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CARBOHYDRATE RESERVE CHANGES IN BELOW-GROUND BIOMASS OF SUBALPINE GRASSLANDS AS A RESULT OF DIFFERENT SNOW CONDITIONS (HRUBÝ JESENÍK MTS., CZECH REPUBLIC)

ABSTRACT: Carbohydrate concentration changes in below-ground biomass of subalpine tall grasslands with *Calamagrostis villosa* (Chaix) J.F. Gmelin were monitored during one year on the slope of Petrovy kameny Mt. (Hrubý Jeseník Mts., Czech Republic). Stands of the community with natural snow conditions were compared with stands on a ski piste. Soil temperature development and snow melting times were also observed in the territory concerned. The difference was stated between mean annual temperature on control stands (4.21°C) and ski piste (3.95°C) in the upper 5 cm of soil. At the average, snow melted on the ski piste two weeks later than that on the natural stands. The natural stands and the stands on the ski piste differ significantly from each other in terms of development of carbohydrate accumulation in the below-ground biomass. Consumption of reserve carbohydrates by the plants at both the ski piste and in the natural stands was nearly similar during the winter. At the beginning of the growing season (July), significant difference in carbohydrate concentration in below-ground organs between stands on the ski piste and natural stands was observed. It was caused by late melting of the snow cover and subsequent delay of the phenologic development and assimilation of the vegetation in the ski piste. Later in season (August, October), the differences in carbohydrate concentration between stands at the ski piste and natural stands disappeared. The mean annual amount of carbohydrates in the upper (0–5cm) and lower (5–10 cm) soil horizons in natural stands and ski piste stands do not differ fundamentally, except for the significant difference in July. The results obtained are discussed in view of abiotic environmental conditions, the plant physiology and strategy of the dominant species.

KEY WORDS: below-ground, carbohydrate reserves, subalpine grassland, snow, ski piste

1. INTRODUCTION

Growth of plants in subalpine habitats demands an appropriate allocation of nutrients. Along with low soil fertility (Bowman and Fisk 2001), duration of snow cover, the amount of water and nutrients available and temperature development during the growth season also play the crucial role (Körner 1999, Hitz *et al.* 2001). From this point of view, it is essential for the plants to accumulate a sufficient amount of reserve substances in the reserve tissues. Their ability to utilise them quickly in their life processes is also of great importance (Bliss 1998). Carbohydrates or lipids (Körner 1999) are the most frequently mentioned reserve sources of carbon for plants. A plant with a sufficient energy reserve is able to survive better in the climate of the subalpine belt, to resist a sudden loss of biomass (Lambers *et al.* 1998, Wyka 1999, Landhäusser and Liefferrs 2002, Weih and Karlsson 2002) and competition with the other species.

Changes in carbohydrate concentrations related to temperature of the environment were recorded for many plants (Eagles 1967, Wielgolaski and Kjelvik 1975). Concentration of carbohydrates in below-ground biomass usually achieves its minimum in a period after snow melting (Wyka 1999), and its maximum between the top and end of the growing season. The above-mentioned changes are connected with respiration and photosynthetic intensity. The highest consumption of carbohydrates is observed during the winter and snow melting. On the other hand, the growing season is a period when the plants create necessary supplies of carbohydrates (Bliss 1998, Weih and Karlsson 2002).

The length and course of the winter season is therefore of key importance for the plant community in the alpine tundra. Quantitative and qualitative changes in the snow cover are reflected directly in changing abiotic factors of the environment (Körner 1999). Most of all, it is soil temperature and length of the growing season which have a crucial influence on composition of the plant communities (Walker *et al.* 1999, Rixen *et al.* 2003, Wipf *et al.* 2005).

