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

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

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Communicated by Prof. V. Westhoff at the meeting of March 29, 1980

b. Equitability component

In plots B1, 2, and 4 in 1978 only a single species once covered over 12.5% of the surface: *Leontodon hispidus.* A few species covered sometimes about 5–10%, like *Briza media, Trisetum flavescens, Lotus corniculatus, Leontodon hispidus*, and *Knautia arvensis.* In the course of the study the occasional dominance of certain species disappeared (Table 2). Most species covered less than 5%, but the number of individuals often fluctuated strongly from one species to another.

In plots B3 and B5 a much stronger dominance could be observed than in the non-fertilized plots (Fig. 5). In 1978 the grasses *Festuca rubra* and *Dactylis glomerata* covered from 10–40% of the surface, the coverage of other species, particularly forbs, amounting to less than 1%, e.g., *Plantago lanceolata, Ononis repens, Ranunculus acris*, and *Chrysanthemum leucanthemum.* A few constantly present forbs, initially covering about 25%, like *Centaurea pratensis* and *Lathyrus pratensis* in plot B5 did not keep up this high coverage. This also holds for forbs that established themselves in the fertilized plots after a few years and attained a rather high coverage, like *Heracleum sphondylium* in plot B3.

Summing up, we may say that species diversity in both components is less in the fertilized plots, with a biomass amounting to much more than 500 g/m^2, than in the other plots whose biomass is usually less than 300 g/m^2 (Table 7).

Table 6. Precipitation data from the Meteorological Station Valkenburg, South-Limburg, at a distance of about 3 km from the experimental site in Gerendal. In 1976 harvesting of the vegetation took place on 10 August. Data after the Royal Dutch Meteorological Institute (K.N.M.I.), De Bilt (U.), The Netherlands.

PRECIPITATION TABLE					
month		1975–76		average	
December 1975		23 mm		59 mm	
January 1976		83 mm		68 mm	
February 1976		34 mm		54 mm	
	winter		140 mm		181 mm
March 1976		27 mm		47 mm	
April 1976		15 mm		55 mm	
May 1976		41 mm		60 mm	
	spring		83 mm		162 mm
June 1976		26 mm		72 mm	
July 1976		47 mm		72 mm	
August 1976		29 mm		78 mm	
	summer		102 mm		222 mm
Total			325 mm		565 mm

3.4. Sod removal

a. Phanerogams

The effect of sod removal in April 1971 on the floristic assemblage obviously was most severe during the next few years. During these first years many weeds of arable land, like *Euphorbia helioscopia, Mercurialis annua, Cirsium arvense, Elytrigia repens*, and *Anagallis arvensis*, established themselves. After about three years they disappeared from both the fertilized and the non-fertilized plots (Tables 3 and 5).

Table 7. Evenness of the plots based upon the cover percentages of the species in 1978. Evenness is expressed as J following Shannon's formula $- \Sigma$ pi log pi/log s, where S is the species number in the plot and pi is the probability of samplin the i th species

treatment / plot	non-fertilized plots (J)	fertilized plots (J)
A 1	0,65	
B 1	0,78	
A 2	0,82	
B 2	0,77	
A 3		0,50
B 3		0,59
A 4	0,86	
B 4	0,87	
A 5		0,59
B 5		0,52
average	0,79	0,55
standard error	0,08	0,05

Observations in the field and experiments in the laboratory, showed that some part of the species settling in the sod-removed plots originated from the seedbank in the soil, e.g. *Mercurialis annua, Plantago major, Euphorbia helioscopia*, and *Cerastium holosteoides*. Other ones grew forth from subterranean parts extending to below 10 cm in the soil, e.g., *Ononis repens, Agrostis stolonifera, Elytrigia repens, Centaurea pratensis, Dactylis glomerata*, and *Taraxacum* species. Again other ones originated from both sources: *Chrysanthemum leucanthemum, Cirsium arvense, Carex flacca, Leontodon hispidus*, and *Plantago media*.

