

Phytosociological affiliation of Annex II species *Tephrosieris longifolia* subsp. *moravica* in comparison with two related *Tephrosieris* species with overlapping distribution

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Abstract: The phytosociological affiliation of *Tephrosieris longifolia* subsp. *moravica*, species of European importance, was studied in relation to two closely related species of the genus *Tephrosieris* which have overlapping distribution within the Western Carpathian Mts: *T. integrifolia* and *T. crispa*. The main aim was to compare plant communities inhabited by the three taxa, to assess the major environmental gradients responsible for variation in their distribution and to estimate ecological indicator values for *Tephrosieris longifolia* subsp. *moravica*. *T. longifolia* subsp. *moravica* was recorded in nine localities in the Slovakia and Czech Republic where it occurs in very specific site conditions of ecotone habitats. Its phytosociological affiliation is restricted to grasslands of the alliances *Bromion erecti* and *Arrhenatherion elatioris* and to the ecotone vegetation between these grasslands and beech forests. *T. integrifolia* occurs most frequently in the *Diantho lumnitzeri-Seslerion*, *Bromion erecti* and *Quercion pubescenti-petraeae* alliances. *T. crispa* occurs predominantly in communities of the *Calthion palustris* alliance and *Scheuchzerio-Caricetea fuscae*, *Mulgedio-Aconitetea* and *Montio-Cardaminetea* classes. The major gradient responsible for variation in species composition of communities inhabited by the studied taxa was associated with moisture and nutrient content. The vascular plant-based ecological indicator values for *Tephrosieris longifolia* subsp. *moravica* calculated from phytosociological relevés with its occurrence were set for light – 6, temperature – 5, continentality – 4, moisture – 5, soil reaction – 6 and nutrients – 5. We conclude that the studied taxon has intermediate relationship to the most of the studied factors in comparison with two related species, *T. crispa* and *T. integrifolia*.

Key words: *Tephrosieris longifolia* subsp. *moravica*; classification; phytosociological affiliation; diversity; Ellenberg indicator values

Abbreviations: CZ, Czech Republic; EIV, Ellenberg indicator values; ES, Electronic expert system for identification of syntax; SK, Slovakia; TLM, *Tephrosieris longifolia* subsp. *moravica*; TL, *Tephrosieris longifolia* s.l.; TI, *Tephrosieris integrifolia*; TC, *Tephrosieris crispa*

Introduction

Tephrosieris longifolia (Jacq.) Griseb. & Schenk is a suboreophyte of Central Europe (Meusel et al. 1992). The easternmost occurrence is restricted to Albania, the westernmost to France, the northernmost to Germany and the southernmost to Italy (Greuter 2006–2009). The majority of population sites are located in the Eastern Alps in Austria, Slovenia and Italy. It is less frequent in Switzerland, northern Croatia, western Hungary, Czech Republic and Slovakia (Meusel et al. 1992). Holub (1979) described the isolated populations from Bílé/Biele Karpaty Mts (Czech/Slovak border area) as an individual subspecies *T. longifolia* subsp. *moravica*. The morphological differences of TLM from the nominal subspecies and its ecological requirements were discussed by Holub (1979, 1982), Kochjarová (1995, 1997, 1998a), Janišová et al. (2005), Hegedúšová et al. (2009) and Janišová et al. (2012). The populations of the Western Carpathians seem to represent an isolated occur-

rence of an alpine migrant with an individual evolution (Holub 1999). Their occurrence is restricted to very specific and vulnerable habitats. Nowadays, four localities in the Czech Republic (Bílé Karpaty Mts) and five in Slovakia (Biele Karpaty Mts, Strážovské vrchy Mts, Trábeč Mts, Vtáčnik Mts, Table 1) are known and monitored (Kochjarová 1998b; Janišová et al. 2004; Chmelová 2007; Gbelcová 2006, 2010), while seven localities are considered to be extinct. It is listed as protected, endangered and rare taxon of the flora of Slovakia (EN) (Feráková et al. 2001) and an endemic taxon of the Western Carpathians (Kliment 1999) included in the European list of important species (NATURA 2000, Directive 92/43/EEC, Annex II). In the Czech Republic it belongs to the protected and critically endangered species (C1 = CR, Procházka 2001; C1-t, Grulich 2012).

The distribution area of *T. longifolia* subsp. *moravica* within the Western Carpathians overlaps with the distribution of two related species of the genus *Tephrosieris*, namely *T. integrifolia* and *T. crispa*.

Table 1. Characteristics of the studied localities of TLM in Czech Republic and Slovakia.

Country	Mts	Locality	Size in m ²	Microlocality	Current management
CZ	Bílé Karpaty	Hodňovská dolina	75,600	Javor Lásca	pasture disturbed site by cattle regularly mown meadow irregularly mown meadow irregularly mown meadow without management
		Hrušová dolina	1,200		
		Hluboče Tratihušť	25,800 100		
SK	Biele Karpaty	Lysá	12,000		longer abandoned but recently irregularly grazed
		Strážovské vrchy	Omšenie	11,000	Trštinárske lúky Hrebeň
		Čavoj	20,000	Pri cintoríne Záhumenie	mostly abandoned meadow, various stages of succession
	Tribeč	Radobica	15,000		mostly mown, partly without management
	Vtáčnik	Stráž	5,000		abandoned for decades and covered by large shrubs and trees

Tephroses integrifolia (L.) Holub belongs to the Eurasian species with occurrence in temperate zone of Europe and Asia. Its southernmost occurrence is in the central Italy; and in the north its distribution area reaches the Baltic States, Kola Peninsula and Novaya Zemlya (Greuter 2006–2009). It belongs to vulnerable species in Slovakia (VU, Feráková et al. 2001) and to the protected and endangered species in the Czech Republic (C2 = EN, Procházka 2001; C2-b, Grulich 2012). Its occurrence is rare and scattered in both countries. It is declared as the characteristic species of the *Festuco-Brometea* class (Mucina 1997), *Quercetea pubescenti-petraeae* class, *Cirsio-Brachypodium* and *Geranion sanguinei* alliances (Soó 1970; Mucina & Kolbek 1993). From the study area, phytosociological data from *Festucion valesiacae*, *Bromo pannonici-Festucion pallentis*, *Geranion sanguinei*, *Cirsio-Brachypodium pinnati*, *Cynosurion cristati* and *Arrhenatherion elatioris* alliances are known (cf. Kochjarová 1997).

