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Agriculture, Ecosystems and Environment 109 (2005) 1–8

Agriculture Ecosystems & Environment

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# Effects of abiotic factors on species richness and cover in Central European weed communities

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Received 15 January 2004; received in revised form 15 February 2005; accepted 17 February 2005

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## Abstract

Plant species richness and cover of 698 samples of weed flora, recorded in standard plots in the Czech Republic from 1955 to 2000, were related to altitudinal floristic regions, soil types, cultivated crops, climate, altitude and year of the record. Stepwise backward elimination of explanatory variables was used to analyse the data, taking into account their interactive nature, until the general linear model contained only significant terms. Net effects of particular variables on weed species number and cover, independent of covariance with other variables, were determined. Weed species number and cover were significantly affected by altitudinal floristic region and its interaction with the year of sampling. Both weed species number and cover decreased over time, more so in the moderate-to-cold than in the warm altitudinal floristic region, due to the increase in agricultural intensification being more profound at higher than lower altitudes. There was no direct effect of soil type on weed species number, whereas the decrease of weed cover with increasing crop cover was more pronounced on nutrient-poor than nutrient-rich soils. Maize fields contained the lowest number of weed species, while root crops and fodder plants were most species rich. Within the group of other cereals than maize, spring barley and oats harboured more weed species than winter wheat and, in particular, than rye. The differences in weed flora were largely attributable to management and partly related to crop-specific agricultural practices as well as general changes in the management of arable fields over the last decades.

*Keywords:* Agricultural management; Arable land; Crop characteristics; Czech Republic; Temporal changes

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## 1. Introduction

Species diversity remains one of the central topics in contemporary ecology and the object of various studies, from community to landscape level and in all types of ecosystems (Huston, 1994). At the regional

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doi:10.1016/j.agee.2005.02.018

level, diversity has been related to various factors such as area, altitude, productivity, landscape heterogeneity, successional status and disturbance (Huston, 1994; Swift and Anderson, 1994; Rosenzweig, 1995). These factors do not act separately but are to some extent mutually correlated, which makes it difficult to assess the role each plays in determining species richness (Kohn and Walsh, 1994; Pyšek et al., 2002a).

Human-made habitats represent extraordinarily species-rich environments (Wittig, 2002) due to habitat heterogeneity, frequent and diverse disturbances creating mosaics of different successional stages, intensive propagule pressure and immigration of alien species (Pyšek et al., 2002b). The factors promoting species richness and structuring vegetation of inhabited areas such as cities, villages or traffic routes are well identified (Wittig, 2002), whereas those acting on arable land are much less known. Arable land is not only disturbed with varying frequency, intensity and predictability but has been directly created by disturbance associated with agriculture since the Neolithic period (Holzner and Immonen, 1982). Disturbance can be described in terms of crop management but is difficult to quantify as it may interact with environmental factors (Pyšek and Lepš, 1991; Dale et al., 1992; Salonen, 1993; Erviö et al., 1994; Andersson and Milberg, 1998; Hallgren et al., 1999). Rigorous studies analysing the determinants of weed species richness are still rare (Stevenson et al., 1997; Kleijn and Verbeek, 2000; Hyvönen and Salonen, 2002).

Using a large data set of vegetation plots and statistical analysis that allows for determining the effect of individual factors unbiased by correlation with other variables, the present paper attempts to answer the following questions. 1. What are the main factors determining the number and cover of weed species on Central European arable land? 2. Do particular crops differ in the number of weed species they harbour? 3. How did the weed species richness change over the second half of the 20th century?

## 2. Materials and methods

### 2.1. Data set

A set of 712 sampling plots was used from the Czech Republic, a country which represents a suitable model for studies of diversity at a landscape scale (Neuhäuslová et al., 2001). Plots of a standard size of 100 $m^2$ were sampled by Z. Kropáč from 1955 to 2000, each plot only once. Plots were selected to cover the geographic, climatic and crop range of the territory, and located where weed vegetation was well developed. Except for maize fields where residues of herbicides were always present, weed communities recorded in the plots can therefore be biased towards higher species richness than average (Chytrý, 2001). However, direct comparisons of weed species richness and cover among these plots are possible as the same sampling strategy was used over the whole study period.

