

Winter climate change at different temporal scales in *Vaccinium myrtillus*, an Arctic and alpine dwarf shrub

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Abstract

Snow cover strongly influences plant growth in Arctic and alpine ecosystems. Snow characteristics and snowmelt timing are likely to change in a warmer climate. We studied year rings and shoot growth of the dwarf shrub bilberry (*Vaccinium myrtillus*), and species abundances of the vegetation, in response to early or late snowmelt at a study site in the Central Alps, near Davos, Switzerland. Snowmelt was manipulated on experimental plots for 3 and 30 years. Additional plots were set up along a natural snowmelt gradient, and at high and low elevation. Growth ring data showed an increasing trend in annual growth increment over the last 20 years, especially in the extraordinarily hot summer of 2003. Comparing high and low elevation sites, growth rings were wider at low elevation, but only in cold years. In years with relatively cold summers, however, xylem ring width was greater in plots with late rather than early snowmelt along the natural snowmelt gradient, possibly indicating drought stress in early snowmelt plots. Snow cover had a strong influence on species abundances along the natural snowmelt gradient, and change (not yet significant) was beginning to be seen in plots with 30 years of snow manipulation. Our results indicate that beneficial effects of early snowmelt for shrub growth may be offset in cold summers. Although early snowmelt prolongs the growing season, harsh conditions and frost events early in the growing season may become more likely, and hamper plant growth, and this could affect plant growth in all Arctic and alpine snow-dominated ecosystems.

Seasonal snow cover is an inherent characteristic of high altitudes and latitudes. Snow cover strongly shapes Arctic and alpine ecosystems, and their plant life, by influencing crucial environmental factors for plant growth, notably winter plant and soil temperatures, and season length (Jones et al. 2001). As a result, plant growth and local species distribution often closely reflect the winter snow characteristics and timing of snowmelt (Friedel 1961; Körner 2003). Usually, steep environmental gradients exist over short distances from areas with little snow, a long vegetation period and extreme temperature fluctuations to those with long-lying snow cover, a short vegetation period and rather stable temperatures (Jones et al. 2001).

Climate change is likely to affect winter snow cover, and changes are expected to be most severe at high latitudes and altitudes (Symon et al. 2005; Solomon et al. 2007). With a temperature rise of 1.3°C in the 20th century, which has markedly accelerated since the 1980s,

the warming in the northern part of the Swiss Alps was higher than the global average (OcCC Consortium 2007). A further increase of 1.8°C (0.9–3.4°C) is predicted for the winter season over the next 50 years (OcCC Consortium 2007). In warmer winters, more of the precipitation will fall as rain, and the snow cover is likely to melt earlier in spring (Knowles et al. 2006). Although temperature effects on the snow cover may be mitigated by increases in winter precipitation in some areas, changes in the duration of the snow cover can already be observed in Arctic and alpine regions (Shabanov et al. 2002; Laternser & Schneebeli 2003; Knowles et al. 2006).

Changes in ecosystem structure and function that are attributed to changing snow cover have already become apparent in tundra ecosystems. Satellite data indicates that the growing season has increased by 12 days in northern America, and by 18 days in Eurasia, in the last 20 years (Zhou et al. 2001), leading to an earlier greening of the Arctic (Myneni et al. 1997; Shabanov et al. 2002).



Another prominent example of an ecosystem change that is attributed to changing snow cover is the enhanced growth of shrubs in Arctic tundra (Sturm et al. 2001; Tape et al. 2006). In the Alps, plant growth can vary considerably from year to year depending on seasonal snow cover characteristics (Jonas et al. 2008).

Numerous experimental studies have estimated the impacts of climate change on tundra ecosystems, but most of them have focused on warming (Dormann & Woodin 2002). Snow cover changes have been addressed by: (1) manipulating snow manually (e.g., Galen & Stanton 1993; Starr et al. 2000; van der Wal et al. 2000; Rixen et al. 2001; Wipf et al. 2006; Rixen et al. 2008); (2) manipulating snow with fences that accumulate snow in their lee (Walker et al. 1999; Wahren et al. 2005); and (3) observing natural patterns or gradients (Galen & Stanton 1995; Schöb et al. 2008). Most of these studies showed fundamental responses in the development, growth, fitness and distribution of plants. The temporal scales of such studies may range from one year (Wipf et al. 2006) to hundreds or thousands of years in the case of natural gradients (Billings & Bliss 1959). In our study, we aim to complement existing knowledge by addressing short-, mid- and long-term snow cover changes simultaneously. For this, we take advantage of a study site where snowmelt has been manipulated experimentally for three years, and for 30 years along snow fences. Additionally, we study natural gradients in snowmelt timing and in altitude.

