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## Assessment of the Ecological and Habitat Preferences of the Species *Sesleria caerulea* and *S. tatrae* (*Poaceae*) in the Western Carpathians

By

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With 5 Figures

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### Summary

MAJEROVÁ BUDZÁKOVÁ M., GALVÁNEK D., MÁJEKOVÁ J. & ŠIBÍK J. 2016. Assessment of the ecological and habitat preferences of the species *Sesleria caerulea* and *S. tatrae* (*Poaceae*) in the Western Carpathians. – *Phyton* (Horn, Austria) 56(2): 161–180, with 5 figures.

The main objective of this study was to investigate the ecological preferences of the species *Sesleria caerulea* (L.) ARD. and *S. tatrae* (DEGEN) DEYL in the Western Carpathians. To achieve that we used two different data sets: the first data set of 1029 relevés was selected from the Slovak vegetation database, the second data set of 201 relevés was collected along 11 transects by the authors of this study (with confirmation of ploidy level of each *Sesleria* species in the relevés). Almost all of our results correspond with the current knowledge obtained with traditional observation methods. Therefore we support a general idea to use phytosociological data as a predictors of plant species occurrence in a certain environment that can be used e.g. for modeling although the critical evaluation of used data must be considered to avoid circular argumentation. At the same time we also emphasize to be critical

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when analyzing data applying general information retrieved from observations only. After the many of done researches where the results have been assumed, we finally did the very detailed analysis which replace assumptions. Our results show, that altitude is one of the most important factors determining the occurrence of the studied *Sesleria* species. *S. tatrae* is restricted to a narrow range at higher altitudes, while *S. caerulea* is found preferentially at lower altitudes, its wide range of altitudinal distribution is typical. Substrate characteristics are also an important driver for the occurrence of the two species. In the Western Carpathians, both species occurred mostly on basiphilous substrates. Our study revealed also an affinity of *S. caerulea* to higher pH values in comparison with *S. tatrae*, which seem to have a wider ecological niche with regard to soil reaction as previously supposed. *S. caerulea* dominates on steep slopes with shallow soils and lower availability of nutrients. *S. tatrae* requires a higher level of nutrients and areas with deeper soils and moderate slopes. *S. caerulea* is better adapted to drought, whereas *S. tatrae* dominates in localities with a higher amount of soil moisture.

#### Zusammenfassung

MAJEROVÁ BUDŽÁKOVÁ M., GALVÁNEK D., MÁJEKOVÁ J. & ŠIBÍK J. 2016. Assessment of the ecological and habitat preferences of the species *Sesleria caerulea* and *S. tatrae* (*Poaceae*) in the Western Carpathians. [Bewertung der ökologischen Ansprüche und der Habitatbindung von *Sesleria caerulea* und *S. tatrae* (*Poaceae*) in den West-Karpaten]. – *Phyton* (Horn, Austria) 56(2): 161–180, mit 5 Abbildungen.

Das Ziel der vorliegenden Untersuchungen war, die ökologischen Ansprüche der beiden Arten *Sesleria caerulea* (L.) ARD. und *S. tatrae* (DEGEN) DEYL in den West-Karpaten zu charakterisieren. Um dies zu erreichen wurden zwei unterschiedliche Datensätze genutzt: der erste Datensatz mit 1029 Vegetationsaufnahmen, ein Auszug aus der Slowakischen Vegetationsdatenbank und der zweite mit 201 Aufnahmen, die im Zuge dieser Untersuchungen entlang von 11 Transekten angefertigt wurden. Dabei ist für jede *Sesleria*-Population in jeder Aufnahme die Ploidiestufe festgestellt worden. Fast alle unsere Ergebnisse stimmen mit den bisher bekannten Fakten überein. Wir unterstützen daher die These, phytosoziologische Daten als Hilfsmittel für die Vorhersage des Vorkommens von Pflanzenarten in einem bestimmten Habitat zu nutzen, z. B. für Modellierungen. Allerdings müssen die benutzten Daten einer kritischen Bewertung unterzogen werden, um Zirkelschlüsse zu vermeiden. Wir möchten aber betonen, bei der Analyse von Daten, die nur aus allgemeinen Informationen allein aus Beobachtungen stammen, kritisch zu sein. Nach vielen Untersuchungen, die auf Vermutungen beruhen, basieren unsere Ergebnisse auf detaillierten Analysen der gesammelten Daten. Unsere Studien haben ergeben, dass die Seehöhe einer der wichtigsten Faktoren ist, der das Vorkommen der beiden *Sesleria*-Arten beeinflusst. *S. tatrae* ist auf einen schmalen Gürtel in höheren Lagen beschränkt, während *S. caerulea* tiefere Lagen bevorzugt, sie ist allerdings durch eine weite Höhenamplitude gekennzeichnet. Auch die Substratbeschaffenheit ist ein wichtiger Faktor, der das Vorkommen der beiden Arten beeinflusst. In den West-Karpaten kommen beide Arten meist über basiphilen Substraten vor. Unsere Untersuchungen zeigen auch eine Präferenz von *S. caerulea* zu höheren pH-Werten im Vergleich mit *S. tatrae*, die eine weitere Amplitude in Bezug auf die Bodenreaktion aufweist als früher angenommen. Gegenüber dem Nährstoffangebot

verhalten sich die beiden Arten unterschiedlich. *S. caerulea* dominiert steile Hanglagen mit flachgründigen Böden und einem geringen Nährstoffangebot. *S. tatrae* benötigt höhere Nährstoffgehalte, tiefgründigere Böden und mäßig geneigte Hänge und dominiert an Standorten mit besserer Wasserversorgung. *S. caerulea* ist gegenüber Trockenheit weniger empfindlich.

## 1. Introduction

The genus *Sesleria* (*Poaceae-Pooideae-Seslerieae*) is comprised of up to 48 species and subspecies which are distributed mainly over Europe (north-westwards to Iceland), marginally in northern Africa and western Asia (eastwards to the Caucasian region; DEYL 1946, 1980, LAZAREVIĆ & al. 2015). It is hypothesised that the genus originated from a region of the Alps, although nowadays the main center of taxonomical and morphological variability is considered to be the Balkan Peninsula (DEYL 1946, STRGAR 1981). Two ploidy levels are known as the most common in the genus:  $2n = 28$ , referred to as a tetraploid taxon, and  $2n = 56$ , referred to as an octoploid taxon. However, other ploidy levels such diploid ( $2n = 14$ ), hexaploid ( $2n = 42$ ) and dodecaploid ( $2n = 84$ ) have also been observed (DEYL 1980, STRGAR 1981, DI PIETRO & al. 2005, LAZAREVIĆ & al. 2015). The genus is taxonomically highly complex and ambiguous, and includes many not clearly distinguishable taxa (DEYL 1946, DI PIETRO 2007, LYSÁK & al. 1997). Hybridisation and introgression between some taxa is assumed. The genus is also known for its strong morphological and phenotypic plasticity as well as a strong similarity in morphological traits, which can lead to misclassifications of the species.