Tephroses crispa (Jacq.) Rchb. has the center of its distribution primarily in the Central European mountains. The northern limit stretches to Germany, Poland and Byelorussia, the western one to Thüringer Wald (Germany), the eastern one to Ukraine and the southern one lies in the Austrian Alps, northern Italy, Slovenia and Bosnia-Herzegovina (Greuter 2006–2009). In Slovakia, the taxon is not protected. In the Czech Republic, the taxon is classified as nearly threatened (C4=NT, Procházka 2001; C4-a, Grulich 2012). This species is considered to be characteristic for the vegetation of the *Molinio-Arrhenatheretea* class (Mucina 1997), wetland vegetation of the *Adenostylin alliariae*, *Petasition officinalis*, *Calthion palustris*, *Caricion fuscae*, *Sphagno warnstorffiani-Tomenthypnion*, *Sphagno recurvi-Caricion canescentis* and *Alnion incanae* alliances (cf. Soó 1970; Rybníček et al. 1984).

We studied phytosociological affiliation of TLM in comparison with two related species TI and TC, focussing on the territory of the Western Carpathians

with the following main aims:

1) to determine plant communities inhabited by TLM, TI and TC; 2) to find the major environmental gradients responsible for variation in the distribution of target species; 3) to estimate average ecological indicator values for TLM.

Material and methods

Based on present occurrence, similar vertical distribution in the studied area, ecological requirements and with respect to the possibility of existence of hybrid populations between TLM and TC (locality Inovec), three from seven known species of the genus *Tephroses* (TLM, TI and TC) were selected for our study. We did not include the other related taxa of the genus *Tephroses* as they differ significantly in their habitat requirements and distribution. *Tephroses papposa* occurs in Slovakia only in the Bukovské vrchy Mts (Eastern Carpathians) and occurrence of *T. capitata* is restricted to the alpine belt of the Belianske and Západné Tatry Mts, predominantly above 1,500–2,200 m a.s.l. and is missing in the Czech part of the Carpathian Mts *Tephroses aurantiaca* inhabits various stands in montane and submontane regions of the Slovenský kras Mts, Veľká Fatra Mts and Muránska planina Mts (660–1,350 m a.s.l.) and is missing in the Czech part of the Carpathian Mts. The phytosociological data used in our study were gathered from the territory of the Western Carpathians including Slovakia (Central Phytosociological Database of Slovakia, code EU-SK-001, Šibík 2012, <http://www.ibot.sav.sk/cdf/index.html>) and Czech Republic (Czech National Phytosociological Database, EU-CZ-001, Chytrý & Michalcová 2012, <http://www.sci.muni.cz/botany/chytry/links.htm>). All phytosociological relevés were recorded according to the principles of the Zürich-Montpellier school (Braun-Blanquet 1928) and stored using the TURBOVEG database software (Hennekens 1996). Records of vascular plants including juvenile individuals of woody species are listed together in the resulting data set (314 relevés). The internal variation within the dataset was assessed by numerical classification using the relative Euclidean distance as a distance mea-

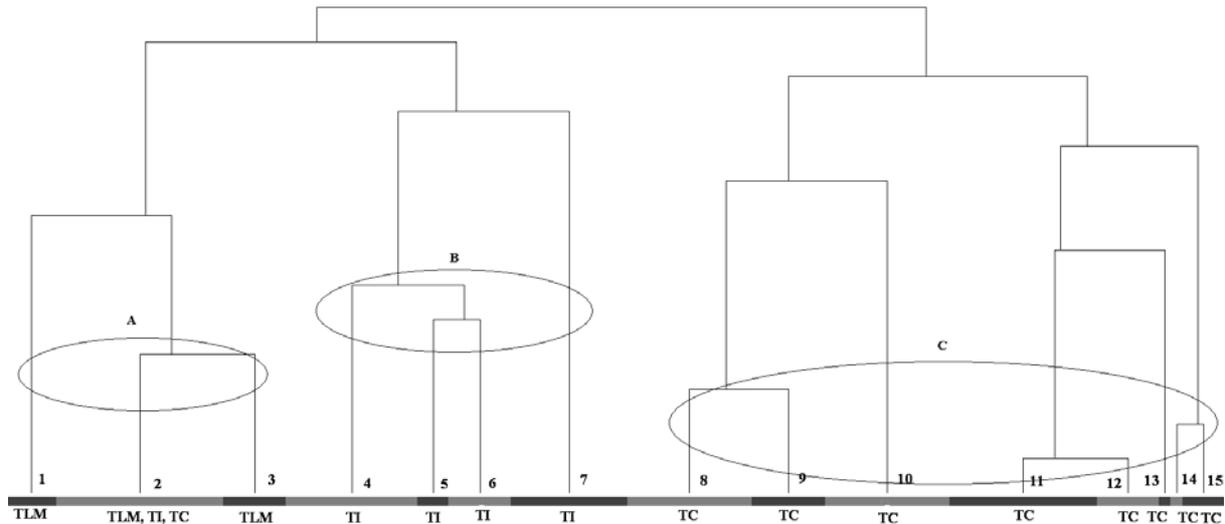


Fig. 1. Dendrogram of the numerical classification by Ward's group linkage method using relative Euclidean distance as a distance measure and logarithmic transformed species data. – The numbers indicate clusters; TLM: clusters 1–3, TI: clusters 2 and 4–7, TC: clusters 2 and 8–15.

sure and Ward's group linkage method on logarithmically transformed species data (PC-ORD 5.0 software package; McCune & Grace 2002). The optimal number of clusters was determined using the Crispness method (Botta-Dukát et al. 2005) contained in the program JUICE (Tichý 2002). Relevés of grassland communities in each cluster were classified according to the electronic expert system (ES) for identification of syntaxa (Janišová et al. 2007, http://ibot.sav.sk/ES_trav_veg-Sk.doc), while communities unknown for ES were classified according to the original classification of each author of relevés. Diagnostic, constant and dominant species for the clusters were calculated by JUICE (Tichý 2002). Diagnostic species were statistically determined on the base of fidelity concept (Bruehlheide 1997; Chytrý et al. 2002, 2006) using the phi coefficient $\Phi \geq 0.25$. Fisher's exact test ($P < 0.001$) was used to eliminate the species with a non-significant pattern of occurrence. Constant species were defined as the species present in more than 40% of relevés (in the text they are ordered according to their frequency). Dominant species are ordered according to the percentage of relevés in which their cover exceeds 25%.