We measured radial and shoot growth increments of the bilberry (*Vaccinium myrtillus*), a dwarf shrub common in Arctic and alpine tundra, and the species abundances of the vegetation in response to different types of snow cover. To study the radial growth of *V. myrtillus*, we made use of the fact that the stems of the dwarf shrub produce one xylem growth ring each year, like trees. As growth rings reflect the growing conditions of a given year, the comparison of ramet age and ring widths from different sites allows for a comparison of growing conditions under different snow regimes over as much as two decades.

We expect early snowmelt to enhance plant growth because the growing season is prolonged. Alternatively, growth may also be reduced because the risk of exposure to harsh conditions early in the year may be higher. Effects of early and late snowmelt may differ depending on the growing conditions in a specific year.

Material and methods

Study site

The investigations were carried out at the Stillberg treeline research station near Davos (Central Alps,

Switzerland, 47°28'N, 7°30'E). The site is located on a 25–30° steep, north-east exposed slope at 2200 m a.s.l., at the treeline. The mean annual precipitation is 1150 mm, and the mean temperature is 2.0°C (July, 9.4°C; January, –5.8°C; weather station at 2090 m a.s.l.). The mean maximum snow depth is 1.50 m, and snow cover lasts on average from 18 October (± 16 days) to 26 May (± 10 days). The main vegetation type, growing on a 5–20 cm deep organic topsoil layer on paragneiss bedrock, is dwarf shrub heath (*Empetro-Vaccinietum cetrarietosum*), dominated by the deciduous dwarf shrub bilberry (*Vaccinium myrtillus*) and other members of the ericaceous family. *V. myrtillus* is a long-lived woody species that can grow up to 50 cm high.

Experimental design

To assess the impact of snowmelt date on the vegetation, plots were established in four different subsets varying in timescale of the snow manipulations: the first subset consisted of plots in an ongoing snow manipulation experiment (Wipf 2006; Wipf et al. 2009); in the second subset the plots were chosen along snow fences that were built 30 years ago; and in the third subset the plots were established along a natural snow gradient at the same elevation. To identify the effect of snowmelt date on the growth performance of *V. myrtillus* at different elevations, a fourth subset was chosen with plots at two different altitudes. All data in this study were collected between June and October 2006. All the plots, except the plots from the elevation gradient, were within a 200-m radius.

The snow manipulation experiment started in spring 2004 in plots of 1 m² (Wipf 2006). In nine plots advanced snowmelt was simulated by removing most of the snow in spring, whereas nine other plots served as controls. In 2006, snow had gone by 24 May (± 0.7 days SE) in early snowmelt plots and by 7 June (± 3.5 days) in the control plots, thereby prolonging the growing season by 13% to 96 days (snow-free to first severe frost days). In 2004 and 2005, snowmelt dates were 29 May and 24 May in early-melting plots, and 9 June and 1 June in control plots, respectively (Wipf et al. 2009).

Three large wooden snow fences, each approximately 20 m long, were built horizontally along the steep slopes 30 years ago to prevent avalanches. Snow accumulates above these snow fences in winter, and hence melts later (16 June ± 1.3 days versus 12 June ± 5.3 days in 2006). Analyses of pictures from three previous winters indicated that snowmelt from 2006 was representative. Nine plots were located close to the fence in undisturbed vegetation (i.e., no signs of disturbance by construction, and plots were not affected by shadow from the fence). Nine control plots were established 8 m uphill (apparently

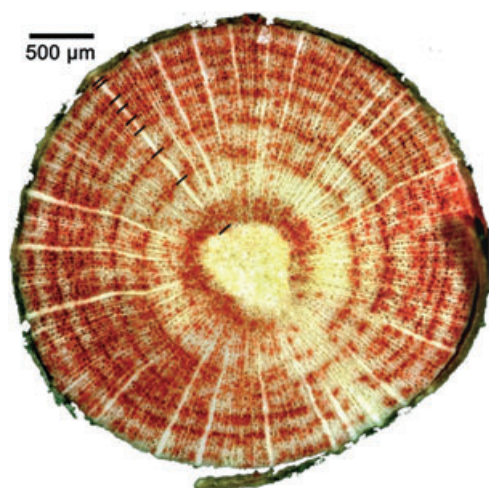


Fig. 1 Cross section of *Vaccinium myrtillus* stained with Safranin to enhance the visibility of the xylem ring boundaries. This specimen was nine years old. Ring boundaries are denoted with black lines.

with the same steepness and abiotic conditions), where snow cover was unaffected by the fence.