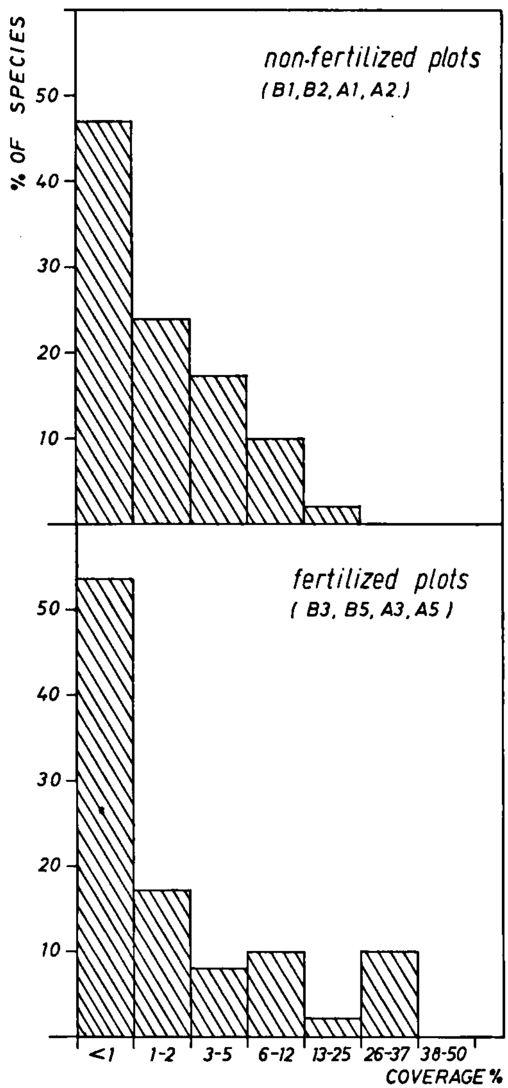

Fig. 5. The distribution of the percentage of species among coverclasses in four fertilized and four non-fertilized plots. In the latter ones the species equitability is higher, i.a., by the absence of dominance.

b. Bryophytes

Following sod removal, the cryptogams were investigated in detail in the winter 1971–72. All species found before the interference were met with afterwards too, though in lower abundances. Furthermore, in many large, open places in the vegetation there was a community consisting mainly of ephemeral acrocarpic species: *Phascum cuspidatum, Pottia davalliana, Barbula convoluta, Bryum biocolor, Ceratodon purpureus, Bryum erythrocarpum, Bryum rubens*, and *Bryum klinggraeffii*. In plots A1–5 about 20 bryophytic taxa were found.

During the vegetational succession this moss community disappeared almost entirely. A few species persisted in small, open places, chiefly caused by animals; e.g. *Bryum rubens* and *Phascum cuspidatum* were still met with in 1975 and 1977. However, this also holds for non-fertilized plots without sod removal. (Table 2).

c. Above-ground plant biomass

In terms of biomass the period from 1973 to 1978 was about 10% less productive for the non-fertilized, sod-removed plots than it was for the non-sod-removed ones. This effect was mainly caused by the biomasses of plots A4 and B4 in 1975: 210 and 500 g/m^2, respectively. When these figures for 1975 are left out of account, the difference is reduced to 5%. We may thus conclude that in non-fertilized plots removal of the top soil layer had, during a period of 2 to 7 years after the interference, almost no influence on the above-ground biomass. Such an influence makes itself felt, however, in the fertilized plots were the biomass of sod-removed plots exceeded that of undisturbed ones by about 50% of the overall biomass of all fertilizer-treated plots.

4. DISCUSSION

4.1. *Phytosociological trends*

a. Phanerogams

During the period from 1970 to 1978 the vegetation on the slope (including the non-fertilized plots) changed from an **Arrhenatheretum elatioris**, with elements of the **Mesobrometum erecti** and the **Poo-Lolietum**, to a **Mesobrometum erecti**. This is expressed by the increase of species like *Brachypodium pinnatum, Leontodon hispidus, Agrimonia eupatoria, Ranunculus bulbosus, Scabiosa columbaria, Helictotrichon pubescens, Briza media, Carex flacca*, and *Linum catharticum*, as well as the new establishment of *Carex caryophyllea, Pimpinella saxifraga, Orchis militaris, Gymnadenia conopsea*, and *Ctenidium molluscum* (Braun-Blanquet & Moor 1938, Westhoff & den Held 1969). A number of species typical of the **Arrhenatheretum elatioris**, like *Heracleum sphondylium, Pimpinella major, Festuca pratensis, Knautia arvensis, Daucus carota*, and *Arrhenatherum elatius* (Westhoff & den Held 1969) are no longer dominant or disapeared altogether.

