Weed vegetation of arable land in Central Europe: Gradients of diversity and species composition

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Abstract.
Question: What are the main broad-scale spatial and temporal gradients in species composition of arable weed communities and what are their underlying environmental variables?
Location: Czech Republic and Slovakia.
Methods: A selection of 2653 geographically stratified relevés sampled between 1954-2003 was analysed with direct and indirect ordination, regression analysis and analysis of beta diversity.
Results: Major changes in weed species composition were associated with a complex gradient of increasing altitude and precipitation and decreasing temperature and base status of the soils. The proportion of hemicryptophytes increased, therophytes and alien species decreased, species richness increased and beta diversity decreased with increasing altitude. The second most important gradient of weed species composition was associated with seasonal changes, resulting in striking differences between weed communities developed in spring and summer. In summer, weed communities tended to have more neophytes, higher species richness and higher beta diversity. The third gradient reflected long-term changes in weed vegetation over past decades. The proportion of hemicryptophytes and neophytes increased, while therophytes and archaeophytes decreased, as did species richness over time. The fourth gradient was due to crop plants. Cultures whose management involves less disturbances, such as cereals, harboured less geophytes and neophytes, and had higher species richness but lower beta diversity than frequently disturbed cultures, such as root crops.
Conclusions: Species composition of Central European weed vegetation is mainly influenced by broad-scale climatic and edaphic factors, but its variations due to seasonal dynamics and long-term changes in agricultural management are also striking. Crop plants and crop-specific management affect it to a lesser, but still significant extent.

Keywords: Alien species; Altitude; β-diversity; Canonical Correspondence Analysis; Cereal; Czech Republic; Plant community; Root crop; Seasonal dynamics; Slovakia; Temporal change.

Nomenclature: Kubát et al. (2002).

Introduction

Weed communities on arable land are widespread and highly dynamic components of Central European vegetation (Holzner 1978; Holzner & Immonen 1982; Ellenberg 1996). So far, major broad-scale patterns of weed species composition and underlying environmental gradients have been studied mainly by phytosociological methods. Earlier studies from various countries of Central and West Europe supposed the main discontinuity in weed species composition to occur between cereal and root-crop cultures, as reflected in the division of high-level phytosociological units (Braun-Blanquet et al. 1936; Tüxen 1950; Oberdorfer 1993). Studies from the last decade, which used larger data sets, supposed the main discontinuity to occur between the weed vegetation of basic soils in drier areas and of more acidic soils in precipitation-rich areas (Hüppe & Hofmeister 1990; Ries 1992; Mucina 1993; Jarolímek et al. 1997). Multivariate analyses of broad-scale gradients in similar weed communities as occur in Central Europe, carried out in northern Europe (Salonen 1993; Erviö et al. 1994; Andersson & Milberg 1998; Hallgren et al. 1999) or southern Canada (Thomas & Dale 1991; Dale et al. 1992) also emphasized the role of geographical variability in climate and soil, which is usually more important for weed species composition than the effect of crops and associated agricultural management. For Central European weed vegetation, however, such an analysis has never been done.

Weed vegetation, consisting predominantly of annual plants, shows a much higher degree of temporal dynamics than other vegetation types in Central Europe. These dynamics operate both on the scale of seasonal changes (Kropáč et al. 1971; Holzner 1973, 1978; Lososová et al. 2003) and on a long-term scale, that corresponds to the gradually increasing intensification of agricultural production during the second half of the 20th century (Hilbig 1987; Kropáč 1988; Andreasen et al. 1996). Thus, gradients in

species composition of weed vegetation cannot be properly investigated without consideration of temporal patterns.

This paper applies multivariate statistical methods to a large data set of weed relevés from two Central European countries. Our objectives were to test the effects of broad-scale environmental gradients, crop plants and time on weed species composition, to rank the importance of these particular factors, and to describe patterns in species composition and diversity of weed vegetation associated with these factors.

Materials

We compiled a data set of 3481 relevés of agricultural weed vegetation of the Czech Republic (2596 relevés) and Slovakia (885 relevés). This data set included 1826 unpublished relevés of our own (in particular by Z.K., Z.O., Š.C. and Z.L.) and relevés taken from literature (e.g. Passarge & Jurko 1975; Mochnacký 1987; Otýpková 2001;) and other sources. The relevés are currently stored in TURBOVEG format (Hennekens & Schaminée 2001) in the Czech and Slovak national phytosociological databases (Chytrý & Rafajová 2003). For the analysis, we deleted all relevés lacking any indication of locality, date of record and crop plant. To achieve a reasonable stratification of the data set by geographical areas and by different vegetation types, we divided the area of the Czech Republic and Slovakia into grid squares of 1.25 longitudinal × 0.75 latitudinal minute (ca. 1.5 km × 1.4 km) and we also divided the relevés into spring (recorded before 1 June) and summer/autumn subsets (recorded on 1 June or later). If two or more relevés were recorded in the same grid square, the same crop plant and in the same period (spring or summer/autumn), we randomly selected only one of them. This procedure eliminated possible bias in the data set that may have been caused by oversampling of some areas, and yielded 2653 relevés, which were further used in analyses. These relevés were recorded between 1954-2003, mostly in the periods 1960-1985 and 1995-2003. Plot sizes ranged from 8 to 100 m^2.

Records of crop plants were deleted from the species data set and used as explanatory variables. A few plant records determined only at the genus level were deleted. Bryophytes were not considered as they play a negligible role in agricultural habitats and often are not recorded by researchers. Species cover values, estimated at different ordinal scales in original relevés, were transformed to percentages and square-rooted.

Four explanatory variables, presumably associated with variation in weed species composition, were compiled for all relevés: Altitude, Season, Year of record and Crop. The variable Season expressed phenological stages of weed vegetation during the growing season. It was derived from the date of record transformed into sequential numbers of half-month periods from the beginning of the year. For instance, 9 and 14 were the values used for the first half of May and the second half of July, respectively. Variable Crop included two broad categories strongly differring in agricultural management, further referred to as Cereals and Root crops, the former without mechanical disturbances applied during the period of crop growth while the latter were subject to regular hoeing, weeding or tilling. 'Cereals' included cereals itself (1355 relevés), recently abandoned fields (206), fodder (128), maize (119), stubble (92), and rapes (69) and the category 'Root crops' involved root crops themselves (427), vegetables (95), vineyards (86), and other crops (76).

