Tuexenia 33: 371–398. Göttingen 2013.
available online at www.tuexenia.de

Phytosociology and ecology of *Avenula adsurgens* subsp. *adsurgens* in Carpathian grasslands

Soziologie und Ökologie von *Avenula adsurgens* subsp. *adsurgens* in Grasländern der Karpaten

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Abstract

This paper focuses on ecological requirements and phytosociological affinity of *Avenula adsurgens* subsp. *adsurgens*. Although this grass is widely distributed in central and south-eastern Europe reaching dominance in certain grassland types, the knowledge on its ecology and coenology is very poor. Moreover, some of the published data on its distribution are wrongly related to *Avenula praeusta*. We studied the taxon within an area of about 300 km^2 (Central Slovakia) where it occurs in diverse habitats. Data from a systematic phytosociological survey were used to assess interspecific associations and ecological indicator values of the taxon. Detailed measurements from a transect along a spruce colonisation gradient were used to evaluate its relationship to a set of topographical, microclimatical, pedological and soil-microbiological characteristics. Tillers of *A. adsurgens* subsp. *adsurgens* were cultivated for two growing seasons to estimate characteristics of its clonal morphology and growth and its ability of spatial spreading. In the studied area, the taxon occurred mainly over the volcanic bedrock along a wide range of altitudes. It was concentrated in slightly managed or abandoned montane grasslands (800–1100 m) of the *Violion caninae* and *Nardo strictae-Agrostion tenuis* alliances. Phytosociologically the taxon seems not to be an important diagnostic species of these communities, rather an indicator of their successional development. Its highest cover was recorded in early to mid-successional stages without significant proportions of woody species. In stands with traditional management by mowing, grazing or their combination, the taxon was common (albeit with lower percentage cover), but more intensive management including amelioration or fencing led to its retreat. Ellenberg ecological indicator values of *A. adsurgens* subsp. *adsurgens* were set as follows: light 7, temperature 5, continentality 4, moisture 4, soil reaction 5 and nutrients 3. Along a successional gradient, the taxon cover was positively correlated with percentage cover of herb litter, catalase activity, canopy openness and potassium content and negativelycorrelated with percentage cover of needles and canopy index reflecting the cumulative effects of spruce colonisation. The horizontal spreading of the taxon was enabled by the formation of spacers with a maximum length of 25.5 cm. We suppose that the ability to spread horizontally by spacers, together with the observed clonal plasticity, tall stature and fast growth by intensive tillering, belong to important attributes of *A. adsurgens* subsp. *adsurgens* promoting its success and dominant role in the abandoned grasslands.

Manuscript received 20 December 2012, accepted 19 March 2013
Co-ordinating Editor: Eszter Ruprecht

Keywords: clonal morphology, ecological indicator values, grassland management, perennial grass, phytosociological affinity, succession

Erweiterte deutsche Zusammenfassung am Ende des Textes

1. Introduction

Avenula adsurgens (Schur ex Simonkai) Sauer et Chmelitschek [Syn: *Avenochloa adsurgens* (Schur ex Simonkai) Holub, *Helictotrichon alpinum* subsp. *adsurgens* (Schur) Soó, *Avenochloa alpina* subsp. *adsurgens* (Schur ex Simonkai) Soo, *Helictotrichon adsurgens* (Schur ex Simk.) Conert, *Helictochloa adsurgens* (Simonk.) Romero Zarco] belongs to the group of *Avenula pratensis*, which is taxonomically difficult and still insufficiently known (HOLUB 1957, 1961, SAUER & CHMELITSCHEK 1976, VALDÉS & SCHOLZ 2009). The genus *Avenula* was studied by J. Holub, and the information concerning morphology, taxonomical relationships, coenology and ecology of the individual taxa can be found in his thesis (HOLUB 1957) and in his subsequently published papers (HOLUB 1959, 1961, 1962, 1972, 1976). A newer evaluation of the genus *Avenula* in the Eastern Alps and adjacent regions was made by SAUER & CHMELITSCHEK (1976). Their concepts were accepted in the most recent descriptions and determination keys (e.g. ADLER et al. 1994, CONERT 1998, VALDÉS & SCHOLZ 2009). According to the accessible literature, *Avenula adsurgens* has an intermediate position between *A. pratensis* and *A. planiculmis*, not only regarding their morphology, but also regarding their ecology. It is considered to be a horizontal vicariant of *A. pratensis* and a vertical vicariant of *A. planiculmis* (HOLUB 1957).

In spite of the fact that several authors consider *Avenula adsurgens* and *Avenula praeusta* Rchb. to be synonyms for the same taxon (HOLUB 1980, MARHOLD & HINDÁK 1998), the newer syntheses of the genus *Avenula* distinguish them as separate taxa (SAUER & CHMELITSCHEK 1976, CONERT 1998, ADLER et al. 1994, VALDÉS & SCHOLZ 2009). According to them, the name *Avenula praeusta* Rchb. should be used exclusively for populations in higher altitudes of the Alps, which most likely belong to the montane types of *Avenula pratensis* L. (HOLUB 1972). In this paper, we use the name *A. adsurgens* subsp. *adsurgens* to distinguish the studied taxon from those alpine populations. In the Western Carpathians, similarly to other parts of its distribution area, the *A. adsurgens* populations are morphologically inconsistent (HOLUB 1957, SAUER & CHMELITSCHEK 1976), which resulted in a very inconsistent taxonomical evaluation of individual populations in the published literature (the studied populations are mostly referred to as *A. planiculmis* or *A. praeusta*). In the future, the taxonomical range of *Avenula adsurgens* s. lat. needs to be elucidated by a morphometrical analysis.

Avenula adsurgens is a polycarpic perennial grass forming loose tussocks by extravaginal tillers (spacers), which can reach up to 30 cm (CONERT 1998). The base of stalks and tussocks is covered by strong straw-like sheaths (HOLUB 1957). It is a hemicryptophyte with at least some leaves remaining green through the winter. Similarly to other *Avenula* species, the studied taxon is highly polyploid with $2n = 18x = \pm 126$ chromosomes being the most common value (SAUER & CHMELITSCHEK 1976). For the genus, however, various other chromosome numbers of 2n = 14, 28, 42, 70, 81, 98, 112, 126, 133, 147 have been reported in the literature. The subspecies *A. adsurgens* subsp. *adsurgens* has a subcontinental distribution including Austria, Slovakia, Hungary, Bosnia, Macedonia, Romania, Bulgaria, Turkey and Ukraine (VALDÉS & SCHOLZ 2009). *Avenula adsurgens* subsp. *adsurgens* inhabits dry and warm habitats in the colline to montane belt (mostly up to 1000 m a.s.l.) and prefers south-facing slopes (HOLUB 1957, SAUER & CHMELITSCHEK 1976). The types of bedrock and habitats vary between the regions. In Transylvania it occurs in vineyards, stony pastures and occasionally in forests (BELDIE 1967). In Ukraine it grows on rocks, rocky slopes and subalpine meadows (ČOPYK 1976), montane meadows in the beech zone (PROKUDIN et al. 1977) and forest clearings and open forests (CVELEV 1976). In the Eastern Alps, on the other hand, it occurs in several types of extreme habitats including alluvia or open pine formations on serpentine bedrock classified as *Avenulo adsurgentis-Festucion pallentis* Mucina in Mucina et Kolbek 1993 (EGGLER 1954, 1955; MUCINA & KOLBEK 1993). Its occurrence in these open and disturbed habitats is explained by its low competitive ability in other grassland types (SAUER & CHMELITSCHEK 1976). In the larch-spruce zone of the Central Alps, *A. adsurgens* subsp. *adsurgens* is locally replaced by *A. adsurgens* subsp. *ausserdorferi* (Ascherson & Graebner) Sauer & Chmelitschek, which is considered to be endemic for the Eastern Alps; however, its taxonomic recognition is questioned by some authors (TRIBSCH & SCHÖNSWETTER 2003).

In Slovakia, *A. adsurgens* subsp. *adsurgens* is considered to be an endangered taxon (FERÁKOVÁ et al. 2001, listed as *A. praeusta*) of the category LR:nt (lower risk, near threatened). It inhabits grasslands from colline to submontane regions where it can become dominant after the cessation of traditional management and grassland abandonment (JANIŠOVÁ et al. 2004, 2007a).

The dominance of tall perennial grasses in plant communities of temperate regions have frequently been attributed to clonal morphology (KLIMEŠ et al. 1997, HALASSY et al. 2005) or specific nutrient use strategies (HOLUB et al. 2012a). The length of spacers has been widely used to classify clonal plants as phalanx or guerrilla (VAN GROENENDAEL et al. 1996, KLIMEŠ et al. 1997): guerilla species infiltrate into the surrounding vegetation by widely spaced ramets, while phalanx species grow tightly packed advancing fronts of ramets with short spacers (LOWETT DOUST 1981). The length of the spacer between mother and daughter ramet effects the plant species' distribution and its response to changing environmental conditions. While species with short spacers prevail in nutrient-poor and other kinds of stressful habitats, species with long spacers are more common in later successional stages (SAMMUL et al. 2004). By means of long spacers, plants are able to explore the habitat and to reach favourable microsites faster than by means of short spacers (DE KROON & HUTCHINGS 1995, SAMMUL 2011).

Perennial grasses can respond to environmental heterogeneity through modifications of their clonal morphology as a trade-off between phalanx and guerrilla forms (POTTIER & EVETTE 2011). Plasticity of clonal growth is profitable mainly in a heterogeneous environment. By means of plasticity of spacer length, plants are able to recognise the quality of the microsite within the patch and adjust their growth in response to the environment (DE KROON & HUTCHINGS 1995). Both properties, production of long spacers and plasticity of spacer length, can bring numerous benefits for a plant, independent of environmental conditions (HUTCHINGS & de KROON 1994, OBORNY 1994).

Recent knowledge on *A. adsurgens* subsp. *adsurgens* regarding its distribution, coenology and ecology is very poor, which may partly be due to the lack of a reliable identification key in national floras. Moreover, we lack the information on its clonal morphology and growth parameters that could help us to understand its success in poorly managed or abandoned grassland communities. In our contribution, we tried to collect relevant information on phytosociological affinity, ecological behaviour and growth of *A. adsurgens* subsp. *adsurgens*. We hope that this information can contribute to the knowledge of this taxon and its relation to grassland management and selected environmental factors and that it will help to estimate its present conservation status. In our paper, we addressed the following main questions: 1) What is the phytosociological affinity of *A. adsurgens* subsp. *adsurgens*? 2) What are the ecological requirements of *A. adsurgens* subsp. *adsurgens*, and what management practices contribute to its success and dominance? 3) How can the clonal morphology of the studied taxon be related to its successful spreading during grassland secondary succession?

2. Material and methods

2.1 Data collection and analysis

The phytosociological affiliation of *Avenula adsurgens* subsp. *adsurgens* was based on a data set of 672 relevés recorded according to the Zürich-Montpellier school (BRAUN-BLANQUET 1964) in the Poľana Mts and the adjacent regions between 1995 and 2005 (SLÁVIKOVÁ & KRAJČOVIČ 1996, 1998; UJHÁZY 2003 and unpublished material). In the study area, *A. adsurgens* subsp. *adsurgens* occurs in numerous localities in a wide range of habitats. A systematic sampling covered the whole area of the Protected Landscape Area and Biosphere Reserve Poľana, whole cadastres of the villages Hrochoť and Strelníky and a part of both Hriňová and Detva cadastres adjacent to the Poľana Mts massif. The 656 species of vascular plants contained in the data set (including all grassland types and their successional stages) were used to calculate interspecific associations and species co-occurrences with *A. adsurgens* subsp. *adsurgens* using the program JUICE (TICHÝ 2002). The subset of 427 relevés recorded in mesophilous grasslands was used for Canonical Correspondence Analysis (TER BRAAK & ŠMILAUER 2002) to evaluate the relation of *A. adsurgens* subsp. *adsurgens* to the main environmental gradients. Easily measured environmental variables were used as input data: altitude, xericity (calculated from the values of slope aspect and slope inclination as cos (aspect − 225°) * tg (slope inclination) and percentage cover of woody species, separately for tree (*E3*) and shrub layer (*E2*), as indicator of successional stage. During the phytosociological sampling, notes on management practices in the sampled plots were made. Based on this information, the relation of *A. adsurgens* subsp. *adsurgens* to the grassland management type was assessed. The 85 relevés with the occurrence of *A. adsurgens* subsp. *adsurgens* were subjected to TWINSPAN classification (HILL 1979, three pseudospecies cut levels: 0%, 5% and 25%) and Detrended Correspondence Analysis (TER BRAAK & ŠMILAUER 2002) to distinguish the vegetation types and evaluate the phytosociological affinity of the taxon. Altitude and environmental variables derived from Ellenberg indicator values (ELLENBERG et al. 1991; unweighted averages calculated for individual relevés from the indicator values of taxa present) were post-hoc correlated with main ordination axes. The TWINSPAN division was used for cluster differentiation in the synoptic table. Diagnostic species for individual clusters were estimated based on the *phi* coefficient tested for significance by Fisher's exact test at a significance level of $P < 0.01$ (JUICE, TICHÝ 2002). The classification of clusters to syntaxa (associations and alliances) was based on the revised review of Slovak grassland vegetation (JANIŠOVÁ et al. 2007b).

