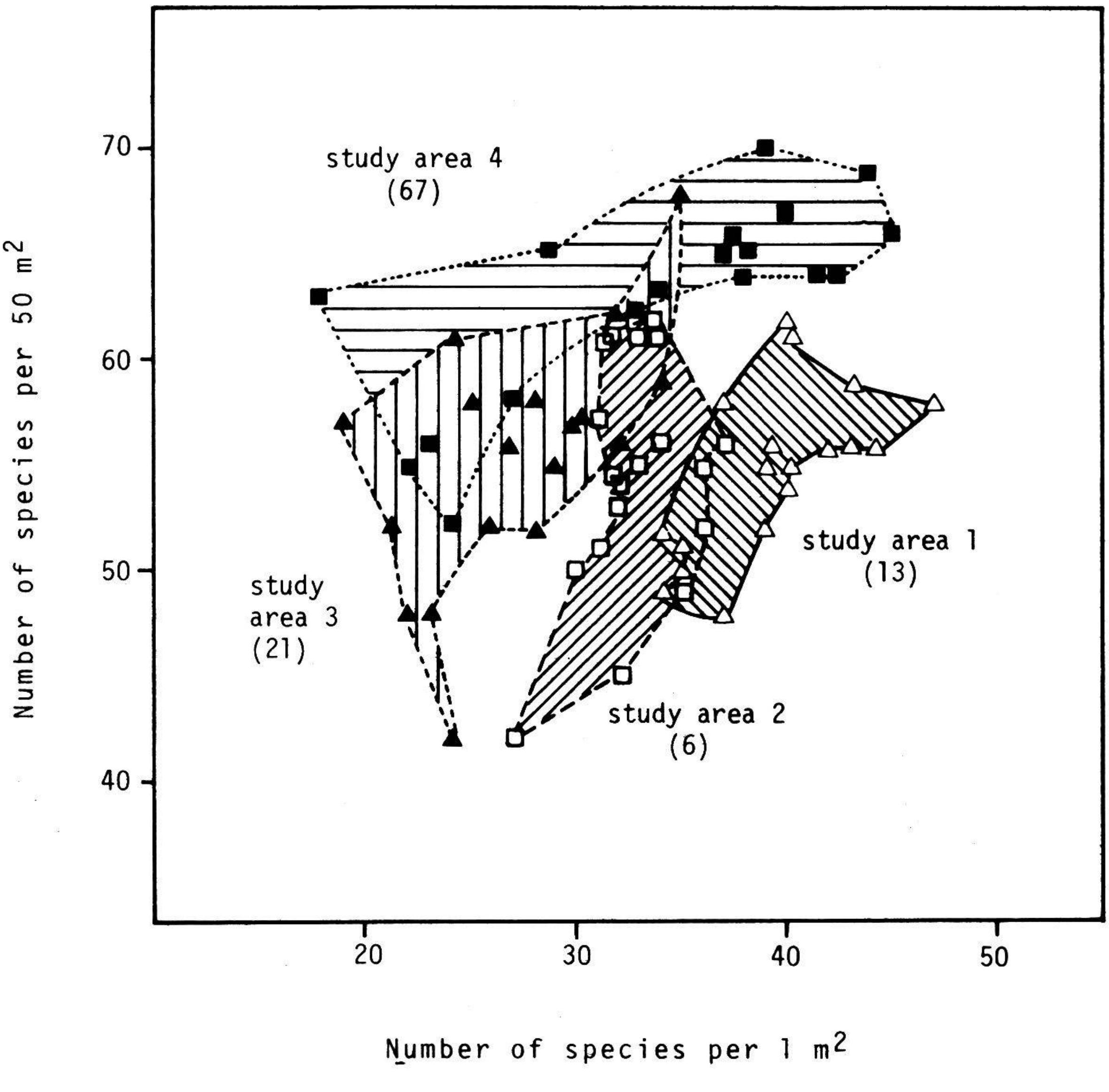


Fig. 60. Number of species per 1 m^2 plotted against the number of species in the surrounding 50 m^2 within successional stages of *Mesobrometum* grassland. 18 samples taken in 1978 were considered per study area. The variances of the 1 m^2 data are shown in parentheses following the area indications.

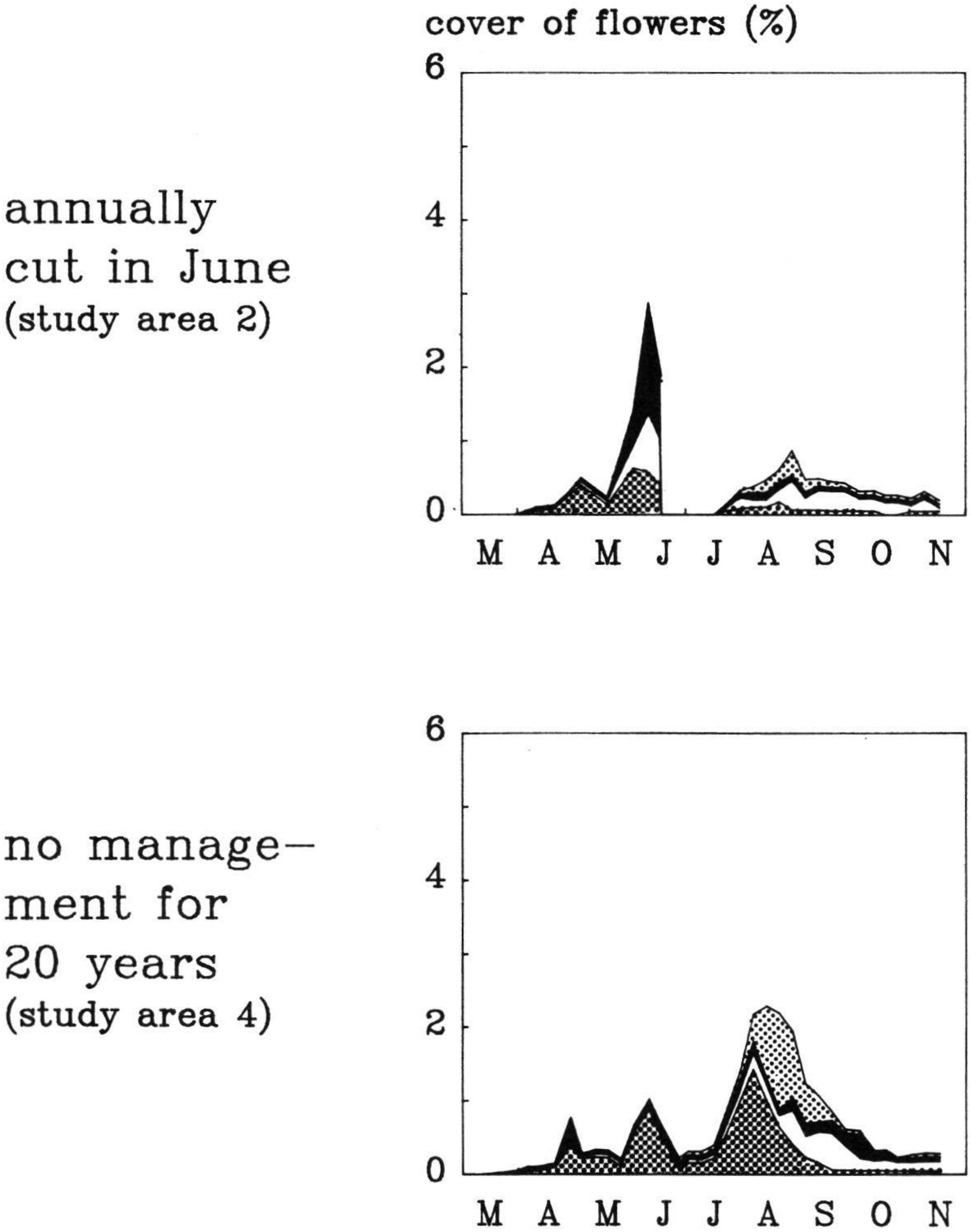


Fig. 61. Synthetic colour diagrams of two successional stages of *Mesobrometum* grassland showing the proportion of different flower colours in the course of the year 1978. (Three samples of 50 m^2 each were considered per study area).

yellow white blue red

succession proceeds. The variance of the 1 m^2 data is equal to 6 for the annually cut area (study area 2), but equal to 67 for the area unused for 20 years (study area 4), the homogeneity decrease in the stand apparently following the advance of succession.

Synthetic colour diagrams

The synthetic colour diagrams show the proportion of different flower colours throughout the year, the sum of the cover percentages being plotted against time. The colour peak in the annually cut study area 2 occurred in mid June, but corresponded to early August in the study area 4, unmanaged for almost 20 years (Fig. 61). In 1978, when study area 1 was experimentally managed for the first time, the diagrams of differently treated plots were quite similar in shape, distinct colour peaks invariably occurring in mid June (Fig. 62). However, only two years later, the diagrams distinctly reflected the different treatments: within plots subject to burning in March as well as those unmanaged from 1978 onwards, the June peak was no longer seen, but instead an August peak appeared. Cutting in October brought about two colour peaks, a higher one corresponding to early June and a lower one to mid August. On the other hand, cutting in mid June i.e. the control treatment resulted in quite stable phenological behaviour in the period 1978-1980 (Fig. 62). The results obtained within study area 2 were generally in accordance with these observations (Fig. 63).

The phenological response of whole communities was less notable within the study areas 3 and 4 than within the study areas 1 and 2 but it was nevertheless recognizable (Figs 64, 65).

4.2.2. *Mathematically processed phytosociological data*

As far as phytosociological data (relevés) is concerned, qualitative alterations of the vegetation due to the different treatments were not clearly recognizable to date. Within the areas studied, different surfaces subjected to a given treatment did not show greater similarity to each other within the first three or four years of experimental management when presence-absence data was used for analysis. No distinct developmental trends were observable as exemplified by the study areas 1, 2 and 4 (Figs 66, 67, 68).

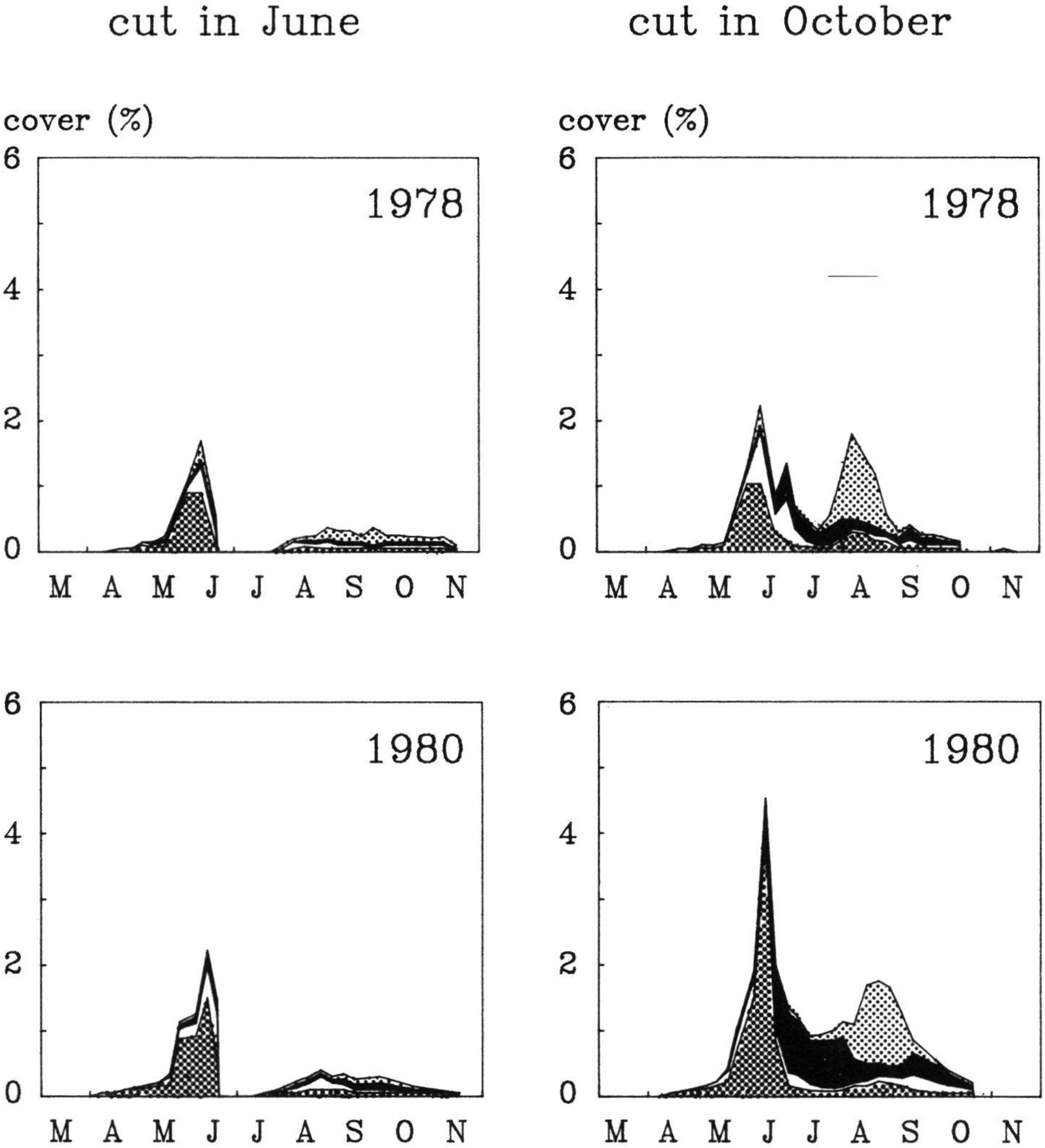
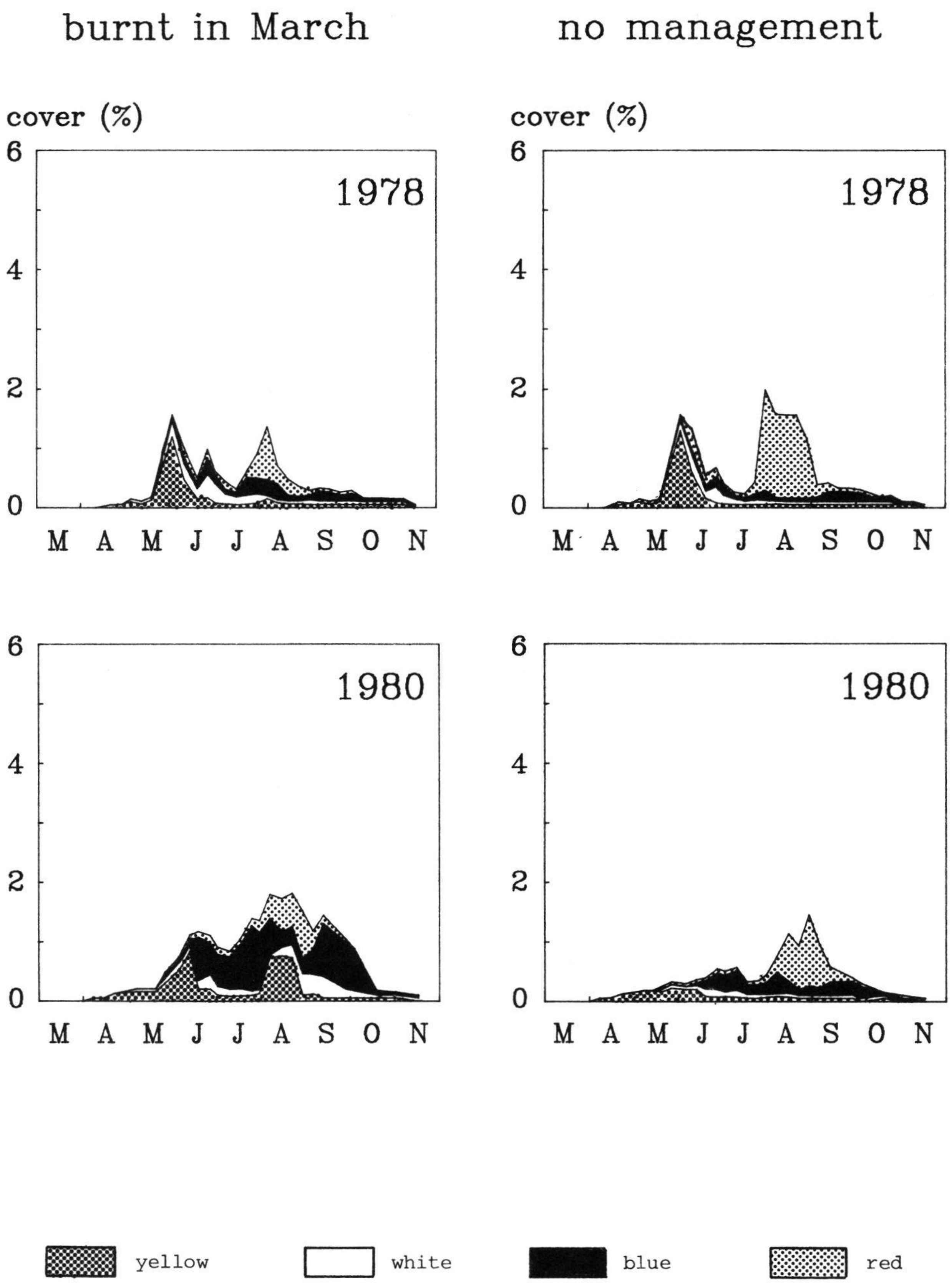


