

Changes during the 20th century in species composition of synanthropic vegetation in Moravia (Czech Republic)

Změny ve složení synantropní vegetace na Moravě v průběhu 20. století

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Variation in species composition and proportion of different plant traits were studied for weed and ruderal vegetation in the eastern part of the Czech Republic (Moravia), especially the temporal changes from the beginning of the 20th century up to 2005. Data sets for 433 weed species and 695 ruderal species were used in the analysis. While historical data on the occurrence of synanthropic species were obtained from floristic literature, that on recent occurrence were extracted from the Czech National Phytosociological Database. Species that were common in the past are still common a century later and rare species are becoming rarer. Almost a quarter of all synanthropic species recorded at the beginning of the last century are endangered species and 12 are now extinct in this country. Some trends in species composition and particular species attributes were found. While mean abundance of archaeophytes and native species decreased, mean abundance of neophytes increased in both vegetation types during the last century. The use of regression tree models revealed that the relative abundance of weed and ruderal species is related to their species attributes, i.e. Ellenberg indicator value, lifespan, life strategy, pollination mode, plant height and flowering period. The most abundant weed species have always been shade-tolerant, relatively small plants that are able to flower for a long time and require high levels of nutrients. The most abundant weed species changed from insect-pollinated to those without any specific pollination mode. A long flowering period is an important attribute of the most abundant ruderal species. There was no significant change in ecological preferences of ruderal species. Regarding the life strategy of these species, CR-strategists were the most abundant in 1908 but less common in 2005 and partly replaced by C-strategists.

Key words: arable land, archaeophytes, Czech Republic, neophytes, regression tree models, ruderal vegetation, weed vegetation

Introduction

The last century saw a shift in traditional land use and lifestyle throughout the Czech Republic: people now keep fewer domestic animals, agricultural technologies have changed, efforts have been made to keep the settlements clean, the use of herbicides and fertilizers has increased etc., all of which are reflected in changes in synanthropic vegetation.

In this study, two main vegetation types are included in synanthropic vegetation. They are (i) weed vegetation in arable fields and (ii) ruderal vegetation of human settlements and their surroundings, waste deposits, railways, verges of roads and trampled habitats. In the traditional phytosociological approach they are both placed in the classes *Stellarietea mediae*,

Agropyreteea repentis, *Artemisietea vulgaris*, *Plantaginetea majoris* and *Galio-Urticetea* (Moravec et al. 1995). Although both of these types of synanthropic vegetation are strongly influenced by human activities, they differ in species composition and species attributes due to the different regimes and intensity of disturbances in fields and ruderal sites (Lososová et al. 2006). These differences are the main reason why these vegetation types are mostly studied separately. Many studies have investigated the temporal changes in these vegetation types on different temporal and spatial scales in Central Europe.

Weed vegetation growing in arable fields is mainly composed of annual species, whose life strategy is closely related to that of planted crops. Species composition of weed vegetation changed considerably, mainly during the second half of the last century. The main reason was the frequent use of modern agricultural techniques such as improved seed-cleaning techniques, chemical weed control and early harvesting. Many studies have shown that specialized weed species have declined or disappeared from European fields (e.g., Holzner & Immonen 1982, Hilbig 1987, Kornaś 1988, Firbank 1990, Andreassen et al. 1996, Sutcliffe & Kay 2000, Lososová 2003, Pinke 2004, Kropáč 2006). Lososová et al. (2004) have shown for the Czech Republic and Slovakia that over the last fifty years the proportion of archaeophytes declined, while that of neophytes increased. Little is known about shifts in species attributes over particular temporal periods.

Temporal changes in ruderal vegetation and vegetation in trampled habitats are studied mainly as part of investigations into the flora and vegetation of big cities. Comparisons of historical floristic data with recent data exist for some Central European cities, e.g. Leipzig (Klotz & Gutte 1992), Zürich (Landolt 2000), Warsaw (Sudnik-Wójcikowska 1987) and Plzeň (Chocholoušková & Pyšek 2003). These floristic studies facilitated the identification of changes that have occurred over relatively long temporal periods. Nevertheless, such studies cover only relatively small areas. On a broader scale, valuable data on changes in species composition and species abundance can be provided by floristic mapping. One such example is the study by Preston et al. (2002), who analysed complete species lists of 100 km² grid squares across Britain and Ireland and compared them with those recorded forty years previously. This study deals with general patterns in species structural changes in large-scale habitats, but little is known about general changes in species composition in particular types of vegetation. Changes in synanthropic vegetation types occupying the whole spectrum of man-made habitats are available for the city of Plzeň (Pyšek et al. 2004a). In this case, two phytosociological data sets were compared to reveal the changes in species composition over thirty years.

The aims of this study are (i) to characterize temporal changes in species composition of synanthropic vegetation at a regional scale over one century; (ii) to analyse differences in the proportion of alien species; and (iii) to evaluate changes in species attributes.

Material and methods

Two sources were used to obtain species data. The data on species composition of weed and ruderal vegetation in the first decade of the 20th century is from the regional flora of anthropogenic habitats made by Laus (1908). Heinrich Laus published his own floristic lists and compiled data on weed and ruderal species found by many regional botanists (F. Böhm, F. Čouka, J. Podpěra, F. Kovář, P. Schreiber, etc) covering the whole region of

Moravia (E part of the Czech Republic). Laus divided Moravia into subregions and characterized the synanthropic flora of these subregions by the most common synanthropic plants and several selected localities, with their species lists. He defined weed species as “every plant which is oppressed by man in arable fields and gardens”. Ruderal species were defined by Laus (1908) as: “...plants which grow close to or inside settlements, villages and towns, on roads, on waste dumps, on walls, by fences, inside railway stations, in stone quarries, etc. Everywhere where this vegetation is unwanted.”

