

Response of a weed community to nitrogen fertilization: a multivariate analysis

Pyšek, Petr¹ & Lepš, Jan²

¹*Institute of Applied Ecology, CS-281 63 Kostelec nad černými lesy, Czechoslovakia;*

²*Department of Biomathematics, Czechoslovak Academy of Sciences, Branisovská 31, CS-370 05 České Budejovice, Czechoslovakia; Tel. +42 38 817 ext. 214; E-mail KRIVAN%CSEARN@SEARN;*

Abstract. The effect of nitrogen fertilizers on the composition of a weed community was investigated in a barley field. Two doses (70 and 140 kg N/ha) of three fertilizers (ammonium sulphate, calcium-ammonium nitrate, and liquid urea) were used. The results were evaluated using the canonical correspondence analysis. Hybrid analyses and various combinations of environmental variables and covariables were used to separate the influence of the dose and the type of fertilizer and to separate the direct and indirect effects of fertilization. The results reveal that both the dose and type of fertilizer have a significant effect on the composition of the weed community. The results suggest that both the direct effect of fertilizer and an indirect effect, through increased competition of the crop, are important determinants of weed community composition.

Keywords: Canonical correspondence analysis; Competition; Direct effect; Diversity; Indicator value; Indirect effect.

Nomenclature: Rothmaler (1986).

Abbreviations: ANOVA = Analysis of Variance; CCA = Canonical Correspondence Analysis; DCA = Detrended Correspondence Analysis; GLM = General Linear Modelling; GLIM = Generalized Linear Modelling.

Introduction

Both observations and experimental studies have shown that nutrient supply can control the occurrence of species in plant communities (e.g. Tilman 1982, 1985). However, it is often difficult to separate the direct effect of a single nutrient on particular species from indirect effects mediated by changes in the community and the environment, even in controlled experiments. The major effect of an increase in nutrient supply may be the faster growth of all species of plants, which increases the competition for light.

The composition of a weed community is determined

by (a) environmental factors and (b) interference (in the sense of Harper 1977) between weeds and crop (e.g. Fogelfors 1972; Spitters & van den Bergh 1982) and among weeds themselves. In agrophytocoenoses, competition for light, water and nutrients are most important (Glauning & Holzner 1982).

The remarkable effect of fertilizers on weed communities has been described by many authors (e.g. Koch 1957; Böhnert 1981; Pyšek 1983; Tilman 1987). There have also been attempts to list species that indicate the nitrogen content of the soil (Walter 1963; Borg 1964). A scale of indicator values has been proposed by Ellenberg (1951, 1979) which has inspired authors from all over Europe (see Holzner 1982b).

Whereas the statistical evaluation of the effect of fertilizer on a single variable is more or less routinely done by using ANOVA, and in more complicated cases GLM or GLIM (see Jongman, ter Braak & van Tongeren 1987), the evaluation of the effect at the community level has long been a difficult task because of the many mutually dependent response variables, non-linear responses, etc. These difficulties can be overcome using Canonical Correspondence Analysis (CCA, program CANOCO, ter Braak 1987 a,b), which enables an evaluation of the influence of the environment on the composition of the community and provides a distribution-free Monte Carlo test of significance. Multivariate analysis was usually used as an explanatory data analysis, i.e. for inferring hypotheses from large observational data sets. CCA is not only designed for such explanatory analysis but also for hypothesis testing using data from controlled experiments.

Our study addresses the following questions:

1. What is the effect of fertilizer on the composition of the weed community of a barley field?
2. What are the differences associated with the dose or type of fertilizer used?
3. Is it possible to distinguish the direct effect of the fertilizer from indirect effects through increased

competition with the crop?

4. Is it possible to use a weed community as an indicator of the dose and/or type of fertilizer applied?

Material and Methods

The experimental summer barley field was located near the village of Samšín, South Bohemia, Czechoslovakia, at an altitude of 500 m a.s.l. This study exploited an experiment designed to evaluate the hydrological consequences of applying fertilizers. As it was not possible to influence the design of the fertilizer experiment, the quadrats are not true replications (they are pseudo-replications sensu Hurlbert (1984)). Consequently, the statistical analyses may be confounded by spatial heterogeneity of the field, which has not been controlled for.