The alpine grassland cannot use lignified parts of their tissues for carbohydrate accumulation. They use the below-ground, overwintering organs to accumulate carbohydrates during the unfavourable period (Skre 1985). Below-ground biomass of alpine grassland in the upper 10 cm of soil achieves up to 80%, while for the topmost 5 cm it is more than 50% of the plant biomass (Hitz *et al.* 2001). Deeper soil layers are not used to a great extent. Downwards, the amount of below-ground biomass decreases by two thirds in every 10 cm of depth (Malinovsky 1997).

Most reserve organs in alpine grassland are thus in a relatively thin layer of soil which can be influenced easily by above-ground abiotic environmental conditions. Changes in the length of growing season and in the temperature mode caused by different snow conditions should therefore be reflected directly in changing carbohydrates concentrations in the below-ground biomass. So far, the issues related to the impact that the different snow conditions have on reserve carbohydrates in subalpine grasslands do not seem to be known.

In the subalpine environment, substantial changes occur in the snow conditions of downhill ski pistes. Comprehensive impacts of changes in physical properties of snow, soil temperature decrease, shortened growing season and subsequent changes in the structure and vitality of the alpine vegetation become evident on the ski piste (Baiderin 1982, Keller *et al.* 2004, Rixen *et al.* 2004, Wipf *et al.* 2005). However, data on the specific impact of these factors on allocation of reserve carbohydrates in below-ground biomass are missing.

Therefore, the present study aims to (1) describe changes in carbohydrate concentration in root biomass of subalpine tall grasslands with *Calamagrostis villosa* (Chaix) J.F. Gmelin during the growing season at the areas with different snow conditions (downhill ski piste *vs.* stands with natural snow conditions). Attention was also paid to (2) differences in carbohydrate concentration depending on the depth of below-ground biomass.

2. STUDY AREA

The research was performed in the north-eastern leeward hillside of the mountain Petrovy kameny (1448 m a.s.l., GPS 50°04´N, 17°14´E), in the subalpine belt of the Hrubý Jeseník Mts. (Jeník 1972; Fig. 1). The mountain range belongs to Hercynian middle mountains of Central Europe (Grabherr *et al.* 2003).

The relief of Petrovy kameny Mt. was reshaped in cryogenic and periglacial ways (Křížek *et al.* 2005). The study area is formed of crystalline bed rocks and gneiss (Demek 1987). In pedological terms, the area is formed of podzols (Kubiena 1953).

The territory is characterized by a short and cold summer and a long, cold and damp winter with a long duration of snow cover (Quitt 1971). The highest parts of the territory have extreme climate which corresponds to high alpine to subarctic areas. The average annual temperature in the top parts is 1.1°C. Long-term annual average rainfall is 1213 mm while the amount of rainfall is influenced significantly by wind. The snow cover lasts for up to 180 days a year, usually from November to May (Lednický 1985).

Subalpine tall grasslands with *Calamagrostis villosa*, which was a study object, predominate on protected, leeward places above the alpine timberline. They belong to the association *Sileno vulgaris-Calamagrostietum villosae* Jeník *et al.* 1980. The community usually grows on drier, deeper soils that are rich in nutrients and humus (Jeník 1961, Kočí 2001). The community is dominated by *Calamagrostis villosa*; the accessoric species are *Rumex arifolius* All., *Silene vulgaris* (Moench) Garcke, *Luzula luzuloides* subsp. *rubella* (Mert. et Koch) Holub, *Luzula sylvatica* (Huds.) Gaudin, *Rubus idaeus* L., *Bistorta major* S.F. Gray, *Ligusticum mutellina* (L.) Crantz and others (Jeník *et al.* 1980).

In the study region, there are the uppermost downhill ski pistes in the Hercynian Middlemountains which reach the subalpine belt. The ski piste examined has been used for skiing since the first half of the last century, and snow grooming is applied since 1980s. Artificial snowing is not carried out in the locality. The relief and vegetation on the ski piste and in its surroundings is of a natural character.

