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Growth of Alpine lady-fern (*Athyrium distentifolium*) and plant species composition on a ski piste in the Hrubý Jeseník Mts., Czech Republic

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This study was focused on identifying the impact of a ski piste on snow conditions, soil temperature, as well as phenological development and growth of *Athyrium distentifolium*, and examining differences in species composition between the ski piste and the natural environment. Longer snow-cover period and deeper snow were observed on the ski piste than in the natural surroundings. Lower soil temperature was found on the ski piste during the peak winter period and at the beginning of the growing period. Different environmental conditions on the ski piste caused a delay and shortening of the phenological development of *A. distentifolium* in the late spring. Individuals of that plant caught up the initial delay in phenological development within 36 days after the beginning of measurement. However, plants only grew to lower height on ski piste as compared with plants in control plots. Even relatively small differences in the time of snow melt and soil temperature development in stands examined on the ski piste resulted in significant changes in the species composition of the studied vegetation towards subalpine tall grasslands.

Key words: alpine plant community, *Athyrium distentifolium*, habitat ecology, phenology, ski piste, species composition

Introduction

Snow cover strongly determines the distribution of plant species in the alpine zone (Billings & Bliss 1959, Körner 1999). Patterns of snow distribution and snow duration in alpine areas create rather stable mosaics of vegetation that follow isolines of snow melt (Körner 1999). The snow cover protects plants from low temperatures, drought and frost (Ellenberg 1988, Jones & Pomeroy 2001). Snow distribution determines the length of the growing season (Körner 1999, Sturm *et al*. 2001), and it influences soil development and the soil environment including soil temperature, freeze-thaw cycles, microbial activity, oxygen–CO_2 balance (Meyer 1993, Körner 1999, Jones & Pomeroy 2001), respiration of plants during the winter, nutrient transport and nutrient availability (Bilbrough *et al*. 2000, Fahnestock *et al*. 2000, Lipson *et al*. 2002, Schimel *et al*. 2004). There is also a close relationship between snow duration, plant cover, phenology of plants and plant productivity (Walker *et al*. 1995, Heegaard 2002, Huelber *et al*. 2006, Kudo & Hirao 2006). Experiments with altered snow depths and snow cover duration have shown significant phenological and growth changes in alpine plants (Galen & Stanton 1993, 1995, Walker *et al*. 1999, Totland & Alatao 2002, Wahren *et al*. 2005).

Skiing in ski areas exerts an important type of land-use that significantly influences the distribution of snow cover and subsequently the development of limiting factors in the mountain environment (Titus & Tsuyuzaki 1998, Rixen *et al*. 2003). Research focused on the impacts of ski piste operation on the mountain environment began to be carried out in the 1970s and 1980s with the expansion of these activities, especially in the European Alps (Weiss *et al*. 1998). Most of those studies focused on direct impacts, especially on the impacts of mechanical disturbances on the soil cover, plant phenology and plant communities (e.g. Bayfield 1980, 1996, Watson 1985, Tsuyuzaki 1993). They also dealt with an evaluation of vegetation succession in areas where grass had been seeded artificially (e.g. Delarze 1994, Urbanska *et al*. 1999, Fattorini 2001, Gros *et al*. 2004). Fewer studies dealt with indirect impacts of downhill skiing, i.e. the impact of altered snow conditions on the soil environment and vegetation on ski pistes (Baiderin 1982, Rixen *et al*. 2003, 2004, Keller *et al*. 2004, Wipf *et al*. 2005).

Manipulation of snow (displacing and compacting the snow cover) on ski pistes and skiers' activities results in a considerable snow compaction (Keller *et al*. 2004). Snow compaction is reflected in changes of its thermal and hydrological properties. Snow density, hardness, heat conductivity, water content and duration increase, while porosity and permeability decrease (Sturm *et al*. 1997, Rixen *et al*. 2003, Keller *et al*. 2004). Heat conductivity is a function of snow density, so heat flow through the compacted snow cover is much higher than in areas with natural snow cover (Sturm *et al*. 1997). This results in more freezing of soil on ski pistes as compared with areas having a natural snow cover (Baiderin 1982, Cernusca *et al*. 1990, Rixen *et al*. 2004), subsequent reduction of soil microbial activity (Meyer 1993) and carbohydrate reserve changes in below-ground biomass (Zeidler *et al*. 2008). Changes in oxygen and carbon dioxide balances, as a result of an increased number of ice layers in the snow, have also been observed at sites with a compacted snow cover (Cernusca *et al*. 1990, Newesely 1997). The lack of oxygen causes an increased susceptibility of plants to frost damage in their shoots and roots (Körner 1999). As a result, plant species with insufficient cold hardiness and plants sensitive to mechanical stress may be damaged, resulting in a shift among functional groups (Wipf *et al*. 2005). Shortening of the vegetation season on ski pistes can also have an impact on some plants, as has been shown in the Alps and Russia. There can be phenological changes in early-flowering species, or they can even disappear from communities (Baiderin 1982, Wipf *et al*. 2005).