A detailed field observation of *A. adsurgens* subsp. *adsurgens* was performed at the locality of Príslopy situated in the central part of the Poľana Mts on andesite bedrock and altitudes between 910 and 920 m. In 2003, a transect was established on a north-facing slope in the abandoned pasture colonised by spruce (JANIŠOVÁ et al. 2007a). On this 160 m long and 20 m wide transect, we studied the process of post-pasture secondary succession speeded up by spruce colonisation. *Avenula adsurgens* subsp. *adsurgens* occurred in parts of the transect less colonised by spruce reaching dominance or subdominance in the understorey vegetation (HRIVNÁK & UJHÁZY 2005). Altogether, 155 circular plots with an area of 0.5 m^2 each were sampled in a grid of 5 m × 5 m along the whole transect for a detailed analysis of the relationship between the understorey vegetation and the relevant environmental factors. In the plots, the percentage cover of all vascular plants and bryophytes was estimated. A set of topographical, microclimatical, pedological and soil-microbiological characteristics was measured: percentage cover of herb litter, percentage cover of needles on the soil surface, thickness of the litter layer, soil acidity (pH-KCl, pH-H_2O), organic matter (humus) content (Tyurin's method), total nitrogen (Kjeldahl's method), phosphorus and potassium content. Soil samples were taken from the uppermost mineral horizon from a depth of 5–10 cm (see JANIŠOVÁ et al. 2007a for the methodological details). From fresh samples, gravimetric moisture, basal soil respiration rate, substrate-induced respiration and catalase activity were determined (see GÖMÖRYOVÁ et al. 2009 for details). To assess the light availability at the understorey level, vertical hemispherical canopy photographs were taken in the middle of each sample plot using a digital camera equipped with a fisheye lens. For the evaluation of the photographs, Gap Light Analyser 2.0 (FRAZER et al. 1999) was used, and the percentage of open sky seen from beneath the forest canopy (percentage canopy openness) was calculated. To characterise the stage of tree colonisation, a canopy index was calculated reflecting both density and size of trees at a particular point (KÜHLMANN et al. 2001): Canopy index $= \Sigma_i BA_i e^{-r_i}(1 + \cos\alpha_i)$, where BA_i is the basal area of the *i*th tree within a 5-m radius of the sampling plot centre, r_i is the distance between the sampling plot centre and the *i*th tree, and α is the angle between the slope line and the sampling plot centre. The relation of *A*. *adsurgens* subsp. *adsurgens* to each of the measured factors was analysed by correlation analysis. Spearman rank correlation coefficients were calculated with the software Statistica 7. Frequency and cover of *A*. *adsurgens* subsp. *adsurgens* in relation to canopy openess and canopy index were compared with frequency and cover of other frequent grass and sedge species to visualise their relationships to light availability and their resistance during the spruce colonisation process. Ellenberg indicator values (ELLENBERG et al. 1991) were calculated from 85 phytosociological relevés and 59 transect plots with occurrence of *A*. *adsurgens* subsp. *adsurgens*, and subsequently the indicator values for the taxon were calibrated using JUICE (TICHÝ 2002).

Nomenclature of vascular plants and syntaxa follows MARHOLD & HINDÁK (1998, available online: http://ibot.sav.sk/checklist/) or JANIŠOVÁ et al. (2007b), respectively.

2.2 Growth characteristics in cultivation

Clonal morphology and growth characteristics of *A*venula *adsurgens* subsp. *adsurgens* were investigated experimentally. Six randomly selected tussocks (genets) were divided into individual tillers (ramets), and ten tillers per tussock (one tiller per pot) were grown during two growing seasons (from April 2004 to October 2005). Pots with a diameter of 14 cm and a soil mixture (soil from the natural habitat, garden substrate and sand in ratio 1:3:3) were used for the growth experiment. To allow free development of extravaginal tillers (spacers), after the first growing season, eight randomly selected tussocks (developed from individual tillers of one from six genets mentioned above) were cultivated in a flower bed (with a 1:1 mixture of sand and garden substrate) at distances of 30 cm between the tussocks. The following growth characteristics were recorded after each of the two growing seasons: number of newly formed daughter tillers, number of both surviving and dead tillers, tussock diameter at the soil surface, maximum horizontal distance of extravaginal tillers from their mother tillers and number of spacers. After the second growing season, number of flowers and length of spacers were recorded, too. The recorded data were used to calculate genet averages for i) tussock diameter (formed since the beginning of the experiment from a single planted tiller); ii) maximum distance of tillers from their mother tiller after two growing seasons; iii) number of flowering tillers; iv) number of spacers and their lengths after two years of cultivation.

Kruskal-Wallis one-way analysis of variance tests were used to compare growth characteristics of plants belonging to different genets. Mann-Whitney U tests were used to compare plants planted in pots with plants planted in the flower bed.

3. Results

3.1 Phytosociological affiliation of *Avenula adsurgens* subsp. *adsurgens*

The inspection of the whole grassland data set (672 relevés containing 656 species of vascular plants) helped us to identify species that were negatively or positively associated with the occurrence of *Avenula adsurgens* subsp. *adsurgens* in the study region (Fig. 1).

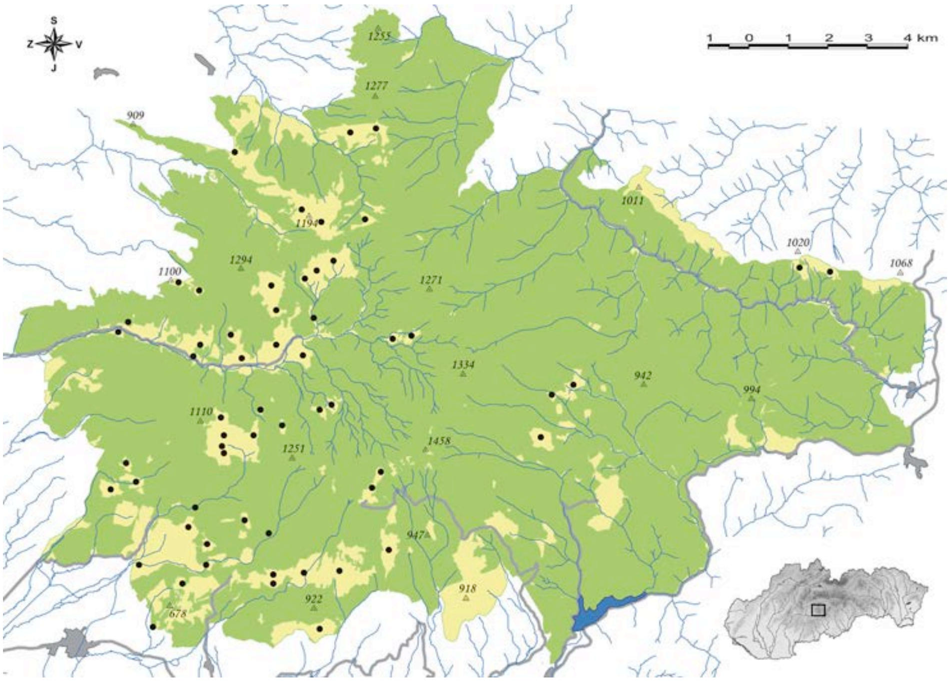

Fig. 1. Distribution of *Avenula adsurgens* subsp. *adsurgens* in the study area. The Landscape Protected Area Poľana is shown in colours, green for forests and yellow for grasslands. Black circles indicating the occurrence of the studied taxon are based on localities published in JANIŠOVÁ et al. (2004).

Abb. 1. Verbreitung von *Avenula adsurgens* subsp. *adsurgens* im Untersuchungsgebiet. Das Landschaftsschutzgebiet Poľana ist farbig dargestellt (grün = Wälder, gelb = Grasland). Die schwarzen Punkte zeigen das Vorkommen der Art entsprechend der in JANIŠOVÁ et al. (2004) aufgeführten Lokalitäten an.

The following taxa were negatively associated with *A. adsurgens* subsp. *adsurgens* (phi coefficient < -0.12, in ascending order): *Myosotis scorpioides* agg., *Lychnis flos-cuculi*, *Poa trivialis*, *Carex nigra*, *Caltha palustris* agg., *Scirpus sylvaticus*, *Filipendula ulmaria*, *Alopecurus pratensis*, *Trisetum flavesens*, *Lysimachia nummularia*, *Juncus effusus*, *Deschampsia cespitosa*, *Ranunculus repens*, *Crepis paludosa*, *Dactylorhiza majalis*, *Holcus lanatus*, *Galium palustre*, *Carex ovalis*, *Festuca pratensis*, *Galium uliginosum*, *Cerastium holosteoides*, *Cirsium rivulare*, *Cirsium palustre*, *Lysimachia vulgaris* and *Equisetum arvense*. Most of these species are typical of wetlands, wet grasslands or intensively used grasslands, which are avoided by *A. adsurgens* subsp. *adsurgens*.

The following species had the highest fidelity to *A. adsurgens* subsp. *adsurgens* (phi coefficient > 0.3, in descending order): *Juniperus communis*, *Knautia arvensis*, *Carlina acaulis*, *Ranunculus polyanthemos*, *Potentilla aurea*, *Brachypodium pinnatum*, *Trifolium flexuosum*, *Viola canina*, *Potentilla erecta*, *Carex pilulifera*, *Fragaria vesca*, *Luzula luzuloides*, *Campanula persicifolia*, *Pyrethrum corymbosum*, *Trifolium montanum*, *Cruciata glabra*, *Veronica officinalis* and *Calamagrostis arundinacea*. The following taxa constantly co-occurred with *A. adsurgens* subsp. *adsurgens* (values over 60%, in descending order) and had also a high fidelity (phi coefficient > 0.2): *Agrostis capillaris*, *Achillea millefolium* agg., *Alchemilla vulgaris* s. lat., *Briza media*, *Hypericum maculatum*, *Nardus stricta*, *Pimpinella* *saxifraga* and *Tyhmus pulegioides*. Both latter groups contain taxa typical of mesophilous grasslands of the order *Nardetalia strictae* (class *Nardetea strictae* Rivas Goday et Borja Carbolell 1961) where *A. adsurgens* subsp. *adsurgens* occurs most frequently.

Based on the results of the TWINSPAN analysis, plant communities containing *A. adsurgens* subsp. *adsurgens* can be divided into two main groups, each of them involving the managed grasslands as well as their successional stages.

a) Grasslands of warmer and drier habitats distributed at lower altitudes (700–1000 m), assigned to the *Campanulo rotundifoliae-Dianthetum deltoidis* Balátová-Tuláčková 1966 association within the *Violion caninae* Schwickerath 1944 alliance (clusters 1 and 2 in Table 1).

b) Montane grasslands of cooler and moister habitats at higher altitudes (900–1325 m) assigned to one of two following associations or having an intermediate position between them: *Festuco capillatae-Nardetum strictae* Klika et Šmarda 1944 (alliance *Violion caninae*) and *Violo sudeticae-Agrostietum capillaris* Ujházy in Janišová et al. 2007 (alliance *Nardo strictae-Agrostion tenuis* Sillinger 1933) (clusters 3, 4 and 5 in Table 1).

In the ordination plot (Fig. 2), these two groups of relevés are well separated along the first ordination axis, which can be interpreted by increasing moisture and decreasing temperature. The second axis reflects mainly the effect of altitude.

Phytosociological interpretation and characteristics of individual clusters (Table 1) are as follows:

Cluster 1 represents a thermophilous variant of *Campanulo rotundifoliae-Dianthetum deltoidis* located on SE-, S- and W-facing slopes at altitudes from 645 to 1020 m. Relevés of this cluster represent regularly mown or grazed grasslands dominated by *Nardus stricta*, *Agrostis capillaris* or *Festuca rupicola*. In contrast to the following vegetation types, they contain several xerothermophilous species (e.g. *Helianthemum ovatum*, *Festuca rupicola*, *Tithymalus cyparissias*), and thanks to their regular management, species of intensive grasslands (*Cynosutus cristatus*, *Trisetum flavescens*, *Plantago lanceolata*, *Leontodon hispidus*, *Taraxacum* sect. *Ruderalia*) are frequent.

Cluster 2 represents typically developed *Campanulo rotundifoliae-Dianthetum deltoidis* and its earlier successional stages. These stands are distributed at altitudes from 780 to 1100 m on S- or SE-(SW-) facing slopes. Most of them are abandoned or used as slightly grazed pastures, which is reflected in high cover values of expansive grasses (*Brachypodium pinnatum*, *Calamagrostis epigejos*, *A. adsurgens* subsp. *adsurgens*), which occur here in combination with oligotrophic species of the alliance *Violion caninae*.

