

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Relative effects of management and environmental conditions on performance and survival of populations of a terrestrial orchid, *Dactylorhiza majalis*

Petra Janečková^a, Kateřina Wotavová^{a,b}, Iva Schödelbauerová^a, Jana Jersáková^{a,c}, Pavel Kindlmann^{a,c,d,*}

^aFaculty of Biological Sciences, University of South Bohemia, Branišovská 31, CZ 37005 České, Budějovice, Czech Republic

^bLaboratory of Applied Ecology, Faculty of Agriculture, University of South Bohemia, Studentská 13, 37005 České Budějovice, Czech Republic

^cInstitute of Systems Biology and Ecology, Academy of Sciences of the Czech Republic, Branišovská 31, 37005 České Budějovice, Czech Republic

^dAgrocampus Rennes, 35042 Rennes Cedex, France

ARTICLE INFO

Article history:

Received 17 February 2005

Received in revised form

3 September 2005

Accepted 21 September 2005

Available online 28 November 2005

Keywords:

Management

Mowing

Shading

Species composition

Weather effects

ABSTRACT

For population viability analysis of endangered orchid populations, it is crucial to disentangle the effects of weather and management from intrinsic orchid dynamics. When doing this, typically several months' average temperatures and/or sums of precipitations are compared with some characteristics of plant performance. Here we tested, whether short averaging intervals (1–2 weeks) are more closely correlated with orchid performance. We used 5 years of data from five *Dactylorhiza majalis* populations, and have shown that the improvement of prediction by shortening the interval over which the temperatures are averaged or precipitation summed, even if detectable, is only weak and not significant. This, however, may be due to low weather variability during the study. Regarding the second aspect, the effect of management (presence or absence of mowing), we have found that leaf area of *D. majalis* at the regularly mown site was larger than that at the sites which were mown only once in 2 years, but we did not detect a significant effect of the absence of mowing on the incidence of flowering. Mowing can affect orchid performance in two ways: by reduced shading of orchids and by reducing competition with other species. Therefore, we have determined the co-occurring species associated with presence or absence of mowing and found that shading significantly affected the length of the flower stalk, the ratio of leaf width to leaf length at the end of the season, but did not affect seed weight and probability of flowering the next year. We conclude that the most appropriate management for *D. majalis* is mowing at least once a year, ideally at the end of June/beginning of July, after its fruiting.

© 2005 Elsevier Ltd. All rights reserved.

1. Introduction

The survival of populations of many European orchid species is strongly dependent on appropriate site management, espe-

cially regular mowing or grazing (Waite and Hutchings, 1991; Lind, 1992; Kull, 2002). Effect of management on orchid populations is best assessed by long-term monitoring (Wells and Cox, 1989, 1991; Vanhecke, 1991; Willems and Bik, 1991; Falb

* Corresponding author: Tel.: +42 604 753 397; fax: +42 38 777 5357.

E-mail address: pavel@entu.cas.cz (P. Kindlmann).

0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2005.09.045

and Leopold, 1993; Sieg and King, 1995; Gill, 1996; Inghe and Tamm, 1988; Wells et al., 1998; Brzosko, 2002; Janečková and Kindlmann, 2002; Jersáková et al., 2002; Kindlmann and Balounová, 2001; Øien and Moen, 2002; Tali, 2002, etc.). However, when such data are analysed, it is crucial to disentangle the effects of *weather* and management (usually *mowing*) from the *intrinsic orchid dynamics* – which is what we concentrate on here.

When effect of *weather* is considered, usually several months' average temperatures and/or precipitation totals are compared with some characteristics of plant performance, such as percentage of flowering plants, flowering shoot height or leaf area. Results of such studies have been conflicting: some studies have confirmed the intuitive assumption that weather does affect plant performance (Wells, 1981; Firmage and Cole, 1988; Wells and Cox, 1989, 1991; Willems and Bik, 1991; Vanhecke, 1991; Wells et al., 1998; Sieg and King, 1995; Brzosko, 2002; Janečková and Kindlmann, 2002), while others have not (Whigham and O'Neill, 1991; Wheeler et al., 1998; Falb and Leopold, 1993; Øien and Moen, 2002). The problem may stem from the fact that the weather effects on orchid behaviour may be associated with some relatively short extreme conditions (e.g. short periods of severe drought or frost), which may cause severe damage to the population (Vanhecke, 1991). This raises the question of whether the often-used temperature means and/or precipitation totals spanning several months are appropriate for detecting weather influences on orchid populations. If short periods of extreme weather matter, then they may be obscured in long-term averages. Therefore, we test here the impact in such analyses of the time period over which weather variables are analysed.

Even if *mowing* is generally considered beneficial to the fitness of meadow orchids (Kull, 2002), its occurrence does not automatically ensure persistence of orchid populations (Tamm, 1991). Therefore, we study here, how plant fitness is affected by various mowing regimes. We use the total leaf area of a plant and its flower stalk height as indicators of plant fitness, because leaf area determines the plant's decision to flower or remain sterile in the next year in orchids (Wells et al., 1998; Kindlmann and Balounová, 1999, 2001) and the amount of stored carbohydrates in the underground storage organs for the next year (Kindlmann and Balounová, 1999), and because the height of the flower stalk is significantly correlated with the number of flowers and ultimately with the number of seeds in the current year (Kindlmann and Balounová, 2001). Consequently, leaf area and flower stalk height are closely correlated with two main fitness components: number of seeds in the current year and the size of the next-year's tuber.

There are two mechanisms, how mowing can affect orchid performance. Early mowing (usually in July, immediately after maturation of orchid seed capsules and seed dispersal), can suppress their competitors – dominant grasses (Willems, 1990; Lepš, 1999). Late mowing (~ August, September) removes the old plant biomass, thus reduces shading of orchids in the subsequent year and increases light available for photosynthesis (Lepš, 1999). This may be especially important for many temperate orchids species which require high light conditions and grow early in the season (Kull, 2002). Therefore

we study here, whether both mechanisms are important in management of our study species: which co-occurring species are characteristic for presence and absence of mowing and how shading affects various aspects of orchid performance, like leaf area and shape, seed weight, and length of the flower stalk.