Methods

First, we subjected the weed data set to Detrended Correspondence Analysis (DCA) from the CANOCO 4.5 package (ter Braak & Šmilauer 2002), in order to assess the overall variation patterns in species composition. DCA, a unimodal method, was used due to rather long gradients in compositional turnover encountered within the data set. For interpretation of DCA results in terms of environmental gradients, the four explanatory variables (Altitude, Season, Year, and Crop) were passively projected on an ordination scatter plot. These variables, however, were not involved in the extraction of ordination axes and the axes therefore correspond to the main gradients in species composition, that are unconstrained by explanatory variables.

Subsequently we tested gross and net effects of each of the four explanatory variables on species composition using canonical correspondence analysis (CCA; ter Braak & Šmilauer 2002). Gross effects were tested using separate CCAs with a single explanatory variable, followed by permutation tests for the first canonical axis (999 permutations were always used). Net effects, i.e. the effects of particular variables after partialling out the effects shared with the other explanatory variables, were tested using partial CCAs, each with a single explanatory variable and the other three variables used as covariables. Significances were again tested by permutation tests for the first canonical axis. Shared effects of different combinations of explanatory variables were tested using a series of partial CCAs. The ratio of particular canonical eigenvalues to the sum of all eigenvalues (total inertia) was used to measure the proportion of explained variation (Borcard et al. 1992). For the four partial CCAs in which a single explanatory variable was used, we listed scores along the first CCA axis for species with the highest fit in the analysis. The resulting species order reflected the

weed vegetation change along the gradient of the particular explanatory variable, after partialling out effects of the other variables. Other possible gradients in species composition that could not be explained by the four variables were assessed by partial DCA, in which these four variables were used as covariables.

Ecological interpretations of the gradients associated with the net effects of each explanatory variable were done by relating these gradients to Ellenberg indicator values for relevés (Ellenberg et al. 1992). To investigate structural changes in vegetation along these gradients, in addition to species composition, we used species richness and species classifications by life forms and by time of immigration for alien species. As the plot size varied in our data set, number of species was replaced by residuals from the regression of the number of species on log plot size, in order to remove variance in species numbers due to species-area relationship (Rosenzweig 1995). In the subsequent analyses, these residuals were used as a measure of species richness. Although the area effect was removed, the results for species richness must be interpreted with caution due to the non-random arrangement of sampling sites (Chytrý 2001). However, as we found no systematic bias in plot size with respect to environmental gradients, we believe that the patterns of species richness detected in our data set approximate the real situation.

Raunkiaer life forms were taken mostly from Ellenberg et al. (1992). Only therophytes, hemicryptophytes and geophytes were used in the analyses, as the other life forms were rare in weed vegetation. Alien species were classified according to Pyšek et al. (2002a) into archaeophytes (non-native species that appeared in the study area before 1500, and many of them already with the advent of Neolithic agriculture) and neophytes (non-native species that appeared during the last five centuries).

The net effects of each of the explanatory variables Altitude, Season, Year and Crop (the effects after subtracting correlated effects of the other three variables) were calculated for species richness and Ellenberg indicator values as dependent variables. For quantitative variables Altitude, Season and Year, net effects were determined using standardized residuals from general linear models in which each of these three variables was in turn used as a dependent variable and the other two plus categorical variable Crop as independent variables. Then species richness and Ellenberg indicator values were regressed on these standardized residuals. Standardization of the residuals enabled direct comparison of regression coefficients among explanatory variables measured on different scales. Net effects of categorical variable Crop were determined using analysis of covariance.

Relationships between life forms or groups of alien species and the net effects of the four explanatory variables were tested with a generalized linear model, using binomial distribution and logit link function (McCullagh & Nelder 1989), where the independent variable was species scores on the 1st canonical axis of partial CCA with the given explanatory variable and dependent categorical variable was species assignment to a particular category of life form or alien status. Only species whose fit in the partial CCA was higher than median were used in the analysis. All univariate statistical analyses in this study were calculated with the STATISTICA program (Anon. 2001).

In order to assess patterns of β-diversity (the mean difference in weed species composition among relevés) along the four major gradients, we partitioned the data set along the gradients, and for each partition we calculated β-diversity as mean Sørensen dissimilarity for all pairs of relevés ($1 - S$, where S is Sørensen similarity; Magurran 1988; Koleff et al. 2003). Then we determined confidence intervals for β-diversity in each partition, using 500 bootstrap samples (Efron & Tibshirani 1993) taken from the relevés belonging to that partition. This procedure was done in program JUICE 6.1 (Tichý 2002).

Results

Fig. 1 shows the variation in weed species composition, as detected by DCA. The first ordination axis explained 1.73% of the total variation in species data and corresponded to the altitudinal gradient, while the second axis (1.46% of total variation) was associated with other explanatory variables. The amount of variation in species data explained by net effects of particular variables, as detected by partial CCAs (Table 1), was highest for Altitude and decreased through Season and Year to Crop. The explained variation attributable to net shared effects of two or three variables was negligible. These four variables together explained 2.30% of the total variation in species data. The first and the second axis of partial

Table 1. Percentage variation in species data attributed to the effects of explanatory variables, as calculated by (partial) CCA. Gross effects include the total variation explained by the particular variable(s), including the variation shared with other variables. Net effects include variation explained by the particular variable(s), not shared with other variables. Percentage of net shared variation (∩) is only shown when exceeding 0.01%. F-values of the permutation tests are shown for partial CCAs, which were used to determine the net effects. ** = $P < 0.01$.