Cluster 3 contains stands of *Festuco capillatae-Nardetum strictae* including transitions to the *Polygono bistortae-Trisetion flavescentis* Br.-Bl. et Tüxen ex Marhall 1947 and the *Arrhenatherion elatioris* Luquet 1926 alliances. These stands are distributed at altitudes from 640 to 1130 m mainly on N-facing slopes. Most of them are managed by mowing or grazing. Species of submontane meadows well supplied with water and nutrients are frequent, e.g. *Hypericum maculatum*, *Trollius altissimus*, *Festuca pratensis*, *Crepis mollis*, *Geranium sylvaticum*, *Myosotis scorpioides* agg., *Primula elatior*.

Cluster 4 includes stands of *Violo sudeticae-Agrostietum capillaris* and *Festuco capillatae-Nardetum strictae* associations distributed mainly at higher altitudes from 900 to 1325 m, which are abandoned or irregularly grazed. In the stands dominated by *Nardus stricta* and *Agrostis capillaris*, species typical of montane grasslands of the *Nardo strictae-Agrostion tenuis* alliance (*Poa chaixii*, *Trommsdorfia maculata*, *Campanula serrata*, *Vaccinium myrtillus*, *Luzula luzuloides*, *Carex pilulifera*) are frequent.

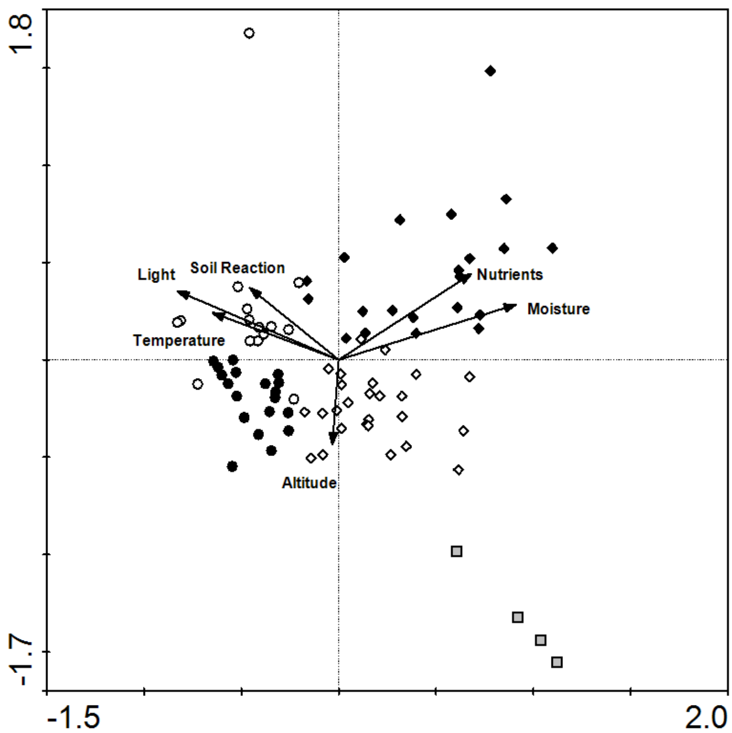

Fig. 2. Detrended Correspondence Analysis (DCA) of 85 relevés containing *Avenula adsurgens* subsp. *adsurgens*. Eigenvalues of the first and the second axes were 0.381 and 0.341, respectively. Post-hoc correlated environmental variables derived from Ellenberg indicator values are shown. Groups of relevés distinguished in the synoptic table (Table 1) are marked by different symbols: ○ – thermophilous variant of *Campanulo rotundifoliae-Dianthetum deltoidis*; ● – typical variant of *Campanulo rotundifoliae-Dianthetum deltoidis*; ♦ – prevailing managed stands of *Festuco capillatae-Nardetum strictae* with transitions to *Arrhenatherion* and *Polygono-Trisetion*; ◊ – prevailing unmanaged *Violo sudeticae-Agrostietum capillaris* and *Festuco capillatae-Nardetum strictae*; □ – advanced successional stages of *Festuco capillatae-Nardetum strictae*.

Abb. 2. *Detrended Correspondence Analysis* (DCA) von 85 Vegetationsaufnahmen mit *Avenula adsurgens* subsp. *adsurgens*. Die Eigenwerte der ersten und zweiten Achse sind 0,381 und 0,341. Vektoren zeigen *post-hoc*-korrelierte Umweltvariablen an, die aus Ellenberg-Zeigerwerten gewonnen wurden. Symbole zeigen die Zugehörigkeit der Aufnahmen zu den in Tabelle 1 unterschiedenen Aufnahmegruppen an: ○ – Thermophile Variante des *Campanulo rotundifoliae-Dianthetum deltoidis*; ● – Typische Variante des *Campanulo rotundifoliae-Dianthetum deltoidis*; ♦ – überwiegend bewirtschaftete Bestände des *Festuco capillatae-Nardetum strictae* mit Übergängen zum *Arrhenatherion* und *Polygono-Trisetion*; ◊ – überwiegend brachliegende Bestände des *Violo sudeticae-Agrostietum capillaris* und *Festuco capillatae-Nardetum strictae*; □ – fortgeschrittene Sukzessionsstadien des *Festuco capillatae-Nardetum strictae*.

Cluster 5 includes advanced successional stages of the *Festuco capillatae-Nardetum strictae* distributed at altitudes between 900 and 1000 m. From the former vegetation types they are dif-ferentiated by a high cover (25–85%) of woody species (*Fagus sylvatica*, *Picea abies*, *Acer pseudoplatanus* etc.) in both shrub and tree layer. Numerous forest understorey species (*Hieracum murorum*, *Viola riviniana*, *Pyrola minor*, *Anemone ranunculoides*, *Mercurialis perennis*) are present, too.

Table 1. Combined synoptic table of grassland communities containing *Avenula adsurgens* subsp. *adsurgens* with species percentage constancy and cover ranges (superscript). The groups of relevés shown as individual columns are described in the text and depicted in the ordination diagram (Fig. 2). Species with high fidelity to individual species groups confirmed by Fisher's exact test at a significance level of $P < 0.01$ are given in bold type. Phytosociological interpretation of individual clusters: 1 – *Campanulo rotundifoliae-Dianthetum deltoidis*, most thermophilous stands; 2 – *Campanulo rotundifoliae-Dianthetum deltoidis*, typical stands and their successional stages; 3 – mown and grazed stands of *Festuco capillatae-Nardetum strictae* with transitions to *Arrhenatherion* and *Polygono-Trisetion*; 4 – *Violo sudeticae-Agrostietum capillaris* and *Festuco capillatae-Nardetum strictae*, mainly unmanaged; 5 – advanced successional stages of the *Festuco capillatae-Nardetum strictae*.

Tabelle 1. Übersichtstabelle der Grasslandgesellschaften mit *Avenula adsurgens* subsp. *adsurgens* mit Prozentstetigkeiten und Deckungsgrad-Spannen (hochgestellte Werte) der Arten. Die Aufnahmegruppen der einzelnen Spalten sind im Text beschrieben und im Ordinationsdiagramm (Abb. 2) dargestellt. Arten mit enger Bindung an einzelne Artengruppen (auf dem Signifikanzniveau $P < 0{,}01$ nach einem Fisher Exact-Test) sind in fett dargestellt. Pflanzensoziologische Zuordnung der Aufnahmegruppen 1–5 s. englischen Tabellenüberschrift.

Group No.	1	2	3	4	5
Number of relevés	15	19	21	26	4
Symbol for the group in Fig. 2	○	●	♦	◊	□
Woody species in the shrub and tree layers					
Juniperus communis	7^{+}	**89^{r-4}**	5^{r}	38^{r-2}	.
Picea abies	7^{r}	37^{r-2}	10^{+}	50^{r-2}	**100^{2-5}**
Acer pseudoplatanus	.	5^{r}	5^{r}	8^{r-+}	**100^{r-+}**
Fagus sylvatica	.	5^{r}	.	12^{r-+}	**100^{+-2}**
Abies alba	.	.	.	4^{r}	**50^{r-1}**
Sorbus aucuparia	.	.	.	.	**50^{r}**
Rosa canina agg.	7^{r}	26^{r-+}	5^{+}	12^{r}	50^{r}
Betula pendula	13^{r-+}	.	.	.	.
Prunus spinosa	.	5^{r}	.	.	.
Malus sylvestris	.	5^{r}	5^{r}	.	.
Salix cinerea	.	.	10^{r}	.	.
Corylus avellana	.	.	10^{+}	4^{r}	.
Sambucus ebulus	.	.	.	.	25^{r}
Avenula adsurgens subsp. adsurgens	100^{r-3}	100^{r-4}	100^{+-3}	100^{r-4}	100^{r-2}
Species with high fidelity to five distinguished clusters (calculated for a subset of relevés containing A. adsurgens *subsp.* adsurgens, *confirmed by Fisher's exact test at a significance level of P < 0.01)*					
Plantago lanceolata	**93^{+-2}**	63^{r-1}	62^{+-2}	58^{r-2}	.
Leontodon hispidus	**87^{+-2}**	53^{+-2}	38^{+-2}	27^{r-2}	.
Dianthus deltoides	**53^{+}**	16^{+}	19^{+}	.	.
Taraxacum sect. Ruderalia	**53^{r-2}**	16^{r}	33^{+-2}	4^{1}	.
Euphrasia rostkoviana	**53^{+-3}**	26^{r-2}	14^{r-2}	15^{r-+}	.
Daucus carota	**33^{r-2}**	5^{r}	5^{r}	.	.
Agrimonia eupatoria	**33^{+-1}**	5^{+}	5^{r}	.	.
Hypochaeris radicata	**27^{r-+}**	5^{r}	5^{+}	.	.
Leontodon autumnalis	**33^{+-2}**	.	5^{+}	.	.
Helianthemum ovatum	**27^{r-2}**	.	5^{1}	.	.
Cynosurus cristatus	**40^{+-1}**	.	.	.	.
Trisetum flavescens	**33^{+-2}**	.	19^{+-2}	.	.
Festuca rupicola	**93^{r-3}**	**100^{+-3}**	10^{+-2}	38^{r-2}	.
Hypericum perforatum	**67^{r-2}**	**79^{r-2}**	.	15^{r-2}	.
Knautia arvensis	73^{+-2}	**100^{r-1}**	67^{r-2}	54^{r-2}	50^{+}
Thymus pulegioides	87^{+-3}	**95^{+-2}**	48^{r-2}	77^{r-2}	.
Plantago media	73^{+-2}	**95^{r-2}**	57^{r-1}	42^{r-1}	.

Group No.	1	2	3	4	5
Carex caryophyllea	80^{+-2}	**89**$^{r-2}$	33^{+-1}	42^{r-2}	.
Silene nutans	47^{r-2}	**89**$^{r-2}$	14^{r-+}	35^{r-+}	.
Galium verum	53^{+-2}	**89**$^{r-2}$	71^{+-3}	38^{r-2}	.
Trifolium montanum	20^{+-1}	**84**$^{r-3}$	33^{r-1}	54^{r-2}	.
Brachypodium pinnatum	40^{+-4}	**74**$^{+-4}$	14^{+-3}	35^{+-4}	25^{4}
Tithymalus cyparissias	47^{+-2}	**68**$^{r-2}$	10^{r-1}	4^{1}	.
Viola hirta	27^{+-2}	**68**$^{r-2}$	10^{+}	8^{r}	.
Silene vulgaris	13^{r-1}	**63**$^{r-2}$	14^{r-+}	19^{+-2}	.
Campanula rotundifolia agg.	7^{+}	**58**$^{r-2}$	33^{+-2}	12^{r-+}	.
Thlaspi caerulescens	7^{r}	**42**$^{r-+}$	10^{+}	8^{r}	.
Potentilla heptaphylla	13^{+}	**32**$^{r-+}$	.	.	.
Astragalus glycyphyllos	7^{+}	**32**$^{r-1}$	.	4^{+}	25^{r}
Arabis hirsuta agg.	.	**21**$^{r-+}$	.	.	.
Ranunculus acris	67^{+-2}	68^{r-2}	**95**$^{+-2}$	69^{r-2}	50^{r-2}
Festuca pratensis	60^{+-2}	.	**76**$^{+-3}$	12^{r-+}	.
Ranunculus auricomus agg.	7^{1}	16^{r-+}	**76**$^{r-2}$	35^{r-2}	50^{r-+}
Vicia cracca	20^{r-+}	11^{r-+}	**71**$^{+-2}$	31^{r-2}	.
Dactylis glomerata	40^{+-1}	5^{+}	**71**$^{+-2}$	8^{+}	25^{+}
Lathyrus pratensis	13^{r-+}	5^{1}	**67**$^{r-2}$	27^{+-2}	.
Primula elatior	.	16^{r-1}	**67**$^{+-2}$	54^{r-2}	75^{r-+}
Carum carvi	40^{r-1}	11^{+}	**57**$^{r-1}$	.	.
Vicia sepium	.	.	**57**$^{r-1}$	8^{+-2}	25^{r}
Arrhenatherum elatius	7^{3}	26^{r-+}	**48**$^{+-2}$	4^{+}	50^{+}
Trollius altissimus	.	.	**48**$^{r-4}$	8^{+-1}	.
Colchicum autumnale	27^{r-+}	11^{r-+}	**43**$^{r-2}$	4^{+}	.
Deschampsia cespitosa	7^{+}	.	**43**$^{r-3}$	31^{r-2}	.
Phyteuma spicatum	.	.	**43**$^{r-2}$	31^{r-+}	25^{r}
Crepis mollis	.	.	**33**$^{r-2}$	4^{2}	.
Phleum pratense	.	.	**24**$^{r-+}$	4^{r}	.
Cirsium arvense	7^{+}	.	**24**$^{r-2}$	.	.
Myosotis scorpioides agg.	.	.	**24**$^{r-+}$	.	.
Alopecurus pratensis	.	.	**24**$^{+-2}$	.	.
Potentilla erecta	67^{+-2}	74^{+-2}	86^{+-2}	**100**$^{r-3}$	100^{2-2}
Hypericum maculatum	53^{+-1}	74^{r-2}	100^{+-3}	**100**$^{+-3}$	100^{1-2}
Luzula luzuloides	.	21^{+-1}	67^{+-3}	**92**$^{+-3}$	100^{r-2}
Veronica officinalis	33^{+-1}	79^{r-2}	43^{r-1}	**85**$^{r-2}$	100^{+-2}
Carex pilulifera	33^{+-2}	32^{+-2}	10^{+}	**69**$^{+-2}$	50^{1-2}
Avenella flexuosa	13^{1-3}	5^{2}	24^{+-2}	**54**$^{+-3}$	75^{+-2}
Poa chaixii	.	5^{+}	29^{r-2}	**54**$^{r-2}$	25^{2}
Vaccinium myrtillus	.	.	.	**15**$^{+-2}$	.
Hieracium murorum	.	.	5^{+}	12^{r-+}	**100**$^{+}$