Fig. 62. Study area 1: development of the synthetic colour diagrams of surfaces under different treatments. Years represented: 1978, 1980.



burnt in March
no management
cover (%)
cover (%)
6
4
2
0
1978
1978
1980
1980
M A M J J A S O N
M A M J J A S O N
M A M J J A S O N
M A M J J A S O N
yellow
white
blue
red

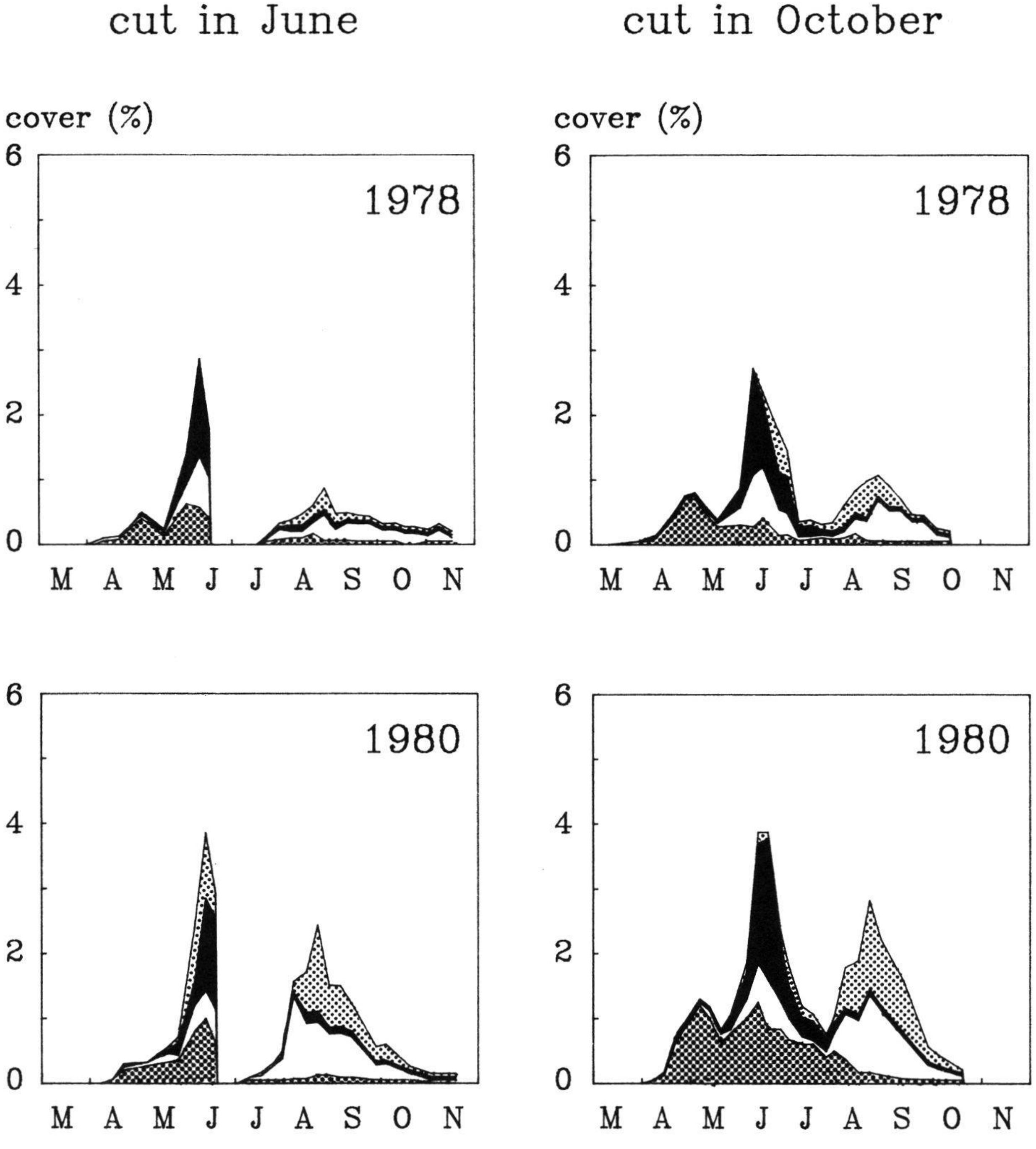
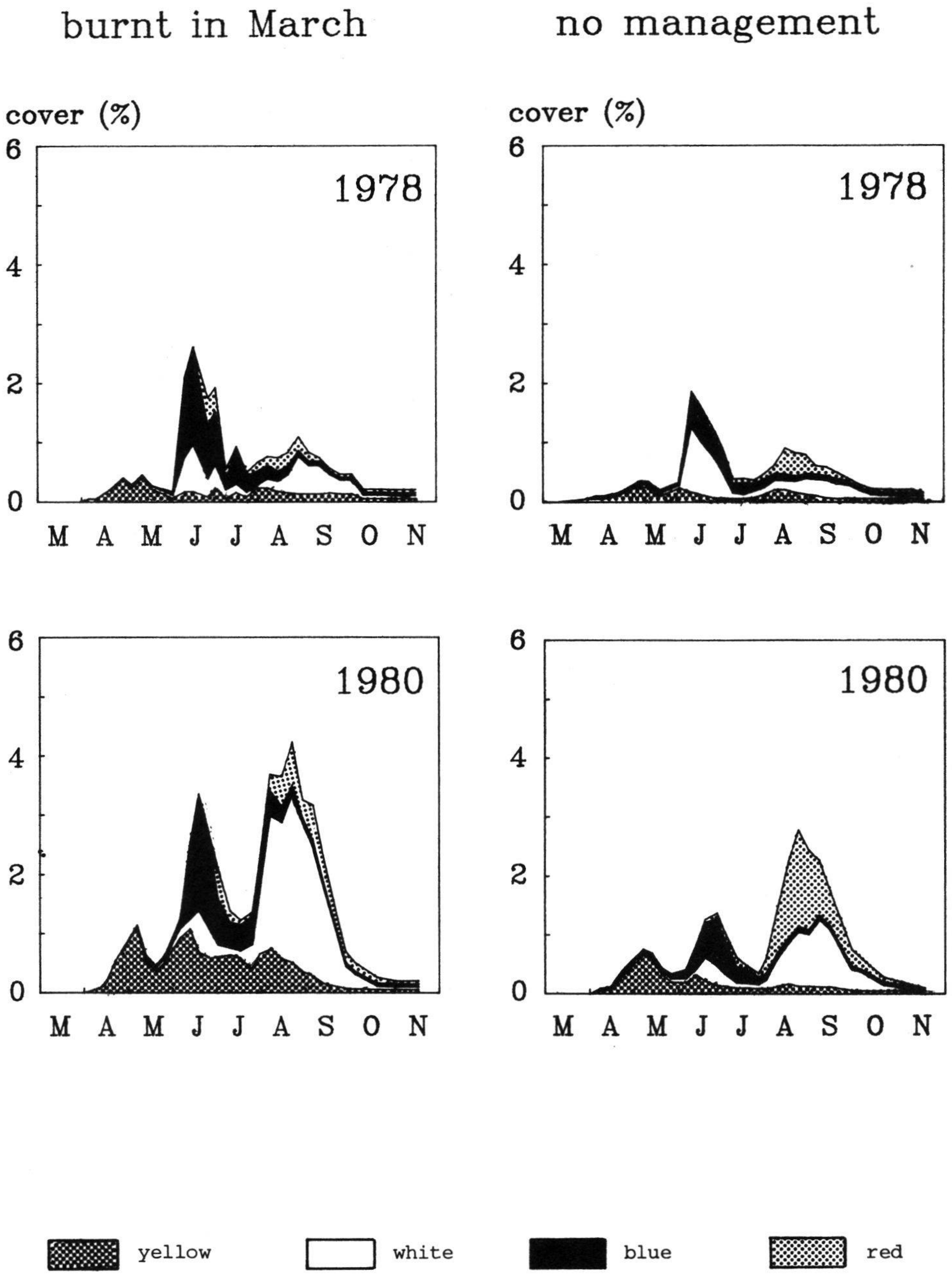


Fig. 63. Study area 2: development of the synthetic colour diagrams of surfaces under different treatments. Years represented: 1978, 1980.


burnt in March
no management
cover (%)
6
4
2
0
1978
1980
M A M J J A S O N
yellow
white
blue
red

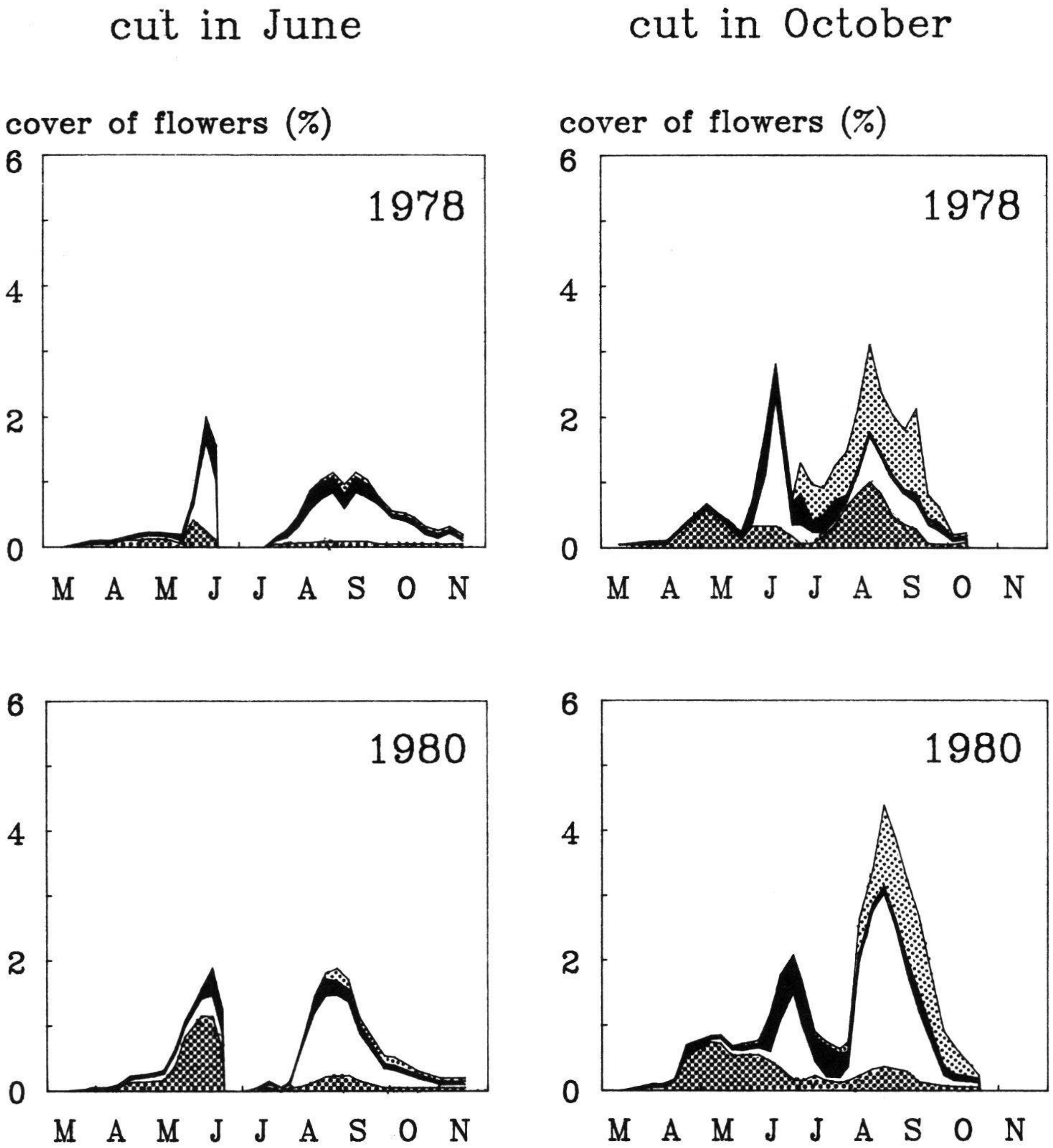
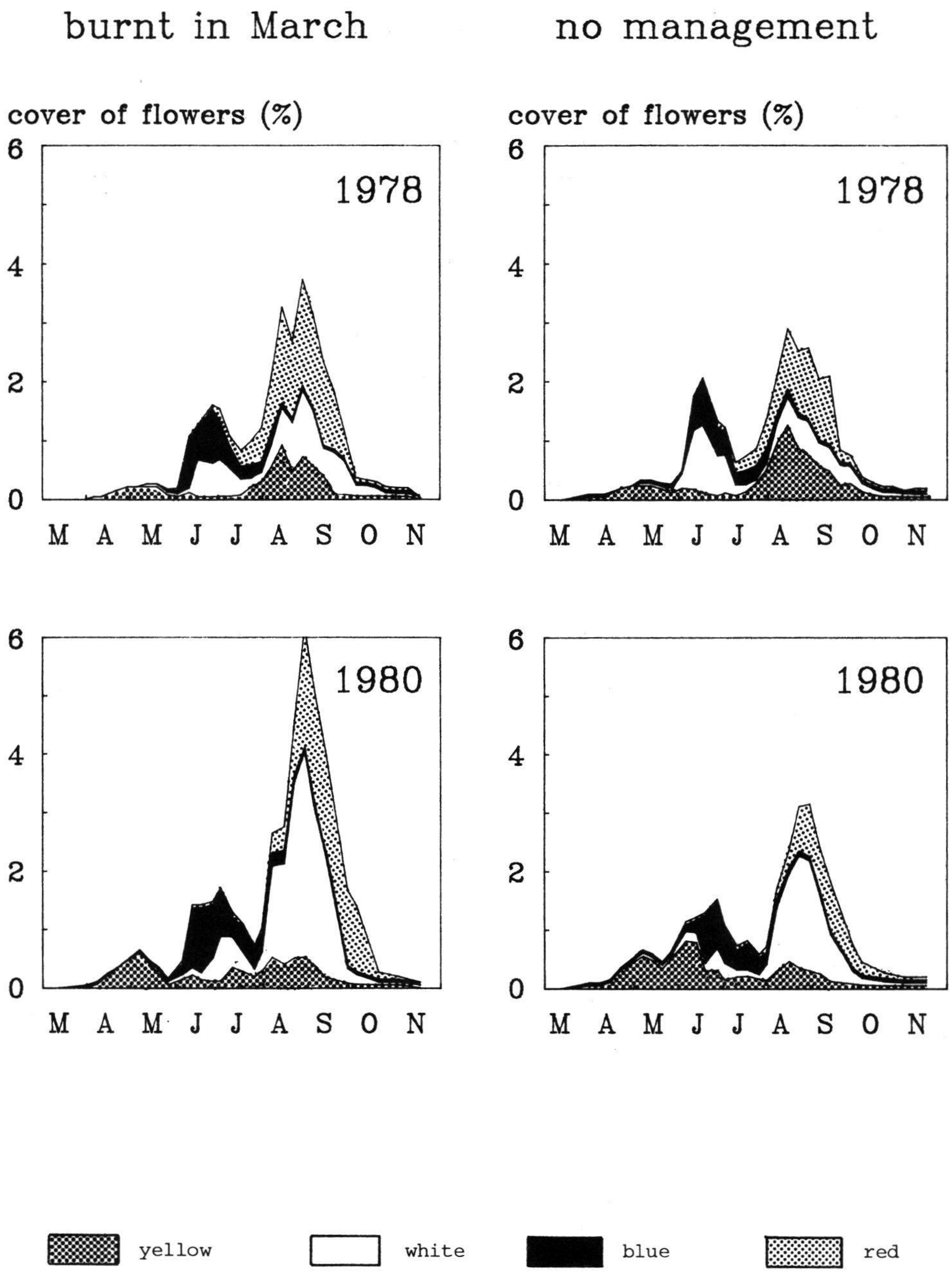


Fig. 64. Study area 3: development of the synthetic colour diagrams of surfaces under different treatments. Years represented: 1978, 1980.



