Effects of harvesting dates and frequencies on above and below-ground dynamics in Belgian wet grasslands[1]

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Abstract: A trial was established to assess the effects of harvesting dates and frequencies on the species, biomass and nutrient dynamics in wet grasslands in Belgium. Above and below-ground developments were analyzed. The vegetation changed evidently from the first spring after the establishment of the harvesting treatments onwards. One or two late summer and/or auturnn harvests (August-October) led to lower productivity and higher species-richness. Generally, the reaction from the individual species was related to their capacity to germinate *(Lychnis flos-cuculi* L.) or initiate new tillers *(Anthoxanthum odoratum* L.), stolons *(Agrostis canina* L.) or rhizomes *(Carex acuta* L.). Not only did the total productivity decrease after one or two late summer and/or autumn harvests, hut even the species increasing their cover/abundance after these treatments simultaneously developed less vigorous shoots. Soil analyses could not detect any changes in substrate fertility. However, analyses of nutrients in roots and rhizomes indicated lower concentrations of phosphorus and potassium in harvested conditions. Thus, the quick response of vegetation to the different treatments was related to its adapting species composition and to a depletion of phosphorus and potassium in roots and rhizomes. A depletion of nutrients in the soil was not detected.

Keywords: wet grasslands, species-rich, harvesting, below-ground.

Résumé: Des essais expérimentaux ont été effectués dans Ie but d'évaluer l'effet des dates et des fréquences de récolte sur Ie dynamisme des espèces, de la biomasse et des minéraux dans les prairies humides de Belgique. Le développement des parties aériennes et racinaires a été analysé. On a noté un changement de la végétation dès Ie premier printemps après la mise en place des traitements lors d'une ou de deux récoltes en fin d'été ou en autornne (aoftt-octobre), entraînant une réduction de la productivité et une augmentation du nombre d'espèces. En général, la réaction des espèces prises individuellement était liée à leur capacité de germination *(Lychnis flos-cuculi* L.) ou de formation de nouvelles pousses *(Anthoxanthum odoratum* L.), de stolons *(Agrostis canina* L.) ou de rhizomes *(Care acuta* L.). Non seulement la productivité totale a diminué à la suite de une ou de deux récoltes en fin d'été ou en automne, mais également les espèces en expansion après ces récoltes ont perdu de la vigueur. Un examen du sol n'a permis de déceler aucun changement de la fertilité, alors qu'on a noté une réduction des concentrations en phosphore et en potassium chez les racines et les rhizomes des prairies étudiées. Ainsi, la réaction rapide de la végétation à ces traitements est liée à l'adaptation des espèces constituantes et à une diminution en phosphore et potassium chez les racines et les rhizomes. Un appauvrissement du sol en éléments minéraux n'a pas été détecté.

Mots-clés: prairies humides, richesse spécifique, récolte, racines.

Introduction

Biodiversity in the densely populated and industrialized northem part of Belgium is rapidly decreasing. Among the last relatively valuable ecosystems are the wet grasslands. They are scattered along the many slow-flowing rivers of the country. These grasslands are unsuitable for modem agriculture and, as a result, still possess a remarkable ecological heterogeneity (Verlinden, Dumortier & Van den Brande, 1989b). The question is, how these grasslands can be managed in order to maintain their ecological richness or, where degradation took or is taking place, how to restore them.

A decrease in soil fertility and plant productivity is often regarded as one of the key processes in the restoration of amenity grasslands (Bakker, 1989; Gough & Marrs, 1990; Olff & Bakker, 1991), although it is not the only one (Berendse *et al.,* 1992). It is of course a reality that modem agriculture bas led to an overall increase in fertility and productivity of the environment in industrialized countries.

More knowledge of the dynamics in these grasslands is required to strengthen the development of effective conservation and rehabilitation strategies for the future (Grime, 1980; Verlinden, Dumortier & Malfait, 1989a). An appropriate management for amenity grasslands will generally not be compatible with agricultural priorities. In many cases, however, a compromise with some low input type of agriculture rnight offer more potential for improvement and sustainability.

The aim of this study is to look into possible management options and their effects on the dynarnics in wet grasslands. Harvesting is the most commonly practised management option in the wet grasslands of northern Belgium. Grazing is less suitable because of the small scale of the patches and the high water table during most of the year. Therefore, the investigation focuses on harvesting. Different harvesting

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treatments are possible. Dates as well as frequencies can vary. The investigation aims to compare a series of harvesting dates and frequencies in order to judge to what extent different harvesting treatments can influence the dynamics in wet grasslands, and which mechanisms are responsible for these influences.

Because of the anticipated role of plant productivity and soil fertility, an analysis of the species dynamics is combined with an analysis of the biomass and the nutrient dynamics, all of them in relation to the harvesting treatment. As the interaction between species, biomass and nutrients often occurs below ground, some emphasis is put on measurement of the below-ground components.

Material and methods

SITE DESCRIPTION

The experiments were conducted in the Bourgoyen-Ossemeersen, a 200-ha complex of wet grasslands in the alluvial plains (5.5 m above sea-level) of the river Leie in the area of the city of Ghent (51° 6' N; 3° 40' E). The investigated grasslands have the status of nature reserve. For the last ten years they have been harvested yearly without fertilizing. In these alluvial ecosystems, the water table is high for most of the year (lowest level: - 60 cm; highest level: + 20 cm). The site is inundated from November to March. The hydrology of the Bourgoyen-Ossemeersen is isolated from its surroundings, which means that all incoming water is raio water. Outgoing water is regulated with a sluice. The soil is hydromorphous. The humified upper layer is restricted to 10-15 cm, while the rest of the profile consists of heavy clay. The availability of nitrogen and calcium in the soil is high (300-400 mg 100 g⁻¹ and 400-450 mg 100 g⁻¹, respectively), while the availability of phosphorus and potassium is rather low (3-4 mg 100 g⁻¹ and 14-15 mg 100 g⁻¹, respectively). Important species in the wetter patches are *Carex acuta* L. (nomenclature follows De Langhe *et al.,* 1983), *Glyceria maxima* (Hartm.) Holmberg, *Ranunculus repens* L., *Phalaris arundinacea* L., *Cardamine pratensis* L., *Lychnis flos-cuculi* L. and *Carex disticha* Huds. As conditions become drier, they are often less productive and accompanied by *Holcus lanatus* L." *Anthoxanthum odoratum* L., *Festuca rubra* L. and *Agrostis canina* L. Productivity varies from 4 ton ha⁻¹ in the drier patches to 8 ton ha⁻¹ in wetter patches. The more productive patches are often less species-rich.