3. MATERIAL AND METHODS

Twenty permanent plots in the ski piste and 20 permanent plots in a reference natural area outside the piste were randomly chosen and delimited in stands of subalpine tall grasslands with *Calamagrostis villosa* (Fig. 1). To record seasonal changes in carbohydrate concentration, four samples were taken repeatedly from each permanent plot during 2005: first one when the snow was melting,

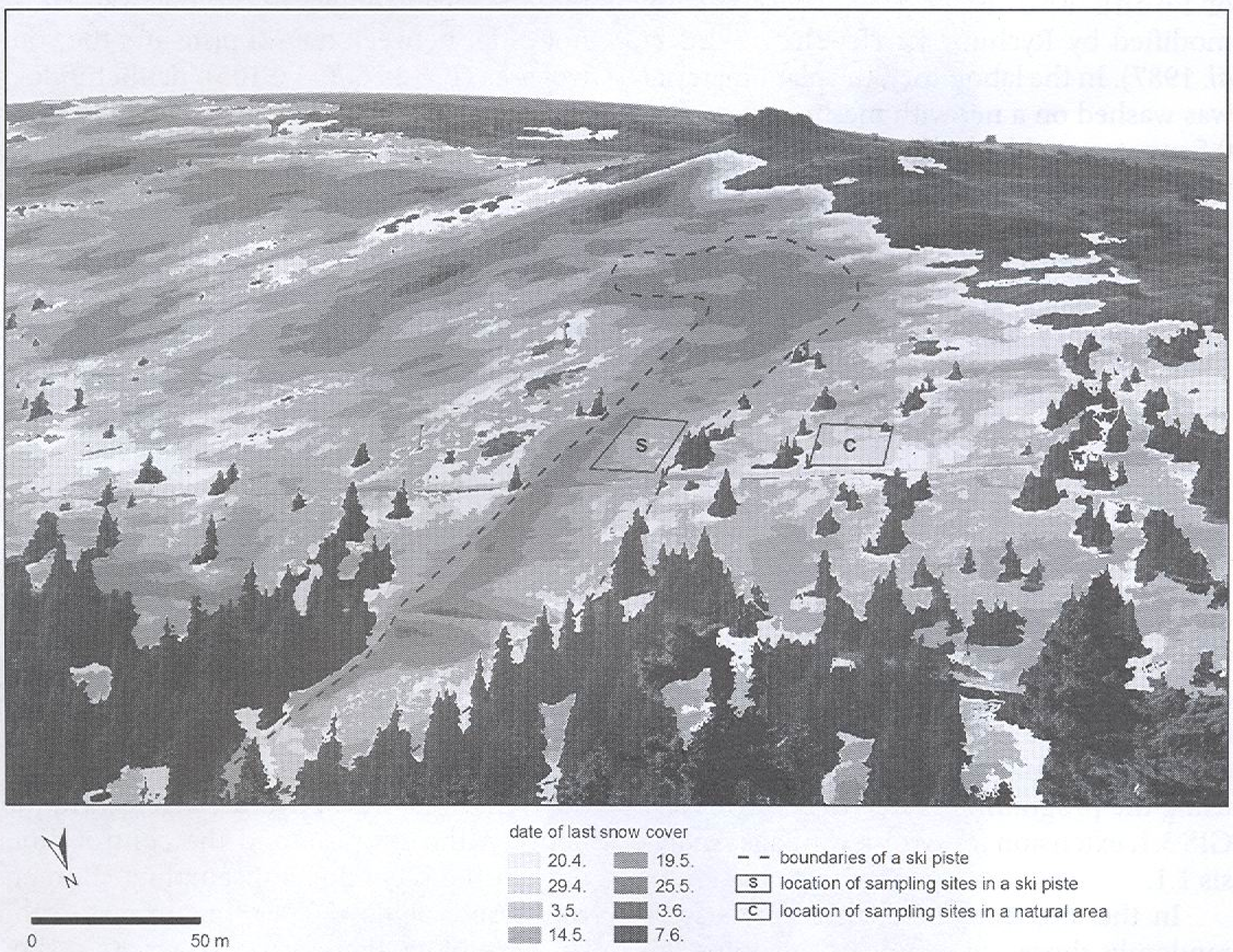

Fig. 1. Snow melting process on the north-eastern slope of Petrovy kameny Mt. in 2005 with sampling areas being marked. The particular colour intensities express the distribution of snow cover on the slope examined in the given time.

