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Inter-annual Variability of the Abundance and Morphology of *Dactylorhiza majalis (Orchidaceae-Orchideae)* in two Permanent Plots of a Mire in Slovakia

By

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With 4 Figures

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Summary

HRIVNÁK R., GÖMÖRY D. & CVACHOVÁ A. 2006. Inter-annual variability of the abundance and morphology of *Dactylorhiza majalis (Orchidaceae-Orchideae)* in two permanent plots of a mire in Slovakia. – Phyton (Horn, Austria) 46 (1): 27–44, 4 figures. – English with German summary.

Inter-annual variability of the abundance and morphology of *Dactylorhiza majalis* (RCHB.) HUNT & SUMMERH. was studied in two monitoring plots (MPs) in a nutrient poor acidic fen in the Veporské Mts, Central Slovakia, during 1997–2004. Stands were regularly mowed in the past. In the late 1980s and during the 1990s, mowing ceased and the area was gradually overgrown by shrubs and trees. Both MPs have been regularly mowed every year since 1999. The initial counts of flowering individuals were 5 and 11 in 1997, and later the population sizes increased to 19 and 145 individuals in 2004 on MP1 and MP2, respectively. Whereas a continuous increase is obvious for MP2, the number of flowering individuals increased until 2002, when a maximum of 51 individuals was observed, but decreased again in 2003 on MP1. The investigated morphological traits were significantly positively correlated,

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whereby the correlations are consistent for both monitoring plots. Nevertheless, correlations are quite weak, mainly those between vegetative traits (plant height, number of leaves) and floral traits (number of flowers, inflorescence length). Except one case, year means of all traits are consistently negatively autocorrelated, which means that the vigorous growth and reproduction in one year are generally followed by poor performance in the subsequent year. No general pattern was found in the correlations between year means and standard deviations of the investigated morphological traits and the population size and/or increment. For MP2, we revealed a correlation between the vegetation changes and the population growth of *D. majalis*.

Zusammenfassung

HRIVNÁK R., GÖMÖRY D. & CVACHOVÁ A. 2006. Die zeitliche Variabilität der Populationsgröße und morphologischen Merkmale von *Dactylorhiza majalis (Orchidaceae-Orchideae)* auf zwei Dauer-Beobachtungsflächen in einem Moor in der Slowakei. – Phyton (Horn, Austria) 46 (1): 27–44, 4 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die zeitliche Variabilität von Häufigkeit und Morphologie von *Dactylorhiza majalis* (RCHB.) HUNT & SUMMERH. zwischen aufeinanderfolgenden Jahren wurde auf zwei Beobachtungsflächen (MP) in einem nährstoffarmen, sauren Moor im Verporské Gebirge, Zentrale Slowakei, von 1997–2004 untersucht. Die Standorte wurden früher regelmäßig gemäht. Ende der 80er-Jahre und in den 90er-Jahren setzte die Mahd aus und das Gebiet wurde allmählich von Sträuchern und Bäumen überwachsen. Beide Beobachtungsflächen wurden seit 1999 wieder regelmäßig jedes Jahr gemäht. Die ersten Zählungen 1997 ergaben 5 bzw. 11 blühende Individuen, danach nahm die Größe der Populationen zu und 2004 wurden 19 bzw. 145 Pflanzen auf MP1 bzw. MP2 gezählt. Während auf MP2 ein kontinuierlicher Anstieg beobachtet wurde, stieg die Zahl auf MP1 bis 2002 (Maximum mit 51 Pflanzen) und nahm dann 2003 wieder ab. Die untersuchten morphologischen Merkmale waren in beiden Flächen übereinstimmend, signifikant positiv korreliert. Dennoch, die Korrelationen waren ziemlich schwach, besonders diejenigen zwischen vegetativen Eigenschaften (Pflanzenhöhe, Zahl der Blätter) und solchen im Blühbereich (Zahl der Blüten, Infloreszenzlänge). Mit einer Ausnahme waren die Jahresmittel aller Eigenschaften übereinstimmend negativ autokorreliert, das heißt, daß kräftiges Wachstum und Blüte in einem Jahr durch schwache Ausbildung im nächsten Jahr gefolgt wurden. Es konnte kein allgemeines Muster der Korrelationen zwischen Jahresmitteln und Standardabweichungen der morphologischen Eigenschaften sowie Populationsgröße und/oder Zunahme gefunden werden. Auf MP2 fanden wir eine Korrelation zwischen Vegetationsveränderungen und Zunahme der Individuenzahl von *D. majalis*.

