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**Competing interests**

No competing interests have been declared.

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## ORIGINAL RESEARCH PAPER

# How alpine heathlands response to the snow cover change on the ski slope? Long-lasting ski slope impact case study from the Hrubý Jeseník Mts (Central Europe)

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The distribution and duration of snow cover are important variables that affect ecosystem processes in the alpine zone. The establishment of ski resorts dramatically change their surrounding environment and ski slopes represent significant anthropogenic impact in the mountains. We assessed the changes in environmental factors, phenology, growth, and reproductive performance of bilberry (*Vaccinium myrtillus*), a dominant species of alpine heathlands, caused by a “nature-friendly” managed ski slope (i.e., without artificial snow and machine grading) at permanent plots established on the ski slope under operations (inside the ski slope) and on an unaffected control area (outside the ski slope). A lower mean temperature and a shorter time of great temperature fluctuation during snow melting, a longer time span of snow cover, and a higher snow water equivalent were observed inside the ski slope compared to outside it. Due to changed environmental conditions, the beginning of growth was postponed, and a delay in phenological development was observed in the bilberry at the ski slope. However, bilberry ripened both inside and outside the ski slope in a similar period and showed similar cover and even higher flower and fruit densities inside the ski slope compared with natural surroundings. The persistence of bilberry was not deteriorated and its performance was even better inside the ski slope. On the ski slope, managed snow cover can reduce the potential vegetation shifts due to expected impact of the climate warming. That should be taken into account in conservation and management planning.

**Keywords**

snow conditions; tourism impact; bilberry; conservation

**Introduction**

Seasonal snow cover is the crucial determinant of plant life at high altitudes and latitudes worldwide [1–3]. Snow also alters other environmental factors affecting plant growth, especially soil temperature, moisture availability, and nutrient cycling [4].

Changes in snow cover are determined by climatic [5,6] and direct human impacts [7–9]. The interplay between global climate change and snow cover became significant research topics during past decades [1,2]. Looking at a more local spatial scale, a number of recent studies demonstrate that the establishment of ski resorts dramatically changes their surrounding environment [7,9–11]. Ski slopes represent complex anthropogenic impact in the mountains. In addition to the direct human impacts on vegetation and soils due to the heavy machinery used to remove barriers and smooth the terrain [9], the main indirect impact of ski slope preparation consists

of the compaction and higher density of snow. A denser snow layer possesses lower insulation capability that evokes soil freezing during winter [7,12] and the postponement of spring snowmelt. Changes in snow cover are also closely linked to shifts in the hydrological regime [7,13] and soil nutrient capacity [10,14].

Plants are finely tuned to the seasonality of their environment, and shifts in the timing of plant activity (i.e., phenology) provide some of the most convincing evidence that species and communities are being influenced by environmental change [15]. Plant ontogeny and growth characteristics in high altitudes closely reflect winter snow parameters and the timing of snowmelt as was shown by both natural observations (e.g., [16]) and manipulative experiments (e.g., [1–3,7]). Spatio-temporal changes in snow cover at ski slopes constitute an important factor to the activity and fitness of most of plant species. At ski slopes the seasonal development of plants is altered [10], which might influence entire plant life cycles and cause changes in the diversity of plant functional groups over a longer time span [3]. Consequently, shifts in soil and ecosystem processes could result in dramatic changes in the composition of plant communities [9,17].

In general, chionophilous species, including dwarf shrubs, are particularly affected by ski slope operations [7,9] but their phenological responses can be ambiguous and species-specific [3]. Dwarf-shrubs belonging to the family Ericaceae are abundant in the cold regions of northern territories, where they often represent the dominant species in both sub-arctic and sub-alpine dwarf-shrub communities [18]. Bilberry (*Vaccinium myrtillus* L.), a deciduous dwarf shrub, is one of the most frequent and abundant vascular plant species in Northern Europe and the high altitudes of European mountains [19]. The chamaephyte is adapted to the protection of snow, and thus snow cover changes are closely connected with its phenology, growth and persistence. Hence, bilberry presents a convenient model plant for examining the effects associated with snow cover changes due to ski slope operations.

In this study, we examined the effects of artificially changed snow conditions due to “nature-friendly” ski slope operations (i.e., ski slope that has never been machine-graded or artificially snowed) in an alpine zone of the High Sudeten Mts (Central Europe) on selected environmental factors and the phenology and performance of bilberry (*Vaccinium myrtillus*), a dominant plant of alpine heathlands. Specifically, we addressed the following questions: (i) how do the ski slope operations influence temperature, snow cover period, and snow water content on stands with alpine heathlands compared with the non-manipulated natural environment; (ii) do cover, reproductive density, and phenological development of bilberry growing inside ski slope differ from outside (natural) conditions; (iii) could the ski slopes impact mitigate the future global warming threats to the alpine heathlands?

## Material and methods

### Study site

The study area is situated in the northeastern part of the Czech Republic in the summit part of the High Sudetes (the Hrubý Jeseník Mts), which belong to the Hercynian Mts. The study was performed at the NW slope of Petrovy kameny Mt (1448 m a.s.l., 50°04' N, 17°14' E, mean inclination 24°) in the alpine belt above timberline [20]. The composition of the alpine vegetation, soil, and several other abiotic and biotic conditions, including the geomorphology of the site, are described in detail by Křížek et al. [21], Treml and Banaš [20], Zeidler et al. [22], Banaš et al. [17], Hédal et al. [14], and Zeidler et al. [23]. One part of the slope is established as the investigated ski slope and an adjacent one left as a natural area under protection. The slope has been used for skiing since the second half of the twentieth century, and snow grooming has been performed since 1980s. Neither artificial snow nor machine grading are used at the ski resort, and snow is maintained only by snowcats during the skiing season without any management in summer. At the downslope lane area, the snow amount is enhanced by a row of snow fences that accumulate wind-drifted snow during whole winter season. Skiing activities are suspended when the snow depth drops below 80 cm to prevent

the mechanical disturbance of vegetation that is considered as “nature-friendly” managed ski slope [11]. There are any other substantial differences between the skiing-affected and skiing-free parts of the slope.