right before the beginning of the growing season (May 3); the second one at the beginning of the growth (July 4); the third one in culminating growth (August 24), and the fourth one at the end of the growing season (October 4). In the natural stands, the first sampling was carried out right after the melting of snow ended. In the ski piste, sampling was performed at the same time, through the remaining and melting snow layer.

All below-ground biomass was taken by means of a cylindrical soil sampling equipment with a circle sampling area $4.90.10^{-3}$ m^2 and depth of 15 cm. All residues of above-ground biomass and waste were removed from the sample, and the monolith was divided into the upper (0–5 cm) and lower part (5–10 cm) of the horizon. The material was transported in plastic bags to the laboratory.

The amount of carbohydrates was determined by hydrolysis and with subsequent quantitative colorimetric measurement to determine reducing sacharides. The method of Fonda and Bliss (1966) was slightly modified by Rychnovská (Rychnovská *et al.* 1987). In the laboratory, the plant material was washed on a net with mesh size equal to 0.5 mm to get rid of mineral admixtures. The next step consisted in drying at 85°C (Dykyjová *et al.* 1989). The dry plant material was hydrolysed with HCl (4%). Concentration of carbohydrates was determined using spectrophotometry and Nelson test solution at 530 nm.

During the 2005 spring season when snow was melting, photographs of the slope examined were taken from a stationary point on the opposite slope, with a fixed focus of the objective. The recording interval was 2–5 days, depending on the weather. Digitalised photographs were incorporated into coordinates, converted to shape file. On the basis of rectified photographs, a map showing the development of snow melting in the natural environment and the ski piste was created using the programmes ArcGIS 8.3, ArcView GIS 3.1, extension for ArcView Image Analysis 1.1.

In the area examined, three plots were randomly chosen in stands of subalpine tall grasslands with *Calamagrostis villosa,* both in the ski piste and in the natural environment. In November 2004, a data logger (Minikin 2T, EMS Brno) was installed in each of six plots to measure temperature 5 cm below the litter surface. The temperature development was recorded on a continual basis, with one-hour intervals. Daily average values have been used to present temperature course in the areas monitored.

Repeated measures ANOVA was used to analyse changes in carbohydrate concentration, with treatment (ski slope *vs.* control ~ natural plots) and horizon as the between-plots factors and sampling date as the within-plots factors. Geisser-Greenhouse corrected probability levels on the within-subject F tests were used (Quinn and Keough 2002). Data were log-transformed before the analysis. The NCSS 2001 (Hintze 2001) package was used for all the statistical analyses.

4. RESULTS

The analysis of carbohydrate concentration in below-ground biomass has proved that the mean content of carbohydrates does not differ between the ski piste and the control area ($F = 2.76$, $P = 0.105$), neither it does between the upper and lower horizon ($F = 0.47$, $P = 0.497$). In 1 g of dry matter from the ski piste below-ground biomass, 95.19 mg of carbohydrates were identified in average. In the control plots, it was 100.21 m g^{-1} of carbohydrates. For the upper horizon – the value was 97.21 mg g^{-1} of carbohydrates and for the lower horizon – it was 98.02 mg g^{-1} of carbohydrates.