We use *Dactylorhiza majalis*, which commonly occurs in wet meadows in central Europe, as our study species. Although the absolute number of extant *D. majalis* sites is not low, their rate of decline is worrisome. The main reasons for this decline are believed to include agricultural practices and the period of collectivisation (transformation of small-scale private farms into large-scale agricultural co-operatives) accompanied by large inputs of fertilizers, drainage, conversion of meadows and pastures into arable land and cessation of both cattle and sheep grazing in sub-montane regions (Wotavová et al., 2004). Thus it is not only the present number of sites, but also the temporal trend in the number of sites that determines this species' "rarity" (Wotavová et al., 2004). Recently, attempts have been made to restore wet meadows by blocking their drainage and reintroducing original plant species, including *D. majalis*. It is therefore important to determine, what is the correct management regime at such sites. Therefore we make here proposals for correct management of this species, which is the practical contribution of this paper for conservation of *D. majalis*.

2. Methods

2.1. The species studied

The western-marsh orchid (*D. majalis* Reichenb. Hunt et Summerh) is the most abundant species in the genus *Dactylorhiza* in Central Europe. The rapid decline of its natural habitats has caused it to be considered an endangered species in the Czech Republic (Wotavová et al., 2004). *D. majalis* has a broad ecological niche and occurs in wet to damp meadows, fenlands, wetlands and peatlands. *D. majalis* tolerates slightly acidic to strongly alkaline soils (pH 5.2–8.1). Its leaves appear above ground usually during April and last until July. The inflorescence contains about 30 nectarless flowers, appears in May and June and is pollinated by bees and bumblebees. For more details, see Wotavová et al. (2004).

2.2. Long term monitoring

Two biometric characteristics, total leaf area (estimated as (leaf length) × (leaf width)/2 summed over all leaves) and flower stalk height, were measured on samples of 50 plants per population in five populations containing several hundreds of individuals each (see Table 1 for site descriptions). None of the sites was fertilized. All plants were permanently marked by a numbered metallic plate staked to the ground by a 100 mm stainless nail, roughly 5 cm from the plant. Monitoring took place twice a year, when the plants achieved maximum size (once at the end of May, once at the end of June), from 1999 to 2003. Mowing, if present, took place in July, after fruiting (see Table 1 for years, when mowing was performed).

Meteorological data on average daily temperatures and precipitation during the 5 years of observation were obtained

Table 1 – Site description and mowing management during 1998–2003 (1 – mown, 0 – unmown); n total number of species at the site

Site	n	Mowing 1998–2003	Site description
Čakov	35	010000	Wet, partially shaded meadow, with increasing litter accumulation, threatened by <i>Filipendula ulmaria</i> invasion. Dominated by <i>Juncus articulatus</i> , <i>Senecio rivularis</i> and <i>Cirsium palustre</i>
Milíkovice	16	101010	Wet, peaty meadow with abundant <i>Serratula tinctoria</i> . Dominated by <i>Carex</i> sp., <i>Galium palustre</i> and <i>Serratula tinctoria</i>
Ohrazení	28	010101	Relatively dry meadow 'endangered by desiccation, with abundant <i>Betonica officinalis</i> . Dominated by <i>Betonica ojjicinalis</i> , <i>Cynosurus cristatus</i> and <i>Viciacracca</i>
Vrbenske	21	111101	Wet meadow, rush litter accumulation. Dominated by <i>Alopecurus pratensis</i> , <i>Poa trivialis</i> , and <i>Ranunculus acris</i> .
Šumava	35	000000	Wet, peaty ridges along a small stream. Dominated by <i>Menyanthes trifoliata</i> , <i>Equisetum fluviatile</i> and <i>Bistorta major</i> .

**Fig. 1 – Map of our sites within South Bohemia.**

from the meteorological station at Česká Budějovice. Four of the sites are located within a 10 km radius from this station (see Fig. 1). From these raw data we calculated average temperature and summary precipitation data for 8 days, 15 days and one- and three-monthly intervals, covering the periods from May to October in the previous year and from March to June in the current year.

2.3. The shading experiment

In 2002, at the beginning of April, at the site Milíkovice, three groups of 32 plants of *D. majalis* with flower buds were caged individually. The cages were covered by three different types of nylon netting: white netting, black netting, and two layers of black netting. The white cages did not reduce light significantly, cages covered by black netting reduced photosynthetically active radiation by 50%, and cages covered by two layers of black netting reduced photosynthetically active radiation by 75% (measured by Li-6400, Li-Cor, USA). Vegetative plants were excluded from the experiment.

Length and width of each leaf, total leaf area (see above), length of the flower stalk, length of inflorescence, and the

number of flowers were measured weekly during the flowering season and their maximum achieved values were used for subsequent analyses. The ratio (leaf length)/(leaf width) was calculated to numerically quantify the shape of the leaf.

We have hand-pollinated 20% of flowers of each of randomly chosen 17 plants per group (to simulate natural pollination, as the cages prevented access of pollinators). At the end of June, when most of the capsules were ripe, average dry weight of all seeds in a capsule was determined for three lowest capsules for each of these plants using analytical scales (precision 10^{-5} g). These plants were checked for flowering once more in 2003. For each of the three experimental groups, probability of flowering was determined as the proportion of plants within the group that flowered in 2003.

2.4. Data analysis

For data-processing we considered total leaf area of the plant and plant status (flowering or vegetative) as characteristics of plant performance. We use the following abbreviations for the variables: LA(t) is the total leaf area in year t, S(t) is the height of flower stalk in year t, F(t) is plant status, where F(t) = 1, if the plant flowered in year t, F(t) = 0 if the plant was vegetative in year t. Prior to the analyses, all variables measured were tested for normality and appropriate transformations used when necessary.

To determine the influence of climatic conditions on plant behaviour we used GLM (general linear model) models (S-plus 2000). We used leaf area and height of flower stalk as the response variables. The predictors were sum of precipitation and average temperature during the interval considered, LA(t – 1), and site. The intervals considered for weather variables were: 3 months, 1 month, 15 days, and 8 days during the period from May to October in the previous year and from March to June in the current year. We did not include winter months (November–February) in the analyses, as the plants are dormant during these months. We used the GLM model with forward selection (S-plus 2000). Only predictors explaining a significant amount of variance were included in the model. Models were tested against each other with F-tests. For modelling the effects of weather conditions on flowering we used the binomial GLM model (S-plus 2000) with flowering as response and the same set of predictors as described above.

Correlations between response and significant predictors were calculated using Statistica 5.5. (StatSoft, Inc., Tulsa, USA).