The locality has a moderately humid climate typical of the highlands (mean annual temperature 6.8 °C, mean annual precipitation 657 mm). The soil is a sandy-clayey brown earth and the pH varied from 5.6 to 6.9. The phreatic level was between 2.6 and 6.0 m depth. The field, 30.5 ha, was divided into plots of ca. 3 ha, each of which was treated with different doses of ammonium sulphate, calcium-ammonium nitrate or liquid fertilizer (DAM 390), the main part of which is urea, combined with ammonium nitrate. For simplicity, the liquid fertilizer was referred to as liquid urea. A mixture of sulphate and nitrate was also applied. The doses of fertilizer used were 0,70 and 140 kg of total nitrogen/ha respectively. The dose of 70 kg corresponds to the agricultural levels in common use in the region for summer barley. The fertilizers were applied in three equal amounts (on April 20, May 20, and June 14) and the samples were taken at the end of June and in July 1983. The experiment started in 1976 using the same crop and fertilization design throughout the whole research period. The results thus represent the long-term effects of different fertilization patterns.

The weed community was sampled by means of randomly located quadrats of 1 m². In each quadrat, species occurrence was estimated using the seven-grade scale of Braun-Blanquet (Mueller-Dombois & Ellenberg 1974). The set of relevés was elaborated by classical non-numerical synthesis, based on methods of the Zürich-Montpellier school. An ordinal transformation (corresponding to that of van der Maarel 1979) on the 1-7 scale was used for calculations. Species diversity was calculated as mean number of species per plot S , as species diversity s.s., H' expressed by the Shannon formula (\log_2) (e.g. Peet 1974), and as species evenness J' according to Pielou (1966).

The changes in the community were evaluated using

Table 1. Characteristics of the experimental plots and frequencies of the most important species. Type of fertilizer used: S = sulphate, N = nitrate, U = urea, regardless of the dose used, regardless of the fertilizer type. Infestation is the sum of importance values (1 to 7 transformed values of Braun-Blanquet scale) of all weed species in a relevé. Species are characterized by their frequency in quadrats. Only species with frequency $\geq 10\%$ in at least one category are listed. Complete data are available upon request.

1 = Unfertilized; 2 = Fertilizer type S; 3 = Fertilizer type N; 4 = Fertilizer type U; 5 = Fertilizer dose 70 kg N/ha; 6 = Fertilizer dose 140 kg N/ha.

	1	2	3	4	5	6
Number of quadrats	19	34	29	10	57	46
Mean no. of species S	8.8	5.0	5.4	1.8	5.2	4.5
Mean diversity H'	2.96	2.00	2.15	1.67	2.21	1.72
Mean evenness J'	0.96	0.91	0.91	0.96	0.89	0.79
Mean infestation	17.1	11.8	12.3	4.8	13.0	10.0
<i>Veronica arvensis</i>	100	15	28	20	35	15
<i>Fallopia convolvulus</i>	79	41	79	20	70	33
<i>Thlaspi arvense</i>	68	18	10	0	12	13
<i>Myosotis arvensis</i>	95	65	52	40	67	54
<i>Viola arvensis</i>	58	47	28	30	42	37
<i>Stellaria media</i>	74	71	83	0	67	76
<i>Veronica persica</i>	79	26	41	0	44	24
<i>Galium aparine</i>	53	91	90	50	82	89
<i>Galeopsis tetrahit</i>	58	26	24	0	25	15
<i>Apera spica-venti</i>	5	6	7	40	7	11
<i>Medicago lupulina</i>	63	12	7	0	9	11
<i>Arenaria serpyllifolia</i>	16	0	0	0	0	0
<i>Equisetum arvense</i>	16	6	0	0	4	0
<i>Vicia angustifolia</i>	16	0	3	0	2	0
<i>Anagallis arvensis</i>	26	3	3	0	2	4
<i>Lamium amplexicaule</i>	21	6	0	0	4	4

CCA. The environmental variables, the type and dose of fertilizer, and estimated cover of the crop (barley) were used. It is clear that the cover of barley is not only correlated, but directly influenced by the fertilizer. Nevertheless, CCA is able to use environmental variables that are correlated; a combination of various analyses gave a rough estimate of the direct effect of fertilizer and the indirect effect due to changes in the cover of the crop.