1. Introduction

Orchids belong to rare and endangered species in Europe. The main reasons are a high sensitivity to negative anthropogenic influences and direct destruction of orchid habitats. Orchids are characterized by specific population dynamics, which are affected mainly by 1) climatic factors (e.g. rainfall, temperature; WELLS & al. 1998, GORCHAKOVSKII & IGOSHEVA 2003, WOTAVOVÁ & al. 2004), 2) habitat deterioration (e.g. effect of fertilization, invasion of trees and shrubs, animal influences; Silvertown & al. 1994, Brzosko 2002), 3) habitat management (mainly meadow species; Hutchings & al. 1998, Jones 1998, Barbaro & al. 2003, Wotavová & al. 2004), and 4) species' biology (e.g. dormancy, irregular flowering; Kindlmann & Balounová 1999; Brzosko 2003). The modifiable morphological traits are influenced by the mentioned factors as well. For example, Balounová 1997 and Wotavová 2001 detected a distinct effect of habitat management on leaf area, length of inflorescence and length of flowering stems of *Dactylorhiza majalis*.

We chose *Dactylorhiza majalis* (Rchb.) Hunt & Summerh. as the object of study because of a relatively wide occurrence on both regional and national scales, supposed importance of findings for the regional management of plant communities with the occurrence of this species, and the availability of comparable studies (e.g. Balounová 1997, Wotavová 2001, Wotavová & al. 2004, Janečková & al. 2006).

D. majalis belongs to the *D. majalis* group, the so-called "tetraploid marsh-orchids", containing numerous, morphologically and ecologically very variable species (Bateman & Denhold 1983, Tyteca & Gathoye 2000). It occurs in most of Western and Central Europe, in the Baltic region and Northern Russia (Soó 1980, Delforge 1995). In Slovakia, *D. majalis* grows in wet meadows more or less over the whole territory and belongs to the vulnerable taxa (Feráková & al. 2001, Vlčko & al. 2003).

The aims of this study were:

- to describe temporal changes in the abundance of flowering individuals of *D. majalis* and their morphological characteristics, as well as possible interactions between population size and morphology, based on a case study of two micropopulations, and to identify factors responsible for the changes of population size and morphology
- to assess whether the changes of vegetation affect the size of the *D. majalis* population.

2. Methods

2.1. Design of Study

Two monitoring plots (designated further as MP1 and MP2) were established in the upper part of the Jasenina Protected Area (further PA), which is situated in the SW part of the Veporské Mts near the Ďubákovo village in Central Slovakia (Fig. 1). The sizes of plots were 300 m^2 and 550 m^2, respectively.

The number of flowering *Dactylorhiza majalis* individuals was recorded for both monitoring plots in the middle of June during the period 1997–2004. Scoring of morphological traits was accomplished at a stage of full flowering, i.e. when all flower buds within inflorescences flushed in an overwhelming majority of individuals. MPs are stabilized in natural margins formed by the morphology of terrain, trunks of trees and shrubs and a power line pylon. For each recorded *D. majalis* individual, the following traits were measured: number of flowers (NuFl), number of leaves (NuLe), plant height (HePl) and inflorescence length (LeIn). Damaged plants, where any of the traits could not be measured, were omitted.

Phytosociological relevés were done according to the Zürich-Montpellier approach. Braun-Blanquet's scale adapted by Barkman & al. (1964; M – 2m, cover about 5 %, A – 2a, 5.1-15 %, B – 2b, 15.1–25 %) was used to describe species abundance in two randomly chosen plots (one plot within each MP) with a standard relevé area (4 × 4 m). Phytosociological relevés were done when vegetation was optimally developed in the second half of June, along with the assessment of the D. majalis population.

Fig. 1. Location of the studied area (monitoring plots MP1 and MP2: tip of arrow head) in Slovakia

2.2. Statistics and Nomenclature

The investigated continuous morphological traits were analysed using a two-way analysis of variance. The distribution of the number of flowers proved to be approximately normal, Anova was thus used for this trait as well (procedure Glm, Anonymous 1988). As the second count variable, the number of leaves, followed Poisson distribution, log-linear model was used for the analysis (procedure Catmod, Anonymous 1988). Both years and monitoring plots were considered fixed-effect factors. Since the interaction terms were found to be significant for most traits, separate one-way analyses were done for each monitoring plot. The pairwise differences of means were tested using Duncan's test.

Correlations among morphological traits were assessed using Pearson's correlation coefficients (procedure Corr, Anonymous 1988). Temporal autocorrelations of trait means in individual years were also calculated. Because of a very short time series (eight years), only autocorrelations over a 1-year lag were considered. The relationships between morphology and abundance of the species, including delayed relationships (morphology in one year affects population size or increment in the next year or vice versa), were assessed as well. Since neither the trait values nor population sizes can be considered independent, statistical significance was based on 100 random permutations over years using an ad hoc program.

Phytosociological relevés were stored in the database program TURBOVEG (HENNEKENS & SCHAMINÉE 2001) and Principal Componets Analysis (PCA) was used to explain their variability, using the CANOCO program (TER BRAAK & ŠMILAUER 1998).