In the Western Carpathians this issue relates mainly to two similar taxa, *Sesleria caerulea* (L.) ARD. [syn. *S. albicans* KIT. ex SCHULT., *S. calcarea* (PERS.) OPIZ, *S. varia* (JACQ.) WETTST.] and *S. tatrae* (DEGEN) DEYL. Both belong to *S. sect. Sesleria* (syn. *S. sect. Calcariae* DEYL) and are very similar in morphology. *S. caerulea* is a tetraploid taxon ( $2n = 4x = 28$ ) with several octoploid individuals, reported in the south-eastern Alps (LAZAREVIĆ & al. 2015) from the submontane (foothills) up to the alpine belt. The species is quite common in north-western and central Europe. It is distributed throughout the Western Carpathians, Pyrenees, Alps and their foothills, northwards to northern Germany, southwards to the northern Apennines and on isolated sites in Spain (Sierra Nevada), Romania, and Poland (DIXON 1982). The species also occurs in the United Kingdom, Ireland and Iceland. *S. tatrae* (an octoploid taxon;  $2n = 8x = 56$ ) is sub-endemic and restricted to montane and alpine elevations, and occurs only in the mountains of the Slovak and Polish Carpathians with the exception of one isolated locality in the Sudetes (Kleśnica valley in the Śnieżnik Kłodzki Mts; FABISZEWSKI 1970). According to the current research, based primarily on field observations, *S. caerulea* and *S. tatrae* colonise habitats with relatively different ecological conditions. *S. caerulea* occurs in highly varied habitats, preferring steeper wind-swept limestone

walls with shallower soil. *S. tatrae* dominates the moderate and more humid limestone slopes with deeper soils, and is not restricted to sites with alkaline conditions (DEYL 1936).

Both species can be found in the same area only in the montane, subalpine and alpine elevations of the Western Carpathian region, especially in the Vysoké Tatry Mts (Belianske Tatry Mts and Západné Tatry Mts), Nízke Tatry Mts, Veľká Fatra Mts and Malá Fatra Mts. It has been reported by some authors (BĚLOHLÁVKOVÁ 1980, DEYL 1938, 1946, KLIMENT & al. 2008) that a high level of morphological variation within the two species was observed in these contact zones. Despite this fact, recent studies have not revealed any intermediary individuals between *Sesleria caerulea* and *S. tatrae* (BUDZÁKOVÁ & al. 2014). Some authors hypothesize the presence of hybridisation and introgression between these two species (DEYL 1938, 1946), which could consequently lead to the above-mentioned existence of morphologically and cytologically aberrant individuals. In course of field determinations of these specimens, the habitat characteristics are therefore sometimes taken into account. This circular reasoning may frequently cause misunderstandings, especially in phytosociology, when the differences in ecology and fidelity to habitats of the two *Sesleria* species can be skewed or mistaken. There is currently still a lack of empirical ecological research, including the precise identification of each taxon by determination of the ploidy level.

The main goal of this study was to examine the ecological preferences of the two *Sesleria* species in the subalpine zone of the Western Carpathians and to compare them with data documented in literature.

## 2. Material and Methods

### 2.1. Data Material

#### 2.1.1. Vegetation Data

Two groups of relevés with the occurrence of *Sesleria caerulea* and *S. tatrae* were subjected to statistical analyses. The first contained 1029 relevés selected from the Slovak vegetation database and the second contained 201 relevés (including determination of the ploidy level of each *Sesleria* population) collected along 11 vertical and horizontal transects in the Belianske Tatry Mts, Malá Fatra Mts and Veľká Fatra Mts (Fig. 1).

#### 2.1.2. Database Data

Relevés were extracted from the Slovak vegetation database (ŠIBÍKOVÁ & al. 2009, ŠIBÍK 2012), in November 2013. From the whole database (which currently contains around 35 000 relevés from Slovakia and the border zones to Poland, Hungary and the Czech Republic) only relevés ranging from montane up to the alpine vegetation belt were selected. That is, from 900 m above sea level upwards, where both species may occur simultaneously. We subsequently excluded relevés not belonging to the syntaxa with common occurrence of *Sesleria caerulea* and *S. tatrae*.

Syntaxa with a common occurrence of *Sesleria caerulea* and *S. tatrae* were considered to be all classes and alliances in which at least one of these species was regarded as diagnostic, constant or dominant, in accordance with JAROLÍMEK & ŠIBÍK 2008. Before geographical stratification relevés with incomplete information regarding GPS coordinates, aspect, slope and cover of the herb layer were excluded from the data set. No more than fifteen relevés were selected per grid cell ( $1.5 \times 1.4 \text{ km} = 1.25$  minutes of longitude and 0.75 minutes of latitude). This data set also contains relevés that meet all above-mentioned criteria, but without the study species. Consequently, the set of 1029 relevés (see Fig. 1B) was prepared for further statistical analyses.

### 2.1.3. Transect Data

During the seasons of 2010–2013, phytosociological relevés with an area  $1 \times 1 \text{ m}$  were collected along the vertical and horizontal transects (11 in total). The smaller area was chosen to record more homogenous environmental conditions in comparison with traditional  $4 \times 4 \text{ m}$  plots (cf. CHYTRÝ & OTÝPKOVÁ 2003). The smaller relevé area has been chosen because of the small scale patchiness of the mountain vegetation, that results in specific spatial dynamics on strongly structured sites. The small-scale multitude of microclimates and stresses together with the edaphic pattern created by relief explain the high biological diversity in the alpine zone (KÖRNER 2003). On the basis of specific environmental conditions and in an effort to focus on preferences of selected *Sesleria* species to their environment, we decided to record relevés from very homogenous plots with almost the same size. Relevés were taken from each transect in 5 m distance. Sampling of relevés followed the standard procedures of the Zürich-Montpellier School (BRAUN-BLANQUET 1964) using the modified 9-degree abundance and dominance scale proposed by BARKMAN & al. 1964. Overall, 201 relevés were collected during this research; 137 relevés with the occurrence of *S. tatrae*, 67 relevés with the occurrence of *S. caerulea* and 3 relevés with the occurrence of both species. The study area chosen encompasses the montane and subalpine vegetation belt in the Western Carpathians, which is the only area where these species are sympatric. Three transects were selected in the Belianske Tatry Mts (81 relevés), four transects in the Veľká Fatra Mts (60 relevés) and four transects in the Malá Fatra Mts (60 relevés) (see Fig. 1C). Fresh leaves (at least two samples per plot) were sampled from each relevé and dried in silica gel for flow cytometry analyses.