To separate the sources of the variability in the weed community, various combinations of unconstrained, constrained and hybrid ordinations with various environmental variables were applied. The unconstrained ordination, DCA, provided an analysis of the overall variability of the whole relevé set. In subsequent analyses, environmental variables were used as follows: D - dose of fertilizer, C - cover of the crop, and T - type of fertilizer; T is a nominal variable, which was coded as four separate variables: S - ammonium sulphate, N - calcium-ammonium nitrate, U - urea, W - unfertilized.

Table 2. Summary of analyses and eigenvalues (λ) corresponding to the first three ordination axes. Eigenvalues corresponding to unconstrained axes are marked by '!'. Names of variables: D = fertilizer dose; C = cover of the crop; T = fertilizer type; No. = Number of analysis; T = type of analysis; EV = environmental variables included; CV = covariables.

No.	T	EV	CV	λ_1	λ_2	λ_3
1	DCA	-	-	0.453!	0.341!	0.262!
2	CCA	D,C,T	-	0.219	0.176	0.382!
2a	CCA	D,C,T	-	0.219	0.176	0.126
3	CCA	D,T	-	0.209	0.176	0.383!
4	CCA	D,T	C	0.177	0.143	0.382!
5	CCA	D	-	0.166	0.451!	0.335!
6	CCA	C	-	0.198	0.447!	0.337!
7	CCA	C	D,T	0.091	0.380!	0.308!

The hybrid analyses were used (only the first two axes constrained) to estimate that part of the variability in the community that can be accounted for by variability in the environment. CCA with all environmental variables was used to estimate the proportion of the community variability attributable to variability in the environment. The community variability attributable to particular environmental variables was estimated using several CCA runs, each with a single variable. However, the cover of the barley crop was highly correlated with dose and type of fertilizer (multiple linear regression, $R = 0.81$, $P < 0.01$). To separate the influence of cover from the direct influence of fertilizers, CCA was computed (1) with dose of fertilizer and composition of fertilizer as environmental variables and cover as a covariable, and (2) with cover as an environmental variable and fertilizer dose and composition as covariables. To determine the effect of a particular fertilizer, plots fertilized with 70 kg N/ha were analysed separately with the type of fertilizers as the environmental variable.

The results of the various species ordinations (i.e. species scores on CCA axes) were compared with the indicator values for these species given by Ellenberg (1979).

Results

Non-numerical analysis

The weed community in the unfertilized plots differed from that in the plots where nutrients were supplied (Table 1). Regardless of the type of fertilizer used there was a marked decrease in S , H' and J' when 70 kg of N was applied. After addition of 140 kg, the differences

were even more profound. The total infestation expressed as mean total dominance per relevé dropped with fertilization.

Of the types of fertilizer, liquid urea had the greatest effect. Plots treated with this fertilizer show the lowest total number of species, mean number of species per plot, species diversity and total infestation. However, it was not possible to distinguish plots fertilized with sulphate from those treated with nitrate. *Veronica arvensis*, *Fallopia convolvulus*, *Thlaspi arvense*, *Myosotis arvensis* and *Veronica persica* indicate low nitrogen, and *Galium aparine* and *Apera spica-venti* high nitrogen contents (Table 1). However, differences in the occurrence of the individual species were not associated with the type of fertilizer used, with the exception of *Veronica persica* and *Fallopia convolvulus*, the percentage occurrence of which was roughly doubled in nitrate-treated plots, and *Thlaspi arvense* and *Viola arvensis*, which occurred more frequently in the plots fertilized with sulphate.

Canonical correspondence analysis

The eigenvalues corresponding to the first three ordination axes were used to characterize the results of particular analyses (Table 2). In all cases but one (2a), the hybrid analysis was used, with only the first two axes constrained (if there was only one environmental variable, then only the first axis was constrained). Comparison of constrained ordinations with detrended correspondence analysis (DCA), and comparison of constrained and unconstrained axes showed that only a small part of the community variability may be ascribed to environmental variables. The correlation of the first DCA axis with environmental variables was relatively low ($R = 0.49$). The highest correlation was found with liquid urea ($r = 0.47$). The high proportion of unexplained variability is partly due to the low number of species per relevé and the strongly aggregated distribution of species within plots. Nevertheless, the first canonical axis was significant in all analyses, for analyses 2 to 6 $P = 0.01$, for analysis 7 $P = 0.05$ (Monte Carlo permutation test, constrained permutations used in analyses with covariables).

The amount of variability unexplained by the environmental variables could be estimated by comparison of the third eigenvalue in analysis 2 (all environmental variables used, hybrid analysis, first two axes constrained) and analysis 2a (the same but all three axes constrained).