We estimated the impact of mowing using ANOVA and ANCOVA (Statistica 5.5, StatSoft, Inc., Tulsa, USA), the former with LA(t) as a dependent variable and mowing as an independent variable, and the latter also including LA(t – 1) as a covariable, because LA(t) may be strongly dependent also on LA(t – 1) (Kindlmann and Balounová, 1999). We used the binomial GLM model for testing the effect of mowing on the proportion of plants that flowered. As flowering can also be determined by LA(t), we included LA(t) in the model with a step-up approach.

The influence of management on species composition was analysed by redundancy analysis (RDA) of the phytocoenological relevés data in the program CANOCO 4.5 (Lepš and Šmilauer, 2003).

Effects of shading on biometric parameters at the end of the season were tested by means of one-way ANOVA with a subsequent Tukey HSD test (Statistica 5.5, StatSoft, Inc., Tulsa, USA). The effects of shading on the probability of flowering the next year were tested by means of a G-test (Zar, 1984).

3. Results

3.1. Climatic conditions

Results of the GLM models with LA(t) as a response are shown in Table 2. LA(t) was always best fitted by LA(t – 1), which explained most of the variation (deviance reduction = 42.7%).

The next best predictors differed with the length of the time interval over which the climatic variables were averaged. When 3 months averages were considered, the correlation between LA(t) and the next best predictor, the sum of precipitations from April to June, was negative. Correlations between the second best predictors for shorter averaging intervals considered were always positive.

The relationship between LA(t – 1), weather variables and the plant status, F(t) (flowering/vegetative), is also shown in Table 2. The pattern for binomial GLM models was similar to that of the GLM model for LA(t) – the best predictor was always the leaf area in the previous year, but in this case no weather variables significantly affected F(t).

Height of the flower stalk, S(t), was more influenced by weather conditions than either leaf area or flowering, as shown in Table 2. Weather variables were the best predictor in all cases, and two weather variables always significantly affected S(t). The correlations between flower stalk height and sums of precipitation and temperature were not all positive. When 3 months, 1 month and 15 days averages were considered, the correlations between flower stalk height and the best predictors (precipitation from April to June, precipitation in August and in the first half of August in the previous year and precipitation in June in the current year), were negative.

3.2. Impact of mowing

Leaf area, LA(t), was significantly larger at the sites mown the previous year ($F = 13.031, P = 0.0003$). However, when LA(t – 1)

Table 2 – GLM for leaf area, LA(t), plant status, F(t) and height of flower stalk, S(t)

Predicted variable	Averaging interval	Significant predictors	F-ratio	P-level	% d	r	
LA(t)	3 Months	+LA(t – 1)	416.5	0.000	42.7	0.654	
		+Precipitation – April–June (t)	30.8	0.000	5.2	–0.113	
	1 Month	+LA(t – 1)	416.5	0.000	42.7	0.654	
		+Temperature – September (t – 1)	32.8	0.000	5.5	0.167	
	15 Days	+LA(t – 1)	416.5	0.000	42.7	0.654	
		+Precipitation – 1st half of March (t)	33.8	0.000	5.7	0.098	
	8 Days	+LA(t – 1)	416.5	0.000	42.7	0.654	
		+Precipitation – 2nd week of March (t)	35.3	0.000	6.0	0.178	
Plant status F(t)	3 Months	+LA(t – 1)	108.1	0.000	14.8		
	1 Month	+LA(t – 1)	108.1	0.000	14.8		
	15 Days	+LA(t – 1)	108.1	0.000	14.8		
	8 Days	+LA(t – 1)	108.1	0.000	14.8		
Height of flower stalk S(t)	3 Months	+Precipitation – April–June (t – 1)	185.5	0.000	34.9	–0.361	
		+LA(t)	75.7	0.000	18.0	0.444	
		+Precipitation – January–March (t)	11.7	0.000	3.2	0.205	
		+Precipitation – August (t – 1)	143.2	0.000	29.3	–0.422	
	1 Month	+LA(t)	87.5	0.000	20.2	0.444	
		+Precipitation – June (t)	32.7	0.000	8.7	–0.388	
		+Precipitation – 1st half of August (t – 1)	172.9	0.000	33.3	–0.379	
		+LA(t)	76.5	0.000	18.2	0.444	
	15 Days	+Precipitation – 2nd half of April (t)	20.4	0.000	5.6	0.108	
		+Temperature – 1st week of April (t)	155.7	0.000	31.0	0.418	
		+LA(t)	76.8	0.000	18.2	0.444	
		+Precipitation – 3rd week of April (t)	32.6	0.000	8.7	0.164	

Predictors considered in the model: LA(t – 1), temperatures and sums of precipitation in the period from March to October (t – 1) and from March to June (t), averaged over the interval indicated in the first column. % d means percentage of decreased deviation, r means correlation coefficient. No r for F(t) given, as F(t) is a 0–1 variable.

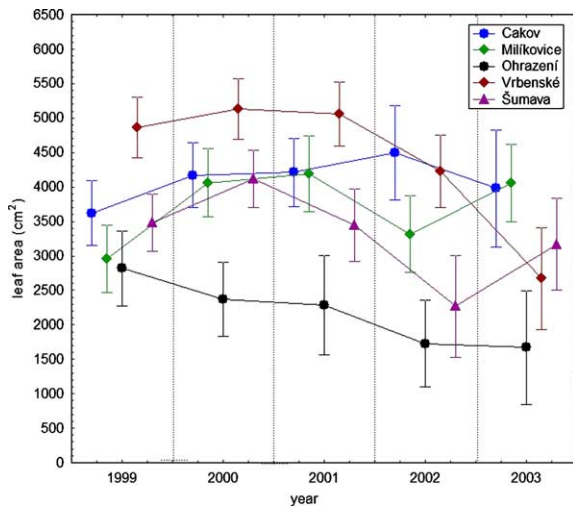


Fig. 2 – Leaf area with standard error between years and sites.

was used as a covariable in ANCOVA, this difference disappeared ($F = 0.189$, $P = 0.6631$). The differences in LA(t) between sites are also evident in Fig. 2 and Table 3. In Fig. 2, LA(t) at one of the sites mown every other year (Milikovice) is not different from that of the unmown sites (Cakov, Sumava) in any year (see also Table 3), while LA(t) at the other site mown every other year (Ohrazení) is clearly the smallest and LA(t) at the regularly mown site Vrbenske is always the largest, except in 2003, which followed a year of no mowing. Similarly, there is a difference between sites in the height of the flower stalk (Fig. 3, Table 3).