burnt in March
no management
cover of flowers (%)
cover of flowers (%)
6
4
2
0
1978
1978
1980
1980
M A M J J A S O N
M A M J J A S O N
M A M J J A S O N
M A M J J A S O N
yellow
white
blue
red

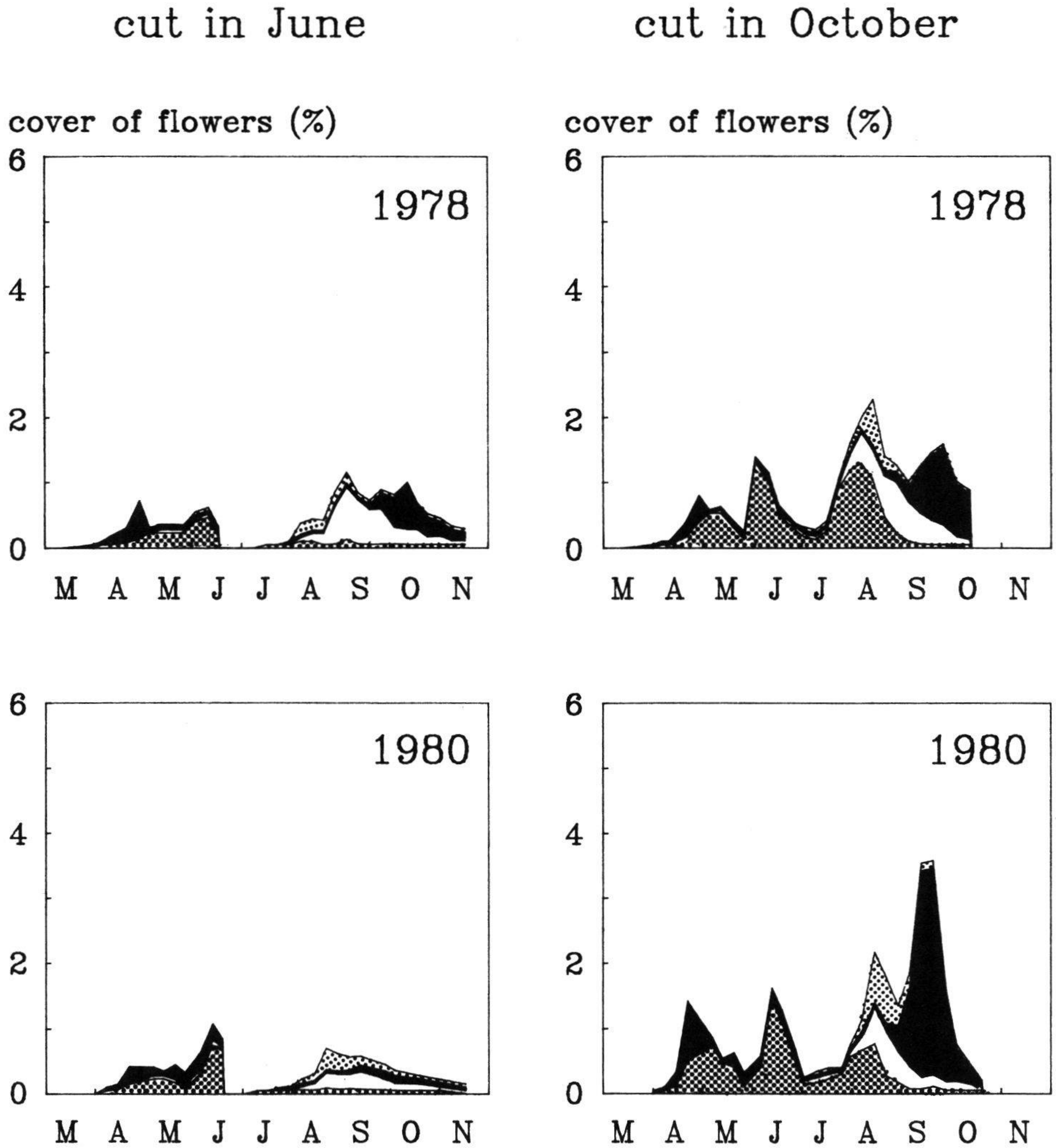
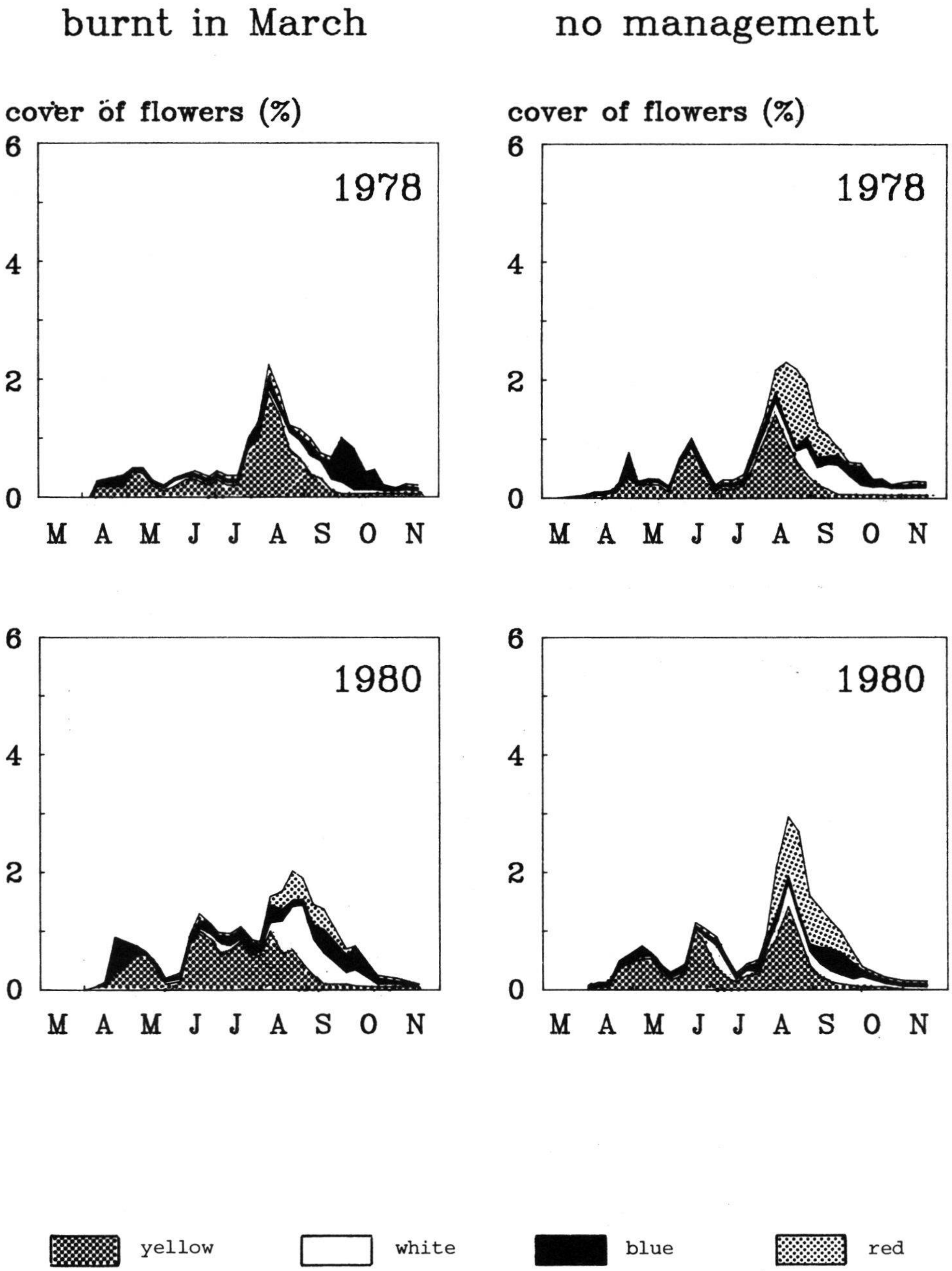


Fig. 65. Study area 4: development of the synthetic colour diagrams of surfaces under different treatments. Years represented: 1978, 1980.


burnt in March
no management
cover of flowers (%)
cover of flowers (%)
6
4
2
0
1978
1978
1980
1980
M A M J J A S O N
M A M J J A S O N
M A M J J A S O N
M A M J J A S O N
yellow
white
blue
red

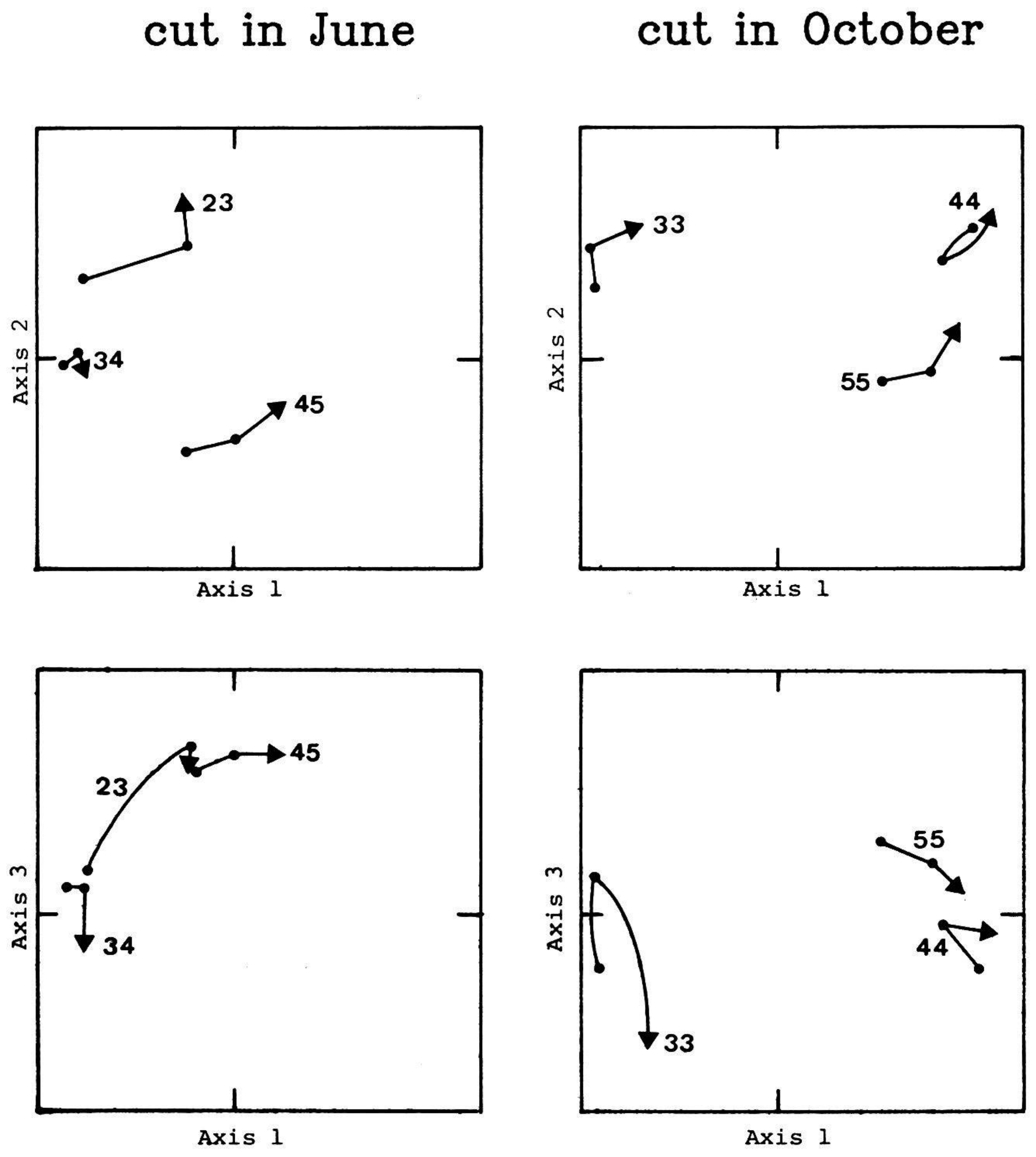


Fig. 66. Study area 1. Ordination of qualitative (presence-absence) vegetation data by principal component analysis. Observation period: 1978-1980.

The positions of the relevés are represented in separate graphs for each treatment. Numbers refer to the surfaces.

Top : Axis 1 and 2
Bottom: Axis 1 and 3

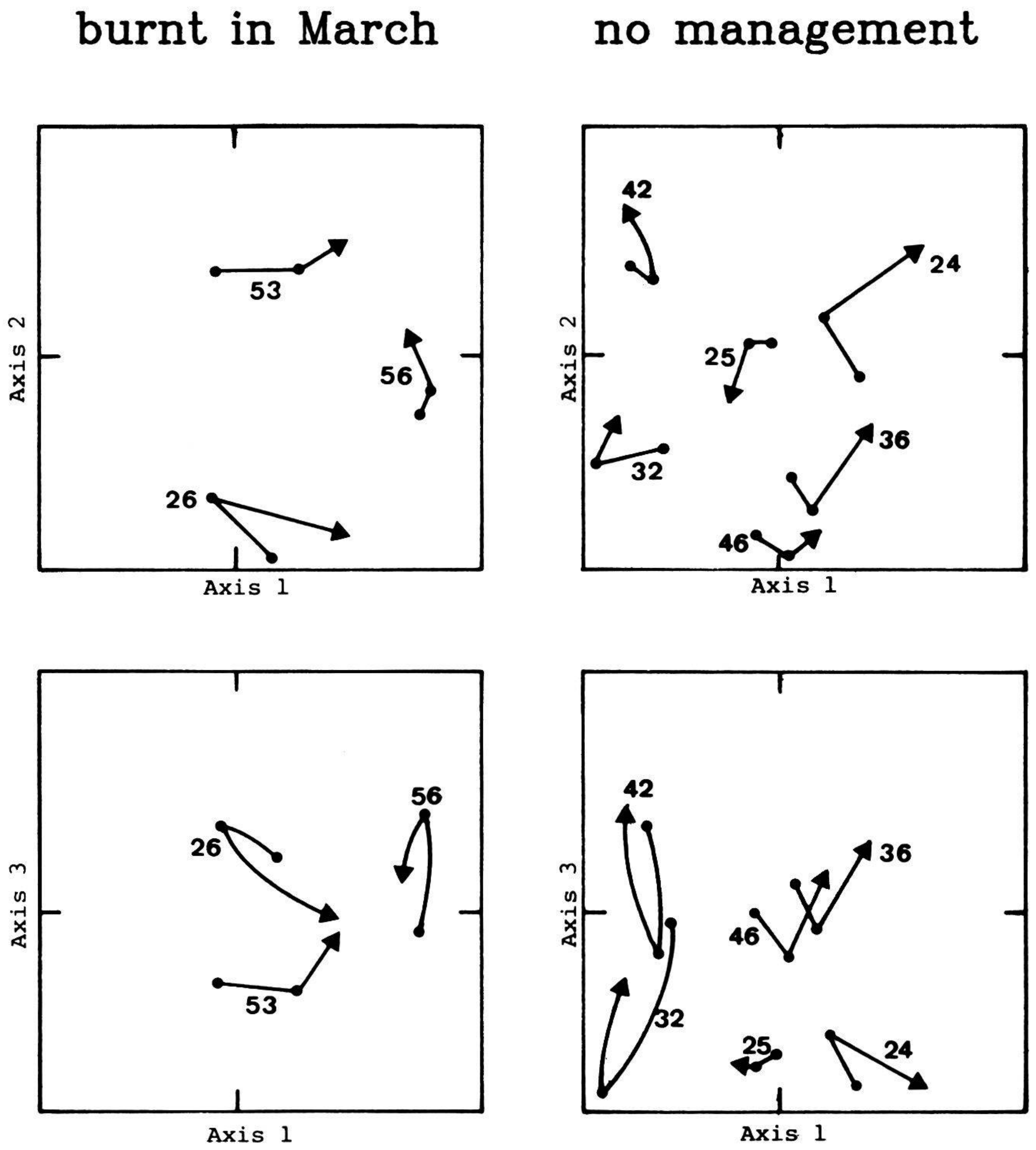


Fig. 66 (continued). Axis 1: percentage of variation accounted for: 10.48%
range of co-ordinates: -1.84 to 2.18

Axis 2: percentage of variation accounted for: 7.70%
range of co-ordinates: -1.98 to 2.04

Axis 3: percentage of variation accounted for: 7.34%
range of co-ordinates: -1.89 to 2.13