Species constantly co-occurring with A. adsurgens *subsp.* adsurgens *(estimated within the large data set containing all relevés recorded in the study region)*

Agrostis capillaris	80^{+-3}	95^{+-2}	100^{+-3}	100^{+-3}	100^{2-2}
Alchemilla vulgaris s. lat.	100^{r-2}	100^{r-2}	90^{+-3}	88^{r-2}	75^{r}
Briza media	100^{+-2}	100^{+-2}	86^{+-2}	85^{r-2}	25^{r}
Nardus stricta	93^{+-4}	84^{+-4}	57^{+-2}	81^{+-4}	75^{+-2}
Achillea millefolium agg.	87^{+-2}	100^{+-2}	90^{+-2}	96^{+-2}	75^{r-+}
Pimpinella saxifraga agg.	87^{r-2}	89^{+-2}	67^{r-1}	73^{r-2}	75^{+}

Other species with high fidelity to relevés containing A. adsurgens *subsp.* adsurgens *(phi > 0.3, calculated for the large data set containing all relevés recorded in the study region)*

Cruciata glabra	87^{+-2}	100^{+-2}	100^{+-3}	96^{+-3}	100^{+-1}
Viola canina	80^{+-2}	100^{+-2}	95^{+-2}	73^{+-2}	50^{r}
Trifolium flexuosum	53^{r-2}	63^{r-3}	38^{+-1}	31^{+-4}	50^{+}

Group No.	1	2	3	4	5
Ranunculus polyanthemos	33^{+-1}	42^{r-+}	48^{r-1}	69^{r-2}	25^{r}
Carlina acaulis	47^{r-2}	95^{r-2}	52^{+-2}	92^{r-2}	100^{r-+}
Potentilla aurea	20^{r-+}	47^{r-2}	38^{r-1}	65^{+-2}	100^{r-1}
Fragaria vesca	20^{r-+}	37^{r-2}	57^{r-1}	54^{r-2}	100^{2-2}
Calamagrostis arundinacea	13^{+}	16^{r-+}	5^{1}	15^{r-1}	25^{+}
Campanula persicifolia	7^{+}	32^{r-+}	5^{+}	35^{r-2}	50^{r-+}
Pyrethrum corymbosum	.	32^{r-1}	10^{r}	12^{r-1}	.
Other species					
Lotus corniculatus	93^{+-2}	95^{+-2}	90^{+-2}	92^{+-2}	75^{r-+}
Festuca rubra agg.	93^{+-2}	89^{r-2}	95^{+-3}	85^{r-3}	75^{2-2}
Veronica chamaedrys	80^{r-2}	89^{r-2}	95^{+-2}	88^{r-2}	75^{r-1}
Acetosa pratensis	80^{+-1}	89^{+-1}	95^{+-2}	88^{r-2}	25^{r}
Prunella vulgaris	60^{+-2}	26^{+}	24^{+-1}	50^{r-+}	100^{r-1}
Ajuga reptans	20^{r-+}	16^{r}	43^{r-2}	62^{r-2}	100^{1-2}
Trifolium repens	80^{+-3}	74^{r-1}	71^{+-3}	58^{r-2}	25^{r}
Pilosella officinarum	67^{+-2}	26^{r-1}	14^{r-+}	62^{r-+}	75^{+-2}
Danthonia decumbens	47^{+-2}	58^{+-2}	10^{+}	46^{+-2}	75^{+-2}
Galium mollugo agg.	33^{r-1}	26^{r-1}	33^{r-+}	12^{r-2}	50^{r}
Carex montana	13^{2-2}	11^{+-2}	5^{+}	15^{r-+}	50^{r-+}
Carex panicea	13^{+}	5^{2}	19^{+-1}	8^{r-+}	25^{r}
Campanula patula	73^{r-+}	74^{r-1}	76^{r-+}	62^{r-1}	.
Luzula campestris s. lat.	93^{+-2}	95^{+-2}	86^{r-2}	65^{r-2}	.
Anthoxanthum odoratum	87^{+-2}	63^{r-2}	76^{+-2}	62^{r-2}	.
Poa pratensis agg.	80^{+-2}	74^{+-2}	86^{+-3}	38^{r-2}	.
Stellaria graminea	73^{r-2}	37^{r-+}	76^{r-2}	73^{r-2}	.
Trifolium pratense	87^{+-2}	68^{r-2}	57^{+-2}	50^{r-2}	.
Leucanthemum vulgare agg.	67^{+-2}	53^{r-1}	62^{r-1}	54^{r-1}	.
Carex pallescens	40^{+-1}	37^{+-1}	48^{+-1}	46^{r-1}	.
Polygala vulgaris	60^{+-2}	21^{r-+}	29^{r-1}	38^{r-1}	.
Tragopogon orientalis	27^{r-1}	42^{r-1}	38^{r-2}	12^{r-+}	.
Cardamine pratensis agg.	.	16^{r-+}	48^{r-1}	35^{r-+}	.
Cerastium holosteoides	40^{r-+}	32^{r-+}	24^{+-1}	12^{r-+}	.
Rhinanthus minor	33^{r-2}	16^{r-+}	38^{r-1}	4^{+}	.
Dianthus carthusianorum agg.	33^{r-+}	32^{r-2}	.	19^{+}	.
Steris viscaria	27^{+-2}	21^{r-2}	14^{r-+}	15^{r-+}	.
Genista tinctoria	40^{r-2}	16^{r-1}	14^{r-+}	12^{+-2}	.
Sanguisorba minor	27^{r-1}	37^{r-+}	10^{+}	4^{+}	.
Salvia pratensis	33^{+-2}	21^{r-2}	19^{r-1}	.	.
Trifolium alpestre	7^{+}	32^{r-2}	19^{r-+}	8^{+}	.
Antennaria dioica	13^{+}	16^{r-2}	.	27^{+-2}	.
Anthyllis vulneraria	13^{2-2}	32^{r-+}	5^{r}	8^{r-+}	.
Trifolium ochroleucon	27^{r-2}	32^{r-1}	5^{+}	.	.
Ranunculus bulbosus	33^{+-2}	16^{r-+}	10^{+}	.	.
Genista pilosa	27^{+-2}	5^{1}	10^{+}	8^{r-+}	.
Botrychium lunaria	13^{r}	5^{+}	14^{r-+}	8^{r-+}	.
Trommsdorfia maculata	.	11^{1}	5^{r}	19^{r-1}	.
Linum catharticum	13^{+-1}	21^{+-2}	.	4^{+}	.
Betonica officinalis	.	11^{+}	10^{r-+}	8^{r-+}	25^{r}
Festuca ovina	7^{2}	16^{+}	.	8^{+-2}	.
Jacea phrygia agg.	.	16^{r-+}	5^{+}	8^{+}	.
Platanthera bifolia	.	5^{+}	.	15^{r-+}	25^{r}
Potentilla collina agg.	20^{1-2}	5^{r}	5^{+}	.	.
Cirsium eriophorum	13^{r-1}	11^{r-+}	5^{r}	.	.
Trifolium aureum	13^{+}	.	5^{r}	8^{r}	.
Pseudolysimachion spicatum	7^{r}	16^{+}	.	4^{+}	.
Rubus idaeus	.	5^{r}	5^{1}	12^{r-2}	.

Group No.	1	2	3	4	5
Asarum europaeum	.	5^{r}	10^{+-2}	4^{r}	25^{2}
Tephroseris integrifolia	.	5^{+}	5^{r}	4^{r}	.
Galium pumilum agg.	.	5^{+}	5^{+}	4^{r}	.
Acetosa arifolia	.	.	5^{+}	4^{+}	25^{+}

Additional species: Acetosella multifida agg. 2:11^{r-+}; Aegopodium podagraria 3:19^{+-2}, 4:8^{+}; Agrostis canina 1:13$^{1-2}$, 3:5^{+}; Allium oleraceum 1:7^{+}, 2:5^{+}; Anemone nemorosa 3:10^{r-+}, 5:25^{2}; Anemone ranunculoides 5:25^{+}; Angelica sylvestris 3:5^{+}; Aquilegia vulgaris 2:5^{+}; Arenaria serpyllifolia agg. 1:7^{r}; Astrantia major 3:14^{+}, 4:4^{+}; Avenula pubescens 1:7^{+}, 3:10$^{2-2}$; Calamagrostis epigejos 2:16$^{4-4}$, 4:8$^{3-4}$; Calamintha species 1:7^{1}; Campanula glomerata 4:4^{r}; Campanula rapunculoides 2:5^{+}; Campanula serrata 3:19^{r-1}, 4:27^{+-2}; Capsella bursa-pastoris 3:5^{r}; Cardaminopsis arenosa 4:4^{r}; Cardaminopsis halleri 2:5^{r}, 4:8^{r}; Carduus acanthoides 3:5^{+}; Carex hirta 3:10^{+-2}, 4:4^{+}; Carex leporina 3:5^{r}, 4:4^{+}; Carex tomentosa 3:5^{+}; Carlina vulgaris 3:5^{r}; Chaerophyllum aromaticum 3:19^{r-1}, 4:4^{r}; Chaerophyllum hirsutum 3:10^{+}; Chenopodium species 1:7^{r}; Cirsium palustre 3:10^{r-+}, 4:4^{r}; Crepis praemorsa 3:5^{2}; Cuscuta epithymum 1:7^{r}; Dactylorhiza sambucina 2:5^{r}, 4:12^{r-+}; Elymus repens 3:5^{2}; Epilobium palustre 3:5^{+}; Equisetum arvense 3:5^{+}; Erophila verna 1:7^{r}; Euphrasia stricta 1:7^{+}; Filipendula ulmaria 3:10^{+}; Filipendula vulgaris 3:5^{+}; Fragaria viridis 3:5^{+}; Gentianella lutescens 2:5^{+}, 4:4^{+}; Geranium sylvaticum 3:14^{r-1}; Geum rivale 2:5^{+}, 3:19^{r-2}; Geum urbanum 4:4^{r}, 5:25^{+}; Gymnadenia conopsea 4:8^{+}; Heracleum sphondylium 1:7^{r}, 3:19^{+-1}; Hieracium cymosum 3:10^{r-+}; Holcus lanatus 1:7^{2}, 3:5^{+}; Juncus effusus 3:5^{+}; Lathyrus sylvestris 3:5^{+}; Lilium martagon 3:10^{+-1}; Listera ovata 3:10^{r-+}; Lychnis flos-cuculi 3:5^{r}; Lysimachia nummularia 3:5^{+}; Maianthemum bifolium 3:10^{r-+}; Mentha arvensis 3:5^{1}; Mercurialis perennis 3:5^{+}, 5:25^{+}; Myosotis arvensis 1:7^{+}, 3:5^{r}; Omalotheca sylvatica 1:7^{r}; Ophioglossum vulgatum 3:5^{1}; Phleum phleoides 2:5^{+}; Pilosella bauhinii 2:5^{r}; Plantago major 1:7^{r}, 3:5^{+}; Poa annua 3:5^{+}; Poa trivialis 3:5^{+}, 4:4^{1}; Polygonatum odoratum 3:5^{+}; Polygonatum verticillatum 3:10^{r-+}; Potentilla rupestris 2:5^{+}; Primula veris 3:5^{+}; Prunella laciniata 1:13^{+-2}, 2:5^{r}; Pyrola minor 5:25^{r}; Ranunculus repens 3:5^{2}, 4:4^{+}; Sanguisorba officinalis 3:5^{+}; Saxifraga granulata 1:7^{+}; Scorzonera humilis 4:4^{r}; Securigera varia 2:5^{2}, 3:5^{+}; Sedum acre 1:7^{r}, 2:5^{r}; Sedum sexangulare 3:5^{+}; Senecio jacobaea 1:7^{+}, 2:5^{r}; Serratula tinctoria 1:7^{r}, 3:5^{+}; Silene nemoralis 2:5^{r}; Stachys sylvatica 3:5^{r}; Stellaria media 1:7^{1}; Symphytum tuberosum 2:5^{+}, 3:10^{r-+}; Thalictrum aquilegiifolium 4:4^{r}; Thesium linophyllon 1:13^{+-2}; Traunsteinera globosa 3:5^{r}, 4:12^{r-+}; Trifolium dubium 1:7^{+}; Trifolium pannonicum 1:7^{+}; Trommsdorfia uniflora 2:5^{1}, 4:8^{r-+}; Tussilago farfara 3:5^{r}; Urtica dioica 3:10^{+}; Valerianella locusta 1:7^{r}; Verbascum densiflorum 1:7^{r}; Veronica arvensis 1:7^{+}; Vicia dumetorum 4:4^{+}; Vincetoxicum hirundinaria 3:5^{+}; Viola lutea 4:4^{+}; Viola reichenbachiana 4:8^{r-+}, 5:25^{+}; Viola riviniana 5:25^{1}; Viola tricolor 1:20^{r-+}, 2:5^{+}.