## 2.2. Karyological Analyses

The estimation of nuclear DNA content was performed by using flow cytometry (FCM) which enables to determine the ploidy level of plants from each relevé (for details see BUDZÁKOVÁ & al. 2014).

## 2.3. Statistical Methods

Phytosociological relevés stored in the TURBOVEG database (HENNEKENS & SCHAMINÉE 2001) were exported into the JUICE 7 software (TICHÝ 2002) for statistical analyses. Multiple regression analyses and t-tests were performed using Statistica 8.0 <<http://www.statsoft.com>>. DCA ordinations were performed using the CANOCO 4.5 package (TER BRAAK & ŠMILAUER 2002). The names of syntaxa follow

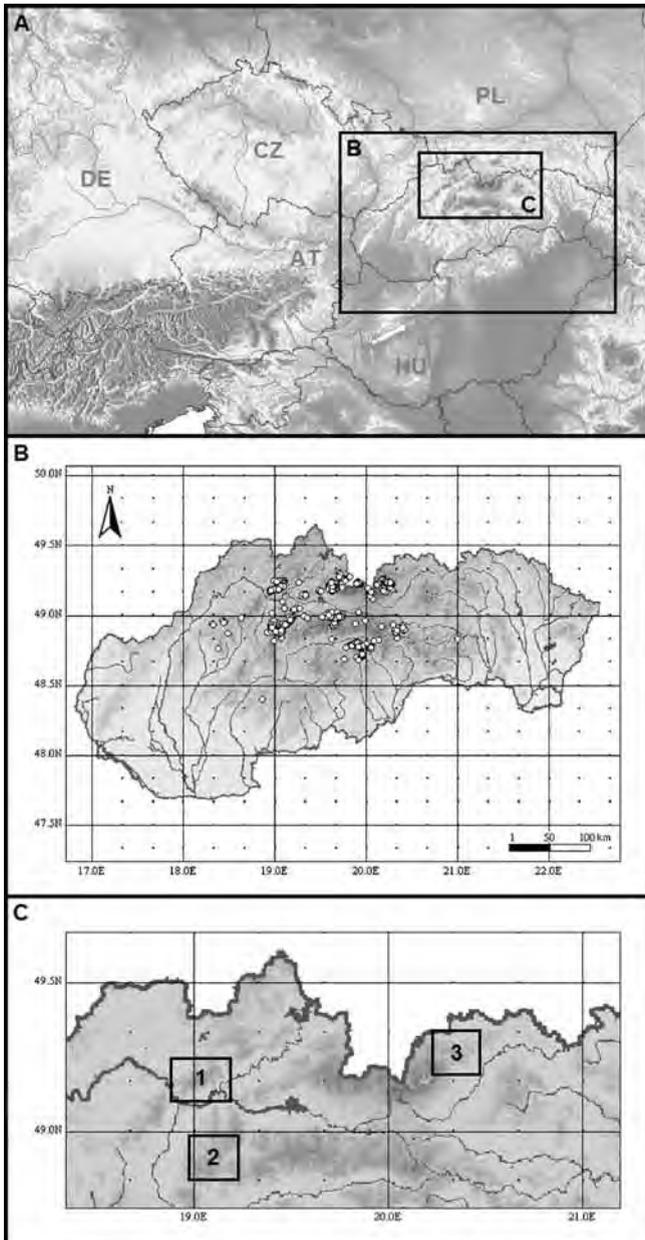


Fig. 1. Map showing the study area within the Europe (A). Map showing the relevés obtained from the Slovak vegetation database (B). Location of the Malá Fatra Mts (1), Velká Fatra Mts (2) and Belianske Tatry Mts, where the transect data were collected (C).

KLIMENT & al. 2010 and JAROLÍMEK & ŠIBÍK 2008. The nomenclature of the vascular plants is in accordance with the checklist by MARHOLD & HINDÁK 1998 with the exception of *Sesleria caerulea*. This name follows the more recent nomenclatural study of *S. caerulea* (L.) ARD. and *S. uliginosa* OPIZ (FOGGI & al. 2001).

We used a number of statistical methods to estimate the relationship between the occurrence of *Sesleria* and environmental variables. Multiple regression, t-test and detrended correspondence analysis were used to evaluate the database data. Transect data were compared using ordination methods (detrended correspondence analysis). Multiple regression was performed to relate the percentage cover of *S. caerulea* and *S. tatrae* to the partial geographical and ecological attributes recorded at each locality. We used the forward stepwise procedure, which selects the best predictors from our list of environmental variables to avoid a possible collinearity among used variables. The analysis comprised four continuous variables: (1) altitude (in m), (2) annual direct radiation (estimated over the slope, aspect and latitude; McCUNE & KEON 2002), (3) Shannon-Wiener's diversity (HILL 1973, TICHÝ & HOLT 2006), (4) cover of herb layer (in %) and 13 categorical variables related to the geographic position (geographical factors) and the character of bedrock: (1) Západné Tatry Mts (comprising relevés from the Západné Tatry Mts and the Skorušinské vrchy Mts), (2) Malá Fatra Mts (relevés from the Malá Fatra Mts and the Strážovské vrchy Mts), (3) Slovenské Rudohorie Mts (comprising relevés from the Muránska planina Plain, Veporské vrchy Mts, Slovenský raj Mts, Volovské vrchy Mts and Štiavnické vrchy Mts), (4) Východné Tatry Mts (comprising the Vysoké Tatry Mts and the Belianske Tatry Mts), (5) Nízke Tatry Mts and (6) Veľká Fatra Mts, (7) neo-volcanic rocks, (8) sedimentary deposits (glacial, glaciofluvial, alluvial and deluvial deposits), (9) marl (marl, calcareous marl, marlite and marl slate), (10) limestone, (11) dolomite, (12) granitoid (granite, granodiorite, tonalite and gneiss) and (13) sedimentary rocks (quartzite, sandstone and slate). Statistical significance was considered to be at the 0.05 level. The Digital Geological Map of the Slovak Republic at a scale of 1: 50 000 (KAČER & al. 2005) was used to classify each relevé to a geological substrate.

A t-test was applied to evaluate database data. This method estimates the significance of altitude, radiation, slope and cover of herb layer in determining the percentage cover of *S. caerulea* and *S. tatrae*. Statistical significance was considered to be at the 0.05 level. Percentage values of the cover of the herb layer were subjected to arcsine transformation to adjust the normal distribution in the data set. The results of the analyses are presented in Box and Whisker plots, which were constructed for all significant and non-significant environmental variables.