The data on recent species composition of vegetation in the same region were taken from identically-defined habitats. Phytosociological relevés stored in the Czech National Phytosociological Database (Chytrý & Rafajová 2003) were used. The assignment of a particular relevé by its original author to phytosociological units of weed vegetation (*Stellarietea mediae*) and ruderal vegetation, together with vegetation of trampled habitats (*Agropyretea repentis*, *Artemisietea vulgaris*, *Galio-Urticetea*, *Plantaginetea majoris* and *Stellarietea mediae*), was the criterion for inclusion of the relevé in further analyses. In total, 1669 relevés of weed vegetation and 1427 relevés of ruderal vegetation made by different authors in Moravia from 1985 to 2005 were obtained. Species lists were completed for both vegetation types.

Phanerophytes were excluded from the species lists, because it was unclear if they were recorded by Laus. Bryophytes, species determined only to the generic level and records of crop plants (only for the data set on weed vegetation) were deleted. Rare species occurring in only one or two relevés were omitted.

After these procedures, only two data sets containing 433 and 695 weed or ruderal species were obtained. Editing these data sets was done using the JUICE 6.3 program (Tichý 2002). Taxonomic concepts and nomenclature of species used in this paper follow Kubát et al. (2002). Information on extinction or threat to species was adopted from Holub & Procházka (2000).

The number of localities for each species and cited by Laus was used as a measure of the regional abundance of each species in 1908. The occurrence of species in plots relative to the total number of plots was used as a measure of the regional abundance of each species in 2005. To minimize differences between data sets, caused by different sampling strategies and scales, values from both periods were standardized to zero mean and variance one.

To describe synanthropic vegetation in both temporal periods, particular species attributes were chosen. First, species were characterized by their immigration status. Three categories defined by Pyšek et al. (2002) were used; natives, archaeophytes and neophytes (see Pyšek et al. 2004b for detailed definitions). Next, Ellenberg indicator values for light, temperature, continentality, moisture, soil reaction and nutrients (Ellenberg et al. 1992) were used to describe the ecological demands of the species. A Bioflor database (Klotz et al. 2002) provided information on lifespan (annuals, biennials and perennials), life strategy (seven CSR strategies, according to Grime 1979), and pollen vector (wind, selfing and insect). Information on the longevity of flowering periods and mean height of each species are those cited in the Key to the Flora of the Czech Republic (Kubát et al. 2002).

The regression tree analysis was used to find the relations between species abundance and their attributes in both the periods studied (Breiman et al. 1984, De'ath & Fabricius 2000). Regression tree models can uncover complex interactions between independent variables used (species attributes). The regression tree provides an hierarchical method of splitting a data set into smaller homogeneous groups in which the within-group variation in the response variable is minimized. At each node of the tree, species are divided into two groups based on a certain value of a selected attribute (splitter independent variable).

In selecting the optimal tree size, the 10-fold cross-validation method with the $SE = 0$ rule was used (Breiman et al. 1984). The cross-validation procedure gives an estimate of the pruning level needed to select (automatically) a particular tree that appears the most stable and valid.

At each node of the tree, besides the splitter variable, surrogate variables are identified. Surrogate variables can separate cases in a similar way to the particular splitter variable. In this study, only those variables whose associated value with respect to the splitter variable was > 0.3 were considered as surrogates.

For each tree the explained variation in the dependent variable was calculated from their resubstitution relative errors, corresponding to residual sums of squares. Each of the explanatory variables used in the model contributes to a different extent to the explained variation in the response variable. The influence of particular explanatory variables can be evaluated by the relative importance values, with the best explanatory variable having the value of 100. The relative importance value reflects the contribution of each variable stemming both from its role as a primary splitter variable and as a surrogate across all branches of the tree.

Regression trees were calculated separately for weed and ruderal species and for both time periods. All calculations were done by the program Statistica 8.0 (<http://www.statsoft.com/>).

Results

Changes in species composition

The total number of weed species recorded in Moravia was 433; 343 species were found in 1908 and 303 species in 2005. From the former species list 107 species were not found in arable fields in 2005. Eight of them are extinct throughout the Czech Republic and 84 species documented in 1908 are now endangered (24.5%). The present species list contains only 35 endangered species (11.5%). The total number of ruderal species recorded in Moravia was 695. At the beginning of the last century, 579 ruderal species were found in anthropogenic localities, of which 95 were not found in 2005; four of these species are now extinct and 120 are endangered (20.7%). In 2005, 477 species were found, of which only 45 are endangered (9.4%).

Comparing differences in the proportion of natives, archaeophytes and neophytes in two different species lists, we found a remarkably high proportion of archaeophytes in weed vegetation, while ruderal vegetation contained relatively more neophytes (Table 1). Nevertheless, the proportions of natives and aliens in weed and ruderal vegetation have hardly changed over time. Some differences were found, however, when mean abundances of species were compared. It was shown that archaeophytes were the most frequent species in both vegetation types, followed by natives and neophytes, in 1908 (Fig. 1A, B). In 2005, archaeophytes were still the most frequent species, but neophytes had become more common. The most common species in the sets of weed and ruderal vegetation are almost the same now as in the past (Table 2). This trend was found in all species groups (natives/archaeophytes/neophytes) in both vegetation types (Fig. 2). For weed vegetation the most common species in both temporal periods were *Capsella bursa-pastoris*, *Chenopodium album* agg., *Cirsium arvense* and *Stellaria media*. The most common ruderal species were *Achillea millefolium* agg., *Artemisia vulgaris*, *Polygonum aviculare* agg. and *Urtica dioica* (Table 2).