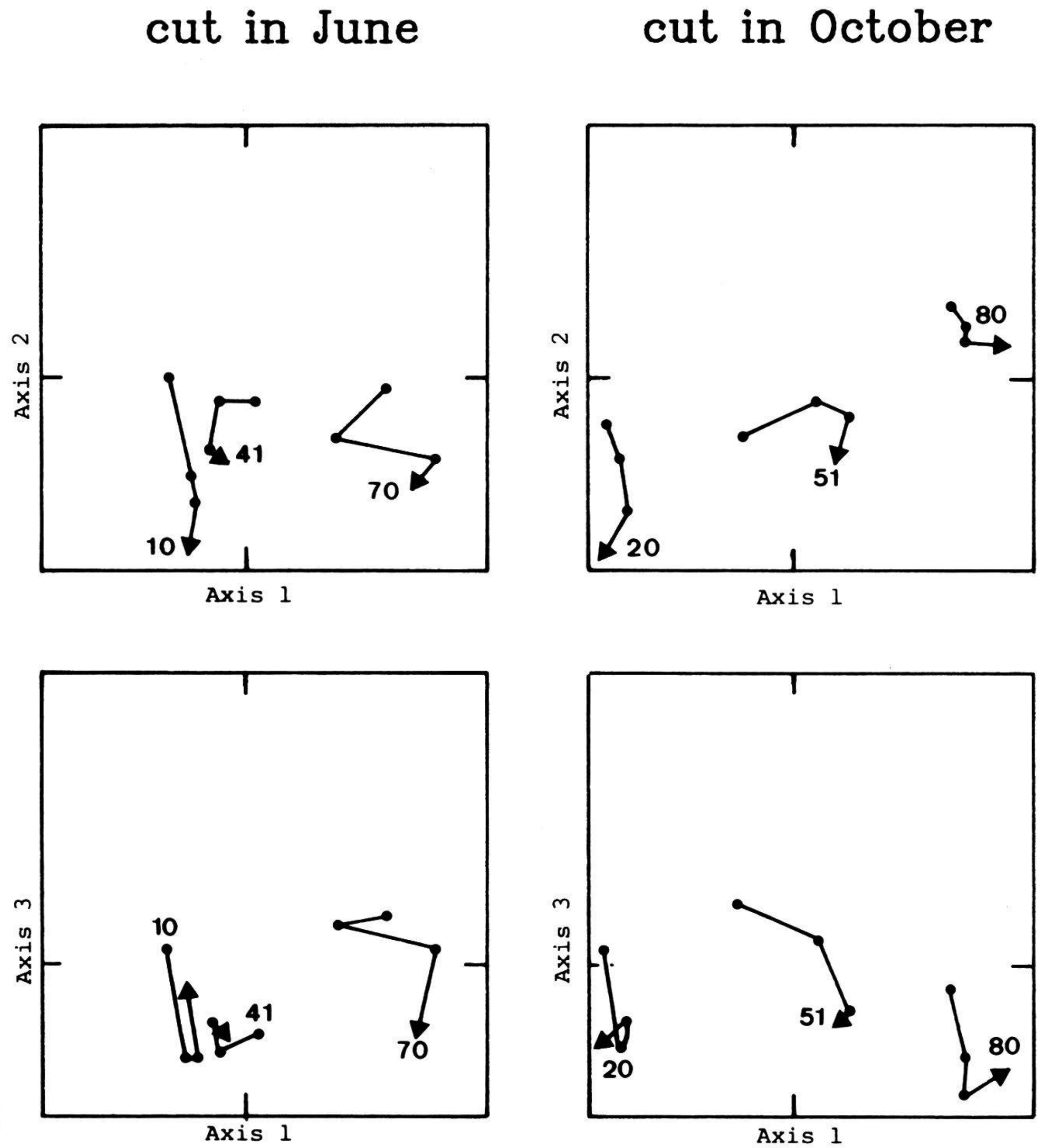


Fig. 67. Study area 2. Ordination of qualitative (presence-absence) vegetation data by principal component analysis. Observation period: 1977-1980.

The positions of the relevés are represented in separate graphs for each treatment. Numbers refer to surfaces.

Top : Axis 1 and 2
Bottom: Axis 1 and 3

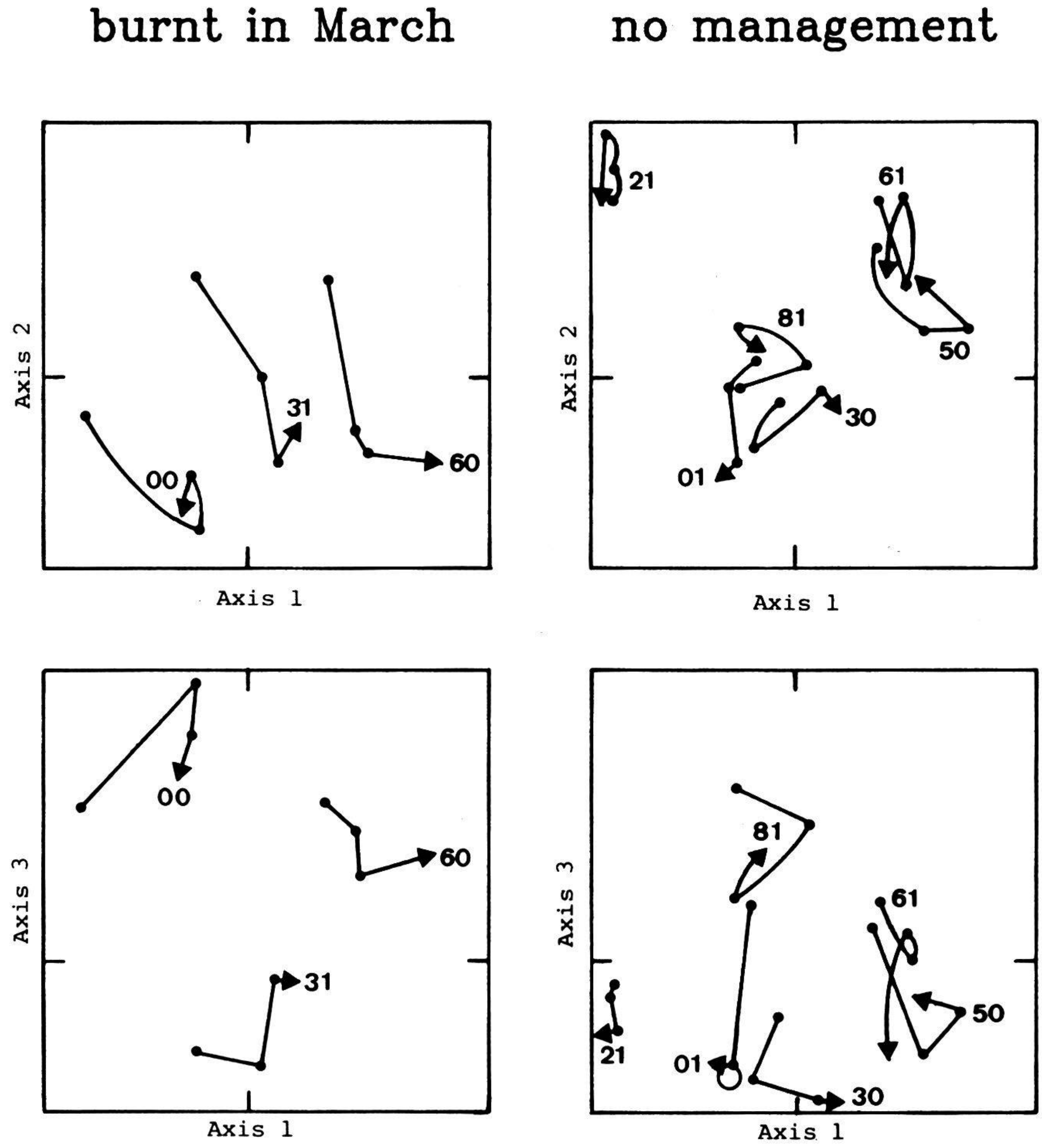


Fig. 67 (continued). Axis 1: percentage of variation accounted for: 10.87%
range of co-ordinates: -1.89 to 2.07

Axis 2: percentage of variation accounted for: 7.99%
range of co-ordinates: -1.70 to 2.26

Axis 3: percentage of variation accounted for: 7.46%
range of co-ordinates: -1.36 to 2.60

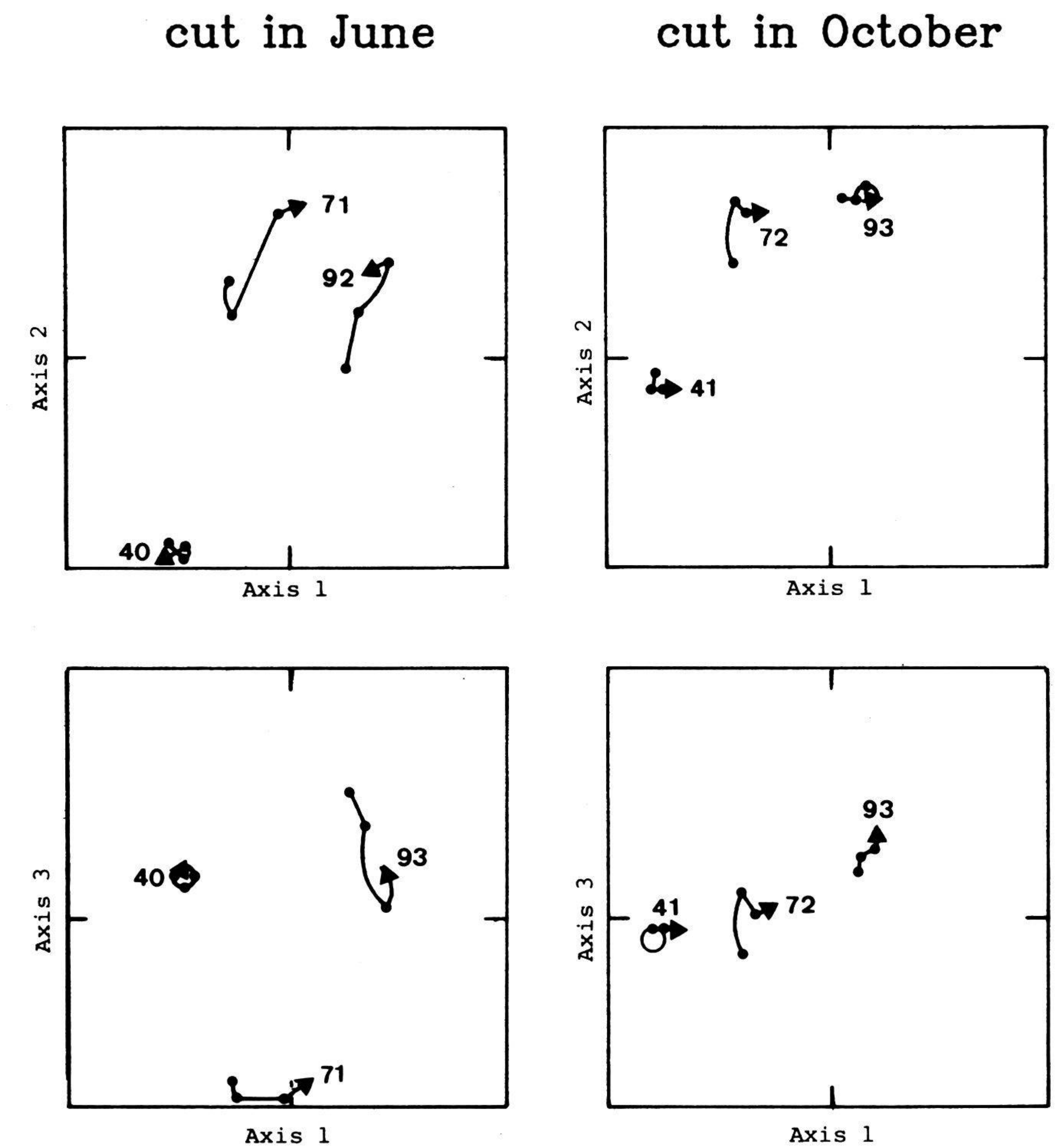


Fig. 68. Study area 4. Ordination of qualitative (presence-absence) vegetation data by principal component analysis. Observation period: 1977-1980.

The positions of the relevés are represented in saparate graphs for each treatment. Numbers refer to surfaces.

Top : Axis 1 and 2
Bottom: Axis 1 and 3

burnt in March   no management

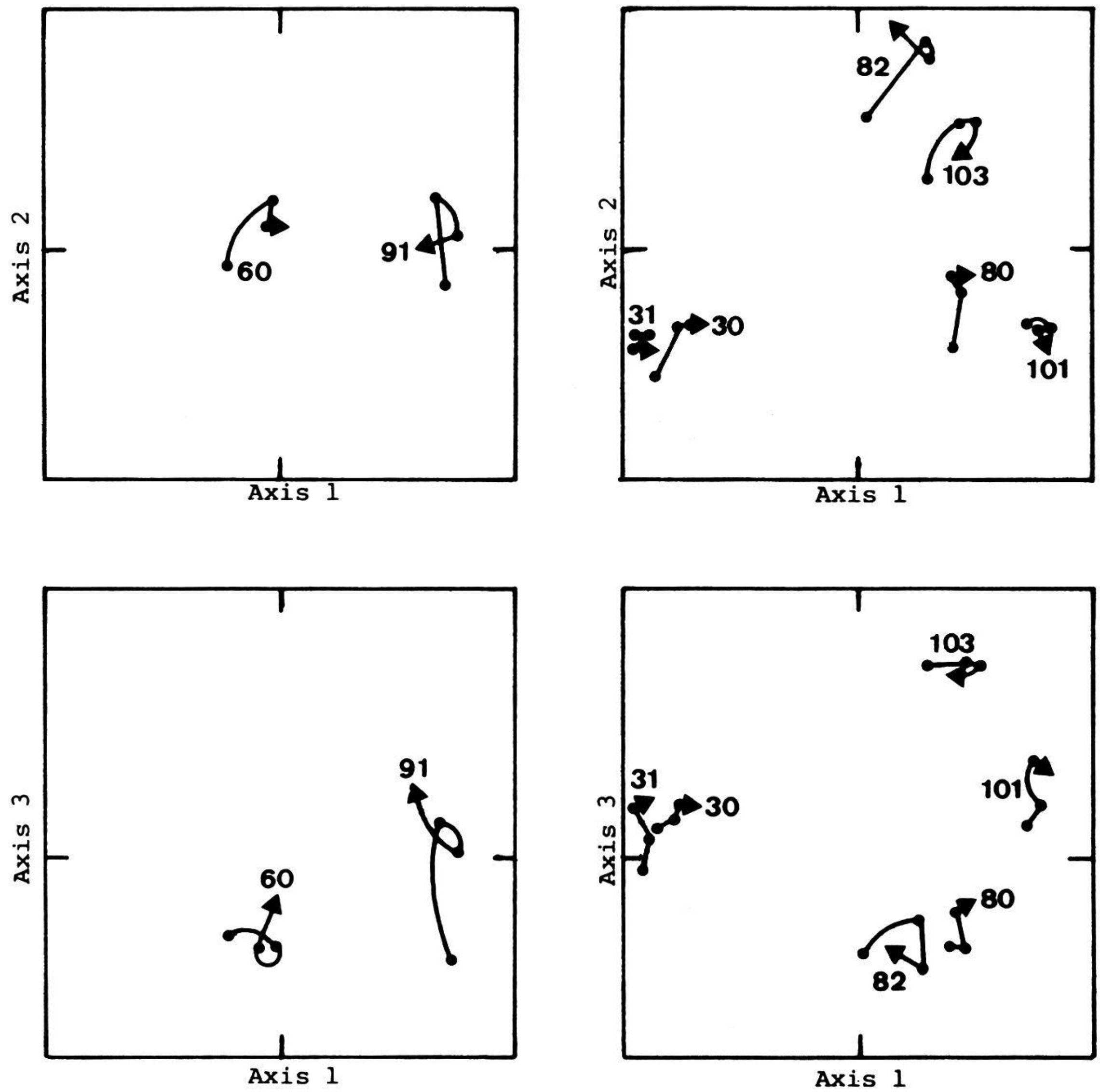


Fig. 68 (continued). Axis 1: percentage of variation accounted for: 14.72%
range of co-ordinates: -2.59 to 2.40

Axis 2: percentage of variation accounted for: 12.06%
range of co-ordinates: -2.45 to 2.54

Axis 3: percentage of variation accounted for: 6.24%
range of co-ordinates: -2.10 to 2.89

On the contrary, mathematical analysis of the relevés taking into account the quantity of the different species (cover-percentage) was found to reveal some developmental patterns. It should be noted, however, that the observable trends appeared to be caused mainly by cover alterations in only very few species.

As far as study area 1 is concerned, the ordination of the relevés by principal component analysis is presented in Fig. 69 and interpreted in Table 8. The first axis mainly reflects cover alterations of *Camptothecium lutescens*, the second axis those of *Bromus erectus* and the third axis those of *Mnium rostratum*. Burning in March was found to damage the bryophytes towards extinction, whereas the influence of the other treatments upon the bryophytes was far less remarkable (Figs 70, 71). The cover of *Bromus erectus* remained relatively stable within the control plots cut in mid June, decreased moderately in surfaces cut in October and quite markedly in those subject to burning, whereas a distinct increase was observed within unmanaged plots (Fig. 29).