To analyse the vegetation along the natural snowmelt gradient, pairs of plots were established at nine sites in close vicinity to the experimental plots (with the same steepness, aspect, etc.). Two plots of a pair were at 8–14 m distance from each other, and half of the plots melted early in the year (before 23 May 2006), with the other half melting later (after 6 June 2006).

Eighteen additional plots were established at two different elevations: nine above the Stillberg site at 2400 m a.s.l. (approximate snowmelt date 14 June) and nine below the Stillberg site at 2000 m a.s.l. (approximate snowmelt date before 23 May). Similar snowmelt patterns were observed in previous years.

Xylem ring width analysis

Three ramets of *V. myrtillus* per plot of 1 m² were randomly sampled in all plots at the end of the growing season in mid September. The ramets were cut 5 cm below the soil surface and dried at room temperature for several weeks. Sections 1–2 cm in length were cut from the base of the ramets with a razor blade. To highlight the growth ring structure, the cut was stained with Safranin. After removing approximately 1 mm, the ring boundaries become clearly visible because of the different capillarity of the larger vessels that were formed early in the year (Fig. 1). If the xylem rings were still difficult to distinguish, chalk was rubbed into the vessels to enhance the contrast (Schweingruber & Poschlod 2005). The samples were fixed on a microscope slide with grafting wax, and

images were taken with a digital camera (Leica DC 200; Leica, Solms, Germany) mounted on the stereomicroscope with a 4× magnification (Olympus BX 51; Olympus, Tokyo, Japan). For the xylem ring width measurement, a cross was drawn on each photograph over the centre of the shoot cross section, with one axis along its widest diameter. Xylem ring widths were then measured along all four axes, starting at the first ring formed. As all of the samples were photographed with a fixed digital camera at the same magnification and resolution, a constant factor (1.66113 pixel = 1 μm) was used to convert the measurements from pixels to μm, and the annual ring width was calculated as the mean of four measurements along the cross axes. All image analyses were carried out with the public-domain software IMAGEJ (Rasband 2006).

Shoot length

The shoot length increments (new growth) of *V. myrtillus* were measured on 16 and 17 September 2006. Shoot length is a good proxy for annual productivity of a shoot (M. Martin, S. Wipf & C. Rixen, unpubl. data). In each plot we measured apical new shoots of four randomly selected ramets with digital calipers.

Species abundance

To record species abundance, vegetation records were made in the centre (0.5 × 0.5 m) of all plots, except those of the elevation gradient. Species abundance was measured as the number of squares in which a species was present in a 0.5 × 0.5 m grid with 25 squares (each 0.1 × 0.1 m). Abundance data were converted to percentage cover. This method allows for rapid assessments that are minimally biased by the individual observer when repeated in different years. However, the method tends to overestimate the cover of plants with small size.

Statistical analysis

For analysis of age distribution, the ramets of *V. myrtillus* were grouped into 5-year age categories (1–5 years old, 6–10 years old, etc.). Differences in age distribution between plots were tested with chi-square tests of association to see whether treatments affected the age structure of ramet populations, and to see if other variables could be analysed irrespective of the age distribution.

The xylem ring widths were analysed separately for every year (counting back from the outermost growth ring of the year of harvest), using a full factorial mixed effects type-I analysis of covariance (ANCOVA). The fixed effect was “snowmelt” (early or late). The age of the

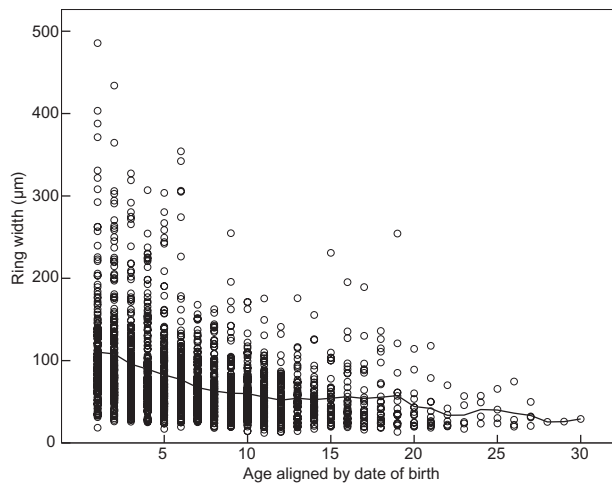


Fig. 2 Relationship between xylem ring width and age aligned by date of birth, i.e., the number of a rings on an individual ramet counted from the centre (ring 1) to the margin (between 4 and 30, depending on the age of the ramet). The numbers do not, therefore, represent specific years. The decreasing trend with increasing ring number is indicated by the interpolation line. Each point on the unsmoothed line represents the mean value of the respective age.