Table 1. – Proportions of native species, archaeophytes and neophytes in weed and ruderal Moravian vegetation in 1908 and 2005. Proportions were calculated for the species lists compiled for each temporal period.

| | Weeds | | Ruderals | |
|-----------------------------|-------|------|----------|------|
| | 1908 | 2005 | 1908 | 2005 |
| Proportion of natives | 51.6 | 49.2 | 62.1 | 63.1 |
| Proportion of archaeophytes | 44.3 | 44.6 | 29.2 | 28.3 |
| Proportion of neophytes | 4.1 | 6.3 | 8.7 | 8.6 |

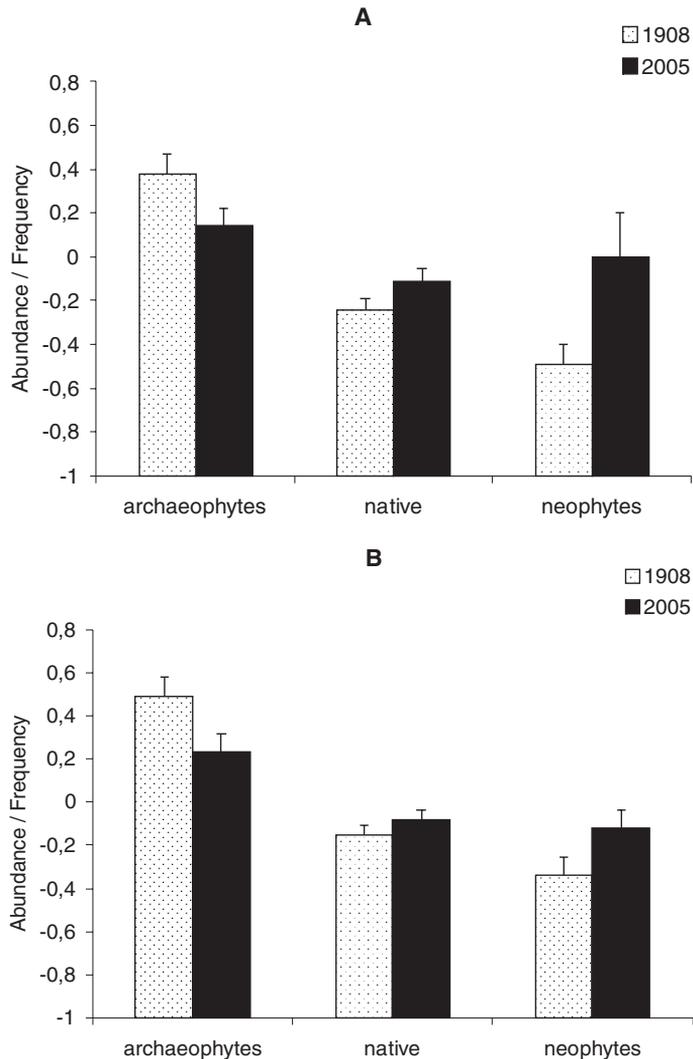


Fig. 1. – Changes in native and alien (archaeophytes, neophytes) species' occurrence in the synanthropic vegetation of Moravia over the last century, shown separately for weeds (A) and ruderals (B). Means of standardized values (zero mean \pm S.E.) of species abundances in 1908 and frequencies in 2005 (see text for details) are shown to make the two periods based on different sampling methods comparable. Period and immigration status were significant factors ($P < 0.001$) in two-way ANOVA with measures of occurrence as response variables.

Table 2. – The most abundant Moravian weed and ruderal species in different temporal periods. Species are listed in decreasing order. Numbers are absolute numbers for localities in 1908 or percentage frequencies in 2005.

| | Number of localities in 1908 | | Frequency (%) in 2005 | |
|----------|--------------------------------|----|----------------------------------|----|
| Weeds | <i>Cirsium arvense</i> | 40 | <i>Stellaria media</i> | 70 |
| | <i>Convolvulus arvensis</i> | 28 | <i>Viola arvensis</i> | 64 |
| | <i>Anagallis arvensis</i> | 27 | <i>Capsella bursa-pastoris</i> | 63 |
| | <i>Sonchus arvensis</i> | 27 | <i>Tripleurospermum inodorum</i> | 61 |
| | <i>Capsella bursa-pastoris</i> | 27 | <i>Galium aparine</i> | 60 |
| | <i>Centaurea cyanus</i> | 26 | <i>Veronica persica</i> | 60 |
| | <i>Chenopodium album</i> | 24 | <i>Cirsium arvense</i> | 59 |
| | <i>Sinapis arvensis</i> | 24 | <i>Taraxacum sect. Ruderalia</i> | 55 |
| | <i>Stellaria media</i> | 24 | <i>Lamium purpureum</i> | 54 |
| | <i>Fallopia convolvulus</i> | 24 | <i>Chenopodium album</i> | 53 |
| Ruderals | <i>Achillea millefolium</i> | 38 | <i>Taraxacum sect. Ruderalia</i> | 48 |
| | <i>Artemisia vulgaris</i> | 32 | <i>Artemisia vulgaris</i> | 43 |
| | <i>Atriplex patula</i> | 32 | <i>Elytrigia repens</i> | 39 |
| | <i>Chenopodium album</i> | 32 | <i>Urtica dioica</i> | 32 |
| | <i>Urtica dioica</i> | 32 | <i>Polygonum aviculare</i> | 32 |
| | <i>Polygonum aviculare</i> | 30 | <i>Lolium perenne</i> | 31 |
| | <i>Carduus acanthoides</i> | 29 | <i>Achillea millefolium</i> | 30 |
| | <i>Daucus carota</i> | 25 | <i>Plantago major</i> | 30 |
| | <i>Bromus tectorum</i> | 24 | <i>Capsella bursa-pastoris</i> | 28 |
| | <i>Conyza canadensis</i> | 24 | <i>Tripleurospermum inodorum</i> | 27 |