We may expect the vegetation development on the slope to lead to a type of vegetation closely resembling the **Prunella vulgaris subassociation** of the

Mesobrometum erecti as described by Bornkamm (1960) from the Leine area near Göttingen in Germany. Just like South Limburg, this region is located at the northern limit of the area in which limestone grasslands belonging to the **Mesobromion** are met with (Braun-Blanquet & Moor 1938, Shimwell 1971). The slope in the Gerendal faces to the North-West, and the community described by Bornkamm occurs predominantly on North-West-facing slopes. The expection regarding this development is substantiated by the occurrence of *Prunella vulgaris, Festuca pratensis, Veronica chamaedrys*, and *Bellis perennis*, and by the new establishment of species like *Senecio jacobaea* and *Luzula campestris* (Tables 2 and 3).

However, development of vegetation is "a much less orderly process than the development of an individual or, perhaps, the evolution of a population" (McNaughton 1977). All kinds of unexpected changes may occur, and therefore it is often hazardous to predict the course of succession. The conduct of *Festuca arundinacea*, for example, is quite unpredictable. In 1975 this species colonized the study area from the valley bottom. In Western Europe it mostly grows on moister soils richer in nutrients than do the great majority of the species on the slope (Kruijne *et al.* 1967, Ellenberg 1974). Nevertheless, during the last three years it is much on the increase.

b. Bryophytes

The bryophyte community met with on the slope in 1970 rather closely resembles the **Rhytidiadelphus squarrosus community (Squarrosion)** as described by von Krusenstjerna (1954) from the vicinity of Uppsala in Sweden. Species common to both communities are *Brachythecium rutabulum, Calliergonella cuspidata, Campylium chrysophyllum, Cirriphyllum piliferum*, and *Rhytidiadelphus squarrosus*. In the course of our observations this community maintained itself virtually unchanged in the non-fertilized plots and elsewhere on the slope. Only a few species increased, like *Ctenidium molluscum* and *Campylium chrysophyllum* (Tables 2 and 3). These species are typical of moderately dry calcarous grassland (Barkman 1966). The changes in the bryophytic vegetation are much less than those in the phanerogams; sometimes there are none. It seems as if the constitution of these two communities is governed by different ecological factors.

The moss community met with in the winter of 1971–72, after sod removal, consisting chiefly of small, annual acrocarpic mosses, is very similar to the subfederation **Phascion cuspidatae** Waldheim 1944 described from South Sweden (Waldheim 1947). The two have the following species in common: *Phascum cuspidatum, Pottia davalliana, Barbula convoluta, Bryum bicolor*, and *Ceratodon purpureus*. Waldheim (1947) emphasized the great floristic homogeneity of this community in Europe.

In the Gerendal this bryophytic community was also met with in small, open places (gaps) in the vegetation, in the years following the winter of 1971–72. It was mostly fragmentary and represented by a few species only. This holds for the entire slope, including the fertilized plots. Establishment of the species constituting this community dependes on the availability of gaps rather than on the trophic condition of the soil (Grubb 1976).

The species composition of the bryophytic vegetation may be governed chiefly by the exposition of the slope and the structure of the phanerogamic vegetation. The combination of autumnal mowing and animal activities (voles, badgers, honey-buzzards, earthworms, etc.) each year produces enough open places which can then be colonized by the community **Phascion cuspidatae.** Richards (1928) called such a bryophytic community a "winter ephemeral community".

4.2. *Species diversity, above-ground biomass, and stability*

In the course of our studies an evident relationship was found between species diversity and biomass: species richness and equitability are linked to low above-ground biomass; and vice versa. This is confirmed by results obtained elsewhere is parallel work (e.g., Golley & Centry 1965, van den Bergh 1979) and also with some of Odum's (1969) hypotheses.

Treatment with fertilizer enhances the biomass (e.g., Smith 1971, Reed 1977) but, in terms of succession it throws the community back to a younger, so-called "bloom" stage (Odum 1969). According to Odum it is one of the characteristics of such a younger stage that external disturbance interferes more strongly with this kind of vegetation than with a more mature, species-rich stage of development. The extreme drought of 1976 may be seen as such an external disturbance (Table 6). As to species numbers, this disturbance affected the fertilized plots more than the non-fertilized. In 1976 the average number of species was about 40% lower in the fertilized plots, as compared with 1975 and 1977, but only 6% in the non-fertilized ones. The above-ground biomass, however, in both kinds of plots shows a decrease of over 40% during the period concerned.