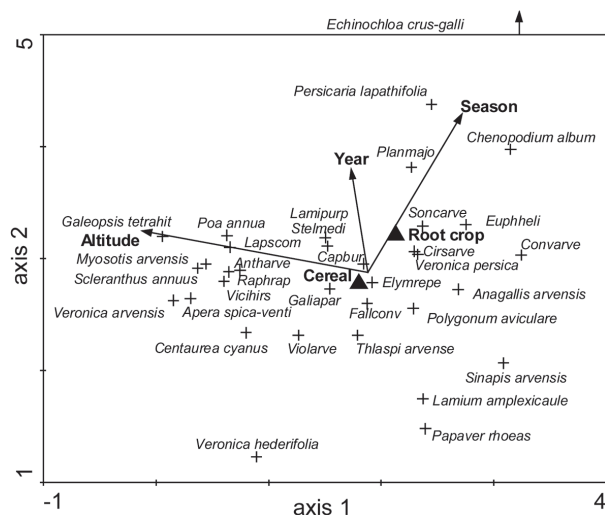|	Gross effects	Net effects	Permutation test: F-value
Altitude	0.84	0.84	22.760 **
Season	0.69	0.61	16.546 **
Year	0.51	0.48	13.201 **
Crop	0.37	0.26	7.143 **
Season ∩ Crop	-	0.08	
Year ∩ Crop	-	0.03	
All explanatory variables	2.30	2.30	

Fig. 1. Detrended correspondence analysis (DCA) diagram of species with passively projected explanatory variables for weed vegetation of the Czech Republic and Slovakia. Species with low weight are not shown. Abbreviations: Antharve = *Anthemis arvensis*, Capbur = *Capsella bursa-pastoris*; Cirsarve = *Cirsium arvense*; Convarve = *Convolvulus arvensis*; Elymrepe = *Elytrigia repens*; Euphheli = *Euphorbia helioscopia*; Fallconv = *Fallopia convolvulus*, Galiapar = *Galium aparine*; Lamipurp = *Lamium purpureum*; Lapscomm = *Lapsana communis*; Planmajo = *Plantago major*; Raphrap = *Raphanus raphanistrum*; Soncave = *Sonchus arvensis*; Stelmedi = *Stellaria media*; Vicihirs = *Vicia hirsuta*; Violarve = *Viola arvensis*.

DCA, calculated after partialling out the variation explained by the four explanatory variables, explained additional 1.59% and 1.10% of the total variation, respectively. Comparable proportions of the total variation explained by variables Altitude, Season, Year and Crop and by partial DCA indicate that these four variables are among the most important variables which affect weed species composition, however, there may also be a few other explanatory variables of comparable importance.

In spite of the low percentage of explained variation, the effects of each of these variables on species composition were highly significant and species ranks along the gradients of each variable had clear ecological interpretations (Table 2; next page). Interpretations of these gradients through Ellenberg indicator values are presented in Table 3. Beside changes in species composition, these four gradients were also correlated with other vegetation characteristics. Species richness was higher at higher altitudes, later in the growing season and in cereal fields, but decreased over the years. β-diversity (Fig. 2) decreased with altitude but increased from spring to summer and autumn. It was higher in root crops than in cereals, but showed no interpretable pattern of change over the years. Therophytes were more common at lower altitudes and in earlier decades of the second half of the
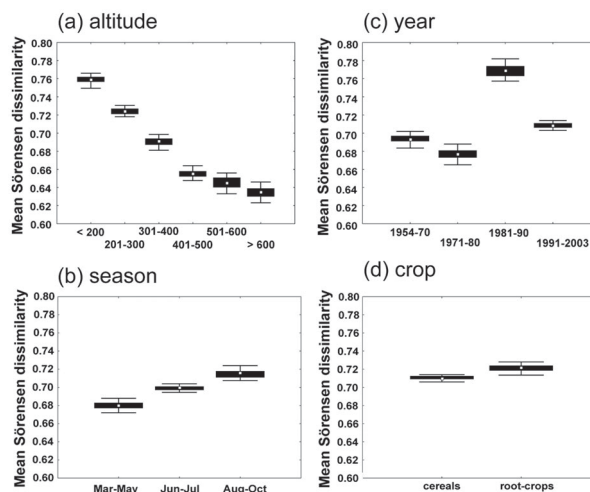

Fig. 2. Differences in β-diversity along four major gradients. β-diversity increases with mean pair-wise Sørensen dissimilarity calculated for groups of relevés. Boxes and whiskers indicate median and 50% and 95% percentiles, calculated from bootstrap resampling.

20th century, while hemicryptophytes showed opposite patterns. Geophytes appeared to be more frequent in root crops (Table 3). Representation of alien species, both archaeophytes and neophytes, decreased with altitude (Table 3). Archaeophytes exhibited a remarkable decline over the years, while neophytes tended to be progressively more common. Neophytes were especially found in root-crops and later in the growing season.

Table 3. Relationships between net effects of the four explanatory variables and vegetation characteristics. Relationships with Ellenberg indicator values and diversity measures were calculated by partial correlation coefficients. Relationships with life forms and alien species were expressed as coefficients of the generalized regression model. In categorical variable Crop, signs of unequality indicate significantly higher values found in either cereals (C > R) or root crops (C < R). ** = $P < 0.01$; * = $P < 0.05$; n.s. = non significant.

	Altitude	Season	Year	Crop
Ellenberg indicator values				
Light	– 0.056**	0.043**	0.010 *	C < R**
Temperature	– 0.111**	0.032**	– 0.012**	C < R**
Continentality	– 0.155**	0.020 *	– 0.044**	n.s.
Moisture	0.132**	0.040**	0.093**	n.s.
Soil reaction	– 0.284**	– 0.031 *	0.083**	n.s.
Nutrients	– 0.067**	0.036**	0.229**	C < R**
Species richness	1.376**	2.384**	– 0.768**	C > R**
Life forms				
Therophytes	– 0.777**	n.s.	– 1.126**	n.s.
Hemicryptophytes	0.677**	n.s.	1.074**	n.s.
Geophytes	n.s.	n.s.	n.s.	C < R*
Alien species				
Archaeophytes	– 0.797**	n.s.	– 0.641**	n.s.
Neophytes	– 0.715**	0.575 *	0.732 *	C < R*

Discussion

Low proportion of explained variation

The present analysis identified main gradients in weed species composition and interpreted them in terms of explanatory variables. Although the gradients had clear ecological interpretations, the variation explained by individual ordination axes was extremely low (< 2%). This could be partly attributed to the fact that some important explanatory variables, such as the effects of herbicides, fertilizing, crop rotation or land use in preceding years, were not considered in our analysis. In search for more powerful explanatory variables, we divided the Crop variable into more categories, but the amount of explained variation did not increase significantly and the results had a much less straightforward interpretation, therefore they are not presented here. Beside the low amount of total variation explained by variables Altitude, Season, Year and Crop, it was striking that unconstrained and partial unconstrained ordination (DCA, pDCA) also detected low variation, which suggested that the potentially missing variables were hardly more important than the four variables included. Thus the low proportion of explained variation was perhaps a consequence of (1) the large data set (2653 relevés × 544 species), resulting in a high amount of noise, and (2) the polynomial distortion of ordination axes, which had been shown by Økland (1999) to increase the total inertia and thus to underestimate the proportion of explained variation. Therefore we use the eigenvalue/total inertia ratio for comparison of the relative importance of individual explanatory variables or ordination axes rather than as real proportion of explained variation.