Detrended correspondence analysis (DCA, logarithmic transformation $b = \log(X_{i,j} + 1)$; downweighting of rare species) from the CANOCO 4.5 for Windows package (ter Braak & Šmilauer 2002) was applied for the ecological interpretation of the main gradients in the data set.

Unweighted averages of EIV for light, temperature, continentality, moisture, soil reaction and nutrients (Ellenberg et al. 1991) calculated for individual relevés were plotted onto a DCA ordination diagram as supplementary environmental variables. Species not included in the Ellenberg's list (*Achillea millefolium* agg., *Allium flavum*, *Alchemilla* spec. div., *Cirsium pannonicum*, *Galium boreale* agg., *Hacquetia epipactis*, *Knautia kitaibelii* and *Taraxacum* sect. *Ruderalia*) and species lacking some indicator value were disregarded in the calculations. The EIV were used also for comparison of relevé groups containing each of the three studied taxa, differences between the groups were tested by one-way ANOVA and Tukey HSD test for unequal sample size N in the Statistica software (STATSOFT INC. 2006). Average EIV calculated from phytosociological relevés with

TLM occurrence were used to estimate the ecological requirements of TLM. The significance of differences in the average EIV among the relevé groups containing three studied taxa was tested.

The probability of occurrence of the studied taxa with respect to altitude, slope and environmental factors expressed by the EIV was calculated by logistic regression fitted by Generalized additive models (GAM, Hastie & Tibshirani 1990). To avoid a circular reasoning, EIV of the two compared species TI and TC were omitted during the calculation of unweighted averages. Binomial distribution and an identical model with three degrees of freedom were applied to all analyses. In order to test the statistical significance of the model, the fitted model was compared with the null model. All species showed significant responses to all studied factors. The calculation was performed in CANOCO for Windows (ter Braak & Šmilauer 2002).

The nomenclature of vascular plants follows Marhold & Hindák (1998). The nomenclature of syntaxa has been unified according to Janišová et al. (2007) and Jarolímek et al. (2008).

Results

Following the numerical classification (Fig. 1), fifteen floristically differentiated vegetation units were distinguished within the data set and assigned to the nine phytosociological classes: *Alnetea glutinosae*, *Carici rupestris-Kobresietea bellardii*, *Elyno-Seslerietea*, *Festuco-Brometea*, *Molinio-Arrhenatheretea*, *Montio-Cardaminetea*, *Mulgedio-Aconitetea*, *Querco-Fagetea*, *Scheuchzerio-Caricetea fuscae*. The distribution map (Fig. 2) shows the occurrence of TLM, TI and TC in the study area. Relationships of the TLM, TI and TC to environmental factors are shown in Fig. 3 and 4. The EIV calculated for TLM are shown in Table 2.

Numerical classification

The results of the numerical classification indicate that there is little overlap in coenological affinity of the stud-

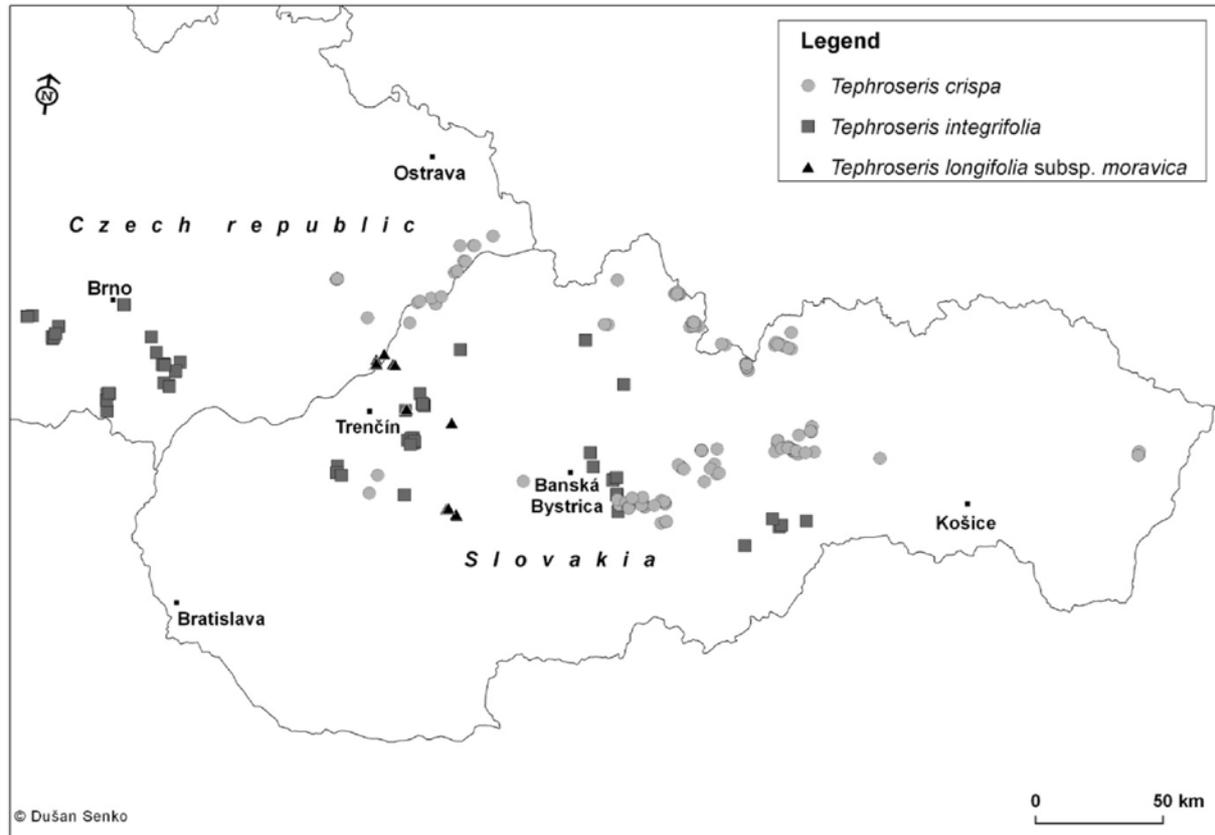


Fig. 2. Distribution of *Tephroseris longifolia* subsp. *moravica*, *T. integrifolia* and *T. crispa* in the Western Carpathians based on plot vegetation databases of Slovakia and the Czech Republic. © Dušan Senko

ied taxa (Fig. 1). The first division separated relevés with occurrence of TI (branch B) from the rest of relevés (branches A and C). Relevés containing TLM were separated in the second division. Altogether, TLM occurs in vegetation classified within three clusters (clusters 1, 2 and 3 within the branch).