The names of the plants follow MARHOLD & HINDÁK 1998 and the names of plant communities follow HÁJEK & HÁBEROVÁ 2001 and MUCINA & MAGLOCKÝ 1985.

3. Study Site

The populations we studied grow on a poor acidic fen, in the Carici echinatae-Sphagnetum association of the Sphagno recurvi-Caricion canescentis alliance (HRIVNÁK & al. 2001). The stands of this community are poor in species, with a low cover of the herb layer, where *Carex canescens, C. echinata, C. nigra, C. panicea, C. rostrata and Eriophorum angustifolium* predominate, and dominance of peat mosses, mainly *Sphagnum recurvum* agg. (HÁJEK & HÁBEROVÁ 2001). It is poor in all mineral nutrients, but rich in organic matter, with pH values of approx. 5–5.5 (HÁJEK & HÁBEROVÁ 2001, HÁJEK & HÁJKOVÁ 2002, HÁJKOVÁ & HÁJEK 2003). Typical for the vegetation in the Jasenina PA is the occurrence of low sedges *(Carex echinata, C. canescens, C. nigra, C. panicea)* and diagnostic species of the class Scheuchzerio-Caricetea fuscae like *Agrostis canina, Eriophorum angustifolium, Potentilla erecta, Viola palustris*. *Sphagnum fallax* is the predominating moss species; *Calliergon cordifolium, C. giganteum* and *Polytrichum commune* are less frequent. In the study area, a gradual succession of Sphagno recurvi-Caricion canescentis stands towards wet meadows of the Calthion or willow shrubs of the Salicion cinereae alliances (unmowed stands) was observed. In the first case, hygrophilous species, which are rare in typical stands of Carici echinatae-Sphagnetum, spread gradually (e.g. *Caltha palustris, Equisetum sylvaticum, Filipendula ulmaria, Lysimachia vulgaris, Salix cinerea, Scirpus sylvaticus*).

The investigated stands of acidic poor fens were regularly mowed every year in the past. At the end of the 1980's and during the 1990's, the area and frequency of mowing rapidly decreased and a part of the studied area has been gradually overgrown by shrubs and trees (mainly *Salix cinerea* and *Alnus glutinosa*). In 1995, all shrubs and trees were removed from both MPs, however, *Salix cinerea* strongly sprouted during the subsequent years. Both MPs have been regularly mowed every year since 1999 (BELANOVÁ 2004 mscr.).

The vegetation was negatively affected by changes of water regime (road construction beneath the mire) and eutrophication (fertilization and cattle grazing in a area above the mire).

4. Results

4.1. Temporal Changes in the Number of Flowering Individuals of *Dactylorhiza majalis*

Dynamics of flowering individuals in the studied MPs during the eight years is illustrated in Fig. 2. The initial number of flowering individuals was low in both MPs (5 and 11 on MP1 and MP2, respectively) at the beginning of our study, but the further development was different. The number of individuals on MP2 markedly increased during our study, the peak abundance on MP2 represents 1318% of the initial status. On MP1, the increase was much less pronounced, the abundance differs up to a factor of 8 between plots. In 2003, a change of the trend was observed: the increase of the abundance of flowering individuals on MP2 became much slower compared to previous years, and even a decrease occurred on MP1. Nevertheless, the counts of flowering individuals are positively autocorrelated over a 1-year lag (r = 0.43, p = 0.34 and r = 0.93, p = 0.03 for MP1 and MP2, respectively).

4.2. Morphological Characteristics of the *Dactylorhiza majalis* Populations

The measured morphological traits over years and MPs are presented in Figs 3a–h. The trait averages exhibit a considerable interannual fluctuations on MP1, whereas they are much less variable on MP2 (except LeIn). The most pronounced fluctuation on MP1 was observed during the period 1997 to 1999, later the averages become more stable, but the observed range of the investigated traits is larger. Increasing variation range during the last years may be associated with increasing population size and thus increasing number of measured individuals (cf. Fig. 2).

The differences in the number of leaves were highly significant for monitoring plots, years as well as MP × year interaction (Table 1). On the