Detrended correspondence analysis (DCA) was used to examine the main gradients in floristic composition of communities with the occurrence of both species. Analysis was applied for both (1) database data, and (2) transect data. As the length of the gradient in both cases exceeded 3 SD units (LEPŠ & ŠMILAUER 2003), unimodal ordination methods (DCA) were used. Altitude, radiation, slope, cover of herb layer ( $E_i$ ), cover of *Sesleria caerulea*, cover of *S. tatrae* and Shannon-Wiener's diversity were post-hoc correlated with the ordination axes to inspect the ecological differences between groups of samples in the first analysed dataset. Ellenberg's indicator values (ELLENBERG & al. 1992) and Shannon-Wiener's diversity were post-hoc correlated with the ordination axes to inspect the ecological differences between groups of samples in the evaluation of transect data.

### 3. Results

#### 3.1. Multiple Regression

We applied a model related to relevé data with *S. caerulea* (Table 1) and a model related to relevé data with *S. tatrae* (Table 2) to estimate the variables, which influenced the occurrence of the *Sesleria* species the most. The majority of the environmental variables used in the multiple regressions did not show significant contribution to species occurrence. The analysis confirmed the positive correlation of radiation and the percentage of the cover of the herb layer with the cover of *S. caerulea* (Table 1). On the other hand, factors such as altitude and character of bedrock (namely granitoid, sediments and marl bedrocks) negatively influenced the cover of *S. caerulea*. In the case of radiation and the cover of the herb layer, a similar positive correlation was obtained when cover data for *S. tatrae* were used. Beside these, altitude and several other geographical factors (Malá Fatra Mts and Západné Tatry Mts) also showed a positive correlation. In our analysis, dolomite bedrocks and locations in the Východné Tatry Mts were significantly negatively correlated with the occurrence of *S. tatrae*. The complete results are presented in the Tables 1 and 2.

#### 3.2. T-test

When comparing means and *p*-values of each dependent variable within each group (Table 3), *t*-test results indicated that two variables (altitude and cover of herb layer) differed significantly, whereas radiation and slope did not differ significantly at the 0.05 level. Means, standard deviations and the number of samples in each group, as well as the *t*-value, *df* and *p*-value are provided in Table 3. The graphical results of *t*-test analyses are represented as Box and Whisker plots in Fig. 2.

#### 3.3. Ordination

The results of DCA analyses of 1 029 relevés extracted from the Slovak vegetation database (Fig. 3, 4) revealed important differences between relevés with the occurrence of *S. caerulea* and relevés with occurrence of *S. tatrae*. The first axis significantly ( $p < 0.05$ ) correlates with altitude (correlation coefficient 0.14), slope (0.40), radiation (0.18), cover of herb layer (0.36) and cover of *S. caerulea* (0.19). The position of the species along the first ordination axis (Fig. 4) shows that the main gradient influencing the distribution of relevés in the ordination diagram is also related to the character of soil reaction and the light availability. On the left side, there is a group of relevés with increasing frequency of acidophilous species such as *Vaccinium myrtillus*, as well as species that prefer shaded and/or forest sites with deeper soils (*Oxalis acetosella*, *Picea abies*, *Luzula sylvatica* and *Homogyne alpina*). All these species can be found in habitats such as forests at lower al-

Table 1. Summary of multiple regression analysis of the dependence of the occurrence of *Sesleria caerulea* on other variables (including four continuous variables and thirteen categorical variables listed in the materials and methods section). Only significant variables selected by forward stepwise method are presented.

Variable	Beta	Std. Error	B	Std. Error	t	p-level
Intercept	–	–	30.8	3.4	9.2	0.000
Altitude	–0.4	0.0	–0.0	0.0	–11.0	0.000
Granitoid	–0.2	0.0	–10.5	1.9	–5.5	0.000
Radiation	0.1	0.0	5.6	1.7	3.3	0.001
Deposits	–0.1	0.0	–5.6	2.0	–2.8	0.005
Cover of herb layer	0.1	0.0	0.1	0.0	2.3	0.021
Marl	–0.1	0.0	–2.6	1.3	–2.0	0.046

Multiple regressions (all significant at  $p < 0.05$ )

Table 2. Summary of multiple regression analysis of the dependence of the occurrence of *Sesleria tatrae* on other variables (including four continuous variables and thirteen categorical variables listed in the materials and methods section). Only significant variables selected by forward stepwise method are presented.

Variable	Beta	Std. Error	B	Std. Error	t	p-level
Intercept	–	–	–13.8	1.8	–7.6	0.000
Altitude	0.2	0.0	0.0	0.0	6.3	0.000
Radiation	0.1	0.0	5.0	1.0	5.0	0.000
Malá Fatra Mts	0.1	0.0	3.1	0.8	3.8	0.000
Dolomite	–0.1	0.0	–1.8	0.6	–2.9	0.004
Východné Tatry Mts	–0.1	0.0	–2.7	1.1	–2.5	0.012
Západné Tatry Mts	0.1	0.0	1.9	0.8	2.4	0.018
Cover of herb layer	0.1	0.0	0.0	0.0	2.1	0.036

Multiple regressions (all significant at  $p < 0.05$ )

Table 3. Summary of *t*-test results for chosen environmental variables (altitude, cover of herb layer, radiation and slope) between group of samples with occurrence of *Sesleria caerulea* and samples with occurrence of *S. tatrae*. Mean 1 and Std. Error 1 correspond to relevés with *Sesleria caerulea*, Mean 2 and Std. Error 2 correspond to relevés with *S. tatrae*.

Variable	Mean 1	Mean 2	t-value	df	p-level	Std. Error 1	Std. Error 2
Altitude	1243.85	1610.09	–21.4	728	0.000	235.9	192.3
E <sub>1</sub> (arcsin)	0.92	1.03	3.8	723	0.000	0.4	0.4
Radiation	0.74	0.69	–1.9	723	0.064	0.3	0.3
Slope	40.58	38.56	1.5	723	0.140	18.9	14.9