In the CCA with all environmental variables (analysis 2a, Fig. 1) the first axis was determined mainly by the dose of fertilizer and cover of the crop, whereas the differentiation along the other axes was mainly due to type of fertilizer, particularly as the urea-treated plots differed considerably. The plots treated with nitrates and

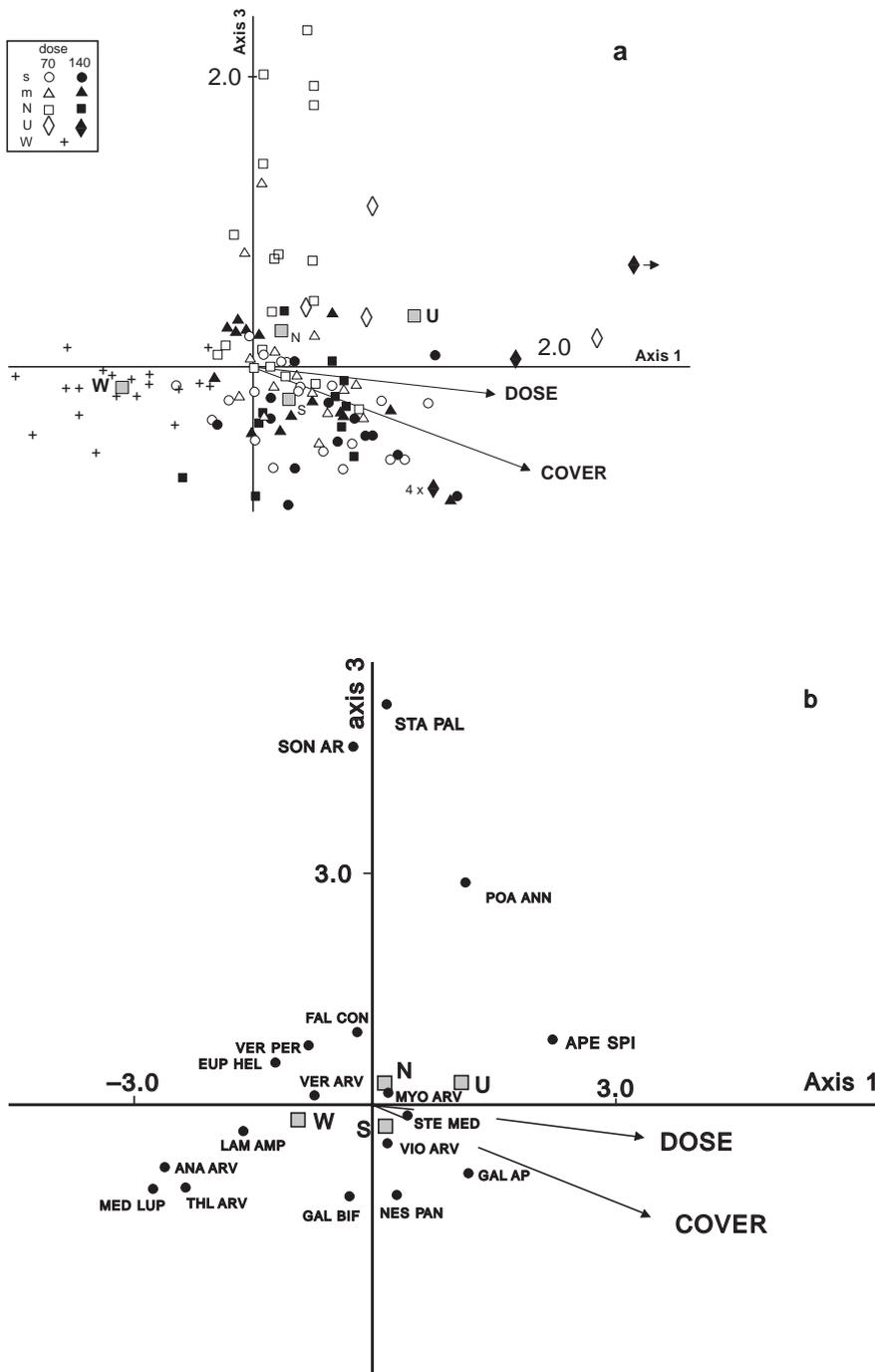


Fig. 1. Ordination diagram referring to analysis 2a (Table 2).