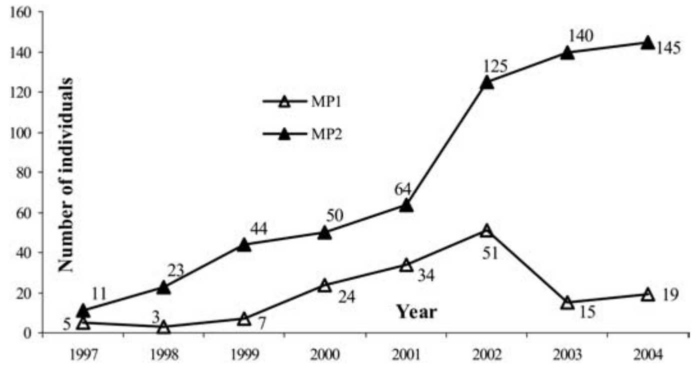

Fig. 2. Interannual changes of the abundance of the flowering individuals of *Dactylorhiza majalis*

other hand, the remaining morphological traits did not differ between the MPs. Plant height and inflorescence length varied significantly among years. Interaction terms (MP × year) for these traits were also significant, indicating that the development of morphological traits over years was not consistent over monitoring plots, especially before regular mowing was applied. This can be clearly demonstrated in Fig. 3a–h. Before mowing, morphological traits strongly and significantly differed even between successive years (Table 2). What is remarkable, the behaviour of floral traits at the beginning of the study strongly differs between plots: the years of the best performance on MP1 are the years of the poorest performace on MP2 and opposite. Later on, during the period of regular mowing, floral traits became more or less stable, mainly on MP1 (the differences between years for this period were generally non-significant), whereas vegetative traits showed less stability (Table 2).

Table 1. Analysis of variance of the investigated morphological traits

	DF	χ^2-test	F-test		
		NuLe	**NuFl**	**HePl**	**LeIn**
MP	1	14.67***	0.08^{ns}	0.95^{ns}	0.29^{ns}
Year	7	90.35***	1.44^{ns}	14,51***	2,53*
MP*Year	7	35.22***	1.18^{ns}	2,78**	2,37*
Residual	720				
	DF	**χ^2-test**	**F-test**		
		NuLe	**NuFl**	**HePl**	**LeIn**
MP1 – Year	7	54.59***	1.09^{ns}	8,76***	2,27*
Residual	146				
MP2 - Year	7	85.67***	2,67*	8,73***	4,13***
Residual	574				

Legend: MP – monitoring plot, NuLe – number of leaves, NuFl – number of flowers, HePl – height of plant, LeIn – lenght of inflorescence, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ns – non-significant; DF – degrees of freedom.

As expected, the investigated morphological traits are significantly positively correlated, whereby the correlations are consistent over both monitoring plots (Table 3). Nevertheless, correlations are quite weak, mainly those between vegetative traits (plant height, number of leaves) and floral traits (number of flowers, inflorescence length).

In spite of a short period of investigation, a preliminary time-series analysis can be done. Neither the means nor the variation of the measured morphological traits exhibit a temporal trend (Fig. 3a–h). Except one case, year means of all traits are consistently negatively autocorrelated (Table 4), whereby several autocorrelations are significant or near the conventional

Table 2. Pairwise comparisons of means of morphological traits among years (Duncan's multiple-range test)

MP1							
NuLe		**NuFl**		**HePl**		**LeIn**	
Year	Mean	Year	Mean	Year	Mean	Year	Mean
2004	4.7895	1998	25.333	1998	51.067	1998	12.033
2001	4.7576	2003	20.400	2002	45.653	2002	10.308
1998	4.6667	2004	20.000	2004	39.979	2004	9.389
2002	4.5686	2002	19.804	1999	39.625	2000	9.137
2000	4.1250	2000	19.792	2000	37.254	2003	8.447
1997	4.0000	2001	18.970	2001	35.867	2001	8.403
2003	3.6667	1997	18.000	1997	31.820	1997	7.940
1999	3.5000	1999	12.750	2003	31.620	1999	7.825
MP2							
NuLe		**NuFl**		**HePl**		**LeIn**	
Year	Mean	Year	Mean	Year	Mean	Year	Mean
2001	5.0323	1997	21.545	2002	42.754	1999	10.5703
2004	4.9655	2004	21.303	1998	41.222	2003	10.0618
1997	4.8182	2003	20.344	1999	37.932	2002	9.9760
1998	4.7391	2000	20.146	2003	37.485	2000	9.3458
2003	4.4351	2001	19.968	1997	36.864	1997	9.3182
2000	4.3125	2002	19.176	2001	36.658	2004	9.2076
1999	4.2162	1999	17.432	2004	35.848	2001	9.0016
2002	4.2080	1998	17.174	2000	35.148	1998	7.6391

Years with regular mowing are marked by shading (1999 beginning of regular mowing). Meaning of symbols and abbreviations as in Table 1.

Table 3. Correlations between the investigated morphological traits

MP		**NuLe**	**NuFl**	**HePl**	**LeIn**
MP1	NuLe	1.000	.	.	.
	NuFl	0.286***	1.000	.	.
	HePl	0.372***	0.418***	1.000	.
	LeIn	0.248**	0.725***	0.599***	1.000
MP2	NuLe	1.000	.	.	.
	NuFl	0.453***	1.000	.	.
	HePl	0.168***	0.356***	1.000	.
	LeIn	0.252***	0.732***	0.496***	1.000
Both MPs	NuLe	1.000	.	.	.
	NuFl	0.422***	1.000	.	.
	HePl	0.203***	0.367***	1.000	.
	LeIn	0.252***	0.731***	0.515***	1.000

Meaning of symbols and abbreviations as in Table 1.

