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Effects of nitrogen fertilization on vegetation structure and dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grassland

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SUMMARY

During the last decade a sharp increase in dominance of *Brachypodium pinnatum* was observed in chalk grasslands. We hypothesize that the enhanced nitrogen input from the atmosphere caused this increase. Therefore, a N-fertilization experiment (with 120 kg N ha^{-1} in the first year, and 50 kg N ha^{-1} in the second and third year) was carried out in two Dutch chalk grassland sites. Phytomass of *Brachypodium* increased significantly in the N-fertilized plots, while the dry weight of other graminoids and forbs decreased. Vertical distribution of phytomass was affected by N-fertilization, too: dry weight of *Brachypodium* increased enormously in the layers 10–40 cm above soil surface. As a consequence, it overtopped most other species and light penetration in the canopy was markedly reduced. Nutrient analyses showed that this increase in *Brachypodium* was possible without enlarged storage of phosphorus in the vegetation. It is concluded that increased nitrogen availability favours dominance of *Brachypodium* in chalk grasslands.

Key-words: Brachypodium pinnatum, chalk grasslands, dominance, nitrogen and phosphorus economy, nitrogen fertilization, vegetation structure.

INTRODUCTION

Chalk grasslands are semi-natural, species-rich plant communities, which were once widespread in Western Europe. They decreased considerably in area during the second half of this century, when they lost their economic function as grazing areas (Wolkinger & Plank 1981; Ratcliffe 1984). A number of remnants of this vegetation have been set aside as nature reserves. Management is needed to prevent their natural succession into woodland (Wells 1974; Willems 1985). During the last decade an increase in dominance of the characteristic chalk grassland species *Brachypodium pinnatum* (L.) Beauv. (subsequently referred to as *Brachypodium*) has been observed in most West-European countries, even under different management practices as grazing (Wilmanns & Kratochwil 1983), mowing (Bobbink & Willems 1987) and burning (Zimmermann 1979). This increase in *Brachypodium* is negatively correlated with species number and diversity (Bobbink & Willems 1987).

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Table 1. Total above-ground phytomass, phytomass of *Brachypodium*, other graminoids and forbs (g dry weight m^{-2}) in the control plots of chalk grassland in August 1984 ($n = 5$)

	Wrakelberg	Gerendal
Brachypodium	185·0 (40·0)	136·1 (87·9)
Other graminoids	93·2 (34·9)	104·6 (50·4)
Forbs	58·6 (30·8)	186·7 (132·8)
Total above-ground	336·8 (31·9)	427·4 (92·5)

Values are means with standard deviations in parentheses.

It is a well-known fact that grasses often increase strongly in the vegetation as a result of enhanced nutrient availability, especially nitrogen (N). Increased inputs have changed *Calluna* and *Erica* heathland in The Netherlands into a monotonous grass vegetation dominated by *Deschampsia flexuosa* or *Molinia coerulea* (Heil & Diemont 1983; Berendse & Aerts 1984). Undoubtedly, a nutrient-limited ecosystem like a chalk grassland (e.g. Smith 1980) is sensitive to such eutrophication. Calculations of total annual input of N, based on wet deposition, in Dutch chalk grasslands yields estimates of 40–60 kg N ha^{-1} $year^{-1}$ (Bobbink *et al.* 1986). We hypothesize that this extra input has caused (1) the strong increase in *Brachypodium* and (2) the drastic change in vegetation structure during recent years. Therefore, we have started experimental research focusing on the question of whether this grass species benefits more than the other chalk grassland species from the extra N supply, and whether this effect has consequences for the vegetation structure and, consequently, species diversity.

SITES AND METHODS

Study sites

The chalk grasslands studied are situated in two nature reserves in Southern Limburg, The Netherlands. The Gerendal site (2 ha) is a north-west-facing slope (inclination 20°). This site has been a fertilized pasture but became a nature reserve in 1967. Since 1970 the investigated part of the slope has been mown annually in late autumn with removal of the litter (Willems 1980).

The second site, the Wrakelberg (4 ha), is a south-facing slope (inclination 15°). The vegetation has been mown annually in late autumn since the early 1960s when the area became a nature reserve (Bobbink & Willems 1987). At present both sites are covered by a phytocoenosis belonging to the *Mesobrometum erecti* Br. -Bl. ex Scherrer 1925 (Willems 1982).