In the summer of 1976 a number of species were missing from the fertilized plots that had been there before, particularly some forbs with a low abundance/dominance value (Tables 4 and 5). Most of them were perennials, present in the year before as well as after the dry year, and we may assume that only their above-ground parts had been killed by the drought. This was not observed in most of the non-fertilized plots. If our assumption is right, it may well be due to the fact that plants in fertilized plots root much more superficially than in untreated ones, as shown by other studies in the same area (S.P.Tjallingii & J.H.Willems, unpublished data). In the fertilized plots the plant roots were mostly concentrated in the uppermost 10–15 cm of the soil; in unfertilized places they were much more homogeneously distributed down to a depth of about 30–35 cm. Deep rooting of herbs in unfertilized limestone grassland was also found in the Sheffield region of England (Al-Mufti *et al.* 1977).

In contrast with the results mentioned above, Knapp (1977) found a considerable decrease in number of species in permanent plots in a non-fertilized, species-riche limestone grassland in North-West Germany, as a consequence of the drought in 1976. This decrease was about 20% compared with the average species number in the two preceding years.

Van der Maarel (1978) did not find a period of drought during spring and early summer in 1970 to affect the species number of a species rich dune grassland on the Isle of Voorne, along the Dutch Northsea coast.

Recently, Al-Mufti *et al.* (1977) and Grime (1978, 1979) pointed out the relationship between species richness and biomass. The greatest species richness in herbaceous vegetation was found when the dry weight of standing crop plus litter was between 350 and 750 g/m^2. Grime (1978) called this range a "corridor of potentially high species density". When the biomass values are above or below these values, species richness declines rapidly though for different reasons. This leads to a "hump-backed relationship" (Grime 1978) when species richness is plotted against the weight of annual biomass plus litter. Above a value of 750 g/m^2 the number of species is reduced by the dominance of one or a few species, below a value of 350 g/m^2 by stress or damage (Grime 1979).

As shown by a glance at fig. 3, in the Gerendal, too, such a "corridor" emerges when species richness and biomass are plotted against each other. The greatest species richness is observed when the weight of the above-ground biomass lies between 150 and 350 g/m^2. Similar values were found for chalk grasslands elsewhere in continental Europe, e.g., in Sweden (Rosén & Sjögern 1973) and in East Germany (Reichhoff 1974). These values are much lower than those given by Al-Mufti *et al.* (1977) and by Grime (1978), though their measurements were also made in species-rich limestone grassland. This discrepancy may be due to the fact that in the Gerendal there is hardly any litter, as the plant material is annually harvested and removed. Here, the biomass is harvested from about 2 cm above the ground surface, without lethal effect on the plants, whereas Grime and his co-workers cut the plants in the laboratory at soil level (Grime, pers. comm.). In chalk grassland the vegetation is densely structured just above the soil level and much biomass is concentrated there.

As fig. 3 shows further, the plots with high species numbers nearly always fluctuate by less than 100 g/m^2 of dry weight per year, a much narrower range than found by Al-Mufti (1977) and Grime (1978). Our observations also show that the range may move from one year to another on the biomass axis. Sometimes, as in 1975, the "corridor" cannot even be clearly made out. This may be due to weather conditions fluctuating from year to year. In the spring and summer of 1976 the drought led to a stress situation as defined by Grime (1974, 1978, 1979). The "corridor" then moves downward on the axis on which the biomass is plotted, as already supposed by Grime (1979).

In 1973 the part of the forbs in the biomass of the non-fertilized plots was between 60 and 80%. Over the years this percentage decreased steadily; in 1978 it amounted from less than 50–60%. (Fig. 4). Such a change was also found by Golley & Gentry (1965) in an abandoned-field community. There during the first seven years the forbs had a greater part in the biomass than the grasses, the overall biomass remaining about equal. In the eight year one grass species, *Andropogon virginicus*, attained domination, and the biomass rose considerably. A parallel development seems to have taken place in the non-fertilized plots of the Gerendal. Locally the grass *Brachypodium pinnatum* became dominant, increasing in coverage as well as in biomass. Future observations must show in how far this expected development is actually taking place.

