The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities*

J. G. Vermeer & F. Berendse**
Department of Landscape Ecology and Nature Management, University of Utrecht, Opaalweg 20, 3523 RP Utrecht, The Netherlands

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Abstract

The relationship was studied between shoot biomass, nutrient concentration in the soil and number of species per unit area. The study was carried out in two different parts of the Netherlands, the Gelderse Vallei (east of Amersfoort) and the Westbroekse Zodden (northwest of Utrecht). Four series of vegetation and soil samples were taken: one series in grassland and wetland communities, one series in grassland communities, one series in fen communities and one series in only one wetland community.

The two series in grassland communities show a negative correlation between shoot biomass and species number and a positive correlation between shoot biomass and nutrient concentration in the soil. The opposite was found in the series in the fen communities: there was a positive correlation between species number and shoot biomass and a negative correlation between shoot biomass and nutrient concentrations. The series of samples that had been taken in only one wetland community showed an optimum curve for the relation between shoot biomass and number of species. It is concluded that in the plant communities studied the species richness per unit area increases with increasing productivity at low production levels (< 400–$500\ g/m^2$) and decreases with increasing productivity at higher production levels (> 400–$500\ g/m^2$).

Introduction

Many of the methods to improve agricultural profits have a detrimental effect on semi-natural landscape elements. Eutrophication is one of the most important problems with which nature management has to deal nowadays.
It can be caused by the application of high levels of fertilizer to agricultural land, from which nutrient transport can occur by water flow to the neighbouring natural areas.

Lowering the groundwater table also causes an increase in nutrient availability by accelerating the mineralization in the soil (Black, 1969; Etherington, 1975; Léon, 1968). From fertilization experiments (van den Bergh, 1979; Golley & Gentry, 1966; Thurston, 1969; Willems, 1980; Williams, 1978; Willis, 1963) it is known that an increase in the nutrients available (N, P, K) can bring about an increase in biomass production together with a decrease in species number per unit area. Al-Mufti *et al.* (1977) and Grime (1973a, 1978, 1979) devised a more detailed model for the relation between species richness and shoot biomass. According to this theory in vegetation of low shoot biomass there will be severe stresses or disturbance factors operating leading to conditions in which only a few species can survive. In conditions where more nutrients are available more species have a chance to establish

* Nomenclature follows Heukels - Van Ooststroom (1977)

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themselves and species number per unit area and biomass production will increase. According to these authors this positive correlation between shoot biomass including litter and species number exists only up to a certain limit. When the availability of nutrients exceeds this limit, dominance of only a few species will occur as a result of competition for light (shoot) and space (root). Under these circumstances a negative correlation between shoot biomass including litter and species richness will be established (see also: Wheeler & Giller, 1982). Hence the relation between biomass and species richness can be described as an optimum curve. Because the main effect of eutrophication is expected to be the enrichment of the soil, together with an increase in biomass production, it is important to pursue the following question: What kind of relationship is there between the shoot biomass and the number of species per unit of area and between the shoot biomass and the availability of nutrients in the soil?

Study area

The study has been carried out in two different parts of the Netherlands: the Gelderse Vallei and the Westbroekse Zodden. In both areas several different plant communities were studied. The Gelderse Vallei is an agricultural area east of Amersfoort. In this area a series of six different plant communities was studied (Table 1: series 1). These plant communities range from a low productive community (dry grassland) to a highly productive one (reed swamp). The Westbroekse Zodden are found northwest of Utrecht. In the past peat was cut in this area traces of which are still to be seen. Some areas of open water were created by cutting the peat. However in other parts of the Zodden a succession of vegetation has led to a floating fen stage. Such fens consist of sods of living plants with many rhizomes (35 cm thick) growing floating on water (Table 1: series 3). Also there are parts of the area which consist of ridges of uncut peat and are mainly

Table 1. Short description of the plant communities of the different series (management, dominant species and soil type).

Study area	Management	Most frequently occurring species	Soil type
Series 1			
dry grassland	mown once a year	*Equisetum arvense, Aira praecox, A. caryophyllea, Hieracium pilosella, Agrostis tenuis*	sandy loam
wet grassland	mown once a year	*Juncus acutiflorus, Molinia caerulea, Carex panicea, Succisa pratensis*	clay on sand
hay field on a dike	mown twice a year	*Arrhenatherum elatius, Anthoxanthum odoratum, Rumex acetosella, Elytrigia repens*	marine clay
moist grassland	mown once a year	*Festuca rubra, Anthoxanthum odoratum, Carex riparia, Agrostis stolonifera, Juncus gerardii*	peat on clay
road verges	mown once a year	*Elytrigia repens, Carex hirta, Holcus lanatus,*	sandy loam
reed swamp	mown irregularly	*Phragmites australis*	clay
Series 2			
grassland	mown once a year	*Phalaris arundinacea, Holcus lanatus, Poa trivialis, Alopecurus pratensis*	ridges of uncut peat on sand (-1 m)
Series 3			
fens	mown once a year	*Juncus subnodulosus, Carex diandra, C. lasiocarpa, C. rostrata, Equisetum fluviatile*	floating peat layer (on water) sand at 1 m
Series 4			
wet grassland	mown once a year	*Succisa pratensis, Carex panicea, Cirsium dissectum, C. palustre, Molinia caerulea*	peat on sand (-1 m)