EXPERIMENTAL DESIGN

In five adjacent fields with a similar soil profile and a slight difference in water table, forty plots (7 m x 7 m) were established (Dumortier, 1990). In each of the five fields, each of eight plots received one of the following treatments:
- one yearly harvest on the lst of June;
- one yearly harvest on the lst of July;
- one yearly harvest on the lst of August;
- one yearly harvest on the lst of September;
- one yearly harvest on the lst of October;
- one yearly harvest on the lst of November;
- two harvests a year: one on the lst of July and one on the lst of October;
- no harvesting.

Each of the five fields served as a replication of the eight treatments. During the location of the plots, attention was paid to minimize the variability in productivity and species composition. A 1-m buffer zone separated the plots. The plots were established in spring 1986. From then onwards, they were managed as mentioned above. After mowing, the hay was removed within ten days. No fertilizers were applied. In all forty plots, species and biomass dynarnics were investigated. Nutrient analyses were conducted in a smaller number of selected plots.

SPECIES DYNAMICS

The vegetation composition was analyzed by recording all species present and their cover/abundance: monthly during the growing season of the first year, and yearly (June) during the following years.

Data were collected from a central 6 m x 1 m monitoring area in all of the forty plots. Cover/abundances were estimated according to the scale of Londo (Londo, 1984). For the data analysis or cover figures below 5%, the abundance figures were used to modify the cover figures as follows:

r *(raro)*	some specimens	(cover %) - 0.3
p *(paupulum)*	some to 20 specimens	(cover %) - 0.1
a *(amplius)*	20 to 100 specimens	(cover %) + 0.1
m *(multum)*	more than 100 specimens	(cover %) + 0.3

In June 1987, the data were refined with estimations (per species) of the percentage of tillers belonging to different phenological phases (germinating, vegetative, flowering/ fruiting).

BIOMASS DYNAMICS

The above-ground biomass was measured by cutting five samples (30 cm x 30 cm) in each of the plots due for mowing. The unharvested plots were sampled together with the last harvested plots (lst of November). The unharvested plots were sampled outside the central 6 m x 1 m monitoring area. The others were sampled randomly. Thus, biomass data were collected at different times for the different treatments. This does not affect the analysis of the development per treatment, which is the aim of these measurements. The hay was dried (24 hours; 90°C) and weighed.

The below-ground biomass is more difficult to investigate (Boehm, 1979; Dumortier, 1991). The reasons are the inaccessibility and variability of the root material, and the impossibility of identifying roots of different species and separating dead and live material. The classica! parameter, the total below-ground biomass, which is obtained after sieving soil samples, was too inaccurate an approach to detect any responses to management. The data displayed much variability due to old thick roots and rhizomes, which were irregularly dispersed according to the presence of (previous) shoot bases.

To avoid confusion with old root material, and limit the variability, root production was measured over a limited period. Therefore root-free soil cylinders were used (Persson, 1984; Hansson & Andren, 1986). The samples were taken in September 1986 with a steel corer (diameter 8.2 cm; height 10 cm). Tuis is the moment of the lowest root growth (Behaeghe, 1979). In each of the forty plots two

samples were taken at random. The roots were extracted manually. This is the best method as wet sieving washes the nutrients out of the soil and dry sieving is too labour-intensive. Some sandy soil was added to the remaining soil to restore the original volume and to conserve the soil structure. The rnîxture was sterilized (8 hours; 110°C) and finally put back in the holes. The soil was compacted to a density similar to that of the surrounding soil. No replanting or resowing was done. The soil cylinders were harvested one year later, in September 1987, with the same steel corer, divided into two parts of 5 cm height, rinsed with water while captured by means of a 450-µm mesh sieve, dried (24 hours; 90°C) and weighed. The resulting biomass figure is subsequently called the "new below-ground biomass". The approach of the new below-ground biomass underestimates the real new below-ground biomass because only lateral growth is measured. Tuis does not affect the comparison between the plots, which is the aim of the measurements.

NUTRIENT DYNAMICS

Soil nutrient reserves were measured in November 1987, after two seasons of harvesting experiments. Samples were taken in the five grasslands, each time in three plots. These plots represented the three harvesting frequencies. In each plot three samples were taken randomly and analyzed for $pH-H_2O$, organic matter, total N, P, K, Ca and Mg according to Cottenie *et al.* (1982).

Below-ground nutrient reserves in the vegetation during winter were measured by cutting rhizomes and thicker roots out of the soil. This was done in November 1987, just before commencement of the winter inundation, In one of the investigated grasslands, samples were taken from each plot. Roots and rhizomes were cleaned thoroughly with a dry towel. The use of water could leach nutrients. They were analyzed for P, K, Ca and Mg according to Cottenie *et al.* (1982).

lnsight into the transfer of nutrients from soil to above-ground vegetation was obtained by strontium absorption experiments (Veresoglou & Fitter, 1984). The experiments were implemented in May, when the vegetation was in full development. A strontium solution (3 mg mL^{-1}) was injected in three different 25 cm x 25 cm grids with a spacing of 5 cm (36 injections per grid). Bach grid was given a different injection depth: 5, 10 and 15 cm. Sirnilar flowering intensities were chosen because preliminary tests indicated that flowering shoots accumulated only half the concentration in comparison with vegetative shoots (Dumortier, 1990). One month after the injection, above-ground biomass was cut, separated according to the species, oven-dried (24 hours; 90°C) and weighed. After ashing, the concentration of strontium was measured by atomie absorption. Tuis measurement could not be repeated for different treatments because of the amount of work involved.

Results

SPECIES DYNAMICS

The response to the treatments was recorded for all 63 species growing in the trial (Table I). Data on their cover/abundances describe the immediate response to the treatments (following months), and the further development (following years).