The effect of altitude

The most important gradient in species composition of weed vegetation covaried with altitude and associated climatic factors (temperature, precipitation) (Table 3). In the Czech Republic and less so in Slovakia the pH and nutrient status of soils is also correlated with altitude, as base-rich soils are mainly found in dry lowlands. Therefore there is a clear distinction between thermophilous, xerophilous and calcicole weed communities at low altitudes and communities of colder and wetter areas with acidic soils at higher altitudes. This result demonstrates that at the broad geographical scale, even the vegetation of a human-made habitat containing a large proportion of alien species and strongly depending on management, is more influenced by primary environmental factors than human activities. Similar results, which stressed the importance of climatic or soil variables on weed vegetation,

Table 2. Species with the highest fit in partial CCAs and their scores along ordination axis 1. Each column represents a separate partial CCA in which Altitude, Season, Year, and Crop were used in turn as the only explanatory variable while the effects of the other variables were subtracted by defining them as covariables. Low values of scores for respective variables are associated in turn with low altitudes, early season, earlier years and cereal fields. For an extended version of this table, see App. 1. [1]*Veronica hederifolia* includes *V. sublobata*.

Altitude Species	Ax 1 score	Fit	Season Species	Ax 1 score	Fit	Year Species	Ax 1 score	Fit	Crop Species	Ax 1 score	Fit
Setaria pumila	-0.97	0.057	Veronica triphyllos	-1.41	0.072	Myosotis stricta	-0.87	0.029	Apera spica-venti	-0.41	0.025
Amaranthus retroflexus	-0.94	0.058	Erophila verna	-1.35	0.053	Silene latifolia	-0.78	0.039	Euphorbia exigua	-0.37	0.022
Echinochloa crus-galli	-0.94	0.072	Veronica hederifolia[1]	-1.24	0.201	Papaver argemone	-0.76	0.028	Consolida regalis	-0.36	0.024
Consolida regalis	-0.63	0.072	Myosotis stricta	-1.07	0.044	Neslia paniculata	-0.60	0.061	Silene noctiflora	-0.28	0.020
Veronica polita	-0.62	0.065	Papaver argemone	-0.84	0.035	Arenaria serpyllifolia	-0.54	0.039	Vicia tetrasperma	-0.28	0.015
Silene noctiflora	-0.49	0.060	Arabidopsis thaliana	-0.73	0.065	Raphanus raphanistrum	-0.53	0.086	Vicia sativa	-0.23	0.020
Myosotis arvensis	0.33	0.089	Lamium amplexicaule	-0.70	0.118	Euphorbia exigua	-0.43	0.029	Anagallis arvensis	-0.17	0.020
Veronica arvensis	0.39	0.051	Descurainia sophia	-0.70	0.043	Sherardia arvensis	-0.42	0.029	Myosotis arvensis	-0.17	0.023
Raphanus raphanistrum	0.41	0.052	Lamium purpureum	-0.46	0.068	Scleranthus annuus	-0.41	0.037	Polygonum aviculare	-0.15	0.022
Vicia sativa	0.42	0.063	Thlaspi arvense	-0.38	0.089	Rumex crispus	-0.37	0.038	Viola arvensis	-0.13	0.022
Achillea millefolium	0.51	0.080	Stellaria media	-0.29	0.061	Taraxacum sect. Ruderalia	0.28	0.045	Euphorbia helioscopia	0.19	0.014
Lapsana communis	0.52	0.116	Capsella bursa-pastoris	-0.27	0.067	Galium aparine	0.29	0.051	Stellaria media	0.20	0.029
Ranunculus repens	0.53	0.074	Galium aparine	-0.25	0.038	Lapsana communis	0.32	0.044	Chenopodium album	0.27	0.049
Mentha arvensis	0.55	0.075	Anagallis arvensis	0.36	0.086	Ranunculus repens	0.34	0.031	Persicaria lapathifolia	0.29	0.023
Tussilago farfara	0.71	0.053	Plantago major	0.38	0.064	Lamium purpureum	0.43	0.058	Echinochloa crus-galli	0.51	0.021
Spergula arvensis	0.79	0.094	Medicago lupulina	0.40	0.034	Geranium dissectum	0.53	0.033	Amaranthus retroflexus	0.60	0.023
Rumex acetosella	0.81	0.063	Sonchus oleraceus	0.48	0.040	Poa trivialis	0.65	0.037	Galinsoga parviflora	0.70	0.030
Galeopsis tetrahit	0.91	0.326	Sonchus asper	0.53	0.090	Aegopodium podagraria	0.96	0.031	Solanum nigrum	0.71	0.016
Holcus mollis	1.32	0.086	Euphorbia exigua	0.54	0.046	Lolium perenne	1.06	0.062	Galinsoga quadriradiata	0.74	0.031
Alchemilla vulgaris	2.12	0.063	Setaria pumila	0.87	0.047	Galinsoga quadriradiata	1.14	0.073	Senecio vulgaris	0.89	0.035

were reported by studies from other geographical areas, such as Manitoba and Saskatchewan (Thomas & Dale 1991; Dale et al. 1992), Finland (Salonen 1993; Erviö et al. 1994) and Sweden (Hallgren et al. 1999). The dominant role of climate and soil in forming broad-scale compositional patterns of weed vegetation in Central Europe was discussed by Holzner (1978) and recognized in recent phytosociological surveys (Hüppe & Hofmeister 1990; Ries 1992; Mucina 1993; Jarolímek et al. 1997).