a. Ordination of plots. Symbols used for plots treated with different fertilizers are indicated in the left top part of the diagram. S = sulphate; m = mixture sulphate/nitrate; N = nitrate; U = urea; W = unfertilized plots. Centroids are indicated by hatched squares.

b. Ordination of species. ANA ARV = *Anagallis arvensis*; APE SPI = *Apera spica-venti*; EUP HEL = *Euphorbia helioscopia*; FAL CON = *Fallopia convolvulus*; GAL AP = *Galium aparine*; GAL BIF = *Galeopsis bifida*; LAM AM = *Lamium amplexicaule*; MED LUP = *Medicago lupulina*; MYO ARV = *Myosotis arvensis*; NES PAN = *Neslia paniculata*; POA ANN = *Poa annua*; SON AR = *Sonchus arvensis*; STA PAL = *Stachys palustris*; STE MED = *Stellaria media*; THL ARV = *Thlaspi arvense*; VER ARV = *Veronica arvensis*; VER PER = *Veronica persica*; VIO ARV = *Viola arvensis*. Species with frequency less than 5% are not displayed.

sulphates were relatively similar to each other and lie between unfertilized and urea treated plots. The second axis is highly correlated with the urea, and the plots treated with fertilizers other than urea are close to each other and difficult to separate. As the distinction of urea-treated plots is obvious, constrained axes 1 and 3 (analysis 2a) were used to construct a diagram in Fig. 1. Species with a high score on the first axis, i.e., those growing where the crop was dense on fertilized sites,

were mostly tall and erect weeds (e.g. *Apera spica-venti* and, with lower frequency, *Avena fatua* and *Chamomilla suaveolens*). Low scores on the first axis were found with low, prostrate, radially spreading species, which were not able to compete successfully for light with the crop, *Medicago lupulina*, *Anagallis arvensis*, *Lamium amplexicaule*, with lower frequency *Arenaria serpyllifolia*, *Vicia angustifolia*, *Spergula arvensis*. Apparently, competition for light increased and species diversity de-