TABLE I. List of all species present in the trial

Achillea ptarmica L.	*Lathyrus pratensis* L.
Agrostis canina L.	*Leontodon autumnalis* L.
Agrostis sto/onifera L.	*Lolium perenne* L.
Alopecurus geniculatus L.	*Lotus uliginosus* Schkuhr *
A/opecurus pratensis L.	*Lychnis flos-cuculi* L.
Anthoxanthum odoratum L.	*Lycopus europeus* L.
Atriplex prostrata Boucher ex DC.	*Lysimachia nummularia* L.
Bromus mollis L.	*Lysimachia vu/garis* L.
Caltha palustris L.	*Mentha aquatica* L.
Cardamine pratensis L.	*Myosotis cespitosa* C.F. Schultz
Carex acuta L.	*Phalaris arundinacea* L.
Carex demissa Homem.	*Phleum pratense* L.
Carex disticha Huds.	*Phragmites australis* (Cav.) Trin. ex Steud.
Carex hina L.	*Poa pratensis* L.
Carex vesicaria L.	*Poa trivia/is* L.
Cerastium fontanum Baumg.	*Polygonum amphibium* L.
Cirsium pa/ustre (L.) Scop.	*Polygonum persicaria* L.
Eleocharis palustris (L.) Roem. et Schuit.	*Ranunculus acris* L.
Epilobium hirsutum L.	*Ranunculus flammula* L.
Equisetum fluviati/e L.	*Ranunculus repens* L.
Equisetum palustre L.	*Ranuncu/us sceleratus* L.
Festuca pratensis Huds.	*Rhinanthus ngustifolius* C.C. Gmel.
Festuca rubra L.	*Rumex acetosa* L.
Filipendula ulmaria (L.) Maxim.	*Rumex crispus* L.
Galium palustre L.	*Rumex hydrolapathum* Huds.
Galium uliginosum L.	*Solanum dulcamara* L.
Glyceria fluitans (L.) R. Brown	*Sonchus arvensis* L.
Glyceria maxima (Hartm.) Holmberg	*Taraxacum sp.*
Ho/cus lanatus L.	*Trifolium repens* L.
Iris pseudacorus L.	*Urtica dioica* L.
Juncus conglomeratus L.	*Va/eriana repens* Host
Juncus effusus L.	

The immediate response of two representative species is shown in Figure 1 and Figure 2. Although the starting cover/abundances are not always the same, the figures reveal whether and how much cover/abundances increased or decreased according to the harvesting treatment. *Ranunculus repens* in Figure 1 represents the species recovering rapidly and increasing their cover/abundance after harvesting. In unharvested plots, *Ranunculus repens* gradually extended its cover, reaching a maximum in August, after which it gradually retreated from the community. After any harvesting date, the species rapidly recovered its pre-harvesting cover/abundance. Harvesting in July was followed by a delayed peak, while harvesting in August or September provided the species with additional expansion opportunities. Harvesting in October or November was not followed by any increase in cover/abundance because by then the species was hardly noticeable in the dense vegetation cover. Species with similar recovery and expansion pattems were *Lychnis flos-cuculi, Taraxacum sp., Cardamine pratensis* and *Ranunculus flammula.* The cover/abundance of some species only increased after particular harvesting dates. *Galium palustre* increased its cover/abundance after harvesting in July, while for *Anthoxanthum odoratum* an increase occurred after harvesting in August or September. After other harvesting dates, these species hardly recovered. *Carex acuta* in Figure 2 represents the species with low recovering after any harvesting date. If not harvested, *Carex acuta* remained dominant in the vegetation until October. After harvesting in June, July or August, the species slightly

Mowing in June | Mowing in July | Mowing in August | Mowing in September

Mowing in October | Mowing in November | Mowing in July and October | No mowing
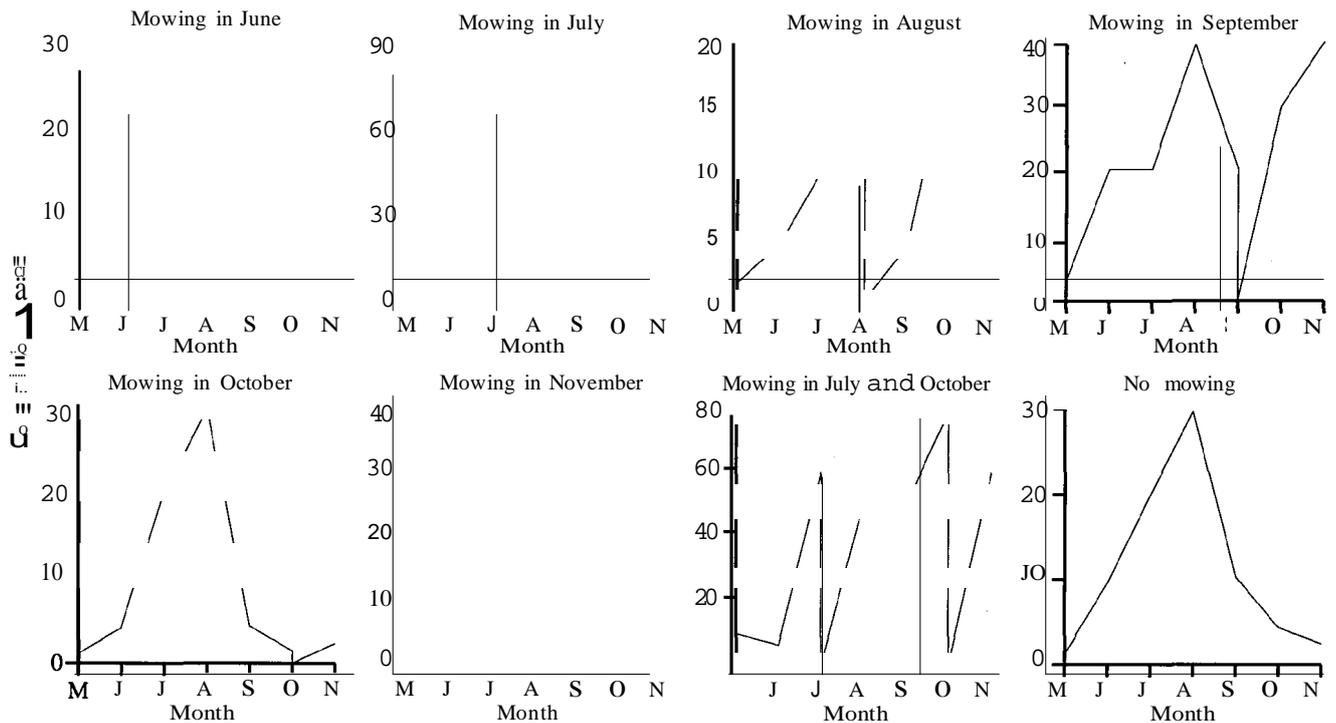
FIGURE 1. Cover/abundance of *Ranunculus repens* L. (percentage of the total area covered by the species) during one growing season (1986), according to the yearly harvesting treatment (0-5% cover percentages with adaptations regarding abundance; see material and methods).