Table 4. Temporal autocorrelations (1-year lag) of morphological traits based on year means

	NuLe	***NuFl***	***HePl***	***LeIn***
MP1	–0.440	–0.604	–0.546	–0.699a
MP2	–0.324	0.001	–0.172	–0.356
Both MPs	–0.227	–0.512a	–0.465a	–0.592*

Meaning of symbols and abbreviations as in Table 1.
a – $p < 0.10$.

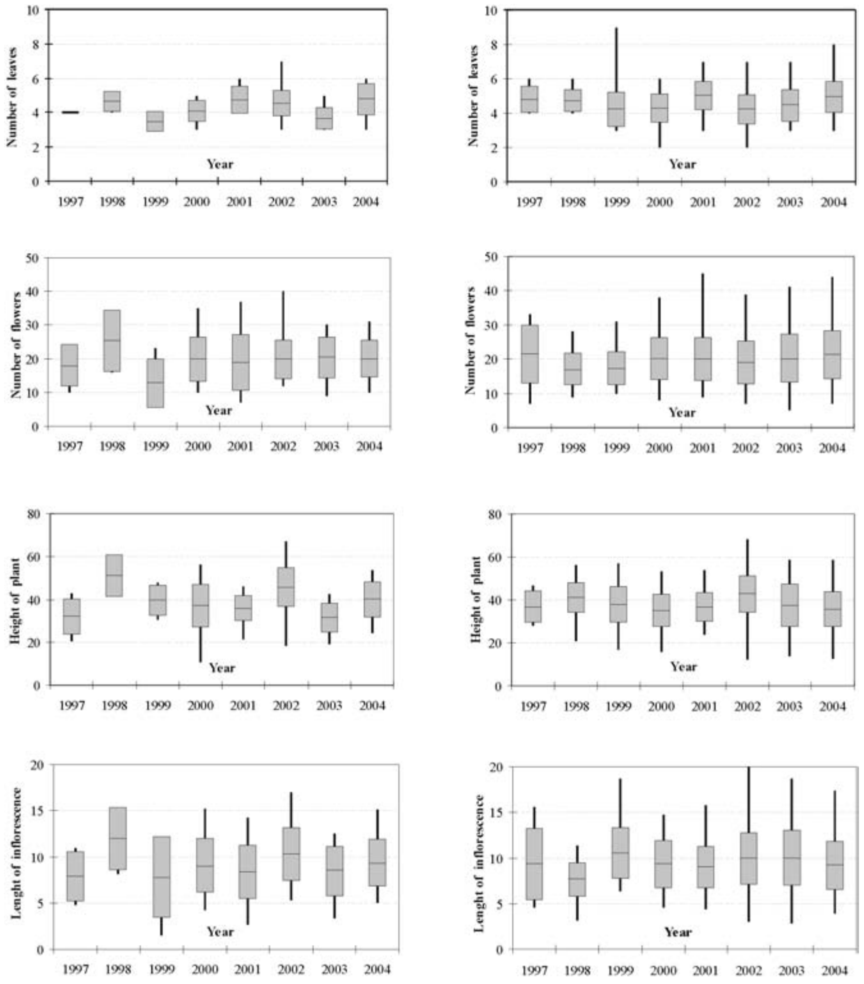

Fig. 3a-h. Morphological characteristics of the flowering individuals of *Dactylorhiza majalis* in 1998–2004. Horizontal bar – mean, box – standard deviation, vertical bars – minimum and maximum values; MP1 – left, MP2 – right.

significance limit of P = 0.05 despite a very small data set (7 mean-mean pairs). The binomial probability of such outcome (assuming no autocorrelation) is 3.5%. This indicates that vigorous growth and reproduction in one year are generally followed by a poor appearance in the subsequent year, whereby this effect is more pronounced on MP1 (Table 4, Fig. 3a–h).

No general pattern was found in the correlations between year means and standard deviations of the investigated morphological traits and the population size and/or increment (Table 5). To account for possible delayed relationships, we included correlations shifted by one year in both directions. Several significant and nearly significant correlations were found, but they were absolutely not consistent over monitoring plots and the pooled population.

