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Ecology and distribution of *Tephroseris longifolia* subsp. *moravica* in relation to environmental variation at a micro-scale

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Abstract: *Tephroseris longifolia* subsp. *moravica* is an endemic endangered taxon of European importance. Within the nine recently known populations it occurs in very specific site conditions of ecotone habitats. In our contribution, we try to quantify its realized niche with regard to the measured components of its biotic and abiotic environment. The main aim was to assess the importance of spatial environmental variation on taxon occurrence and performance and to relate the obtained ecological information to data on taxon abundance and demography. Possible reasons of taxon rarity are discussed, too. Comparison of plot pairs indicated that plots containing the taxon had deeper soil and higher soil Na and Mg contents than plots without it. They also contained higher number of species, especially forbs. Several soil parameters were positively correlated with taxon size and density while light parameters played minor role. Negative correlations between cover of vascular plants, especially grasses and taxon size and density suggest its reduced competitive ability. Vascular plant-based ecological indicator values were set for light (6), temperature (5), continentality (4), moisture (5), soil reaction (7) and nutrients (5). The studied sites differed in topography, soil characteristics (pH, soil Na, K, Ca, P and NH_4) and cover of herb litter. Size of taxon populations was negatively related to their finite rate of increase which varied between 1.25 and 2.04 and was most sensitive to demographic parameters related to growth. We conclude, that the studied taxon is not strictly stenotopic as the ranges of several environmental variables were rather wide. We suppose, that the narrow limits of recent taxon occurrence are consequences of its low competitive ability and demographic processes related to germination and seedling establishment. The differing requirements of its ontogenetic stages (seedlings and generative individuals) may define the final limits of its small-scale distribution.

Key words: ecological indicator numbers; ecological niche; endangered taxon of European importance; finite rate of increase; habitat conditions; light parameters; soil properties

Abbreviations: TLM, *Tephroseris longifolia* subsp. *moravica*; EIV, Ellenberg indicator values.

Introduction

Tephroseris longifolia subsp. *moravica* Holub is an endemic subspecies with geographically restricted distribution isolated from the distribution area of other taxa belonging to *Tephroseris longifolia* s.l. Recently, nine populations of TLM were recorded in western Slovakia and eastern Czech Republic, and seven populations are considered to be extinct (Fig. 1). The population sizes are low and the taxon abundance fluctuates rather strongly (Kochjarová 1998; Janišová et al. 2005; Chmelová 2007; Gbelcová 2010). Due to the high risk of extinction, the taxon was declared endangered and included in the European list of important species (NATURA 2000, Directive 92/43/EEC, Annex II). According to the preliminary results of our research on the taxon reproductive biology (Janišová et al. submitted), habitat degradation by abandonment combined with demographic and climatic stochasticity seem to be the most important factors determining the long-term survival of the studied taxon. The precise determination of both biotic and abiotic environmental factors responsible for rarity of the studied taxon can provide relevant information necessary for its effective conservation.

Within the nine recently known populations the taxon occurs in ecotone habitats between beech forests and sub-xerophilous grasslands (Holub 1999; Janišová et al. 2005; Chmelová 2007; Kochjarová & Hrouda 2004; Hegedüšová et al. submitted). The very specific site conditions of taxon occurrence, in some sites restricted to several meters wide belt along the forest/shrub margin suggest that TLM is a stenotopic taxon with narrow habitat requirements. However, this statement should be supported by exact measurements of a wide set of environmental factors. Otherwise there are several other possible explanations of restricted distribution of TLM within its sites, exclusion by competitively stronger species or demographic processes related to seed dispersal and germination being the most important.

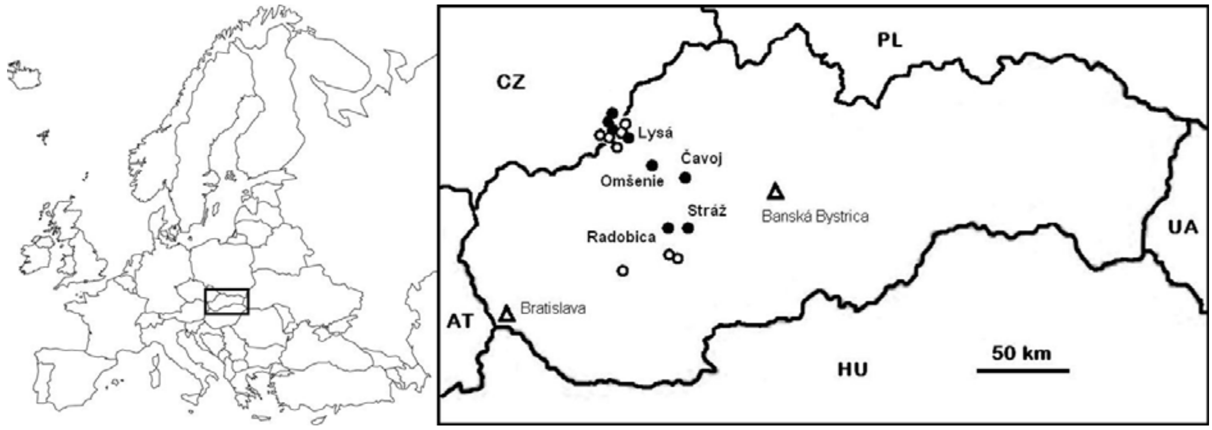

Fig. 1. Distribution of *Tephroseris longifolia* subsp. *moravica* in the Czech Republic and Slovakia. Empty circles show historic sites where the taxon is recently considered to be extinct. Solid circles show sites with recent evidence of taxon occurrence. The studied population sites are indicated by their names.

For plant populations, describing the microhabitat for individual plants quantifies the realized niche – the actual relationship between the plant and its habitat (Gibson 2002). There are many biotic and abiotic components of the microhabitat, and their importance varies in both space and time. In our study, we search for relevant environmental factors which determine the taxon distribution at a small scale. Within its habitat and within the spatial bounds of its populations there, individuals of the study taxon may be located preferentially in specific microsites, and within these microsites may show enhanced performance on certain type of microsites. Characteristics of the microsites that individuals of the selected taxon are located in can be determined by comparing the values of environmental variables at sites containing the taxon to values obtained from random points where the taxon is absent (Gibson 2002; Griffith 1996). We adopted this approach in assessing the microsite preference for TLM individuals in relation to environmental heterogeneity in five of nine naturally grown field populations.

To relate the measured environmental factors to population characteristics of TLM we studied several demographic parameters of TLM at each of the sites. Along with the estimation of population sizes at the level of both genets and ramets, we studied stage-structured life cycle in order to understand the status of the populations (whether they are increasing, decreasing or stable). The finite rate of increase (λ) provided a measure for population change and elasticity analysis allowed to identify the life history stages that are most limiting to population growth. These are potentially very useful in conservation management as they can influence the short-term survival potential of a population, as well as extinction threats (Gibson 2002).

The aims of our study were: a) to quantify the realized niche of TLM with regard to the measured components of its biotic and abiotic environment; b) to assess the importance of spatial environmental variation on plant occurrence and performance; c) to estimate the ecological indicator values of TLM from data recorded at a micro-scale; d) to estimate finite rate of increase of the studied TLM populations; e) to relate the obtained information on TLM distribution and habitat conditions to data on TLM population abundance and demography and to discuss possible reasons of taxon rarity and chances of its survival.

Material and methods

Brief description of five TLM population sites studied (Fig. 1) – Čavoj (Strážovské vrchy Mts, 560–585 m a.s.l.), Lysá (Biele Karpaty Mts, 740–780 m a.s.l.), Omšenie (Strážovské vrchy Mts, 570–670 m a.s.l.), Radobica (Tríbeč Mts, 480–560 m a.s.l.) and Stráž (Vtáčnik Mts, 770–780 m a.s.l.) – is in Table 1, including size of the sites, their recent management and several population characteristics. Environmental variables (Table 2) and species data were recorded within one week in June 2009 so that temporal variation of individual factors during sampling was minimal. In each site, the sampling was done with regard to the existing variability in habitat conditions of TLM occurrence, so that populations from environmentally more heterogeneous sites are represented by more sample plots than populations from homogeneous sites. Plots containing TLM individuals were selected randomly within each type of habitat with the only condition that at least one individual of TLM (vegetative, generative, seedling or juvenile) is present.