Cluster 1 – Fringe vegetation with occurrence of TLM (13 relevés, CZ)

Diagnostic species: *Dentaria bulbifera*, *Sanguisorba officinalis*, *Quercus robur*, *Geranium pratense*, *Alliaria petiolata*, *Anthriscus sylvestris*, *Myosotis arvensis*, *Heracleum sphondylium*, *Aegopodium podagraria*, *Avenula preusta*, *Tephroseris longifolia* subsp. *moravica*, *Astrantia major*, *Polygonatum multiflorum*, *Taraxacum* sect. *Ruderalia*, *Vicia sepium*, *Primula elatior*.

Constant species: *Tephroseris longifolia* subsp. *moravica*, *Veronica chamaedrys* agg., *Symphytum tuberosum* agg., *Ranunculus acris*, *Primula elatior*, *Heracleum sphondylium*, *Cruciata glabra*, *Alchemilla* spec. div., *Vicia sepium*, *Taraxacum* sect. *Ruderalia*, *Dentaria bulbifera*, *Ajuga reptans*, *Sanguisorba officinalis*, *Hypericum maculatum*, *Dactylis glomerata*, *Astrantia major*, *Acetosa pratensis*.

Dominant species: *Poa trivialis*, *Festuca rubra* agg., *Fraxinus excelsior*, *Quercus robur*, *Avenula praeusta*.

These successional, species-rich grasslands of the *Arrhenatherion elatioris* alliance occur on the north-facing slopes at the edge of deciduous forests, mainly on

the locality Hodňov, Bílé Karpaty Mts. Species composition is a mixture of the meadows species (e.g. *Acetosa pratensis*, *Arrhenatherum elatius*, *Campanula patula*, *Dactylis glomerata*, *Festuca rubra* agg.), forest species (e.g. *Asarum europaeum*, *Athyrium filix-femina*, *Dentaria bulbifera*, *Mercurialis perennis*) and fringe herbs (e.g. *Fragaria moschata*, *Geranium sanguineum*, *Peucedanum cervaria*). The majority of stands are abandoned.

Cluster 2 – Heterogeneous grassland vegetation with occurrence of all studied *Tephroseris* taxa (relation to the submontane and montane *Arrhenatherion elatioris* communities, *Bromion erecti* and *Cirsio-Brachypodium pinnati* alliances, 43 relevés, 14 CZ, 29 SK)

Diagnostic species: *Agrimonia eupatoria*, *Campanula patula*, *Arrhenatherum elatius*, *Knautia arvensis*, *Allium schoenoprasum*, *Carpinus betulus*, *Quercus petraea*, *Linaria vulgaris*, *Hypericum hirsutum*, *Galium odoratum*, *Tephroseris longifolia* subsp. *moravica*, *Poa pratensis* agg., *Colchicum autumnale*, *Verbascum lychnitis*.

Constant species: *Arrhenatherum elatius*, *Achillea millefolium* agg., *Veronica chamaedrys* agg., *Ranunculus acris*, *Tephroseris longifolia* subsp. *moravica*, *Primula veris*, *Campanula patula*, *Dactylis glomerata*, *Acetosa pratensis*, *Lathyrus pratensis*, *Vicia cracca*, *Poa pratensis* agg., *Cruciata glabra*, *Alchemilla* spec. div., *Hypericum maculatum*, *Symphytum tuberosum* agg., *Ajuga reptans*, *Ranunculus auri-*