3.2 Habitat preferences and ecological requirements of *Avenula adsurgens* subsp. *adsurgens*

In the study region, *A. adsurgens* subsp. *adsurgens* is distributed at altitudes between 480 m and 1325 m and found mainly on volcanic bedrock; only few localities were found on crystalline bedrock. Localities of all aspects are similarly frequent; however, there are only few localities on east-facing slopes due to the lack of available grassland areas on the eastern slopes of the Poľana massif. Concerning the grassland management, *A. adsurgens* subsp. *adsurgens* occurred mainly in pastures (25%), slightly or irregularly grazed pastures (38%) or in long-term unmanaged grasslands (21%). Exceptionally, it could be found in formerly recultivated or fenced pastures. Less frequently and with low cover, it occurred on meadows (5%) or in plots managed by a combination of mowing and grazing (categories MG and AMG, 11%). In the Hriňová region, *A. adsurgens* subsp. *adsurgens* was found in the irregularly burned meadow community. None of the studied stands was treated with manure or fertiliser. In summary, about one third (34%) of the sampled stands was regularly utilised in a traditional way during the sampling period. The two remaining thirds were either abandoned or utilised only irregularly.

In the data sub-set of mesophilous grasslands (427 relevés), the main environmental gradient along the first CCA axis (Fig. 3) was best correlated with altitude (r = 0.71), and the gradient along the second axis was best correlated with mowing (r = -0.48). According to the

Monte Carlo permutation test, these two variables together with xericity had significant effects upon the vegetation variability. Eigenvalues of the first and second axis were 0.267 and 0.171, respectively. The variance of the species-environment relationship was 32.5% (first axis) and 53.3% (first and second axes). In the ordination plot (Fig. 3), the preference of *A*. *adsurgens* subsp. *adsurgens* for grasslands at higher altitudes and less intensive utilisation is obvious.

Based on our calculation of Ellenberg indicator values (Table 2), *A*. *adsurgens* subsp. *adsurgens* can be characterised as follows: **light: 7** (plant occurring chiefly in full light, but sometimes surviving in slight shade); **temperature: 5** (plant occurring chiefly in the sub

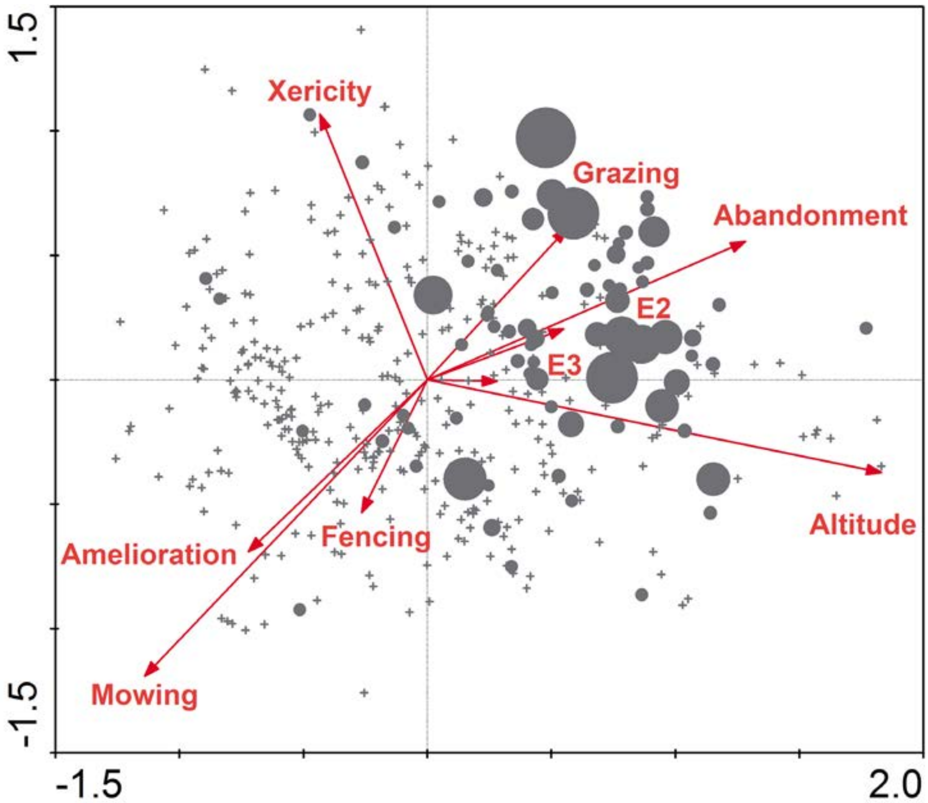

Fig. 3. Canonical Correspondence Analysis (CCA) of mesophilous grasslands in the study region (427 relevés). Relevés with occurrence of *Avenula adsurgens* subsp. *adsurgens* are depicted by circles with diameters proportional to its percentage cover. Nine environmental variables are shown. Eigenvalues of the first and second axes were 0.267 and 0.171, respectively; percentage variance of species-environment relationship was 32.5 (first axis) and 53.3 (first and second axes).

Abb. 3. *Canonical Correspondence Analysis* (CCA) des mesophilen Grasslands im Untersuchungsgebiet (427 Aufnahmen). Aufnahmen mit Vorkommen von *Avenula adsurgens* subsp. *adsurgens* sind als Kreis dargestellt (der Durchmesser der Kreise symbolisiert die Deckung der Art). Neun Umweltvariablen sind dargestellt. Die Eigenwerte der ersten und zweiten Achse sind 0,267 und 0,171. Die Anteile erklärter Varianz der Arten-Umwelt-Zusammenhänge liegen bei 32,5% (erste Achse) und 53,3% (erste und zweite Achse).

montane temperate zone, often also in colline and subalpine zones, indicators of moderate temperatures); **continentality: 4** (plant occurring chiefly in regions with sub-oceanic climate, mostly in Central Europe, but spreading towards the East); **moisture: 4** (plant occurring on medium dry soils, usually avoiding very dry and very wet areas); **soil reaction: 5** (plant occurring on moderately acid soils, seldom found on very acid or neutral to alkaline soils); **nutrients/productivity: 3** (plant occurring chiefly on nutrient-poor soils, usually not found on moderately rich and rich soils).

3.3 Relation of *A*venula *adsurgens* subsp. *adsurgens* to light reduction and spruce colonisation

Along the spruce colonisation gradient, *A. adsurgens* subsp. *adsurgens* dominated in most of the plots of early successional stages and was present with lower percentage cover also in several plots of mid-successional stages, but it was absent from all plots of late successional stages (Fig. 4). Considering the combined effects of shading, needle fall and duration of tree influence expressed by the canopy index, *A. adsurgens* subsp. *adsurgens* had low to intermediate successional resistance during the spruce colonisation process compared to other grass and sedge species. A rapid retreat of *A. adsurgens* subsp. *adsurgens* from plots of higher canopy index values was obvious (Fig. 5). Its response to spruce colonisation was compared to several widespread co-occuring grass and sedge species. Similar response was detected in the case of *Agrostis capillaris* and *Danthonia decumbens*. Least resistant were *Briza media* (occurring only at low index values) and *Nardus stricta* (rapidly retreating at higher index values). *Brachypodium pinnatum* was least affected by spruce colonisation as it reached similar percentage cover values at various canopy index levels. *Avenella flexuosa* was most resistant to spruce colonisation, keeping high percentage cover also in later colonisation stages.

Regarding the species response to reduced light availability (represented by a reduced percentage canopy openness), *A. adsurgens* subsp. *adsurgens* was less sensitive than the typical heliophilous grassland species *Briza media*, *Nardus stricta* and *Danthonia decum-*

Table 2. Ellenberg indicator values for *Avenula adsurgens* subsp. *adsurgens* calibrated from our coenological data and those published by BORHIDI (1995) and SIMON (2000).

Tabelle 2. Auf Basis der eigenen Vegetationsdaten errechnete Ellenberg-Zeigerwerte für *Avenula adsurgens* subsp. *adsurgens* sowie die von BORHIDI (1995) und SIMON (2000) für *A. praeusta* angegebenen Zeigerwerte.

Ellenberg indicator value	The whole data set (85 relevés)		99 most frequent co-occurring species		Transect data	BORHIDI (1995)	SIMON (2000)
	Average (median)	Standard deviation	Average	No. of missing values	Average	*Avenula praeusta*	*Avenula praeusta*
Light	7.0 (7.0)	1.1	6.9	8	6.6	8	–
Temperature	5.3 (5.4)	1.0	5.4	50	5.3	4	5
Continentality	3.8 (3.7)	1.2	3.9	15	4.0	4	–
Moisture	4.6 (4.6)	1.1	4.5	20	4.3	4	3
Soil reaction	5.5 (5.5)	3.7	5.8	35	5.4	5	4
Nutrients/ Productivity	3.6 (3.5)	2.7	3.5	14	3.2	2	–

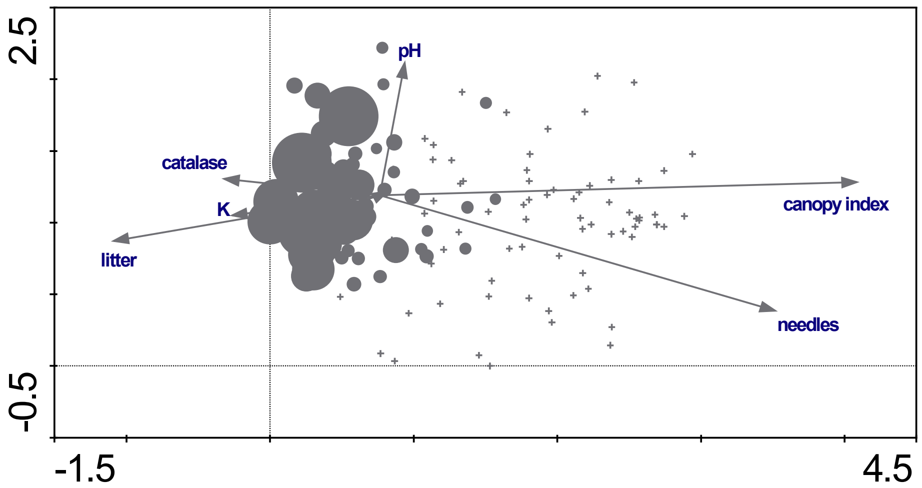

Fig. 4. Detrended Correspondence Analysis (DCA) of 155 circular transect plots. The first ordination axis represents the spruce colonisation gradient and is strongly correlated with the canopy index (r = 0.76). Plots containing *Avenula adsurgens* subsp. *adsurgens* are depicted by circles with diameters proportional to its percentage cover. Positions of other plots are depicted by cross marks. Environmental variables that are significantly correlated with the percentage cover of *A. adsurgens* subsp. *adsurgens* are shown.