Circular plots of 0.5 m^2 were used for sampling of co-occurring species and environmental factors. This plot size was estimated to be optimal in terms of encompassing only the ecologically relevant radius of the presumed microsite (the radius was slightly less than the mean height of TLM individuals). In total, 25 pairs of plots (50 plots altogether) were sampled. In plots containing the study taxon, one of the involved TLM individuals was located in the plot centre. The paired plot to each sample containing TLM was recorded in the distance of 2 m from its centre in direction set as random angle; the only condition was the absence of TLM individuals. For each of the 50 plots, a set of environmental variables was measured or calculated including topographic, edaphic, bioclimatic and biological habitat characteristics (Table 2).

Soil samples were taken from the uppermost mineral horizon from the depth of 5–10 cm. This is the zone most

Table 1. Characteristics of the studied population sites and respective TLM populations.

Population site	Radobica	Čavoj	Omšenie	Lysá	Stráž
Size in m^2	15000	20000	11000	12000	5000
Current management	mostly mown, partly without management	mostly abandoned, various stages of succession	site of one subpopulation mown, two subpopulations without management	long time without management or irregularly grazed	abandoned for decades and covered by large shrubs
Population size of TLM in 2009					
Number of genets	758*	399	188	448	197
Proportion of generative genets (%)	40.8	77.7	71.3	92.2	49.2
Number of ramets per vegetative genet	2.1	1.4	3.9	1.9	1.8
Number of flowering shoots per generative genet	1.3	1.1	1.5	1.5	1.2
Population size of TLM in 2010					
Number of genets	1021*	331	169	299	246
Proportion of generative genets (%)	7.3	41.7	48.5	95.3	5.3
Number of ramets per vegetative genet	2.0	2.0	3.5	1.1	2.3
Number of flowering shoots per generative genet	1.2	1.2	2.1	1.3	1.0
Other population characteristics					
Finite rate of increase (λ) based on 2009–2010 transition rates (number of marked plants)	1.25 (96)	1.36 (60)	2.04 (98)	1.50 (44)	1.66 (47)
Germination percentage *in situ* (mean + standard deviation)	1.9±2.6	0.9±2.0	2.1±5.1	0.9±1.4	2.1±2.1

* in the site Radobica small forest clearing with the densest stand of TLM was not included into this census

densely rooted by TLM and other herb species where the interaction between plants and soil factors is most intensive. Three subsamples were taken for each plot and bulked together to form composite samples. The samples were air-dried and used for measurement of soil acidity in water and 1 M KCl suspension (20 g soil plus 50 mL water and KCl respectively), soil organic carbon content (standard Tyurin titrimetric method, Tyurin 1951), accessible phosphorus (P, Bray & Kurtz 1945), exchangeable potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na) were estimated in NH_4Cl extract using atomic absorption spectrometry. Nitrogen was estimated separately for ammonia (NH_4) by SFS-EN ISO 11732: 2005 and nitrate (NO_3) by SFS-EN ISO 13395:1996.

At each plot, canopy light transmission was characterized using vertical hemispherical photographs taken 50 cm above the soil surface with a Nicon Coolpix 5400 digital camera equipped with a fisheye FC E9 objective. Canopy openness, leaf area indices and variables reflecting the amount of direct and diffuse solar radiation (Table 2) were estimated from the photographs using Gap Light Analyser 2.0 (Frazer et al. 1999). The co-occurring taxa of vascular plants and bryophytes present in at least 20% of plots were used as variables, too.

Interspecific associations between TLM and each other species gives information on their reciprocal affinity in the data set (consisting of both plots containing TLM and plots without TLM). Differently from the species co-occurrence, interspecific associations reflect also the occurrence of each of the species in the plots without TLM. Phi coefficient was used as fidelity measure, calculation was performed in program JUICE (Tichý 2002). Positively and negatively associated species with the highest values of phi coefficient are reported.

In the plots containing TLM individuals, several characteristics of TLM were recorded at the level of both genetic individuals (genets) and shoots (ramets). These characteristics were used as fitness parameters for correlation with the recorded abiotic environmental variables and percentage cover of co-occurring species (see electronic appendix for the data). The characteristics of sites (size, management) and TLM populations (population size, proportion of flowering individuals, size of vegetative and generative genets, finite rate of increase and germination rates *in situ*) were used to evaluate the suitability of the studied sites for potential survival of TLM populations.

Population size was estimated in 2009 and 2010 within the annual monitoring program at each of the studied sites. Number of vegetative and generative genets was counted and their size was given as number of vegetative ramets and generative ramets (flowering shoots). To estimate the finite rate of increase (λ) for the studied populations we used single sets of transition rates 2009–2010 between three stage classes: seedlings, vegetative genets and generative genets (Caswell 2001). In total, 345 TLM individuals (47 seedlings, 144 vegetative and 154 generative plants) marked at the permanent plots in May 2009 were used to set the transition rates. First, we constructed composite matrix for all marked individuals and used its transition rates for each site with insufficient number (less than 20) of marked individuals in some of the stage class (mostly seedlings and vegetative individuals). For stage classes with sufficient number of marked individuals (20 and more), transition rates were calculated for each site separately. Rate of reproduction (number of seedlings developed from one generative individual) was estimated as mean number of well-developed seeds produced by one flowering shoot (592 seeds; estimation based on Janišová et al., submitted) multiplied by site-specific data of mean number of flowering shoots per genet and mean germination rate *in situ*. Lefkovitch matrices for stage-classified models were used to calculate λ and contribution of individual matrix elements to fitness (elasticity values). PopTools

Table 2. Environmental variables measured in five naturally grown field populations.

Environmental variable	Description
Slope	Inclination of micro-relief measured in degrees (0–90§).
Solar radiation	Potential direct solar irradiation (heat index) calculated from the slope and aspect data according to Parker (1988).
Cover_herbs	Percentage cover of herb layer.
Cover_moss	Percentage cover of bryophytes.
Cover herbs-litter	Percentage cover of plant dead biomass (litter) in the herb layer.
Cover bare soil	Percentage cover of bare soil on the plot surface.
Cover trees-litter	Percentage cover of dead leaves of woody species on the plot surface.
Distance from woody species	Distance of plot centre from the nearest trunk of woody species in cm.
Distance from disturbance	Distance of plot centre from the nearest disturbed soil surface in cm.
Disturbed surface	Percentage cover of disturbed soil surface within the plot area.
Soil depth	Depth of soil measured by metallic rod with diameter of 4 mm. Average of ten measurements in cm.
Soil depth_SD	Variability of soil depth expressed as standard deviation from average computed out of ten measurements of Soil depth.
Canopy Openness	Percentage of open sky seen from beneath a forest canopy calculated from hemispherical photography.
LAI 4 Ring	Effective leaf area index integrated over the zenith angles 0 to 60° (Stenberg et al. 1994).
LAI 5 Ring	Effective leaf area index integrated over the zenith angles 0 to 75° (Welles & Norman 1991).
Trans Direct	Amount of direct solar radiation transmitted by the canopy (Mols m^{-2} d^{-1}).
Trans Diffuse	Amount of diffuse solar radiation transmitted by the canopy (Mols m^{-2} d^{-1}).
Trans Total	Sum of Trans Direct and Trans Diffuse (Mols m^{-2} d^{-1}).
Soil pH-H_2O	Soil acidity estimated in water.
Soil pH-KCl	Soil acidity estimated in KCl suspension.
Soil Na	Natrium (mg kg^{-1} of dry matter).
Soil K	Kali (mg kg^{-1} of dry matter).
Soil Mg	Magnesium (mg kg^{-1} of dry matter).
Soil Ca	Calcium (mg kg^{-1} of dry matter).
Soil P	Phosphorus (mg kg^{-1} of dry matter).
Soil humus	Soil humus content calculated from carbon content (%).
Soil cox	Organic carbon content (%).
Soil NH_4	NH_4 (mg kg^{-1} of dry matter).
Soil NO_3	NO_3 (mg kg^{-1} of dry matter).
Number of all species	Number of all species in the plot except TLM.
Number of vascular plants	Number of vascular plants in the plot except TLM.
Number of bryophytes	Number of bryophyte species in the plot.
Number of woody plants	Number of woody plant species in the plot.
Number of forbs	Number of forb species in the plot except TLM.
Number of grasses	Number of grass and graminoid species in the plot.
% cover of all species	Sum of percentage cover of all species in the plot except TLM.
% cover of vascular plants	Sum of percentage cover of vascular plant species in the plot except TLM.
% cover of bryophytes	Sum of percentage cover of bryophyte species in the plot.
% cover of woody plants	Sum of percentage cover of woody plant species in the plot.
% cover of forbs	Sum of percentage cover of forb species in the plot except TLM.
% cover of grasses	Sum of percentage cover of grass and graminoid species in the plot.
Vascular to all species	Proportion of % cover of vascular plants to % cover of all species.
Bryophytes to all species	Proportion of % cover of bryophytes to % cover of all species.
Grasses to vascular	Proportion of % cover of grasses to % cover of vascular plants.
Forbs to vascular	Proportion of % cover of forbs to % cover of vascular plants.
Woody plants to vascular	Proportion of % cover of woody plants to % cover of all species.

software was used for calculations (Hood 2005).