As far as study area 2 is concerned, the ordination of the relevés by principal component analysis is presented in Fig. 73 and interpreted in Table 9. The first axis primarily reflects cover alterations of *Thuidium abietinum*, the second axis those of *Festuca ovina* and the third axis mainly those of *Bromus erectus* but also to some extent those of *Festuca ovina*. The cover of *Thuidium abietinum* remained stable within plots subject to cutting in October, increased slightly in those cut in June and decreased slightly in unmanaged surfaces, whereas burning in March was found to severely damage this species (Fig. 72). The cover of *Festuca ovina* increased quite remarkably within the unmanaged plots, decreased moderately in burnt surfaces but only slightly decreased within the plots subject to one of the other treatments (Fig. 74). *Bromus erectus* behaved in almost the same way exhibiting an increase of the cover within unmanaged plots and a decrease in the otherwise treated surfaces (Fig. 75).

The relevés taken within the study areas 3 and 4 for the most part did not to date reflect any quantitative alteration of the vegetation due to different treatments; the only exceptions were the burnt surfaces where the bryophytes were apparently severely damaged (Figs 76, 78, 79). As far as study area 4 is concerned, the ordination of the relevés by principal component analysis is presented in Fig. 77 and interpreted in Table 10. The first axis mainly reflects cover alterations of the bryophyte *Rhytidium rugosum* and also to some extent those of *Thuidium abietinum*, the second axis primarily those of *Thuidium abietinum* and partly those of *Hylocomium splendens*, whereas the third axis chiefly reflects cover alterations of *Carex montana* and *Rhytidiadelphus triquetrus*.

On the whole, the observations described above corroborate the hypothesis that changes in the phenological behaviour precede by far the actual physical alterations of a given community. The analysis of phenological records yielded many more distinct results than phytosociological data gathered during the same observation period. In this respect phenological data seems to have a positive advantage over the phytosociological records.

Table 8. Interpretation of the scatter diagrams of study area 1 (Fig. 69)

Treatment	Cover development	
	Camptothecium lutescens (Axis 1)	*Bromus erectus* (Axis 2)
cutting in June	∿	=
cutting in October	↓	↓↓
burning in March	↓↓↓	↓↓
no management	(↓)	↑↑

↑, ↑↑, ↑↑↑: increase (slight, moderate, marked)

↓, ↓↓, ↓↓↓: decrease (slight, moderate, marked)

∿ : fluctuation

= : no change

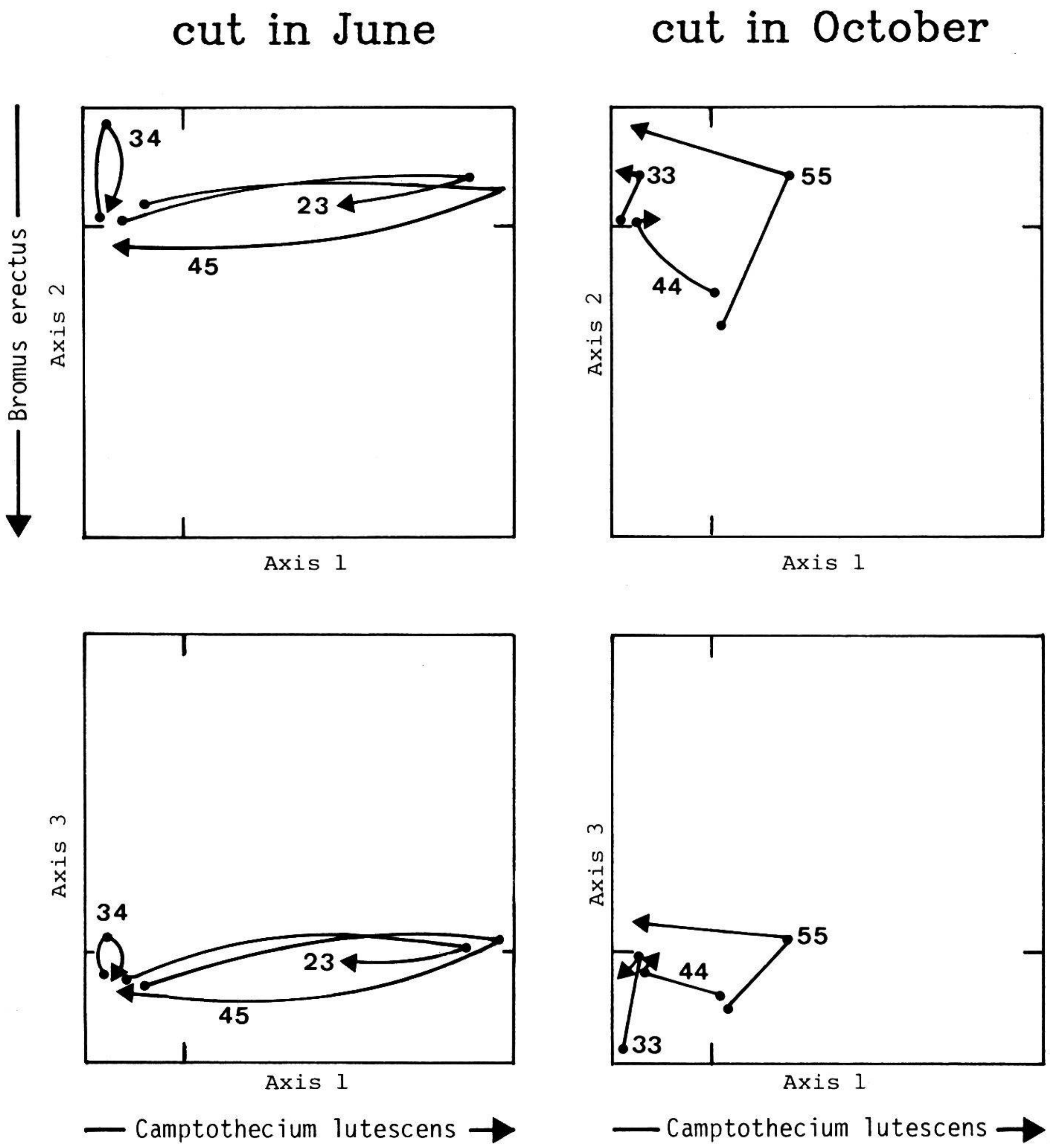


Fig. 69. Study area 1. Ordination of quantitative (cover-percentage) vegetation data by principal component analysis. Observation period: 1978-1980.

The positions of the relevés are represented in separate graphs for each treatment. Numbers refer to the surfaces.

Species highly correlated with an ordination axis are indicated; an arrow shows the direction from low to high cover percentage.

Top: Axis 1 and 2 Bottom: Axis 1 and 3

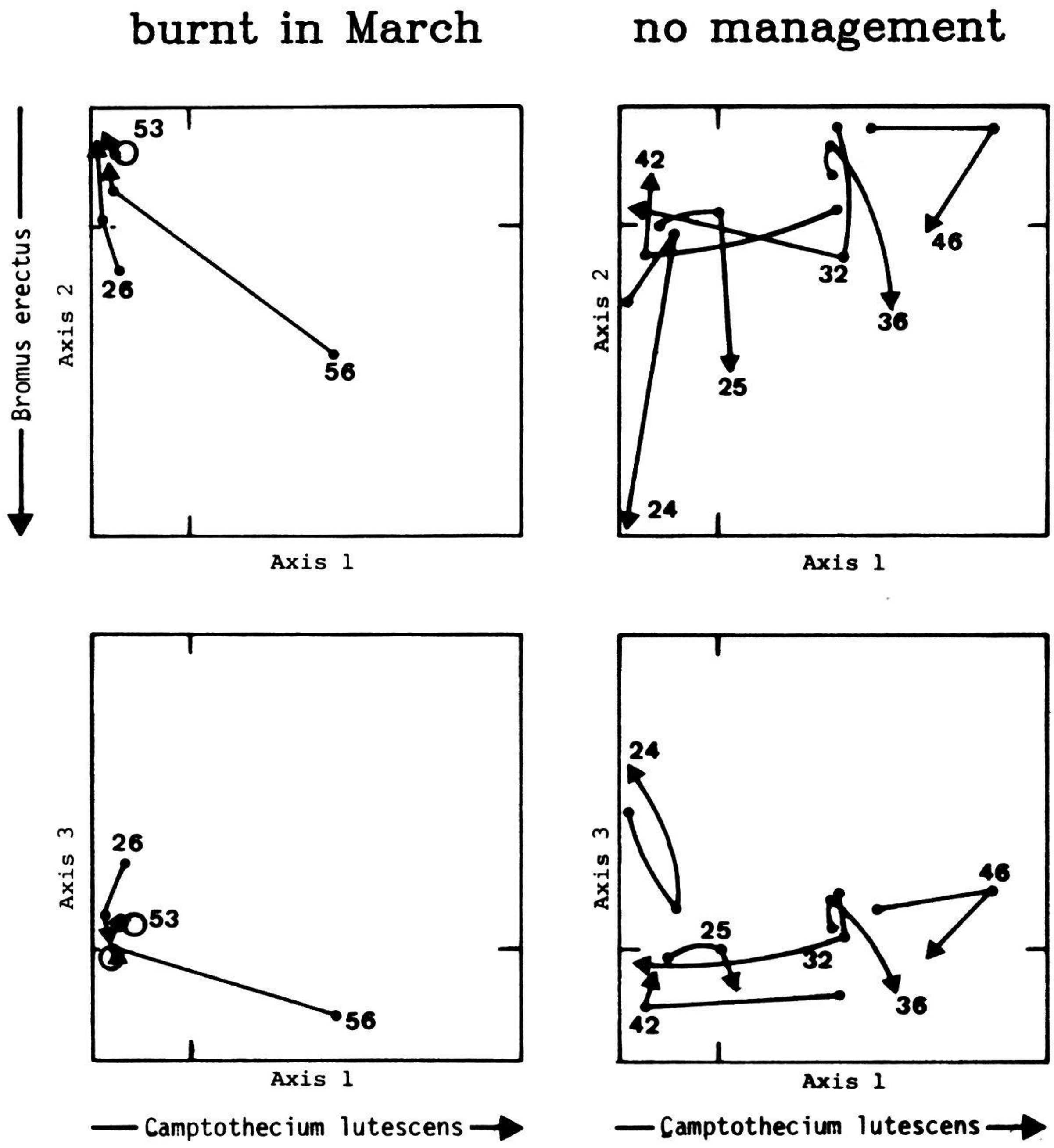


Fig. 69 (continued). Axis 1: percentage of variation accounted for: 43.19%
range of co-ordinates: -256.24 to 772.64

Axis 2: percentage of variation accounted for: 18.55%
range of co-ordinates: -768.15 to 260.73

Axis 3: percentage of variation accounted for: 8.10%
range of co-ordinates: -264.10 to 764.78

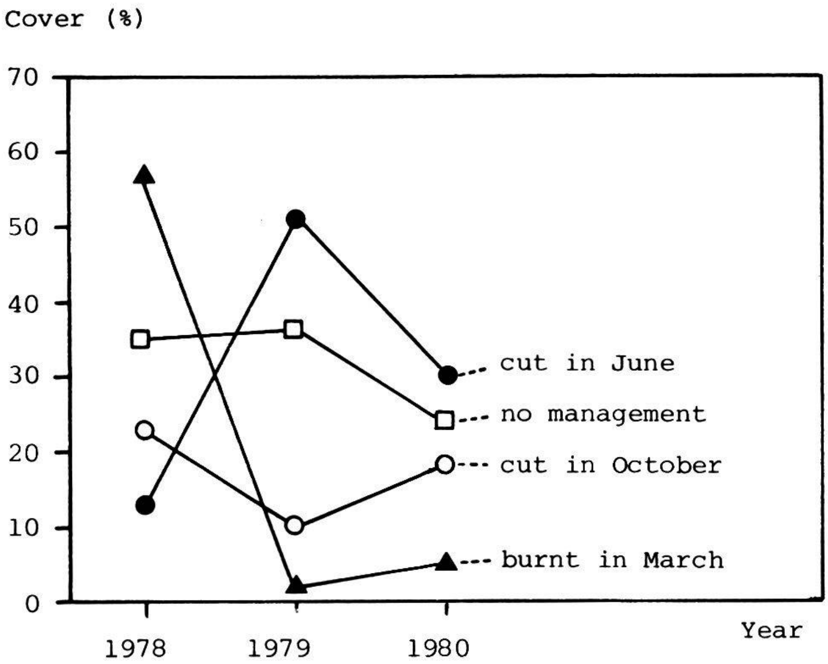


Fig. 70. Bryophytes within study area 1: development of the cover under different treatments for the period 1978-1980. (Ten relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m^2 each were evaluated).

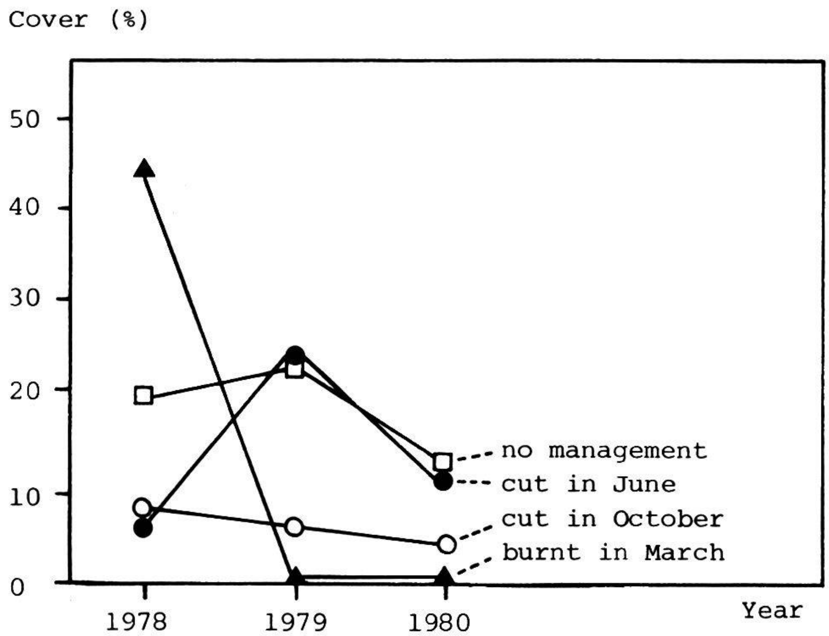


Fig. 71. *Camptothecium lutescens* within study area 1: development of the cover under different treatments for the period 1978-1980. (Ten relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m^2 each were evaluated).

Table 9. Interpretation of the scatter diagrams of study area 2 (Fig. 73).