We studied stands of alpine heathlands dominated by *Vaccinium myrtillus* (association *Festuco supinae-Vaccinietum myrtilli* Šmarda 1950, alliance *Genisto pilosae-Vaccinion* Br.-Bl. 1926) that are characterized by a deep continuous snow cover which protects against frost and strong winds in winter. The dominant *Vaccinium myrtillus* (cover >75%) is sporadically accompanied by *Vaccinium vitis-idaea*, *Avenella flexuosa*, *Calamagrostis villosa*, and *Luzula luzuloides* [24]. Alpine heathlands cover the upper parts of the study area close above the treeline and our plots were established 1380–1410 m a.s.l. The nomenclature of plant species follows Kubát et al. [25] and the nomenclature of the vegetation types was modified according to Chytrý [26].

### Permanent plots establishment

The design of the permanent plots setting followed Banaš et al. [17]. We randomly selected 20 permanent plots 0.5 × 0.5 m on the ski slope under operations (henceforth “inside the ski slope”) and 20 identically sized control plots on the unaffected (“control”) area (“outside the ski slope”). Distances between adjacent plots were at least 10 m. The control plots were located 10–40 m from the 10-meter buffer zone between the ski slope and unaffected areas on both sides of the ski slope. No significant differences were found in geomorphological conditions (elevation, aspect, and inclination of the slope) between the plots on the ski slope and control plots (all  $p > 0.20$ ; data not shown).

### Snow cover and snow water equivalent

At all permanent plots, the onset of continual snow cover and its melt-down was registered during the winter 2003–2004 to compare the duration of snow inside and outside the ski slope. Snow density was estimated by a snow corer at three measuring points each inside/outside the ski slope at the same altitude (ca. 1390 m a.s.l.) on 29 January, 27 February, 1 April, and 14 April 2004. A snow sample of known volume was subsequently removed from the top to the bottom of a snow corer and weighed ( $\pm 5$  g). Snow water equivalent ( $SWE = Density \times Snow\ depth \times Sample\ area$ ;  $kg\ m^{-2}$ ) was computed.

### Soil temperature measurements

Data loggers with temperature sensors (Minikin 2T, EMS Brno) were placed near the three randomly selected plots inside and outside the ski slope (six data loggers in total). The temperature was measured 3 cm below the litter surface from December 2003 until the end of 2004. The soil temperature course was recorded continuously in 1-hour intervals and a daily means curve was visualized.

To measure the temperature demand of flowering onset inside and outside the ski slope, the effective cumulative temperature (ECT) above 5°C [16] was calculated from the snowmelt date to the beginning of the bilberry flowering phase based on output of all data loggers.

### Phenology, cover, and reproductive density

The phenology of *V. myrtillus* was recorded at permanent plots during the growing season in 2004. The observations began after snowmelt on 13 May and terminated on 20 September. During this period, 17 phenological surveys were carried out at approximately 1-week intervals with shorter intervals in the beginning of the season. Following the methodology of the Czech Hydrometeorological Institute, seven phenophases were distinguished:

- Phase 1: sprouting initiation. Terminal buds swell up but are still unfurled, without apparent green tips.
- Phase 2: budburst. Bud scales unfasten partially because of the growing leaf. Green leaf tips are apparent.
- Phase 3: prematuration of leaves. Leaf blades are incompletely unfurled with apparent folds.
- Phase 4: floral bud emergence. Floral buds are markedly distinguished in leaf axils.
- Phase 5: flowering. Flowers are fully developed and open with functional anthers.
- Phase 6: flower fade. Anthers are empty and become darker and dry; some of them drop off.
- Phase 7: ripening fruits. Berries attain their characteristic shape, color, final proportion, and grow and soften.

For each phenophase, the median day from the beginning of the year 2004 when the respective phenological phase was reached and median duration of each phase was calculated from records at permanent plots.

Bilberry cover was estimated simultaneously with each phenological investigation at the permanent plots. The Braun-Blanquet 9-grade abundance–dominance scale [27] was used to record cover.

The number of bilberry flowers was counted on permanent plots during the peak of the flowering phenophase. At the end of the ripening phenophase (20 September), all berries were picked off the shrubs on permanent plots and counted as the maximum yield.

## Data analyses

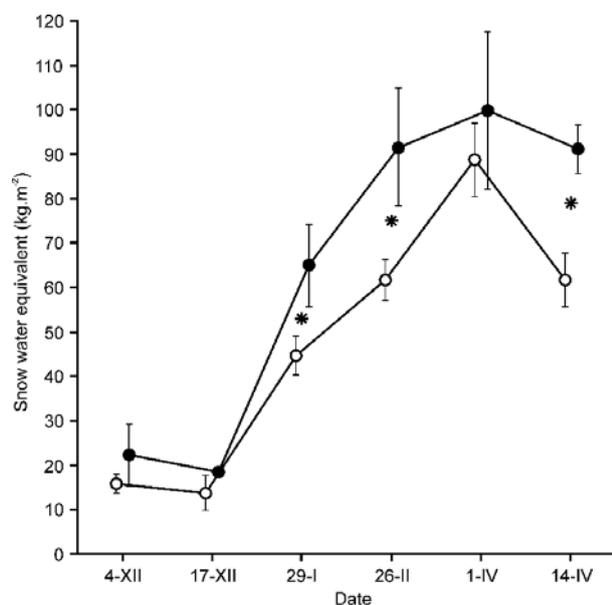
Differences in the snow cover period and ECT between the inside and outside of the ski slope were tested with the *t*-test. Changes in snow water equivalent during winter and the cover of bilberry at permanent plots during the season were tested by linear mixed models with random coefficients with the ski slope as fixed factor, time as a covariate, plots/points as subjects, and using AR(1) covariance pattern structure. To determine the appropriate variance–covariance structure for a model, we used AIC [28]. *F*-test for each component of the fixed component model was calculated according to the methods described by Kenward and Roger [29]. Before analysis, the Braun-Blanquet abundance–dominance scale underwent van der Maarel transformation into a 9-graded numerical scale (1–9) [27]. Differences in the phenological development of bilberry inside and outside the ski slope were separately tested for each date by the likelihood ratio test. The difference between inside and outside the ski slope in the reproductive density, median day when the respective phenological phase was reached, and duration of each phenophase were tested by Mann–Whitney *U*-test. All calculations were performed using NCSS 9 (NCSS, LLC., Kaysville, Utah, USA).