Two non parametric tests for dependent samples (Wilcoxon signed ranks test for symmetric distributed variables and sign test for the rest of variables, Zar 1999) were used to determine differences of the measured variables between the plots containing TLM individuals and the plots without TLM. As the number of plot pairs was rather low, some of existing differences might be indicated as insignificant and the results should be interpreted with caution. Differences between sites in the measured environmental variables were tested by Kruskal Wallis test using only plots containing TLM. For correlation of the measured variables and fitness components to TLM, Spearman rank correlation coefficient was used. Plots 12a and 12b were omitted from analysis of paired samples as both of them contained TLM, however, sample 12a was used in correlation and Kruskal-Wallis test as well as in calculation of ecological indicator values for TLM. The statistical package IMB SPSS Statistics 18 was used for calculations.

The relationship among individual sample plots containing TLM were visualized in unconstrained ordination graphs. Detrended correspondence analysis was used to relate species composition of individual plots (length of gradient being 3.765). Percentage cover of species was log-transformed and data on TLM were deleted prior to analysis. Principal components analysis was used to relate individual plots based on the measured environmental variables (length of gradient being 0.782).

Ellenberg indicator values (EIV) of co-occurring species of vascular plants and bryophytes were used to characterize ecological requirements of TLM for light, temperature, continentality, moisture, soil reaction and nutrients (the last not set for bryophytes; Ellenberg et al. 1991). Unweighted averages were computed for individual plots

Table 3. Descriptive statistics of the measured variables for two groups of plots, P – plots containing TLM individuals, A – plots without TLM. W – Wilcoxon signed ranks test, S – sign test, * $P \leq 0.05$, ** $P \leq 0.01$.

Environmental variable	Plots containing TLM (P)					Plots without TLM (A)					P vs. A	Differences between sites
	Mean	Median	Std. Deviation	Min	Max	Mean	Median	Std. Deviation	Min	Max		
Slope	19.08	19.5	9.03	0	32	19.50	20.5	9.14	0–35	35	n.s.	*
Solar radiation	−0.22	−0.20	0.15	−0.46	0	−0.21	−0.22	0.16	−0.52	−0.08	n.s.	n.s.
Cover_herbs	68	70	17.6	11	90	62.08	67.5	23.5	11	95	n.s.	n.s.
Cover_moss	19.54	7.5	26.27	0	80	23.92	3	33.42	0	90	n.s.	n.s.
Cover herbs-litter	30.21	22.5	30.5	0	95	37	37.5	32.58	0	85	n.s.	*
Cover bare soil	3.04	1	5.23	0	20	3.58	0	9.5	0	35	n.s.	n.s.
Cover trees-litter	25.63	20	28.13	0	90	24.04	15	30.9	0	97	n.s.	n.s.
Distance from woody species	503	375	470	0	2100	489	400	493	0	2200	n.s.	n.s.
Distance from disturbance	441	200	460	0	1000	467	200	440	0	1000	n.s.	n.s.
Disturbed surface	2.04	0	6.4	0	30	3.75	0	10.63	0	40	n.s.	n.s.
Soil depth	25.23	21.3	10.5	13.5	52.7	22.85	20.7	9.67	12.7	51	> ** (S)	n.s.
Soil depth_SD	7.07	6.2	3.7	1.6	14	7.53	6.1	4.33	2.6	17.1	n.s.	**
Canopy Openess	38.38	34.74	22.85	7	85	37.19	31.11	23.62	6	86	n.s.	n.s.
LAI 4 Ring	1.23	0.91	1.8	0	3.69	1.31	1.08	1.1	0	3.77	n.s.	n.s.
LAI 5 Ring	1.24	1.1	0.95	0	3.23	1.28	1.27	0.94	0	3.13	n.s.	n.s.
Trans Direct	8.15	8.88	5.84	0.3	18.3	8.07	8.46	5.71	0.2	18.3	n.s.	n.s.
Trans Diffuse	9.06	9.67	5.1	1.4	17.6	8.77	8.58	5.22	1.1	17.6	n.s.	n.s.
Trans Total	17.20	17.93	10.65	2.8	35.9	16.84	17.04	10.62	2.5	36	n.s.	n.s.
Soil pH-H_2O	5.76	5.5	0.64	4.9	7.1	5.81	5.7	0.69	4.8	7	n.s.	*
Soil pH-KCl	5.21	4.93	0.81	4.1	6.7	5.29	5.18	0.93	3.7	6.8	n.s.	*
Soil Na	102.4	94.5	49.5	38.0	216.7	83.99	89.61	44.01	3.7	180.2	> * (S)	**
Soil K	155.8	147.4	72.17	69.8	358.7	150.1	128.9	72.02	69.3	338.4	n.s.	*
Soil Mg	498.6	374.5	281.5	276	1176	472.3	385.1	257.59	221	1070	> * (S)	n.s.
Soil Ca	3422	3322	657.12	2378	4385	3371	3411	738.51	1970	4620	n.s.	**
Soil P	7.45	6	4.82	1	20	6.7	6.5	3.96	1	18	n.s.	*
Soil humus	10.78	10.7	2.46	6.9	14.8	10.52	10.35	2.7	5.7	14.4	n.s.	n.s.
Soil cox	6.24	6.2	1.42	4	8.6	6.1	6	1.57	3.3	8.4	n.s.	n.s.
Soil NH_4	12.57	11.36	5.23	6.4	24.6	13.67	10.71	6.63	6.4	30.6	n.s.	*
Soil NO_3	6.21	4.23	4.8	1.1	17.8	5.53	4.31	3.98	1	15.2	n.s.	n.s.
Number of all species	24.5	25.5	8.2	6	38	21.8	19	9.74	5	42	> * (W)	n.s.
Number of vascular plants	22	23.5	7.37	6	32	20	18.5	8.38	5	38	n.s.	n.s.
Number of bryophytes	2.46	2	1.5	0	6	1.79	1.5	1.79	0	5	n.s.	n.s.
Number of woody plants	1.42	1	1.38	0	5	1.67	1	1.47	0	6	n.s.	n.s.
Number of forbs	15.54	15.5	5.69	5	25	13.63	13.5	6.18	3	28	> * (W)	n.s.
Number of grasses	5.04	6	2.84	0	9	4.71	4.5	2.88	0	10	n.s.	n.s.
% cover of all species	99.08	91.5	47.81	11	219	95.92	95.5	46.79	13	164	n.s.	n.s.
% cover of vascular plants	80.83	80.5	30.72	11	139	71.29	73.5	28.7	13	135	n.s.	n.s.
% cover of bryophytes	18.13	5	25.77	0	80	24.58	4	33.96	0	90	n.s.	n.s.
% cover of woody plants	11.71	2	22.8	0	76	7.13	2	11.8	0	42	n.s.	n.s.
% cover of forbs	44.42	48.5	21.3	10	101	37.83	41	19.1	9	65	n.s.	n.s.
% cover of grasses	24.71	24.5	16.65	0	70	26.33	25.5	19.43	0	72	n.s.	n.s.
Vascular to all species	0.87	0.93	0.15	0.53	1	0.83	0.95	0.22	0.39	1	n.s.	n.s.
Bryophytes to all species	0.13	0.07	0.15	0	0.47	0.17	0.05	0.22	0	0.61	n.s.	n.s.
Grasses to vascular	0.30	0.31	0.19	0	0.76	0.33	0.34	0.21	0	0.79	n.s.	n.s.
Forbs to vascular	0.57	0.56	0.22	0.23	0.97	0.54	0.58	0.18	0.2	0.85	n.s.	n.s.
Woody plants to vascular	0.13	0.03	0.22	0	0.73	0.13	0.04	0.19	0	0.79	n.s.	n.s.
Ranunculus acris (% cover)	0.79	1	0.18	0	3	0.42	0	0.13	0	2	>* (S)	n.s.