4.3. *The effect of sod removal*

Bornkamm's findings (1974) showed that after about 3 years the effect of sod removal in calcareous grassland near Göttingen is no more evident in the species composition. In the Gerendal about 3 years after the interference most weeds of arable land had disappeared.

In 1977 the vegetation of non-fertilized, sod-removed plots still differed slightly from that of undisturbed plots. The sod-removed plots in 1977 still had more rosette plants. In that year speces like *Scabiosa columbaria, Bellis perennis*, and *Prunella vulgaris* occurred only in these plots.

Most weeds disappear from the fertilized, sod-removed plots after a few years. According to Al-Mufti *et al.* (1977) this is due to competition in the soil, the moisture content during certain periods being of particular importance. The first to disappear after the weeds are low forbs like *Prunella vulgaris* and *Leontodon hispidus*, then often follow species like *Plantago lanceolata* and *P. media*. This occurs despite the fact that these species are able to produce larger leaves when fertilized and put them in a more vertical position, as observed during the study. Some tall-growing species are able to maintain themselves in the fertilized plots, or even to establish themselves there newly (Smith *et al.* 1971). In our study area this is exemplified by forbs like *Centaurea pratensis, Knautia arvensis, Hypericum perforatum,* and *Heracleum sphondylium.* This may be due to agricultural management, i.e., cutting of the stand which enables the rosette plants to thrive in autumn and early spring when they do not have to compete for light with tall grasses (Newman 1973) and when soil temperatures start reaching a critical level (Brouwer 1978). Mobilization of reserves from usually well-developed roots permits certain forbs in spring to compete successfully with fast growing grasses for light and space (Al-Mufti *et al.* 1977).

Production is strikingly higher in the sod-removed than in the undisturbed, fertilized plots; in fertilized plots where the top layer was removed in 1971 it was one-and-a-half times as much as in the plots then left undisturbed. As the humus-rich top layer was almost entirely removed, this difference was not expected. It did not occur in the non-fertilized plots. At present no explanation for the difference can be offered.

4.4. *Concluding remarks and prognoses*

The development of the vegetation in a number of fertilized and non-fertilized plots on former pastures mown annually for almost ten years has been followed closely. The observations lead to the conclusion that the quantity of above-ground biomass is inversely correlated with the species diversity of the vascular vegetation.

The largest fluctuations observed in the course of the experiments occurred in the plots with the highest biomass and the lowest species diversity. This highly productive vegetation is effected more largely by external interference than the vegetation with lower biomass. These observations confirm certain hypotheses concerning the correlation between above-ground biomass, species diversity, and the rate of change in species composition, as formulated by, i.a., Odum (1969) and van Leeuwen (1966, 1970).

Thus, concerning the two problems mentioned in the beginning of this paper, it can be concluded that:

– An obvious negative correlation between productivity and species diversity was found in chalk grassland vegetation, and

– A vegetation with a high species diversity proved to change less in species composition during a period of almost ten years, than a vegetation with a lower species diversity.

It will be necessary to continue the observations during the coming years, in order to distinguish certain trends in vegetation development from temporary fluctuations. It remains difficult to distinguish these two factors in the development of an ecosystem, as shown by van den Bergh (1979) on the basis of observations in grassland plots at Rothamsted which have now been studied for more than 120 years (Williams 1978).

During the next years the study will be continued and expanded. Further research will concentrate on, e.g., the seed bank and the possibility of regeneration of the vegetation in natural gaps (Grubb 1976, 1977) linked with the studies on sod-removed plots. Observations on soil and micro-climatic factors will be extended, and the structure of the vegetation will be taken into account to a greater extent (Barkman 1979), in order to gain more insight into the processes involved in the development of a plant community.

ACKNOWLEDGEMENT

The author likes to express appreciation and gratitude to the students in Biology at the Utrecht University for their pleasant and useful assistance during the fieldwork: Henk Greven, Hans van der Mast, Karin Noordam, Annie Verbiest, Chris Vlietstra, and Gerard Voskuilen. He is also much indebted to Dr. P.J. van den Bergh (Wageningen) for his useful comments on the manuscript, to Prof. Dr. K.U. Kramer (Zürich) for translating the manuscript, and to J. Wiegers (Amsterdam) for his yearly assistance on "harvesting-day" in the Gerendal.

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