Altitude also influences the diversity of weed vegetation. Unexpectedly, species richness increases with altitude, which is in contrast with the decreasing patterns that are more commonly found in temperate regions (Begon et al. 1990; Pyšek et al. 2002c). Higher numbers of species per relevé plot at higher altitudes are probably due to a lower degree of agricultural intensification in less productive upland areas. By contrast, β-diversity, i.e. between-site variation in species composition, decreases with altitude (Fig. 2a). This pattern is consistent with the contrast observed between the remarkable seasonal dynamics and pronounced differentiation due to crop plants in the lowlands and warmer parts of Europe on the one hand and the rather uniform floristic composition throughout the season and across different crop plants in the highlands and cooler parts of Europe on the other hand (Holzner 1978; Holzner & Immonen 1982; Glemnitz et al. 2000). Similar relationships of floral and vegetation diversity to altitude as found in this study were reported for Central European urban vegetation (Pyšek 1993).

Altitude and associated environmental factors do not only influence species composition and diversity, but also a proportion of dominant life forms of weed vegetation, therophytes and hemicryptophytes. The proportional change from therophytes to hemicryptophytes along the altitudinal gradient, revealed in our study, suggests that at higher altitudes weed communities contain more species of adjacent vegetation, e.g. meadows and pastures, while the performance of ecologically specialized annual weeds decreases.

Our study also demonstrated that alien weeds, both archaeophytes and neophytes, showed a remarkable concentration of occurrences at lower altitudes, which corresponds to analogous patterns found in various vegetation types of Central Europe (Kowarik 1990; Mihulka 1998; Pyšek 1998a, b, 2002b; Sukopp 2002). In the context of the present paper this is not surprising for neophytes, recent newcomers from regions with often a warmer climate than the target area of Central Europe (Pyšek et al. 2003). However, our results indicate that also for archaeophytes, a group with thousands of years of invasion history in the territory studied, climate still acts as a major constraint to their wider distribution even in habitats to which they are perfectly suited.

Seasonal changes

The second most important gradient in weed species composition is related to seasonal dynamics. Short-living annual weeds form remarkably different communities in the course of a single growing season, with late-germinating thermophilous species appearing only in late spring and summer (Ellenberg 1996). In a phytosociological context, this observation led Kropáč et al. (1971) and Holzner (1973, 1978) to a proposal for a classification of spring, summer and autumn phenological aspects found on the same field as separate associations. The dynamics of thermophilous annuals, many of them neophytes, probably cause the increase in species richness and β-diversity during the growing season (Table 3, Fig. 2b). Increasing performance of heliophilous plants later in the season (Table 3) is probably caused by an increased light availability after crop harvest.

Changes over past decades

The third gradient in species composition is a historical gradient, reflecting the changes of weed vegetation over past decades. Our data set contained many relevés from the 1960s, as well as many relevés made after the mid-1990s, but only 13 relevés were from before 1960. This means that the vast majority of our relevés were from the period when most agricultural land in former Czechoslovakia was owned by large co-operative farms that had changed small fields into vast tracts of arable land with intensive management and heavy use of herbicides. This management resulted in a dramatic decline of diversity of Central European weed vegetation (Kropáč 1988; Hilbig & Bachthaler 1992; Lososová 2003). It is therefore possible that temporal trends in weed vegetation were not so striking as they would have been if relevés from the 1940s would have been involved in the comparison. In this respect, our results were similar to those of Hallgren et al. (1999), who found weak temporal trends in Swedish weed data from 1970-1994. Still, species order along the time axis (Table 2) and regression analyses (Table 3) indicate a decline in archaeophytic annuals (e.g. *Papaver argemone, Neslia paniculata, Raphanus raphanistrum, Euphorbia exigua, Sherardia arvensis*) and increase in neophytes, which is most striking in the American species *Galinsoga quadriradiata*. The overall decrease in species richness over time (Table 3) confirmed the results of the above mentioned studies on biodiversity decline in Central European weed vegetation. The pattern of β-diversity through time (Fig. 2c) had no clear interpretation. A pronounced peak in the 1980s was probably influenced by a lower intensity of sampling and associated bias in this period.

The effect of the crop plant

The type of crop affected weed species composition: thermophilous and nutrient-demanding weeds were more frequent in root crops. Cereal fields had higher species richness, lower β-diversity (Fig. 2d), and fewer geophytes and neophytes than root crop cultures (Table 3). The effect of the crop plant, however, was less pronounced than the effects of altitude, season or year (Table 1). This result contradicts the earlier phytosociological concepts of two major units of Central European weed vegetation, one for cereal fields and the other for root crops. Such a distinction has been made either at the level of classes, e.g. *Secalietea* and *Chenopodietea,* or orders within a single class, mostly the class *Stellarietea mediae* (e.g. Braun-Blanquet et al. 1936; Tüxen 1950; Mucina & Maglocký 1985; Krippelová & Mucina 1988; Kropáč 1988; Oberdorfer 1993; Moravec et al. 1995). This contradiction indicates that in the traditional phytosociological approach, emphasis on a subjectively selected environmental factor such as the crop plant may lead to a failure to identify properly the main gradients in species composition, especially in a vegetation type driven simultaneously by several environmental factors. Statistical analyses of large data sets appear to be a more suitable tool for identifying the importance of particular environmental factors.

The overriding effect of climatic and soil factors revealed in the current study is in accordance with the results of Hüppe & Hofmeister (1990) who proposed a new syntaxonomical system of German weed vegetation with two main groups of communities, i.e. calcifuge and calcicole. Similar divisions, which put less emphasis on the differentiation of weed vegetation due to the crop, were accepted by Ries (1992) and Mucina (1993) for Austria, Jarolímek et al. (1997) for Slovakia, and Haveman et al. (1998) for The Netherlands.

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App. 1. Extended version of Table 2. Species with the highest fit in partial CCAs and their scores along the first ordination axes. Each column represents a separate partial CCA in which Altitude, Season, Year, and Crop were used in turn as the only explanatory variable while the effects of the other variables were subtracted by defining them as covariables. Low values of scores for respective variables are associated in turn with low altitudes, early season, earlier years and cereal fields.