Methods

In April 1984 six permanent plots, each 2×3 m, were laid out on both sites in a homogeneous part of the vegetation with a relatively low proportion of *Brachypodium*. Half of the plots were fertilized with 120 kg N ha^{-1} (as ammonium nitrate) in 1984, and with 50 kg N ha^{-1} in 1985 and 1986. The high N application in 1984 was added to accelerate the effects of fertilization. Phytomass distribution of the unfertilized plots in August 1984 is given in Table 1. All permanent plots were mown in November or December 1984 and 1985 with removal of the mown plant material.

Table 2. Total above-ground phytomass and litter (g dry weight m^{-2}) in chalk grassland with (N) or without nitrogen (O) fertilization in August 1986

	Wrakelberg		Gerendal	
	O	N	O	N
Total above-ground phytomass	366·9 (40·9)	485·4 (60·8)	479·0 (56·4)	566·1 (41·6)
Litter	6·1 (3·0)	6·6 (2·0)	7·2 (2·4)	7·3 (2·4)

Values are means with standard deviations in parentheses.

In August 1986 the vegetation was harvested: in each treatment six subplots (0·16 m^{-2}) were randomly chosen and clipped at the soil surface. The samples were sorted into: *Brachypodium*, other graminoids (grasses, *Carex* spp., *Luzula* spp.), forbs, bryophytes and litter. In all groups, except litter, standing dead and living plant material were taken together. After drying at 70°C for 48 h dry weight was measured.

In half of the plots, randomly chosen, light profiles and vegetation structure were analysed. Before sampling, vertical profiles for photosynthetically active radiation (PAR, 400–700 nm) through the canopy were measured at 5–10 cm intervals on bright sunny days with a line sensor (TFDL, Wageningen), with a light sensitive surface of 50 × 0·4 cm. In the samples from these plots dry weight of the different species groups was quantified in strata of 10 cm.

Special attention was paid to morphological characteristics of *Brachypodium*: the number of the flowering stalks was counted and their dry weight was measured. From each sample 20 vegetative shoots were randomly taken and individual shoot dry weight, shoot length and number of leaves were determined. The number of shoots of *Brachypodium* per m^2 was calculated from these data.

Nitrogen and phosphorus (P) concentration of the plant material of all species groups were measured colorimetrically after wet digestion with a continuous-flow auto-analyser (Skalar analytical; Breda).

Data were statistically analysed using BMDP4V for two-way analysis of variance. If necessary, data were log or arc-sine transformed (Sokal & Rohlf 1981).

RESULTS

Phytomass

Three years of N-fertilization resulted in an increase in total above-ground phytomass, 30% on the south-facing Wrakelberg and 20% on the north-west-facing slope in the Gerendal, compared with control treatment ($P < 0·01$, Table 2). Dry weight of the different species groups of the vegetation was affected too (Fig. 1). The phytomass of *Brachypodium* in the N-fertilized plots increased strongly ($P < 0·001$), dry weight in these plots became 50% higher than in the control plots on the Wrakelberg, and even 80% higher in the Gerendal. Dry weight of the other species groups, however, decreased: that of the graminoids by 24% and 67% ($P < 0·01$) and of the forbs by 28% and 62% ($P < 0·05$)

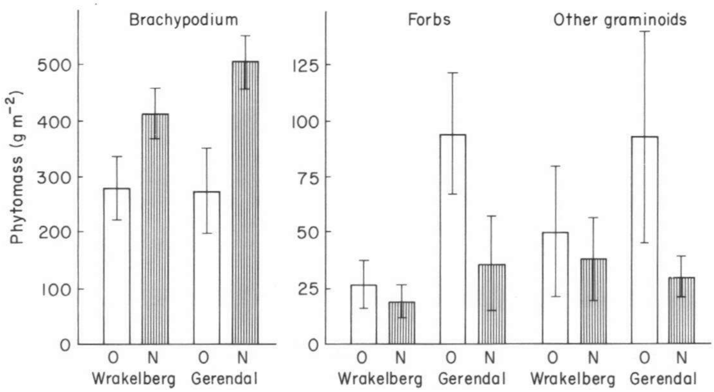

Fig. 1. Phytomass of *Brachypodium*, other graminoids and forbs (g dry weight m^{-2}; mean $\pm$ 1 SD) in August 1986 with (N) or without (O) nitrogen fertilization on two chalk grassland sites in Southern Limburg (the Wrakelberg and the Gerendal).

on the Wrakelberg and in the Gerendal, respectively. Results of the analysis of variance are given in Table 3.