## Results

### Snow cover and snow water equivalent

The onset of continual snow cover was 7 December 2003. The mean number of days with continual snow cover was higher inside (mean  $\pm$ SD: 166  $\pm$ 6) than outside (148  $\pm$ 2) the ski slope (*t*-test:  $t = 9.1$ ,  $p < 0.001$ ). The last snow melted outside the ski slope on 5 May, but on 27 May inside the ski slope. The snowmelt delay inside the ski slope is thus approximately 18 days.

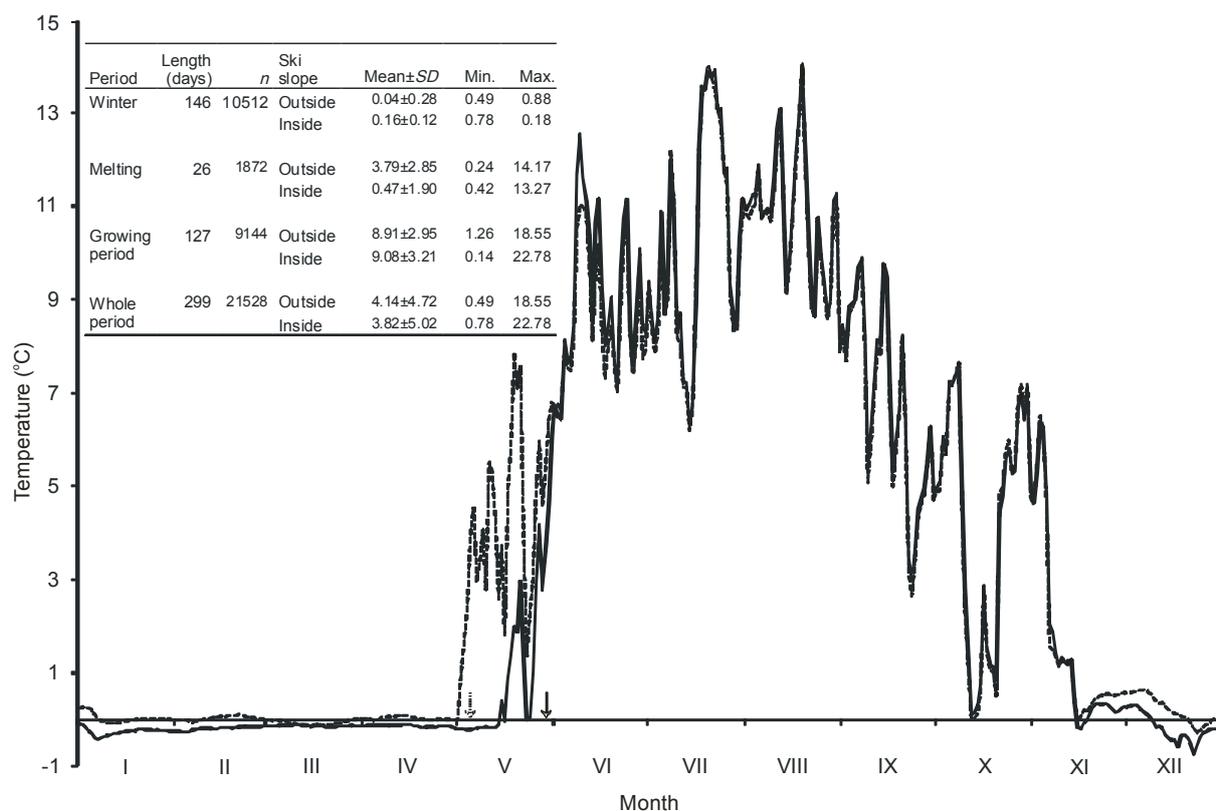
Snow water equivalent increased during winter and reached maximal values on the 1 April both inside and outside the ski slope (Fig. 1). SWE was significantly higher inside than outside the ski slope but greater differences in SWE between inside and outside ski slope were found later in winter [mixed-models; ski slope:  $F(1, 6.3) = 5.87$ ,  $p = 0.049$ ; time:  $F(5, 19.5) = 24.2$ ,  $p < 0.001$ ; Ski slope  $\times$  Time:  $F(5, 19.5) = 1.62$ ,  $p = 0.202$ ; Fig. 1].



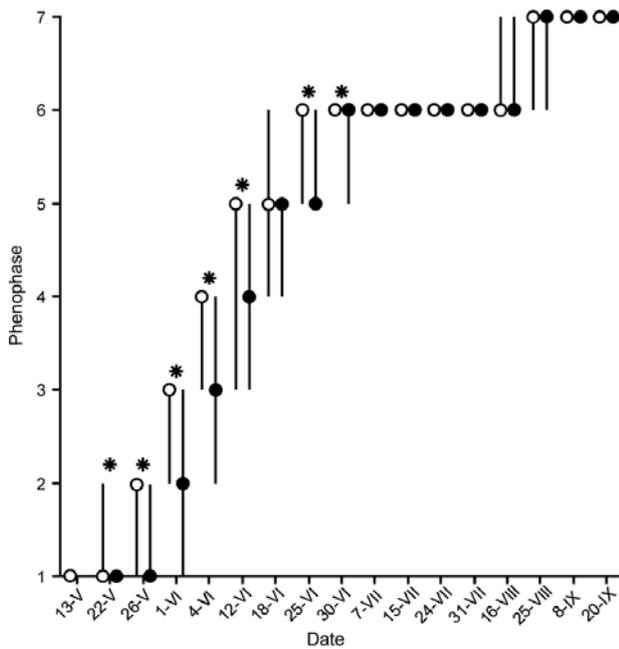
**Fig. 1** Changes in snow water equivalent (SWE; mean  $\pm$ SE) inside (black circles) and outside the ski slope (empty circles) during the winter 2003/2004. Asterisks indicate significant differences in the mean SWE (at  $p \leq 0.05$ ) between the inside and outside of the ski slope for the respective sampling date (mixed models individual comparison hypothesis  $F$ -test).