The presence of all vascular plant species was recorded in each plot and their cover estimated visually using the Domin 11-degree scale (Westhoff and van der Maarel, 1978). Average crop height was measured with an accuracy of 5 cm. Each plot was assigned to a soil type according to the FAO-UNESCO classification (1988) and to either the warm altitudinal floristic region (Thermophyticum sensu Skalický, 1988), or the moderate-to-cold altitudinal floristic region (combined Mesophyticum and Oreophyticum sensu Skalický, 1988). The other variables recorded in each plot are summarized in Table 1.

To verify that the data set was reasonably stratified by area and different habitats, the following procedure of stratified resampling was performed prior to data analysis. Only one plot per each phytosociological association, to which particular plots were assigned by Z. Kropáč, was randomly selected from each quadrangle of a geographical grid of 1.25 longitudinal × 0.75 latitudinal minute (ca. 1.5 km × 1.4 km). Oversampling in some areas was thereby eliminated. This procedure removed only 14 plots, and the remaining 698 were analysed. The plot records are stored in the Czech National Phytosociological Database (Chytrý and Rafajová, 2003; nos. 342001–342781).

### 2.2. Statistical analysis

The response variables were weed species number and weed cover. Species numbers were square-rooted to obtain an appropriate transformation for count data (Sokal and Rohlf, 1981). Cover values were expressed in % (Westhoff and van der Maarel, 1978) and arcsine transformed. All the data were evaluated using normal

Table 1
Environmental variables (covariates) recorded for the sampling plots

| Variable | Range |
|---|---|
| Year of record | 1955–2000 |
| Season | March–October |
| Altitude | 145–950 m |
| Climatic districts | 3–12 |
| Mean annual temperature | 4.5–9.5 °C |
| Mean temperature in January | −5.5 to −0.5 °C |
| Mean temperature in June | 11.0–18.5 °C |
| Annual precipitation | 425–1300 mm |

'Season' refers to the date of record given as the number of fortnights from 1 January. 'Climatic districts' were recorded on an ordinal scale increasing from cold/wet to warm/dry according to Quitt (1975). Temperature and precipitation were taken from Vesecký et al. (1958).

errors and identity link function. The explanatory variables were three categorical variables, further referred to as factors, i.e. crop identity (Table 2), altitudinal floristic region and soil type, and 10 ordinal or continuous variables, further termed covariates, including crop height, crop cover, and abiotic environmental variables (Table 1). All covariates measured on different scales were standardized to zero mean and unit variance.

Analyses of covariance (ANCOVAs) in GLIM® Version 4 (Francis et al., 1994) were done for the entire data set ($n = 698$), where cereals (except maize) were considered as a single group, and then repeated for the subset of cereals with four categories: barley, oats, rye and wheat ($n = 377$). The adequacy of the fitted models was confirmed by plotting standardized residuals against fitted values, and by normal probability plots of fitted values (Crawley, 1993). The aim of each analysis was to determine the minimal adequate model, in which the effects of all explanatory variables (factors and covariates) were significantly ($P < 0.05$) different from zero and from one another, and all non-significant explanatory variables were removed. This was achieved by a stepwise process of model simplification, beginning with the maximal model containing all factors, interactions and covariates and deleting non-significant to retain significant terms. This evaluation was carried out using a newly developed approach (Pyšek et al., 2002a, 2003), based on Lonsdale (1999). To prevent biases to the model structures caused by correlation between variables, model simplifications were made by backward elimination from the maximal models by using stepwise analysis of deviance tables (Crawley, 1993). The results obtained were thus not affected by the order in which the explanatory variables were removed in the stepwise process of model simplification.

## 3. Results

Overall variation explained by particular minimal adequate models was between 29.4 and 39.3%, except weed cover in cereals ($R^2 = 18.8\%$) (Table 3). Weed