Relative dry weight of *Brachypodium* increased towards *c.* 90% of total above-ground phytomass in all N-fertilized plots within 3 years ($P<0.001$). Remarkably, relative phytomass of *Brachypodium* in the unfertilized plots increased also since 1984: from 55 to 75% on the Wrakelberg, and from 32 to 55% on the slope in the Gerendal ($P<0.05$) (Fig. 2).

Morphological characteristics of Brachypodium

The effects of N-fertilization on morphological characteristics of *Brachypodium* were obvious: shoot length and shoot dry weight increased considerably ($P<0.001$) after 3 years. The number of leaves per shoot increased slightly ($P<0.01$). However, the number and dry weight of flowering stalks of *Brachypodium* and the total number of shoots per m^2 was not affected by N application (Table 4).

Light transmission and vegetation structure

The vertical distribution of phytomass was influenced by enhanced N availability (Fig. 3). On both slopes less dry weight is concentrated in the 0–10 cm layer after N-fertilization and total phytomass increased somewhat in the layers 10–40 above soil surface. Dry weight distribution of *Brachypodium* changed enormously in the N-treated plots: in all layers from 0 to 50 cm, especially in those 10–40 cm above soil surface, the amount of *Brachypodium* increased significantly (see also Table 3). Since no increase in flowering shoots after N treatment was found, this higher phytomass should be ascribed to an enhanced vegetative shoot phytomass of *Brachypodium*. The amount of other graminoids and forbs decreased in most layers on the Gerendal site, whereas the amount of forbs on the Wrakelberg site remained constant, or even increased, especially in the vegetation strata above 20 cm.

In line with these changes in vertical structure, penetration of radiation (PAR) through the canopy was considerably reduced in the N-fertilized plots (Fig. 4). In the more open vegetation of the Wrakelberg, the 50% light transmission point increased to more than 20 cm ($\pm$3·5) after N-fertilization, compared with *c.* 9 cm ($\pm$1·7) in the control plots ($P<0.01$). At 5 cm above soil surface the light penetration was reduced from *c.* 32%

Table 3. Summary of ANOVA results

	Source of variations		
	Site (S)	Fertilization (F)	Interaction (S × F)
Brachypodium	—	***	*
Graminoids	—	**	*
Forbs	**	*	*
Bryophytes	—	—	—
Litter	—	—	—
Total above ground DW	***	***	—
% *Brachypodium*	—	***	*
DW *Brachypodium* 0–10 cm	—	*	—
10–20 cm	—	**	—
20–30 cm	**	***	—
30–40 cm	***	***	***
40–50 cm	—	**	**
50–60 cm	—	—	—
50% light transmission point	***	**	—
% PAR near soil surface	***	**	**
% PAR at 25 cm	**	**	—
Shoot length BP	***	***	***
Number of leaves BP	***	**	—
Shoot dry weight BP	*	***	—
Number of flowering stalks	—	—	—
Number of shoots	—	—	—
% N in			
Brachypodium	**	—	—
Graminoids	—	***	—
Forbs	—	—	—
% P in			
Brachypodium	***	—	*
Graminoids	—	—	**
Forbs	*	—	—
Amount of N in			
Brachypodium	**	***	**
Graminoids	—	**	—
Forbs	**	—	**
Total above-ground	***	***	—
Amount of P in			
Brachypodium	**	**	*
Graminoids	—	**	—
Forbs	***	*	**
Total above-ground	***	—	—

BP = *Brachypodium*.
— Not significant, * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