Only a few studies have dealt with the relation between snow cover and alpine vegetation of the Hercynian Mountains of central Europe (*sensu* Grabherr *et al*. 2003), particularly from the High Sudeten Mts. (Jeník 1958, Štursa *et al*. 1973, Klimešová 1993, Hejcman *et al*. 2006). Data concerning the impact of ski pistes on alpine vegetation of these mountains is lacking. In addition, the alpine tundra of Hercynian Mts., including the studied territory in the Hrubý Jeseník Mts., covers only about 10.48 km^2 and is therefore threatened by the development of anthropogenic activities (Jeník 1998, Grabherr *et al*. 2003). An important community of the alpine belt of the Hrubý Jeseník Mts. is the *Athyrium distentifolium* community [association *Adenostyli-Athyrietum alpestris* (Zlatník 1928) Jeník 1961]. Within the Hercynian Mts. of central Europe, this is a rare alpine community (Kočí 2001), potentially endangered by downhill skiing development. Nevertheless, potential changes of the community under influence of ski piste have been neglected up until now.

This study of the alpine plant community dominated by *A. distentifolium* is focused on (1) identifying the difference in snow conditions and soil temperature between the ski piste and the natural environment, (2) examining if the ski piste causes a delay of phenological development and decrease of growth in *A. distentifolium,* as the community's dominant species, and (3) examining if there are differences in species composition between stands of the community on the ski piste and the natural environment.

Material and methods

Study site

The study area (about 10 000 m^2) is situated in northeastern Czech Republic, in the Hrubý Jeseník Mts., which is the second highest mountain range within the Hercynian Mts. of central Europe (*sensu* Grabherr *et al*. 2003). The research locality is situated on the northeastern leeward hillside of Petrovy Kameny Mt. (1448 m a.s.l., 50°04´N, 17°14´E) in the alpine belt above timberline (Jeník 1972, Treml & Banaš 2008).

The relief of the slope of Petrovy Kameny Mt. has been shaped by cryogenic and periglacial processes (Křížek *et al*. 2005). The study area is formed of crystalline bedrock and gneiss (Demek 1987) with podzolic soils (Kubiena 1953).

The territory is characterized by a short and cold summer and a long, cold and damp winter with long snow cover duration (Quitt 1971). The highest parts of the territory have an alpine climate, with an average annual temperature of 1.1 °C, an average temperature in January is –7.5 °C, in July 9.7 °C. Long-term annual average rainfall is 1200–1300 mm, and the amount of rainfall is influenced significantly by wind (Lednický 1985). The mesoclimate and subsequently also the biota of the area are significantly influenced by snow accumulation on the leeward side of the anemo-orographic system during the winter (Jeník 1961, 1997). The snow cover lasts up to 180 days per year, usually from November to the end of May.

The stands of alpine vegetation containing *A. distentifolium* (association *Adenostyli-Athyrietum alpestris* (Zlatník 1928) Jeník 1961 from the alliance *Dryopterido-Athyrion* Holub *ex* Sýkora et Štursa 1973) occur in protected, shaded and moist places with long-lasting snow cover at and around the alpine timberline. The stands are dominated by *A. distentifolium*, but *Adenostyles alliariae*, *Rumex arifolius*, *Silene dioica*, *Stellaria nemorum*, *Oxalis acetosella* occur as well. In lower areas, the vegetation gradually changes into a mountain spruce forest of the association *Athyrio alpestris–Piceetum* Hartmann 1959.

The study region has the highest situated downhill ski pistes in the Hercynian Mts., reaching into the alpine zone. The ski piste examined has been used for skiing since the first half of the 20th century, and snow grooming has been performed since the 1980s. There is no artificial snow-making on the ski piste and natural snow accumulation is supported only by 1-m-heigh snowfences. The relief and vegetation on the ski piste and surroundings are of natural character. Use as a pasture ceased in the 1940s, and there have been no important mechanical disturbances — particularly because the location is part of a national nature reserve. The mechanical disturbance of plants on the ski run is prevented by operating rules. Skiing activities are suspended when snow depth drops below 80 cm.