in use as grassland (Table 1: series 2). Another type of plant community is found at sites which are under the direct influence of a high water table (wetland – Table 1: series 4). We studied these different plant communities in a series ranging from low to high productivity in order to examine the relationship between nutrient availability, biomass production and species number per unit of area within one plant community and even within one vegetation type (wetland, Table 1: series 4).

Material and methods

In each series samples of vegetation and soil were taken at random in the central part of the area, so that edge effects were avoided. The samples were taken in the period in which the total aboveground biomass was expected to be at its maximum. In series 1 the samples were taken just before the first cut in the hay field which was mown twice a year. 30 samples of 10 by 10 cm were cut out down to 10 cm below the soil surface in series 1. In the other series the samples measured 20 by 20 cm. 40 samples were taken in series 2, 50 samples in series 3 and 104 samples in series 4.

Aboveground biomass – excluding bryophytes and litter – was harvested by clipping the vegetation at soil surface (Litter was difficult to sample because the removal of the gross biomass after mowing was irregular. Bryophytes, if occurring, mainly *Sphagnum* species, were excluded in sampling because of the difficulties in determination of the transition zone between living biomass and peat). The biomass was weighed after drying for 48 hours at 70 °C. The soil was sampled directly under the vegetation samples that were taken. Concentrations of nitrate, ammonium and the pH and the conductivity were determined after shaking 20 g of dry soil with 50 ml of distilled water and concentrations of potassium after shaking 20 g of dry soil with 100 ml of a mixture of hydrochloric acid (0.2 M) and oxalic acid (0.4 M). Concentrations of phosphate were measured after shaking 5 g of dry soil with 100 ml of distilled water. In series 1 dry soil was used; in series 2 and 4 weights of fresh soil were used which were equivalent to the amounts of dry soil mentioned. Because of a yellow brown colouring of the soil extracts in series 3, we took soil water samples at a depth of –15 cm in this series. Nitrate, ammonium, phosphate and chloride were determined colorimetrically and potassium by atomic absorption spectrophotometry.

Results

Series 1

In this series six plant communities (Table 1) were sampled ranging from middle to high shoot biomass (400–1000 g/m^2). Correlations between the several studied parameters were determined by means of linear regression analysis. The results show a significant negative correlation between biomass and species number (1–13 ssp/100 cm^2) and a significant positive correlation between shoot biomass and concentrations of PO_4^{3-} and NO_3^- (Table 2). This means we should find a high biomass when there is a high concentration of nutrients in the soil.

There is also a significant positive correlation between shoot biomass and pH (range 4.3–7.0). This is to be expected because a low pH has an inhibitory effect on root growth and therefore on the absorption of mineral nutrients and on the biomass production. The amount of mineral nutrients due to mineralization will also be very small under these low pH conditions (non-calcareous).

Series 2

Four grassland communities were sampled, which varied from medium to high shoot biomass (450–1150 g/m^2). Again a negative correlaton is found between shoot biomass and species richness per unit of area (range 3–12 ssp/400 cm^2; $p < 0.10$) and a significant positive correlation between shoot biomass and the concentrations of mineral nutrients K^+ and NH_4^+. There is also a significant positive correlation between plant biomass and the conductivity, the concentration of Cl^- and the water content of the soil.

Series 3

Five different fen communities were studied. In this series in contrast to the results found in series 1 and 2, there is an increase in the number of species (range 8–16 ssp/400 m^2) with increasing shoot biomass (175–500 g/m^2). It is evident that the plant

Table 2. The values of the correlation coefficient (r) for the correlations between biomass and species density and biomass and soil parameters. The level of significance is given by: * $= p < 0.05$; ** $= p < 0.01$; not det. = not determined.

		Species density (ssp/m²)	NO_3^- (ppm)	NH_4^+	PO_4^{3-}	K^+	Cl	pH	Conductivity (mS)	water content (%)
Biomass	series 1	-0.52**	0.54**	not det.	0.40*	0.17	-0.05	0.76**	not det.	not det.
	series 2	-0.21 (p<0.1)	0.06	0.72**	0.21	0.61**	0.54**	-0.06	0.39**	0.08
	series 3	0.42**	0.13	-0.31*	0.13	-0.05	-0.38**	0.24*	-0.46**	0.08
	series 4	-0.046	0.38**	0.08	0.32**	0.25**	-0.04	0.20*	0.08	-0.34**
	series 4a	-0.52*	0.28	-0.15	0.48*	0.53*	0.29	0.11	0.47*	-0.26
	series 4b	0.31**	0.17	0.05	0.07	0.03	-0.06	0.23*	-0.03	-0.27**

communities of the fens have a low productivity.