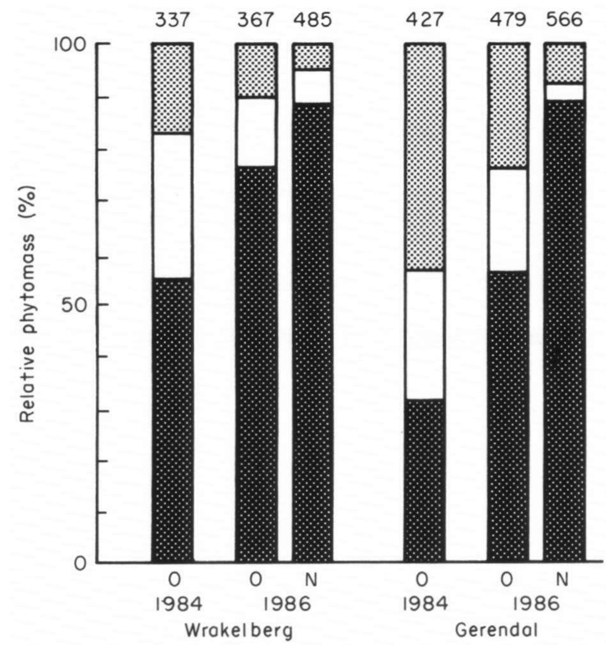

Fig. 2. Relative phytomass (%) of *Brachypodium* (■), other graminoids (□) and forbs (▨) in August 1984 (O) and in August 1986 with (N) or without (O) nitrogen fertilization on two chalk grassland sites in Southern Limburg. Numbers on top of the columns indicate peak standing crop in g dry weight m^{-2}.

Table 4. Morphological characteristics of *Brachypodium* in the N-fertilized (N) and control plots (O) in August 1986

		O		N	
Shoot length (mm)	Wrakelberg	44·5	(14·8)	59·1	(25·8)
	Gerendal	125·9	(42·9)	194·5	(67·0)
Number of leaves per shoot	Wrakelberg	1·7	(0·1)	2·0	(0·2)
	Gerendal	2·3	(0·2)	2·6	(0·4)
Vegetative shoot dry weight (mg)	Wrakelberg	89	(72)	133	(88)
	Gerendal	111	(70)	169	(102)
Number of flowering stalks (m^{-2})	Wrakelberg	265	(112)	320	(96)
	Gerendal	173	(94)	241	(110)
Number of vegetative shoots (m^{-2})	Wrakelberg	3041	(460)	2747	(457)
	Gerendal	2366	(420)	2854	(454)

Values are means with standard deviations in parentheses.

($\pm$4·1) of incoming radiation in the control treatment to 4% ($\pm$2·7) in the N-treated plots. On the north-facing slope in the Gerendal with a taller vegetation, N application resulted in similar changes in light transmission as in the vegetation on the Wrakelberg, except that light absorption occurred at a higher level above the soil surface (15 cm) in the Gerendal than on the Wrakelberg (Fig. 4).

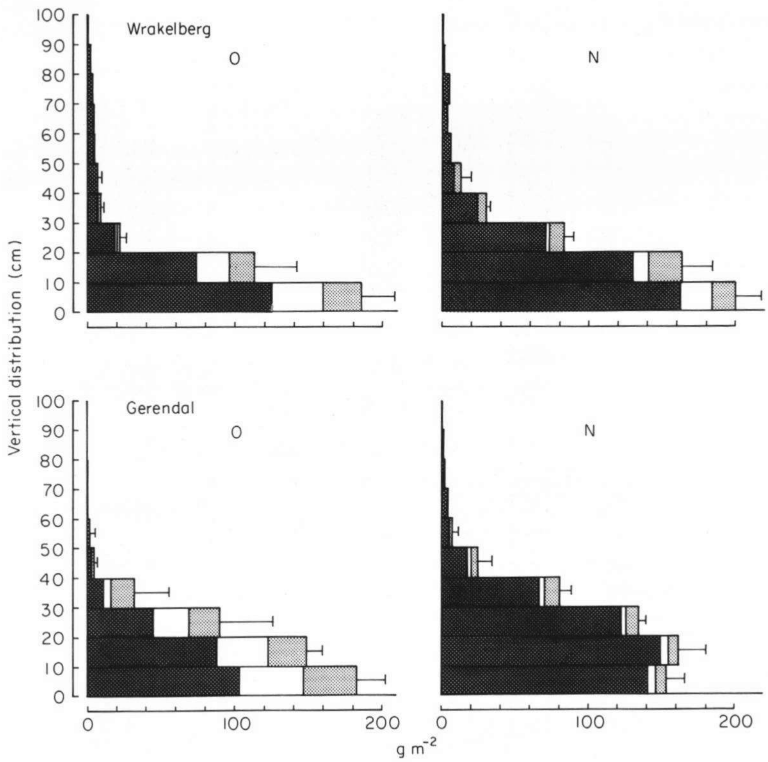

Fig. 3. Vertical distribution of above-ground phytomass of *Brachypodium* (■), other graminoids (□) and forbs (▨) (g dry weight m^{-2}; mean ± 1 SD) in August 1986 with (N) or without (O) nitrogen fertilization on two chalk grassland sites in Southern Limburg.