We used the binomial GLM model to investigate the impact of mowing on plant status, $F(t)$. To eliminate the impact of

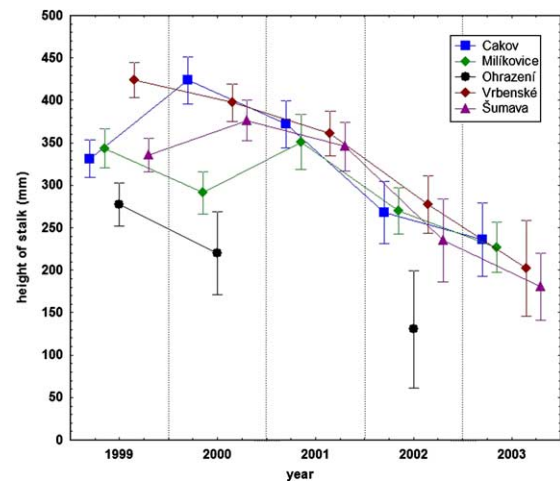


Fig. 3 – Height of flower stalk (t) at individual sites.

plant size on plant status (see Table 2), we included leaf area as a predictor in the model. This resulted in 15.1% of decreased deviation ($F = 110.5$, $P = 0.00$). However, the addition of mowing as another predictor caused a decrease in the deviance of only 0.1% ($F = 0.676$, $P = 0.41$), which means that mowing did not influence the plant status.

3.3. Two aspects of mowing – plant shading and affecting species composition

Fig. 4 shows results of RDA regarding the impact of mowing on the composition of other species at the sites. There is a high species-environment correlation (0.919) on the first (horizontal) axis, but the second (vertical) canonical axis explained most of the variability (53.2%, compared to 20.7% for

Table 3 – ANOVA – summary of all effects and post hoc comparisons

		df	F	P	
Height of flower stalk (t)	Year	4	60.7	0.00000	
	Site	3	7.1	0.000104	
	Year ^a Site	12	6.2	0.000000	
Leaf area (t)	Year	4	7.8	0.000003	
	Site	4	37.9	0.000000	
	Year ^a Site	16	3.7	0.000001	
Leaf area (t) – Year	1999	2000	2001	2002	2003
	ab	c	bc	a	a
Mean	3550	3971	3838	3208	3110
Leaf area (t) – Site	Cakov	Milikovice	Ohrazení	Vrbenske	Sumava
	cd	bc	a	d	b
Mean	4096	3716	2174	4392	3298
Height of stalk (t) – Year	1999	2000	2001	2002	2003
	c	c	c	b	a
Mean	359	372	357	262	211
Height of stalk (t) – Site ^a	Cakov	Milikovice	Vrbenske	Sumava	
	b	a	b	a	
Mean	326	296	332	295	

In each row, significantly different values are indicated by different letters ($P < 0.05$, Tukey HSD test).

a The site Ohrazení is not included, as there were no flowering individuals here in some years.

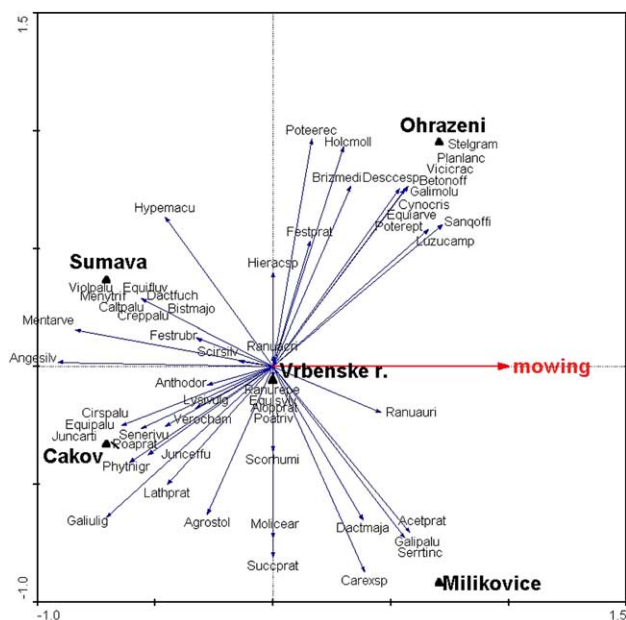


Fig. 4 – RDA ordination diagram showing species (arrows) composition and sites (centroids) in relation to mowing (species relative cover increases in the direction of arrows). See appendix for abbreviation of plant names. Test of all canonical axes was not significant ($F = 0.784$, $P = 0.664$).

Legend: Acetprat – *Acetosella vulgaris*; Agrostol – *Agrostis stolonifera*; Alopprat – *Alopecurus pratensis*; Angesilv – *Angelica silvestris*; Anthodor – *Anthoxanthum odoratum*; Brizmedi – *Briza media*; Betooffi – *Betonica officinalis*; Bistmajo – *Bistorta major*; Carexsp - *Carex* sp.; Cirspalu – *Cirsium palustre*; Galpalu – *Caltha palustris*; Cynocris – *Cynosurus cristatus*; Creppalu – *Crepis paludosa*; Dactmaja – *Dactylorhiza majalis*; Desccesp – *Deschampsia cespitosa*; Dactfuchs – *Dactylorhiza fuchsii*; Equipalu – *Equisetum palustre*; Equifluv – *Equisetum fluviatile*; Equisylv – *Equisetum sylvatica*; Equiarve – *Equisetum arvense*; Festprat – *Festuca pratensis*; Festrubr – *Festuca rubra*; Galiulig – *Galium uliginosum*; Galipalu – *Galium palustre*; Galimolu – *Galium molugo*; Hierasp – *Hieracium* sp.; Holcmoll – *Holcus mollis*; Hypemacu – *Hypericum maculatum*; Juncarti – *Juncus articulatus*; Junceffu – *Juncus effusus*; Lathprat – *Lathyrus pratensis*; Lysivulg – *Lysimachia vulgaris*; Luzucamp – *Luzula campestris*; Mentarve – *Mentha arvensis*; Menytrif – *Menyanthes trifoliata*; Molicaer – *Molinia caerulea*; Phytynigr – *Phyteuma nigra*; Planlac – *Plantago lanceolata*; Poaprat – *Poa pratensis*; Poatriv – *Poa trivialis*; Poteerac – *Potentilla erecta*; Poterept – *Potentilla reptans*; Ranuacri – *Ranunculus acris*; Ranuauri – *Ranunculus auricomus*; Ranurepe – *Ranunculus repens*; Sangoffi – *Sanguisorba officinalis*; Scirsilv – *Scirpus silvaticus*; Succprat – *Succisa pratensis*; Scorhumi – *Scorzonera humilis*; Senerivu – *Senecio rivularis*; Serrtinc – *Serratula tinctoria*; Stelgram – *Stellaria graminea*; Verocham – *Veronica chamaedrys*; Vicicrac – *Vicia cracca*; Violpalu – *Viola palustris*.