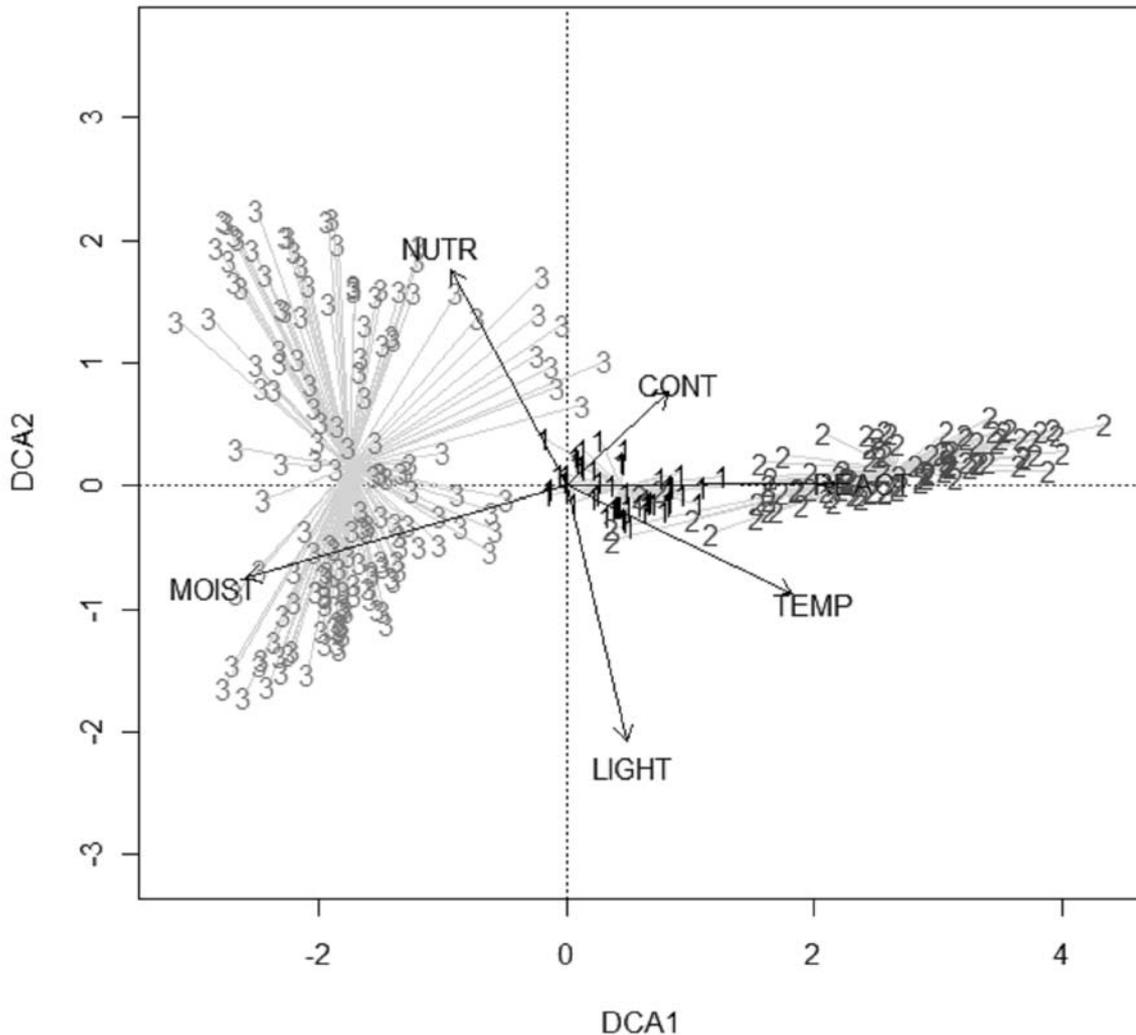


Fig. 3. DCA ordination diagram with Ellenberg indicator values plotted as supplementary variables. Each spider connects individual relevés with the average score for relevés belonging to the same group. The first and the second axes are shown (logarithmic transformation; downweighting of rare species; the first two eigenvalues are 0.7843 and 0.4126). Groups: 1 – *T. longifolia* subsp. *moravica*, 2 – *T. integrifolia*, 3 – *Tephrosieris crispa*.

comus agg., *Potentilla erecta*, *Luzula luzuloides*, *Colchicum autumnale*, *Asarum europaeum*.

Dominant species: *Arrhenatherum elatius*, *Brachypodium pinnatum*, *Agrostis capillaris*, *Bromus erectus*, *Trisetum flavescens*, *Tephrosieris longifolia* subsp. *moravica*.

This is the only cluster including vegetation with occurrence of all three studied taxa. The cluster includes mesic meadows dominated by *Agrostis capillaris*, *Arrhenatherum elatius*, *Trisetum flavescens*, *Bromus erectus* and their successional stages. In abandoned stands, expansive grasses (*Calamagrostis epigeios*, *Brachypodium pinnatum* and *Bromus erectus*) spread into the grasslands. This type of vegetation inhabits moderately humid soils, preferably north- and north-west-facing slopes at the altitudes ranging from 500 to 1,000 m, with typical occurrence of mesophilous species.

Cluster 3 – *Brachypodium pinnati*-*Molinietum arundinaceae* association with occurrence of TLM (16 relevés, 6 CZ, 10 SK)

Diagnostic species: *Plantago lanceolata*, *Trisetum flavescens*, *Vicia cracca*, *Jacea pratensis*, *Thymus pulegioides*, *Carex montana*, *Potentilla alba*, *Tephrosieris longifolia* subsp. *moravica*, *Tragopogon orientalis*, *Valeriana stolonifera* subsp. *angustifolia*, *Cirsium pannonicum*, *Campanula glomerata*, *Trommsdorffia maculata*, *Lotus corniculatus* agg., *Phyteuma spicatum*.

Constant species: *Tephrosieris longifolia* subsp. *moravica*, *Vicia cracca*, *Lotus corniculatus* agg., *Dactylis glomerata*, *Achillea millefolium* agg., *Acetosa pratensis*, *Ranunculus acris*, *Potentilla erecta*, *Cruciata glabra*, *Ajuga reptans*, *Veronica chamaedrys* agg., *Primula veris*, *Leucanthemum vulgare* agg., *Lathyrus pratensis*, *Arrhenatherum elatius*, *Trisetum flavescens*, *Plantago lanceolata*, *Hypericum maculatum*, *Heracleum sphondylium*, *Briza media*, *Anthoxanthum odoratum* agg.

Dominant species: *Arrhenatherum elatius*, *Rhytidiadelphus triquetrus* (E₀), *Laserpitium latifolium*, *Rhytidiadelphus squarrosus* (E₀).

These species-rich semi-dry grasslands inhabit relatively deeper soils on calcareous bedrock. The characteristic feature of this vegetation type is the occur-