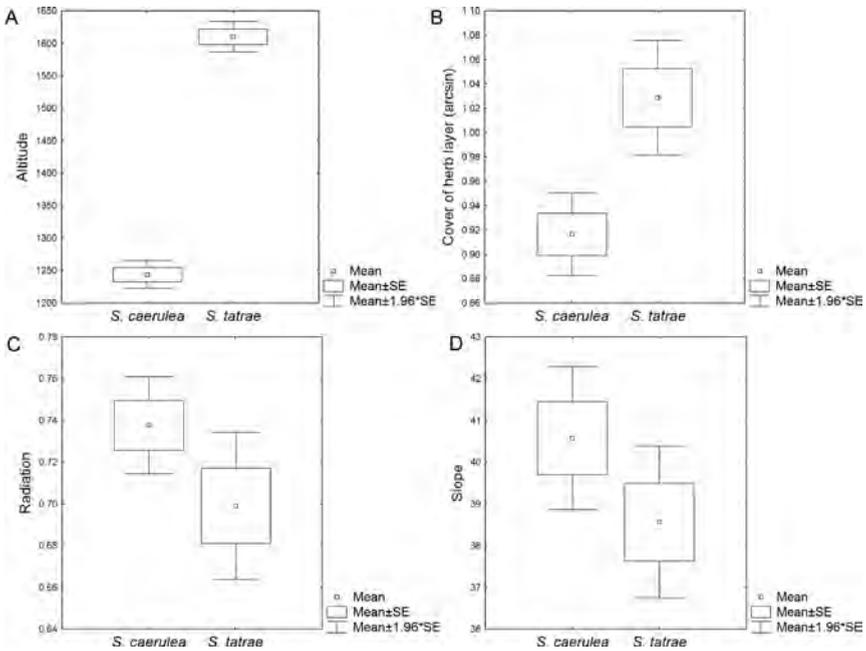


Fig. 2. Box and Whisker plots showing the results of t-test analyses for two groups of relevés: those with occurrence of *Sesleria caerulea* and those with occurrence of *S. tatrae*. Graphs were constructed for all variables used in this analysis: altitude (A), cover of herb layer (B), radiation (C) and slope (D), but only altitude and cover of herb layer differed significantly at the 0.05 level.

titudes as well as tall herb mesophilous communities of the supramontane and subalpine belt. Species typical for more open and exposed sites such as *Primula auricula*, *Trisetum alpestre* and *Saxifraga paniculata*, are situated on the right side of the diagram. These species represent basiphilous taxa that are common in the first successional stages or pioneer plant communities in which the total cover is not so dense. The second axis significantly ( $p < 0.05$ ) correlates with altitude (0.78), radiation (0.31), cover of *S. caerulea* (0.41) and cover of *S. tatrae* (0.16). The most important is altitude, which is illustrated by the occurrence of typical high-altitude species such as *Dryas octopetala*, *Carex firma* and *Festuca versicolor* in the upper part of the diagram. Thermophilous species such as *Carex humilis* and *Pulsatilla slavica* have been placed into the bottom right corner, and they correlate with irradiation. Relevés without occurrence of any *Sesleria* species were more or less scattered in the diagram. One larger cluster of these relevés can be recognised on the left side of the diagram and can be associated mostly with nutrient-poorer soils, dense cover of herb layer, and/or with moderate inclina-

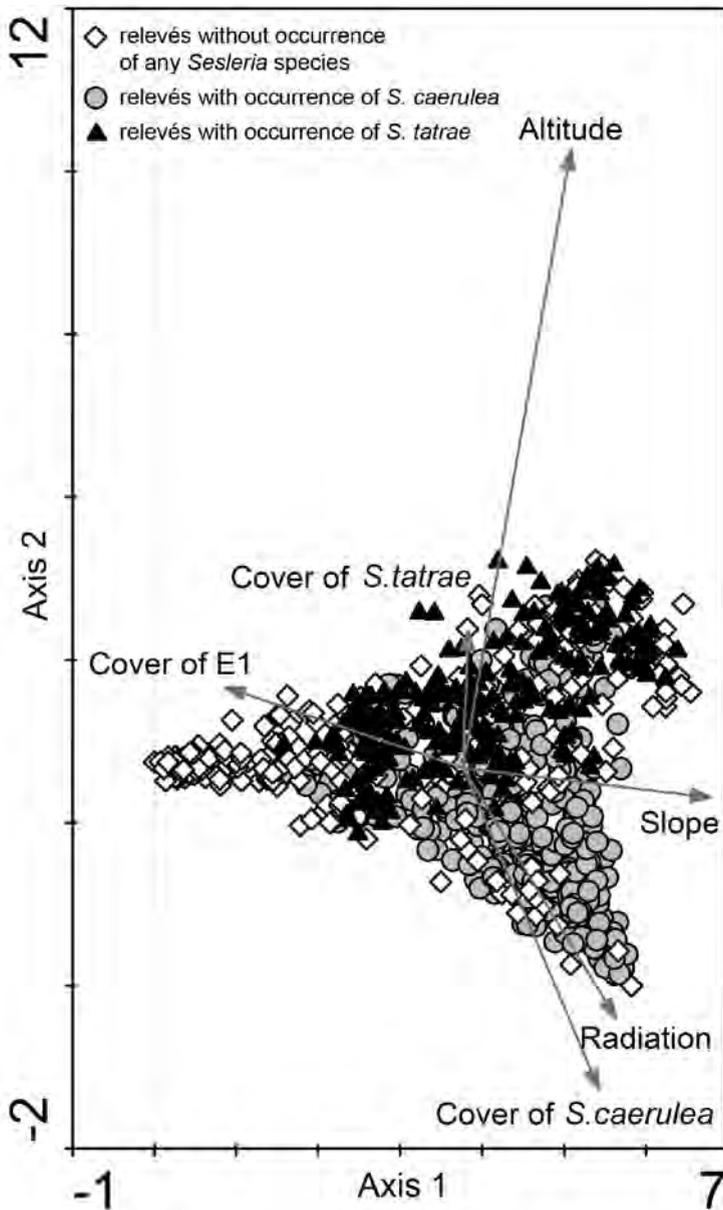


Fig. 3. Detrended correspondence analysis (DCA) of 1 029 relevés obtained from the Slovak vegetation database. Continuous variables [altitude, slope, radiation, cover of herb layer ( $E_1$ ), Shannon-Wiener's diversity], cover of *Sesleria caerulea* and cover of *S. tatrae* were used as supplementary environmental variables. Length of gradients: 6.545 (1. axis), 5.224 (2. axis); eigenvalues: 0.725 (1. axis), 0.492 (2. axis).