However, carbohydrate concentration was changing substantially in time ($F = 475.43$, $P < 0.001$), and it also had a different dynamics in the ski piste and on the control plots (interaction treatment × time, $F = 4.60$, $P = 0.008$). In the first sampling (May), the carbohydrate concentrations were very similar for the ski piste and control areas, and they were significantly lower than those in the other samplings. There was a significant difference in carbohydrate concentration between the ski piste and the control plots only in the second (July) sampling (Bonferroni test at alpha = 0.05). In contrast to the ski piste plots, there were 20% more carbohydrates in the upper horizon and 13% in the lower one on the control plots in July. On top of the growing season and at its end (August and October), the carbohydrate concentrations in the ski piste and on the control area were quite similar again (Fig. 2).

A different dynamics of carbohydrate concentration between the horizons over time was also observed (interaction: horizon × time, F = 4.57, $P = 0.008$), while its development was similar for both the ski piste and the natural site (interaction horizon × treatment × time, F = 1.16, $P = 0.326$). However, the only difference was found out in the third sampling (August) when carbohydrate concentration in the upper horizon was significantly lower than that in the lower horizon (Bonferroni test at alpha = 0.05; Fig. 2).

An analysis of the snow melting course in the territory examined (Fig. 1) showed that snow melting in the community observed in the natural environment ended on May 3rd approximately, and the melting time differences among the single sampling places were several days only (± 4 days). In the ski piste, snow melting ended about May 17, and the time differences among the single sampling places were ± 5 days.

It follows from the course of daily soil temperatures (Fig. 3) that temperature in the ski piste is lower than that in the natural plots during the winter season and it more often achieves negative values. The mean soil temperature in the upper 5 cm in the ski piste was by 0.26°C lower than that on the natural plots.