Measurement of snow conditions

In the winter of 2004, the snow depth was measured along three transects (each 110 m long), which crossed both the ski piste (40 m), and the natural environment (60 m) on both sides, through the examined vegetation stands. Snow depth was measured at 4-m intervals. Three depth measurements (0.7-m apart) were taken at every measuring point of the transect using a calibrated telescoping avalanche probe and the average depth for the given point was calculated. Measurements were carried out on 5 January, 29 January, 27 February, 1 April, 14 April, and 27 April 2004.

During the 2004 spring season, snow melting process at the study area was evaluated from the photographs taken from a stationary point on the opposite slope. Depending on the weather, the pictures were taken every 2–5 days. Digitized images were incorporated into coordinates and converted to a shapefile. Using the programs ArcGIS 8.3, ArcView GIS 3.1, and the extension for ArcView Image Analysis 1.1, a map of the snow-melting process in the natural environment and on the ski piste was created on the basis of rectified photographs. This map was then used to establish the time when snow had melted from each of the plots used for phenology and growth sampling.

Permanent plots establishment and soil temperature measuring

In *A. distentifolium* stands, ten 0.5 × 0.5-m plots on the ski piste and ten identically-sized control plots outside the ski piste were randomly selected and marked. Distances between adjacent plots were at least 10 m. The control plots were located 10–40 m from the 10-m buffer zone between the ski piste and unaffected area on both sides of the ski run. No significant differences in the environmental conditions (elevation, aspect and inclination of the slope, soil conditions) among plots on the ski piste and control plots were found (all $P > 0.25$, data not shown).

Three spots were randomly selected within permanent plots on the ski piste and in the natural environment. A datalogger (Minikin 2T, EMS Brno) with a temperature sensor, placed 3 cm below the litter surface, was positioned at each location on 17 November 2003. Soil temperature development was then recorded continuously in 1-h intervals until 30 November 2004. Average daily temperatures for every datalogger were then calculated and used in the analysis.

Phenology and growth of *A. distentifolium*

Basic phenophases that express significant stages in the life cycle of *A. distentifolium* were chosen to monitor seasonal changes in this species' phenology. The single phenophases was recorded for each individual on the marked plots. The methodology for particular phenophases followed that of the Czech Hydrometeorological Institute (Valter 1985) but was modified for ferns. The following phenophases were defined:

Phase 1: *Initial emerging fronds* — hibernating buds formed of young unfurling fronds, coiled in a spiral, are noticeable in the plant detritus, at the apical parts of rhizomes. No green parts of leaves are visible.

Phase 2: *Emerging fronds* — the buds have unfurled partly, so parts of leaves are noticeable at their apical parts or around the buds.

Phase 3: *Young fronds* — the leaves have already partly unfurled and all the single leaves are visible, but they have not reached their final size corresponding to maturity.

Phase 4: *Maturing of leaves* — leaves are fully developed. Sori have not reached their full size and have light colour.

Phase 5: *Maturation of sori* — sori on the leaves are getting brown, but the walls of the sori are not yet broken.

Phase 6: *Dehiscence of sori* — the sori are breaking and the spores are released.

Phenological stages and lengths of the fronds of *A. distentifolium* were monitored on each plot during the 2004 growing season. Along with phenological stages, the height of all fronds on plots from the ground to the top of the bud or to the end of the frond was measured. The monitoring began immediately after the snow had melted on all control plots (13 May). In total, 17 phenological and growth investigations were carried out in 2004, approximately on a weekly basis, between 13 May and 20 September.

Plant species composition

For examination of plant species composition in the stands of *A. distentifolium*, 10 already fixed plots for phenological observation and another 20 randomly selected plots were used for both ski-piste and control area. Hence, 30 plots 1 × 1-m on the ski piste and the same number of plots in the natural environment were established. No significant differences in the environmental conditions (elevation, aspect and inclination of the slope, soil conditions) among plots on the ski piste and control plots were found (all $P > 0.21$, data not shown). During the peak of the vegetation season (the first half of August 2004), the plant-species composition on these plots was recorded by means of phytosociological relevés. Species cover was estimated using Braun-Blanquet's nine-grade abundance–dominance scale (Moravec 1994), and the nomenclature of the plant species followed Kubát *et al*. (2002).