## Soil temperatures

The mean annual average soil temperature 3 cm below the litter surface inside the ski slope was  $0.313^{\circ}\text{C}$  lower than outside the ski slope during study period. However, temperature differences between the inside and outside of the ski slope stands were not uniform throughout the year. During winter, the temperature inside the ski slope was slightly below zero, while outside, the soil temperature varied near or slightly above zero (Fig. 2). Great differences in the temperature course occurred during the spring snowmelt, when temperatures rose rapidly above zero, first outside the ski slope, and with a delay in temperature rise inside the slope. During the snowmelt period, high temperature fluctuations occurred outside the ski slope. On the other hand, temperature rather rapidly increased inside the ski slope after snowmelt. Temperature differences between the environments disappeared in late June. Later in the season, the temperature course inside and outside the ski slope did not differ (Fig. 2).



**Fig. 2** Soil temperatures ( $^{\circ}\text{C}$ ; daily means) 3 cm below the litter surface in *Vaccinium myrtillus* stands inside (full line) and outside (broken line) the ski slope during the 2003/2004 winter season and the 2004 growing season. Each line is an average of data from three data loggers. Arrows inside the plot mark snowmelt dates inside and outside the ski slope. Descriptive statistics (mean  $\pm$ SD, minimum, and maximum) of soil temperatures for three distinct periods (winter = 7th December 2003 – 30th April 2004, melting = 1st – 26th May 2004, growing period = 27th May – 30th September 2004) and over whole period (7th December 2003 – 30th September 2004) are presented in the table ( $n$  – number of hourly means used for the calculations).



**Fig. 3** Course of phenological development of *V. myrtillus* inside and outside the ski slope. For each sampling date and separately for the inside and outside of the ski slope plots, the earliest and latest phenological phase (length of the vertical line) and median phenological phases observed are shown (inside the ski slope = full circle, outside the ski slope = empty circle). Asterisk denotes a significant difference (likelihood ratio test at  $p \leq 0.05$ ) in phenological development between the inside and outside of the ski slope for the respective sampling date. Absence of the phenological record for the first date inside the ski slope is due to the presence of snow cover.

## Phenology

The phenological development of *V. myrtillus* differed between the inside and outside of the ski slope in the first part of the season (Fig. 3, Tab. 1). In general, plants growing outside the ski slope were ahead of plants inside ski slope from the beginning of the growing season until the end of June. Later in the season (July), the phenological development of *V. myrtillus* inside the ski slope drew level abreast of that outside and bilberry ripened both inside and outside the ski slope in a similar period (Fig. 3, Tab. 1). We observed a trend towards shortened periods of three phenological phases (Nos. 1, 2, and 4) inside the ski slope (Tab. 1). ECT from snowmelt to the first flowering of *V. myrtillus* were not different between the inside ( $193 \pm 7$ ; mean  $\pm$ SE) and outside ( $196 \pm 6$ ) ski slope plots ( $t$ -test:  $t = 0.345$ ,  $p = 0.732$ ).

## Changes in *V. myrtillus* cover

The *V. myrtillus* cover increased continuously both inside and outside the ski slope during spring and the cover was significantly higher outside the ski slope than inside it during the first half of the growing season. However, the cover increased more rapidly at the ski slope than outside it during late spring, resulting in similarly high covers of *V. myrtillus* at both sites in summer [mixed models; ski slope:  $F(1, 97.9) = 39.0$ ,  $p < 0.001$ ; time:  $F(15, 586.1) = 113.1$ ,  $p < 0.001$ ; Ski slope  $\times$  Time:  $F(15, 586.1) = 10.3$ ,  $p < 0.001$ ; Fig. 4].

## Reproductive density

The number of flowers, fruits and ratio fruits/flowers per  $0.25 \text{ m}^2$  were higher inside than outside the ski slope. However, due to large variation of all studied traits observed especially inside the ski slope, only reproductive density of fruits was significantly higher inside than outside the ski slope (Mann-Whitney  $U$ -test; flowers:  $Z = 1.79$ ,  $p = 0.073$ ; fruits:  $Z = 2.01$ ,  $p = 0.045$ ; fruits/flowers:  $Z = 1.78$ ,  $p = 0.075$ ; Fig. 5).

## Discussion

### Snow cover and snow water equivalent

We showed that the studied attributes of snow cover differ between the inside and outside of the ski slope, i.e., the observed differences are caused by snow manipulation due to the ski slope operations. This result is in line with other studies from various alpine sites [7,9] and with studies from other vegetation types at the study area [17,22,23]. The changes in the snow quality were mirrored by SWE that increased during winter both inside and outside the ski slope, but were even faster inside the slope due to snow fences functioning. The systematic increase in the snow cover density during winter is a common trend for natural (not prepared) and prepared snow cover, including artificial snow [7,13]. However, our data showed that using just a snowcat obviously accelerated snow compaction. Because SWE is correlated with density and hence the water content of the snow cover [13], a denser and thicker snow cover inside a ski slope contains more water than the outside. According to other studies