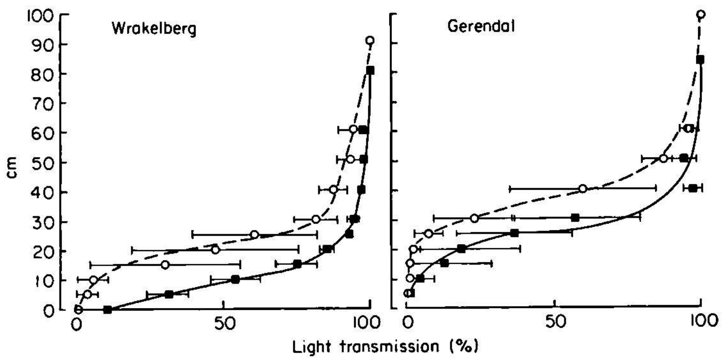

Fig. 4. Light transmission (% PAR; mean ± 1 SD) in the canopy (30 and 31 July 1986) after 3 years of N-fertilization (○) and in the control treatment (■) of two chalk grassland sites in Southern Limburg.

Nitrogen and phosphorus economy

Concentration of nitrogen and phosphorus in the above-ground plant material were only occasionally influenced by 3 years of N-fertilization. Only the concentration of N in the plant material of the graminoids increased, compared with the control treatment ($P < 0{\cdot}001$), while in the other species groups no differences were found (Fig. 5). The P

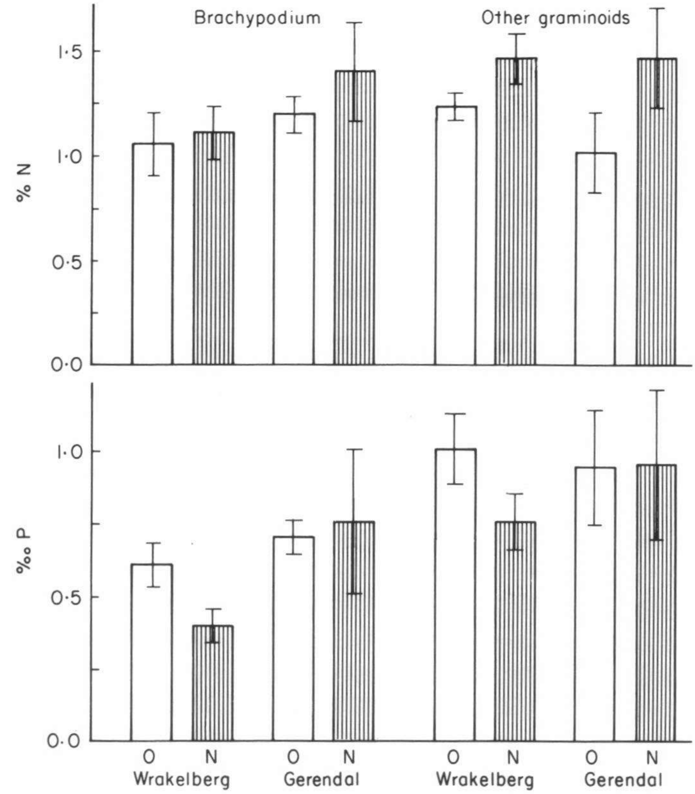

Fig. 5. Nitrogen (% N) and phosphorus concentration (‰ P) in the above-ground plant material of *Brachypodium* and the other graminoids in August 1986 with (N; hatched columns) or without (O; open columns) nitrogen fertilization on two chalk grassland sites in Southern Limburg. Bars indicate ± 1 SD.

concentration in the other graminoids ($P<0{\cdot}01$) and in *Brachypodium* ($P<0{\cdot}05$) was, however, lower in the plant material of the N-treated plots from the Wrakelberg. This difference was not found in the Gerendal where the concentration of both nutrients in the plant material mostly was higher than on the Wrakelberg, probably caused by the former agricultural fertilization of the Gerendal site until 1967.