recovered, while after later harvesting dates it did not recover at all. Species with similar characteristics were *Carex disticha, Cirsium palustre, Lysimachia vulgaris* and *Filipendula ulmaria.*

During the first spring after harvesting, when vegetation developed new green shoots after winter dormancy, divergent developments of the vegetation cover according to the previous harvesting treatment were evident. For most species, development during the following years was sirnilar to the immediate response to harvesting. Species

Mowing in June | Mowing in July | Mowing in August | Mowing in September

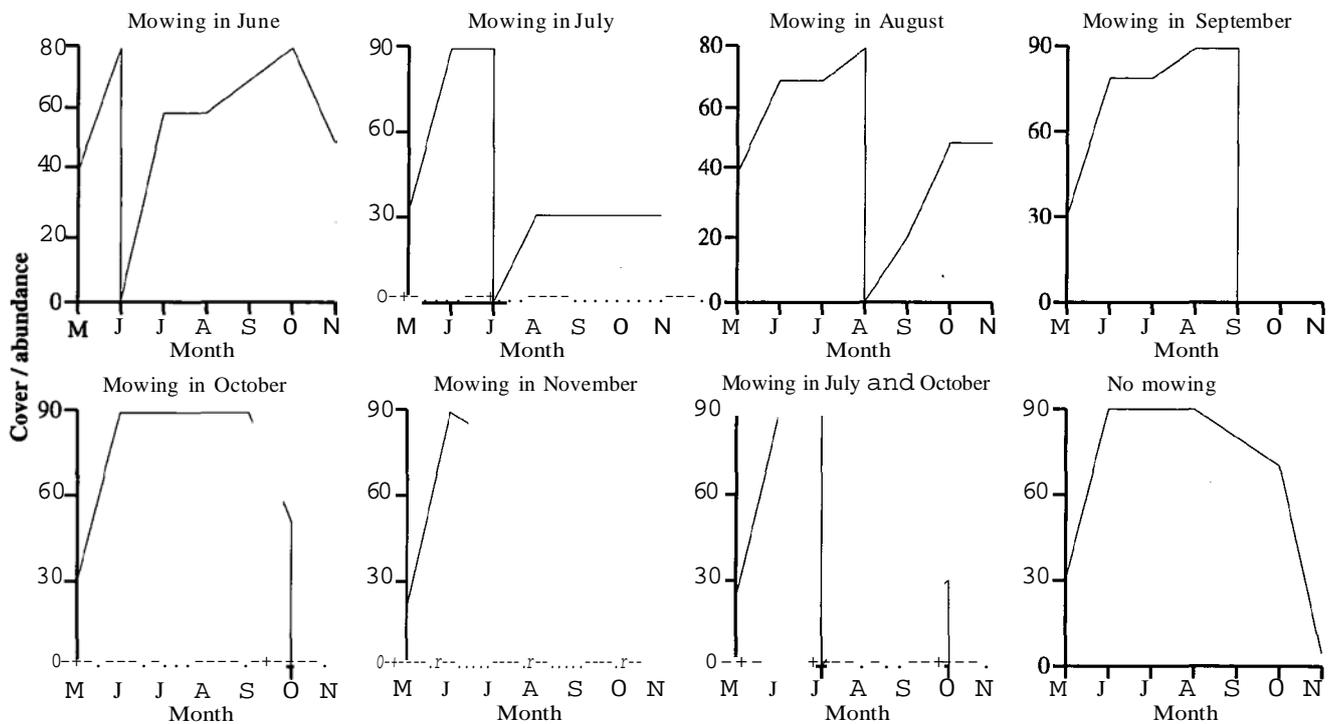Mowing in October | Mowing in November | Mowing in July and October | No mowing

FIGURE 2. Cover/abundance of *Carex acuta* L. (percentage of the total area covered by the species) during one growing season (1986), according to the yearly harvesting treatment (0-5% cover percentages with adaptations regarding abundance; see material and methods).

which recovered rapidly and increased their cover/abundance after certain harvests, generally maintained an increased cover/abundance during the following years *(e.g. Ranunculus repens* while harvesting in August). Species curtailed by certain treatments remained restricted in their development during the following years, if they did not disappear completely *(e.g. Cirsium palustre* after harvesting in July). For a few species, further development was opposite to the immediate response. *Carex acuta* slightly recovered after early-season harvesting, while it did not recover after late-season harvesting. From the first spring after harvesting onwards, the density and height of the *Carex acuta* shoots remained restricted in the early-season harvested plots, while the cover was dense and vigorous in the late-season harvested plots. *Lysimachia vulgaris* and *Carex disticha* responded similarly. These three species are rhizomatous.

The records on the phenological stages add more information to the cover/abundance data (Table Il). Some species were able to increase their cover/abundance rapidly after certain harvests because of their germination capacity at that specific time. Germination was then facilitated by the open canopy after the harvest. Examples are *Lychnis flos-cuculi, Ranunculus flammula, Taraxacum sp.* and *Cardamine pratensis.* Often the germination capacity was high because seed setting occurred just before mowing. Sometimes a delay or some specific environmental conditions were required between seed setting and germination. *Ranunculus repens* seeds germinated during the following spring. Table Il shows the percentages of tillers of this species belonging to different phenological phases, according to harvesting treatment during the previous year. *Ranunculus repens* preferably germinated in the late-season harvested plots (Table Il), where the canopy was still open. The cumulation of vegetative expansion immediately after harvesting between June and September and an abundant germination during spring after harvesting between September and November, made this species particularly competitive in harvested conditions.

Harvesting directly influenced species coexistence, enhancing development opportunities for some species and reducing these for other species, thus affecting species richness. Figure 3 shows the average number of species during three seasons according to the treatment. The number of species increased after harvesting either in July, August, September or October or harvesting in July and

October. A decline was noticed in the unharvested plots

TABLE Il. Average percentage of *Ranunculus repens* L. tillers belonging to different phenological phases Guvenile, vegetative, flowering/fruiting), according to the yearly harvesting treatment, after one year of comparative experiments (June 1987)

	Juvenile	Vegetative	Flowering/fruiting
Harvesting in June	Ha	rvesting in July	

and in the plots harvested in November. After harvesting in June, the number of species remained equal. Thus, a higher number of species was favoured by one or two harvests between July and October.