Data analysis

Differences in snow depth and the temperature development in the topsoil during the season between the ski piste and natural environment (= control) were analysed with the general linear model (GLM) with sampling points or data-loggers as subjects, 'ski piste' as the between-subject fixed factor and sampling date as the within-subject fixed factor. Changes in phenological stages and plant height during the season on the ski piste and in natural environment were analysed either using the generalized linearized model (GLIM) or GLM, with plots nested within the fixed factor 'ski piste' (ski piste *vs*. control), and sampling date as the within-plots fixed factor. In GLIM, we used the ordinal multinomial model and logit link function (Crawley 1993) with the frequency of plants in each respective phenological stage as a count variable. For visualisation purposes, we first estimated the most frequent phenological stage observed in *A. distentifolium* plants in each plot for each date, and then we calculated the means of phenological stages from these data for each date and environment. For each date, variation in the phenological development and plant height between ski piste and natural stands was analysed using either the *t*-test (Zar 1996) or nested ANOVA (Quinn and Keough 2002). All statistical analyses were performed using Statistica 6.0 (Statsoft Inc. 2001).

Floristic composition was analysed with CANOCO 4.5 (ter Braak & Šmilauer 2002). We first analysed the data set with DCA using Hill's scaling. The results indicated that a linear approach is appropriate for the elucidation of a relationship between floristic composition and environmental factors (Lepš & Šmilauer 2003). Then we compared floristic composition between the control plots and plots on the ski piste using the redundancy analysis (RDA). The Monte Carlo permutation test (499 permutations) was used to assess the significance of the first canonical axis. For each plot the mean value of Ellenberg's indicator values for moisture, light, soil reaction and nitrogen (Ellenberg *et al*. 1991) was calculated without species weighting. We did not analyse the indicator values for temperature, because more than one third of the species in the analysed data set had unknown values for temperature.

Results

Snow conditions

Snow depth differed significantly between the ski piste and control plots ($F_{1,52}$ = 12.17, P = 0.001) and among the sampling dates ($F_{5,260}$ = 90.87, P < 0.001). Because the ski piste × sampling date interaction was also significant ($F_{5,260}$ = 8.52, P < 0.001), we performed a separate analysis for each habitat and each sampling date. In the control plots, snow depth differed among the sampling dates, with the exception of the second and the fifth date. On the ski piste, in the middle of the season (27 February), the snow depth differed from the beginning of the season (5 January, 29 January) and from the end of the season (14 April and 27 April). In both habitats the greatest depth was recorded on 27 February (Fig. 1). On the last four dates, the snow depth on the ski piste was much greater than that on the control plots, while no differences were found on the first sampling date (P = 0.59). On the plots intended for phenological monitoring and measuring of *A. distentifolium* growth, the snow cover lasted until 5 May in the natural environment, while on the ski piste, the snow melted with a 16-day delay (21 May).

Soil temperatures

The analysis of the soil temperature 3 cm below the litter surface showed that the annual average temperature on the ski piste was approximately 0.3 °C lower than that in the natural environment ($F_{1,4}$ = 10.03, P = 0.034). However, temperature differences between the ski piste and natural stands were not uniform throughout the year (ski piste × sampling date interaction, $F_{365,1460}$ = 1.24,

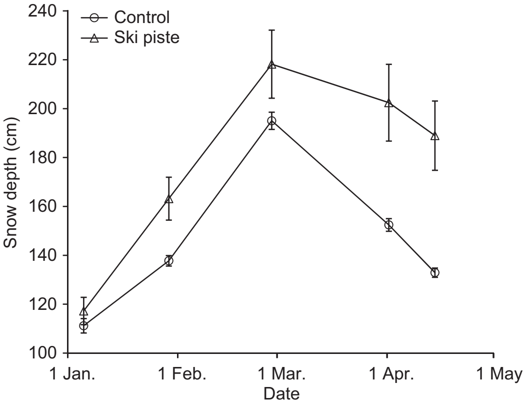

Fig. 1. Changes in snow depth on the control plots and ski piste during peak and cessation of the 2004 winter season (mean ± SE).

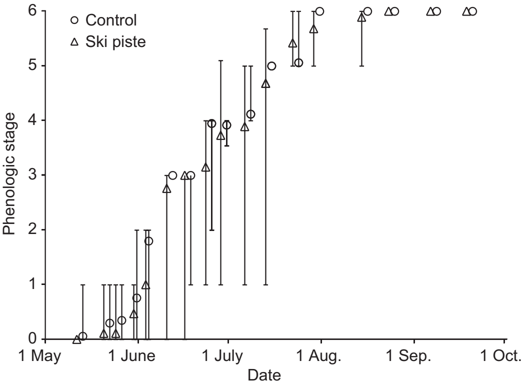

Fig. 2. Phenological development of *Athyrium distentifolium* on control plots and ski piste during the 2004 growing season. For each habitat and date the mean, minimum and maximum of the phenologic stage (0: dormant stage, 1: initial emerging fronds, 2: emerging fronds, 3: young fronds, 4: maturing of leaves, 5: maturation of sori, 6: dehiscence of sori) were calculated.