After N application the total amount of N in the above-ground phytomass increased significantly at both sites ($P<0{\cdot}001$). This increase is completely accounted for by a higher amount of N in the above-ground plant parts of *Brachypodium* in the N-treated plots ($P<0{\cdot}001$). In these plots N storage in *Brachypodium* was almost 2 g N m^{-2} higher on the Wrakelberg and 4 g N m^{-2} in the Gerendal (Fig. 6). In contrast to N, no significant difference in the total amount of P in the vegetation was found between treatments. On the Gerendal site the amount of P in *Brachypodium* increased ($P<0{\cdot}01$) after N-fertilization, but at the same time the amount of P in the other species groups of the vegetation decreased.

DISCUSSION

The well-known low productivity of chalk grasslands is usually ascribed to deficiency of nutrients, mostly of phosphate and nitrate (e.g. Smith 1980). Application of large

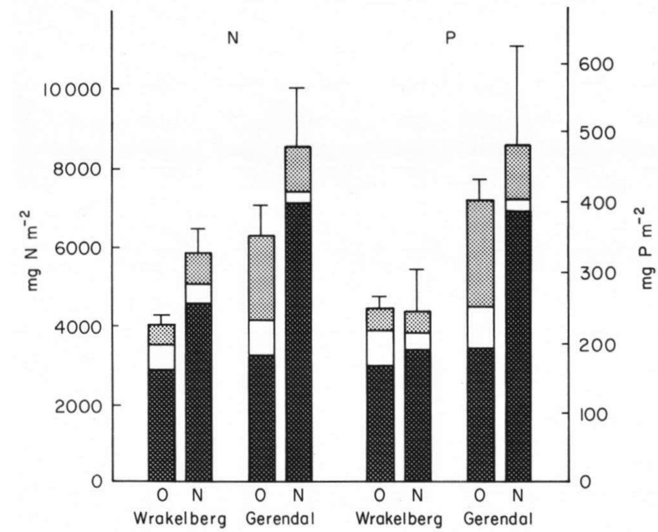

Fig. 6. The amount of nitrogen (mg N m^{-2}; mean$\pm$1 SD) and phosphorus (mg P m^{-2}; mean $\pm$1 SD) in the above-ground phytomass of *Brachypodium* (■), other graminoids (□) and forbs (▩) in 1986 with (N) or without (O) nitrogen fertilization on two chalk grassland sites in Southern Limburg.

amounts of artificial fertilizer (NPK) alters chalk grassland into tall, species-poor grassland, dominated by a few highly productive crop grasses (Willems 1980). Data from fertilization experiments with single nutrients in chalk grasslands are very scarce. Nitrogen application of 50 kg N ha^{-1} year^{-1} in a chalk grassland in England has caused an increased dry matter yield and a strong dominance of *Festuca rubra* (Smith *et al.* 1971). However, the most frequent grass species of continental European chalk grasslands, namely *Brachypodium* and *Bromus erectus*, were absent in the British site, and so results are difficult to compare. Although *Festuca rubra* occurred in our research sites, no increase in phytomass of this species was observed (Bobbink, unpubl.)

The primary aim of this study is to determine to what extent N availability limits *Brachypodium* in chalk grasslands. Fertilization with 120 kg in the first and 50 kg N ha^{-1} year^{-1} in two successive years, resulted in a vegetation with a slightly higher peak standing crop and in a sharp increase in *Brachypodium* (Figs 2 and 3; Table 2). The experimentally applied amount of N is probably somewhat more than the 'normal' input of N from the atmosphere. However, percolation of N from the soil of chalk grassland plots, receiving a similar amount of N-fertilization, is very low (less than 2 kg N ha^{-1} year^{-1}, D. Van Dam personal communication), which indicates that the extra input of N is retained within the system. Therefore, it is likely that the increased input of N in the last decades is responsible for the strong dominance of *Brachypodium*. The observed increase in dominance of this species in the unfertilized plots is in good agreement with this statement, because, unfortunately, N input has not stopped since 1984.