Table 5. Correlations between year means and standard deviations of morphological traits and population size and increment

		N	**Inc**	**N_{del}**	**Inc_{del}**	**N_{adv}**	**Inc_{adv}**
MP1	NuLe	0.480	–0.018	–0.110	0.405	0.148	–0.626
	NuLe SD	0.532	–0.141	0.191	0.238	0.590	0.051
	NuFl	0.102	0.024	0.108	0.087	–0.304	–0.788*
	NuFl SD	–0.289	–0.110	–0.411	0.793a	0.156	0.094
	HePl	0.122	–0.148	–0.442	–0.273	–0.321	–0.053
	HePl SD	–0.021	0.523	–0.471	–0.666	–0.517	–0.320
	LeIn	0.140	–0.044	–0.198	–0.265	–0.409	–0.457
	LeIn SD	–0.395	–0.180	–0.515	–0.124	–0.011	0.896**
MP2	NuLe	–0.089	–0.366	0.253	–0.704	–0.140	0.902**
	NuLe SD	0.507	–0.340	0.422	0.521	0.353	–0.718a
	NuFl	0.324	–0.910**	0.830*	–0.498	0.161	0.183
	NuFl SD	0.219	–0.813*	0.888**	–0.484	0.095	0.226
	HePl	0.046	0.843*	–0.346	–0.165	0.216	–0.118
	HePl SD	0.701a	–0.153	0.569	0.477	0.518	–0.865*
	LeIn	0.376	–0.136	0.275	0.676	0.322	–0.723a
	LeIn SD	–0.028	–0.357	0.582	0.505	–0.171	0.000
Both MPs	NuLe	0.281	–0.088	0.244	0.209	0.254	–0.447
	NuLe SD	0.537*	–0.193	0.527a	0.085	0.574*	–0.084
	NuFl	0.157	–0.030	0.256	0.008	–0.008	–0.697**
	NuFl SD	–0.048	–0.106	0.093	0.582*	–0.134	0.129
	HePl	–0.030	–0.045	–0.337	–0.229	–0.063	–0.045
	HePl SD	0.243	0.422	0.109	–0.525a	0.048	–0.329
	LeIn	0.235	–0.050	0.081	–0.206	0.111	–0.454
	LeIn SD	–0.237	–0.092	–0.168	–0.032	–0.286	0.618*

Legend: SD – standard deviation, N – population size, Inc – population increment, N_{del} (Inc_{del}) – population size/increment in the current year correlated with the population morphology of the previous year, N_{adv} (Inc_{adv}) – population size/increment in the previous year correlated with the population morphology of the current year. Other symbols and abbreviations as in Table 1.

4.3. Vegetation characteristics

Fig. 4 shows the general variability of vegetation on both MPs during the whole research period. The first two axes explain more than 80 % of the variation in both MPs.

Within MP1, the highest loadings on the first axis (61 %) have *Carex panicea, Eriophorum angustifolium, C. echinata, Galium uliginosum, C. nigra*, which are typical mire species. Temporal fluctuation over the 7 years of investigation was substantial, but no trend could be identified, the plot preserves the character of a mire.

On the other hand, in addition to typical mire species as *Carex echinata* and *Eriophorum angustifolium*, wetland species like *Salix cinerea, Galium palustre* and *Caltha palustris* exhibited the highest loading on the first axis on MP2. The relevés are ordered along the second axis more or less temporally, so that this axis (although representing only 10.5 % of variation) seems to be associated with a directed vegetational change from a mire towards a wet meadow or willow shrubland.

For MP2, we revealed a correlation between the position of relevés along the second PCA axis and the abundance of flowering individuals of *Dactylorhiza majalis* ($r = 0.881$, $p < 0.01$). This suggests an interaction between the development of vegetation and increase of number of flowering individuals of the monitored species. However, such relationship was not detected for MP1.

No relationships were found between the morphology of *D. majalis* and the vegetation.

5. Discussion

5.1. Abundance and Morphology of Dactylorhiza majalis

Actually, our study was based on flowering individuals only. The estimation of the population size is a difficult task in orchids. A thorough counting of individuals in the vegetative stage is possible on a small scale, but requires an enormous effort on a plot of more than 300 m^2. In addition, flowering is frequently followed by dormancy or sterility in the subsequent year (KINDLMANN & BALOUNOVA 1999, TALI & KULL 2001, KERY & al. 2005).

An important hint for practical implications is whether the population size was really growing or the observed increase of the count of flowering individuals was only due to a shift towards visible life stages. To answer this question, we have to take into account that the investigated populations were exposed to a rather long period when mowing was interrupted (approx. 15 years) and when conditions for survival of *D. majalis* were strongly unfavourable. This is reflected also in very low numbers of flowering individuals recorded at the beginning of the observation period on both monitoring plots. Theoretically, the populations may have persisted