P = 0.004). Separate analyses for each month revealed that only in three months (February, March and May) was the temperature on the ski piste consistently lower than that on the control plots (Table 1). Temperature differences between the environments gradually decreased during February and March and almost disappeared in June. Later in the season, neither the effect of ski piste (Table 1) nor the ski piste × sampling date interaction had significant effects on the temperature (all $P > 0.08$).

Phenology and growth of *A. distentifolium*

The phenological development of *A. distentifolium* differed between the ski piste and control plots (GLIM ski piste × sampling date interaction, $\chi^2 = 43.7$, $P < 0.001$; Fig. 2). At the beginning of the season (13, 22 and 26 May), no significant phenological difference between plants on the control plots and on the ski piste was observed. Significant differences between environments were observed from 1 June to 16 June (early summer), when plants on the control plots showed earlier development than plants on the ski piste (*t*-test: all $P < 0.05$). Later in the season (late summer and autumn), no significant phenological differences between plants on the control plots and on the ski piste was observed (Fig. 2).

The results also show that the development of the early phenological stages (initial germination and germination) was shortened on the ski piste, specifically between the fifth and sixth measurement dates (4 June to 11 June) (Fig. 2).

Table 1. Soil temperatures (°C; mean and SE per month) 3 cm below the litter surface in *Athyrium distentifolium* stands on the control plots and on the ski piste during the 2003/2004 winter season and the 2004 vegetation season. Results of repeated-measures ANOVA testing the effect of the between-subject factor "ski piste" within each month are given.

	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Mean
Control	–0.18	–0.06	–0.04	–0.04	–0.06	4.80	10.14	10.65	11.46	7.26	4.46	1.65	4.19
	(0.05)	(0.01)	(0.01)	(0.01)	(0.01)	(0.38)	(0.22)	(0.22)	(0.19)	(0.22)	(0.26)	(0.20)	(0.15)
Ski piste	–0.34	–0.65	–0.29	–0.33	–0.15	3.24	9.51	10.78	11.19	7.16	4.48	1.48	3.86
	(0.08)	(0.06)	(0.03)	(0.02)	(0.01)	(0.29)	(0.21)	(0.23)	(0.14)	(0.21)	(0.27)	(0.21)	(0.14)
F	0.38	3.09	8.11	8.03	0.78	7.55	0.91	0.29	0.25	0.09	0.01	0.77	
P	0.57	0.15	0.04	0.04	0.43	0.05	0.39	0.62	0.64	0.79	0.91	0.43	

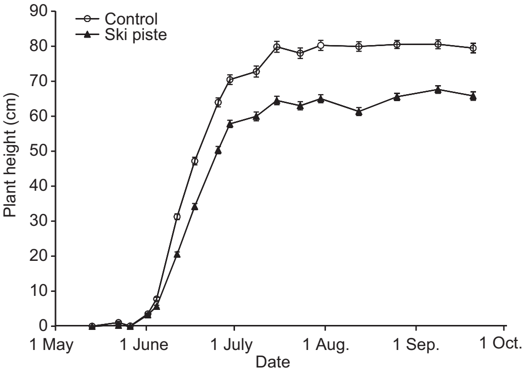

Fig. 3. Changes in plant height (mean ± SE) of *Athyrium distentifolium* growing on the ski piste and on the-control plots during the 2004 growing season.