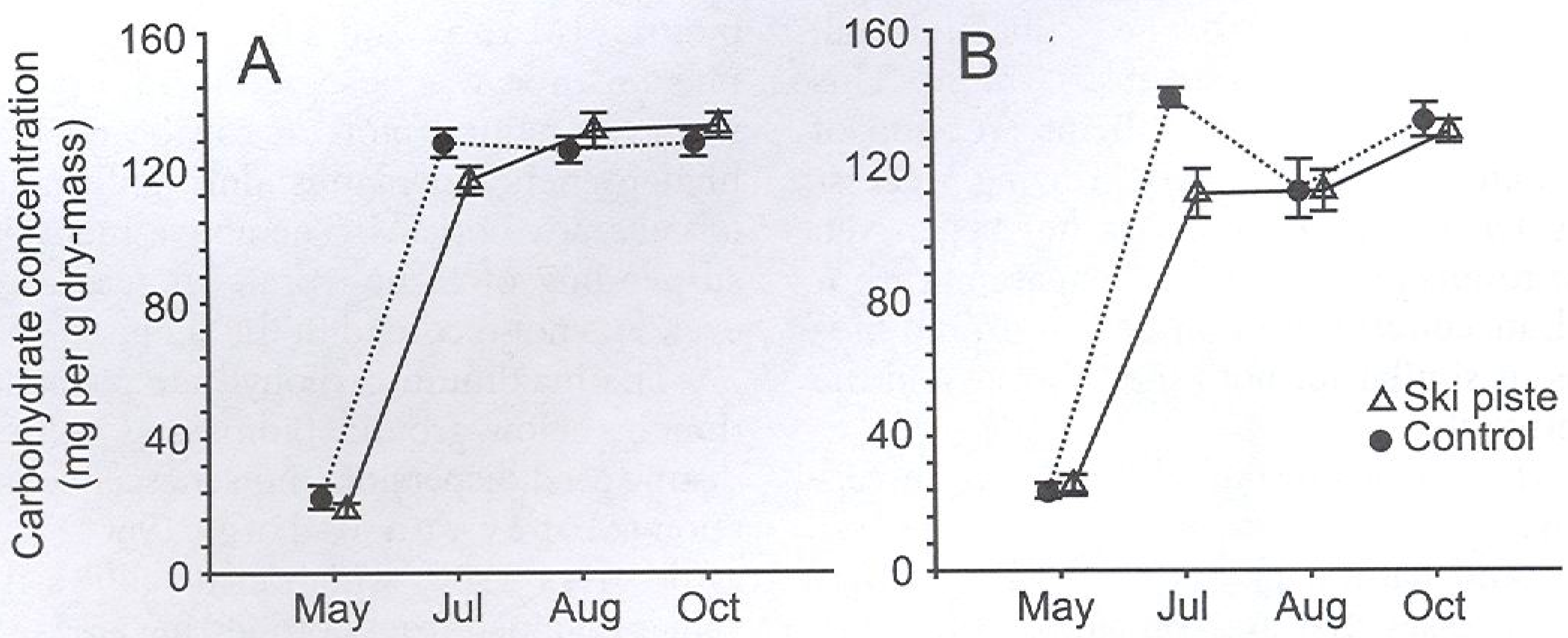

Fig. 2. Temporal changes of carbohydrate concentration in below-ground biomass (means ± SE) of subalpine tall grasslands with *Calamagrostis villosa* in the ski piste and control plots in (A) the lower horizon (5–10 cm) and in (B) the upper soil horizon (0–5cm).