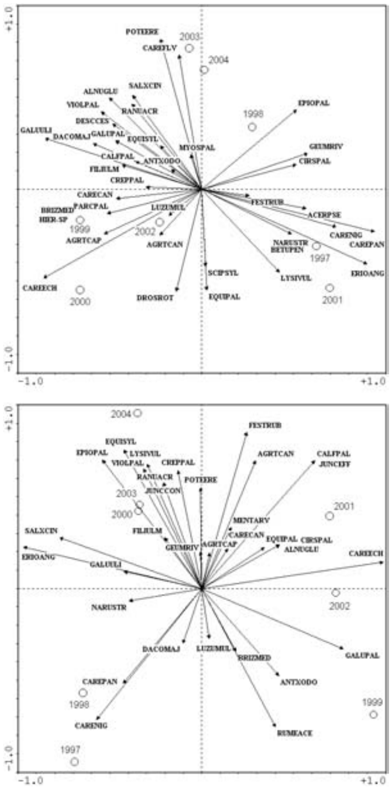

Fig. 4. PCA analysis of relevés on MP1 (upper; eigenvalues: axis 1 – 0.619, 2 – 0.198) and MP2 (lower; eigenvalues: axis 1 – 0.764, 2 – 0.105) over years

Legend: RUMEACE – *Acetosa pratensis*, ACERPSE – *Acer pseudoplatanus*, AGRTCAN – *Agrostis canina*, AGRTCAP – *Agrostis capillaris*, ALNUGLU – *Alnus glutinosa*, ANTXODO – *Anthoxanthum odoratum*, BETUPEN – *Betula pendula*, BRIZMED – *Briza media*, CALFPAL – *Caltha palustris*, CARECAN – *Carex canescens*, CAREECH – *Carex echinata*, CAREFLV – *Carex flava*, CARENIG – *Carex nigra*, CAREPAN – *Carex panicea*, CIRSPAL – *Cirsium palustre*, CREPPAL – *Crepis paludosa*, DACOMAJ – *Dactylorhiza majalis*, DESCCES – *Deschampsia cespitosa*, DROSROT – *Drosera rotundifolia*, EPIOPAL – *Epilobium palustre*, EQUIPAL – *Equisetum palustre*, EQUISYL – *Equisetum sylvaticum*, ERIOANG – *Eriophorum angustifolium*, FESTRUB – *Festuca rubra* agg., FILIULM – *Filipendula ulmaria*, GALUPAL – *Galium palustre*, GALUULI – *Galium uliginosum*, GEUMRIV – *Geum rivale*, HIER-SP – *Hieracium* sp., JUNCCON – *Juncus conglomeratus*, JUNCEFF – *Juncus effusus*, LUZUMUL – *Luzula multiflora*, LYSIVUL – *Lysimachia vulgaris*, MENTARV – *Mentha arvensis*, MYOSPAL – *Myosotis scorpioides* agg., NARUSTR – *Nardus stricta*, PARCPAL – *Parnasia palustris*, POTEERE – *Potentila erecta*, RANUACR – *Ranunculus acris*, SALXCIN – *Salix cinerea*, SCIPSYL – *Scirpus sylvaticus*, VIOLPAL – *Viola palustris*.

underground, since orchids are generally capable to survive up to several years in the dormant stage. Nevertheless, the duration of adverse conditions seems to be too long. WOTAVOVÁ & al. 2004 considered the absence of aboveground organs in 3 consecutive years a strong indication (although not a proof) of the extinction of this species on a site. Therefore, we interpret increasing counts of flowering individuals as an increase of the population size as such. However, since we have neither marked nor genotyped the flowering individuals, the fraction of dormant individuals or the share of clonal growth and the recruitment of new genets on population growth could not be directly estimated.

Our assumption of the increase of flowering individuals after regular mowing was not completely confirmed. The numbers of flowering individuals developed differently. Whereas a continuous increase is obvious for MP2, the number of flowering individuals has increased until 2002 but decreased in 2003 in MP1 (cf. Fig. 2). Some authors report significant fluctuations of flowering and fruiting from year to year (WHIGHAM & O'NEILL 1991, FALB & LEOPOLD 1993), but others hardly detect any big differences (BRZOSKO 2002). We know that flowering of orchids depends on several abiotic and biotic factors (KINDLMANN & BALOUNOVÁ 2001) and management (including mowing of biotopes) is only one of them. Weather, nutrient level, shading, and competition influence the existence, development, flowering, morphology and size of populations of *D. majalis* as well (WOTAVOVÁ & al. 2004). Generally, after appropriate management is applied, the abundance of orchid species usually increases (e.g. WILLEMS 1989, HUTCHINGS & al. 1998, JERSÁKOVÁ & KINDLMANN 2004). Management positively influences population structure, e.g. in favour of flowering individuals compared to vegetative or dormant plants (WOTAVOVÁ & al. 2004) and/or increasing the number of young individuals compared to old plants (HUTCHINGS & al. 1998). The effect of management on morpohological traits was reported as well; e. g. JANEČKOVÁ & al. 2006 observed that leaf area on regularly mown sites is larger than on sites, which were mown only once in 2 years. Cessation of mowing as well as other negative anthropic factors lead to a rapid decline of the number of flowering individuals. Such development was observed both on the local level, e.g. in Germany (HAMEL 1977, WEGENER 1994), and the national level, e.g. in the Czech Republic (JATIOVÁ & ŠMITÁK 1996, WOTAVOVÁ 2001) and Slovakia (POTŮČEK 1990). A marked change of abundance in MP1 in 2003 was probably due to other factors than management. Extremely low population censuses at the beginning of the observation period indicate that the populations probably suffered from a bottleneck that may have strongly decreased genetic variation and increased the vulnerability of the populations and their sensitivity to environmental fluctuations. Delayed density dependence can also explain such population fluctuation. In *Orchis morio*, a negative autocorrelation of the population size over a 5-year lag was observed (GILLMAN