Treatment	Cover development		
	Thuidium abietinum (Axis 1)	*Festuca ovina* (Axis 2, Axis 3)	*Bromus erectus* (Axis 3)
cutting in June	↑	↓	↓
cutting in October	∿ =	∿ (↓)	↓
burning in March	↓↓↓	↓↓	↓↓
no management	↓	↑↑	↑↑↑

↑, ↑↑, ↑↑↑: increase (slight, maderate, marked)

↓, ↓↓, ↓↓↓: decrease (slight, moderate, marked)

∿ : fluctuation

= : no change

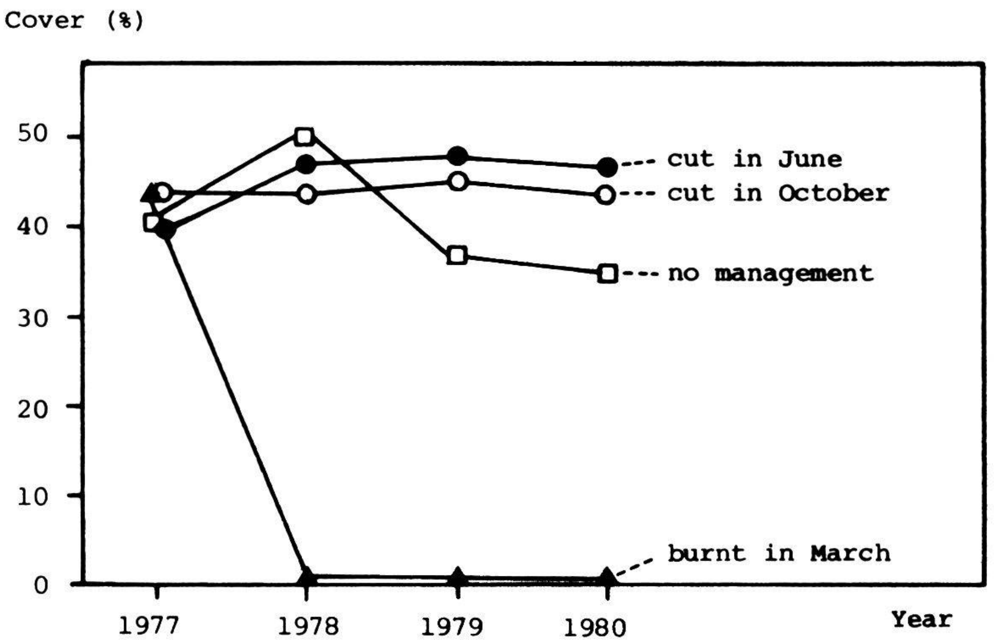


Fig. 72. *Thuidium abietinum* within study area 2: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

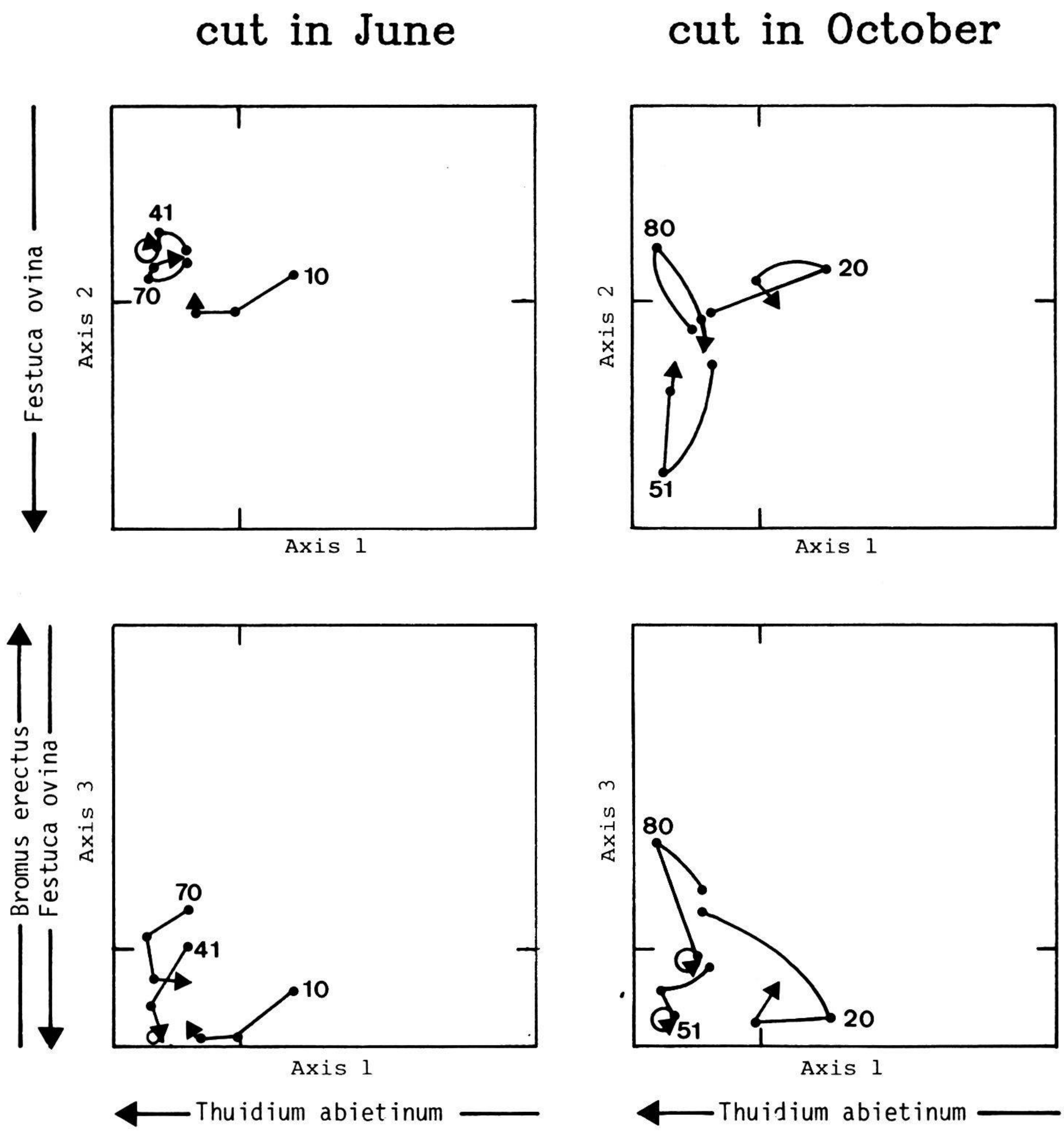


Fig. 73. Study area 2. Ordination of quantitative (cover-percentage) vegetation data by principal component analysis. Observation period: 1977-1980.

The positions of the relevés are represented in separate graphs for each treatment. Numbers refer to the surfaces.

Species highly correlated with an ordination axis are indicated; an arrow shows the direction from low to high cover percentage.

Top: Axis 1 and 2 Bottom: Axis 1 and 3

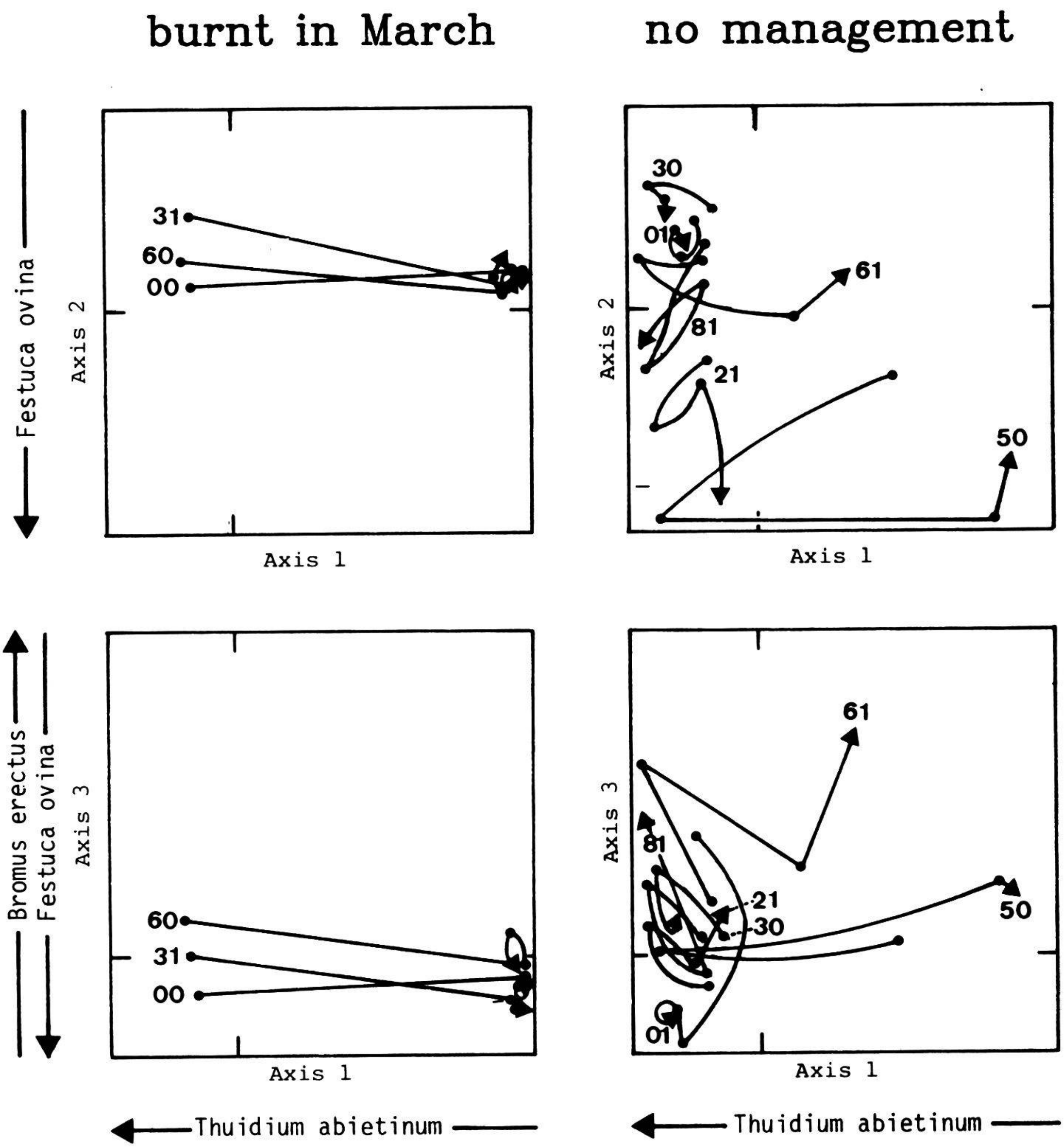


Fig. 73 (continued). Axis 1: percentage of variation accounted for: 51.37%
range of co-ordinates: -355.47 to 777.84

Axis 2: percentage of variation accounted for: 18.33%
range of co-ordinates: -601.48 to 531.84

Axis 3: percentage of variation accounted for: 12.28%
range of co-ordinates: -263.35 to 869.97

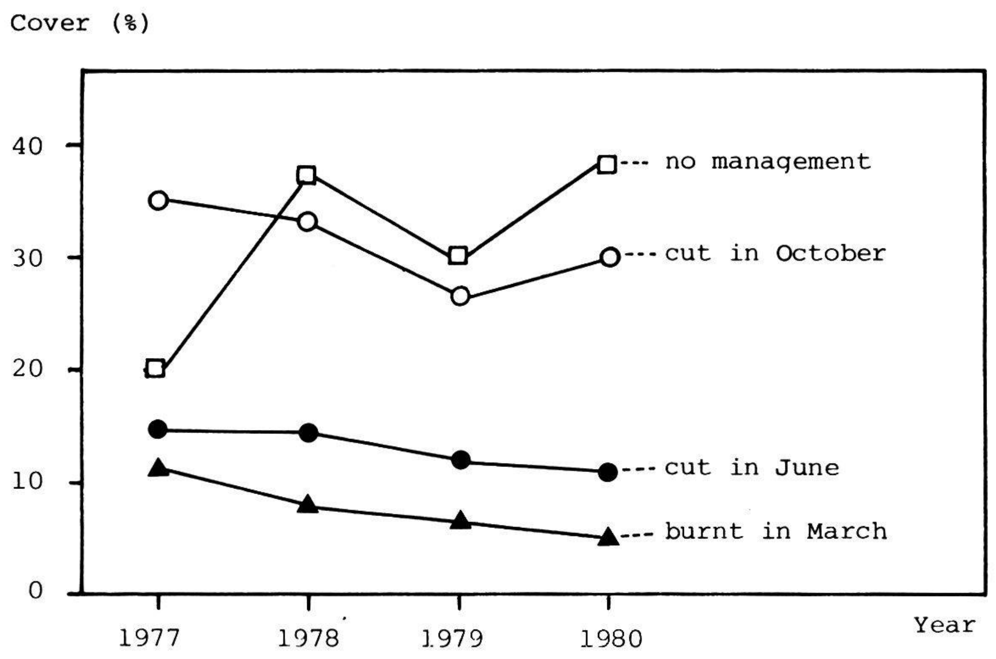


Fig. 74. *Festuca ovina* within study area 2: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

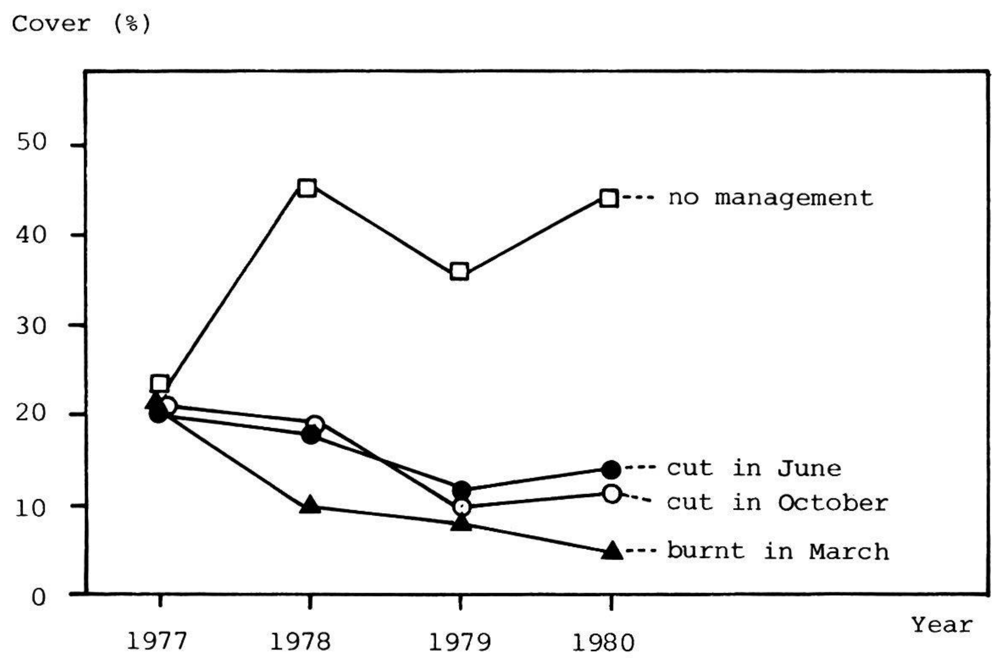


Fig. 75. *Bromus erectus* within study area 2: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

Table 10. Interpretation of the scatter diagrams of study area 4 (Fig. 77)

Treatment	Cover development		
	Rhytidium rugosum (Axis 1)	*Thuidium abietinum* (Axis 2, Axis 1)	*Hylocomium splendens* (Axis 2)
cutting in June	↑	↑	↓
cutting in October	↑↑	∿	-
burning in March	↓	↓↓↓	-
no management	↑↑	↑	↑

↑, ↑↑, ↑↑↑: increase (slight, moderate, marked)

↓, ↓↓, ↓↓↓: decrease (slight, moderate, marked)

∿ : fluctuation

= : no change

\- : no observation

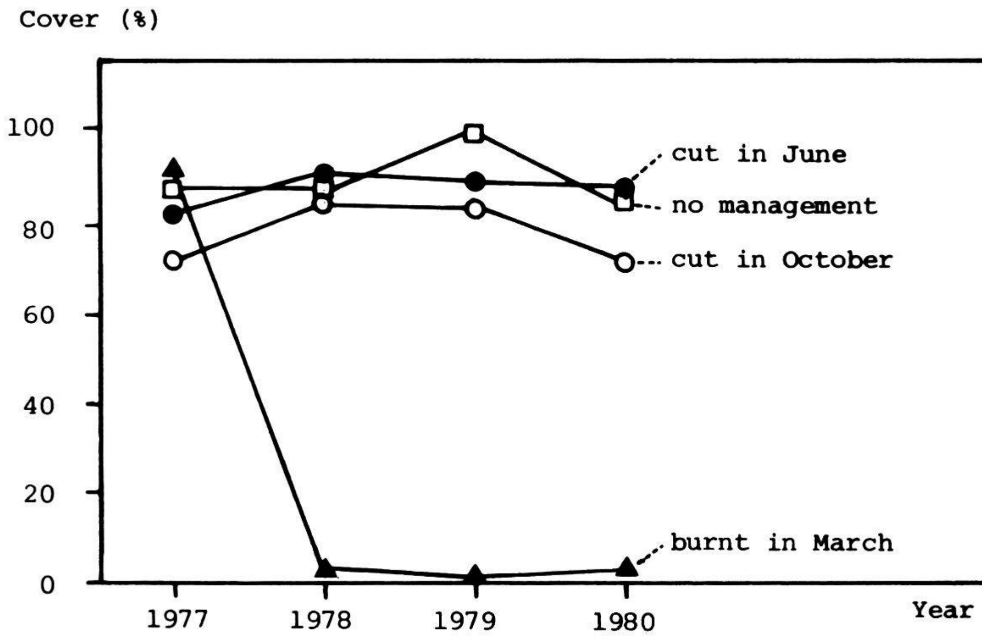


Fig. 76. Bryophytes within study area 4: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