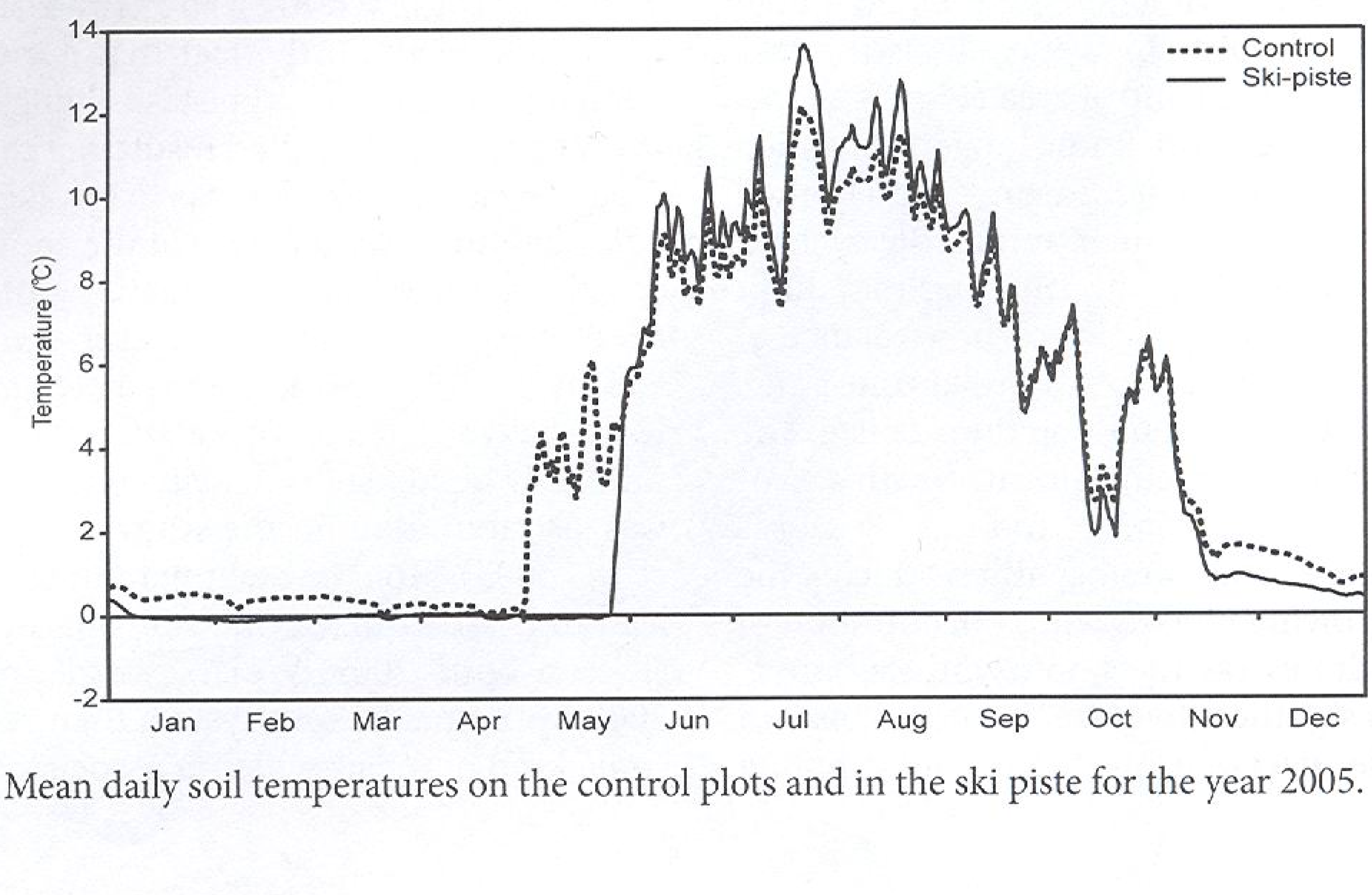

Fig. 3. Mean daily soil temperatures on the control plots and in the ski piste for the year 2005.

5. DISCUSSION

The course of changes in carbohydrate concentrations in below-ground biomass in areas examined during the season is related to physiological processes in plants and it does not differ from developments in the other alpine communities (Money and Billings 1960, Fonda and Bliss 1966, Brocklebank and Hendry 1989). The amount of carbohydrates in below-ground biomass of *Kobresia bellardii* (All.) Degl. (8–18%) in the mountains of Colorado (Bell and Bliss 1979) is very close to our results. The beginning of the growing season in the alpine belt is correlated with low carbohydrate concentration in below-ground biomass (Fonda and Bliss 1966, McCown and Tiezsen 1972), which can also be observed in the community examined, i.e. subalpine tall grasslands with *Calamagrostis villosa*. This decrease is connected with interruption of dormancy and initiation of growing processes when photosynthesis has not began yet. Our results prove that the decrease of carbohydrate concentration in below-ground biomass is similar for both the ski piste and the control plots.

There is a substantial difference in carbohydrate concentration among the ski piste and natural plots on July. Physiological processes that are connected with early phenophases are limited by temperature and duration of the snow cover. This is closely related to light conditions and availability of nutrients (Wipf *et al.* 2005). It was found out that snow is lying in the stands examined within the ski piste in average by two weeks later than on the control area (Fig. 1). Plants that are covered with snow longer, i.e. which have a shorter growing season, have a limited time to get through their annual life cycle. It is also obvious that the time lag may limit achievement of a positive carbon balance of the stand (Körner 1999). Similar time stress can be expected in stands on the ski piste. The photosynthetic system is formed with a two-week delay in the ski piste and this lag causes lower inflow from photosynthesis during the spring growing phases. The concentration of carbohydrates (as the photosynthesis product) was significantly lower in the ski piste in the earlier part of growing season (sampling on July). Therefore, the time stress resulting from a longer duration of snow cover on the ski piste was reflected in reserve carbohydrate concentration as late as 48 days after the melting of snow ended in the ski piste.

Data concerning carbohydrate concentration in below-ground biomass between ski piste and control plots in the top and end of the growing season suggest that the community is able to eliminate the above-mentioned time stress during season. This proves capability of some alpine communities to accelerate its seasonal development (Holway and Ward 1963, Shibata and Nishida 1993, Bliss 1998, Körner 1999). The top of growing season in natural plant communities is characterised by suspending advance of growth or possibly by decreasing carbohydrate concentration in the bellow-ground biomass (Money and Billings 1960). This phenomenon was observed in root biomass from the natural plots. It can be related to higher energy demands during formation of generative organs. The above-mentioned suspending of carbohydrate increase, however, was not recorded in the ski piste.