in three separate runs: one based on vascular plants, one on bryophytes and one on both groups combined. Species not included in the Ellenberg's list (vascular plants *Allium flavum*, *Cirsium pannonicum*, *Glechoma hirsuta*, *Isopyrum thalictroides*, *Knautia kitaibelii* and bryophyte *Homalia besseri*) and species lacking some indicator value were disregarded in the calculations. Spearman Rank Correlation Coefficients were calculated between EIV plot averages and relevant environmental variables measured. Vascular plant-based EIV had strongest correlation with the measured variables in light, temperature, soil reaction and nutrients. Bryophytes-based EIV had strongest correlation with the measured variable in moisture. EIV based on combination of vascular plants and bryophytes yielded similar but slightly less significant correlation to the measured variables than EIV based on vascular plants only. Concerning these facts, ecological indicator values of TLM were set mainly with regards to vascular plant-based EIV from plots containing TLM. Unweighted averages of Ellenberg indicator values for plots were used also as variables to test differences between plots containing TLM individuals and those without TLM by Wilcoxon Signed Ranks Test. As none of these variables differed between the two plot groups, the results were not shown.

Names of bryophytes and vascular plants are according to Marhold & Hindák (1998).

Results

Ecological niche of TLM

Survey of the measured components of TLM realized

Table 4. Spearman rank correlation coefficients between selected TLM characteristics and measured variables. Only significant relationships are shown (* $P < 0.05$, ** $P < 0.01$).

	% cover	All genets	G genets	V genets	Juv.	All ramets	V ramets	G ramets	Size V	Size G
Cover trees-litter	0.40 *					0.40 *				
Distance from disturbance								0.44 *		0.41 *
Soil Na			0.42 *					0.42 *		
Soil Ca								0.44 *		0.42 *
Soil P						0.40 *	0.45 *			
Number of grasses			0.41 *	−0.45 *						
% cover of vascular plants				−0.43 *			−0.43 *			
% cover of grasses				−0.53 **						
Grasses to vascular				−0.41 *						
Forbs to vascular								−0.41 *		−0.43 *
Achillea millefolium (% cover)				−0.43 *						
Cruciata glabra (% cover)				−0.40 *						
Fragaria moschata (% cover)		−0.45 *								
Fragaria vesca (% cover)		0.56 **		0.40 *	0.50 **	0.56 **				0.54 **
Poa pratensis agg. (% cover)				−0.44 *						
Primula veris (% cover)		0.40 *			0.48 *	0.44 *	0.44 *			
Vicia cracca (% cover)										−0.46 *

% cover: % cover of TLM in the plot; All genets: number of TLM genets per plot (0.5 m^2); G genets: number of generative TLM genets per plot (0.5 m^2); V genets: number of vegetative TLM genets per plot (0.5 m^2); Juv.: number of seedlings and juveniles of TLM per plot (0.5 m^2); All ramets: number of TLM ramets (vegetative plus generative) per plot (0.5 m^2); V ramets: number of TLM vegetative ramets per plot (0.5 m^2); G ramets: number of TLM generative ramets per plot (0.5 m^2); Size V: number of vegetative ramets per TLM genet; Size G: number of generative ramets per TLM generative genet.

niche is in Table 3 including mean, median, standard deviation, minimum and maximum values recorded in plots containing TLM individuals. Full data set is placed in an electronic appendix.

Co-occurring species and interspecific associations

In total, 213 taxa of vascular plants and bryophytes were recorded in the plots, 176 of them occurred also in samples containing TLM individuals. TLM most frequently co-occurred with the following species (percentage of plots containing the species pair is shown in parentheses): *Cruciata glabra* (88), *Festuca rubra* (72), *Asarum europaeum* (68), *Arrhenatherum elatius* (64), *Primula veris* (64), *Achillea millefolium* (52), *Plagiomnium affine* (56), *Ranunculus acris* (56) and *Veronica chamaedrys* (56). Only in plots containing TLM the following species were recorded (ordered according to frequency, number of plots in parentheses): *Hypericum hirsutum* (4), *Trifolium pratense* (3), *Anthriscus sylvestris* (3), *Chaerophyllum aromaticum* (3), *Brachythecium velutinum* (2), *Solidago virgaurea* (2), *Urtica dioica* (2) and *Myosotis arvensis* (2). On the other hand, several species did not occur in plots containing TLM although they were present in their plot pairs (species present in ≥2 plots): *Tithymalus cyparissias* (5), *Cephalanthera damasonium* (2), *Cornus sanguinea* (2), *Myosotis sylvatica* (2), *Plantago media* (2), *Potentilla heptaphylla* (2) and *Teucrium chamaedrys* (2).

Species positively associated with TLM (phi ≥ 20, shown in the parentheses) were the following: *Achillea millefolium* (29), *Hypericum hirsutum* (28), *Plagiomnium affine* (25), *Chaerophyllum aromaticum* (24), *Trifolium pratense* (24), *Anthriscus sylvestris* (24), *Anthoxanthum odoratum* (22), *Ranunculus acris* (21), *Jacea pratensis* (20) and *Salvia pratensis* (20). Species negatively associated with TLM (phi ≤ −20, shown in the parentheses) were the following: *Tithymalus cyparissias* (−35), *Cornus sanguinea* (−21), *Cephalanthera damasonium* (−21), *Myosotis sylvatica* (−21), *Teucrium chamaedrys* (−21), *Potentilla heptaphylla* (−21) and *Plantago media* (−21).

Effect of small-scale environment variation on TLM occurrence and performance

Comparison of plots containing TLM and plots without TLM indicated significant differences in 6 variables (Table 3). Plots containing TLM had deeper soil and higher soil Na and Mg contents than plots without TLM. They also contained higher number of species, especially forbs. There were no differences in light parameters. Average plot EIV (based on vascular plants, bryophytes or both of them) did not differ between the plot groups (results not shown). Among the co-occuring species, significant differences were revealed only in *Ranunculus acris* which had higher cover values in plots containing TLM.

Correlation coefficients of TLM characteristics (percentage cover, number of genets and ramets, size of vegetative and generative genets) with the measured variables are shown in Table 4. Among the soil parameters, contents of Na and Ca positively correlated with density of generative ramets, soil Na positively correlated also with density of generative genets and soil Ca positively correlated also with the size of generative genets. Soil P content showed positive correlation with density of both all ramets and vegetative ramets. Light parameters seem not to play a role in determination of TLM size and density neither at the level of genets nor at the level of ramets. On the other hand, biological variables performed multiple correlations with TLM characteristics. Cover and density of TLM was positively correlated with cover of tree litter (fallen leaves). Density of vegetative genets (in one case also ramets) was negatively correlated with percentage cover of vascular plants and grasses, number of grass and graminoid species and their proportion in plots. Number of vegetative genets was negatively correlated with percentage cover of *Poa pratensis* agg., *Achillea millefolium* and *Cruciata glabra*. Density of generative ramets and size of generative genets was negatively correlated with proportion of forbs in plots and positively correlated with distance from disturbance. Positive correlations were indicated between % cover of *Fragaria vesca* and *Primula veris* and numerous TLM characteristics (Table 4). Percentage cover of *Fragaria moschata* was negatively correlated with density of all genets and % cover of *Vicia cracca* with size of generative genets.