**Tab. 1** Timing of phenological phases Nos. 1–7 in *Vaccinium myrtillus* inside and outside the ski slope.

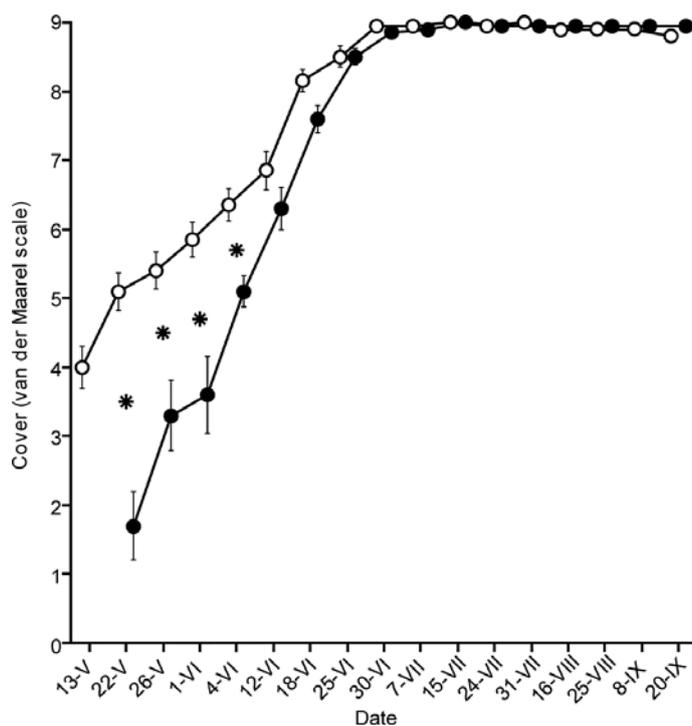
	<i>n</i>	Day when the respective phenological phase was reached			Duration of each phase		
		median (25–75% percentile)	Z-value	<i>p</i>	median (25–75% percentile)	Z-value	<i>p</i>
Phase 1							
Outside	15	134 (134–143)	–4.38	<0.001	9 (4–13)	1.96	0.050
Inside	20	147 (143–153)			6 (3–10)		
Phase 2							
Outside	20	147 (143–147)	–4.90	<0.001	7.5 (6–10)	3.22	0.001
Inside	20	153 (153–156)			3 (3–8)		
Phase 3							
Outside	20	153 (153–156)	–4.36	<0.001	3 (3–8)	–2.53	0.012
Inside	20	156 (156–164)			8 (6–8)		
Phase 4							
Outside	18	156 (156–164)	–3.55	<0.001	8 (7–8)	3.63	<0.001
Inside	18	164 (164–164)			6 (6–7)		
Phase 5							
Outside	17	164 (164–170)	–3.64	<0.001	12.5 (6–13)	0.322	0.747
Inside	18	170 (170–172)			12 (12–12)		
Phase 6							
Outside	17	177 (177–180)	–3.11	0.002	61 (53–70)	1.67	0.093
Inside	18	182 (180–189)			56 (51–62)		
Phase 7							
Outside	16	238 (231–249)	–0.48	0.628	-	-	-
Inside	16	238 (238–249)			-		

The difference between inside and outside the ski slope in the median day from the beginning of the year 2004 when the respective phenological phase was reached and median (25–75% percentile) duration of each phase was tested by Mann–Whitney *U*-test. Different sample sizes are caused by failure to record some phases on some plots. Duration of the Phase 7 was not estimated.

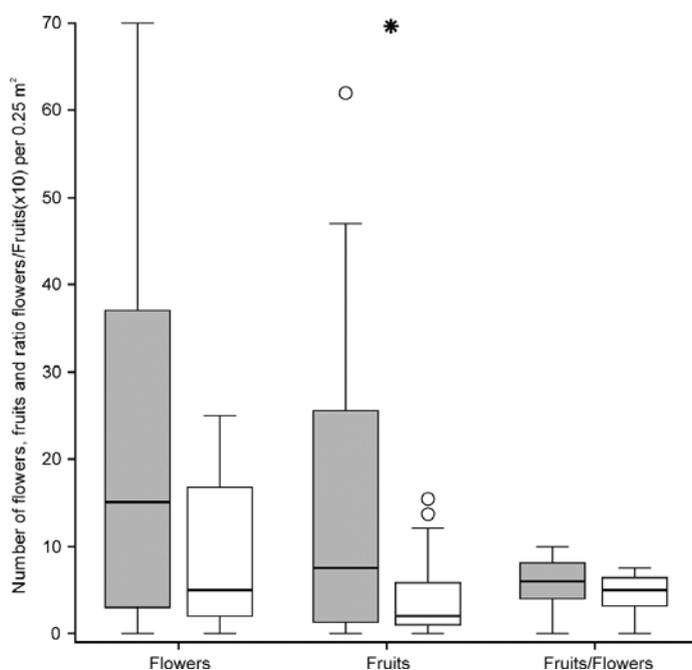
[9,10,14,30], soil developmental changes, including alterations in nutrient cycling and nutrient ratios are expected under shifted hydrological conditions.

#### Soil temperatures

We found that different soil thermal conditions exist inside and outside the ski slope as a consequence of ski slope management. The compacted and hence denser snow cover decreases the insulation capacity, and winter snow temperatures on prepared ski slopes may drop by several degrees compared with natural plots [7]. Our observations confirmed lower average daily temperatures of approximately 0.3°C in bilberry stands inside compared to outside the ski slope. Similar values were found under groomed snow at alpine grasslands in the Alps [31] and the inside stands of some other vegetation types at the ski slope in the Hrubý Jeseník Mts [17,23]. Despite higher snow



**Fig. 4** Changes in *V. myrtillus* cover (mean  $\pm$  SE) inside (full circle) and outside (empty circle) the ski slope during the growing season in 2004. Asterisks indicate significant differences in mean cover (at  $p \leq 0.05$ ) between the inside and outside of the ski slope for the respective sampling date (mixed models individual comparison hypothesis *F*-test). Absence of the mean for the first date inside the ski slope is due to the presence of snow cover.



**Fig. 5** Box plots of number of flowers, fruits, and ratio fruits/flowers ( $\times 10$ ) per  $0.25 \text{ m}^2$  inside (grey box) and outside (empty box) the ski slope at the peak of flowering/fruiting. Asterisk indicates significant difference between the medians inside and outside the ski slope (Mann–Whitney *U*-test at  $p \leq 0.05$ ).

compaction, the relatively slight temperature drops inside the ski slope are a consequence of the increased thickness of the snow cover inside ski slope due to snow interception by snow fences installed along studied ski slope [17,23]. The same effect can be achieved by huge amounts of artificial snow that counteract the reduced insulating properties of the snowpack in some parts of the Alps [12]. However, lower temperatures inside the ski slope occur more frequently during winter, and this environment should be considered colder than the natural environments outside of the ski slope.

Essential differences in the temperature course between the ski slope and natural plots appeared during the spring and snowmelting period. Because the prepared compacted snow cover remains longer than the natural snow [7,9,23,31], the soil warming and beginning of the snow-free season inside ski slope under consideration is delayed approximately 3 weeks compared with the outside, which is the prevalent interval at ski slopes in general [7,12,17]. Consequently, the ground soil of the ski slope receives less solar radiation in spring when it is still covered with snow, while the outside areas are already snow free. Outside the ski slope, snowmelt is connected with temperature fluctuation compared with later snowmelt following by rapid rise of temperature inside ski slope. During the summer until the start of new snow preparation (the skiing season), the soil temperature course does not differ inside and outside the ski slope. The lack of the difference in thermal regime during summer is typical for ski slopes and their surroundings [12,23].