Table 2
Summary of study crops and weed performance

| | No. of plots | Weed species number | | Weed cover (%) | | Crop height (cm) | | Crop cover (%) | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Barley (*Hordeum vulgare*) – 89% spring-sown | 65 | 33.4 | 7.7 | 49 | 12 | 52 | 17 | 65 | 11 |
| Oats (*Avena sativa*) – 100% spring-sown | 28 | 34.4 | 8.6 | 50 | 12 | 71 | 32 | 69 | 8 |
| Rye (*Secale cereale*) – 100% winter-sown | 110 | 29.4 | 8.3 | 47 | 12 | 98 | 63 | 65 | 9 |
| Wheat (*Triticum aestivum*) – 98% winter-sown | 174 | 31.5 | 8.0 | 50 | 10 | 68 | 38 | 67 | 9 |
| Maize (*Zea mays*) | 18 | 31.4 | 6.5 | 53 | 7 | 169 | 60 | 69 | 8 |
| Oilseed rape (*Brassica napus* ssp. *napus*) | 24 | 33.3 | 5.3 | 55 | 7 | 104 | 39 | 71 | 8 |
| Fodder | 95 | 33.3 | 8.0 | 49 | 13 | 49 | 34 | 65 | 14 |
| Stubble | 68 | 37.2 | 7.9 | 68 | 15 | 4 | 9 | 10 | 21 |
| Root crops (*Beta vulgaris* and *Solanum tuberosum*) | 90 | 39.8 | 9.6 | 56 | 11 | 37 | 15 | 45 | 21 |
| Vegetables | 19 | 33.4 | 6.7 | 54 | 11 | 34 | 17 | 49 | 17 |

*Fodder* includes mainly legume-grass mixtures, alfalfa (*Medicago sativa*) and alsike clover (*Trifolium hybridum*), *stubble* remains of crop after harvest and fields temporarily abandoned for less than one year. *Others* consist of 7 plots with flax (*Linum usitatissimum*), poppy (*Papaver somniferum*), sunflower (*Helianthus annuus*) and millet (*Panicum miliaceum*) (not shown).

Table 3
Overall significance and variation ($R^2$) explained by minimal adequate models (MAM), and parameters and significance of variables representing methodological biases (crop height, season; see text for explanation)

| | MAM | | | | Crop height | | | | Season | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $F$ | d.f. | $P$ | $R^2$ (%) | slope ± S.E. | $F$ | d.f. | $P$ | slope ± S.E. | $F$ | d.f. | $P$ |
| Species number: entire data set | 14.1 | 20,677 | <0.001 | 29.4 | 0.10 ± 0.035 | 8.7 | 1,678 | <0.01 | 0.25 ± 0.040 | 39.4 | 1678 | <0.001 |
| Species number: cereals | 20.7 | 8,368 | <0.001 | 31.0 | 0.36 ± 0.040 | 81.1 | 1,369 | <0.001 | – | – | – | – |
| Weed cover: entire data set | 9.9 | 43,654 | <0.001 | 39.3 | 0.017 ± 0.007 | 6.2 | 1,655 | <0.05 | [a] | 3.3 | 8662 | <0.01 |
| Weed cover: cereals | 9.4 | 9,367 | <0.001 | 18.8 | 0.042 ± 0.007 | 40.0 | 1,368 | <0.001 | – | – | – | – |

[a] Slopes co-vary differently ($F = 2.2$; d.f. = 7, 661; $P < 0.05$) in individual crops.

species number and weed cover increased throughout the growing season, as did the crop height. As a consequence, all the relationships of weed species number and cover with season and crop height were positive and consistent for all crops, except the relationship between weed cover and season for the entire data set, which differed significantly among crops (Table 3).

Species number and weed cover positively depended on season and crop height, reflecting the development during the growing season. In some analyses, response variables were significantly affected by both season and crop height (Table 3), while in others only one of them had a significant effect. For that reason, during the process of backward elimination from the maximal models only the variable that explained greater deviance when removed from the maximal model was accepted.

To reveal unbiased effects of other explanatory variables on weed species number and cover, significant effects of season and crop height were removed from further analyses. The residuals after removing these significant effects were then re-examined by the stepwise backward procedures and the net effects were identified of the (i) year of record and altitudinal floristic region, (ii) soil type, and (iii) crop identity. The net effects of year and altitudinal floristic region were analysed first. The analyses of the net effects of soil type and crop identity were made after removing the variables representing significant effects of the year of record and altitudinal floristic region.

The average number of weed species decreased significantly from 1955 to 2000 (Fig. 1) in both altitudinal floristic regions. At the beginning of the study period, species numbers were higher in the moderate-to-cold than in the warm region. Because the decrease in species numbers was significantly faster in the former region, at the end of the study period, the warm region had more species per plot than the moderate-to-cold one (Fig. 1). Weed cover remained significantly higher in the moderate-to-cold than in the warm altitudinal region (entire data set: $F = 6.28$; d.f. = 1, 696; $P < 0.05$; cereals: $F = 5.37$; d.f. = 1, 375; $P < 0.05$), independently of the year of record. Climate variables and altitude had no significant effect on weed species number and cover.