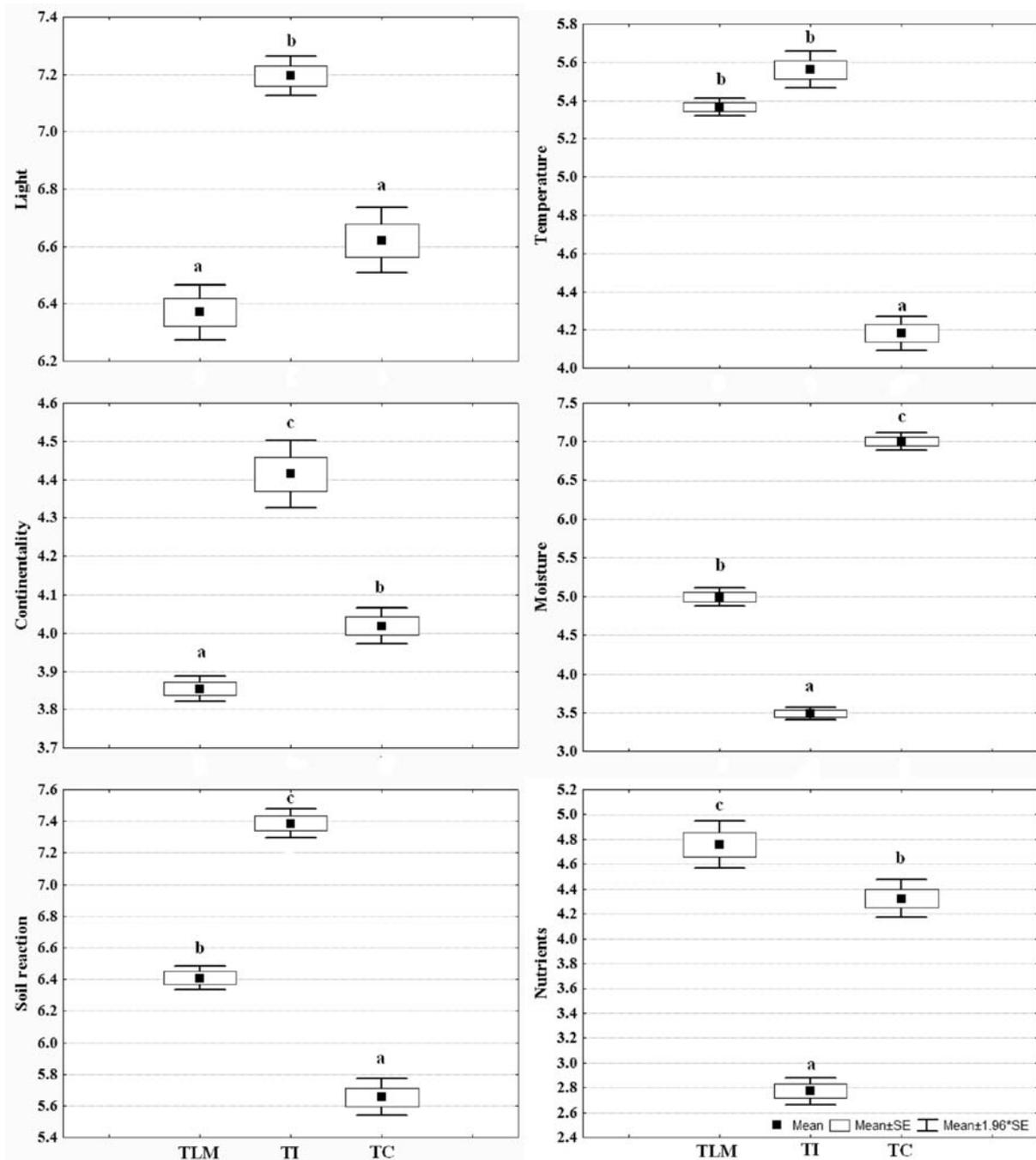


Fig. 4. Relationship of the studied species to the environmental factors estimated according to the Ellenberg indicator values. Boxes and whiskers include 25–75% and 0–100% of the observed values, respectively, and squares inside the boxes are medians. TLM – *Tephrosia longifolia* subsp. *moravica*, TI – *T. integrifolia*, TC – *Tephrosia crispa*.

rence of mesophilous species of the *Molinion caeruleae* alliance (*Betonica officinalis* and *Serratula tinctoria*) in combination with thermophilous species of the *Festuco-Brometea* class (*Dianthus carthusianorum* and *Helianthemum nummularium* agg.). The cluster includes localities of TLM with the largest TLM populations (Lysá, Čavoj, Radobica and Javor).

Relevés containing TI were well separated in dendrogram within the branch B including clusters 4–7 (Fig. 1). TI occurs predominantly in the communities of the *Bromion erecti*, *Cirsio-Brachypodium pinnati*, *Diantho lumnitzeri-Seslerion*, *Festucion valesia-*

cae, *Quercion pubescenti-pretraeae*, alliances. Relevés containing TC were most diverse, clearly separated in the first division in branch C containing clusters 8–15 (Fig. 1). The occurrence of TC is typical in the communities of the *Caricion davallianae*, *Caricion fuscae*, *Calthion palustris* and *Sphagno warnstorffiani-Tomenthypnion* alliances. In the montane, supramontane or rarely subalpine tall-herb broad-leaved natural riparian communities and forest shady spring areas (fragments of alliances *Caricion remotae*, *Petasition officinalis* and *Alnion incanae*) it occurs with less frequency.

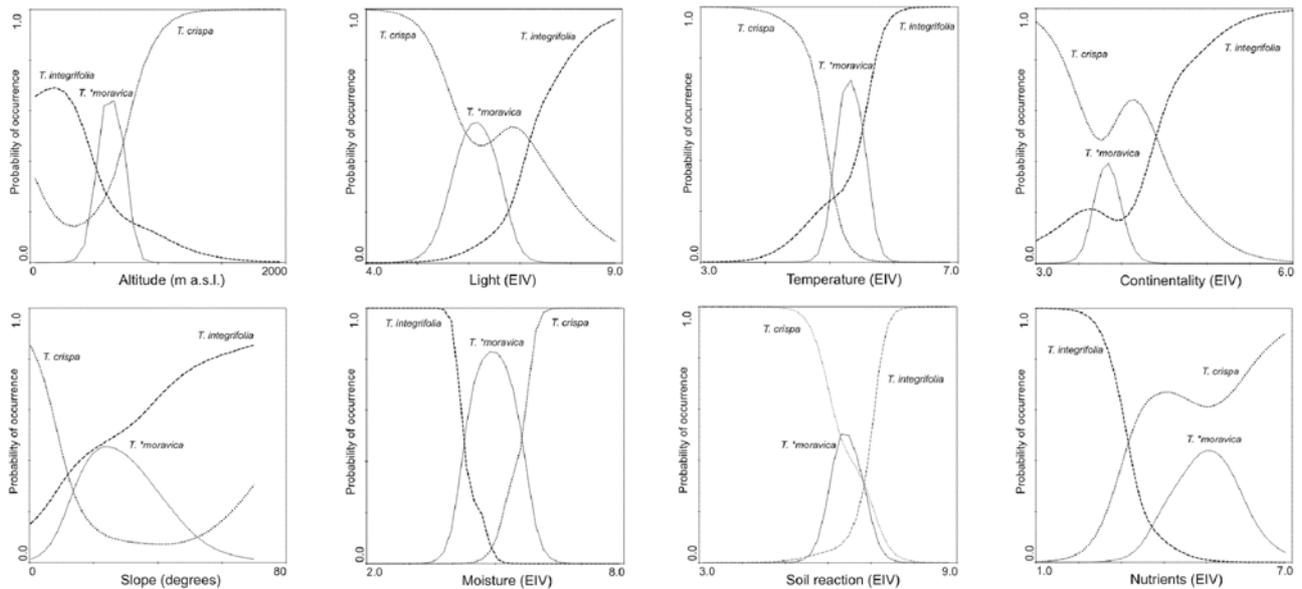


Fig. 5. Species response curves with respect to altitude, slope and six environmental factors expressed by the EIV. Logistic regression fitted by GAM (3 d.f.) were used on the presence/absence data.

Table 2. Ellenberg indicator values for *Tephrosieris longifolia* subsp. *moravica* based on indicator values of vascular plants in relevés containing TLM.