#### Phenology and changes of cover

Emergence and initial stages of plant development of many species in the arctic and alpine zones are triggered by snowmelt and temperature [6,16,32,33]. In the case of delayed snowmelt, the phenological phases of many alpine species are realized in a shorter time span compared with unchanged conditions [34]. Walker et al. [1] referred to such plant species as having “compressed phenology”, and a similar pattern is mentioned for several plant species from Japanese mountains [16], arctic tundra [35], and also from the Hrubý Jeseník Mts [17]. We found that bilberry developed with a delay inside the studied ski slope from the beginning until the end of June. Hence, bilberry belongs to alpine species that delay development as their response to postponed snowmelt [7,16]. This is partly in agreement with other papers [36,37] that consider bilberry as a conservative species with relatively fixed phenological timing. Borner et al. [38] observed similar conservative phenological pattern in related *V. vitis-idaea* at sites with increasing snow depth in Alaskan arctic tundra.

Therefore, even a short delay of snowmelt can evoke shifts of bilberry phenophases that is apparent several weeks after snowmelt [31,39].

The cover also showed delay in development as the onset of growth and increased cover of alpine shrubs is closely linked to snowmelt timing [35]. Accordingly, the growth of bilberry shoots was delayed due to the snowmelt postponement at the studied ski slope. Growth differences evoked by the snowmelt postponement were documented for several other species at groomed ski slopes [7,17].

Flowering phenology is a temperature-dependent phenomenon in many plants, and the ECT has often been used as an indicator of flowering traits [32]. We showed that temperature affects bilberry phenological development because the onset of its flowering needs the identical ECT regardless of the time of snowmelt. The shorter time span of some bilberry phenological phases inside the ski slope despite a delayed start can be thus explained by higher daily temperatures during the critical period which temporarily increased its developmental rate. As clarified by Wipf [33], early phenophases respond to snowmelt (as a phenological trigger), whereas the later phases are controlled by temperature rather than snowmelt.

The phenological difference between the ski slope and natural surrounding disappeared at the phase of flower fade. The ontogenetic development of bilberry is linked with its cover that increased more rapidly at the ski slope compared with the outside resulting in similar cover at both habitats later in the growing season. Hence, the approximately 3-week delay caused by the ski slope operations at the beginning of the season is not crucial for the ontogeny of the species because bilberry successfully finished its phenological development at both sites. Similar to our findings, Borner et al. [38] documented that only the late phenological phases of deciduous shrubs occurred at approximately the same time in different snow depths, suggesting that differences in the timing of the early phenological stages are diminished over the course of the growing season. We suggest several possible causes explaining observed findings. First, in contrast with outside the ski slope, less fluctuating and rapidly increasing daily temperatures inside the ski slope after snowmelt likely influenced ECT which temporarily increased developmental rate of bilberry and may contributed to the shortening of phenological differences between habitats from ca. 20 days at the beginning of the season to ca. 5–7 days in June. Second, the greater temperature fluctuation outside the ski slope may cause frost damages [6] and spring frost events can unequivocally evoke growth and reproduction shifts [40]. In addition, life cycle of bilberry may be codetermined by other factors that were not evaluated by us, especially by nitrogen availability, soil moisture, and carbon gain efficiency [41,42]. Several studies suggest that growth processes are likely related to the temperature (see above) and amount of nitrogen [35]. The nitrogen availability depends on the snow bulk [35] that is also influenced by higher atmospheric depositions at the High Sudetes Mts [43]. In accordance with Sweet et al. [35] the nitrogen influence on timing of some phenophases can be expected.

Lower average temperatures at the ski slope can also indirectly influence the rate of increase of bilberry cover through carbon gain efficiency. Low temperatures reduce carbohydrate consumption by respiration in storage organs during winter [44], which was also demonstrated at the studied ski slope [22]. High concentrations of carbohydrates are attributed to cold hardiness during winter [45] and serve to accelerate spring growth processes after snowmelt [4]. Moreover, from the higher SWE we infer better water availability at least during the beginning of the growing season at the ski slope that can have profound effect on the development, activity and duration of the source and sink organs of bilberry plants [46,47].

### Flowering and fruiting output

The mean densities of flowers and fruits were three times higher at the ski slope than outside it despite similar covers of bilberry. However, only ca. 50% of the flowers successfully matured into fruits and the rate was similar both inside and outside the ski slope. Similar mean densities of flowers, fruits and constant fruits:flowers ratio in *V. myrtillus* observed Pato and Obeso [48] at elevation gradient in the Cantabrian Range (Spain). Similar fruits:flowers ratio at both habitats suggest similar availability

of pollinators and/or similar level of self-pollination [48], and similar site conditions during pollination and ripening phase. Fruiting output at compared sites is thus result of earlier events.

Temperature, especially its periodic spring fluctuation connected with frost injury, is a limiting factor for bilberry sexual reproduction [18,40]. Gerdol et al. [18] revealed a negative influence of low spring temperature on production of flowers during a 3-year snow manipulative experiment. Moreover, seed-set success is higher in later snowmelt habitats where is bilberry protected against too low temperature during winter and spring [40]. We suggest that temperature course is a plausible explanation for both flowering and fruiting differences between the inside and outside of the studied ski slope. In our case, spring temperatures particularly fluctuate on plots without snow (outside the ski slope), which can have a negative effect on frost-sensitive reproductive organs and subsequently on flowering and berry production.

As already discussed some non-evaluated factors including nutrient and soil moisture availability might play significant role in the allocation of plant resources into generative reproduction that corroborate study on *Vaccinium* species [18,46–50].

## Conclusions

Our results revealed that even “nature-friendly” managed ski slope had significant effect on several environmental variables including snow water content, snowmelt timing, and soil temperature. The influenced environmental conditions are mirrored by the seasonal development, growth, and reproduction of bilberry as a dominant shrub of alpine heathlands.

We are aware of several potential drawbacks that may affect the generalization. Our study was conducted over 1 year and in a single location (one ski slope). Only limited number of environmental factor were taken into account, hence caution should be taken in extrapolating our findings to determine the potential impacts of “nature-friendly” ski slopes on phenology and performance of bilberry. Despite the limitations, this study shows that the impact of the altered snow conditions on ski slope did not negatively affect or even support the performance (cover, reproductive density) of the *Vaccinium myrtillus*. The longer period of snow cover on the ski slopes could thus support and protect the vegetation from expected impacts of early snow melt due to the global warming. Those facts should be considered in the conservation and management of the protected alpine areas where “nature-friendly” ski slopes are operated or planned in future.