Abb. 4. *Detrended Correspondence Analysis* (DCA) von 155 kreisförmigen Transektaufnahmen. Die erste Ordinationsachse spiegelt einen Gradienten zunehmender Besiedlung durch Fichten wider und ist eng mit dem Kronenschlussindex korreliert (r = 0,76). Aufnahmen mit *Avenula adsurgens* subsp. *adsurgens* sind als Kreis dargestellt (der Durchmesser der Kreise symbolisiert die Deckung der Art). Aufnahmen ohne die Art sind als Kreuze dargestellt. Es wurden diejenigen Umweltvariablen dargestellt, die signifikant mit der Deckung von *A. adsurgens* subsp. *adsurgens* korrelieren.

bens (Fig. 6). On the other hand, *Agrostis capillaris*, *Carex pilulifera*, *Avenella flexuosa*, *Brachypodium pinnatum* and *Luzula luzuloides* (common species of grassland and forest communities) were less sensitive, and *Festuca rubra* (a shade-tolerant grassland species) responded similarly to *A. adsurgens* subsp. *adsurgens*.

The survey of pedological, microclimatical and biological variables recorded in 59 transect plots containing *A. adsurgens* subsp. *adsurgens* is shown in Table 3.

3.4 Clonal morphology and growth characteristics of *Avenula adsurgens* subsp. *adsurgens*

During one growing season, separately planted tillers formed tussocks with an average diameter of 5.2 cm (range 2.7–8.5 cm) consisting of 11 living (range 5–18) and 1 dead (range 0–3) tillers. Five (range 0–10) of the newly formed tillers were extravaginal. After the first growing season, the average distance between two adjacent tillers at soil surface reached 2–3 cm with a maximum value of 6 cm.

After two growing seasons, the average tussock diameter was 8.7 cm (range 3.7–12.5 cm), and the tussocks contained 15 living (range 6–42) and 6 dead (range 0–14) tillers (Table 4). The autumn tillering resulted in 5 new tillers (range 1–12), and an average tussock had four (range 0–13) 0.5–21 cm long spacers. The spacers were formed from buds at the

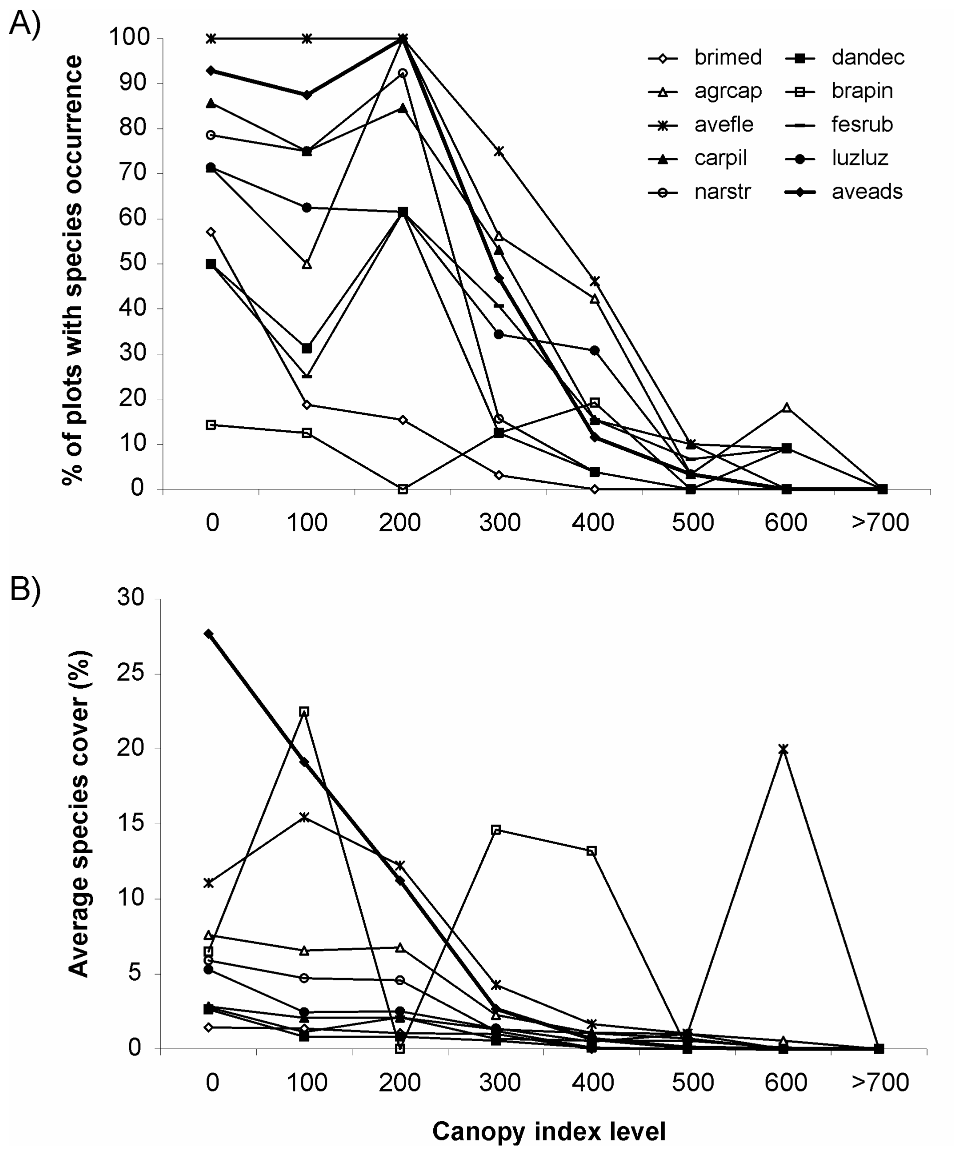

Fig. 5. Relation of *Avenula adsurgens* subsp. *adsurgens* to the canopy index level (which represents the intensity of spruce colonisation) in comparison to other frequent grass and sedge species. A) Percentage of plots with species occurrence at individual canopy index levels. B) Average species cover in plots with species occurrence. Response of *A. adsurgens* subsp. *adsurgens* is shown by a bold line. Species abbreviations: agrcap – *Agrostis capillaris*, aveads – *Avenula adsurgens*, avefle – *Avenella flexuosa*, brapin – *Brachypodium pinnatum*, brimed – *Briza media*, carpil – *Carex pilulifera*, fesrub – *Festuca rubra*, luzluz – *Luzula luzuloides*, narstr – *Nardus stricta*.

Abb. 5. Beziehung zwischen dem Auftreten von *Avenula adsurgens* subsp. *adsurgens* und dem Kronenschlussindex als Maß für das Ausmaß der Besiedlung durch Fichten. Weitere häufige Gras- und Seggenarten sind zum Vergleich dargestellt. A) Anteil der Aufnahmen mit Vorkommen der Art für die einzelnen Intervalle des Kronenschlussindex. B) Mittlerer Deckungsgrad verschiedener Arten in Aufnahmeflächen mit der untersuchten Sippe. Für *A. adsurgens* subsp. *adsurgens* ist der Verlauf fett dargestellt. Die Bedeutung der Kürzelungen der Arten siehe in der englischen Abbildungsunterschrift.

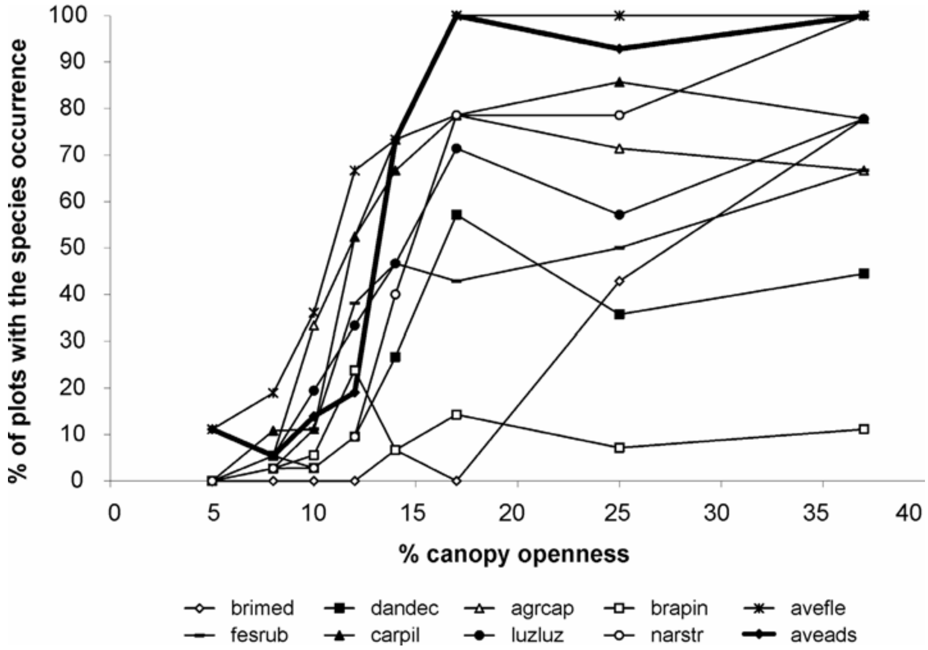

Fig. 6. Relation of *Avenula adsurgens* subsp. *adsurgens* to light availability represented by canopy openness (percentage calculated from vertical hemispherical canopy photographs) in comparison to other frequent grass and sedge species. The species' responses are illustrated by the percentage of plots with their occurrence (in relation to all plots recorded) at the respective level of the measured variable. The response of *A. adsurgens* subsp. *adsurgens* is shown by a bold line. Species abbreviations are explained in Fig. 5.

Abb. 6. Beziehung zwischen dem Anteil der Aufnahmeflächen mit *Avenula adsurgens* subsp. *adsurgens* und der aus hemisphärischen Vertikalfotos errechnen Offenheit der Beschirmung (als Maß für die Lichtverfügbarkeit) im Vergleich zu anderen häufigen Gras- und Seggen-Arten. Die Reaktion der Arten ist durch den Prozentsatz an Aufnahmeflächen dargestellt, in denen sie vorkommen. Die Reaktion von *A. adsurgens* subsp. *adsurgens* ist als fette Linie dargestellt. Abkürzungen der Arten s. Abb. 5.

bottom of mother tillers and grew usually downwards. They were covered with a firm and sharp sheet of pale yellowish colour, easily penetrating the soil layers. The proper green leaves started to form only when the spacer turned to grow upwards. Tissues containing chlorophyll were formed also beneath the soil surface. In the restricted space of a pot, spacers that reached the pot wall usually grew along it and later turned to the soil surface. Thus they reached a considerable length (maximum values of 21, 16, 15.5 and 15 cm were recorded in pots and 25.5 cm in the flower bed). Most tussocks derived from individual tillers flowered in the second year after planting. The average number of flowering tillers per tussock was 4 (range 0–15).

Some tussocks did not form spacers, but for most genets, both types of tussocks were recorded: those with and those without spacers. In the flower bed, only 38% of tussocks formed spacers in comparison to 97% of tussocks planted in pots. Tussocks planted in the flower bed produced significantly less spacers than tussocks in pots. The proportion of spacers in all tillers was lower in the flower bed than in pots, too. Plants growing in the flower

Table 3. Variables measured along the spruce colonisation gradient (averages of 59 plots containing *Avenula adsurgens* subsp. *adsurgens*). Spearman correlation coefficients (SCC) between the percentage cover of *A. adsurgens* subsp. *adsurgens* and environmental variables were calculated for all 155 transect plots (values significant at $P < 0.01$ are given in bold). For details on individual variables, see chapter "Material and methods".

Table 3. Umweltvariablen entlang eines Gradienten zunehmender Besiedlung durch Fichten (Mittelwerte von 59 Aufnahmeflächen mit *Avenula adsurgens* subsp. *adsurgens*). Die Spearman-Korrelationskoeffizienten (r) der Beziehungen zwischen der Deckung von *A. adsurgens* subsp. *adsurgens* und den Umweltvariablen wurden auf Basis aller 155 Transektflächen errechnet (signifikante Werte bei $P < 0,01$ sind fett dargestellt). Details zu den Variablen s. Kapitel "Material und Methoden".

	Mean	Std. Dev.	Min.	Max.	r
Percentage cover of herb litter (%)	14.4	15.6	0	70	**0.79**
Percentage cover of needles (%)	9.7	24.7	0	97	**-0.71**
Thickness of dead biomass layer (cm)	3.3	1.1	1.3	6.9	0.12
Gravimetric moisture (%)	41.8	5.5	32.1	55.4	0.09
Basal soil respiration rate (μg CO_2 g^{-1} h^{-1})	6.2	2.9	2.1	13.9	0.03
Substrate-induced respiration (μg CO_2 g^{-1} h^{-1})	30.9	10.1	4.7	57.8	0.16
pH H_2O	4.4	0.2	3.7	4.8	-0.03
pH KCl	3.4	0.2	3.0	4.0	0.03
Humus content (%)	8.3	2.5	0.7	13.6	-0.12
Catalase activity (ml O_2 g^{-1} min^{-1})	1.6	0.4	0.3	2.7	**0.31**
Canopy openness (%)	20.1	9.4	4.2	42.4	**0.72**
Total nitrogen (mg·kg^{-1} of dry matter)	5.8	1.6	3.6	12.4	0.15
Phosphorus (mg·kg^{-1} of dry matter)	4.0	2.4	1.2	15.3	0.13
Potassium (mg·kg^{-1} of dry matter)	194.8	90.6	90.8	582.6	**0.22**
Canopy index	220.2	124.5	39.3	502.9	**-0.77**

bed differed from those in pots also in maximal distance between tillers at soil surface, number of living, newly formed and all tillers and number of flowering tillers. Tussock diameter, number of dead tillers and the length of spacers did not differ between the pots and the flower bed (Table 4).