Soil types had no significant net effect on the number of weed species. Weed cover significantly decreased with the increase in crop cover on podzol, luvisol, phaeozem, calcaric regosol, chernozem and cambisol (Table 4). The decrease was particularly striking on nutrient-poor soils like podzol, and least on nutrient-rich like chernozem and cambisol.

Species richness in particular crops (Table 2) was highest in root crops, stubble and oats, and lowest in rye. After partialling out the correlations of crop identity with the year of record and altitudinal floristic region, maize was identified as species-poorest and root crops and fodder as richest in weed species (Fig. 2A). Within cereals, weed communities in barley fields were richest in species, while those in rye were the poorest (Fig. 2B).

Within cereals, a significant decrease of weed cover with increasing crop cover was found in barley and oats ($F = 9.80$; d.f. = 1, 375; $P < 0.01$), while it did not depend on crop cover for rye and wheat ($F = 2.69$; d.f. = 1, 374; NS).

## 4. Discussion

The decrease in richness of weed flora revealed in the present analysis over the period of 1955–2000 is

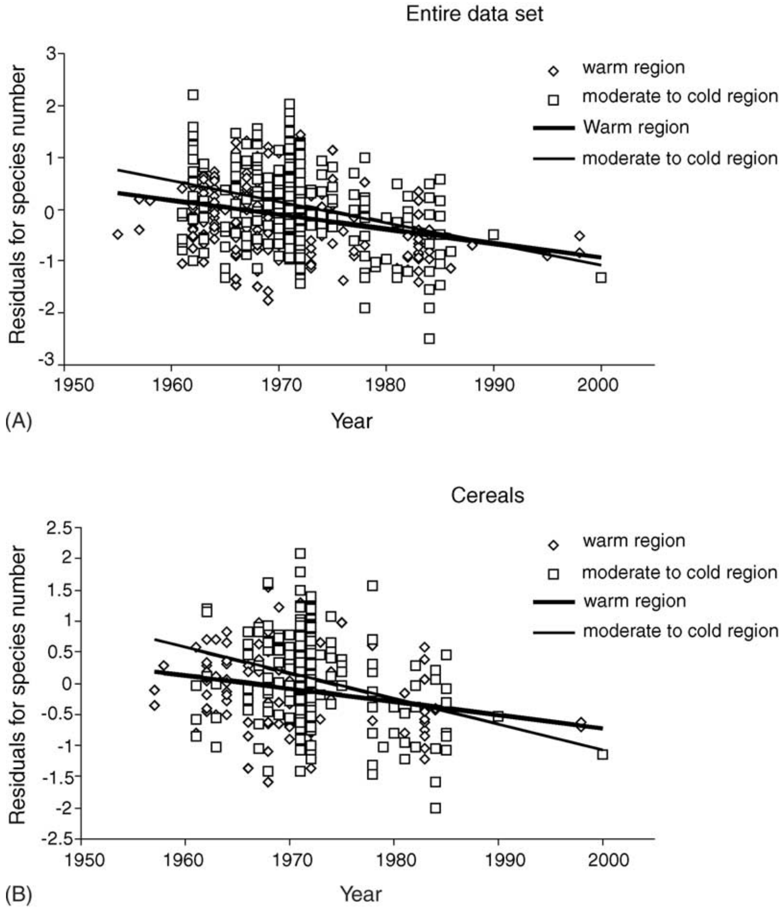

Fig. 1. Trends in weed species number analysed separately for the warm altitudinal and moderate-to-cold floristic region as residuals after subtracting the effects of seasonal development and crop height. (A) Entire data set: $S_W = -0.13–0.16 \times$ year; $S_{MC} = 0.11–0.24 \times$ year; $F = 26.07$; d.f. = 3, 694; $P < 0.001$; $R^2 = 10.1\%$. (B) Cereals: $S_W = -0.10–0.12 \times$ year; $S_{MC} = 0.12–0.24 \times$ year; $F = 11.49$; d.f. = 3, 373; $P < 0.001$; $R^2 = 8.5\%$. $S_W$ and $S_{MC}$ denote number of species in warm and moderate-to-cold region, respectively. Standardized data for years on horizontal axes are shown on the original scale.