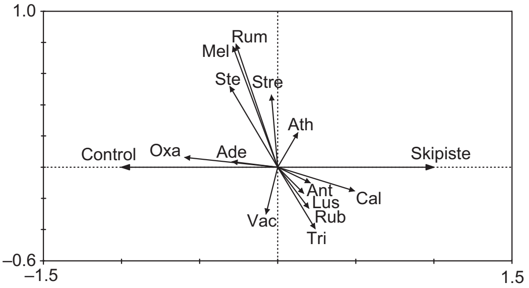

Fig. 4. RDA biplot of the species and the environmental factor 'ski piste' (with two categories: ski piste and control) of the *Athyrium distentifolium* community. Only species with a higher fit in the analysis are displayed. Abbreviations: Ade (*Adenostyles alliariae*), Ant (*Anthoxanthum odoratum-alpinum*), Ath (*Athyrium distentifolium*), Ave (*Avenella flexuosa*), Bis (*Bistorta major*), Cal (*Calamagrostis villosa*), Dry (*Dryopteris dilatata*), Hom (*Homogyne alpina*), Lus (*Luzula sylvatica*), Mai (*Maianthemum bifolium*), Mel (*Silene dioica*), Oxa (*Oxalis acetosella*), Polyg (*Polygonatum verticillatum*), Rub (*Rubus idaeus*), Rum (*Rumex arifolius*), Ste (*Stellaria nemorum*), Strept (*Streptopus amplexifolius*), Tri (*Trientalis europaea*), Vac (*Vaccinium myrtillus*), Ver (*Veratrum album* subsp. *lobelianum*).

The growth of *A. distentifolium* differed between the ski piste and control plots (GLM, ski piste: $F_{1,18} = 3.8$, $P = 0.067$; sampling date: $F_{16,288} = 339.9$, $P < 0.0001$; interaction ski piste × sampling date, $F_{16,288} = 3.2$, $P < 0.001$; Fig. 3). At the beginning of the season, no difference in the *A. distentifolium* plant height between the ski piste and control was observed, but later in the season plants on the control plots grew in height more rapidly than those on the ski piste. Separate analyses for each sampling date showed that plants on the control plots were significantly taller ($P < 0.05$) than those on the ski piste on all sampling dates, with exception of the first, third and fourth sampling dates (13 , 22 and 26 May) when no differences in plant height between the habitats were observed.

Plant species composition

There was no significant difference in species richness between the stands on the ski piste (mean ± SE per square; 5.5 ± 0.3) and on the control plots (5.2 ± 0.3) (two-sample *t*-test: $t_{58} = 0.77$, $P = 0.45$). Although the vegetation was almost closed in both habitats, the total cover was significantly higher on the ski piste (median, 25th and 75th percentile; 100%, 95–100%) than on the control plots (95%, 90%–97%; Mann-Whitney test: $Z = 2.1$, $n_1 = n_2 = 30$, $P = 0.04$). The stands on the ski piste differed significantly in species composition from the control stands (RDA, Monte Carlo permutation test of the first axis: $F = 6.65$, $P = 0.002$; Fig. 4). On the control plots, additional species were mainly *Oxalis acetosella, Adenostyles alliariae* and *Stellaria nemorum*. In contrast, mainly *Calamagrostis villosa*, *Trientalis europaea*, *Luzula sylvatica* and *Rubus idaeus* occured on the ski piste.

The control stands differed from the stands in the ski piste in mean indicator values for all the factors tested (Table 2). Stands in the ski piste showed higher demands for light and moisture in comparison with the control stands. In addition, control stands indicated more fertile and less

Table 2. Mean indicator value (SE) of selected ecological factors (*sensu* Ellenberg *et al.* 1991) based on plant species composition on the natural (control) plots and on the ski piste. Differences between the habitats were tested using a two sample *t*-test ($n = 30$ plots for each habitat).

Factor	Control	Ski piste	*P*
Light	4.4 (0.1)	4.8 (0.1)	0.008
Moisture	5.2 (0.1)	5.7 (0.1)	< 0.001
Soil reaction	5.0 (0.2)	4.3 (0.2)	< 0.001
Nitrogen	5.8 (0.2)	4.8 (0.2)	< 0.001

acidic soils as compared with the stands on the ski piste (Table 2).

Discussion

Snow and soil conditions

The longer snow-cover period and deeper snow observed by us on the ski piste than in the natural surroundings is in agreement with data from Alps and Oregon (Titus 1999, Rixen *et al*. 2003, Wipf *et al*. 2005), and is caused by the manipulation of snow by means of ski piste preparation.

The parallel study by Banaš *et al*. (2005) showed a significantly higher snow density on this ski piste as compared with the natural environment which is caused by modified properties of the snow cover on the ski piste (Rixen *et al*. 2008). With increasing snow density, the insulation capacity of the snow cover decreases (Sturm *et al*. 1997). In some instances, winter temperatures under a compacted snow cover on treated ski pistes can on average be lower by 1 °C (Rixen *et al*. 2004a) or even more (Baiderin 1982) as compared with those in the natural environment. Our results showed lower soil temperatures on the ski piste in the peak winter period and at the beginning of the growing period. The annual average difference between the ski piste and the natural environment was approximately 0.3 °C. Though large temperature differences were not observed in the area examined, the snow depth and soil temperature measurements show that even with the significantly higher depth of snow cover in the ski piste, its insulation capacity is lower. The lower soil temperature found on the ski piste at the beginning of the growing season (May and the beginning of June) was caused by the fact that in May the vegetation on the ski piste still lies partly under the snow cover and the surrounding soil is cooled by water from this melting snow. At the beginning of June, this cooling effect of melting snow subsides in the upper parts of the ski piste.