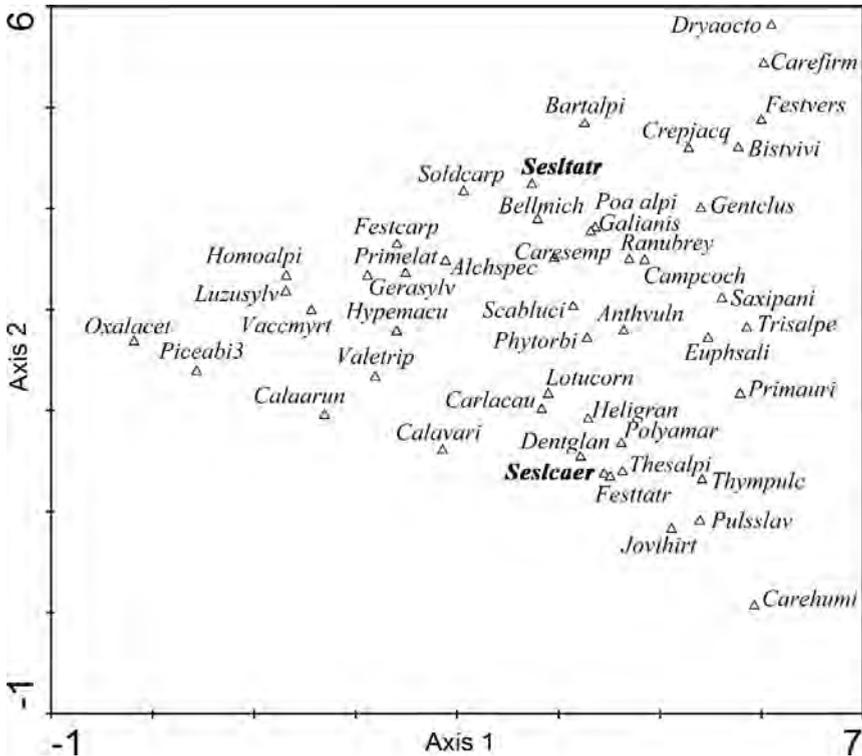


Fig. 4. Species diagram of detrended correspondence analysis (DCA) of 1 029 relevés obtained from the Slovak vegetation database – position of species data alone. The length of gradients and the eigenvalues are the same as states Fig. 2; Species Weight Range from: 20%. *Alchspect*: *Alchemilla* species, *Anthvuln*: *Anthyllis vulneraria* subsp. *alpestris*, *Bartalpi*: *Bartsia alpina*, *Bellmich*: *Bellidiastrum michelii*, *Bistvivi*: *Bistorta vivipara*, *Calaarun*: *Calamagrostis arundinacea*, *Calavari*: *Calamagrostis varia*, *Carehumi*: *Carex humilis*, *Campcoch*: *Campanula cochlearifolia*, *Carefirm*: *Carex firma*, *Caresemp*: *Carex sempervirens*, *Carlacau*: *Carlina acaulis*, *Crepjacq*: *Crepis jacquinii*, *Dentglan*: *Dentaria glandulosa*, *Dryaocto*: *Dryas octopetala*, *Euphsali*: *Euphrasia salisburgensis*, *Festcarp*: *Festuca carpatica*, *Festtatr*: *Festuca tatrae*, *Festvers*: *Festuca versicolor*, *Galianis*: *Galium anisophyllum*, *Gentclus*: *Gentiana clusii*, *Gerasylyv*: *Geranium sylvaticum*, *Heligran*: *Helianthemum grandiflorum* agg., *Homoalpi*: *Homogyne alpina*, *Hypemacu*: *Hypericum maculatum*, *Jovihirs*: *Jovibarba globifera* subsp. *hirta*, *Lotucorn*: *Lotus corniculatus*, *Luzusylv*: *Luzula sylvatica*, *Oxalacet*: *Oxalis acetosella*, *Piceabi3*: *Picea abies* (E<sub>3</sub>), *Phytorbi*: *Phyteuma orbiculare*, *Poa alpi*: *Poa alpina*, *Polyamar*: *Polygala amara*, *Primauri*: *Primula auricula*, *Primelat*: *Primula elatior*, *Pulsslav*: *Pulsatilla slavica*, *Ranubrey*: *Ranunculus breyninus*, *Saxipani*: *Saxifraga paniculata*, *Scabluci*: *Scabiosa lucida*, *Seslcaer*: *Sesleria caerulea*, *Sesltatr*: *Sesleria tatrae*, *Soldcarp*: *Soldanella carpatica*, *Thesalpi*: *Thesium alpinum*, *Thympulc*: *Thymus pulcherrimus* agg., *Trisalpe*: *Trisetum alpestre*, *Vaccmyrt*: *Vaccinium myrtillus*, *Valetrip*: *Valeriana tripteris*.

tion of the stands. DCA analysis of the 201 relevés collected along longitudinal transects (Fig. 5) divided the data set into two quite well separated groups. The presence of Ellenberg's indicator values helped to determine the main factors responsible for distribution of individual relevés along the main axes. The first axis significantly ( $p < 0.05$ ) correlates with Shannon-Wiener's diversity (correlation coefficient 0.24), temperature (0.26), moisture (0.18), soil reaction (0.54), and nutrients (0.15); the second axis significantly ( $p < 0.05$ ) correlates with continentality (0.51) and soil reaction (0.26). Relevés with the occurrence of *S. caerulea* are slightly more scattered on the diagram, which may be caused by the fact that *S. caerulea* shows a wider ecological niche. Species diversity is also higher at those localities. However, the soil reaction is the main factor affecting the position of the relevés in the diagram. The soil reaction positively correlates with the occurrence of *S. caerulea* and negatively with the occurrence of *S. tatrae*. The factors temperature, moisture and nutrients correlated with relevés with *S. tatrae*. Based on these results, we can conclude that *S. tatrae* prefers moister locations with higher nutrient availability.

The cover of the herb layer was investigated by statistical analyses to estimate the species habitat structure. Based on the results of multiple regression (Table 1, 2), the cover of the herb layer was a significant feature and correlated with the occurrence of both *Sesleria* species. T-test results (Table 3, Fig. 2) and DCA analysis (Fig. 3) show in more detail that the cover was higher in communities with presence of *S. tatrae*. We can conclude that *S. tatrae* prefers dense and closed stands, whereas *S. caerulea* can occur also in more open communities on extremely skeletal, shallow soils on steep slopes.

Flow cytometry did not reveal any intermediate ploidy level between the species. All individuals were found to be tetraploids ( $2n \sim 4x \sim 28$ ; *S. caerulea*), or octoploids ( $2n \sim 8x \sim 56$ ; *S. tatrae*). Hexaploid individuals were not recorded in this study.

#### 4. Discussion

Our statistical analyses and their interpretation revealed important and noticeable differences in ecological requirements between *Sesleria caerulea* and *S. tatrae*. The most important ecological factors that differentiate stands of the study species are related to altitude, substrate, soil reaction, nutrients, moisture, temperature, radiation (related to slope and aspect) and the geographical position of each location. We thus confirm earlier assumptions based on extensive field experiences and emphasise some of them using exact statistical analyses.