Ecological indicator values of TLM

Correlations between average plot EIV and adequate measured environmental variables are shown in Table 5. Ecological indicator values of TLM were set as follows (Table 6): light 6 (semi-shade to partial-shade plant occurring also in well lit places), temperature 5 (semi-thermophilous plant distributed mainly in sub-montane temperate regions), continentality 4 (plant occurring mainly in regions with sub-oceanic climate), moisture 5 (moist-site indicator occurring mainly on fresh soils of average dampness), soil reaction 7 (indicator of weekly acid to weekly basic conditions, never found on very acid soils) and nutrients 5 (indicator of sites of intermediate fertility). Estimation based on bryophytes (Table 6) indicated slightly different values for temperature – 4 (plants of montane regions), continentality – 5 (slightly sub-oceanic to slightly sub-continental plant) and soil reaction – 5 to 6 (plant of moderately acid soils, or on neutral to basic soil).

Comparison of sites and TLM populations

Regarding the population abundance, population of Radobica was the largest followed by populations in Čavoj and Lysá, and the smallest were populations in Stráž and Omšenie (Table 1). In all populations, finite rates of increase (λ) calculated for transition period 2009–2010 indicated increase in population size. Population size was negatively related to λ, the two smallest populations had the highest rates and the largest population had the lowest rate (Table 1, Fig. 2). Based on a composite matrix for all marked individuals (including values from all sites), finite rate of increase of TLM was most sensitive to transition between vegetative and generative stages (elasticity value $e_{VG} = 0.261$). Transitions between generative and seedling stages ($e_{GS} = 0.231$) and between seedling and vegetative stages ($e_{SV} = 0.231$) were also important. Summing the elasticity values to components representing growth (G), survival (S) and fecundity (F) we obtained the following values: $G = e_{SV} + e_{VG} = 0.492$, $L = e_{VV} + e_{GG} + e_{GV} = 0.277$, $F = e_{GS} = 0.231$. These values indicate, that λ of TLM was most sensitive to demographic parameters related to growth. Elasticity analysis of matrices for individual populations showed similar results with exception of the Radobica population where λ was most sensitive to survival due to high elasticity value of the transition between vegetative and vegetative stages ($e_{VV} = 0.475$).

Table 5. Spearman rank correlation coefficients of Ellenberg indicator values (EIV) and best correlated measured environmental variables. Average unweighted EIV were based on vascular plants (VP), on bryophytes (B) or on both of them (VP+B). * $P < 0.05$, *** $P < 0.01$, *** $P < 0.001$.

	VP	B	VP+B
EIV Light : LAI5_ring	−0.60***	0.09	−0.57***
EIV Temperature : Solar radiation	0.49***	0.20	0.38*
EIV Moisture : Soil depth	−0.01	−0.45**	−0.11
EIV Soil reaction : pH_KCl	0.67***	0.50**	0.64***
EIV Nutrients : Soil NO3	0.57***	–	–

The studied population sites differed in topography (slope), numerous soil characteristics (soil depth_SD, pH-H_2O, pH-KCl, contents of soil Na, K, Ca, P and NH_4) and cover of herb litter (Fig. 3, Table 3). Light variables and most of biological variables did not differ between sites. Complex comparison of individual plots based on their species composition is shown in Fig. 4. Species-rich grassland vegetation dominates in plots from sites Lysá and Čavoj in the right part of the ordination graph. Plots in the left graph part represent transitional types of ecotone vegetation ranging from grass-rich grassland margins in localities Omšenie and Stráž (upper left part) to forest edge understorey in

Table 6. Estimation of Ellenberg indicator values (EIV) for *Tephroseris longifolia* subsp. *moravica* based on indicator values of vascular plants and bryophytes in plots containing TLM. EIV for nutrients are not available for bryophytes (Ellenberg et al. 1991).

	EIV based on vascular plants					EIV based on bryophytes					EIV set for TLM
	Mean	Median	SD	Min	Max	Mean	Median	SD	Min	Max	
Light	6.3	6.5	0.6	4.8	7.0	5.9	6.0	0.7	4.5	6.7	6
Temperature	5.5	5.5	0.2	5.3	5,8	3.5	3,5	0.4	3	4.5	5
Continentality	3.8	3.8	0.2	3.3	4.2	5.3	5.3	0.4	4.5	6.0	4
Moisture	4.8	4.8	0.2	4.4	5.4	4.8	4.7	0.5	4	5.7	5
Soil Reaction	6.6	6.7	0.6	5.5	7.6	5.4	5.5	0.7	4.3	6.3	7
Nutrients	4.9	4.7	0.8	3.7	6.4	–	–	–	–	–	5

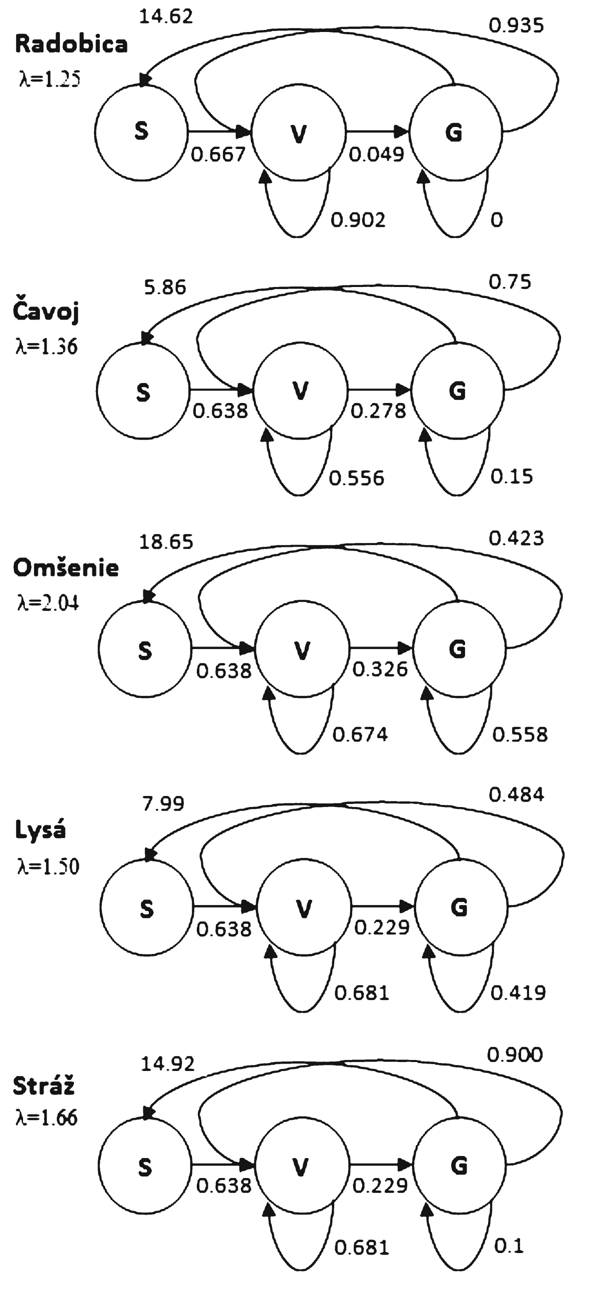

Fig. 2. Stage-structured life cycle diagram of *Tephroseris longifolia* subsp. *moravica*. Transition probabilities between ontogenetical stages (S – seedlings, V – vegetative genets, G – generative genets) and population finite rate of increase (λ) are shown for each population site.

several plots from Radobica (lower left part). Slightly different pattern is shown in Fig. 5 displaying relationships among plots containing TLM based merely on the environmental data (33 measured variables). According to the principal component analysis, sites Čavoj and Radobica provide most similar habitat conditions although very diverse as shown by their wide distribution along the second ordination axis. Two plots from site Omšenie (O2, O4) are close related to plots from site Lysá, while other two plots (O1, O3) are more similar to plots from sites Stráž and Radobica. Both unconstrained ordinations confirmed the highest diversity of abiotic and biotic habitat conditions in Radobica and Čavoj which represent sites having both the largest spatial extent and the most abundant populations.