Changes in species attributes

To determine the changes in species abundance and particular species attributes, regression trees were used. Regression tree models were constructed separately for weeds and ruderals and for both time periods (Fig. 3).

The optimal regression tree for weeds recorded in Moravian arable fields in 1908 is divided into four terminal nodes. This tree explains 29.4% of the variation in the relative abundance of weeds. It shows that the most common Moravian weeds were relatively small, insect-pollinated, annual species with a R- or S- combined life strategy, and in particular a tolerance of shade (Fig. 3A).

The optimal regression tree for weeds recorded in 2005 shows that the most common species are those that have a high demand for nutrients (Fig. 3B). Among them, the most abundant are those flowering more than 3.5 months in the season. In this group of species, the next splitter separates shade-tolerant species, then annual species, with ruderal life strategy being the most abundant. In the group of species with a low nutrient requirement, the most common species are again shade-tolerant plants. This tree explains 31.1% of the variation in the relative abundance of species.

The optimal regression tree for ruderal species recorded in Moravia in 1908 explains 13.4% of the variation in regional abundance (Fig. 3C). The most abundant ruderal species were those flowering for longer than 4.5 months in the year and having less need of moisture. Among species with a shorter flowering period (< 4.5 months) the most abundant species were CR-strategists.

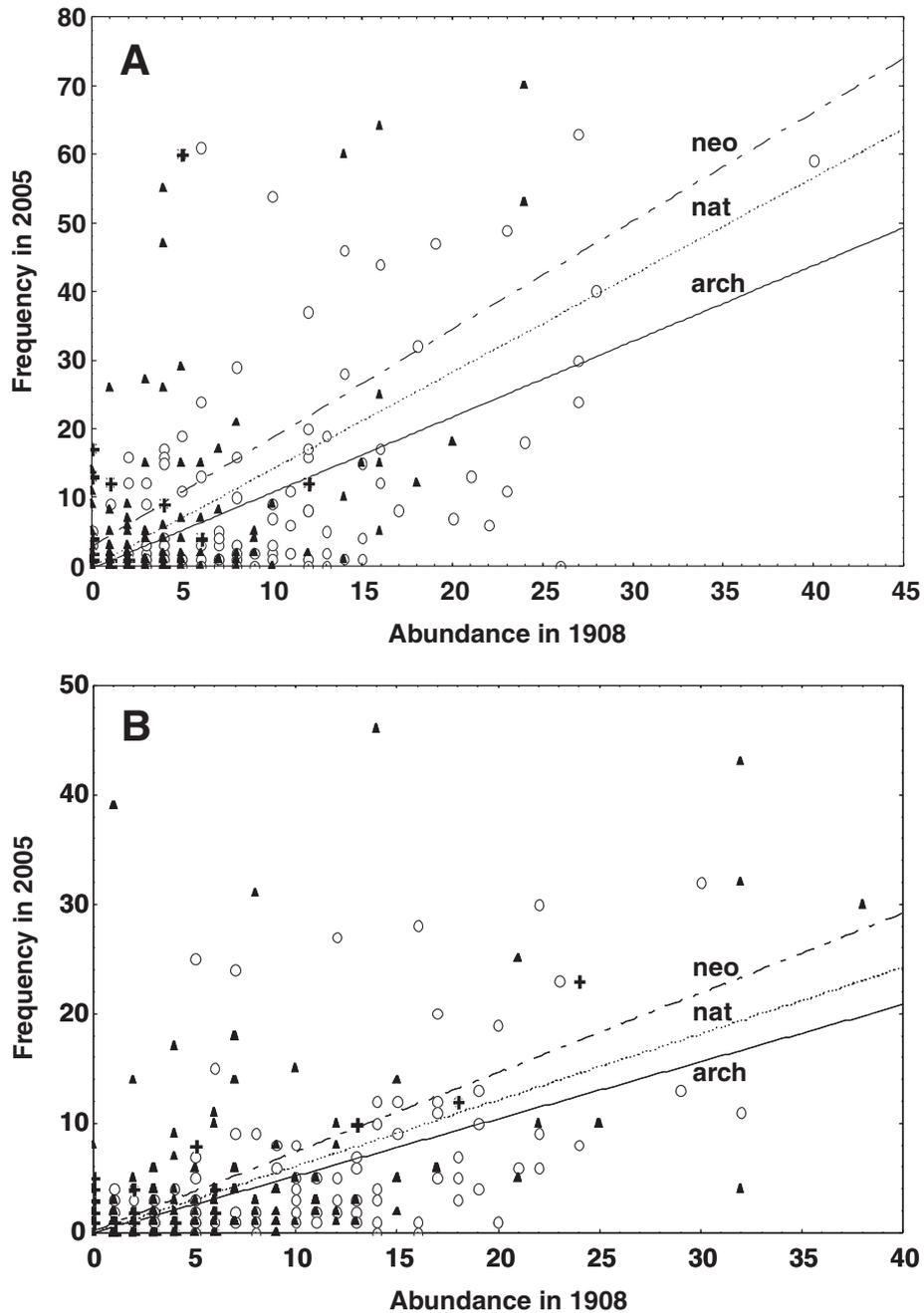
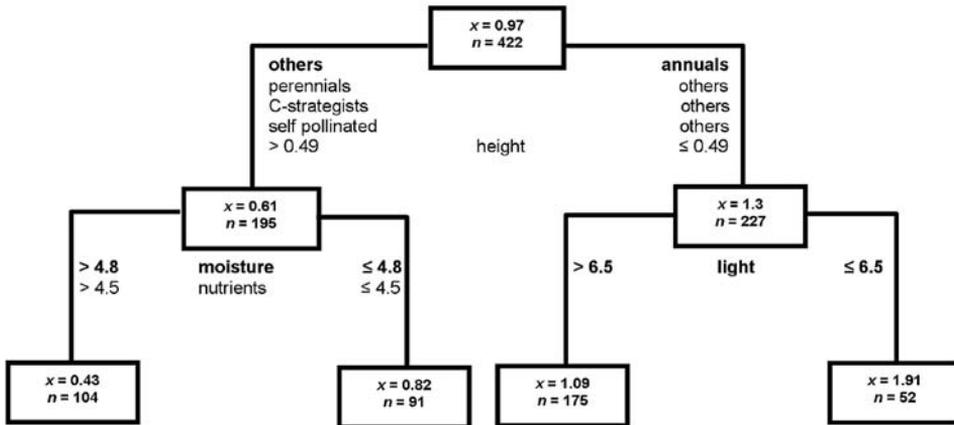
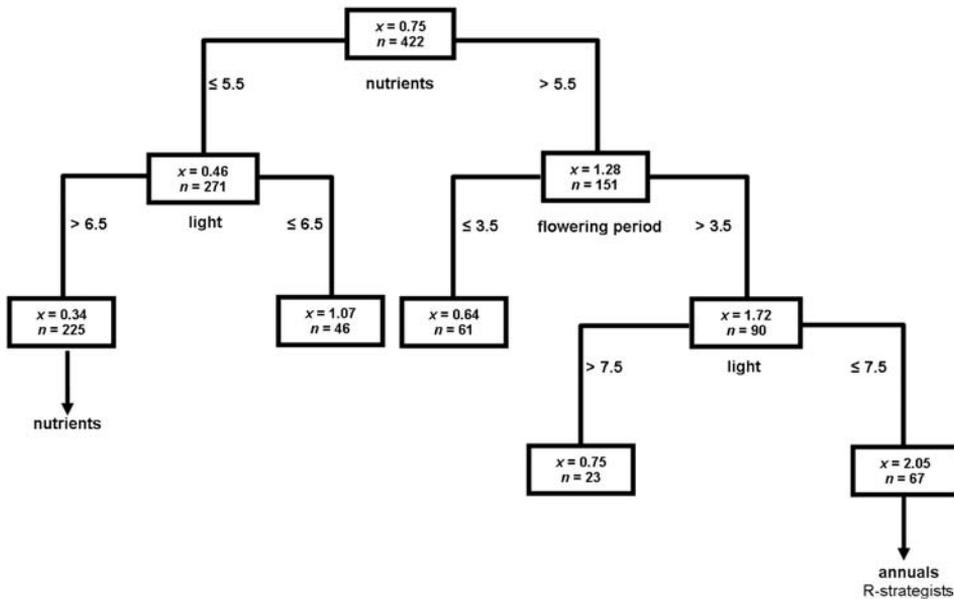


Fig. 2. – Relationship between occurrence of weed and ruderal species occurring in Moravia in 1908 and 2005. Species frequencies in 2005 are plotted against species abundances in 1908. Species are divided into three groups: native (nat), archaeophytes (arch) and neophytes (neo) according to their immigration status. A. Weeds: nat, $r^2 = 0.33$, $P < 0.001$; arch, $r^2 = 0.38$, $P < 0.001$; neo, $r^2 = 0.12$, $P < 0.05$; B. Ruderal: nat, $r^2 = 0.33$, $P < 0.001$; arch, $r^2 = 0.36$, $P < 0.001$; neo, $r^2 = 0.68$, $P < 0.001$.

A. Relative abundance of weed species in 1908

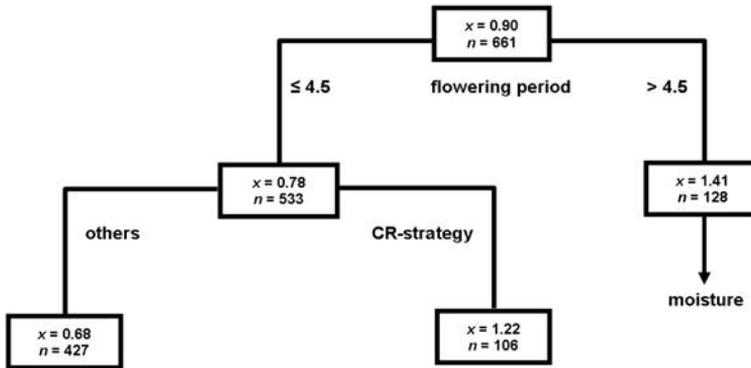


B. Relative abundance of weed species in 2005



The optimal regression tree for present ruderal species has three terminal nodes and explains 10.5% of the variation in regional species abundance (Fig. 3D). The most common species are those with high requirements for nutrients and moisture. Among them, the most common species are plants with a long flowering period (> 3.5 months).