the first axis). The two sites that were mown every other year (Ohrazeni and Milikovice) are on the right of the figure, the two unmown sites (Cakov, Sumava) on the left, and the

regularly mown Vrbenske site at the middle. So the first (horizontal axis) seems to represent the effect of mowing.

Shading significantly affected the length of the flower stalk and the ratio of leaf width to leaf length at the end of the season (Tukey HSD test, Table 4). Flower stalks of the shaded plants were longer and their leaves were more elongated (Table 4). Shading did not significantly affect the inflorescence length, number of flowers, total leaf area or average weight of seed per capsule (Tukey HSD test, Table 4, Fig. 5).

The probabilities of flowering in the following season were 0.76, 0.94 and 0.88 for the control, moderately shaded and heavily shaded groups respectively. G-test did not reveal any significant differences between the groups in the probability of flowering (G_{adj} was 2.03 for control vs. moderate, 0.76 for control vs. heavily and 0.32 for moderate vs. heavily shaded groups, while the critical χ^2 at the 5% significance level is 3.84).

4. Discussion

4.1. Climatic conditions

In all models, leaf area in the previous year was always by far the best predictor of the leaf area in the current year – much better than any of the climatic variables considered. This is in accord with many previous studies (Kindlmann and Balounová, 1999, 2001; Janečková and Kindlmann, 2002 and references therein) and implies that last year's leaf area affects the current year's leaf area via carbohydrates stored as reserves in the tubers (Kindlmann and Balounová, 1999). Thus leaf area in *D. majalis* is a stable, relatively weather-independent characteristic of each plant. Weather can, however, affect the average leaf area and other biometric characteristics of the whole population, as shown here and in many other studies.

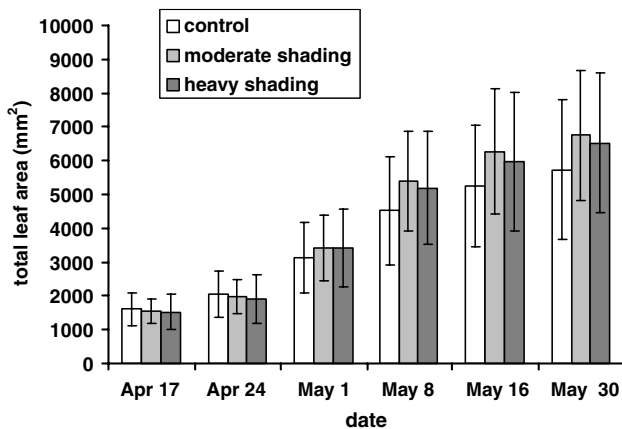
We expected that the 1- or 3-months average temperatures or sums of precipitation commonly used in studies of the relationship between weather and orchid performance (Carey et al., 2002; Øien and Moen, 2002; Wells, 1981; Wells et al., 1998; Wheeler et al., 1998, etc.) may be too long to assess this relationship correctly, because short periods of severe drought or extreme temperatures may have a large effect on orchid performance (Vanhecke, 1991, implicitly also Tali, 2002 and many others). This suspicion was only very weakly supported by our results for both leaf area and height of the flower stalk. That is, in Table 2, for both LA(t) and S(t), the percentage of decreased deviation caused by weather factors (one significant factor for LA(t) in Table 2 and sum of two significant factors for S(t)) was consistently, but not significantly, increased with decreasing length of the interval, over which the weather values were averaged. This may be because weather was not variable enough during our study period. Thus we can conclude that if the extreme events are rare, then the improvement of prediction by shortening the interval over which the temperatures are averaged or precipitation summed, even if detectable, may be only weak or even not significant.

We can only hypothesize about the biological explanation for the significant effects of particular weather conditions on leaf area and/or height of the flower stalk.

Table 4 – Means + SD of biometric parameters in groups differing in the degree of shading

	Control	Moderate shading	Heavy shading
Stalk length (mm)	269 ± 69a	299 ± 60ab	326 ± 55b
Inflorescence length (mm)	67.1 ± 14.1a	63.3 ± 14.2a	60.2 ± 14.1a
Number of flowers	18.8 ± 5.8a	18.7 ± 5.1a	18.3 ± 5.9a
Total leaf area (mm ²)	5729 ± 2068a	6759 ± 1923a	6521 ± 2063a
(Leaf length)/(leaf width)	3.84 ± 0.59a	4.38 ± 0.75b	4.6 ± 0.79b
Average seed weight (mg)	0.009 ± 0.004a	0.007 ± 0.003a	0.007 ± 0.003a

In each row, significantly different values are indicated by different letters ($P < 0.05$, Tukey HSD test). Each group consisted of 32 plants.

**Fig. 5 – Effect of shading on the relationship between the total leaf area and time. Horizontal axis shows dates of measurements.**

- One possible explanation for the negative effect of the sum of precipitation from April to June on both leaf area and height of flower stalk may be that this sum can possibly affect growth of co-occurring plant species, thus increasing interspecific competition and negatively affecting growth of *D. majalis*.
- The end of August and September is the period for new root formation (Leeson et al., 1991) and reinfection of roots by mycorrhizal fungi (Hadley, 1982) in *D. majalis*; leaves cease to grow in June (Kindlmann and Balounová, 1999). This may account for the positive correlations between orchid performance and temperature and/or precipitation during these periods when the 1-month averaging intervals were used.
- March precipitation may affect the initiation of leaf growth, while April precipitation may affect the initiation of flower stalk growth, which is only slightly behind leaf growth (Kindlmann and Balounová, 1999). At these times, the plants can suffer from a lack of water availability, especially if the soil is still frozen. In August, the flower buds for the next year are formed (Leeson et al., 1991). This may account for the correlations found in the short (15- and 8-days intervals).