BIOMASS DYNAMICS

Figure 3 shows the above-ground biomass during three seasons according to the treatment. Not harvesting was followed by an increase in biomass, which was due to an increased productivity and an accumulation of litter (Figure 4). Harvesting in June, July or November was followed by a slightly increased productivity. Harvesting in August, September or October or harvesting in July and October was followed by a decreased productivity. The below- and above-ground biomass according to the harvesting frequency is summarized in Figure 4. The new below-ground biomass in the unharvested plots was about double the new below-ground biomass in the harvested plots. Differences in new below-ground biomass between the different harvests could not be measured. The technique was probably too inaccurate to detect the more subtle effects of the harvesting dates. Only the difference between unharvested and harvested conditions, which also above-ground was the most visible, could be identified (Figure 3).

Biomass production was inversely proportional to the number of species (except for the July harvest) (Figure 3). The decrease in productivity was partially related to the decrease in the cover/abundance of a few taller species in favour of a collection of smaller species. Figure 4 shows how species other than *Carex acuta* represent a higher biomass in the unharvested plots. This is caused by the presence of a few other taller species *(Phalaris arundinacea* and *Filipendula ulmaria).* In the plots harvested twice, these other species are a variety of smaller species *(Lychnis flos-cuculi, Ranunculus flammula, Ranunculus repens, Cardnmine*

3.3

79.
5
86.
7

14 20.2

JO
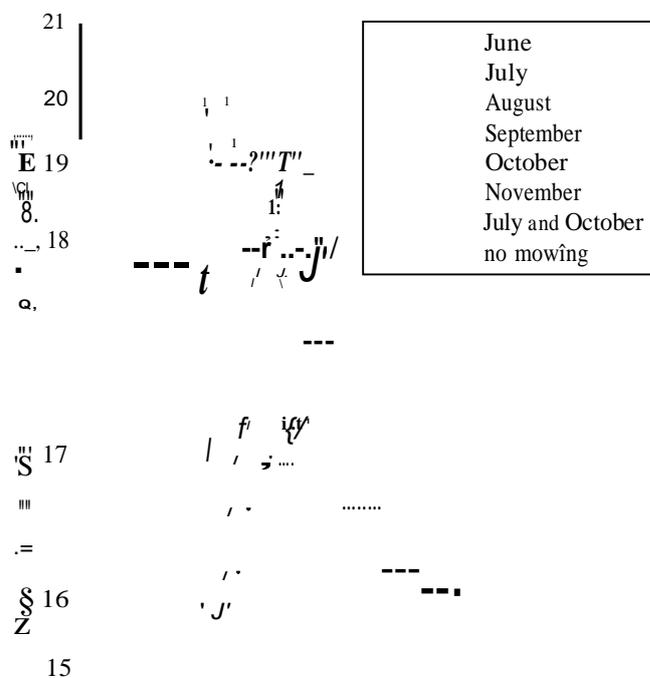
Harvesting in August	1.7	86.7	11.7
Harvesting in September	9.3	80	10.7
Harvesting in October	28.4	59	12.7
Harvesting in November	46.7	51.7	1.7
Harvesting in July and October	23.3	53.3	23.3
No harvesting	3	96	1

200   400   600   800   1000   2000

Above-ground biomass (g/m2)

FIGURE 3. Species-richness (number of species per 6 m2) and above-ground biomass (g m.^{2}), according to the yearly harvesting treatment, during three years of comparative experiments (1986, 1987, 1988). Lines correspond to periods of mowing. Arrows show direction of increasing years.
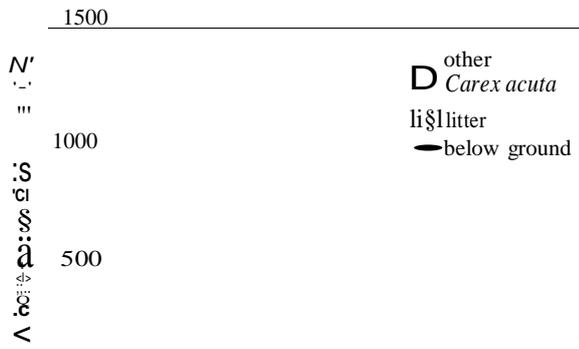
1500

N'

1000

500

D other
Carex acuta

li§l litter
— below ground

TABLE 111. Concentrations of nitrogen, phosphorus, potassium, calcium and magnesium (mg 100 g^{-1}), acidity (pH) and content of carbon (%) (average and standard deviation) in the upper 5 cm of soil, according to the yearly harvesting frequency, and two seasons of comparative experiments (November 1987)

	No harvest		One harvest		Two harvests	
	x	SD	x	SD	x	SD
N	292	119	400	196	376	222
p	4	3	3	2	3	1
K	14	4	14	3	15	4
Ca	390	92	464	100	426	53
Mg	20	7	24	7	20	4
pH	5.0	0.1	5.3	0.3	5.0	0.1
C						

0

1500

500

1000

Below-ground biomass (g m-2)

wing ...ncy/ye
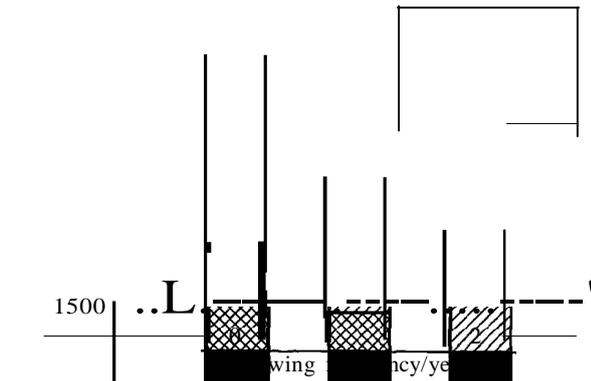
FIGURE 4. Total above...d biom...er biom... *rex acuta* L. biomass and biomass of other species) and new below-ground biomass (g m-2), according to the yearly ha... frequency, after two ...s of comparative experiments (June 1988).

pratensis and *Galiu... ...lustre*). The variety of smaller species replaced a portion of. *Carex acuta* and a few other taller species.