Table 4
Net effects for the entire data showing significant ($P < 0.05$) regression slopes of weed cover on soil types with standard errors (S.E.)

| Soil type | Slope | S.E. | L.S.D. test |
|---|---|---|---|
| Podzol | −0.120 | 0.022 | a |
| Luvisol | −0.061 | 0.012 | b |
| Phaeozem | −0.045 | 0.022 | b,c |
| Calcaric regosol | −0.029 | 0.013 | b,c |
| Chernozem | −0.024 | 0.012 | c |
| Cambisol | −0.019 | 0.006 | c |

Slopes followed by the same letters are not significantly different in L.S.D. tests. $F = 75.77$; d.f. = 5, 692; $P < 0.001$; $R^2 = 9.9\%$.

consistent with the results of other studies from Central Europe (Hilbig, 1987; Kropáč, 1988; Hilbig and Bachthaler, 1992; Andreasen et al., 1996; Lososová, 2003, 2004; Lososová et al., 2004). It is usually attributed to technological changes leading to higher crop management intensity, such as increasing use of herbicides. The moderate-to-cold floristic region was more affected than warm lowlands as indicated by the trends in weed species number over time. At the beginning of the study period, arable fields in the moderate-to-cold altitudinal floristic region were richer in weed species than those in the

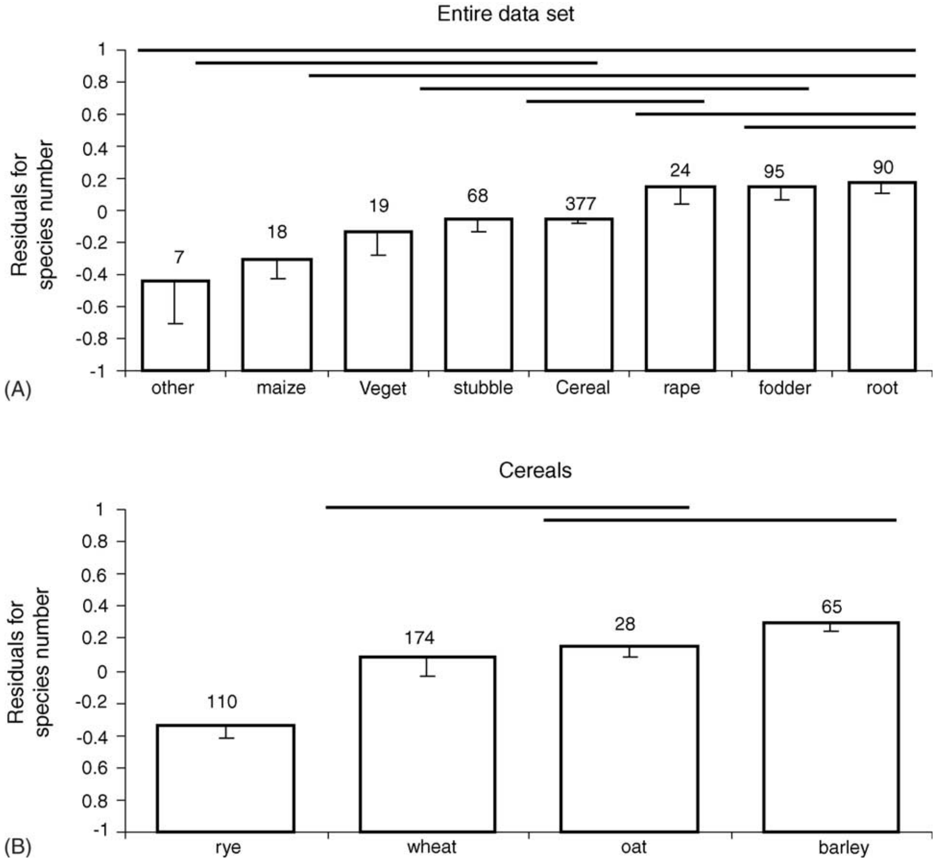

Fig. 2. Weed species number according to crops, analysed after subtracting the effects of seasonal development, crop height, altitudinal region and the interaction of the latter with the year of record. Horizontal lines indicate crop groups with average weed numbers not significantly different by least significant differences (L.S.D.), with sample sizes and S.E. (A) Entire data set: $F = 3.31$; d.f. = 7, 690; $P < 0.01$; $R^2 = 3.3\%$. (B) Cereals: $F = 17.72$; d.f. = 3, 373; $P < 0.001$; $R^2 = 12.5\%$.