Clearly, additional experiments are needed to support these speculations.

To put our results into context with other literature: Tali (2002) noticed considerable fluctuation of plant height between years that was greater than differences between populations or subspecies of *Orchis ustulata*. The fluctuations were attributed to spring weather. Wells and Cox (1991) found a positive correlation between flower spike height and summed precipitation in the periods August–September of the previous year and March–July of the current year. If our results can be generalized, then it is early spring (and maybe August) precipitation that plays an important role (Table 2). We found that the incidence of flowering is influenced by leaf area, rather than by weather conditions, which is in accord with other results (Dijk and Olf, 1994; Wells and Cox, 1989; Whigham and O'Neill, 1991; Willems and Dorland, 2000), but in contradiction to Wells et al. (1998).

4.2. Impact of mowing

It has been shown that infrequent mowing (e.g. less than once every 2 years) may lead to sub-optimal performance of orchid populations (Jersáková et al., 2002; Janečková et al., 2005). Increased nitrogen depositions via atmospheric pollution or fertilizer addition compound the problem (Silvertown et al., 1994; Bobbink and Willems, 1987). Generally speaking, mowing favours smaller species while suppressing the dominant grasses (Lepš, 1999). The performance of orchid populations seems to be determined by light availability and competition with the surrounding vegetation (Dorland and Willems, 2002; McKendrick, 1996; Willems et al., 2001). In our study, leaf area at the regularly mown site Vrbenke was larger than that at the sites which were mown only once in 2 years, with the exception of 2003, following a year when Vrbenke was not mown (Fig. 2). This indicates that mowing every year appears necessary to maintain the large size, even if for maintenance of a stable population mowing once in two years may be sufficient (see also Wotavová et al., 2004).

We did not detect a significant effect of the absence of mowing on the incidence of flowering in *D. majalis*, contrary to Jersáková et al. (2002). However, at the site Vrbenke, which was not mown in 2002, the percentage of vegetative plants increased from 62% in 2002 to 100% in 2003. The absence of a general trend might be due to the irregular mowing regime and large differences in species composition between sites (see Fig. 3).

4.3. Two aspects of mowing – plant shading and affecting species composition

Fig. 5 shows that both unmown sites (Cakov and Vrbenske) are dominated by tall broad-leaved herbs (*Angelica silvestris*, *Cirsium palustre*, *Mentha arvensis*, *Phyteuma nigra*, *Senecio rivularis*), robust sedges (*Scirpus silvaticus*) and rushes (*Juncus articulatus* and *J. effusus*), while regularly mown sites are dominated by minute herbs (*Acetosella vulgaris*, *Galium palustre*, *Luzula campestris*, *Plantago lanceolata*, *Ranunculus auricomus*, *Stellaria graminea*). As tall and dense vegetation can strongly compete with orchids (Jersáková et al., 2002), it is clear that mowing might influence orchid performance at the sites via its effect on species composition.

Shade-tolerant plants often grow bigger leaves and increase their photosynthetic efficiency in order to deal with the decreased rate of photosynthesis, and thus manage to maintain high levels of photosynthesis (Stoneman and Dell, 1993; Wiebel et al., 1994; Messier and Puttonen, 1995; Marenco et al., 2001). Our results demonstrate that in *D. majalis* shading caused elongation of the flowering stalk and of the shape of the leaves at the end of the season. The latter was associated with a slight, statistically non-significant enlargement of the leaf area. All this indicates that the plants tend to “escape” from the shade. Similar results regarding leaf area and shape were obtained by Willems et al. (2001) on *Spiranthes spiralis* and by McKendrick (1996) on seedlings of *Orchis morio* and *Dactylorhiza fuchsii*. Willems et al. (2001) hypothesize that the growth of both flower stalk and leaves depend on underground stored resources.

We found that shading itself did not affect the probability of flowering of a plant in the following season, however. One would expect that shading would negatively affect plant photosynthesis, which would be translated into smaller storage organs and lower probability of flowering of a plant in the following season. This is what Willems et al. (2001) observed on *S. spiralis*. Our results do not support this expectation. Thus *D. majalis* is probably a quite shade-tolerant plant.

4.4. Conservation implications

The long persistence of plant populations is primarily determined by their vital rates (i.e. recruitment, death and growth rates). As disturbances (such as mowing) may affect each rate differently, it is essential to investigate different stages of the life cycle, and the effects of management on each life cycle transition and the overall population growth rate. This has mostly been done by matrix transition models. In addition, the use of life table response experiments (LTRE) and stochastic matrix models allows resolving the life cycle transitions that are most important in determining population growth rates and determining the ideal management interval for long term survival of the species (e.g. Oostermeijer, 2000). Clearly, this supposes data that have been gathered for multiple years and for each life cycle stage. In this study, we adopted a different, less data demanding approach, based on following the fate of individual plants.

It is clear from the literature that if population viability analysis of endangered orchid populations is performed, climatic parameters should be included, if possible, as 1–2

weeks' averages, especially if extreme climatic conditions are present during the period studied. However, our results indicate that the improvement of prediction by shortening the interval over which the temperatures are averaged or precipitation summed, even if detectable, may be only weak or even not significant.

Sections 3.2 and 4.2. indicate that the most appropriate management for *D. majalis* is mowing at least once a year. Other authors suggest that ideally, the meadows or pastures with *D. majalis* should be mown after its fruiting at the end of June/beginning of July, to reduce the abundance of grasses (Lepš, 1999), and then once more in September, to remove the old biomass before the next season. For the same reasons, when only one mow can be performed for financial reasons, the best time is August/September. Mowing may be less frequent on peat bogs, where the soils are naturally less fertile (our personal observation during this study).

Characteristics of our study sites given in Table 1 indicate that the water regime required by *D. majalis* (a high moisture regime) must be ensured. This means that drainage of meadows should be avoided, and provision of small dams may be necessary to avoid drying of the site in spring. The incursion of eutrophic water from adjacent fields (and therefore site fertilization) should be prevented. Springs and peat bogs may often be damaged by wild pig grazing of tubers or roe deer grazing of shoots (our personal observation during this study). If this is the case, then fencing the sites may help.