The significantly greater snow depth and density on the ski piste during the winter resulted in an increased water content, which is in agreement with the data from the Alps (Keller *et al*. 2004, Rixen *et al*. 2003). Our analysis of Ellenberg's indicator values also confirm that soils on the ski piste are moister than in the natural stands. On the ski piste, increased soil moisture and leaching are probably closely connected to the increased soil acidity as pointed out by Ellenberg's indicator values.

Growth and phenology of *A. distentifolium*

The longer snow-cover period and deeper snow observed by us on the ski piste should, considering the ecology of *A. distentifolium*, generally be advantageous by protecting buds and young unfurling fronds from spring freezing. However, our results show that on the ski piste some phenophases are delayed and shortened, and that fronds are smaller.

A close connection between soil temperature and growth speed has been observed for *A. distentifolium* (Odland 1995). Results from Norway show that the main phase of growth of fronds does not begin before the soil temperature reaches 6–7 °C (Odland 1995), regardless of the time when the snow melted (Mchaffie 2005). In the natural environment of the area we examined, the first signs of frond growth (the initial emerging fronds phenophase) were recorded on 13 May. The average soil temperature during the seven days prior to this initial germination was 3.3 °C, and on 12 May, the soil temperature of 6.5 °C was recorded for the first time. The first signs of initial germination were recorded on the ski piste on 22 May. In this case, the average soil temperature during the previous seven days was 4.9 °C, and on 19 May the soil temperature was higher than 6 °C (7.2 °C) for the first time. It follows from this data that the fronds of *A. distentifolium* began to grow within approximately one day (in the natural environment) up to three days (in the ski piste) after the average temperature exceeded 6 °C in the upper part of the soil profile. Similar results were obtained from Norway (Odland 1995). When the soil temperature isotherm reaches approximately 6–7 °C, growth of the fronds of *A. distentifolium* is controlled mainly by air temperature, and it takes 24–27 days for the leaves to grow to their full size (Odland 1995). Mchaffie (2005) states that in

Scotland, fronds of *A. distentifolium* require six or seven weeks to fully expand. In the more oceanic climate of the Scottish Highlands, the average July air temperature in a locality where *A. distentifolium* occurs is 10 °C, while in Norway it is 12 °C (Mchaffie 2005). Data from a meteorological station at the stands we studied show that the average July air temperature in 2004 was 11 °C. In the area examined, fronds of *A. distentifolium* grew to their full size (reached the "maturing of leaves" phenological stage) both on the ski piste and in the natural environment at the same time. A closer comparison of the history of phenological phases with the soil temperature development reveals a difference between the ski piste and control plots. While in the natural environment fronds reached the phase of 'maturing of leaves' during six weeks from the moment the average daily soil temperature reached 6 °C, on the ski piste this period was shorter by one week. Differences in the height of fronds and delay in the phenological development in the ski piste as opposed to the natural environment are apparent at the beginning of the vegetation season. It is caused by the fact that the start of growing is blocked by the presence of snow cover and subsequently also by lower soil temperature, which do not enable the initiation of growth. The delay in phenological development and reduced growth of *A. distentifolium* in the ski piste are also influenced by the lower quantity of soil nitrogen available for the spring growth of plants (Schimel *et al*. 2004, Schmidt & Lipson 2004). This lower quantity of available nitrogen is associated with the soil's lower decomposition activity under the compacted snow cover on the ski piste due to lower soil profile temperatures. A significantly lower litter decomposition rate was found in *A. distentifolium* stands on the ski piste examined (Banaš *et al*. 2005). Also, the analysis of Ellenberg's indicator values confirm that soils on the ski piste are less fertile than natural stands.

Between 23 May and 26 May, unfurling buds (fronds) of *A. distentifolium* dried up in the plots, both in the ski piste and in the natural environment. Data from the meteorological station at the locality show that the average air temperature decreased on 22 May and 23 May to –0.3 °C and –2.2 °C, respectively, with an absolute minimum of –3.3 °C. This confirms the susceptibility of *A. distentifolium* to frost damage (Sato *et al*. 1989, Mchaffie 2005). These results show that in the initial stages of development, fronds of *A. distentifolium* are much more susceptible to frost damage than they are in maturity. Experiments on frost tolerance of leaves of *A. distentifolium* illustrate that they can withstand freezing of up to –15 °C for one day (Sato & Saki 1981). Bigger leaves can survive frost of up to –7 °C for a longer period (Mchaffie 2005).