The correlation between shoot biomass and the determined soil parameters is significantly negative for the concentrations of Cl and NH_4^+ and for the conductivity (Table 2). Also remarkable is the positive correlation between the biomass and the pH (4.8–7.4). In the floating fen stage there is no correlation between the water content of the soil and the biomass because of the permanently waterlogged condition of the soil.

Series 4

This series was sampled in only one wetland community. The results for the total number of samples show no correlation between biomass and species number (2–13 ssp/400 cm²), but there is a significant positive correlation between shoot biomass and soil parameters such as concentrations of NO_3^-, PO_4^{3-}, K^+ and pH (range 3.8–6.6) and a significant negative correlation between shoot biomass and the water content of the soil. Because of the wide range in values for shoot biomass (110–940 g/m²) the samples were divided arbitrarily into those more than 425 g/m² (group 4a) and those less than 425 g/m² (group 4b). When we study these groups separately, we find a significant positive correlation between shoot biomass and species richness for series 4b, and a significant negative correlation between these parameters for series 4a (Table 2). There also are significant positive correlations between biomass and conductivity and the concentrations of K^+ and PO_4^{3-} at high productivity (4a). For the samples of low shoot biomass (4b) there is only a significant negative correlation between biomass and the water content of the soil and a significant positive correlation between biomass and the pH. The results on the relationship between biomass and species richness show the same correlations within one plant community as those found in series 2 and 3.

In accordance with all the results found in this study, we can expect an optimum curve for the relation between biomass and species richness. The top of the curve is at 425 g/m² for the wetland community, but this may be different in other plant communities.

Discussion

The results concerning the relationship between biomass and species number are in accordance with the model devised by Al-Mufti *et al.* (1977) and Grime (1979). We too found an optimum curve for the correlation between the studied factors for structurally similar plant communities and even for one plant community. Before we compare our results with the model of Grime and Al-Mufti *et al.* we shall comment on the way they assembled their optimum curve. Not only was this based on very few data, but these data were obtained in structurally different plant communities, which were situated on various soil types. In a study on the relationship between species number per unit of area and shoot biomass data can only be taken together if they are obtained in plant communities with a comparable structure. Series 2, 3 and 4 meet these demands as well as the demand that the plant communities have been under the same management for a long period.

There is also a difference in the optimum found by Grime (510 g/m²) and the optima found in our study (series 1, 2, 3: 400–500 g/m²; series 4: 425 g/m²). This difference may be the result of a different sampling method both in size of the samples and the measurement of the aboveground biomass. We excluded the biomass of the bryophytes and the litter, whereas Grime did not.

When we consider the correlations which were found for the fen communities (series 3) we see a significant positive correlation between biomass and species number. A possible explanation for this is that in the floating fen stage the conditions are not favourable for plant growth (high water table, low pH, anaerobic rhizosphere) and only a few species will be adjusted to these (Grime, 1979). An improvement of these conditions gives more opportunity for other species to establish themselves and to regenerate, because there are sufficient gaps in the comparatively open plant communities (Grubb, 1977).

Particularly the pH has a detrimental effect on the root growth (Brouwer, 1978), the mineralization in the soil and the availability of mineral nutrients (Armstrong, 1975; Black, 1968; Ernst, 1978; Léon, 1968). Therefore the uptake of water and nutrients, especially N, will be low. This is confirmed by the negative correlation found for the pH and the concentration of NH_4^+ (-0.41; $p < 0.05$). However we must realize that the nutrient content in the soil of series 3 was determined in soil water, in contrast with that of the other series. We consider the content of nutrients (N, P, K) in the plant material a more trustworthy parameter for the total amount of nutrients available during the growing season.

At the high production level there is a negative correlation between species number and biomass production (series 1, 2, 4a). This relationship is found in many fertilization experiments (van den Bergh, 1979; Thurston, 1969; Willems, 1980; Williams, 1978) and is in accordance with the theory of Grime (1979). Grime assumes that at high productivity the conditions are favourable for plant growth and this will lead to the dominance of a few species. Newman (1973) and Berendse (1981) refer to a shift in competition from root (nutrients) to shoot (light). From our study (Table 2) we can conclude that biomass increases with improvement of the nutrient supply and the species number decreases.

As an overall conclusion to our study we can say that the theory of Al-Mufti *et al.* (1977) and Grime (1979) is supported by the results found in series of samples which were taken in structurally similar plant communities and even within one wetland community. It is possible to construct an optimum curve for the relationship between species number per unit of area and shoot biomass. However the optimum can be expected to differ from one plant community to another. In further investigations the implications of these relationships will be studied, in particular in the border zones between semi-natural and agricultural ecosystems.

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