It has to be admitted, however, that many examples exist in which populations of various *Dactylorhiza* species (*D. fuchsii*, *D. maculata*, *D. majalis*, *D. incarnata*) maintain their size and “survive” for many years even without management. Sudden explosions in population size may occur, often a few years after management (mostly mowing) is started (Hamel, 1977; Hermý and Vanhecke, 1989; Reinecke, 1982, 1988), when new open areas are created (Richardson, 1957), or after a disastrous event such as flooding (Vanhecke, 1991). Thus for survival of *Dactylorhiza* species, lack of management spanning several years may not be fatal. However, for optimal performance, regular yearly mowing, especially late in the season, is necessary. Expansion of grasses has to be controlled for, and – if detected – early (just after orchid fruiting) mowing can act against it.

Acknowledgments

This work has been supported by the grant 206/03/H034 of the GA ČR. We thank Mike Hutchings, Rich Shefferson, Tiiu Kull, Pete Carey, eight anonymous reviewers and many other unnamed colleagues for valuable comments on the earlier versions of this manuscript.

REFERENCES

- Bobbink, R., Willems, J.H., 1987. Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands: a threat to species-rich ecosystem. *Biol. Conserv.* 40, 301–314.

- Brzosko, E., 2002. Dynamics of island populations of *Cypripedium calceolus* in the Biebrza river valley (north-east Poland). *Botanical J. Linnean Soc.* 139, 67–77.
- Carey, P.D., Farrell, L., Stewart, N.F., 2002. The sudden increase in the abundance of *Himantoglossum hircinum* in England in the past decade and what has caused it. In: Kindlmann, P., Willems, J.H., Whigham, D.F. (Eds.), *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations*. Backhuys Publishers, Leiden, pp. 187–208.
- Dijk, E., Olff, H., 1994. Effects of nitrogen, phosphate and potassium fertilization on field performance of *Dactylorhiza majalis* (Rchb.) hunt & summerh. *Acta Botanica Neerlandica* 43, 383–392.
- Dorland, E., Willems, J.H., 2002. Light climate and plant performance of *Ophrys insectifera*: a 4-year field experiment in The Netherlands 1998–2001. In: Kindlmann, P., Willems, J.H., Whigham, D.F. (Eds.), *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations*. Backhuys Publishers, Leiden, pp. 225–238.
- Falb, D.L., Leopold, D.J., 1993. Population dynamics of *Cypripedium candidum* muhl. ex willd., small white lady's slipper, in a Western New York fen. *Natural Areas J.* 13, 76–86.
- Firmage, D.H., Cole, F.R., 1988. Reproductive success and inflorescence size of *Calopogon tuberosus* (Orchidaceae). *Am. J. Botany* 75, 1371–1377.
- Gill, D.E., 1996. The natural population ecology of temperate terrestrials: pink lady's slippers, *Cypripedium acaule*. In: Allen, C. (Ed.), *Proceedings of the North American Native Terrestrial Orchids: Propagation and Production*, North American Native Terrestrial Orchid Conference, Germantown, MD, pp. 91–106.
- Hadley, G., 1982. Orchid mycorrhiza. In: Arditti, J. (Ed.), *Orchid Biology: Reviews and Perspectives II*. Cornell University Press, Ithaca, NY, USA, pp. 83–118.
- Hamel, G., 1977. Beobachtungen zur Populationsdynamik der *Dactylorhiza majalis* (Rchb.) hunt & summerh. *Mitteilungen des Arbeitskreises Heimische Orchideen der DDR* 7, 86–89.
- Hermy, M., Vanhecke, L., 1989. Orchids and nature management in flanders: results of a mail questionnaire and a timely review of the situation. *Mémoires de la Société Royale de Botanique de Belgique* 11, 87–105.
- Inghe, O., Tamm, C.O., 1988. Survival and flowering of perennial herbs. V. Patterns of flowering. *Oikos* 51, 203–219.
- Janečková, P., Kindlmann, P., 2002. Key factors affecting shoot growth and flowering performance of *Dactylorhiza fuchsii*. In: Kindlmann, P., Willems, J.H., Whigham, D.F. (Eds.), *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations*, pp. 99–113.
- Jersáková, J., Kindlmann, P., Striteský, M., 2002. Population dynamics of *Orchis morio* in the Czech Republic under human influence. In: Kindlmann, P., Willems, J.H., Whigham, D.F. (Eds.), *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations*. Backhuys Publishers, Leiden, pp. 209–224.
- Kindlmann, P., Balounová, Z., 1999. Energy partitioning in terrestrial orchids – a model for assessing their performance. *Ecol. Modelling* 119, 167–176.
- Kindlmann, P., Balounová, Z., 2001. Irregular flowering patterns in terrestrial orchids: theories vs. empirical data. *Web Ecol.* 2, 75–82.
- Kull, T., 2002. Population dynamics of north temperate orchids. In: Kull, T., Arditti, J. (Eds.), *Orchid biology: Reviews and perspectives, VIII*. Kluwer Academic Publishers, Dordrecht, pp. 139–165.
- Leeson, E., Haynes, C., Wells, T.C.E., 1991. Studies of the phenology and dry matter allocation of *Dactylorhiza fuchsii*. In: Wells, T.C., Willems, J.H. (Eds.), *Population Ecology of Terrestrial Orchids*. SPB Academic Publishing, The Hague, pp. 125–138.
- Lepš, J., 1999. Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow. *J. Vegetation Sci.* 10, 219–230.
- Lepš, J., Šmilauer, P., 2003. *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press, Cambridge.
- Lind, H., 1992. Förekomst, beståndsutveckling och fruktsättning hos salesprot på Öland. *Svensk Botaniska Tidskrift* 86, 329–336.
- Marenco, R.A., Goncalves, J.F.D., Vieira, G., 2001. Leaf gas exchange and carbohydrates in tropical trees differing in successional status in two light environments in central Amazonia. *Tree Physiol.* 21, 1311–1318.
- McKendrick, S.L., 1996. The effects of shade on seedlings of *Orchis morio* and *Dactylorhiza fuchsii* in chalk and clay soil. *New Phytol.* 134, 343–352.
- Messier, C., Puttonen, P., 1995. Growth, allocation, and morphological responses of *Betula pubescens* and *Betula pendula* to shade in developing scots pine stands. *Canadian J. Forest Res.* 25, 629–637.
- Oostermeijer, J.G.B., 2000. Population viability analysis of the rare *Gentiana pneumonanthe*: the importance of genetics, demography and reproductive biology. In: Young, A.G., Clark, G.M. (Eds.), *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, pp. 313–334.
- Øien, D.I., Moen, A., 2002. Flowering and survival of *Dactylorhiza lapponica* and *Gymnadenia conopsea* in the Sølendet Nature Reserve, Central Norway. In: Kindlmann, P., Willems, J.H., Whigham, D.F. (Eds.), *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations*. Backhuys Publishers, Leiden, pp. 3–22.
- Reinecke, F., 1982. Zur gezielten vegetativen Vermehrung einheimischer Orchideen. *Die Orchidee* 33, 58–62.
- Reinecke, F., 1988. Bericht über die Pflege eines *Dactylorhiza incarnata*-Biotops und die Entwicklung der population. *Die Orchidee* 39 (140–144), 173–176.
- Richardson, J.A., 1957. The development of orchid populations in claypits in county Durham. *Proc. Botanical Soc. British Isles* 2, 354–361.
- Sieg, C.H., King, R.M., 1995. Influence of environmental factors and preliminary demographic analyses of a threatened orchid, *Platanthera praecleara*. *Am. Midland Naturalist* 134, 307–323.
- Silvertown, J., Wells, D.A., Gillman, M., Dodd, M.E., Robertson, H., Lakhani, K.H., 1994. Short-term effects and long-term after-effects of fertilizer application on the flowering population of green-winged orchid *Orchis morio*. *Biol. Conserv.* 69, 191–197.
- Stoneman, G.L., Dell, B., 1993. Growth of *Eucalyptus marginata* (Jarrah) seedlings in a greenhouse in response to shade and soil-temperature. *Tree Physiol.* 13, 239–252.
- Tali, K., 2002. Dynamics of *Orchis ustulata* populations in Estonia. In: Kindlmann, P., Willems, J.H., Whigham, D.F. (Eds.), *Trends and Fluctuations and Underlying Mechanisms in Terrestrial Orchid Populations*. Backhuys Publishers, Leiden, pp. 33–42.
- Tamm, C.O., 1991. Population Ecology of Terrestrial Orchids. In: Wells, T.C., Willems, J.H. (Eds.), *SPB Academic Publishing, The Hague*, pp. 1–13.
- Vanhecke, L., 1991. Population dynamics of *Dactylorhiza praetermissa* in relation to topography and inundation. In: Wells, T.C., Willems, J.H. (Eds.), *Population Ecology of Terrestrial Orchids*. SPB Academic Publishing, The Hague, pp. 15–32.
- Waite, S., Hutchings, M.J., 1991. The effects of different management regimes on the population dynamics of *Ophrys sphegodes*: analysis and description using matrix models. In: Wells, T.C., Willems, J.H. (Eds.), *Population Ecology of Terrestrial Orchids*. SPB Academic Publishing, The Hague, pp. 161–175.
- Wells, T.C.E., 1981. Population ecology of terrestrial orchids. In: Syngé, H. (Ed.), *The Biological Aspects of Rare Plant Conservation*. Wiley, Chichester, pp. 281–295.