	Mean	Median	Min	Max	Mode	Variance	SD	EIV set for TLM (Janišová et al. 2012) circular plots 0.5m ²	EIV set for TLM relevés 16–20m ²
Light	6.4	6.4	5.5	7.1	5.9	0.1	0.4	6	6
Temperature	5.4	5.4	4.9	5.7	5.5	0.0	0.2	5	5
Continentality	3.9	3.8	3.6	4.2	3.7	0.0	0.1	4	4
Moisture	5.0	5.0	4.2	5.7	5.0	0.2	0.4	5	5
Soil reaction	6.4	6.4	5.8	7.2	6.2	0.1	0.3	7	6
Nutrients	4.8	4.9	3.6	5.9	5.3	0.5	0.7	5	5

Main environmental gradients responsible for the variation in floristic composition of the studied vegetation
Relationship of all species to the individual environmental gradients is shown in Fig. 3 (the eigenvalues of the first and second axes are 0.7843 and 0.4126, respectively). The main environmental gradient was strongly positively correlated with soil reaction and negatively correlated with moisture. The second axis is positively correlated with nutrients and negatively with light. The most basiphilous and dry soils are occupied by communities with *Tephrosieris integrifolia*, while communities with *T. crispa* occur mostly on the wet and slightly acidic soils. Stands with the occurrence of *T. longifolia* subsp. *moravica* show intermediate position between the two other species. The existing co-occurrence of TLM and TI in the same habitats (e.g. the locality Omšenie) is reflected also in the results of cluster analysis. Although in term of evaluation of the ecological factor moisture TI occupies habitats with very variable moisture condition, its occurrence is restricted in the ordination space along the second axis which represents the nutrient status and light conditions of habitats. Similar is the situation of TLM. Relationship of the studied species to individual environmental factors

is shown in Fig. 4 and 5. Significant differences between the studied species were indicated in all calculated variables (ANOVA, Tukey HSD test, $P < 0.05$). TLM obviously prefers habitats with the highest nutrient content in comparison to the two remaining species and the lowest light requirements with the occurrence on north-facing slopes; TC prefers the moistest stands with least thermophilous species and TI has optimum of the occurrence in the driest types of stands with the highest light and the lowest nutrient requirements. Species response curves (Fig. 4) indicate the intermediate position of TLM in most of the studied factors, namely altitude, slope, temperature (EIV), moisture (EIV), light (EIV) and soil reaction (EIV) and partly also continentality (EIV).

Ecological indicator values of TLM

The ecological indicator values for *Tephrosieris longifolia* subsp. *moravica* (Table 2) calculated from phytosociological relevés with occurrence of TLM are: light – 6 (semi-shade to partial-shade plant occurring also in well lit places), temperature – 5 (semi-thermophilous plant, often interfere to the sub-montane temperature sites), continentality – 4 (plant occurring mainly in most parts

Table 3. Comparison of ecological indicator values set for TLM, TI and TC based on our analyses with the Ellenberg ecological indicator values (Ellenberg et al. 1991).

	Ecological indicator values set by our analyses			Ecological indicator values based on Ellenberg et al. 1991	
	TLM	TI	TC	TI	TC
light	6	7	7	7	6
temperature	5	6	4	6	4
continentality	4	4	4	7	4
moisture	5	3	7	4	8
soil hreaction	6	7	6	8	6
nutrients	5	3	4	?	5

of Central Europe with sub-oceanic climate), moisture – 5 (moist-site indicator occurring mainly on fresh soils of average dampness), soil reaction – 6 (plant of moderately acid soils or weakly acid to weakly basic conditions; never found on very acid soils), nutrients – 5 (indicator of sites of intermediate fertility).

Discussion

Phytosociological affiliation of TLM in comparison with TI and TC

Our study confirmed that the plant communities inhabited by the studied taxa are quite different. TLM occurs mainly in vegetation classified within the alliances *Bromion erecti* and *Arrhenatherion elatioris*. Some populations grow in the ecotone vegetation between meadows and beech forests/shrubs, which is difficult to classify (cluster 1). The very specific site conditions of taxon occurrence in this case, suggest that TLM is taxon with narrow habitat requirements, which is obvious also from the ordination diagram (Fig. 3). In spite of narrow range of TLM recent distribution, it hardly can be considered as strictly stenotopic. Based on our measurements (Janišová et al. 2012), 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. The statement of Kochjarová (1998b) that, TLM occurs also in the *Polygono-Trisetion* and *Cirsio-Brachypodium pinnati* alliances was not confirmed by our study. With respect to ecological conditions, we can assume the possible occurrence of TLM in the *Trifolion medii* alliance.

In comparison with TLM, the phytosociological affiliation of *T. integrifolia* is rather broad. It was recorded in communities of the *Arrhenatherion elatioris*, *Cirsio-Brachypodium pinnati*, *Bromion erecti*, *Diantho lumnitzeri-Seslerion*, *Festucion valesiacae*, *Quercion pubescenti-pretraeae* alliances (clusters 2, 4–7). We are assumed that both studied taxa TLM and TI have specific soil nutrient requirements (Table 3). According to Kochjarová (1995) TI prefers localities on the alkaline soils, which is obvious also in our analysis (Fig. 3, Table 3). Some of these differences may be explained by different geological bedrock and management (Myklestad 2004). *T. crispata* occurs mainly in communities of the *Calthion palustris*, but occasionally

it grows in wetlands of the *Alnion incanae*, *Caricion remotae*, *Caricion davallianae*, *Caricion fuscae* and *Petasition officinalis* alliances and alpine and subalpine communities of the *Carici rupestris-Kobresietea belardii* and *Elyno-Seslerietea* classes (clusters 8–15).

There is an obvious overlap in coenological affinities of TLM and TI. The common occurrence of both taxa is possible in the communities of the *Bromion erecti* alliance, which was observed on the locality Omšenie. Although TC usually occur in well water-saturated or constantly moist or damp soils it was recorded also on occasionally moist or drying places (cluster 2, 6 relevés). We suppose that it is conditioned by a succession as well as the response to abandonment and ruderalization of the man-influenced localities (vicinity of the railway station – Horehronské podolie, non-grazed and abandoned meadows – Slovenský raj, Poľana, Pohronský Inovec and Veporské vrchy) or partially affected by overgrowth by competitively stronger grassland species (e.g., *Lolium perenne* or *Taraxacum* sect. Ruderalia). TLM has the narrowest ecological niche and it is not a characteristic or diagnostic species of any one of the vegetation units presented here.

In localities with common occurrence of the studied taxa (TLM and TI in Omšenie, TLM and TC in Pohronský Inovec Mts, Kochjarová in verb.) there is a probability of occurrence of hybrid populations. All three studied taxa are polyploids with the same chromosome number, $2n = 48$ (Kochjarová 1997, 1998b, 2005, 2006). Despite the fact that no records of hybrids between *Tephroseris* taxa in the distribution area of the studied species have been found in the relevant literature, the existence of hybrids cannot be ruled out definitely.