NUTRIENT DYNAMICS

Table I shows the average concentrations of soil nutrients according to the harvesting frequency, after two

years of comparative treatments. Concentrations of phosphorus (3-4 mg 100 g-1) and potassium (14-15 mg 100 g-1) were similar after any harvesting frequency. Concentrations of nitrogen, calcium and magnesium as well as pH were highest in the plots harvested once. The content of organic matter was highest in the plots harvested twice. Statistica! analysis could not prove any significant differences. Thus, changes in soil fertility could not be detected.

The concentrations of nutrients in roots and rhizomes were also analyzed. While no differences were measured for calcium and magnesium, some differences appeared for phosphorus and potassium. The concentration of phosphorus was higher in the rhizomes from the plots not harvested or

harvested in November (233 and 250 mg 100 g-1, respectively) than in the rhizomes from the other plots (± 200 mg 100 g-1).

The concentration of potassium was highest in the rhizomes (1020 *versus* 649 mg 100 g-1 in the other plots) and in the roots (450 *versus* 271 mg 100 g-1 in the other plots) from

the unharvested plots. As the below-ground biomass was also higher in the unharvested plots, the total below-ground

reserve of potassium in the vegetation was evidently higher in these conditions. Differences in concentrations of potassium among harvesting dates could not be measured. Also here, the technique probably lacked sensitivity. Further, it was remarkable how concentrations of phosphorus and especially potassium were higher in the rhizomes than in the roots (206 *versus* 168 mg 100 g-[1] for phosphorus, respectively, and 695 *versus* 294 mg 100 g-[1] for potassium, respectively). This was not the case for calcium and magnesium.

To measure the nutrient transfer from soil to vegetation, absorption experiments were conducted. We measured the accumulation of strontium in the above-ground parts of six species after its injection at three soil depths (Table IV). When vegetation was in full development in May, the six species absorbed altogether 112 mg m-[2] of strontium. Because strontium absorbtion is comparable to calcium absorption (Creger *et al.,* 1970; Soileau, 1973), the avail- ability of calcium in the same soil profile was compared. The concentration of calcium in the soil varied from 428 to 797 mg 100 g-[1] (0-20 cm depth). Thus, the absorption of calcium was not related to its availability in the soil. For phosphorus and potassium, with concentrations of 2 to 3 mg 100 g-1 and 11 to 23 mg 100 g-[1] respectively, the availability seemed more critical for the uptake by the plants.

Moreover, the data in Table IV illustrate how the absorption activity of *Ranunculus repens* and to a lesser extent of *Carex acuta* declined rapidly between 5 and 15 cm depth. This was not the case for *Glyceria maxima, Agrostis canina, Phalaris arundinacea* and *Equisetum palustre.* The total absorption activity of *Carex acuta* was high.

TABLE IV. Absorbed strontium (μg) in the above-ground biomass of six species, one month after injection at three depths in the soil (5, 10 and 15 cm) (May 1986)

	- S em	- lO cm	- 15 cm
Carex acuta L.	1290	924	914
Glyceria maxima (Hartm.) Holmberg	317	457	408
Agrostis canina L.	162	58	123
Phalaris arundinacea L.	177	45	228
Ranunculus repens L.	1004	249	213
Equisetum palustre L.	183	267	n.a.•

• n.a.: not available.

Discusion

Harvesting influenced the grassland ecosystem. From the first spring after the establishment of the treatments, divergence in grassland development became evident. The influence on the species composition was the most obvious outcome. Some species had the capacity to increase their cover/abundance after harvesting, while the development of other species was curtailed by harvesting. Survival strategies among species can be summarised in four categories. They are based on reproductive capacities. Some species rely on more than one of these strategies, which enhances their competitiveness in harvested grasslands *(Ranunculus repens).*

HAR.VESTING INTERACTS WITH THE GERMINATION CAPACITY

Four types can be distinguished.

- *Galium palustre, Lychnis flos-cuculi* and *Taraxacum sp.* seeds germinated immediately after seed setting. When vegetation was harvested at that time, numerous seeds germinated in the open space. Some species germinated after one specific harvesting time *(e.g. Galium palustre* after harvesting in July). Others also reacted, although at a lower intensity, to harvesting during the subsequent months *(e.g. Lychnis flos-cuculi* after harvesting in July, August or September). As flowering and fruiting are prevalent in summer, most of these species are favoured by summer harvests.

- *Ranunculus repens* seeds did not germinate immediately after seed set; a dormancy period was necessary. During the following spring, germination preferentially occurred in late-auturnn harvested conditions. The open canopy, which was created before the winter, facilitated germination in spring. This species is favoured by harvesting in late auturnn.

- *Cardamine pratensis* and *Ranunculus flammula* were able to germinate after any harvesting date. The act of harvesting was more important than the timing. Seeds germinated during the whole year. After cessation of harvesting these species soon disappeared due to competition for light and suffocation by litter. These species are favoured by any harvesting treatment.

- The fructification opportunities of *Cirsium palustre* were more critica} than its germination opportunities. Fructification of *Cirsium palustre* was restricted by harvesting in July or July and October. Not harvesting, on the other hand, imposed no harm on this species. Seedlings were strong enough to penetrate through the litter and limited space. This species is favoured by a cessation of harvesting.

HAR.VESTING INTERACTS WITH THE INTENSITY OF TILLERING

Grasses have the capacity to initiate new tillers at certain stages of their development. The creation of space just before tillering enhances tiller development. *Anthoxanthum odoratum* was favoured by harvest in August or September. *Holcus lanatus* was favoured by any harvest between August and November. Most of these species are favoured by late summer or auturnn harvests.

HARVESTING INTERACTS WITH THE CAPACITY TO DEVELOP

After harvesting, species with stolons have the capacity to increase their cover/abundance quickly. For *Ranunculus repens,* this occurred after harvesting in June, July, August or September (Figure 1). Tuis species is favoured by summer harvests.