Our investigation revealed that altitude is one of the most important factors determining the occurrence of the studied species. According to a study by RYCHLEWSKI 1955 in the Polish High Tatra Mts, *S. tatrae* can be found at altitudes of 1,100–1,750 m, although the most numerous stands of

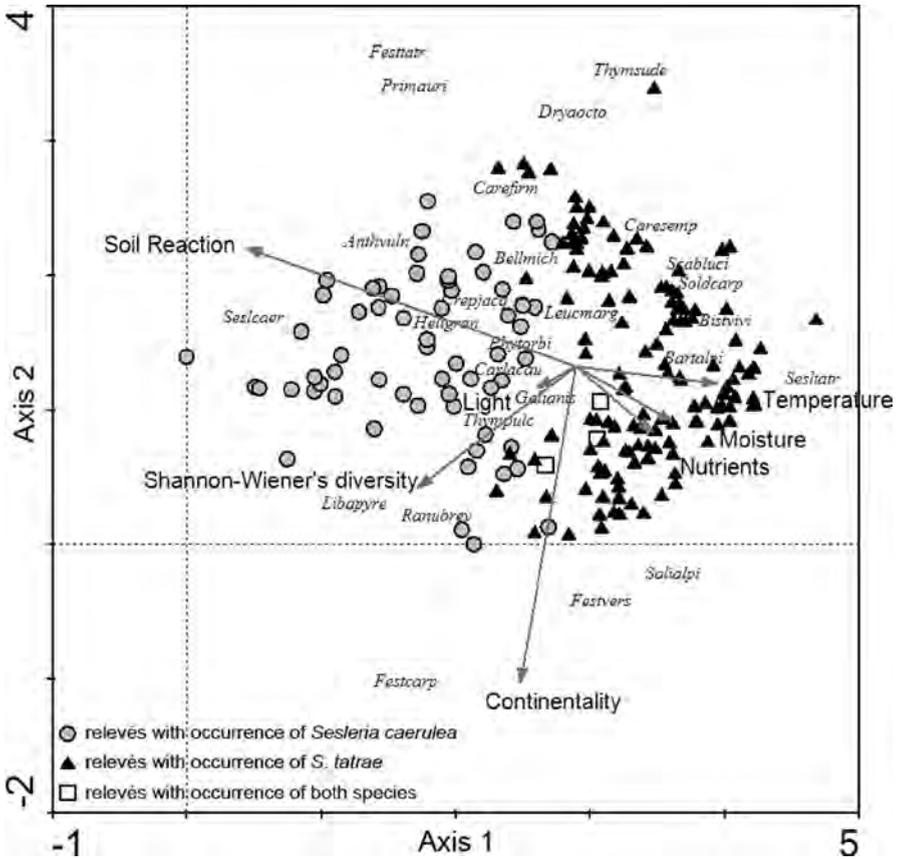


Fig. 5. Detrended correspondence analysis (DCA) of species and relevés with occurrence of *Sesleria caerulea* and *S. tatrae* collected along longitudinal transects in Belianske Tatry Mts, Velká Fatra Mts and Malá Fatra Mts. Ellenberg's indicator values were used as supplementary environmental variables. The length of gradients: 4.681 (1. axis), 3.385 (2. axis); the eigenvalues: 0.551 (1. axis), 0.424 (2. axis); Species Weight Range from: 3%. *Anthvuln*: *Anthyllis vulneraria* subsp. *alpestris*, *Bartalpi*: *Bartsia alpina*, *Bellmich*: *Bellidiastrum michelii*, *Bistvivi*: *Bistorta vivipara*, *Carefirm*: *Carex firma*, *Caresemp*: *Carex sempervirens*, *Carlacau*: *Carlina acaulis*, *Crepjacq*: *Crepis jacquinii*, *Dryaocto*: *Dryas octopetala*, *Festcarsp*: *Festuca carpatica*, *Festatr*: *Festuca tatrae*, *Festvers*: *Festuca versicolor*, *Galians*: *Galium anisophyllum*, *Heligran*: *Helianthemum grandiflorum* agg., *Leucmarg*: *Leucanthemum margeritae*, *Libapyre*: *Libanotis pyrenaica*, *Phytorbi*: *Phyteuma orbiculare*, *Primauri*: *Primula auricula*, *Ranubrey*: *Ranunculus breyninus*, *Salialpi*: *Salix alpina*, *Scabluci*: *Scabiosa lucida*, *Seslcaer*: *Sesleria caerulea*, *Sesltatr*: *Sesleria tatrae*, *Soldcarp*: *Soldanella carpatica*, *Thympulc*: *Thymus pulcherrimus* subsp. *pulcherrimus*, *Thym suede*: *Thymus pulcherrimus* subsp. *sudeticus*.

*S. tatrae* occur at altitudes of 1,400–1,500 m. The species was not found below 1,100 m. Our research correlates with these results, and also with that of other authors (RYCHLEWSKI 1955, LYSÁK 1996, KLIMENT 1999) who define the distribution of *S. tatrae* as restricted to montane and alpine altitudes. Only one occurrence was documented at an altitude of approximately 840 m in the Sudetes (Kleśnica valley in the Śnieżnik Kłodzki Mts; FABISZEWSKI 1970). Conversely, according to some authors, the altitudinal range of *S. caerulea* occurrence varies widely from the colline to the alpine vegetation belt (DEYL 1946, LYSÁK 1996, LYSÁK & DOLEŽEL 1998). Therefore it is assumed that elevation is not the primary driver of the ecological distribution of this species, but by characteristics of microsite conditions (cf. BUDŽÁKOVÁ & al. 2014). Our target sampling was focused on a specific range of altitudes (above 900 m), where both species can occur simultaneously. Despite this limitation, altitude was shown to be one of the most important factors determining the presence or absence of each species at a given location. Our analyses (Table 1, 2, 3 and Fig. 2, 3) confirm that *S. caerulea* prefers lower altitudes (the montane belt) whereas *S. tatrae* was found mostly in higher altitudes (the subalpine-alpine belt).

The character of the substrate and soil reaction are also important drivers for the occurrence of both species. In the Western Carpathians, they occur mostly on basiphilous bedrock such as limestone and dolomite (DEYL 1936, RYCHLEWSKI 1955, DIXON 1982, LYSÁK & DOLEŽEL 1998). Results of multiple regression did not strongly confirm the relationship between *Sesleria* species and basiphilous substrates. In case of *S. caerulea*, only a negative correlation between its occurrence and some substrates (granitoids, sediments and marl) was clearly proved (Table 1). On the other hand, our DCA analyses of transect data using Ellenberg's indicator values (Fig. 5) as well as DCA analyses of database data (Fig. 4) revealed clearly the affinity of *S. caerulea* to higher pH values. Soil reaction of sites of *S. caerulea* was investigated by DIXON 1982 on island populations of the British Isles. At stands with dominance of *S. caerulea*, the soil reaction was mostly alkaline or neutral. According to DEYL 1946, *S. caerulea* grows mostly in rocky stands rich in Ca and Mg (limestone, dolomite and serpentine), although it could occasionally grow even on silicate soils. A different situation was observed in *S. tatrae*, which does not depend strictly on the soil reaction and can also be found at localities with lower pH values (Fig. 5). The range of pH values of soil samples of *S. tatrae* in the Belianske Tatry Mts were previously studied by DEYL 1936. According to his findings, *S. tatrae* is most common in calcareous communities with alkaline, neutral or slightly acid soil reaction, but was also found in communities with lower pH, meaning that *S. tatrae* shows a quite wide pH range and does not depend strongly on the soil reaction (DEYL 1936). This is well demonstrated by the associated taxa including basiphilous and neutral, as well as slightly acidophilous species. The reason for the spread of acidophilous species to the calcicolous communities is mostly