The most important environmental factors

Many studies have shown that abiotic environmental factors can be important sources of variation of plant diversity (Bennie et al. 2006; Marini Lorenzo et al. 2007; Fattahi & Ildoromi 2011). However, the impact of environmental factors may vary spatially, and environmental and community factors may interact in such a way that the outcome of species interaction is moderated by spatial environmental heterogeneity (Law et al. 1993, Bullock 1996). Soil nutrients and soil pH have been shown to be an important factor for plant diversity and variability of vegetation (Moles et al. 2003; Zechmeister

et al. 2003). Results of indirect gradient analysis with EIV as supplementary environmental data EIV, showed that the occurrence of three studied species TLM, TI and TC is differentiated along the main environmental gradient interpreted by interplay of four main environmental factors – soil reaction, moisture, nutrients and light. The soil reaction and moisture play the crucial role among them (Fig. 3). As follows from the results the transition between the communities with TLM and TI occurrence is more or less continuous (they overlap to some extent at the ordination plot). In some cases, it suggests similar condition for occurrence of both taxa conditioned by similar ecological requirements. On the other hand there is a clear isolation between vegetation with occurrence of TC from vegetation containing other two species which suggest sharp boundaries in an occurrence of the communities on the wet and slightly acidic soils. Our results correspond with information on ecology of the studied species involved in other studies and European floras. In Europe TI grows mostly in dry grasslands or open oak forests on calcareous or basic bedrock (Hegi 1929; Tutin 1976; Smith 1979; Widén 1987; Isaksson 2009). TC occurs predominantly on wet peaty meadows, forest wetlands, banks of brooks, alluvial plains on acid soils (Hegi 1929; Tutin 1976; Slavík et Štěpánková 2004). TLM inhabits ecotone habitats, forest edges, bushy hillsides, light forest clearings or sometime on mesophilous meadows on deeper neutral or lightly acid soils (Slavík et Štěpánková 2004; Janišová et al. 2012). The light conditions are dependent on the geographic location and also different altitudes but mainly by the vegetation in the surrounding. The solar irradiation limits directly species distribution and abundance by extreme drought and high temperatures during the summer period (Janišová 2005). Climatic differences between TLM, TI and TC are shown partially by continentality (Fig. 4). According to Janišová (2005) the environmental factors are either topographically dependent or directly topographical. The resulting ordination diagram expresses not only relationships between the relevés with occurrence of TLM, TI and TC and each of the environmental variables but also demonstrates patterns of variation in the floristic composition.

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. The Ellenberg numbers (Ellenberg et al. 1991), as widely used indicator values in Central Europe, were applied in our study to express the habitat conditions. According to Diekmann (1995), Ewald (2009) and Janišová et al. (2012), estimation of ecological indicator values based on only bryophytes showed less close relationships to the measured variables than vascular plant-based EIV. Following this study, we decided to use the estimation of vascular plant-based EIV calculated from average EIV of co-occurring vascular plant species. The average EIV used to set ecological indicator values for

TLM provide important information on average habitat conditions of species occurrence (Janišová et al. 2012). Despite of it, the average EIV hardly indicate the full range of conditions where the taxon is able to survive and its tolerance to individual environmental factors. Janišová et al. (2012) calculated EIV for the studied taxon based on small circular plots with area of 0.5 m² (average number of species per plot was 23, Table 2) and the results were compared with several measured environmental factors. The ecological indicator values were set as follows: light 6, temperature 5, continentality 4, moisture 5, soil reaction 7 and nutrients 5. Our calculation of ecological indicator values for TLM was based on phytosociological relevés with plot size 16 and 25 m². Although our results were calculated from bigger plots (16–25 m², average number of species per plot was 48) covering the whole area of TLM occurrence (CZ, SK), the results were very similar to those indicated by Janišová et al. (2012; Table 2). It is questionable, which result fits better to real TLM ecological requirements. Our results pointed out that the differences are caused by different species composition in the both studied cases and different size of relevés plot, which is reflected in variability of vegetation and ecological conditions. The differences were found also between EIV of TI and TC set by our analyses and its EIV based on Ellenberg et al. (1991; Table 3).

Based on the EIV, TLM (654565) has most similar ecological requirements to the following species: *Galium sylvaticum* (554565, slightly less heliophilous), *Crataegus laevigata* (664575, slightly more thermo- and basiphilous), *Dactylis polygama* (564565, slightly less helophilous and more thermophilous), *Fragaria moschata* (664566, slightly more thermo- and nitrophilous), *Pulmonaria mollis* (554585, slightly less helophilous and more basiphilous), *Cerasus avium* (454575, less helophilous and slightly more basiphilous), *Stellaria holostea* (563565, slightly less helophilous and slightly more thermophilous with slightly more oceanic distribution). However, the list of co-occurring species includes also a lot of shade-tolerant plants (EIV for light – 2-3, e.g. *Carex sylvatica*, *Galium odoratum*, *Neotia nidus-avis*, *Acer campestre*, *Asarum europaeum*, *Athyrium filix-femina*, *Brachypodium sylvaticum*, *Dentaria bulbifera*, *Fagus sylvatica*, *Mercurialis perennis*), light-loving plants and plants in full light (EIV for light – 8-9, e.g. *Carduus acanthoides*, *Carlina acaulis*, *Festuca rupicola*, *Scabiosa lucida*, *Bromus erectus*, *Crepis mollis*, *Dianthus carthusianorum*, *Jacea phrygia*). Regarding the nutrient supply, as well as plants of nutrient-poor sites (EIV for nutrients – 1-2, e.g. *Genista pilosa*, *Potentilla collina*, *Sedum sexangulare*, *Briza media*, *Carex caryophylla*, *Filipendula vulgaris*, *Galium molugo*, *Nardus stricta*, *Viola canina*) and nutrient-rich sites (*Alliaria petiolata*, *Rumex obtusifolius*, *Sambucus nigra*, *Aegopodium podagraria*, *Anthriscus sylvestris*, *Galium aparine*, *Chaerophyllum aromaticum*, *Lunaria rediviva*, *Senecio nemorensis*, *Stellaria media*). We can assume higher ecological tolerance of TLM. With respect to the ecological conditions together with co-

occurring species our results pointed out that TLM has intermediate character for all factors accounted. Finally, this study revealed that the following indicator values can be used for assessment of the ecological preferences of *Tephroses longifolia* subsp. *moravica*: light 6, temperature 5, continentality 4, moisture 5, soil reaction 6 and nutrients 5.

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