C. Relative abundance of ruderal species in 1908



D. Relative abundance of ruderal species in 2005

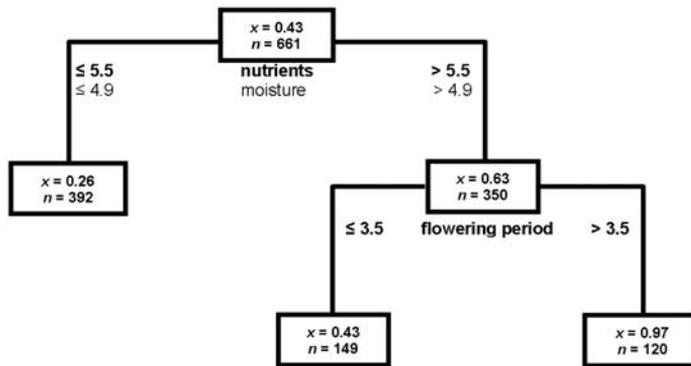


Fig. 3. – Regression tree models explaining the abundance of weed and ruderal Moravian species in 1908 and 2005. Boxes on the nodes contain information on the mean abundance (x) and the number of species assigned to that node (n). Splitter variables and their split values are given in bold type at each node. Surrogates are given in non-bold letters below the main splitter variable. Abundances of species are standardised by use of logarithmic transformation.

The most important attributes related to the relative abundance of weed species have changed slightly from 1908 to 2005 (Table 3). In 1908, the most important attributes of weeds were long flowering period, a low light and moisture requirement, insect-pollination, high requirement for nutrients and small size. In 2005, the most important attributes are represented by especially long flowering periods, shade-tolerance and high requirements for nutrients. Comparing the importance of these attributes for ruderal species in 1908 and 2005 we found that they were as important in the past as now (Table 3). They are long flowering period and high nutrient and moisture requirement. The importance of other attributes, except for the remarkably high representation of CR-strategists in 1908, is lower.

Table 3. – Importance of species attributes in explaining the abundance of weed or ruderal Moravian species in 1908 and 2005. The first and second columns for weed and ruderal species include a sign which indicates the relationship between species attribute and species abundance. A set of linear regressions was used to determine relationships between individual attribute and species abundance. Numbers in third and fourth columns are values of relative importance, which are scaled from 0 to 100. They are related to optimal regression trees, in which abundance of species was used as the dependent variable and species attributes as independent variables. Values > 75 are in bold type.

| | Weeds | | | | Ruderals | | | | |
|---------------------------|-------|------|------------|------------|---------------------------|------|------|------------|------------|
| | 1908 | 2005 | 1908 | 2005 | 1908 | 2005 | 1908 | 2005 | |
| Flowering period | + | + | 100 | 70 | Flowering period | + | + | 83 | 100 |
| Height mean | – | – | 75 | 27 | Height mean | – | + | 32 | 21 |
| Ellenberg indicator value | | | | | Ellenberg indicator value | | | | |
| Light | – | – | 92 | 100 | Light | + | + | 46 | 15 |
| Temperature | – | – | 45 | 66 | Temperature | – | – | 22 | 27 |
| Continentality | – | – | 47 | 37 | Continentality | + | + | 27 | 20 |
| Moisture | – | + | 91 | 54 | Moisture | – | – | 64 | 54 |
| Reaction | + | – | 27 | 29 | Reaction | + | + | 23 | 46 |
| Nutrients | + | + | 77 | 78 | Nutrients | + | + | 64 | 63 |
| Life strategy | | | | | Life strategy | | | | |
| R | + | + | 39 | 23 | R | + | + | 4 | 7 |
| C | – | – | 32 | 4 | C | – | + | 1 | 31 |
| S | – | – | 5 | 3 | S | – | – | 8 | 5 |
| CR | + | + | 42 | 31 | CR | + | + | 100 | 20 |
| CS | – | – | 28 | 17 | CS | – | – | 50 | 56 |
| SR | + | – | 8 | 20 | SR | – | – | 12 | 24 |
| CSR | – | – | 13 | 25 | CSR | – | – | 3 | 5 |
| Life span | | | | | Life span | | | | |
| Annual | + | + | 72 | 57 | Annual | + | + | 30 | 3 |
| Biennial | – | – | 16 | 11 | Biennial | + | + | 28 | 3 |
| Perennial | – | – | 52 | 31 | Perennial | – | – | 50 | 3 |
| Pollination mode | | | | | Pollination mode | | | | |
| Wind | – | + | 77 | 1 | Wind | – | + | 1 | 18 |
| Insect | + | – | 83 | 1 | Insect | + | – | 6 | 6 |
| Selfing | + | + | 20 | 6 | Selfing | + | + | 3 | 0 |

Discussion

Changes in species composition

Comparison of historical with present floristic data is very difficult because of the differences in the data sets. The most important difference is in the sampling methods used for obtaining the data. Some differences arise because of differences in sampling intensity and difficulty of comparing data sources provided by different authors. For these reasons present data sets cannot be easily used for comparing floristic diversity and indicating increases or decreases in the species number in Moravian synanthropic vegetation. However, by including many types of synanthropic vegetation occurring in many habitats (i.e., various types of arable fields and ruderal habitats in human settlements and their surroundings) it is possible to partially eliminate these discrepancies and reveal trends in the distribution of individual species groups.