nutrient leaching of the upper soil layers, which is most common in a humid climate. As a consequence, some acidophilous species with shallow root systems penetrate the upper soil layers. In addition, high rates of organic litter occasionally cause acid soil reaction (DEYL 1936). According to results of multiple regression, *S. tatrae* was even negatively correlated with dolomite substrate (Table 2). Several factors may contribute to this situation. The first one may be related to the potential relationship between *S. tatrae* and the higher content of magnesium in dolomite rocks, although there is no evidence regarding an unfavorable influence of magnesium on the occurrence of the species under study. The situation can be related also to the different weathering of dolomite rocks. Dolomite might be characterised as a harder rock than limestone which produces more debris, and thus more porosity and less soil moisture (ZÓLYOMI 1942). Solubility is also different in both substrates. In comparison with limestone, the calcium (Ca) in dolomite is more strongly bounded and is therefore not as available to plants.

On the basis of the results of both DCA analyses (Fig. 3–5), we can conclude that both species grow under different soil nutrient conditions. *S. caerulea* dominates on steep slopes with shallow soils (DIXON 1982), where nutrients are quickly leached away. Conversely, *S. tatrae* requires a higher level of nutrient availability given on sites with deeper soils situated on moderate slopes. However, properties of slopes as a driver for the distribution of the study species were non-significant by the t-test analysis (Table 3).

Microclimate conditions also influence the ability of both species to grow at a given location. Our study demonstrates that *S. caerulea* is more resistant to drought (Fig. 5) and occurs in areas together with typical xerophilous species such as *Carex humilis* (Fig. 4). Similar results were suggested by DIXON 1986, who pointed out that the species requires good soil aeration with drainage ability (DIXON 1982). However, literature data indicate that this species is able to grow across a wide range of moisture conditions, and tolerates even wet conditions (PIGNATTI & PIGNATTI 1975, DIXON 1996). In contrast, the *S. tatrae* dominates on locations with higher amount of soil moisture and humidity (cf. Fig. 5). Gentler slopes, deeper soils and a relatively narrow altitudinal range also indicate that *S. tatrae* has a greater affinity to humid conditions in comparison with *S. caerulea*.

*S. caerulea* is highly eurythermal species (DIXON 1982) that occurs across a wide range of temperatures. Previous studies have also shown that the species was fresh and green during an exceptionally hot summer (DIXON 1986). *S. tatrae* is usually found at higher altitudes, which are characterised by lower temperatures and a more humid climate. Despite this, our analyses (Fig. 5) show that temperature and the occurrence of thermophilous species correlate more with occurrence of *S. tatrae*. This fact may be due to the study design, as we compared only the communities at higher altitudes (from 900 m). Generally, *S. caerulea* grows in more extreme conditions (steeper, windy and freezing stands where temperature may change rapidly in both

directions) that are not suitable for thermophilous species at such altitudes. Conversely, the less extreme habitats of *S. tatrae* provide more stable conditions for thermophilous species. Thick layers of snow provide sufficient shelter for these plants, especially on southern slopes, where the snow melts quickly in the early springtime. Most of these thermophilous species are separated from populations at lower elevations. We can term their distribution as disjunctive-bi-horizontal (KLIMENT & al. 2007). Several authors regard the isolated occurrence of sub-continental forest species above the tree line as a relic from warm periods of the postglacial period (cf. LOŽEK 1972, OBERDORFER 1978, KLIMENT & al. 2007).

Our research emphasises that the distribution of both species correlates highly with increased radiation (related mostly to slope, aspect and latitude; Table 1, 2). Previous research (DIXON 1982) reported that *S. caerulea* does not require, but is tolerant to, a high value of insolation. According to SCHUBERT 1963, *S. caerulea* can be found mostly on south-facing slopes in France, whereas in the Czech Republic and Slovakia the species is most common on north facing slopes.

Based on our analysis (Table 2), the distribution of *S. tatrae* appears to be closely interwoven with geographical factors. The species shows an affinity for growth in some regions of the Western Carpathians (such as the Malá Fatra Mts and the Západné Tatry Mts). An interesting result is the slight negative correlation with the Východné Tatry Mts. We interpret this discrepancy as a consequence of the fact that the Východné Tatry Mts include not only the Belianske Tatry Mts (known by their limestone and dolomite bedrocks), but also the Vysoké Tatry Mts (granite bedrocks) where the species does not occur abundantly or frequently. Connection between the sub-endemism of *S. tatrae* (KLIMENT 1999) may be related to the occurrence in the mountain range. In contrast, *S. caerulea* is one of the most widespread, as well as most abundant species of the genus *Sesleria* (DEYL 1946).

## 5. Conclusions

We can conclude that the most important factors influencing the occurrence of individual species at different habitats are altitude, substrate and subsequent soil reaction, nutrients, moisture, temperature, radiation and the geographical position of each location. Almost all of our results correspond roughly to the current knowledge about study species until now. However we have found also several discrepancies between previous studies and our findings. As a novelty we consider the negative correlation of *S. tatrae* with dolomite substrates. These results point out the bigger tolerance of that species to acidophilous substrates as previously supposed. Differences with literature data we recognised also in moisture preferences of *S. caerulea*. Based on our analysis, this species dominated at drought sites and its tolerance to moist conditions was not so evident. Differences were found also in tem-

perature preferences. According to current knowledge, *S. caerulea* is a eurythermal species occurring in a quite wide range of temperatures, whereas *S. tatrae* can be found only at higher altitudes where the climate is colder. In our study such correlation was not observed since *S. tatrae* co-occurred with thermophilous species. The reason for such a distribution might be that in higher altitudes *S. caerulea* still dominated on very extreme sites (steep, windy and freezing stands) whereas *S. tatrae* was found on gentle and lee slopes that provide more stable conditions for thermophilous species.

Based on our results, all the study species grow in relatively different habitats, but can also occupy locations with similar environmental conditions. That's the reason why we should be careful when predicting the occurrence of species on the basis of site characteristics. Differentiation of the species based on habitat preferences is not reliable and more important is the determination based on morphological characteristics, in ideal case also on ploidy level determination.

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