Discussion

Co-occurring species and interspecific associations

TLM frequently co-occurs with common species of mesophilous grasslands (*Arrhenatherum elatius*, *Festuca rubra*, *Cruciata glabra*, *Ranunculus acris*, *Achillea millefolium*, *Veronica chamaedrys*, *Anthoxanthum odoratum*, *Trifolium pratense*, *Jacea pratensis*), semi-dry grasslands (*Primula veris*) or species of beech-forest understorey (*Asarum europaeum*). Sporadically, it is accompanied by species of nutrient-rich or disturbed grasslands such as *Anthriscus sylvestris*, *Chaerophyllum hirsutum*, *Urtica dioica* and *Myosotis arvensis*. This fact can be explained by successful TLM recruitment in disturbed microhabitats indicated also in our sowing experiment (Janišová et al. submitted). Negative association of TLM with several species of dry grasslands (*Tithymalus cyparissias*, *Teucrium chamaedrys*, *Potentilla heptaphylla*) suggests its susceptibility to longer-lasting water deficiency in sun-exposed open dry grassland habitats.

Effect of small-scale environment variation on TLM occurrence and performance

In the ecotone habitats, abiotic resources are patchily distributed with different resource levels. In order to determine if the presence and performance of TLM individuals are correlated with microsite resource levels we used the paired plot approach. The indicated differences in soil depth might be related to moisture conditions at a micro-scale. Deeper soils in plots containing TLM suggest that the taxon small-scale distribution could be promoted by sufficient water-retaining capacity of soil. The availability of water seems to be important especially for germination and seedling establishment, higher seedling survival in moister microhabitats could result in a clumped distribution of adult individuals.

Plots containing TLM individuals showed increased content of several nutrients and humus, although the difference between the plot pairs was significant only in two soil variables, soil Na and Mg contents. This pattern suggests but does not prove that greater resource levels might result in differential rates of growth and survival for TLM individuals among microsites. Several processes and interactions between them could cause the observed pattern, however, and experimental approach would be needed to explain it.

The surprising finding that light parameters did not differ between the plot pairs and were correlated with none of TLM fitness characteristics offers two possible explanations. According the first of them, TLM is extraordinary tolerant to both extremes of the light gradient and thus light plays none or only a minor role in determination of its occurrence and performance. However, light is one of environmental factors which under-

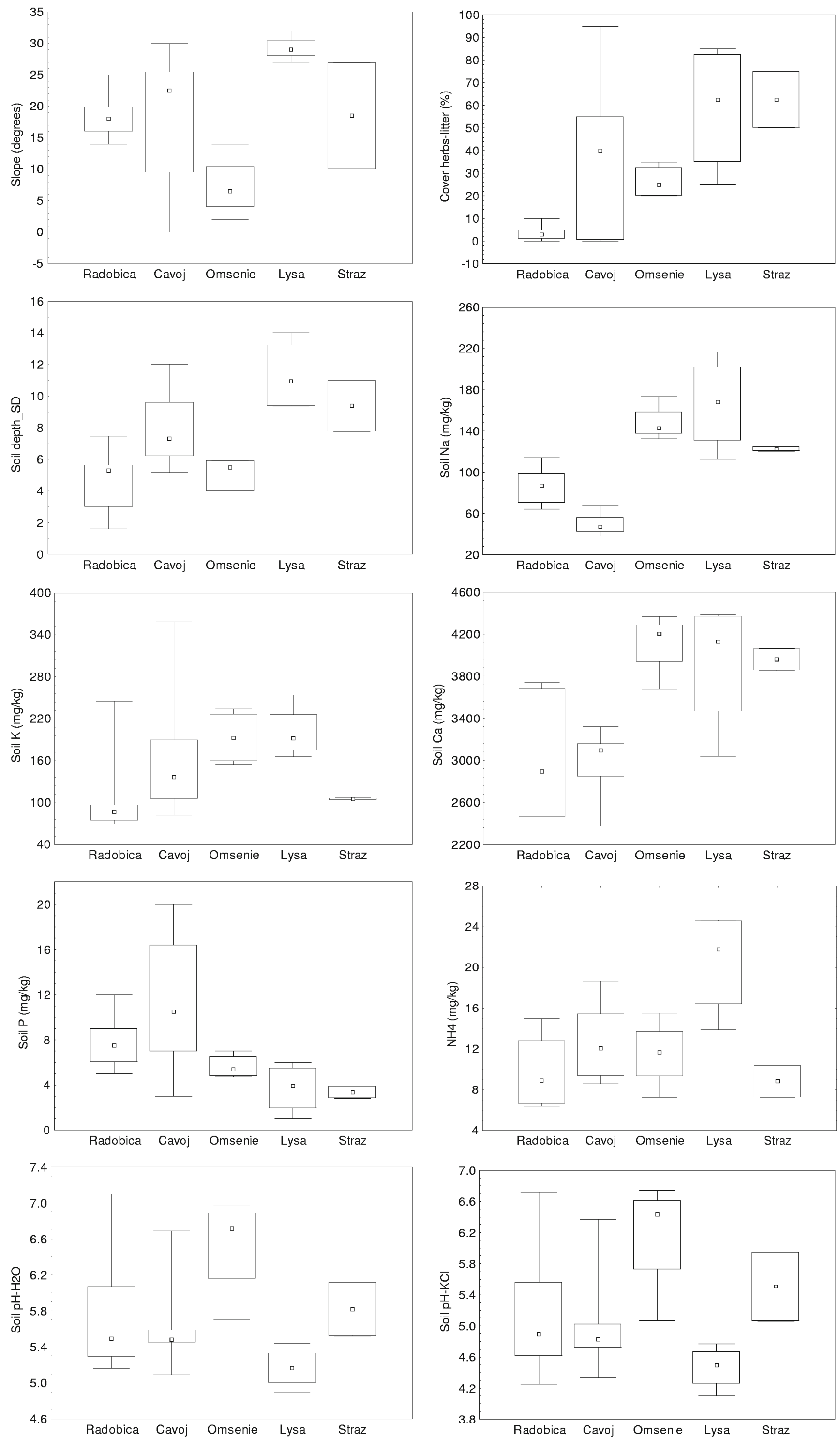

Fig. 3. Comparison of population sites: environmental variables which differ between sites (Kruskal-Wallis test, Table 3) are shown. Median value, 25% and 75% quartiles, minimum and maximum values are shown in each box & whisker plot.

lie significant temporal variation. Light conditions during the peak growing season when our measurements were performed could be irrelevant in our analyses but the situation might be different during early spring. According to the second explanation, TLM requires high light intensity mainly during its early annual development and its obvious phenological shift towards an early growing season is a result of its avoidance from strong competitors for light represented by woody species, tall grasses and forbs.

Although the plots containing TLM had higher number of all species (including vascular plants and bryophytes) and forbs, several negative correlations between the cover, number or proportion of vascular plants (especially grass and graminoid species) and TLM characteristics reveal the tendency of TLM to oc-