HARVESTING INTERACTS WITH THE CAPACITY TO GENERATE RHIZOMES

From the first spring after the instal ment of the treatments, shoots of *Carex acuta , Carex disticha* and *Lysimachia vulgaris* grew more vigorously in late-season harvested plots (September-October) than in early-season harvested plots (June-July). Spring-shoots remained small, particularly in the plots that were harvested twice. This contrasted with the recovery immediately after harvesting, which only occurred if harvested earlier than September. The three species are rhizomatous. Rhizomes develop more slowly than stolons and are only indirectly affected by harvesting. The initiation of new rhizomes coincides with shoot senescence. This was observed between August and October. During this pei"iod metabolites and inorganic materials are translocated from shoots back to roots and/or rhizomes. When the vegetation was harvested before this redistribution could take place, metabolites and inorganic materials were exported from the ecosystem. Immediate regrowth after early-season harvesting exhausted the underground reserves even more. Although the translocation process from regrown shoots back to roots and/or rhizomes was postponed (October-November), these weak shoots failed to initiate sufficient rhizomes to form shoots the following spring. Thus, the spring-shoots remained small. It is evident that harvesting more than once is even more pernicious for rhizomatous plants. The higher concentrations of phosphorus and potassium in roots and rhizomes in the plots which were not harvested or which were harvested in November, confirm the theory developed above. Rhizomatous species are favoured by late autumn harvesting and if the rhizomes are strong enough to penetrate the litter they are favoured by the cessation of harvesting.

In many of the strategies identified above, the species involved are favoured by summer or autumn harvests. Data on the number of species according to the harvesting treatment, suggest that one or two summer and/or autumn harvests (July-October) are beneficia} for species diversity. The increasing species diversity after these treatments is related to the opportunity for more species to initiate and fulfil their regeneration cycle. Also Olff *et al.* (1994), who analyzed grassland succession after cessation of fertilizing and with continued harvesting, noticed how during early productive stages, species escaped from competition for light by germinating when the canopy was still open after cutting. Later, in less productive stages, this competition for light would be replaced by competition for nutrients (Olff *et al.,* 1994). One or two late summer and/or auturnn harvests (August-October) also caused a decrease in productivity. Within three years, the average productivity dropped from 6-8 to 4-6 ton ha-[1], a level which is considered essential for the restoration of species-rich grasslands (Oomes, 1992). However, this productivity level does not guarantee successful restoration of species-rich grasslands. Other essential factors are the presence of a seed bank and a certain level of disturbance to create space for germination and seedling establishment (Berendse *et al.,* 1992). The loss of produc-

tivity is a result and cause of the higher species richness. The fact that the majority of the species favoured by one or two summer and/or autumn harvests (July-October) are less productive *(e.g. Cardamine pratensis, Ranunculus flam- mula, Ranunculus repens, Lychnis flos-cuculi* and *Galium palustre)* implies a lower productivity. This lower productivity, with its more open stand character, increases the opportunities for more of these species to establish (Olff *et al.,* 1994). Early-season mowing (June), which farmers prefer for their livestock because of the palatability of tender young shoots, restricts many species in their regeneration cycle. Seed set is cancelled or delayed and the regrowth is too dense to allow the expansion of less productive species. Late-season harvesting (November), and particularly a cessation of harvesting, provides seed set opportunities for all species but is actually more detrimental for the less productive species, which receive insufficient light and space in the dense vegetation cover. Only a few vigorous species *(e.g. Filipendula ulmaria* and *Phalaris arundinacea)* have the capacity to increase their cover/abundance in these condi- tions. Within three years, the above-ground biomass in the unmown plots increased from 6-8 ton ha-^{1} to more than 10 ton ha-^{1}, a level considered restrictive for species diversity (Oomes, 1992).

Often, the effect of harvesting treatment on vegetation cover can be explained by the interaction between changing species composition and changing productivity. But this is not always the case. All species, including those with low productivity which hardly survived in unharvested conditions, initiated more productive spring-shoots in these circum-stances. Only the strongest shoots of the less productive species can maintain themselves in unharvested conditions. On the other hand, all species, including the few individuals of the vigorous species which survived in harvested conditions, initiated smaller spring-shoots under a harvesting regime. Changing species composition and productivity cannot provide the explanation in this case. Some influence from the nutrient dynarnics is suggested here. After two years of experimenting and identifying clear differences in above and below-ground productivity, changes in the availability of nutrients in the soil could not be detected. The slow reaction of the soil fertility (or the difficulty of detecting any changes) was also observed by others (Van Andel & Van den Bergh, 1987; Parr & Way, 1988; Verlinden, De Becker & Dumortier, 1990; Van der Woude, Pegtel & Bakker, 1994). However, changes in concentration of nutrients in roots and rhizomes were detected. Concentration of phosphorus and potassium in roots and rhizomes as well as biomass of roots and rhizomes decreased in harvested conditions (except for November harvests). The exhaustion of the reserves of phosphorus and potassium is related to the mobility of these nutrients in plant tissues. They are easily translocated to rhizomes and newly developing shoots. If green shoots are harvested, they are removed from the ecosystem. Immobile nutrients like calcium are not redistributed and remain stored in older plant tissues. Late-season harvesting removes relatively more calcium, but this was not reflected by its concentration in the roots, probably because of the abundant availability of calcium in the soil. The finding that phosphorus and potassium, as compared with the other nutrients, were more

concentrated in rhizomes than in roots, confirms their mobility, their comparative importance for rhizome and shoot development and their tendency to be exhausted sooner than other nutrients. Thus, the second reason for the lower productivity after certain harvests is the exhaustion of the reserves of phosphorus and potassium in roots and rhizomes. Differences in concentration of phosphorus and potassium in roots and rhizomes and differences in root and rhizome biomass could only be proved for the most obvious contrast between harvested and unharvested conditions. There was no difference found among harvesting treatments. As the above-ground productivity decreased after one or two summer and/or autumn harvests (July-October), it may be expected that below-ground biomass and the concentration of phosphorus and potassium could also decrease after those harvests. The differentiation between the harvesting dates could then be explained by the fact that nutrients are consumed for seed set in summer (difference with June harvest), while redistribution to roots and/or rhizomes in autumn is not taking place (difference with November harvest). However, these are assumptions which could not be proved.