- Wells, T.C.E., Cox, R., 1989. Predicting the probability of the bee orchid (*Ophrys apifera*) flowering or remaining vegetative from the size and number of leaves. In: Pritchard, H.W. (Ed.), *Modern Methods in Orchid Conservation: The Role of Physiology, Ecology, and Management*. Cambridge University Press, Cambridge, pp. 127–139.
- Wells, T.C.E., Cox, R., 1991. Demographic and biological studies of *Ophrys apifera*: some results from a 10 year study. In: Wells, T.C., Willems, J.H. (Eds.), *Population Ecology of Terrestrial Orchids*. SPB Academic Publishing, The Hague, pp. 47–61.
- Wells, T.C.E., Rothery, P., Cox, R., Bamford, S., 1998. Flowering dynamics of *Orchis morio* L. and *Herminium monorchis* (L.) R.Br. at two sites in eastern England. *Botanical J. Linnean Soc.* 126, 39–48.
- Wheeler, B.D., Lambley, P.W., Geeson, J., 1998. *Liparis loeselii* (L.) rich. in eastern England: constraints on distribution and population development. *Botanical J. Linnean Soc.* 126, 141–158.
- Whigham, D.F., O'Neill, J., 1991. The dynamics of flowering and fruit production in two eastern North American terrestrial orchids, *Tipularia discolor* and *Liparis lilifolia*. In: Wells, T.C., Willems, J.H. (Eds.), *Population Ecology of Terrestrial Orchids*. SPB Academic Publishing, The Hague, pp. 89–101.
- Wiebel, J., Chacko, E.K., Downton, W.J.S., Ludders, P., 1994. Influence of irradiance on photosynthesis, morphology and growth of mangosteen (*Garcinia mangostana* L.) seedlings. *Tree Physiol.* 14, 263–274.
- Willems, J.H., 1990. Calcareous grasslands in continental Europe. In: Hillier, S.H. et al. (Eds.), *Calcareous Grasslands: Ecology and Management*. Bluntisham Books, Bluntisham, pp. 3–10.
- Willems, J.H., Balounová, Z., Kindlmann, P., 2001. The effect of experimental shading on seed production and plant survival in the threatened species *Spiranthes spiralis* (Orchidaceae). *Lindleyana* 16, 31–37.
- Willems, J.H., Bik, L., 1991. Long-term dynamics in a population of *Orchis simia* in the Netherlands. In: Wells, T.C., Willems, J.H. (Eds.), *Population Ecology of Terrestrial Orchids*. SPB Academic Publishing, The Hague, pp. 33–45.
- Willems, J.H., Dorland, E., 2000. Flowering frequency and plant performance and their relation to age in the perennial orchid *Spiranthes spiralis* (L.) Chevall. *Plant Biol.* 2, 344–349.
- Wotavová, K., Balounová, Z., Kindlmann, P., 2004. Factors affecting persistence of terrestrial orchids in wet meadows and implications for their conservation in a changing agricultural landscape. *Biol. Conserv.* 118, 271–279.
- Zar, J.H., 1984. *Biostatistical Analysis*. Prentice Hall Press, Englewood Cliffs, NJ.