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## References

1. Walker MD, Walker DA, Welker JM, Arft AM, Bardsley T, Brooks PD, et al. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrol Process*. 1999;13:2315–2330. [http://dx.doi.org/10.1002/\(SICI\)1099-1085\(199910\)13:14/15%3C2315::AID-HYP888%3E3.0.CO;2-A](http://dx.doi.org/10.1002/(SICI)1099-1085(199910)13:14/15%3C2315::AID-HYP888%3E3.0.CO;2-A)
2. Wahren CHA, Walker MD, Bret-Harte MS. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Glob Chang Biol*. 2005;11:537–552. <http://dx.doi.org/10.1111/j.1365-2486.2005.00927.x>
3. WipfS, Rixen C. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Res*. 2010;29:95–109. <http://dx.doi.org/10.1111/j.1751-8369.2010.00153.x>
4. Körner C. *Alpine plant life*. Berlin: Springer; 2003. <http://dx.doi.org/10.1007/978-3-642-18970-8>

5. Grabherr G, Gottfried M, Pauli H. Climate effects on mountain plants. *Nature*. 1994;369:448. <http://dx.doi.org/10.1038/369448a0>
6. Wipf S, Stoeckli V, Bebi P. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Clim Change*. 2009;94:105–121. <http://dx.doi.org/10.1007/s10584-009-9546-x>
7. Rixen C, Stoeckli V, Ammann W. Does artificial snow production affect soil and vegetation of ski pistes? A review. *Perspect Plant Ecol Evol Syst*. 2003;5:219–230. <http://dx.doi.org/10.1078/1433-8319-00036>
8. Rixen C, Haeberli W, Stoeckli V. Ground temperatures under ski pistes with artificial and natural snow. *Arct Antarct Alp Res*. 2004;36:419–427. [http://dx.doi.org/10.1657/1523-0430\(2004\)036\[0419:GTUSPW\]2.0.CO;2](http://dx.doi.org/10.1657/1523-0430(2004)036[0419:GTUSPW]2.0.CO;2)
9. Wipf S, Rixen C, Fischer M, Schmid B, Stoeckli V. Effects of ski piste preparation on alpine vegetation. *J Appl Ecol*. 2005;42:306–316. <http://dx.doi.org/10.1111/j.1365-2664.2005.01011.x>
10. Roux-Fouillet P, Wipf S, Rixen C. Long-term impacts of ski piste management on alpine vegetation and soils. *J Appl Ecol*. 2011;48:906–915. <http://dx.doi.org/10.1111/j.1365-2664.2011.01964.x>
11. Kašák J, Mazalová M, Šipoš J, Kuras T. The effect of alpine ski-slopes on epigeic beetles: does even a nature-friendly management make a change? *J Insect Conserv*. 2013;17:975–988. <http://dx.doi.org/10.1007/s10841-013-9579-3>
12. Keller T, Pielmeier C, Rixen C, Gadiant F, Gustafsson D, Stähli M. Impact of artificial snow and ski-slope grooming on snowpack properties and soil thermal regime in a sub-alpine ski area. *Annals of Glaciology*. 2004;38:314–318. <http://dx.doi.org/10.3189/172756404781815310>
13. Jonas T, Marty C, Magnusson J. Estimating the snow water equivalent from snow depth measurements in the Swiss Alps. *J Hydrol (Amst)*. 2009;378:161–167. <http://dx.doi.org/10.1016/j.jhydrol.2009.09.021>
14. Hédl R, Houška J, Banaš M, Zeidler M. Effects of skiing and slope gradient on topsoil properties in an alpine environment. *Pol J Ecol*. 2012;60:381–389.
15. Cleland EE, Chuine I, Mooney HA, Schwartz MD. Shifting plant phenology in response to global change. *Trends Ecol Evol*. 2007;22:357–365. <http://dx.doi.org/10.1016/j.tree.2007.04.003>
16. Kudo G, Suzuki S. Flowering phenology of alpine plant communities along gradient of snowmelt timing. *Polar Biosci*. 1999;12:100–113.
17. Banaš M, Zeidler M, Duchoslav M, Hošek J. Growth of alpine lady-fern (*Athyrium distentifolium*) and plant species composition on a ski piste in the Hrubý Jeseník Mts., Czech Republic. *Ann Bot Fenn*. 2010;47:280–292. <http://dx.doi.org/10.5735/085.047.0404>
18. Gerdol R, Siffi C, Iacumin P, Gualmini M, Tomaselli M. Advanced snowmelt affects vegetative growth and sexual reproduction of *Vaccinium myrtillus* in a sub-alpine heath. *J Veg Sci*. 2013;24:569–579. <http://dx.doi.org/10.1111/j.1654-1103.2012.01472.x>
19. Ritchie JC. *Vaccinium myrtillus* L. *J Ecol*. 1956;44:291–299. <http://dx.doi.org/10.2307/2257181>
20. Treml V, Banaš M. The effect of exposure on alpine treeline position: a case study from the High Sudetes, Czech Republic. *Arct Antarct Alp Res*. 2008;40:751–760. [http://dx.doi.org/10.1657/1523-0430\(07-060\)\[TREML\]2.0.CO;2](http://dx.doi.org/10.1657/1523-0430(07-060)[TREML]2.0.CO;2)
21. Křížek M, Treml V, Engel Z. Periglacial landforms in the High Sudetes (the Czech Republic). *Anales Universitatii de Vest din Timisoara – Geograe*. 2005;14:51–58.
22. Zeidler M, Banaš M, Duchoslav M. Carbohydrate reserve changes in below-ground biomass of subalpine grasslands as a result of different snow conditions (Hrubý Jeseník Mts., Czech Republic). *Pol J Ecol*. 2008;56:75–83.
23. Zeidler M, Duchoslav M, Banaš M. Effect of altered snow conditions on decomposition in three subalpine plant communities. *Cent Eur J Biol*. 2014;9:811–822. <http://dx.doi.org/10.2478/s11535-014-0312-3>
24. Krahulec F, Chytrý M, Härtel H. Nardus grasslands and heathlands. In: Chytrý M, editor. *Vegetation of the Czech Republic*. 1. Grassland and heathland vegetation. Praha: Academia; 2007. p. 281–319.
25. Kubát K, Hrouda L, Chrtek J jun, Kaplan Z, Kirschner J, Štěpánek J. *Klíč ke květeně České republiky*. Praha: Academia; 2002.