The effect of harvesting on the grassland ecosystem after two years of comparative experiments, can be explained by the interaction between the changing species composition, the changing productivity and the changing nutrient dynarnics within the vegetation. At this stage, the soil was not involved. When the availability of nutrients in the soil is compared with the intensity of nutrient absorption by vegetation, most nutrients were sufficiently available in the soil, except for phosphorus and potassium. The nutrients related to changes in productivity were also most limited in the soil. This is most probably a result of the fact that, preceding the establishment of the experiments, the grass- lands were harvested without fertilizing for a period of ten years. This suggests a future difference in the availability of phosphorus and potassium in the soil according to the harvesting treatment. The availability of sufficient nitrogen might even accelerate phosphorus and potassium depletion in harvested plots (Van der Woude, Pegtel & Bakker, 1994). The changing availability of nutrients in the soil will internet with change in species composition, change in productivity and the changing nutrient dynarnics within the vegetation. If the depletion of phosphorus and potassium is most pronounced in the upper soil layers, *Ranunculus repens* with its shallow nutrient absorption activity would be most affected. This species, which is now evidently favoured by harvesting, would then be disadvantaged by continued harvesting. Also, *Carex acuta* would be hampered by its shallow nutrient absorption activity, although its total absorption capacity is higher. These assumptions indicate that during the following yars more (unexpected) changes will take place in the grassland ecosystem according to the harvesting treatments. Mechanisms playing an important role during certain stages of succession will be less important during other stages, *e.g.* with decreasing productivity, competition for light might be replaced by competition for nutrients (Olff *et al.,* 1994). Also other factors, which are beyond the reach of this study *(e.g.* invertebrate dynarnics), are expected to interact with the mechanisms described above.

In this study, the effect of different harvesting treatments on the dynamics in wet grasslands, during the first three years of implementation, has been analyzed and explained. Tuis knowledge will assist planners and managers to judge observations in the field and to develop effective strategies for the conservation and/or rehabilitation of amenity grasslands for the future.

Literature cited

Bakker, J. P., 1989. Nature Management by Grazing and Cutting. Kluwer Academie Publishers, Dordrecht.

Behaeghe, T. J., 1979. De seizoenvariatie in de grasgroei. Aggregation Thesis, Faculty of Agricultural Sciences, University of Ghent, Ghent.

Berendse, F., M. J. M. Oomes, H. J. Altena & W. T. Elberse, 1992. Experiments on the restoration of species-rich meadows in The Netherlands. Biological Conservation, 62: 59-65.

Boehm, W. (ed.), 1979. Methods of Studying Root Systems. Ecological Studies, 33. Springer-Verlag, Berlin.

Cottenie, A., M. Verloo, L. Kiekens, G. Velghe & R. Camerlynck, 1982. Chemica! Analysis of Plants and Soils. I.W.O.N.L" Brussel.

Creger, C. R., E. C. Holt & D. A. Lovelace, 1970. Calcium and strontium relationship in various commercially important plants. Agronomy Journal, 62: 297-299.

De Langhe, J. E" L. Delvosalle, J. Duvigneaud, J. Lambinon & C. Van den Berghen, 1983. Flora van België, het Groot Hertogdom Luxemburg, Noord-Frankrijk en de aangrenzende gebieden. Nationale Plantentuin, Meise.

Dumortier, M" 1990. Invloed van maaibeheer op de boven- en ondergrondse ecosysteemdynamiek in vochtige graslanden. Ph.D. Thesis, Faculty of Agricultural Sciences, University of Ghent, Ghent.

Dumortier, M" 1991. Below-ground dynamics in a wet grassland ecosystem. Pages 301-309 *in* D. Atkinson (ed.). Plant Root Growth: An Ecological Perspective. Special Publication Series of the British Ecological Society, Number 11, Blackwell, London.

Gough, M. W. & R. H. Marrs, 1990. A comparison of soil fertility between semi-natura! and agricultural plant communities: lmplications for the creation of species-rich grassland on aban- doned agricultural land. Biological Conservation, 51: 83-96.

Grime, J. P., 1980. An ecological approach to management. Pages

13-55 *in* 1. H. Rorison & R. Hunt (ed.). Amenity Grassland: An Ecological Perspective. John Wiley & Soos, Chichester.

Hansson, A. C. & 0. Andren, 1986. Below-ground plant produc- tion in a perennial grass ley *(Festuca pratensis* Huds.) assessed with different methods. Journal of Ecology, 23: 657-666.

Londo, G., 1984. The decimal scale for relevés of permanent quadrats. Pages 45-49 *in* R. Knapp (ed.). Sampling Methods and Taxon Analysis in Vegetation Sience. Dr W. Junk Publishers, The Hague.

Olff, H. & J. P. Bakker, 1991. Long-term dynamics of standing erop and species composition after cessation of fertilizer appli- cation to mown grassland. Journal of Applied Ecology, 28: 1040-1052.

Olff, H., D. M. Pegtel, J. M. Van Groenendael & J.P. Bakker, 1994. Germination strategies during grassland succession. Journal of Ecology, 82: 69-77.

Oomes, M. J. M., 1992. Yield and species density of grasslands during restoration management. Journal of Vegetation Science, 5: 271-274.

Parr, T. W. & J. M. Way, 1988. Management of roadside vegeta- tion: The long-term effects of cutting. Journal of Applied Ecology, 25: 1073-1087.

Persson, H., 1984. The dynamic fine roots of forest trees. Pages 193-204 *in* G. 1. Agren (ed.). State and Change of Forest Ecosystems: Indications in Current Research. Swedish Report 13, Department of Ecology and Environmental Research, University of Agricultural Sciences.

Soileau, J. M" 1973. Activity of barley seedling roots as measured by strontium uptake. Agronorny Journal, 65: 625-628.

Van Andel, J. & J. P. Van den Bergh, 1987. Disturbance in grass- lands, outline of the theme. Pages 3-13 *in* J. Van Andel, J. P. Bakker & R. W. Snaydon (ed.). Disturbance in Grasslands. Dr W. Junk Publishers, Dordrecht.

Vand der Woude, B. J" D. M. Pegtel & J. P. Bakker, 1994. Nutrient limitation after long-term nitrogen fertilizer applica- tion in cut grasslands. Journal of Applied Ecology, 31: 405- 412.

Veresoglou, D. S. & A. H. Fitter, 1984. Spatial and tempora! pat- terns of growth and nutrient uptake of five coexisting grasses. Journal of Ecology, 72: 259-272.

Verlinden, A., M. Dumortier & J. P. Malfait, 1989a. Graslanden, ruigten en zomen. Pages 87-103 *in* M. Hermy (ed.). Natuurbeheer. Van de Wiele, Brugge.

Verlinden, A., M. Dumortier & M. Van den Brande, 1989b. Overstro-ming in graslanden en gevolgen voor natuurbeheer. De levende natuur, 4: 100-105

Verlinden, A., P. De Becker & M. Dumortier, 1990. Sorne Iong- term management experiments in three wet and moist grass- lands in Flanders. Pages 473-482 *in* Actes du colloque "Gérer la nature?", Ministère de la Région Walonne, Bruxelles.