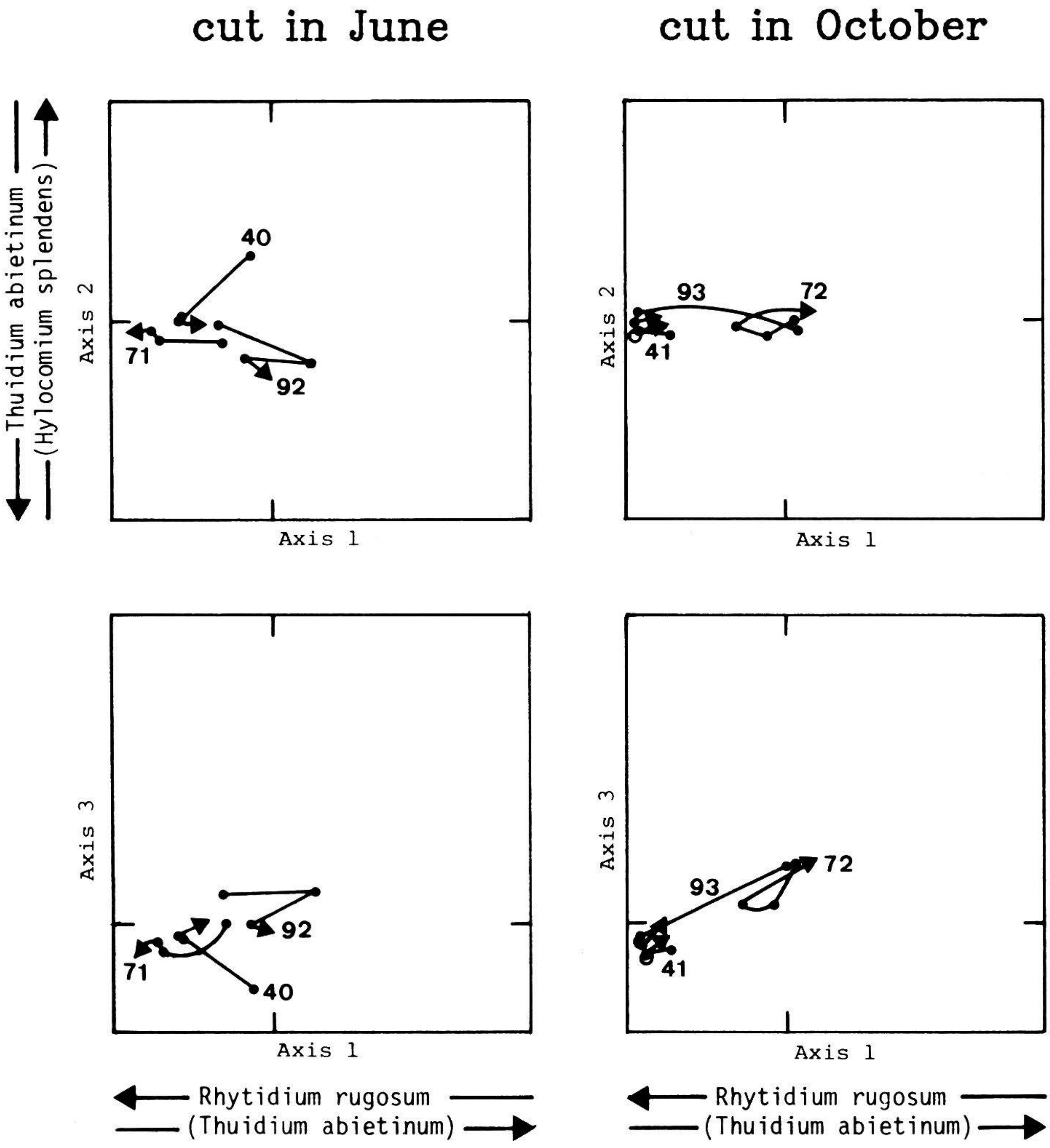


Fig. 77. Study area 4. Ordination of quantitative (cover-percentage) vegetation data by principal component analysis. Observation period: 1977-1980.

The positions of the relevés are represented in separate graphs for each treatment. Numbers refer to the surfaces.

Species highly correlated with an ordination axis are indicated; an arrow shows the direction from low to high cover percentage.

Top: Axis 1 and 2 Bottom: Axis 1 and 3

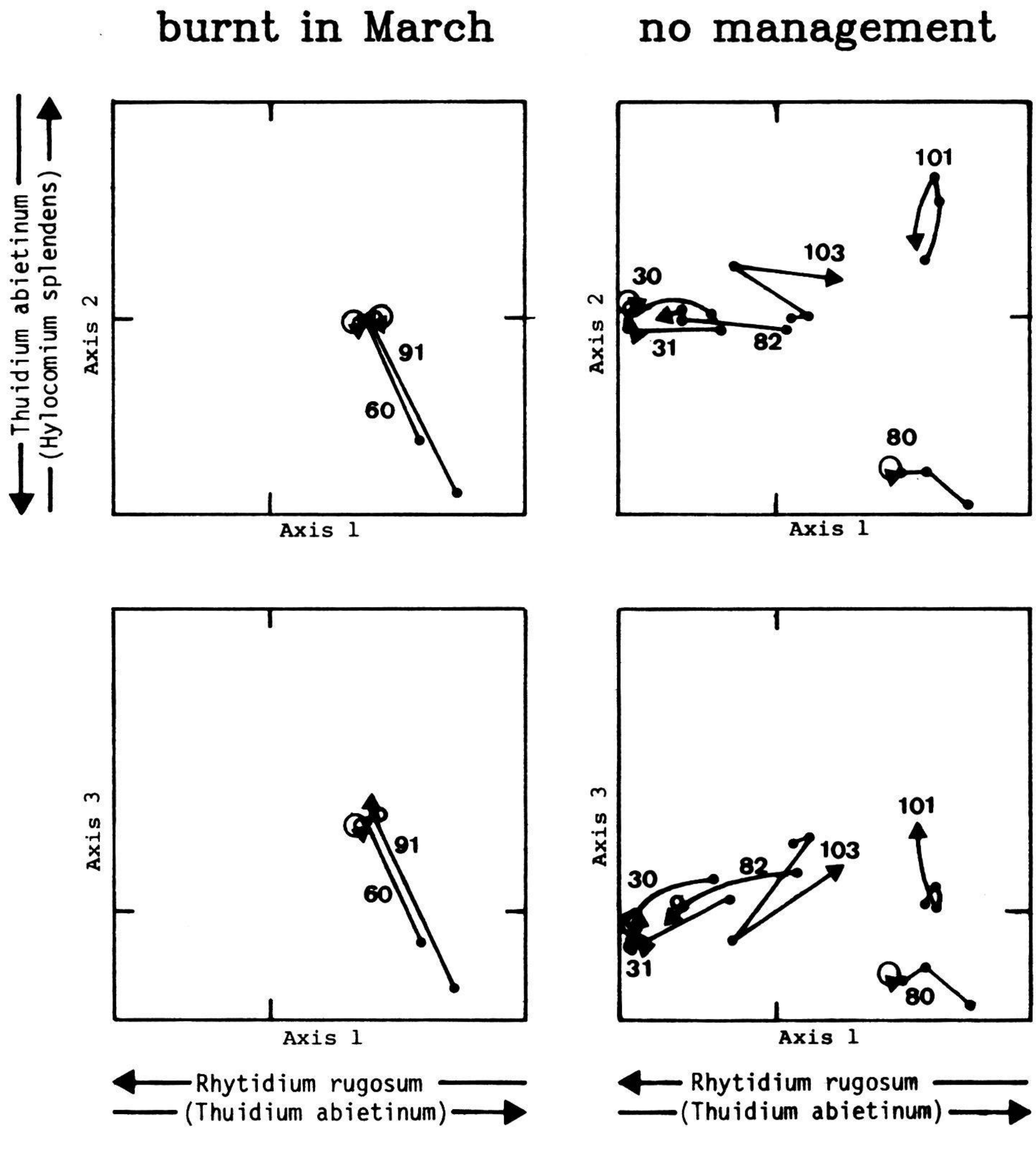


Fig. 77 (continued). Axis 1: percentage of variation accounted for: 47.75%
range of co-ordinates: -558.01 to 886.09

Axis 2: percentage of variation accounted for: 21.88%
range of co-ordinates: -684.67 to 759.43

Axis 3: percentage of variation accounted for: 8.44%
range of co-ordinates: -344.81 to 1099.29

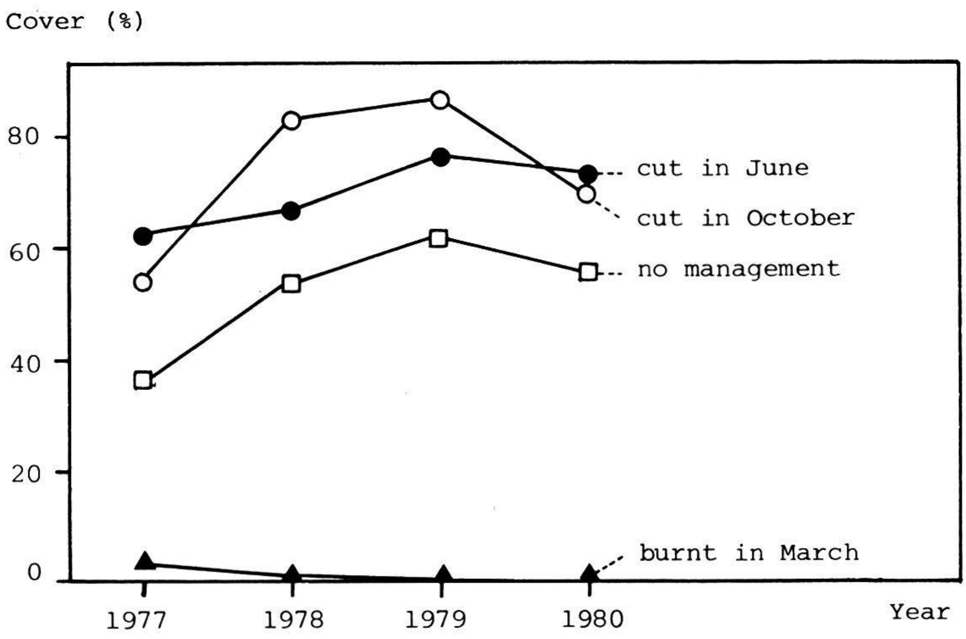


Fig. 78. *Rhytidium rugosum* within study area 4: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management' where six samples of 1 m^2 each were evaluated).

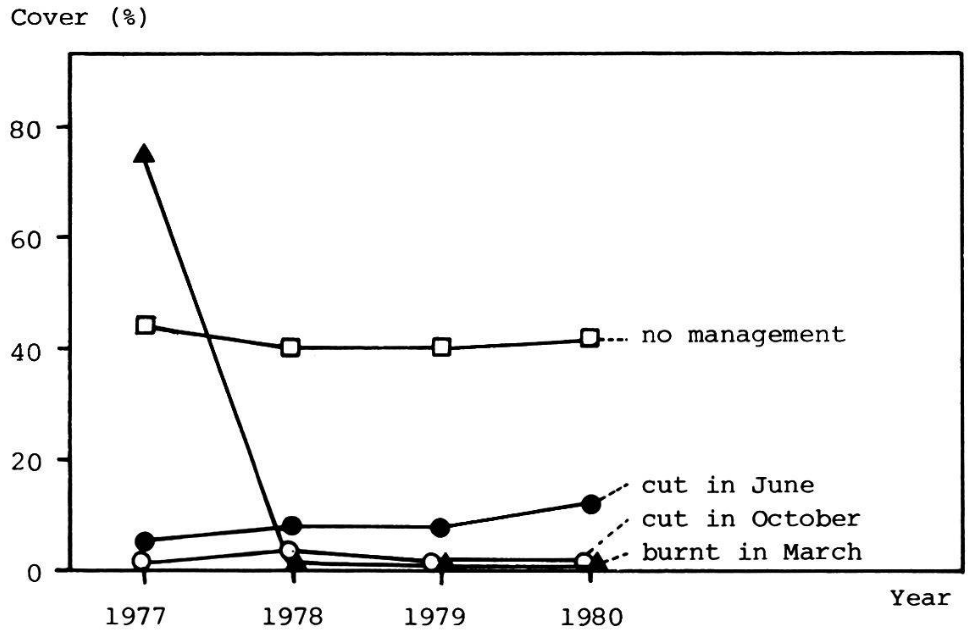


Fig. 79. *Thuidium abietinum* within study area 4: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m^2 each were considered per treatment, save for the condition 'no management where six samples of 1 m^2 each were evaluated).

5. Discussion

Based upon short-term phenological data, predictions concerning the future development of a particular species under given conditions are not infallible; the present study shows no consistent behaviour pattern emerging from observations collected through only one growing season. For instance, elimination of the generative phase in *Bromus erectus* and *Buphthalmum salicifolium* turned out to be unfavourable solely for the latter species, the former species remaining apparently undamaged. On the other hand, reproduction by seed in *Aster amellus* and *Pimpinella saxifraga* did not coincide with cutting in mid June but the performance of the former species weakened towards extinction, whereas the latter was not influenced to any great extent by this treatment. Burning in March did not affect any actual aspect of sexual reproduction in *Brachypodium pinnatum* yet proved to be of competitive advantage for this species. The uncertain indicative value of short-term phenological records undoubtedly results from an insufficient knowledge of the competitive abilities of given species as well as their reproductive strategies, balance between sexual and vegetative reproduction being of particular importance. Relationships between life strategies of some species inhabiting calcareous grassland, the communities in which they occur and the way in which the present grazing intensity influences the survival of populations were recently studied in Great Britain by BRADSHAW and DOODY (1978). Some species were found to reproduce solely by seed (e.g. *Draba incana, Polygala amarella, Viola rupestris, Potentilla crantzii, Primula farinosa*), others by seed and vegetative means (e.g. *Viola riviniana*) whereas some species reproduced only vegetatively (e.g. *Carex ericetorum, Gentiana rupestris, Viola rupestris x riviniana*). From the great variety of life strategies exhibited by these species, BRADSHAW and DOODY (1978) concluded that no single overall management would ensure the survival of them all; our present results corroborate these conclusions. The variable behavioural pattern noticed in calcareous grassland apparently also occurs in other ecosystems. Species growing in the herb layer of deciduous woodland reproduce in general by vegetative means (KNIGHT 1964, MORGAN 1971, WIGHAM 1974, PERSSON 1975, HUTCHINS and BARKHAM 1976); however, sexual reproduction was found to be much more important than vegetative reproduction to the success of *Allium ursinum* (ERNST 1979). According to BRAUN-BLANQUET (1964, p. 509), reproduction phenomena such as blossom formation and ripening or fruit are much less important for competition than germination, sprouting, shoot formation, duration of foliage, falling of foliage and regeneration of roots.

The present results support the opinion that sexual vigour and competitive ability are not interdependent (e.g. SUKATSCHEV 1928, SAKAI 1961, 1965, SAKAI and GOTOH 1955, SOLBRIG and SIMPSON 1974). On the other hand, they point out the importance of studies dealing with the reproductive strategies of higher plants (e.g. HARPER and OGDEN 1970, OGDEN 1974, BARKHAM 1980a, b, URBANSKA-WORYTKIEWICS 1980, URBANSKA in press) as well as their regeneration niche (GRUBB 1977).

As long as little is known about the factors controlling the rank of an individual species in a plant community, mid-term phenological records seem to be a promising way of revealing developmental trends as reliably but earlier than traditional relevés. Observations on flowering intensity appear to be of particular interest. The predictive value of our conclusions drawn from mid-term phenological observations obviously could not have been verified directly, the study having been carried out for an insufficient period of time. However, some of the predictions could be partly confirmed by comparing different successional stages of *Mesobrometum* grassland. Mid-term phenological data indicated no management to be a less favourable treatment than cutting in mid June for *Bromus erectus* and *Ranunculus bulbosus*. These conclusions were corroborated by the fact that the above mentioned species either did not occur in later successional stages of the investigated communities or were present there to a much lesser degree than in regularly cut areas.

Evidence that mid-term observations of phenological phenomena are in the long term quite good indicators of habitat alterations also comes from the long-range observations of other authors. Within populations of *Primula veris* monitored over a period of twenty-eight years, TAMM (1972) found the frequency of flowering sharply declining about ten years earlier than the number of plants and thus the cover, due to changing conditions leading to increasing shade and leaf litter fall. WELLS (1972) described a population of *Pulsatilla* *vulgaris* where the percentage of flowering plants decreased quite remarkably after grazing stopped, the most drastic differences (65 vs. 9.3 per cent) appearing in the two first years.

The mid-term development of cover due to changing habitat conditions may sometimes be misleading in the long term. This phenomenon was observed in the course of the present study in *Bromus erectus*, a remarkable increase of cover being recorded in the three years following cessation of cutting; however, observations on communities representing more advanced successional stages showed a decline of cover appearing in the long term. A similar development was reported by WELLS (1972) in his study on the response of a population of *Pulsatilla vulgaris* towards the cessation of grazing: the number of plants increased notably during the first four years after grazing had stopped (90 vs. 849 plants) and decreased only later. However, the long-range development of both species referred to was indicated by a sharp decline in flowering intensity in the first two years following cessation of management.