26. Chytrý M. Vegetation of the Czech Republic. 1. Grassland and heathland vegetation. Praha: Academia; 2010.
27. van der Maarel E. Vegetation ecology. Malden, MA: Blackwell Publishing; 2005.
28. Akaike H. Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F, editors. The second international symposium on information theory. Budapest: Akadémiai Kiado; 1973. p. 267–281.
29. Kenward MG, Roger JH. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics*. 1997;53:983–997. <http://dx.doi.org/10.2307/2533558>
30. Edwards AC, Scalenghe R, Freppaz M. Changes in the seasonal snow cover of alpine regions and its effect on soil processes: a review. *Quat Int*. 2007;162–163:172–181. <http://dx.doi.org/10.1016/j.quaint.2006.10.027>
31. Rixen C, Stoeckli V, Huovinen C, Huovinen K. The phenology of four subalpine herbs in relation to snow cover characteristics. In: Dolman AJ, Hall AJ, Kavvas ML, Oki T, Pomeroy JW, editors. Soil–vegetation–atmosphere transfer schemes and large-scale hydrological models. Proceedings of an international symposium held during the Sixth Scientific Assembly of the International Association of Hydrological Sciences (IAHS); 2001 Jul 18–27; Maastricht, the Netherlands. Wallingford: IAHS; 2001. p. 359–362. (IAHS Publication; vol 270).
32. Molau U, Nordenhäll U, Eriksen B. Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. *Am J Bot*. 2005;92:422–431. <http://dx.doi.org/10.3732/ajb.92.3.422>
33. Wipf S. Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecol*. 2010;207:53–66. <http://dx.doi.org/10.1007/s11258-009-9653-9>
34. Kawai Y, Kudo G. Local differentiation of flowering phenology in an alpine snowbed herb *Gentiana nipponica*. *Botany*. 2011;89:361–367. <http://dx.doi.org/10.1139/b11-024>
35. Sweet SK, Gough L, Griffin KL, Boelman NT. Tall deciduous shrubs offset delayed start of growing season through rapid leaf development in the Alaskan arctic tundra. *Arct Antarct Alp Res*. 2014;46:682–697. <http://dx.doi.org/10.1657/1938-4246-46.3.682>
36. Walker MD, Ingersoll RC, Webber PJ. Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology*. 1995;76:1067–1083. <http://dx.doi.org/10.2307/1940916>
37. Jonas T, Rixen C, Sturm M, Stoeckli V. How alpine plant growth is linked to snow cover and climate variability. *J Geophys Res*. 2008;113:G03013. <http://dx.doi.org/10.1029/2007JG000680>
38. Borner AP, Kielland K, Walker MD. Effects of simulated climate change on plant phenology and nitrogen mineralization in Alaskan arctic tundra. *Arct Antarct Alp Res*. 2008;40:27–38. [http://dx.doi.org/10.1657/1523-0430\(06-099\)\[BORNER\]2.0.CO;2](http://dx.doi.org/10.1657/1523-0430(06-099)[BORNER]2.0.CO;2)
39. Dvořák IJ, Kociánová M, Hejcman M, Tremel V, Vaněk J. Linkage between geo- and biodiversity on example of snow-patch “Map of Republic” (Modrý důl Valley). *Opera Corconica*. 2004;41:100–110.
40. Tolvanen A. Recovery of the bilberry (*Vaccinium myrtillus* L.) from artificial spring and summer frost. *Plant Ecol*. 1997;130:35–39. <http://dx.doi.org/10.1023/A:1009776200866>
41. Molau U. Relationships between flowering phenology and life history strategies in tundra plants. *Arctic and Alpine Research*. 1993;25:391–402. <http://dx.doi.org/10.2307/1551922>
42. Hülber K, Winkler M, Grabherr G. Intraseasonal climate and habitat specific variability controls the flowering phenology of high alpine plant species. *Funct Ecol*. 2010;24:245–252. <http://dx.doi.org/10.1111/j.1365-2435.2009.01645.x>
43. Fabiszewski J, Brej T. Contemporary habitat and floristic changes in the Sudeten Mts. *Acta Soc Bot Pol*. 2000;69:215–222. <http://dx.doi.org/10.5586/asbp.2000.029>
44. Higgins PD, Spomer G. Soil temperature effects on root respiration and the ecology of alpine and subalpine plants. *Bot Gaz*. 1976;137:110–120. <http://dx.doi.org/10.1086/336849>
45. Ögren E. Premature dehardening in *Vaccinium myrtillus* during a mild winter: a cause for winter dieback? *Funct Ecol*. 1996;10:724–732. <http://dx.doi.org/10.2307/2390507>
46. Mingeau M, Perrier C, Améglio T. Evidence of drought-sensitive periods from flowering to maturity on highbush blueberry. *Sci Hortic (Amsterdam)*. 2001;89:23–40. [http://dx.doi.org/10.1016/S0304-4238\(00\)00217-X](http://dx.doi.org/10.1016/S0304-4238(00)00217-X)
47. Percival D, Murray A, Stevens D. Drought stress dynamics of wild blueberry (*Vaccinium*

- angustifolium* Aiton). Acta Hort. 2003;618:353–362. <http://dx.doi.org/10.17660/ActaHortic.2003.618.41>
48. Pato J, Obeso JR. Growth and reproductive performance in bilberry (*Vaccinium myrtillus*) along an elevation gradient. Ecoscience. 2012;19:59–68. <http://dx.doi.org/10.2980/19-1-3407>
49. Miina J, Hotanen JP, Salo K. Modelling the abundance and temporal variation in the production of bilberry (*Vaccinium myrtillus* L.) in Finnish mineral soil forests. Silva Fennica. 2009;43:577–593. <http://dx.doi.org/10.14214/sf.181>
50. Piňosová J. Některé výsledky měření sněhové pokrývky v Hrubém Jeseníku. Zprávy Československé Botanické Společnosti. 1986;21:69–78.