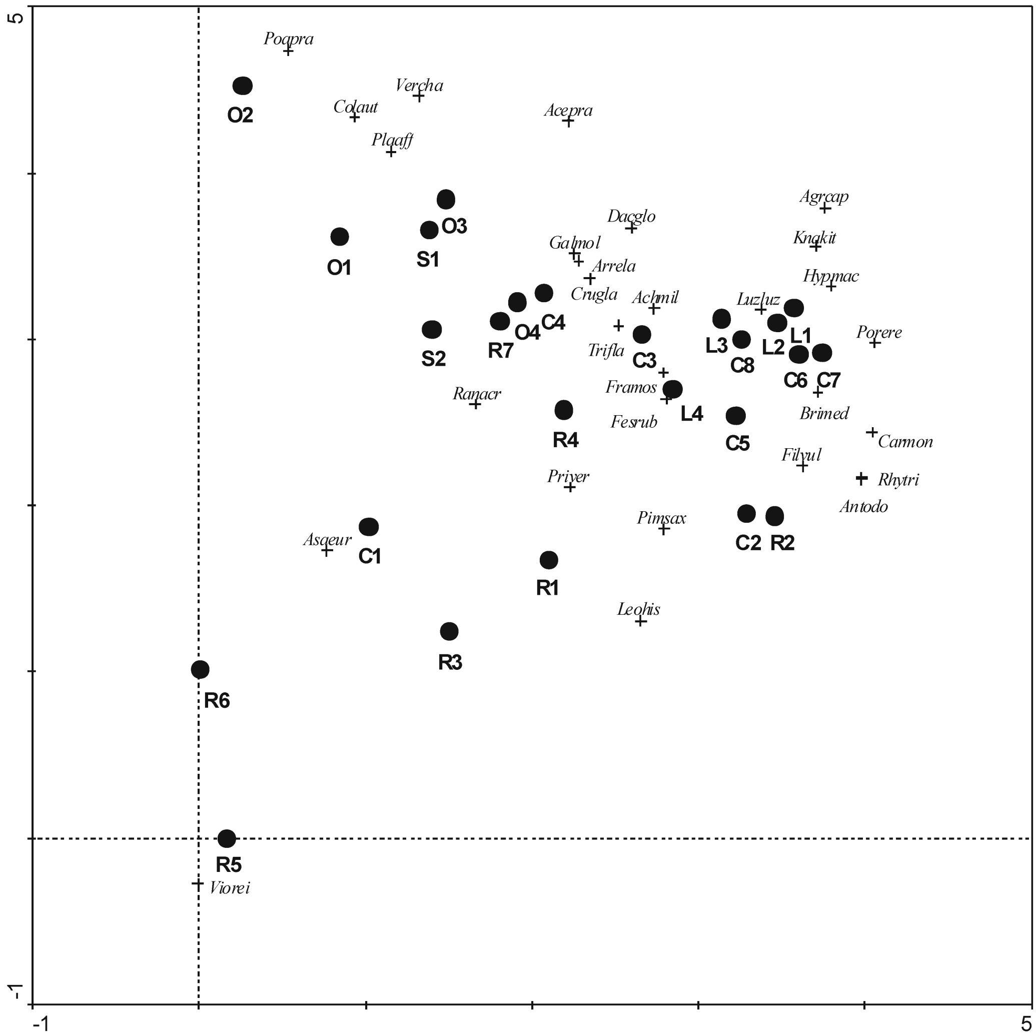

Fig. 4. Detrended correspondence analysis of 25 samples containing TLM. Eigenvalues: 1st axis: 0.545, 2nd axis: 0.487, percentage variance of data explained by the 1st axis: 7.7%, by the 2nd axis: 6.5%. Notation of sites follows the Appendix: C – Čavoj, L – Lysá, O – Omšenie, R – Radobica, S – Stráž. Only 29 species with weight over 25 are shown: *Acepra* – *Acetosa pratensis*, *Achmil* – *Achillea millefolium*, *Agrcap* – *Agrostis capillaris*, *Antodo* – *Anthoxanthum odoratum*, *Arrela* – *Arrhenatherum elatius*, *Asaeur* – *Asarum europaeum*, *Brimed* – *Briza media*, *Carmon* – *Carex montana*, *Colaut* – *Colchicum autumnale*, *Crugla* – *Cruciata glabra*, *Dacglo* – *Dactylis glomerata*, *Fesrub* – *Festuca rubra*, *Filvul* – *Filipendula vulgaris*, *Framos* – *Fragaria moschata*, *Galmol* – *Galium mollugo*, *Hypmac* – *Hypericum maculatum*, *Knakit* – *Knautia kitaibelii*, *Leohis* – *Leontodon hispidus*, *Luzluz* – *Luzula luzuloides*, *Pimsax* – *Pimpinella saxifraga*, *Plaaff* – *Plagiomnium affine*, *Poapra* – *Poa pratensis*, *Potere* – *Potentilla erecta*, *Priver* – *Primula veris*, *Ranacr* – *Ranunculus aris*, *Rhytri* – *Rhytidiadelphus triquetrus*, *Trifla* – *Trisetum flavescens*, *Vercha* – *Veronica chamaedrys*, *Viorei* – *Viola reichenbachiana*.

cur in microhabitats with reduced competition from other plants. Based on our results from experiments with TLM germination in field conditions (Janišová et al. submitted) we suggest that this pattern is a consequence of increased germination of TLM at special microsites (regeneration niche) with opener soil surface and reduced competition from other plants. Positive correlations between % cover of both *Fragaria vesca* and *Primula veris* and numerous TLM characteristics (Table 4) suggest that these species could indicate habitat conditions most suitable for TLM individual development.

Ecological indicator values of TLM

The relationship of TLM to the environmental factors can be expressed by directly measured variable values as well as by indirect indication by co-occurring species. Ellenberg numbers (Ellenberg et al. 1991) belong to widely used indicator values and were used also in our study. As we had also direct measurements for several relevant factors, we could relate the computed EIV values (unweighted) for plots to measured values of related environmental variables. According to our data, vascular plant-based EIV showed closer relationships to the measured variables than bryophytes-based EIV (except relationship between EIV for moisture and soil depth, Table 5) and EIV based on both groups. In our estimation of TLM indicator values we therefore regarded mainly vascular plant-based EIV. Higher indication potential of vascular plants in comparison to bryophytes was reported by several other authors (Diekmann 1995; Ewald 2009) and is attributed mainly to a more pronounced response of vascular plants to ecological gradients, low species number of bryophytes in ecosystems,

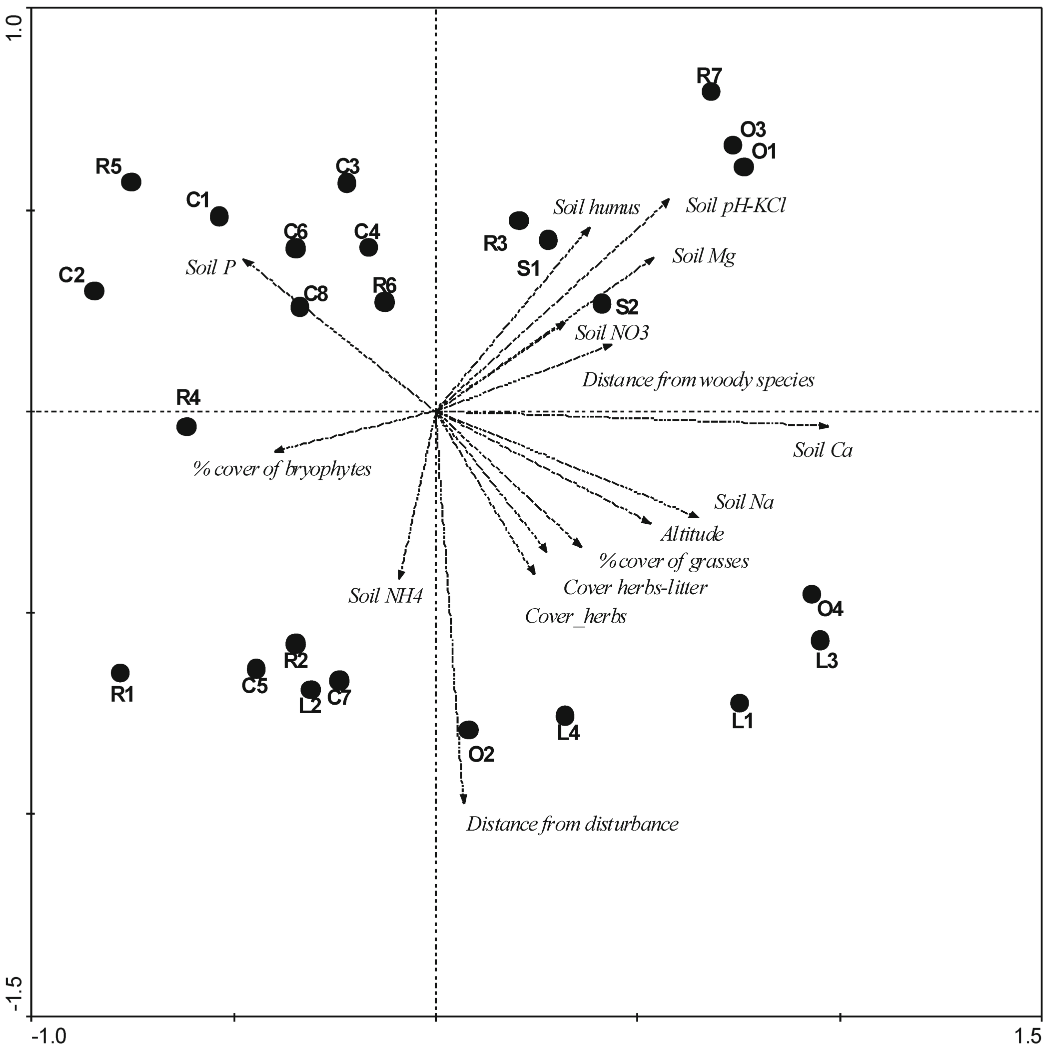

Fig. 5. Principal components analysis of 33 environmental variables. Eigenvalues: 1st axis: 0.496, 2nd axis: 0.234, percentage variance of data explained by the 1st axis: 49.6%, by the 2nd axis: 23.4%. Only 15 most important variables with fit range over 15 are shown, their notation follows Table 2.

or more reliable calibration of EIV for vascular plants.