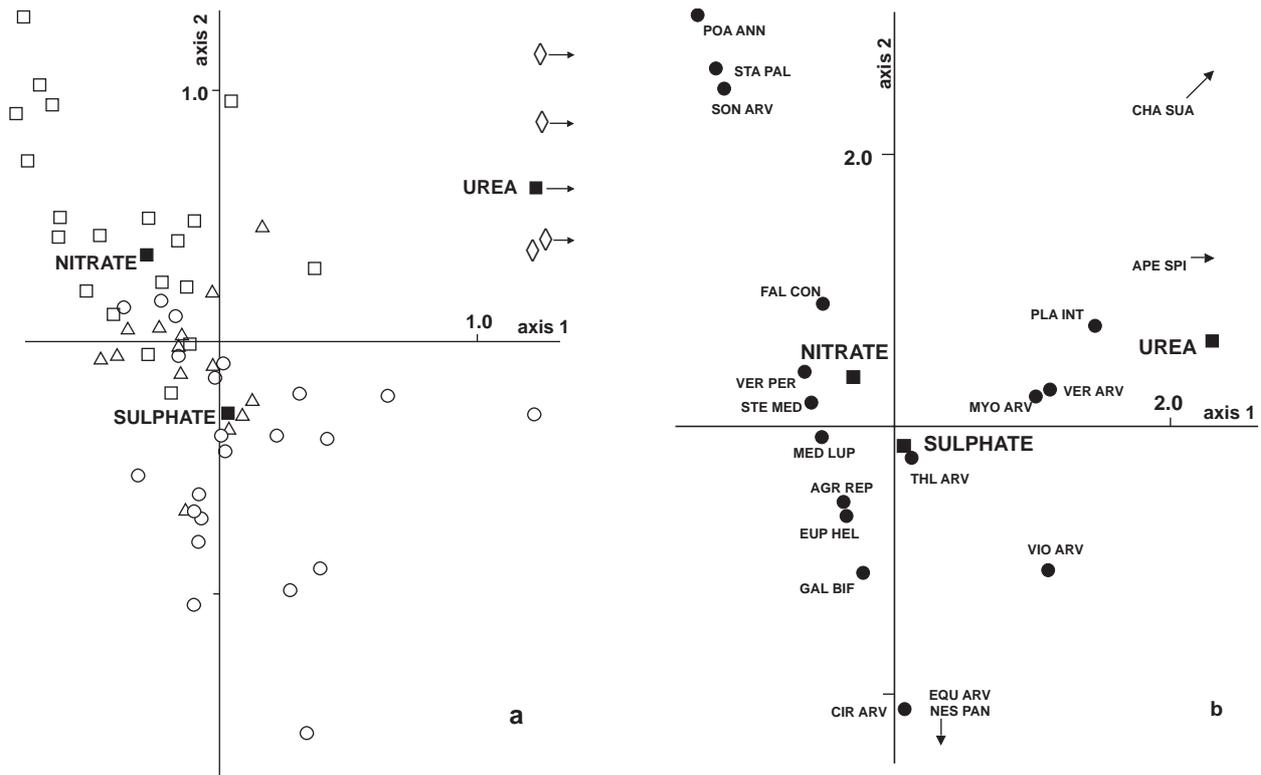


Fig. 2. Ordination diagram referring to a CCA of plots receiving 70 kg N.

a. Ordination of plots. Squares = nitrate; triangles = mixture nitrate/sulphate; circles = sulphate; diamonds = urea. Centroids are shown by full squares.

b. Ordination of species. AGR REP = *Agropyron repens*; CHA SUA = *Chamomilla suaveolens*; CIR ARV = *Cirsium arvense*; EQU ARV = *Equisetum arvense*; PLA INT = *Plantago major* ssp. *intermedia*. For other species abbreviations, see Fig. 1.

creased with increasing score on the first axis.

As the cover of the crop was highly correlated with dose and type of fertilizer, omitting the degree of crop cover or even dose and type of fertilizer (analyses 3 and 6) did not significantly decrease the first eigenvalue. On the contrary, only a small part of the variability was explained by the dose (analysis 5).

The hypothesis that the application of a fertilizer has only an indirect effect (mediated through the cover of the crop) was tested by analysis 4 (fertilizer dose and type as environmental variables and cover as the covariable). If there was only an indirect effect, then all the variability should be explained by the covariable. As there was a highly significant first canonical axis, it may be concluded that fertilizers had a direct effect on the species composition of the community. The first axis was mainly

determined by urea with the species *Avena fatua*, *Apera spica-venti*, and *Chamomilla suaveolens* having high scores.

The other question is whether there is any effect of crop cover that may not be ascribed directly to fertilizer dose and type. Analysis 7 (cover as environmental variable, dose and type as covariables) yielded the smallest eigenvalue and the first canonical axis was only marginally significant ($P = 0.05$). This was partly due to a high number of the covariables, which were highly correlated with the only explaining variable. *Poa annua*, and *Agropyron repens* had a high score on the first axis, i.e., they occurred in plots that had a relatively dense crop canopy. On the contrary, *Anchusa arvensis*, *Equisetum arvense*, and *Galeopsis pubescens* grew mainly in plots with low crop cover.

Because of the strong correlation between the use of fertilizers and crop cover it was very difficult to separate their effects on the composition of weed communities. Nevertheless, the analysis revealed that there was some effect of fertilizers that may not be ascribed to cover and vice versa. Consequently, both the direct effect of fertilizers and the indirect effect through increased competition with the crop were suggested by our data.

To reveal the precise effect of a fertilizer type, only plots receiving 70 kg of N were analysed (Fig. 2) with the type of fertilizer as (nominal) environmental variable. The first axis ($\lambda_1 = 0.252$) was determined mainly by urea treatment ($r = 0.82$) and the second one ($\lambda_2 = 0.158$) separates nitrate- and sulphate-treated plots ($r = 0.61$ and -0.73 respectively). A high proportion of variability remained unexplained; the third ('unconstrained') eigenvalue $\lambda_3 = 0.377$. The plots treated with nitrate and sulphate were only slightly separated; plots treated with a mixture of fertilizers were situated in between, whereas plots treated with urea were very different. Species ordination revealed those species typical of particular fertilizer types (Fig. 2).

Ordinary correlation coefficients were computed for the species' scores on the first (i.e. constrained) ordination axis of analyses 5 and 6 and their indicator values for light, moisture and nitrogen given by Ellenberg (1979). The indicator values for moisture and light were also considered, as they are thought to be secondarily affected by application of fertilizers. The correlation coefficients were used as a first approximation. Because the coefficient in no case exceeded 0.3, no further analysis was carried out and it was concluded that there is no relationship between the ordination scores and indicator values.