Altitude Species	Ax 1 score	Fit	Season Species	Ax 1 score	Fit	Year Species	Ax 1 score	Fit	Crop Species	Ax 1 score	Fit
Portulaca oleracea	−1.61	0.010	Cerastium brachypetalum	−2.43	0.007	Agrostemma githago	−1.15	0.014	Galeopsis angustifolia	−0.79	0.003
Diplotaxis muralis	−1.05	0.009	Tragopogon dubius	−2.03	0.005	Galium tricornutum	−1.14	0.017	Trifolium medium	−0.65	0.003
Setaria pumila	−0.96	0.057	Gagea pratensis	−1.60	0.006	Ranunculus sardous	−0.93	0.007	Kickxia elatine	−0.64	0.014
Amaranthus retroflexus	−0.94	0.058	Holosteum umbellatum	−1.53	0.021	Galeopsis ladanum	−0.92	0.013	Cerastium glomeratum	−0.55	0.003
Echinochloa crus−galli	−0.94	0.072	Veronica triloba	−1.46	0.034	Plantago media	−0.91	0.016	Agrostis gigantea	−0.54	0.005
Conyza canadensis	−0.93	0.038	Veronica triphyllos	−1.41	0.072	Crepis capillaris	−0.91	0.010	Misopates orontium	−0.53	0.008
Mercurialis annua	−0.91	0.016	Erophila verna	−1.35	0.053	Misopates orontium	−0.89	0.009	Galeopsis ladanum	−0.51	0.004
Solanum nigrum	−0.89	0.026	Veronica praecox	−1.32	0.014	Myosotis stricta	−0.87	0.029	Tanacetum vulgare	−0.45	0.003
Ajuga chamaepitys	−0.88	0.011	Veronica hederifolia	−1.24	0.201	Myosotis discolor	−0.85	0.018	Odontites ruber	−0.42	0.007
Veronica hederifolia	−0.86	0.010	Thlaspi perfoliatum	−1.23	0.024	Rubus fruticosus agg.	−0.84	0.014	Apera spica-venti	−0.41	0.025
Amaranthus powellii	−0.85	0.010	Bromus tectorum	−1.10	0.005	Contingia orientalis	−0.78	0.017	Phleum pratense	−0.41	0.006
Gypsophila muralis	−0.85	0.017	Myosotis stricta	−1.07	0.044	Misopates orontium	−0.78	0.017	Lolium multiflorum	−0.40	0.003
Euphorbia falcata	−0.84	0.021	Myosurus minimus	−1.03	0.008	Silene latifolia	−0.76	0.008	Juncus bufonius	−0.39	0.005
Reseda lutea	−0.81	0.011	Bromus sterilis	−0.89	0.007	Alchemilla vulgaris	−0.76	0.028	Euphorbia falcata	−0.38	0.004
Anagallis foemina	−0.80	0.026	Papaver argemone	−0.84	0.035	Papaver argemone	−0.75	0.020	Trifolium arvense	−0.38	0.006
Stachys annua	−0.78	0.032	Valerianella locusta	−0.78	0.009	Veronica triphyllos	−0.72	0.015	Caucalis platycarpos	−0.38	0.004
Cardaria draba	−0.78	0.016	Myosotis discolor	−0.77	0.006	Erophila verna	−0.71	0.008	Euphorbia exigua	−0.37	0.022
Setaria viridis	−0.77	0.031	Arabidopsis thaliana	−0.73	0.065	Veronica triloba	−0.67	0.011	Trifolium campestre	−0.37	0.006
Kickxia spuria	−0.74	0.019	Lithospermum arvense	−0.70	0.031	Gypsophila muralis	−0.64	0.012	Consolida regalis	−0.36	0.024
Chenopodium hybridum	−0.74	0.024	Lamium purpureum	−0.70	0.068	Consolida regalis	−0.64	0.007	Stachys annua	−0.36	0.012
Galinsoga parviflora	−0.72	0.032	Papaver dubium	−0.46	0.005	Papaver dubium	−0.63	0.014	Poa trivialis	−0.31	0.005
Arctium tomentosum	−0.71	0.010	Veronica polita	−0.43	0.027	Veronica opaca	−0.63	0.007	Vicia tetrasperma	−0.29	0.004
Descurainia sophia	−0.71	0.045	Thlaspi arvense	−0.40	0.089	Sagina procumbens	−0.62	0.007	Sagina procumbens	−0.28	0.020
Cichorium intybus	−0.68	0.010	Ranunculus arvensis	−0.38	0.007	Spergularia rubra	−0.60	0.025	Vicia villosa	−0.28	0.004
Anthemis austriaca	−0.65	0.012	Adonis aestivalis	−0.38	0.012	Linaria vulgaris	−0.60	0.061	Maricaria recutita	−0.28	0.003
Lactuca serriola	−0.64	0.024	Anthemis austriaca	−0.37	0.031	Silene noctiflora	−0.60	0.015	Euphorbia exigua	−0.28	0.015
Consolida regalis	−0.63	0.072	Fumaria vaillantii	−0.34	0.021	Neslia paniculata	−0.58	0.010	Daucus carota	−0.28	0.007
Veronica polita	−0.62	0.065	Contingia orientalis	−0.32	0.006	Trifolium arvense	−0.58	0.015	Centaurea cyanus	−0.26	0.012
Falcaria vulgaris	−0.57	0.009	Cardaria draba	−0.31	0.017	Vicia villosa	−0.57	0.008	Galium spurium	−0.25	0.004
Euphorbia exigua	−0.55	0.049	Lamium amplexicaule	−0.31	0.012	Hylotelephium maximum	−0.55	0.013	Aethusa cynapium	−0.24	0.012
Microrrhinum minus	−0.54	0.017	Papaver rhoeas	−0.29	0.061	Adonis aestivalis	−0.54	0.039	Papaver rhoeas	−0.24	0.014
Adonis aestivalis	−0.51	0.012	Consolida regalis	−0.27	0.067	Arenaria serpyllifolia	−0.53	0.086	Vicia cracca	−0.24	0.004
Silene noctiflora	−0.49	0.060	Lolium perenne	−0.25	0.006	Raphanus raphanistrum	−0.51	0.007	Vicia sativa	−0.23	0.020
Lathyrus tuberosus	−0.47	0.031	Neslia paniculata	−0.25	0.038	Cardaria draba	−0.51	0.008	Adonis aestivalis	−0.23	0.005
Papaver rhoeas	−0.45	0.047	Fumaria officinalis	−0.24	0.010	Anthemis austriaca	−0.49	0.011	Valerianella dentata	−0.22	0.005
Lamium amplexicaule	−0.39	0.036	Stellaria media	−0.21	0.013	Papaver rhoeas	−0.49	0.025	Daucus carota	−0.20	0.007
Artemisia vulgaris	−0.34	0.010	Capsella bursa-pastoris	−0.21	0.015	Trifolium campestre	−0.45	0.013	Medicago lupulina	−0.19	0.008
Sonchus oleraceus	−0.33	0.019	Aphanes arvensis	−0.15	0.030	Erodium cicutarium	−0.43	0.029	Veronica arvensis	−0.19	0.012
Chenopodium polyspermum	−0.33	0.012	Galium aparine	−0.15	0.007	Valerianella dentata	−0.42	0.025	Descurainia sophia	−0.19	0.003
Sinapis arvensis	−0.29	0.024	Geranium pusillum	−0.11	0.007	Sherardia arvensis	−0.42	0.008	Lathyrus tuberosus	−0.18	0.005
Sonchus asper	−0.29	0.027	Poa annua	−0.08	0.005	Scleranthus annuus	−0.41	0.012	Lapsana communis	−0.17	0.023
Arenaria serpyllifolia	−0.29	0.011	Veronica arvensis	0.08	0.006	Arabidopsis thaliana	−0.39	0.019	Vicia hirsuta	−0.17	0.003
Convolvulus arvensis	−0.28	0.044	Viola arvensis	0.18	0.008	Consolida regalis	−0.37	0.037	Anagallis arvensis	−0.17	0.008
Medicago lupulina	−0.27	0.015				Rumex crispus	−0.35	0.011	Myosotis arvensis	−0.17	0.012
Chenopodium album	−0.24	0.039				Aphanes arvensis	−0.34	0.014	Anthemis arvensis	−0.17	0.020
Anagallis arvensis	−0.19	0.024				Gnaphalium uliginosum	−0.32	0.025	Maricaria discoidea	−0.16	0.006
Fallopia convolvulus	−0.10	0.013				Lamium amplexicaule	−0.31	0.010	Polygonum aviculare	−0.16	0.023
Viola arvensis	0.12	0.020				Rumex acetosella	−0.31	0.023	Anthemis arvensis	−0.15	0.003
Galium aparine	0.16	0.016				Anthemis arvensis	−0.31	0.010	Atriplex patula	−0.15	0.022
Campanula rapunculoides	0.25	0.011				Myosotis arvensis	−0.28	0.025	Sinapis arvensis	−0.15	0.005
						Silene noctiflora	−0.28	0.023	Campanula rapunculoides	−0.14	0.004
						Medicago lupulina	−0.28	0.016			