warm region, but the decrease in species number over time was more pronounced in the former. It can be hypothesized that the intensification of crop production was already high in fertile lowland at the beginning of the study period. At higher altitudes, crop production was intensified later, decreasing the weed flora more progressively during the study period. An additional explanation may be based on the fact that at low altitudes, the beta-diversity of weed vegetation is higher than in submontane and montane areas (Lososová et al., 2004). Thus in the warm altitudinal region, the local loss of weed species richness due to agricultural intensification of the past decades may have been partly compensated for by the spread of adaptable species from different habitats. In the more homogeneous moderate-to-cold region, however, the local loss of species could not be balanced by the immigration of species from other habitats, which resulted in a more striking decrease in alpha-diversity.

After removing the effect of crop height and cover, soil type per se was not an important predictor of weed species richness. Species richness was possibly controlled through the soil fertility on crop production, which decreased weediness by competition (Pyšek and Lepš, 1991; Kleijn and van der Voort, 1997; Kleijn and Verbeek, 2000; Hyvönen and Salonen, 2002; but see Stevenson et al., 1997). Nutrient rich, productive habitats supported low species richness due to competitive exclusion by potential dominants (Grime, 1979; Huston, 1994). Fertilization and the intensity and mode of crop-specific disturbances can be therefore considered to override the effect of soil types on weed species richness.

Soil type had an effect on the generally negative relationship between weed cover and crop cover. Increasing crop cover caused a more profound decrease in weed cover on nutrient-poor than on nutrient-rich soils, suggesting that competition between weeds and crops was lower on nutrient-rich than on nutrient-poor soils (Ellenberg, 1950, 1988). The present results contradict the prediction of Grime (1979) that the strength of competition is greater in more productive habitats, and support the alternative hypothesis, i.e. that competition is most intense in plots with lowest resource levels (Tilman, 1988; Wilson and Tilman, 1993).

When the effects of climate, time, and crop growth characteristics were removed from analyses, the crop identity per se explained only little of the variation in species richness (3.3 and 12.5% depending on sample size). Obviously, a high proportion of unexplained variation was associated with factors beyond the scope of the present data set, such as the recent site history including crop rotation. Maize had the species-poorest and root and fodder crops the richest weed communities. Weed control in maize was based on pre-emergent application of triazine herbicides (Ballantine et al., 1998) which strongly reduced the development of weed communities. Weed control practices were traditionally less intensive in fodder crops (Kropáč et al., 1971) leading to a more diverse weed flora.

Weed communities of cereals other than maize were species richest in barley, poorest in rye. The fact that rye is the tallest of the cereal crops while barley is the shortest (Table 2) does not play a role here as the effect of crop height was removed from the model. Rye is well known for its ability to suppress weeds via allelochemicals (Barnes et al., 1986). Differences in weed species numbers among cereals could be related to either winter or spring sowing. As winter crops, rye and wheat, occupied the space already in autumn, they competed intensively with weeds in spring. This effect could be more profound in rye which grows faster and tends to be more productive in autumn than wheat. Oats and barley, which are mainly spring crops (93% of plots), were unable to exert such strong competitive effects on weeds. Differences in weed cover in cereals could also be attributed to the time of crop planting. Over the season weed cover in barley and oats decreased with increasing crop cover in spring cereals but not in winter cereals.

The pattern of species richness of weed communities in Central European arable land is complex, driven by a number of mutually correlated, often interacting factors. Differences in weed floras are largely attributable to management, which is partly related to crop-specific agricultural practices (Froud-Williams, 1988), and partly to broad-scale variation in environmental factors and to general changes in management of arable fields over the last five decades.

## Acknowledgement

We thank Ivan Ostrý, Jan Pergl, Irena Perglová, Katrin Karimová, Zdeňka Lososová, Marie Rafajová and Jiří Sádlo for technical support and Martin Chytrý, J.P. Aeschlimann and two anonymous referees for helpful comments. The work was supported by grant no. 526/00/1443 from the Grant Agency of the Czech Republic, the institutional long-term research plan AV0Z60050516 funded by the Academy of Sciences of the Czech Republic, and project MSM 0021620828 from the Ministry of Education of the Czech Republic. M.C. and L.T. were supported by grant MSM 0021622416 from the Ministry of Education of the Czech Republic.

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