Discussion

Recently, weed vegetation has progressively impoverished over central Europe (Hilbig 1982). Weed communities are now very uniform, consisting typically of widespread, nitrophilous and shade tolerant species. Consequently, the use of weed communities as ecological indicators is more restricted nowadays. It is frequently reported that nutrient-poor environments have a great diversity of weed species (e.g. Glauning & Holzner 1982; Hilbig 1982; Holzner 1982a; Pyšek & Pyšek 1987; Ellenberg 1988). Tilman (1987) reported for American weeds that 60% of the species were replaced on high nitrogen plots during secondary succession in abandoned fields. Correspondingly, our results, showing that species richness decreased markedly with increased dosage of fertilizer, agree with the general trend.

Our study also shows that fertilizers have a signifi-

cant effect on the species composition of weed communities. Further, the results support the hypothesis that the species composition is influenced by both the direct effect of the fertilizer and an indirect effect mediated by increased competition with the crop. However, cover of the crop was not manipulated and all the evidence for indirect effect should be considered as correlation only. The cover of the crop is a non-manipulated part of the causal chain here; the rationale of using covariables for separating the direct effect from the indirect effect in CCA, as used in this study, is approximately equivalent to the estimation of causal relationships in Path Analysis (Jöreskog & Sörbom 1981). Because of the high correlation between the amount of fertilizer used and the cover of the barley crop, it was impossible to separate the direct from the indirect effect. This is probably the reason why there was no relationship between the response of the particular species to fertilization and their indicator values. Some species were greatly affected by an increase in nitrogen supply, whereas others were more affected by competition. For some species, mainly prostrate, low, laterally spreading ones, the dense cover of the crop deprived them of light so that they were unable to respond to an increase in nitrogen supply. Erect weeds similar in height to the crop were not shaded out and were able to take advantage of the increased nitrogen supply. So, although the effect of fertilizer treatment on the species composition was significant, it was not related to a single environmental variable in a simple way.

Both climatic and edaphic factors control the distribution of weed species. Moreover, their distribution is further complicated by agricultural practice. Whereas climatic factors influence the distribution of a species on a large scale, soil conditions influence the local patterns of distribution. The 'indicator value' of a weed species varies from area to area and is influenced by competition with other species, both weeds and crop plants (Holzner 1982b). Despite these difficulties, the species composition of a community may be indicative of environmental conditions. In many cases, the prevailing growth form is also an important indicator.

Ter Braak & Gremmen (1987) investigated the internal consistency of Ellenberg's indicator values for moisture in a large set of phytosociological data from natural and seminatural communities (more than 1000 relevés) and found the system to be reasonably consistent. However, they investigated the internal consistency only; they used relevés without environmental variables. We were not able to find any correlation between the response of species to nitrogen fertilization and its Ellenberg's indicator value. Perhaps Ellenberg's indicator values reflect phytosociological responses better on a large scale.

Canonical Correspondence Analysis proved to be a very useful tool for the analysis of controlled experiments. By various combinations of environmental variables and covariables it was possible to determine that the fertilizers had both a direct and an indirect effect through increased competition with the crop.

Conclusions

1. There was a clear effect of fertilizer on the weed species in a barley field, which resulted in a decrease in species diversity, changes in composition of species and of growth forms.
2. Both the dose and type of the fertilizer had a significant effect on the weed community. The plots treated with liquid urea differed markedly from the other plots, whereas those treated with sulphate and nitrate were relatively similar.
3. The weed community was influenced both directly by the fertilizer and indirectly by increased competition with the crop. The complete separation of these effects would, however, need further manipulative experiments.
4. The response of particular species to fertilizers was not related to the published indicator values.
5. The canonical correspondence analysis (via the program CANOCO) proved a useful tool for the analysis of controlled experiments.

Acknowledgements. Thanks are due to Anthony F. G. Dixon for critical reading of the manuscript and for linguistic help, František Krahulec for comments on the first draft, and Jana Pyšková for drawing the figures.