Evidence that reproductive efficiency may be strongly influenced by stress conditions, has been shown by several authors both by field and laboratory observations. KICKUTH (personal communication 1980), observed in *Phragmites communis* a remarkable negative correlation between nutrient stress and flowering intensity as well as flowering time. LANDOLT et al. (1975) reported a strong positive influence of available nitrogen on the number of flowerheads with *Scabiosa columbaria* and *Scabiosa gramuntia*; at high nitrogen treatments the flowering began on average four to eight days earlier than at low treatments. In *Narcissus pseudonarcissus*, BARKHAM (1980a) found the percentage of shoots producing flowers to be strongly related to growing space. In *Trifolium repens*, stress due to interspecific competition resulted in remarkably reduced productivity and vigour (TURKINGTON et al. 1979). HARPER and OGDEN (1970) reported that plants of *Senecio vulgaris* grown within a limited pot space allocated less of their gross energy budget to seeds than individuals of the same species cultivated in favourable conditions. These few selected examples underline the importance of auto-phenological data in giving a better understanding of relations between plants and their biotic as well as abiotic environment.

The loss of the ability to reproduce by seed, however, does not mean that a population inevitably moves towards extinction. Some plants exhibit an astonishing ability to persist in unfavourable habitats where the conditions seem to be completely unsuitable for the development of seed and seedling establishment but apparently are not severe enough to eradicate the population entirely. This phenomenon has been observed e.g. by AUER (1923) in *Phragmites communis* and more recently by GORHAM (1957) in mire-inhabiting species. SUMMERFIELD (1972) described a population of *Narthecium ossifragum* which persisted in a particular mire site in Cheshire, Great Britain, without seedlings or any flowering individual over a period of at least 70 years. WELLS (1968) observed *Pulsatilla vulgaris* surviving in a no longer grazed, dense *Bromus erectus* sward for 30 years although plants became etiolated and did not flower; they subsequently flowered when the surface was grazed again. The survival ability is apparently related to the clonal growth, a condition that is often found in perennial Angiosperms combined in various proportions with reproduction by seed.

Nevertheless, the lack of sexual reproduction represents a serious handicap from a genetic point of view. Without sexual reproduction, no recombination is generated in a population and changing environmental conditions may lead in the long term to a genetic death preceding the actual disappearance of unfit individuals (GRANT 1963, 1975, URBANSKA in press).

Not only the phenological behaviour of individual species but also that of whole communities was found to be a good indicator of transformations taking place in the environment. The phenological response of whole communities towards habitat alterations proved to be rapid and very marked and to precede by far actual physical changes in the floristic composition of a given vegetation. In the second growing season following cessation of cutting, no actual change of the floristic composition was recognizable, but the June peak value of the number of flowering species had already fallen by about 50 per cent indicating a future physical decline of the small-scale homogeneity of the stand; this suggestion was confirmed by investigating the homogeneity in communities representing various successional stages. The synthetic colour diagrams were found to be clearly distinct from each other in the differently treated plots already in the third year of experimental management; previously they were quite uniform for all surfaces within the separate study areas. Changes in phenological behaviour of whole communities as described above could reasonably be expected; it is highly probable that the phenological rhythm of the whole community changes as well when the phenological behaviour of its individual components is changing.

Different plant communities have repeatedly been observed to show different phenological rhythms (e.g. MARCELLO 1962, TüXEN 1962, BALÁTOVÁ-TULÁČKOVÁ 1971, BOTTLÍKOVÁ 1973, FALIŃSKA 1972, 1973a, b, 1976, NEUHäUSL and NEUHäUSLOVA 1977, KRüSI 1980). For this reason, some authors have used phenological behaviour as a criterion for delimitation of phytosociological units (e.g. ZOLLER 1954, FALIŃSKA 1973a, b, HEJNÝ 1978). Very little work has been done so far using synthetic colour diagrams in the field of vegetation science. Instructive examples were furnished by the studies of FüLLEKRUG (1967, 1969) on three subassociations of the *Melico-Fagetum*, *Arrhenatheretum* and *Gentiano-Koelerietum*. FüLLEKRUG (1969) observed in a regularly cut *Arrhenatheretum* a colour peak occurring in late May whereas in an unused or only irregularly used *Gentiano-Koelerietum* a colour peak appeared in late August; these observations correspond quite well with our results obtained in managed and unmanaged surfaces of *Mesobrometum* communities studied in the present work. Synthetic colour diagrams were also worked out by BALÁTOVÁ-TULÁČKOVÁ (1971) for alluvial meadows in Silesia, by FALIŃSKA (1976) for ten forest communities in the Białowieża National Park and by NEUHäUSL and NEUHäUSLOVA (1977) for *Querco-Populetum* and *Galio-Carpinetum*. Unfortunately, all these authors did not estimate the percentage covered by the flowers but that covered by the whole plants, or referred to another unit, for example the 'degree of flowering of species' (FALIŃSKA 1976). A comparison of their results with the present data was therefore not very conclusive, colour diagrams based upon cover records and not upon phenological ones being of no particular predictive value.

It goes without saying that phenological methods have their limitations. One of the factors influencing the predictive value of phenological phenomena is their rather high sensitivity towards fluctuations in the environment. Even if a plant community is in 'equilibrium' this equilibrium is highly dynamic (RABOTNOV 1974, GRUBB 1977). Side by side with successional (i.e.

directional) changes there are fluctuational ones (e.g. BORNKAMM 1961, 1974, RABOTNOV 1974, BYKOV 1974, KNAPP 1974, KRÜSI 1978), caused by weather conditions and/or due to the intrinsic behaviour pattern of individual species. A good example of annual fluctuations in flowering intensity apparently influenced by meteorological conditions is represented by *Ranunculus bulbosus* studied in the course of the present work. Further information in this subject is provided e.g. by WELLS (1967, 1972) for *Spiranthes spiralis*, by ERNST (1979) for *Allium ursinum* or by BARKHAM (1980b) for *Narcissus pseudonarcissus*. Control plots are thus exceedingly important when using phenological methods, especially in a mid-term study; however, they can obviously fulfil their purpose only as long as the fundamental environmental conditions of the respective sites are fairly comparable. For example, BARKHAM (1980b) reports a negative population response of *Narcissus pseudonarcissus* L. in open sites and a positive response in shaded sites towards mean daily hours of sunshine for the period March - September. Individuals of a given species may apparently respond quite differently to weather variation within two adjacent but contrasting habitats.

In addition, the indicator value of phenological phenomena may be limited by microdifferentiation leading to a possible development of local races. Genetic differentiation within species influenced by various abiotic and biotic factors has been repeatedly observed. It seems that in some cases development of local races may occur over short distances and arise rather rapidly, as exemplified by the few selected data.

Investigating the *Ranunculus montanus* group in the alpine zone of Davos, DICKENMANN (1980) found that on an uniform siliceous substrate a microdifferentiation pattern emerged where diploid *R. greneriarus* (2n = 16) alternated with tetraploid *R. montanus* s.str. (2n = 32) within distances of about 5 to 10 m, exactly following the pattern of local relief. TURKINGTON and HARPER (1979) report microevolution in *Trifolium repens*; in response to diversifying selection pressures exerted by the neighbourhood of different species of grass with quite different seasonal rhythms of growth (*Lolium perenne, Holcus lanatus, Cynosurus cristatus, Agrostis tenuis*) *T. repens* developed four different types. SNAYDON (cited by BRADSHAW et al. 1965) found plants of *Agrostis canina* and *Festuca ovina* growing immediately below a zinc coated fence to be significantly more tolerant to zinc than the plants a few inches away on both sides of the fence.

That microdifferentiation really can occur over a short period of time, was elegantly demonstrated by ANTONOVICS (1978). He found with *Plantago lanceolata* that adaptation can take place within a single generation by screening appropriate individuals from a genetically variable seed pool.

According to MATHER (1953, 1955), development of local races is influenced by disruptive selection. If microdifferentiation occurs in a particular species, the extinction of a given population may be prevented; phenological phenomena may accordingly turn out to be misleading at the species level - at the race level, however, they hold true.

In conclusion, phenological observations can be considered to contribute more information on the structure and function of communities than traditional phytosociological methods. They also indicate transformations taking place in plant communities earlier than traditional relevés, this aspect being particularly important not only in studies on succession or the effect of different treatments but also in conservation management of communities containing threatened rare species. Owing to economic or technical factors, it is not always possible to continue the management by which the communities to be preserved have been created within a reserve of man-made ecosystems. Under such circumstances, early indicators revealing the effect of active conservation management are greatly needed; should the treatment used prove unsuitable for a threatened species, it may be possible to change the management plan in time.

Thus, phenological methods turned out to be a rather promising way to reveal developmental trends in plant communities. They are worthy of promotion.

Summary

The present paper deals with the possible indicative value of short- and mid-term phenological observations. The investigations were carried out in *Mesobrometum* limestone grassland in northern Switzerland. The first data on the phenological behaviour as well as the cover of seven plant species within surfaces subjected to one of four different treatments (cutting in June, cutting in October, burning in March, no management) is presented. In addition, the phenological response of whole communities to the aforementioned treatments as represented by synthetic colour diagrams is considered.

Short-term phenological records collected throughout a single vegetation season led to conclusions that were not always found to be infallible. Mid-term observations, on the other hand, turned out to be quite good predictors of future development; conclusions based upon these observations were corroborated by comparing communities representing various successional stages as well as by the long term data of other authors. Phenological observations were shown to indicate habitat alterations earlier than traditional relevés, not only when considering individual species, but also where whole communities are concerned; the time difference sometimes reached as much as ten years. Conclusions drawn from mid-term phenological data were in the long term often more correct than those based upon mid-term phytosociological records.

As far as the cover of a given species is concerned, the response to changing environmental conditions was found to be mostly slow and sometimes rather ambiguous. On the other hand, the different treatments affected the flowering intensity of the seven presented species in the following way:

- Cutting in June proved to be rather unfavourable for *Aster amellus, Buphthalmum salicifolium, Brachypodium pinnatum* and *Primula veris* s.l., advantageous for *Bromus erectus, Ranunculus bulbosus* and *Orchis pallens.*
- Burning in March was not shown to date to cause severe damage to any of the studied species, excepting *Ranunculus bulbosus*; it turned out to be advantageous for *Aster amellus* and particularly so for *Brachypodium pinnatum.*
- Cutting in October was observed to considerably damage *Bromus erectus* and *Ranunculus bulbosus*; the performance of *Buphthalmum salicifolium* was only slightly affected whereas the behaviour of *Primula veris* s.l., *Aster amellus* and *Brachypodium pinnatum* apparently remained unaltered. *Orchis pallens* was not observed in those surfaces.
- 'No management' proved to have a highly unfavourable influence upon *Bromus erectus* and *Ranunculus bulbosus*; it was apparently advantageous for *Primula veris* s.l., *Aster amellus* and *Buphthalmum salicifolium. Orchis pallens* and *Brachypodium pinnatum* appeared to remain unaffected.

The limitations of phenological methods are briefly discussed. Phenological phenomena being very responsive to meteorological conditions, the use of control plots is most important. Furthermore, microdifferentiation occurring in some species may limit the indicator value of phenological data.

In conclusion, the significance of phenological methods in active conservation management is stressed; particularly in this connection, early indicators revealing possible unfavourable effects of a given treatment on threatened species are greatly needed.

Zusammenfassung

Die vorliegende Arbeit befasst sich mit dem prognostischen Wert von kurz- bis mittelfristigen phänologischen Beobachtungen. Bei traditionellen Dauerquadratuntersuchungen sind bekanntlich schlüssige Ergebnisse erst nach relativ langer Zeit zu erwarten, und Schlüsse aus dem örtlichen Nebeneinander auf ein zeitliches Nacheinander haben den Nachteil, dass man nie sicher sein kann, ob die verglichenen Bestände sowohl vom Standort als auch von der Bewirtschaftung in der Vergangenheit her wirklich vergleichbar sind. Um schon nach relativ kurzer Zeit Trendprognosen über den Sukzessionsverlauf bzw. über die Wirkung verschiedener Bewirtschaftungsmassnahmen stellen zu können, lag es nahe, die Verwendbarkeit phänologischer Methoden abzuklären.

Die entsprechenden Untersuchungen wurden in Halbtrockenrasen (Mesobrometen) in der Nord-Schweiz durchgeführt. Es werden die Auswirkungen von vier verschiedenen Bewirtschaftungsmassnahmen (Schnitt im Juni, Schnitt im Oktober, kontrolliertes Abbrennen im März und keine Bewirtschaftung (Brachlegung)) sowohl auf das phänologische Verhalten als auch auf die Deckung von sieben verschiedenen Arten dargestellt. Ausserdem wurde auch der Einfluss dieser Massnahmen auf den phänologischen Rhythmus ganzer Pflanzengesellschaften, wie er z.B. in den synthetischen Farbspektren zum Ausdruck kommt, untersucht.

Schlüsse auf Grund nur kurzzeitiger phänologischer Beobachtungen erwiesen sich nur zum Teil als zuverlässig. Wesentlich besser war hingegen der prognostische Wert über mehrere Jahre gesammelter phänologischer Daten. Einige unserer Trendprognosen, die auf mehrjährigen phänologischen Beobachtungen basieren, konnten zum Teil durch Langzeit-Beobachtungen anderer Autoren, zum Teil durch Vergleich verschieden lange brachliegender Halbtrockenrasen gestützt werden. Insgesamt reagierten phänologische Merkmale einzelner Arten wie auch ganzer Gesellschaften wesentlich rascher auf sich verändernde Standortsbedingungen als andere traditionellerweise beobachtete Charakteristika, wie z.B. die Deckung; Standortsveränderungen waren mit Hilfe phänologischer Methoden bis zu zehn Jahre früher zu erkennen als auf Grund der üblichen Vegetationsaufnahmen. Trendprognosen, gestützt auf nur während weniger Jahre gesammelte Deckungsdaten, erwiesen sich zum Teil auf längere Sicht als irreführend - im Gegensatz zu den entsprechenden phänologischen Daten.

Im Beobachtungszeitraum von 1977 bis 1980 änderte sich der Deckungsgrad der sieben untersuchten Arten nur geringfügig und im allgemeinen nicht bewirtschaftungsspezifisch. Im Gegensatz dazu zeichneten sich auf Grund der phänologischen Beobachtungen die folgenden Vor- und Nachteile der verschiedenen Bewirtschaftungsmassnahmen für die sieben untersuchten Arten ab:
- Juni-Schnitt scheint ungünstig zu sein für *Aster amellus*, *Buphthalmum salicifolium*, *Brachypodium pinnatum* und *Primula veris* s.l., günstig für *Bromus erectus*, *Ranunculus bulbosus* und *Orchis pallens*.
- Kontrolliertes Abbrennen im März wirkte sich bis zum jetzigen Zeitpunkt auf die untersuchten Arten - mit Ausnahme von *Ranunculus bulbosus* - nicht besonders negativ aus; für *Aster amellus* und insbesondere auch für *Brachypodium pinnatum* scheint Abbrennen im März im Gegenteil sehr förderlich zu sein.
- Oktober-Schnitt erwies sich als eher ungünstig für *Bromus erectus* und *Ranunculus bulbosus* und scheint auch *Buphthalmum salicifolium* eher zu schädi-

gen, während das phänologische Verhalten von *Primula veris* s.l., *Aster amellus* und *Brachypodium pinnatum* nicht oder eher günstig beeinflusst wird. *Orchis pallens* kam in den im Oktober geschnittenen Flächen nicht vor.
- Keine Bewirtschaftung (Brachlegung) scheint besonders für *Bromus erectus* und *Ranunculus bulbosus* ungünstig, für *Buphthalmum salicifolium*, *Aster amellus* und *Primula veris* s.l. günstig zu sein; auf das phänologische Verhalten von *Orchis pallens* und *Brachypodium pinnatum* wirkte sich Brachlegung nicht oder eher leicht günstig aus.

Die Grenzen phänologischer Methoden werden kurz diskutiert. So reagieren empfindliche Methoden, wie die Phänologie, auch auf Bestandesfluktuationen, die nicht sukzessions- oder bewirtschaftungsbedingt sind, rascher als weniger empfindliche, wie z.B. Aufnahmen nach BRAUN-BLANQUET; Kontrollflächen sind bei derartigen Untersuchungen deshalb besonders wichtig. Ausserdem kann die Bildung lokaler Rassen (Mikrodifferentiation) den prognostischen Wert phänologischer Beobachtungen auf Artebene - nicht aber auf dem Niveau der Rasse - einschränken.

Schliesslich wird noch auf die mögliche Verwendung phänologischer Methoden bei der Ueberwachung von Pflegemassnahmen in Naturschutzgebieten aufmerksam gemacht; gerade hier sind frühzeitige Hinweise auf eine für bedrohte Arten allenfalls ungünstige Pflegemassnahme besonders erwünscht.

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