4. Discussion

4.1 Habitat preference and phytosociological affiliation of *Avenula adsurgens* subsp. *adsurgens*

According to the data of SAUER & CHMELITSCHEK (1976) and HOLUB (1957), the centre of the *A. adsurgens* distribution in the Western Carpathians is in the submontane to montane belt up to altitudes of about 1000 m where it prefers south-facing slopes. According to our results, the species can also occur at higher altitudes (in the study region, a maximum altitude of 1325 m was recorded), without any specific aspect preference. Within the wide variety of bedrock types recorded for *A. adsurgens* subsp. *adsurgens* in the published literature (limestone, dolomites, andesite, serpentine, melaphyr, flysh sandstone), the majority of localities in the studied region were situated on andesite bedrock. Based on our results, we agree with the opinion of HOLUB (1957) that *A. adsurgens* subsp. *adsurgens* can tolerate moderate grazing, while more intensive management leads to its retreat.

Table 4. Characteristics of clonal fragments (tillers) belonging to six genets of *Avenula adsurgens* subsp. *adsurgens* after the second year of their cultivation in pots and in a flower bed (values in parentheses). In the last column, *P*-values for differences (Kruskal-Wallis ANOVA) among genets in pots are given. *P*-values (Mann-Whitney U tests) for differences between plants cultivated in pots and those cultivated in the flower bed are given in parentheses. Significant differences are given in bold.

Table 4. Eigenschaften von Ausläufern von sechs Geneten von *Avenula adsurgens* subsp. *adsurgens* nach zwei Jahren Kultur in Töpfen und einem Anzuchtsbeet (die Werte für das Anzuchtsbeet in Klammern). Die *P*-Werte (Kruskal-Wallis-ANOVA) in der letzten Spalte beziehen sich auf Unterschiede zwischen Geneten in Töpfen. *P*-Werte (nach einem Mann-Whitney-U-Test) für Unterschiede zwischen Pflanzen in Töpfen und im Anzuchtbeet sind in Klammern dargestellt. Signifikante *P*-Werte sind fett dargestellt.

Growth characteristics	Mean	Min.	Max.	Std. Dev.	*P*
Tussock diameter (cm)	8.7 (10.4)	3.7 (5)	12.5 (22)	2.4 (6.9)	0.338 (0.599)
Maximal distance between tillers at soil surface (cm)	2.7 (3.2)	0 (0)	4.9 (11.5)	1.4 (4.1)	0.473 (**0.047**)
Number of living tillers	15.3 (37)	6 (17)	42 (61)	8.2 (15.4)	0.105 (**<0.001**)
Number of dead (vegetative) tillers	5.8 (7.3)	0 (2)	14 (14)	3.8 (4.3)	0.717 (0.283)
Number of newly formed tillers	4.9 (18.6)	1 (11)	12 (26)	2.8 (5.9)	0.309 (**<0.001**)
Number of flowering tillers	4.0 (2.8)	0 (0)	15 (9)	3.1 (3.1)	**0.047** (0.207)
Number of spacers	3.6 (2.9)	0 (0)	13 (11)	2.5 (4.6)	**0.025** (**0.043**)
Number of all tillers	30.0 (65.9)	16 (42)	72 (91)	11.6 (16.8)	0.105 (**<0.001**)
Length of the longest spacer (cm)	8.0 (14.5)	1.5 (2)	21 (25.5)	4.8 (11.8)	0.547 (0.349)
Average length of spacers (cm)	5.0 (8.5)	0.5 (2)	21 (25.5)	2.7 (5.8)	0.419 (0.333)
Proportion of spacers in all tillers (%)	0.11 (0.03)	0 (0)	21 (14)	0.05 (0.06)	0.066 (**0.003**)

Phytosociologically *A. adsurgens* was regarded to be bound to the *Potentillo albae-Quercetum* Libb 1933 (MAGIC 1998, listed as *A. paeusta*) preferring forest openings, successional pastures and open deciduous or pine forests (HOLUB 1957). The last mentioned habitat type classified within the alliance *Pino-Ericion carnae* (Br.-Bl. 1939) Eggler 1952 represents the occurrence of *A. adsurgens* subsp. *adsurgens* on serpentine bedrock in Austria (EGGLER 1954, 1955). HOLUB (1957) considered *A. adsurgens* subsp. *adsurgens* to be characteristic for the orders *Festucetalia valesiacae* and *Quercetalia pubescentis-petrae*. According to our results, *A. adsurgens* subsp. *adsurgens* occurs frequently in diverse grassland communities of the order *Nardetalia strictae* with transitions to the communities of the order *Arrhenatheretalia elatioris*. It was found to be a diagnostic species of a thermophilous variant with *Festuca rupicola* of the *Campanulo rotundifoliae-Dianthetum deltoidis* association and differential species of this association within *Violion caninae* alliance in Slovakia (JANIŠOVÁ et al. 2007b). However, as the occurrence of the studied taxon is concentrated in early to mid-successional stages, the classification of particular communities is often difficult. The taxon seems not to be an important diagnostic species of these communities, rather an indicator of their successional development (Figs. 7, 8 and 9).

4.2 Ecological requirements of *Avenula adsurgens* subsp. *adsurgens*

To determine the ecological behaviour of a species by a calibration of original indicator values of co-occurring species, usually the weighted averages were used (DIEKMANN 2003). It has been discussed repeatedly that – using strict mathematical criteria – the calculation of weighted averages of ecological indicator values is not appropriate, considering the ordinal

Fig. 7. The locality of Príslopy in the central part of the Poľana Mts. The transect for the detailed observations of post-pasture secondary succession speeded up by spruce colonisation was established on a north-facing slope (upper middle part of the picture) (Photo: M. Janišová, 4.9.2003).

Abb. 7. Die Lokalität Príslopy im zentralen Teil des Poľana-Gebirges. Der Transekt der Detailuntersuchung zur Auswirkung von Sekundärsukzession (Besiedlung durch Fichten) nach Nutzungsaufgabe wurde an dem Nordhang in der oberen Bildmitte plaziert (Foto: M. Janišová, 4.9.2003).

nature of the values. Median indicator values were proposed as a statistically sounder alternative. In our study, we calculated the unweighted means. Mean and median values usually do not differ much, except in some species-poor communities (DIEKMANN 2003). The responses of species were entered as presence-absence data (qualitative) rather than the cover values (quantitative) because a species' cover is not only dependent on environmental site conditions, but also on its specific growth form (and in certain conditions it can give a biased results). According to several authors (DIEKMANN 2003, KOWARIK & SEIDLING 1989), in species-rich vegetation types (meadows), both approaches give similar results.

The ecological indicator values calculated from the set of phytosociological relevés were similar to those calculated from the transect data. Differences between our calculated values and those published by BORHIDI (1995) and SIMON (2000) were also small. The calculated indicator values for temperature, continentality and moisture were the same as estimated by at least one of the mentioned literature sources. According to our results, *A. adsurgens adsurgens* is more shade tolerant (calculated indicator value for light was 7 in stead of 8 estimated by BORHIDI 1995) and occurs also in habitats moderately rich in nutrients (the calibrated value for nutrients was 3 instead of 2 estimated by BORHIDI 1995). Regarding the shade tolerance, the behaviour of frequent grass species along a light availability gradient (Fig. 6) confirmed the position of *A. adsurgens* subsp. *adsurgens* between heliophilous

Fig. 8. Circular transect plot in a grassland community dominated by *Avenula adsurgens* subsp. *adsurgens*. Co-occurring species in order of descending cover: *Potentilla erecta*, *Avenella flexuosa*, *Agrostis capillaris*, *Hypericum maculatum*, *Luzula luzuloides*, *Briza media*, *Carex pilulifera*, *Danthonia decumbens*, *Cruciata glabra*, *Festuca rubra*, *Nardus stricta* and *Acetosa pratensis*. The moss layer covered 55% and was dominated by *Rhytidiadelphus squarrosus* and *Pleurozium schreberi* (Photo: M. Janišová, 4.8.2004).

Abb. 8. Kreisförmige Transekt-Aufnahmefläche in einem von *Avenula adsurgens* subsp. *adsurgens* dominiertem Grassland. Weitere vorkommende (nach abnehmender Deckung angeordnete) Arten werden in der englischen Abbildungsunterschrift aufgeführt. Die Moosschicht der abgebildeten Fläche bedeckte 55 % und war von *Rhytidiadelphus squarrosus* und *Pleurozium schreberi* dominiert (Foto: M. Janišová, 4.8.2004).

grasses (*Briza media*, *Nardus stricta*, *Danthonia decumbens*, indicator value for light: 8) and shade tolerant grasses commonly entering forest communities (e.g. *Avenella flexuosa*, *Brachypodium pinnatum* and *Luzula luzuloides*; indicator value for light: 6, 6 and 4, respectively).

4.3 Clonal morphology and growth characteristics of *Avenula adsurgens* subsp. *adsurgens*

Our cultivation experiment showed that repeated spacer formation during several growing seasons may lead to extensive horizontal spreading of individual plants. Accordingly, *A. adsurgens* subsp. *adsurgens* can be classified as a grass with guerrilla strategy of clonal growth (LOWETT DOUST 1981). The maximum distance from the tussock centre recorded after the second growing season was 29 cm, and the maximum spacer length was 25.5 cm. The volume of the newly grown roots was considerable: Starting with almost zero (as most

Fig. 9. Abandoned pasture colonised by spruce in the locality of Príslopy, Poľana Mts. In late summer, tall stalks of *Avenula adsurgens* subsp. *adsurgens* are most conspicuous (Photo: K. Ujházy, 11.9.2003).

Abb. 9. Aufgegebene, von Fichten besiedelte Weide im Poľana Gebirge bei Príslopy. *Avenula adsurgens* subsp. *adsurgens* fällt im Spätsommer besonders durch seine langen Blühtriebe auf (Foto: K. Ujházy, 11.9.2003).

tillers had no roots when they were planted), the cultivated plants developed a dense root system reaching down to 15 cm. Similar growth characteristics have been recorded in several grass species (*Brachypodium pinnatum*, *Calamagrostis epigejos*, *Bromus inermis*, *Elymus repens* or *Arrhenatherum elatius*), which are common components of semi-natural grassland communities, but in certain circumstances spread expansively after grassland abandonment (DE KROON, H. & BOBBINK, R. 1997, HOLUB et al. 2012a, b, POTTIER & EVETTE 2012).

During secondary succession, these grasses can reach dominance and cause decline in species diversity of grassland communities by production of high above-ground biomass and intensive litter accumulation (HOLUB et al. 2012b, POTTIER & EVETTE 2012).

In cultivation, genets of *A. adsurgens* subsp. *adsurgens* differed significantly in number of produced spacers. Certain tussocks did not form spacers at all. Tussocks planted in the flower bed formed less spacers than tussocks of the same genets planted in pots. This plasticity in clonal growth may be an important precondition for spread of the studied taxon during secondary succession. It is possible that spacer formation is induced by an increasing lack of space in the rhizome layer or by increasing competition. The spacers could thus serve to search for open space and to occupy it (de KROON & HUTCHINGS 1995, SAMMUL 2011). Modification of clonal morphology including switching between phalanx and guerrilla forms is especially advantageous in heterogeneous environmental conditions (OBORNY 1994, DE KROON & HUTCHINGS 1995, POTTIER & EVETTE 2012). As the community heterogeneity increases during the secondary succession, clonal perennial grasses profit from their clonal plasticity, and this advantage may lead to a gradual increase in their cover and reaching dominance in the given plant community.

We suppose that the growth characteristics and clonal plasticity may partly explain the dominance of *A. adsurgens* subsp. *adsurgens* in the studied grasslands. Together with a tall stature and a large amount of annually produced litter, these properties are probably responsible for a successful spreading of the taxon in abandoned grasslands of the study region. The susceptibility to disturbance by mowing and intensive grazing probably limited the taxon occurrence in the traditionally managed grasslands. On the other hand, the taxon's sensitivity to light reduction was probably the main factor limiting its distribution in more advanced successional stages with higher proportion of woody species.