The maximum carbohydrate concentration in below-ground biomass is achieved during seed dispersion and senescence initiation (Money and Billings 1960, Fonda and Bliss 1966) which also follows from values obtained from both testing areas.

Nevertheless, not only the length of the growing season but also the temperature development during the whole year is crucial for carbohydrate concentration in below-ground biomass (Eagles 1967, Brocklebank and Hendry 1989). So the fact that during the winter, vegetation in ski pistes is lying under snow cover with a limited insulating capacity caused by its compaction has to be taken into consideration. Compaction of the snow cover and increased heat conductivity of snow result in lower soil temperatures in the upper soil layers in the winter (Sturm *et al.* 1997, Keller *et al.* 2004, Rixen *et al.* 2004). A significantly higher snow density in the ski piste was also found out in the study site (Banaš *et al.* 2005). Too low temperatures of soil lead to destruction of fine roots particularly (Rixen *et al.* 2003, Weih and Karlsson 2002). A damaged root system then requires some kind of repair which is associated with an increased consumption of carbohydrates. Under these conditions, the plant community would be limited in growth, including production of above-ground biomass, quite because of more investments into repairing the root system (Bliss 1998). The minimum differences in carbohydrate concentration identified among the areas examined at the beginning and at the end of the season are rather suggesting that temperatures under a more compacted snow cover in the ski piste observed do not get down to values that would cause more serious damage to the fine fibrous roots. Such losses are possibly compensated to a sufficient extent. The compensation follows from lower temperatures that slow down respiration processes in the ski piste during the winter season. In this way, consumption of carbohydrates is also reduced (Mooney and Billings 1965, Weih and Karlsoon 2002).

It is also necessary to take into account the fact that areas with longer and physically altered snow cover (i.e. the ski piste) are, especially when the snow is melting, exposed to almost anaerobic conditions, resulting from presence of a higher number of thin ice layers in the snow profile and a higher water capacity of the snow (Rixen *et al.* 2003, Keller *et al.* 2004). These conditions, which Larcher (2003) compares to flooding, cause considerable reduction of productivity and intensity of physiological processes in plants (Wipf *et al.* 2005). These conditions therefore can be supposed to take part in reduction and lags in phenologic development of subalpine tall grassland, including subsequent reduction of reserve carbohydrate allocation.

When looking at carbohydrate concentration in the single soil horizons, we found out that the upper horizon has greater fluctuations while the lower horizon reacts slowly and tends to accumulate carbohydrates during the growing season. Soil temperature in deeper horizons remains relatively low, without significant fluctuations during the season, which reduces the roots respiration intensity, and at the same time it enables storing of carbohydrates (Fonda and Bliss 1966).

The research was dealing with the whole community and it did not take into account reactions of the single plant species. The plants differ among each other in their responses to the environments with different lengths of snow cover (Mooney and Billings 1960, Shibata and Nishida 1993, Walker *et al.* 1994), and their adaptation mechanisms of matter synthesis were being formed in mutual balance between the root and shoot biomass (Ziroian *et al.* 1998). Generally, the longer is duration of the snow cover, the less species are able to survive (Körner 1999). However, grasses and some forbs are better adapted to the short growing period (Kudo 1991). Most dicotyledonous species show lower carbohydrate concentration (McCown and Tiezsen 1972) and thus they will be more sensitive to temperature development in the environment and to the length of the growing season. That is why, as a result of changing abiotic environmental factors associated with different snow conditions, some species are excluded from the community (Walker *et al.* 1999). Elimination of early-flowering species of dicotyledonous herbs was also mentioned in the case of downhill ski pistes (Baiderin 1982, Wipf *et al.* 2005, Rixen *et al.* 2003). On the other hand, the species *Calamagrostis villosa* cannot be expected to recede from the ski piste areas due to its wide ecological amplitude. This fact, together with its ability to adapt to changing soil properties and to alter its own environment are good preconditions for a strong competitiveness of this species (Pyšek 1993).

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