App. 1. Internet supplement to: Lososová, Z.; Chytrý, M.; Cimalová, Š.; Kropáč, Z.; Otýpková, Z.; Pyšek, P. & Tichý, L. 2004. Weed vegetation of arable land in Central Europe: Gradients of diversity and species composition. *J. Veg. Sci.* 15: 413-420.

App. 1, cont.

Altitude Species	Ax 1 score	Fit	Season Species	Ax 1 score	Fit	Year Species	Ax 1 score	Fit	Crop Species	Ax 1 score	Fit
Rumex crispus	0.28	0.023	Spergula arvensis	0.18	0.005	Lathyrus tuberosus	−0.24	0.008	Tripleurospermum inodorum	−0.13	0.012
Poa annua	0.32	0.030	Avena fatua	0.19	0.008	Avena fatua	−0.23	0.011	Viola arvensis	−0.13	0.022
Myosotis arvensis	0.33	0.089	Sonchus arvensis	0.19	0.012	Aethusa cynapium	−0.22	0.010	Scleranthus annuus	−0.13	0.004
Agrostis stolonifera	0.33	0.012	Equisetum arvense	0.20	0.009	Vicia hirsuta	−0.22	0.014	Avena fatua	−0.12	0.003
Vicia hirsuta	0.35	0.036	Chenopodium album	0.21	0.031	Galeopsis tetrahit	−0.15	0.009	Fallopia convolvulus	−0.07	0.007
Gnaphalium uliginosum	0.36	0.016	Convolvulus arvensis	0.24	0.032	Anagallis arvensis	−0.10	0.007	Taraxacum sect. Ruderalia	0.11	0.007
Scleranthus annuus	0.38	0.032	Daucus carota	0.26	0.011	Myosotis arvensis	0.11	0.009	Capsella bursa−pastoris	0.12	0.013
Persicaria maculosa	0.38	0.032	Persicaria lapathifolia	0.27	0.020	Stellaria media	0.13	0.013	Lamium purpureum	0.12	0.005
Veronica arvensis	0.39	0.051	Persicaria hydropiper	0.28	0.006	Tripleurospermum inodorum	0.13	0.012	Persicaria maculosa	0.14	0.004
Raphanus raphanistrum	0.41	0.052	Mentha arvensis	0.28	0.021	Veronica persica	0.17	0.021	Raphanus raphanistrum	0.14	0.006
Anthemis arvensis	0.42	0.038	Atriplex patula	0.31	0.023	Euphorbia helioscopia	0.17	0.011	Euphorbia helioscopia	0.19	0.014
Vicia sativa	0.42	0.063	Aethusa cynapium	0.31	0.020	Veronica arvensis	0.18	0.011	Stellaria media	0.20	0.029
Stachys palustris	0.46	0.042	Persicaria maculosa	0.33	0.024	Persicaria lapathifolia	0.28	0.022	Geranium pusillum	0.21	0.008
Matricaria discoidea	0.51	0.031	Erysimum cheiranthoides	0.33	0.009	Taraxacum sect. Ruderalia	0.28	0.045	Chenopodium polyspermum	0.22	0.005
Achillea millefolium	0.51	0.080	Plantago lanceolata	0.34	0.012	Galium aparine	0.29	0.051	Lamium amplexicaule	0.22	0.012
Lapsana communis	0.52	0.116	Stachys palustris	0.35	0.023	Echinochloa crus−galli	0.30	0.007	Erodium cicutarium	0.25	0.009
Ranunculus repens	0.53	0.074	Oxalis fontana	0.35	0.010	Lapsana communis	0.32	0.044	Chenopodium album	0.27	0.049
Poa trivialis	0.53	0.025	Anagallis arvensis	0.36	0.086	Sonchus oleraceus	0.33	0.019	Persicaria lapathifolia	0.29	0.023
Potentilla anserina	0.54	0.024	Sherardia arvensis	0.38	0.024	Erysimum cheiranthoides	0.34	0.010	Fumaria officinalis	0.32	0.013
Cerastium holosteoides	0.54	0.039	Plantago major	0.38	0.064	Matricaria discoidea	0.34	0.014	Lolium perenne	0.42	0.009
Mentha arvensis	0.55	0.075	Medicago lupulina	0.40	0.034	Ranunculus repens	0.34	0.031	Echinochloa crus−galli	0.51	0.021
Persicaria hydropiper	0.64	0.033	Gnaphalium uliginosum	0.41	0.021	Rumex obtusifolius	0.37	0.013	Chenopodium ficifolium	0.51	0.005
Tussilago farfara	0.71	0.053	Microrrhinum minus	0.42	0.010	Chenopodium polyspermum	0.40	0.019	Chenopodium hybridum	0.52	0.012
Galeopsis pubescens	0.72	0.011	Sonchus oleraceus	0.48	0.040	Amaranthus retroflexus	0.41	0.058	Malva neglecta	0.54	0.005