The results of the N application reported here show a strong increase in *Brachypodium*. Not only is this species limited by nutrient availability in the chalk grassland ecosystem, but also the other components of the vegetation. Low productivity of this community is mostly ascribed to deficiency of both nitrate and phosphate, since the availability of the latter nutrient is very low in such soils with a high pH (Lloyd & Pigott 1967;

Grime & Curtis 1976). Therefore, we also measured the P concentration in the plant material. In the Gerendal site the increased dry matter production of *Brachypodium* did not affect the P concentration in the shoot of this species (Fig. 5). This suggests that N is the most deficient nutrient at this site. The enhanced amount of P in the phytomass of *Brachypodium* might be caused by higher phosphate concentrations in the soil of this site, probably a result of the formerly agricultural use of this grassland. Another explanation of the observed higher P storage in *Brachypodium* after N-fertilization might be a more efficient nutrient uptake from the soil by *Brachypodium* than is the case with the other chalk grassland species. This may be caused by: (1) a higher uptake capacity of the root system (Brouwer 1977; Nye 1977); (2) a higher degree of mycorrhizal infection of the roots (e.g. Sanders & Tinker 1973) or (3) a more 'acid' nutrient uptake due to the fertilization with ammonium nitrate (Glass & Siddiqi 1982), with a higher rate of H^+ efflux resulting in a lowering of pH of the rhizosphere causing a better availability of P in these soils (Kinzel 1983).

However, on the Wrakelberg, the significant increase in phytomass of *Brachypodium* after N-fertilization is accompanied by a lower P concentration in this species (Fig. 5). These results suggest that at this slope (i) N and P both limit dry matter production and (ii) *Brachypodium* is better able to grow at low P levels than other chalk grassland species. The latter impression is also supported by the measurement of P in the control plots, in which in *Brachypodium* a lower concentration of this element has been found than is present in the other graminoids (Fig. 5). However, the properties of *Brachypodium* that enable this species to produce more phytomass in spite of a very low P concentration are still unclear.

The effect of fertilization on dry matter production in grasslands is a well-known phenomenon (e.g. Willems 1980; Van den Bergh 1979). Total phytomass, especially of grasses, increases and usually a taller vegetation is reported. The vertical structure of the canopy, a very important feature for the functioning of the vegetation (Barkman 1979; Werger *et al.* 1986), has mostly not been quantified. Since vertical architecture of the stand is strongly determined by the more abundant species (Fliervoet 1984), changes in abundance of these species can considerably affect the vertical structure of the canopy. After N-fertilization, vertical distribution of phytomass has changed in this experiment (Fig. 3), but total dry weight increased only *c.* 25%, compared with control plots. Therefore, the drastic changes in canopy structure could be largely ascribed to the changed morphology of the increasing dominant *Brachypodium*. In these stands the PAR penetration through the canopy is significantly reduced (Fig. 4). Thus, N application leads to overtopping of most of the other species by *Brachypodium* and, therefore, to a decrease in lower forbs and graminoids. Removal experiments of both predominant or less abundant species have confirmed this functional dominance of *Brachypodium* (Bobbink *et al.* 1987).

Many characteristic chalk grassland species are short-lived or of low stature, e.g. rosette plants. Apart from the lower light quantities near soil surface, the R:FR ratio will be lowered in these dense *Brachypodium* stands (Schenkeveld & Verkaar 1984). This might reduce germination of many short-lived species (Silvertown 1980; Schenkeveld & Verkaar 1984). When seedlings still emerge, the reduced light intensity at the level of their leaves, caused by the increased leaf mass of *Brachypodium*, will strongly hamper the growth and persistence of these species (Verkaar & Schenkeveld 1984). The decrease in species diversity with increasing dominance of *Brachypodium*, observed in this experiment after 3 years of enhanced N availability, is in accordance with these predictions.

The overall conclusion concerning the effects of increased nitrogen availability in chalk grasslands is that, in spite of a small change in peak standing crop, the vertical distribution of phytomass is strongly affected by increased dominance of *Brachypodium*. Extra nitrogen input favours the growth of this grass species. Due to the resulting change in vegetation structure, the light penetration in the canopy is reduced and germination and growth of many characteristic chalk grassland forbs are restricted. Analyses of nitrogen and phosphorus have revealed a very efficient nutrient economy of *Brachypodium*. In order to preserve the highly esteemed species diversity of chalk grassland, a management regime has to be developed that prevents nitrogen monopolization in *Brachypodium* and thus dominance of this species.

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