Vascular plant-based EIV for light were significantly correlated with all measured light variables, highest correlation showed LAI5_ring and TransTotal. EIV for soil reaction were significantly correlated with pH_H_2O, pH_KCl, Soil Mg, soil humus, soil cox, soil NH_4 and soil NO_3 (Spearman correlation coefficients 0.64, 0.67, 0.57, 0.44, 0.42, 0.44 and 0.36, respectively, pH_KCl showed the strongest correlation, Table 5). EIV for nutrients were significantly correlated with the measured variables pH_H_2O, pH_KCl, Soil P, soil humus, soil cox and soil NO_3 (Spearman correlation coefficients 0.40, 0.44, 0.30, 0.40, 0.40 and 0.57; soil NO_3 showed the strongest correlation, Table 5).

According to EIV analysis, TLM belongs to species with intermediate requirements for all factors accounted. Based on the combination of Ellenberg indicator values, TLM (654575) has most similar habitat requirements to the following species: *Bromus benekenii* (554575, slightly less helophilous), *Crataegus laevigata* (664575, slightly more thermophilous), *Primula vulgaris* (652575, slightly more oceanic distribution), *Cerasus avium* (454575, less helophilous), *Cruciata glabra* (764575, slightly more helo- and thermophilous), *Euonymus europaeus* (653585, slightly more oceanic and acidophilous), *Fragaria vesca* (7x55x6, slightly more helo- and nitrophilous), *F. moschata* (664566, more thermo- and nitrophilous and less acidophilous) and *Brachypodium pinnatum* (655474, more continental and xerophilous, grows in slightly less fertile habitats). Almost identical EIV for TLM were calculated from phytosociological data set consisting of relevés with occurrence of TLM (Hegedüšová et al. submitted). These phytosociological data were obtained independently from our plot data by numerous authors in nearly all TLM population sites in Slovakia and Czech Republic.

Although the average EIV used to set ecological indicator numbers for TLM provide important information on average habitat conditions of species occurrence, they hardly indicate the full range of conditions where the taxon is able to survive and its tolerance to individual environmental factors. Some of these features is possible to assess using the indicator capacity of individual co-occuring species. The list of co-occurring species is rather heterogeneous including species of open grassland habitats (*Acetosa pratensis*, *Arrhenatherum elatius*, *Briza media*, *Festuca rupicola*, *Leontodon hispidus*, *Salvia pratensis*), fringe species (*Fragaria moschata*, *F. vesca*) as well as typical forest species (*Asarum europaeum*, *Isopyrum thalictroides*, *Symphytum tuberosum*, *Viola reichenbachiana*). This is probably due to the transitional character of ecotone habitats where TLM is mainly distributed. Co-occurring with indicators of nutrient-rich habitats (*Aegopodium podagraria*, *Anthriscus sylvestris*, *Chaerophyllum aromaticum*, *Heracleum sphondylium*, *Taraxacum* sect. Ruderalia, *Urtica dioica*) simultaneously with co-occurring with species of nutrient-poor habitats (*Genista pilosa*, *Teucrium chamaedrys*, *Thesium linophylon*, *Thymus pulegioides*) suggests high tolerance of TLM to the nutrient status of its habitats.

Comparison of sites and TLM populations

In our study, we used a matrix approach where the only transition period (between years 2009 and 2010) was included. In spite of this limitation, in combination with the data on population size and vitality (proportion of flowering individuals), we have a rather reliable information on the status of each of the studied populations which can be related to the local environmental conditions measured. One of the advantages is that both data (environmental and demographic) were recorded during the same period.

The values of finite rate of increase (λ) were positive in all populations studied. Similar values of λ (1.32, 1.33 and 2.18) were calculated by Gbelcová (2010) who analyzed three TLM populations in the Czech Republic based on composed data recorded during 2007–2009. According to these results, all studied populations of TLM show the trend to increase in size. However, the high values of λ should be interpreted with caution. λ is an asymptotic growth rate assuming indefinite maintenance of the vital rates in the matrix. In reality, demographic parameters vary due to the stochastic nature of environmental conditions (Gibson 2002). Many demographic parameters such as flowering and seedling recruitment are episodic. Due to these facts, the real trends in development of TLM populations should be generalized from data containing at least three transition periods and accounting the temporal demographic stochasticity. Therefore, we used the matrix models only to compare the populations and omitted wider predictions and generalizations.

The differences of the measured environmental variables between the sites indicate that the TLM populations are supported by a wide variety of environmental conditions. Naturally, we would like to know which of the sites offers the best condition for TLM populations to survive and grow. According to our analyses, population size and finite rate of increase were negatively correlated (Table 1). The most abundant population in Radobica had (along with population in Stráž) the lowest proportion of generative individuals in 2010 and no transition from generative to generative stages were recorded (Fig. 2). As a result, the finite rate of increase calculated for this population was the lowest for the recorded period. If the habitat quality is assessed by its regeneration potential for TLM (germination *in situ*, Table 1), slightly different conclusion would be obtained. Best conditions for seedling recruitment of TLM showed populations in Omšenie and Stráž which were least abundant.

Most remarkable differences between population sites were found in soil chemical properties (mainly Na, Ca and NH_4 content) and herb-litter cover (Fig. 3). Some of these differences may be explained by different geological bedrock and management (Myklestad 2004). More than two-times higher NH_4 content in site Lysá is probably result of occasional cattle grazing realized during the last few years. In this site, the lowest pH was recorded although the soil Ca content is high. This disproportion might be related to the deep soil and changes in the topsoil due to successional development of the vegetation. The regular mowing in sites Radobica and Omšenie (site of one subpopulation) resulted in low percentage cover of litter in the herb layer, while in longer abandoned sites (Stráž, Čavoj and Lysá) intensive litter accumulation was obvious. The reasons of differences in soil Na content and the role of Na in the development of both studied taxon and vegetation, remains unclear.

Conclusions and implications for the taxon conservation

In spite of narrow range of TLM recent distribution, TLM hardly can be considered as strictly stenotopic. Based on our measurements, the ranges of several environmental variables in plots inhabited by TLM were rather wide. Also the cultivation experiments supported the idea, that TLM does not require specific habitat conditions to survive (easy cultivation, tolerance to different light and soil conditions). Even so, TLM natural populations are restricted to small areas of specific, mainly transitional habitat conditions of ecotone character. Why TLM grows mainly in ecotone habitats and why is it so rare? To answer this question, additional research would be needed based on longer time observations and manipulative experiments. Based on our results we suppose, that the narrow limits of recent taxon occurrence are related to sensitivity to exclusion by competitively stronger species and demographic processes related to germination and seedling establishment. The differences in requirements of TLM ontogenetic stages (especially between seedlings and generative individuals) may define the final limits of the taxon small-scale distribution. Microsites optimal for germination and seedling establishment (shadow forest margins with open soil surface) represent only suboptimal conditions for the development of generative ramets, which prosper best in open grassland communities (better conditions for pollination and seed dispersal). Within this narrow range of acceptable habitat conditions, the man-made management can become important limiting factor at its two extreme positions:

long-term abandonment leading to out-competing of TLM by competitively stronger plants and too intensive mowing and/or grazing damaging adult individuals and hindering proper seed development. Habitat types suitable for all TLM ontogenetic stages might have been commoner in the past and thanks to that its populations survived until the recent times.

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