Vicia cracca	0.76	0.036	Trifolium hybridum	0.49	0.006	Lamium purpureum	0.43	0.058	Amaranthus retroflexus	0.60	0.023
Spergula arvensis	0.79	0.094	Galinsoga quadriradiata	0.49	0.014	Glechoma hederacea	0.47	0.011	Euphorbia peplus	0.62	0.006
Rumex acetosella	0.81	0.063	Echinochloa crus−galli	0.50	0.021	Agrostis stolonifera	0.51	0.028	Galinsoga parviflora	0.70	0.030
Prunella vulgaris	0.81	0.016	Setaria viridis	0.51	0.014	Geranium dissectum	0.53	0.033	Solanum nigrum	0.71	0.016
Vicia sepium	0.81	0.010	Chenopodium polyspermum	0.52	0.031	Lactuca serriola	0.55	0.018	Holosteum umbellatum	0.71	0.004
Veronica serpyllifolia	0.83	0.013	Sonchus asper	0.53	0.090	Artemisia vulgaris	0.56	0.028	Bromus sterilis	0.72	0.004
Stellaria graminea	0.88	0.043	Euphorbia exigua	0.54	0.046	Poa trivialis	0.65	0.037	Galinsoga quadriradiata	0.74	0.031
Galeopsis tetrahit	0.91	0.326	Anagallis foemina	0.54	0.011	Arctium tomentosum	0.69	0.009	Senecio vulgaris	0.89	0.035
Veronica chamaedrys	0.94	0.015	Stachys annua	0.57	0.017	Malva neglecta	0.69	0.008	Hibiscus trionum	0.95	0.003
Phleum pratense	0.96	0.031	Gypsophila muralis	0.58	0.008	Leucanthemum vulgare	0.71	0.015	Mercurialis annua	0.80	0.012
Agrostis gigantea	1.04	0.020	Reseda luteola	0.61	0.007	Rubus caesius	0.71	0.011	Amaranthus viridis	0.81	0.003
Hylotelephium maximum	1.06	0.026	Galinsoga parviflora	0.62	0.024	Poa pratensis	0.79	0.023	Armoracia rusticana	0.83	0.005
Leucanthemum vulgare	1.06	0.033	Ajuga chamaepitys	0.67	0.007	Pastinaca sativa	0.83	0.011	Atriplex sagittata	0.87	0.006
Rumex acetosa	1.20	0.047	Amaranthus retroflexus	0.68	0.030	Euphorbia peplus	0.84	0.012	Atriplex oblongifolia	0.97	0.004
Trifolium hybridum	1.23	0.039	Kickxia spuria	0.71	0.017	Crepis biennis	0.85	0.012	Chenopodium glaucum	0.97	0.010
Rhinanthus alectorolophus	1.28	0.023	Euphorbia falcata	0.74	0.016	Symphytum officinale	0.91	0.024	Urtica urens	1.27	0.008
Lathyrus pratensis	1.32	0.028	Misopates orontium	0.75	0.015	Arrhenatherum elatius	0.95	0.011	Erucastrum gallicum	1.30	0.003
Holcus mollis	1.32	0.087	Solanum nigrum	0.80	0.021	Aegopodium podagraria	0.96	0.031	Eragrostis minor	1.30	0.004
Sanguisorba officinalis	1.38	0.011	Amaranthus hybridus	0.84	0.007	Leontodon autumnalis	1.04	0.009	Aristolochia clematitis	1.36	0.004
Hypericum maculatum	1.43	0.026	Kickxia elatine	0.86	0.024	Lolium perenne	1.06	0.062	Amaranthus blitum	1.60	0.004
Festuca pratensis	1.48	0.037	Amaranthus powellii	0.86	0.010	Urtica dioica	1.12	0.026	Pulegium vulgare	1.78	0.004
Agrostis capillaris	1.63	0.033	Setaria pumila	0.87	0.047	Galinsoga quadriradiata	1.14	0.073	Coronopus squamatus	1.81	0.004
Lolium temulentum	2.03	0.010	Salvia verticillata	0.88	0.007	Chaerophyllum aromaticum	1.19	0.008	Muscari comosum	1.88	0.003
Equisetum sylvaticum	2.07	0.022	Galeopsis angustifolia	1.00	0.006	Trisetum flavescens	1.20	0.012	Gagea villosa	2.19	0.006
Alchemilla vulgaris s. lat.	2.12	0.063	Carduus nutans	1.71	0.007	Trifolium medium	1.25	0.010	Ornithogalum boucheanum	2.20	0.003
Melampyrum pratense	3.24	0.018	Achillea setacea	1.97	0.006	Persicaria mitis	1.30	0.015	Tragopogon dubius	2.30	0.007
Rumex arifolius	3.25	0.011	Scabiosa ochroleuca	2.03	0.007	Cerastium glomeratum	1.37	0.020	Cerastium brachypetalum	2.43	0.007