Of course, plants behave differently in natural conditions, and the results of a cultivation experiment can hardly replace *in-situ* experiments in natural communities with presence of pests and competitors. In the future, nutrient use strategy and decomposition of *A. adsurgens* subsp. *adsurgens* should be studied as well, as these processes may also influence its success in plant communities.

4.4 Implication for nature conservation

We suppose that the ability to spread horizontally by spacers together with the observed clonal plasticity, tall stature and fast growth by intensive tillering are among the most important attributes of *A. adsurgens* subsp. *adsurgens* promoting its success and dominant role in the abandoned grasslands. Considering the present distribution of *A. adsurgens* subsp. *adsurgens* in Slovakia, its ecological requirements and growth characteristics, we suggest that the taxon is presently beyond actual or potential threat and can be removed from the Red list of the Slovak flora (FERÁKOVÁ et al. 2001).

Erweiterte deutsche Zusammenfassung

Einleitung – Diese Arbeit behandelt die ökologischen Ansprüche und die pflanzensoziologische Anbindung von *Avenula adsurgens* (Schur ex Simonkai) Sauer & Chmelitschek subsp. *adsurgens*, um ihre Rolle in Graslandgesellschaften sowie ihre erfolgreiche Ausbreitung nach Nutzungsaufgabe zu klären. Obwohl diese Grassippe in Mittel- und Südost-Europa weit verbreitet ist und hier bestimmte Graslandtypen sogar dominiert, ist wenig über ihre Ökologie und Vergesellschaftung bekannt. Zudem beziehen sich einige Publikationen über ihre Verbreitung fälschlicherweise auf *Avenula praeusta*. *Avenula adsurgens* subsp. *adsurgens* ist hoch polyploid ($2n = 18x = \pm 126$ Chromosomen). Der ausdauernde und polykarpe Hemikryptophyt bildet mithilfe von bis zu 30 cm langen extravaginalen Ausläufern lockere Horste. Die Sippe ist subkontinental verbreitet und kommt in Österreich, der Slowakei, Ungarn, Bosnien, Mazedonien, Rumänien, Bulgarien, der Türkei und der Ukraine vor. In der Slowakei gilt die Sippe als potenziell gefährdet (IUCN-Kategorie LR:nt, ut. *A. praeusta*). Sie wächst in Grasländern der kollinen bis submontanen Stufe und kann dort nach Aufgabe der traditionellen Landnutzung zur Dominanz gelangen. Allgemein wird die Dominanz hochwüchsiger mehrjähriger Gräser in Grasländern der temperaten Zone dem klonalen Wuchs dieser Arten oder besonderen Strategien zur Nährstoffnutzung zugeschrieben. So ist zu erwarten, dass die Bildung langer Ausläufer und auch die Plastizität der Ausläuferlänge unabhängig von den Umweltbedingungen Vorteile bedeuten. In dieser Arbeit beschäftigen wir uns mit den folgenden Fragen: 1) Wie ist *A. adsurgens* subsp. *adsurgens* vergesellschaftet? 2) Welche ökologischen Ansprüche hat die Sippe und welches Management fördert ihre Entwicklung? 3) Gibt es einen Zusammenhang zwischen klonalem Wuchs und erfolgreicher Ausbreitung der Sippe im Zuge des Brachfalles von Grasländern?

Material und Methoden – Wir untersuchten *A. adsurgens* subsp. *adsurgens* in einem etwa 300 km² großen Gebiet im Poľana Gebirge (Zentral-Slowakei, Abb. 1) in verschiedenen Lebensräumen. Die Assoziationen mit *A. adsurgens* subsp. *adsurgens* bzw. die ökologischen Zeigerwerte der Sippe wurden mit Hilfe einer systematischen pflanzensoziologischen Erfassung (672 Vegetationsaufnahmen zwischen 1995 und 2005 mit insgesamt 656 Gefäßpflanzenarten) bestimmt. Die Abhängigkeit der Sippe von den wichtigsten Umweltgradienten sowie von der Landnutzung wurde mit einem Teildatensatz von 427 Aufnahmen mesophiler Wiesen mithilfe von Kanonischer Korrespondenzanalyse (CCA) analysiert. 85 Vegetationsaufnahmen mit *A. adsurgens* subsp. *adsurgens* wurden mit einer TWINSPAN-Analyse in Vegetationstypen klassifiziert und damit die Vergesellschaftung der Sippe analysiert. Die Zuordnung der Aufnahmegruppen zu Syntaxa (Assoziationen und Verbände) basierte dabei auf der überarbeiteten Übersicht der slowakischen Vegetation (JANIŠOVÁ et al. 2007b). In einem Transekt entlang eines Gradienten zunehmender Besiedlung durch Fichten wurden genaue topografische, mikroklimatische, edaphische und bodenmikrobiologische Messungen durchgeführt, und Zusammenhänge zwischen dem Vorkommen von *A. adsurgens* subsp. *adsurgens* und den gemessenen Variablen wurden mit Hilfe von Korrelationsanalyse analysiert. Dieser Transekt bestand aus 155 kreisförmigen 0,5 m²-Aufnahmeflächen in einem 5 m × 5 m-Raster auf einer Gesamtfläche von 160 m × 20 m. Der klonale Wuchs und andere Wuchseigenschaften von *A. adsurgens* subsp. *adsurgens* wurden in Kultur untersucht. Die Wuchseigenschaften (Durchmesser der Horste, Anzahl und Länge der Ausläufer, Anzahl der Blüten) wurden zwischen den Pflanzen (Geneten) sowie zwischen getopften und in einem Beet wachsenden Pflanzen mit Hilfe von nichtparametrischen Tests verglichen.

Ergebnisse – *A. adsurgens* subsp. *adsurgens* kam im Untersuchungsgebiet hauptsächlich auf vulkanischem Grundgestein in Höhenlagen von 480 bis 1325 m NN vor und zeigte keine Präferenz an bestimmte Hangexpositionen. Sie wurde vor allem in wenig bewirtschafteten oder brachliegenden montanen Wiesen (800–1100 m NN) der Verbände *Violion caninae* und *Nardo strictae-Agrostion tenuis* festgestellt (Tab. 1, Abb. 2). Ihre höchsten Deckungsgrade erreichte sie in frühen bis mittleren Sukzessionsstadien der Wiesen, wenn diese noch nicht von Gehölzen besiedelt sind. In traditionell genutzten Wiesen (Mahd und/oder Beweidung) war die Sippe ebenfalls häufig, erreichte dort jedoch eine geringere prozentuale Deckung. Eine intensivere Nutzung (Düngung bzw. Standweide) bewirkte einen Rückgang der Sippe. Im Ordinationsdiagramm (Abb. 3) wird die Präferenz von extensiv genutzten Grasländern in höheren Lagen durch die untersuchte Sippe ebenfalls deutlich. Die ökologischen Zeigerwerte von *A. adsurgens* subsp. *adsurgens* wurden von uns wie folgt festgelegt (Tab. 2): Licht: 7 (meist bei vollem Licht wachsend, manchmal auch im Halbschatten); Temperatur: 5 (meist in submontan-temperaten Lagen, insgesamt von der kollinen bis subalpinen Stufe, Mäßigwärmezeiger); Kontinentalität: 4 (in Regionen mit subozeanischem Klima, hauptsächlich Mitteleuropa, z. T. auch Osteuropa); Feuchtigkeit: 4 (auf frischen Standorten, sehr trockene und sehr nasse Bereiche meidend); Reaktion: 5 (auf mäßig sauren Böden, selten auf stärker sauren oder neutral-basischen Böden); Nährstoff: 3 (auf stickstoffarmen Böden, nur ausnahmsweise auf mittelmäßig bis stickstoffreichen Böden). In dem untersuchten Transekt (Gradient der Besiedlung durch Fichten) war die prozentuale Deckung von *A. adsur-*

gens subsp. *adsurgens* positiv mit der Deckung der Streu, Kronenoffenheit, Katalaseaktivität des Bodens sowie dem Bodengehalt an Kalium und negativ mit der Deckung an Nadeln und dem Kronenschlussindex (als kumulatives Maß der Effekte der aufkommenden Fichten) korreliert (Tab. 3). Die untersuchte Sippe dominierte in den meisten Probeflächen der frühen Sukzessionsstadien und kam ebenfalls mit geringerer prozentualer Deckung in Probeflächen der mittleren Sukzessionsstadien vor. Dagegen fehlte sie in späten Sukzessionsstadien völlig (Abb. 4). *A. adsurgens* subsp. *adsurgens* war ähnlich empfindlich gegenüber geringerer Lichtverfügbarkeit wie *Festuca rubra*, weniger empfindlich als *Briza media*, *Nardus stricta* und *Danthonia decumbens*, aber empfindlicher als *Agrostis capillaris*, *Carex pilulifera*, *Avenella flexuosa*, *Brachypodium pinnatum* und *Luzula luzuloides* (Abb. 6). Im Vergleich mit den genannten Gras- und Seggen-Arten zeigte die Art zudem eine mittlere Widerstandsfähigkeit gegen Verdrängung durch Fichten (Abb. 5). Die horizontale Ausbreitung der Sippe wird durch die Ausbildung von Ausläufern mit langen Internodien ermöglicht. Deren maximale Länge nach zwei Vegetationsperioden betrug 25,5 cm. Einige Horste bildeten keine Ausläufer; allerdings wurden bei den meisten Geneten Horste mit und ohne Ausläufer beobachtet. Im Anzuchtbeet bildeten lediglich 38% der Horste Ausläufer, wohingegen 97% der in Töpfen wachsenden Horste Ausläufer bildeten. Die getopften Pflanzen bildeten zwar mehr Ausläufer als die im Anzuchtbeet wachsenden Individuen, hatten aber kleinere Horste mit weniger Sprossen als diese (Tab. 4).

Diskussion – Die Klassifikation der Grasländer mit *A. adsurgens* subsp. *adsurgens* erweist sich wegen deren Präferenz von frühen bis mittleren Sukzessionsstadien oftmals als schwierig. *Avenula adsurgens* subsp. *adsurgens* ist weniger eine strenge Charakterart einer bestimmten Pflanzengesellschaft als vielmehr für bestimmte Sukzessionsstadien typisch. Die mithilfe der pflanzensoziologischen Aufnahmen ermittelten ökologischen Zeigerwerte stimmten weitgehend mit den aus der Transekt-Analyse gewonnenen überein. Auch waren die Unterschiede zwischen unseren und den von BORHIDI (1995) und SIMON (2000) publizierten Zeigerwerten gering. Die berechneten Zeigerwerte für Temperatur, Kontinentalität und Feuchtigkeit waren die gleichen wie in mindestens einer der genannten Publikationen. Unseren Ergebnissen zufolge weist *A. adsurgens* subsp. *adsurgens* jedoch eine höhere Toleranz gegenüber Schatten auf und kommt auch in Habitaten mit mäßig guter Stickstoffverfügbarkeit vor. Unser Anzuchtexperiment zeigte, dass die wiederholte Bildung von Ausläufern über mehrere Vegetationsperioden zu einer starken horizontalen Ausbreitung von *A. adsurgens* subsp. *adsurgens* führen kann. Entsprechend ihrer Fähigkeit, reichlich Biomasse zu produzieren und viel Streu zu akkumulieren, kann sie der Gruppe der hochwüchsigen Gräser zugeordnet werden, zu denen beispielsweise auch *Brachypodium pinnatum*, *Calamagrostis epigejos*, *Bromus inermis*, *Elymus repens* und *Arrhenatherum elatius* zählen. Diese Arten sind normalerweise nur ein Bestandteil von halb-natürlichen Grasland-Gesellschaften, können sich aber bei Brache stark ausbreiten und so auch zu einem Verlust an Artenreichtum dieser Grasländer führen.

Wir halten die Fähigkeit zu horizontaler Ausbreitung mithilfe von Ausläufern sowie die beobachtete klonale Plastizität, die Größe und das rasche Wachstum durch intensive Ausläuferbildung für die wichtigsten Gründe des Erfolgs und der Dominanz von *A. adsurgens* subsp. *adsurgens* in brachgefallenen Grasländern. Bei Betrachtung ihrer heutigen Verbreitung in der Slowakei sowie ihrer ökologischen Ansprüche und Wuchseigenschaften kommen wir zu dem Schluss, dass ihre Gefährdung momentan überschätzt wird. Wir empfehlen daher die Streichung der Sippe von der Roten Liste der gefährdeten Pflanzenarten der Slowakei (FERÁKOVÁ et al. 2001).

Acknowledgements

We thank Izabela Háberová, Richard Hrivnák and Dušan Gömöry for field assistance, Erika Gömöryová for providing the data on soil pedological and microbiological variables, Thomas Becker for the translation into German, Aiko Huckauf for English proofreading, Imelda Somodi and an anonymous reviewer for valuable comments on the manuscript. This research project was supported by the Scientific Grant Agency of the Ministry of Education of the Slovak Republic and the Slovak Academy of Sciences (VEGA 2/0099/13).

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