& DODD 2000). However, a time span of 8 years is too short to test such assumption.

As mentioned, the morphological traits under study were found to be significantly positively correlated, and the correlations were consistent over monitoring plots. This is in agreement with KINDLMANN & BALOUNOVÁ 1999, indicating that vegetative growth and reproduction are based on the same energy supply. A general trend of alternating good and poor performance of plants over years (although derived only from population averages, not from single-plant data) also may be associated with resource accumulation and allocation (ŠERÁ & BALOUNOVÁ 1999, VALLIUS 2001, VALLIUS & SALONEN 2000), but the absence of data at the individual plant level does not allow to test this assumption explicitely.

The inconsistency of correlations between the population average of morphological traits and the number of flowering plants over years (including delayed relationships) does not support the assumption that individual plant performances and population size commonly respond to environmental variation. Although this conclusion is based on population averages rather than individual plant behaviour, it is in full agreement with the results reported by KINDLMANN & BALOUNOVÁ 2001 for *Epipactis albensis* and *Dactylorhiza fuchsii*. Nevertheless, these results need to be considered as very preliminary, since the length of the time series under study was quite small.

5.2. Vegetation Dynamics and Interaction Between Vegetation and Abundance of *Dactylorhiza majalis*

Ecological interpretation of the variability along the first PCA axis is not unequivocal. Probably, there are several factors affecting spatial and temporal variation of the vegetation, mainly water level fluctuation or water and soil chemistry. These ecological factors are determining for poor acidic fen vegetation (cf. HÁJEK & HÁJKOVÁ 2002, HÁJKOVÁ & HÁJEK 2003). Moreover, the fluctuation of the species cover due to phenological variation associated with differences in the course of weather conditions among years, which is a kind of sampling error, may play a role as well. The same applies to the interpretation of the second PCA axis on MP1. However, for MP2, the second axis may be interpreted in terms of a directed change. At this stage, it is difficult to assess whether this change is associated with regular mowing or with decreased water level caused by the construction of a road beneath MP2.

The coincidence between the growth of the *D. majalis* population and the vegetation change on MP2 suggests the existence of an interaction between the monitored species and the plant community. However, it remains questionable whether the vegetation is a mere indicator of environmental change or if it has a direct impact on *D. majalis* through competition or facilitation. We tend to prefer the former possibility. Among the recorded species, there is actually none which could affect the survival and growth of *D. majalis* by shading, root competition or other effects.

The vegetation on the surveyed monitoring plots developed in different directions. In spite of temporal fluctuations, MP1 remained essentially a poor acidic fen, thus not providing optimum site conditions for the species under study, since *D. majalis* does not occur on such sites often (cf. HÁJEK & HÁBEROVÁ 2001, HÁJEK & HÁJKOVÁ 2002). MP2 exhibits signs of a development towards a wet meadow, which is the preferred habitat of *D. majalis* (PROCHÁZKA & VELÍSEK 1980, POTŮČEK 1990, JATIOVÁ & ŠMITÁK 1996, STANOVÁ & VALACHOVIČ 2002, WOTAVOVÁ & al. 2004).

6. Conclusion

Differential responses of the *Dactylorhiza majalis* populations between MPs may be attributed to several causes. First, although both populations have undergone a strong bottleneck, the population on MP2 retained a higher number of individuals than MP1 so that genetic drift depleting genes with adaptive significance and the resulting decrease of the adaptive potential could have been less severe. Population size is also reflected in variation levels. Variation ranges increased, but the variation of population averages decreased with increasing population size on both MPs. Second, a differential development of vegetation indicates increasing differences in site conditions between plots. The causes of these differences may be both natural and anthropic, and were not objective of this study. However, the development towards a wet meadow on MP2 indicates gradual amelioration of the biotope, in contrast to MP1. On the other hand, the temporal development associated with mowing is similar on both plots: strong interannual fluctuations in floral and vegetative traits were observed at the beginning of the study, whereas the average performance of plants became more stable after mowing was applied.

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