From the results of the present study it seems that species that were common in the past are still common a century later and rare species are becoming rarer, so they are rarely

present or absent from vegetation plots. A similar trend was found in a study of the temporal dynamics of urban flora of Plzeň (Chocholoušková & Pyšek 2003) and changes in structure of German weed vegetation (Baessler & Klotz 2006). A comparison of all these data sets is difficult, however, because of the different temporal and spatial scales at which the comparisons were made.

At the beginning of the last century, Laus (1908) recorded rather long lists of weed and ruderal species, which were not documented in 2005. Some of these species are extinct or rare today (e.g., weeds: *Agrostemma githago*, *Camelina alyssum*, *Cuscuta epilinum*, *Scandix pecten-veneris*; ruderals: *Atriplex rosea*, *Euclidium syriacum*, *Geranium molle*, *Chenopodium urbicum*), some of them occur in Moravia in other habitats or they were not found in the samples (e.g., weeds: *Centaurea scabiosa*, *Melampyrum arvense*, *Myosotis discolor*; ruderals: *Asparagus officinalis*, *Bidens cernua*, *Lithospermum arvense*, *Onobrychis viciifolia*). The number of localities for extinct and endangered weed species mentioned by Laus (1908) indicates that currently rare or extinct species were also relatively rare at the beginning of the last century. Extinct or endangered ruderal species, which were frequently recorded in 1908, but not in 2005, include, for example, *Anthemis cotula*, *Atriplex rosea* and *Chenopodium vulvaria*. These species are generally rare in Moravia today. A marked decline in the localities for *Atriplex rosea* in the 1950s is repeatedly documented (see Kopecký & Lhotská 1990, Mandák 2003). Nevertheless, the reason for its scarcity throughout the Czech Republic is still rather unclear. Decline in the localities for *Anthemis cotula* and *Chenopodium vulvaria* follows changes in rural lifestyle, which is related, for example, to the decline in keeping small animals, cleaning and paving the streets and village squares and consequently the loss of habitats enriched by ammoniacal nitrogen.

Changes in the proportion of alien species in synanthropic floras is repeatedly reported and an increasing occurrence of neophytes, combined with a decrease in occurrence of natives and archaeophytes, is generally accepted (Mandák et al. 1993, Lososová et al. 2004, Pyšek et al. 2004a, Pyšek et al. 2005). Given this trend, the species lists of both temporal periods considered did not differ. The proportion of alien species found in weed and ruderal vegetation accords, however, with results for the species composition of Central European arable field weed vegetation, ruderal vegetation (Lososová et al. 2004, Pyšek et al. 2005, Wania et al. 2006, Sádlo et al. 2007, Simonová & Lososová 2008) and of Czech settlement flora (Pyšek 1998, Chocholoušková & Pyšek 2003, Pyšek et al. 2004a). This study did not find any decrease in the proportion of archaeophytes and natives, but revealed a decrease in mean abundances of archaeophytes and natives combined with an increase in that of neophytes (e.g., *Galinsoga parviflora*, *G. quadriradiata*, *Matricaria discoidea*, *Veronica persica* in weed vegetation; *Erigeron annuus*, *Helianthus tuberosus*, *Solidago canadensis* in ruderal vegetation). This decrease is due to the decline in traditional arable weeds and ruderals, which grew on disappearing ruderal habitats, such as dumps, rubbish tips or garbage holes.

Changes in species attributes

Some clear trends in changes in species attributes were revealed for both vegetation types in the present study. One of the most important attributes of weed and ruderal species is high requirement for nutrients and long flowering periods.

The number of species of weeds that require high inputs of nutrients reflects habitat changes in the studied area since the beginning of the last century (Fig. 3B). It is probably associated with intense application of fertilizers and abandoning of dry and nutrient-poor fields, which were commonly cultivated in the past. Unlike plants characteristic of soils with high nutrient levels, there has been a general decline in species growing in extremely nutrient-poor and often dry habitats (e.g., *Filago arvensis*, *Galeopsis ladanum*, *Galium tricornerutum*, *Melampyrum arvense*). These species have decreased in abundance or disappeared from Moravian fields, unlike the species with high requirements for nutrients and moisture (e.g., *Galium aparine*, *Persicaria lapathifolia*, *Taraxacum* sect. *Ruderalia*), which have become more abundant.

High input of nutrients has always been an important factor for ruderal vegetation, especially for annual ruderal vegetation. Most abundant ruderal species are able to grow in a variety of ruderal habitats and have wide ecological amplitude. Such species (e.g., *Artemisia vulgaris*, *Chenopodium album* agg., *Lamium album*, *Poa annua*, *Taraxacum* sect. *Ruderalia*, *Urtica dioica*) were common throughout the last century. These species are at an advantage in contemporary landscapes, in which there is increased eutrophication caused by human activities.