The start and development of the 'young fronds' phenophase (phase 3) are same for both environments. Therefore, *A. distentifolium* growing on the ski piste recovered from the initial delay of phenological development in 36 days from the beginning of measurements. These results are thus in accordance with the data from the Alps which show that even a very short difference during melting of the snow cover (several days) can cause a change in the plants' phenological development that lasts for several weeks after the snow disappears (Rixen *et al*. 2001). The fact that the phenological development of *A. distentifolium* on the ski piste "caught up" during the vegetation season is a manifestation of accelerated phenological development when each phenophase takes place within a shortened period of time. Such development has been reported from areas with artificially manipulated snow cover depth and duration (Walker *et al*. 1999). Nevertheless, as follows from seasonal measurements of frond height, this "catching up" of phenological development is associated with the permanently reduced growth of *A. distentifolium* on the ski piste. Using *A. distentifolium* as an example, it is therefore possible to illustrate the way in which some species can react to adverse environmental conditions caused by a ski piste. This strategy consists of decreasing investment into the length and size of leaves, and in the simultaneous quick development to reach the generative phase. The data collected thus confirm the fact that alpine plant species tend to go through their whole year-long life-cycle even if the vegetation season is shortened (Billings & Bliss 1959, Walker *et al*. 1995).

Athyrium distentifolium may dominate in large stands even though their fertility is low or zero, which indicates that, under certain ecological conditions (e.g. the very long-lasting snow beds found in Norway), they reproduce mainly vegetatively (Odland 1998). Presumably, a season that is too short does not allow sufficient reserves to be built up for the production of sori (Mchaffie 2005). On the ski piste examined, *A. distentifolium* reached the phenological stage of maturity approximately at the same time as in the natural environment. Therefore, it is clear that the later snow melt on the ski piste is not sufficient to cause the 'snow beds' effect with consequent impact on the fertility of *A. distentifolium* as described by Odland (1991).

Composition of associated vegetation

In connection with the altered abiotic environmental conditions on the ski piste, changes in the representation of some plant species can be expected (Baiderin 1982, Wipf *et al*. 2005). When comparing species compositions of ski piste and control plots, species typical for alpine tall grassland of the alliance *Calamagrostion villosae* Pawlowski *et al*. 1928 were more common on the ski piste, while species typical for alpine tall fern of the alliance *Dryopterido-Athyrion* (Holub *ex* Sykora et Štursa 1973) Jeník *et al*. 1980 occur more often in the natural environment. The explanation for this fact lies in a combination of several factors. As mentioned above, a lower litter decomposition rate has been shown in the plant litter of *A. distentifolium* community on the ski piste (Banaš *et al*. 2005). Therefore, we can expect an increased accumulation of litter on the ski piste and a subsequent suppression of ecesis of other plant species, as observed previously by several authors (Gjaerevoll 1950, Seastedt *et al*. 2001, Shaw & Harte 2001). This influence concerns mainly dicotyledonous species that are less competitive and have more difficulties to embed in a thicker litter layer, in our case the typical species of alpine tall-fern vegetation (e.g. *Oxalis acetosella*, *Stellaria nemorum*). In contrast, typical species of alpine tall grassland (e.g. *Calamagrostis villosa*, *Rubus idaeus*, *Anthoxanthum alpinum*) are well adapted to life in habitats with a thicker plant litter layer and in sites with increased levels of other stress types (Pyšek 1990, 1993, Kočí 2001). These ecological characteristics thus support the higher presence of such species on the ski piste.

The supression of species typical for the alpine tall-fern vegetation and hemicryptophytes with subnival initiation of phenological development (e.g. *Adenostyles alliariae*) on the ski piste examined is apparently related to the longer-lasting snow cover (shortening of the vegetation season) and to increased mechanical pressure (weight) of snow. We can assume that the higher layer and increased density of snow result in increased mechanical pressure on the vegetation and soil profile. This pressure can cause damage to plants, whose hibernating buds lie near the soil surface.

Our results show that even a relatively small difference in the time of snow melting and in the development of soil temperature can produce significant changes in the growth of *A. distentifolium* and the species composition of the entire community. Hence, the aforesaid tendency for the higher penetration of typical species of alpine tall grassland into stands on the ski piste could in future result in changes at the community level.

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