References

- Böhnert, W. 1981. Ergebnisse von Strukturuntersuchungen in unterschiedlich begünstigten Ackerunkrautphytozöosen. *Wiss. Z. Univ. Halle* 81: 103-114.
- Borg, P. 1964. Über die Beziehungen der Ackerunkräuter zu einigen bodenökologischen Faktoren in der Landgemeinde Helsinki. *Ann. Bot. Fenn.* 1: 146-160.
- Ellenberg, H. 1951. Landwirtschaftliche Standortkartierung auf pflanzengemässer Grundlage. *Z. Pflanzenern. Düng. Bodenk.* 53: 204-224.
- Ellenberg, H. 1979. Liste der Gefäßpflanzen Mitteleuropas. *Scr. Geobot.* 9: 1-122.
- Ellenberg, H. 1988. *Vegetation ecology of Central Europe*. 4th ed. Cambridge University Press, Cambridge.
- Fogelfors, H. 1972. The development of some weed species under different conditions of light and their competition ability in barley stands. In: *Weeds and weed control*, 13th Swed. Weed Conf., Uppsala 1: 4-5.
- Glauning, J. & Holzner, W. 1982. Interference between weeds and crops: A review of literature. In: Holzner, W. & Numata, N. (eds.) *Biology and ecology of weeds*, pp. 149-159. Junk, The Hague.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London.
- Hilbig, W. 1982. Preservation of agrestal weeds. In: Holzner, W. & Numata, N. (eds.) *Biology and ecology of weeds*, pp. 57-59. Junk, The Hague.
- Holzner, W. 1982a. Concepts, categories and characteristics of weeds. In: Holzner, W. & Numata, N. (eds.) *Biology and ecology of weeds*, pp. 3-20. Junk, The Hague.
- Holzner, W. 1982b. Weeds as indicators. In: Holzner, W. & Numata, N. (eds.) *Biology and ecology of weeds*, pp. 187-190. Junk, The Hague.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54: 187-211.
- Jongman, R. H., ter Braak, C. J. F. & van Tongeren, O. F. R. 1987. *Data analysis in community and landscape ecology*. Pudoc, Wageningen.
- Jöreskog, K. G. & Sörbom, D. 1981. LISREL V. *Analysis of linear structural relationships by maximum likelihood and least squares methods*. International Educational Services, Chicago.
- Koch, F. 1957. Die Unkrautgemeinschaften der deutschen Dauerdüngungsversuch Dikopshof (1904-1979). *Bayer. Landwirtsch. Jahrb.* 34: 403-457.
- Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. J. Wiley & Sons, New York.
- Peet, R. K. 1974. The measurement of species diversity. *Ann. Rev. Ecol. Syst.* 5: 285-307.
- Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13: 131-144.
- Pyšek, A. 1983. Differenzierung der Unkrautvegetation durch unterschiedliche Düngung mit Stickstoffhaltigen Mitteln. *Preslia* 55: 173-179.
- Pyšek, P. & Pyšek, A. 1987. Analyse der Unkrautvegetation eines Gerstenfeldes mit Berücksichtigung des Deckungsgrades und der Wuchshöhe des Gerstenbestandes. *Folia Geobot. Phytotax.* 22: 225-239.
- Rothmaler, W., 1986. *Exkursionsflora für die Gebiete der DDR und der BRD*. Volk und Wissen, Berlin.
- Spitters, C. J. T. & van den Bergh, J. P. 1982. Competition between crop and weeds: A system approach. In: Holzner, W. & Numata, N. (eds.) *Biology and ecology of weeds*, pp. 137-148. Junk, The Hague.
- ter Braak, C. J. F. 1987a. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69: 69-77.
- ter Braak, C. J. F. 1987b. *CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis*. TNO, Wageningen.
- ter Braak, C. J. F. & Gremmen, N. J. M. 1987. Ecological amplitudes of plant species and the internal consistency of Ellenberg's indicator values for moisture. *Vegetatio* 69: 79-87.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton.
- Tilman, D. 1985. The resource ratio hypothesis of succession. *Am. Nat.* 125: 827-852.
- Tilman, D. 1987. Secondary succession and the pattern of plant

- dominance along experimental nitrogen gradients. *Ecol. Monogr.* 57: 189-214.
- van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effect on community similarity. *Vegetatio* 39: 97-114.
- Walter, H. 1963. Über die Stickstoffansprüche (die Nitrophilie) der Ruderalpflanzen. *Mitt. Flor. Soz. Arb. Gem.* 10: 56-69.
- Walter, H. 1984. *Vegetation und Klimazonen*. Eugen Ulmer, Stuttgart.

Received 29 May 1990;
Revision received 25 January 1991;
Accepted 10 February 1991.