Results

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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 m² 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 m² 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 incompleteanalytical-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.1. 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

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



Generative phases: flower buds bloom fading

fruit seed dispersal

(...) 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.



bloom

fruit seed dispersal

(...) 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: \blacksquare .

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



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

E



•••• time of cutting

Generative phases: flower buds bloom fading

fruit seed dispersal

(...) 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.



Generative phases: fading

flower buds bloom

fruit seed dispersal

(...) 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 D = dispersion value

> F = humidity value L = light value R = reaction value T = temperature value N = nutrient value K = continentality value H = humus value l 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	Т	к
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.1. (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 m² each were considered per treatment, save for the condition 'no management' where six samples of 50 m² each were evaluated).



Cover (\$, 1977 = 100\$)

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 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² 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 m² each were considered per treatment, save for the condition 'no management' where six samples of 50 m² 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 m² each were considered per treatment, save for the condition 'no management' where six samples of 50 m² 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 m² each were considered per treatment, save for the condition 'no management' where six samples of 50 m² 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 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² 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 m² each were considered per treatment, save for the condition of 'no management' where six samples of 50 m² 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 m² each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m² 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.1. 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.1. 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

Number of flowering individuals



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:



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

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cut in June



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 $0.25~{\rm m}^2$ cuttings aligned on a distance of 0.5 m.

cut in October

no management





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).

Mean number of inflorescences per 1 m^2



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 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² 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 m² each were considered per treatment, save for the condition 'no management where six samples of 1 m² each were evaluated).



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





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).

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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 m² 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.





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). Flowering intensity (%, 1977(1976) = 100%)"



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 m² each were considered per treatment, save for the condition 'no management' where six samples of 50 m² 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 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² each were evaluated).

Mean number of flowerheads per 50 m^2



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 m² each were considered per treatment, save for the condition 'no management' where six samples of 50 m² 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 m² each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m² each were evaluated).



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

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

Flowering intensity (%, 1977(1976) = 100%)



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 m² each were considered per treatment save for the condition 'no management' where six samples of 1 m² each were evaluated).

Mean number of flowerheads per 50 \mbox{m}^2



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 m² each were considered per treatment, save for the condition 'no management' where six samples of 50 m² 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 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² 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.



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:

; 1: • ; 4: • ; 5: • . +/r: • ; 3: • ; 2: • (...): 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 m² each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m² 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).

Mean number of inflorescences per 1 m^2



Fig. 50. Brachypodium pinnatum within study area 2: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² 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 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² each were evaluated).

Mean number of inflorescences per 1 m^2



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 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² 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 m² each were considred per treatment, save for the condition 'no management' where six samples of 1 m² each were evaluated).

Mean number of inflorescences per 1 m^2



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 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² 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.





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 m² 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 m² (upper curve) and per 1 m² (lower curve) recorded weekly throughout 1978 within two successional stages of *Mesobrometum* grassland. Three samples per location were considered.



no management



Fig. 59. Study area 1: development of the number of species in blossom per 50 m² (upper curve) and per 1 m² (lower curve) in surfaces under different treatments. Years represented: 1978, 1980. (Three samples per treatment were considered).



Number of species per $1 m^2$

Fig. 60. Number of species per 1 m^2 plotted against the number of species in the surrounding 50 m² within successional stages of *Mesobrometum* grassland. 18 samples taken in 1978 were considered per study area. The variances of the 1 m² data are shown in parentheses following the area indications.



Fig. 61. Synthetic colour diagrams of two successional stages of *Mesobro-metum* grassland showing the proportion of different flower colours in the course of the year 1978. (Three samples of 50 m² each were considered per study area).

yellow	
--------	--

white

blue

red 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 neverthe-less 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.







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







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







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





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

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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

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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



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

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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)

	Cover development		
Treatment	Camptothecium lutescens (Axis l)	Bromus erectus (Axis 2)	
cutting in June	۰.	=	
cutting in October	÷	++	
burning in March	+++	++	
no management	(+)	††	

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

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

- ∿ : fluctuation
- = : no change

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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 m² each were considered per treatment, save for the condition 'no management' where 20 samples of 1 m² each were evaluated).

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

	Cover development		
Treatment	Thuidium abietinum	Festuca ovina	Bromus erectus
	(Axis l)	(Axis 2, Axis 3)	(Axis 3)
cutting in June	+	÷	¥
cutting in October	∿ <i>≕</i>	∿ (∔)	¥
burning in March	+++	++	++
no management	¥	† †	† ††

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

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

 \sim : 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 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² 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)

	Cover development		
Treatment	Rhytidium rugosum	Thuidium abietinum	Hylocomium splendens
	(Axis l)	(Axis 2, Axis 1)	(Axis 2)
cutting in June	†	†	+
cutting in October	††	\sim	-
burning in March	ŧ	+++	-
no management	† †	+	+

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

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

 \sim : 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 m² each were considered per treatment save for the condition 'no management' where six samples of 1 m² 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

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Fig. 78. Rhytidium rugosum within study area 4: development of the cover under different treatments for the period 1977-1980. (Three relevés of 1 m² each were considered per treatment, save for the condition 'no management' where six samples of 1 m² 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 m² each were considered per treatment, save for the condition 'no management where six samples of 1 m² each were evaluated).