Long flowering periods seem to be a very important attribute of abundant weed and ruderal species. Many of these recently abundant plants are able to flower and to set seed for more than four months in the year. Some common species (e.g., *Capsella bursa-pastoris*, *Poa annua*, *Stellaria media*) can flower the whole year round. In contrast is the decrease in specialized weed species typical of traditional cereal fields, whose lifecycle is adapted to that of the crop. Most of them flowered and set seed at the same time as cereals and their seed was collected and dispersed along with the seed of the crop. The decline of these so-called speirochorous species over the last few decades is documented for many European countries (Holzner & Immonen 1982, Hilbig 1987, Kornaš 1988, Firbank 1990, Andreassen et al. 1996, Sutcliffe & Kay 2000, Lososová 2003, Pinke 2004, Kropáč 2006).

It is not surprising that a long flowering period is an advantage for ruderal species. Ability to flower for a long time and produce abundant seed is an advantage when colonizing newly-created niches in disturbed habitats. These results are consistent with the published results for Mediterranean agricultural habitats (Lloret et al. 2005), Czech arable field vegetation (Lososová et al. 2008) and studies on the biological traits of potentially successful invasive plants (e.g., Rejmánek & Reichard 2001, Pyšek et al. 2003).

Our study suggests that only small (most smaller than crop plants) and shade-tolerant species are able to survive in densely planted crops. Similarly, this is documented for weed vegetation throughout the Czech Republic (Lososová et al. 2008) and synanthropic vegetation in other European countries (e.g., Hilbig 1987, Kornaš 1988, Smart et al. 2003, Pinke 2004). The results yielded by the comparison of the current state of the weed flora with that reported in the past suggest that during the last century the importance of an annual lifespan and R- or S-combined life strategy for species abundance have declined. While species of annual weeds were the most abundant at the beginning of the last century, many of them are now rare. There has been a significant change in the mode of pollination of current weeds. Our study shows that the most important change in species composition of weed vegetation was a decline in the number of insect-pollinated weed species. This decline follows a general decline in insect population densities. Usage of pesticides together with destruction of nesting sites has reduced numbers of insect-pollinators. Such trends

are reported elsewhere in Europe (Benedek 1997, Kearns et al. 1998, Robinson & Sutherland 2002, Biesmeijer et al. 2006).

In ruderal vegetation, there has been little change in species attributes over the time period studied. There is a general decrease in the abundance of CR-strategists and increase in that of species with high competitive ability (C-strategists). These species mainly represent plants with wide ecological amplitudes that require a high nutrient supply and less frequent disturbances. In the present landscape there are many such sites (derelict areas, building sites, etc.). On the other hand, ruderal sites typical of former rural landscapes (e.g., fowl outlets, dunghills or wall footings enriched by ammoniacal nitrogen) colonized by CR-strategists (e.g., *Anthemis cotula*, *Atriplex rosea*, *Diplotaxis tenuifolia*, *Hyoscyamus niger* and *Malva pusilla*) are vanishing.

Comparisons of the species composition of vegetation of larger areas or specific types of habitats over a particular period of time contribute to the knowledge of the changes that have occurred in the landscape and land use. Although the drivers of change in species composition cannot be directly identified by such studies, they indicate the effect on species of human activities and environmental and land use changes that have occurred the time period studied. The changes in abundance of weed and ruderal species and their attributes revealed by this study might reflect the gradual loss of typical rural habitats, increasing input of nutrients (application of fertilizers and increased eutrophication) or an increase in the number of introduced species and their naturalization.

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Souhrn

Práce se zabývá změnami v druhovém složení a ve vlastnostech druhů plevelové a ruderální vegetace Moravy v průběhu minulého století. Údaje o plevelové a ruderální vegetaci Moravy do roku 1908 byly převzaty z práce Lause (Laus 1908), zatímco jako zdroj informací o složení současné synantropní vegetace sloužily fytoecologické snímky uložené v České národní fytoecologické databázi. Vybrány byly snímky zapsané v letech 1985–2005 ve vhodném území a ve vegetačních typech, které odpovídaly definici stanovišť sledovaných Lausem.

Bylo zjištěno, že druhy, které byly časté na začátku minulého století, jsou časté i nyní. Téměř čtvrtina druhů plevelové i ruderální vegetace zaznamenaná Lausem je v současnosti považována za ohrožené druhy, 12 druhů je v současnosti vyhynulých v celé České republice. Zatímco porovnání procentuálního zastoupení původních druhů, archeofytů a neofytů v synantropní vegetaci Moravy neukázalo žádné výrazné rozdíly, porovnáním průměrných frekvencí výskytu druhů bylo zjištěno, že zatímco frekvence archeofytů a původních druhů během studovaného časového úseku klesá, frekvence výskytu neofytů naopak stoupá.

Pro zjištění, které vlastnosti druhů byly důležité k tomu, aby se druh mohl úspěšně vyskytovat na ruderálních stanovištích nebo jako plevel na polích v minulosti a nyní, byly použity modely regresních stromů. Mezi časté druhy polních plevelů patřily vždy (v minulosti i nyní) spíše nízké rostliny tolerantní k zastínění, mající vyšší nároky na obsah živin v půdě a schopné kvést po dlouhou časovou periodu. Oproti minulosti, kdy u nejčastějších plevelů převládaly druhy opylované hmyzem, nejsou dnes hojně plevele přizpůsobeny na specifické způsoby opylování. Dlouhá doba kvetení je stále důležitou vlastností také pro nejčastější ruderální druhy. Co se týká ekologických nároků, u ruderálních druhů nebyly pozorovány žádné větší změny během sledovaného časového úseku. Oproti minulosti výrazně poklesl počet ruderálních druhů majících CR-strategii a naopak vzrostl počet druhů s C-strategií.

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