respective ramet was used as a covariable (mean per plot), as xylem ring width shows a significant correlation with plant age (see Fig. 2). Separate analyses were performed for each set of plots. Additionally, the factor “snowmelt” was tested across all years, where “year” was included in the model as a random factor (without ramet age as a covariable).

Relationships of xylem ring width with climate variables were tested with single and multiple (stepwise) linear regression techniques. Climate variables were mean summer temperatures (June–August) and the number of frost events (days with subzero air temperatures) after snowmelt, as measured as air temperature at 2 m height at a nearby climate station. To identify the effect of temperature on the difference in growth of early and late melting plots, the mean xylem ring widths of the late melting plots were subtracted from the mean xylem ring widths of the early melting plots. The mean values per plot were used for all analyses.

Year ring width across all snow types is presented with original and detrended data (Fig. 3). The ring width clearly decreases in the later year rings (Fig. 2); therefore, the year rings were detrended by aligning the data by date of ramet birth, fitting the number of the year ring (first year, second year, etc., counted from the centre to the margin of the cross section) and plotting the residuals (Fig. 3). This procedure is in accordance with the regional curve standardization (RCS) method that is often applied in dendrochronology to reduce “biological noise” in data (Esper et al. 2003).

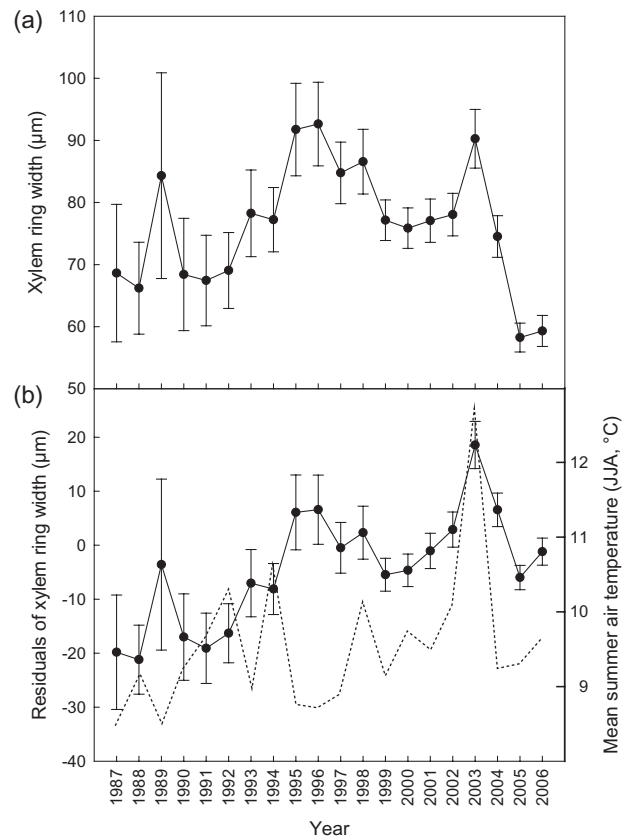


Fig. 3 Mean xylem ring width of *Vaccinium myrtillus* for the years 1987 to 2006 across all snow and elevation plot types: (a) original data and (b) detrended data (residuals after fitting the number of the year ring; see Fig. 2); the secondary x-axis and the dotted line show the mean summer temperatures. Shown are mean values \pm 1 SE.

Shoot length and species abundance per plot were analysed with one-way analyses of variance (ANOVA). Shoot length was log-transformed and species abundance arcsin-transformed to meet the requirement of normal distribution and homoscedasticity. All residuals were checked visually for their homogeneity and normality of variance. Where several measurements were made per plot, mean values were used in the analysis.

All statistical analyses were performed with SPSS 16 (SPSS Inc., Chicago, IL, USA).

Results

Age of ramets

The age of the majority of ramets was between 6 and 15 years, 7% of them were more than 20 years and the oldest ramet was 30 years old. The age distribution of ramets was similar under late and early snowmelt for the natural snow gradient, the snow fences and the snow

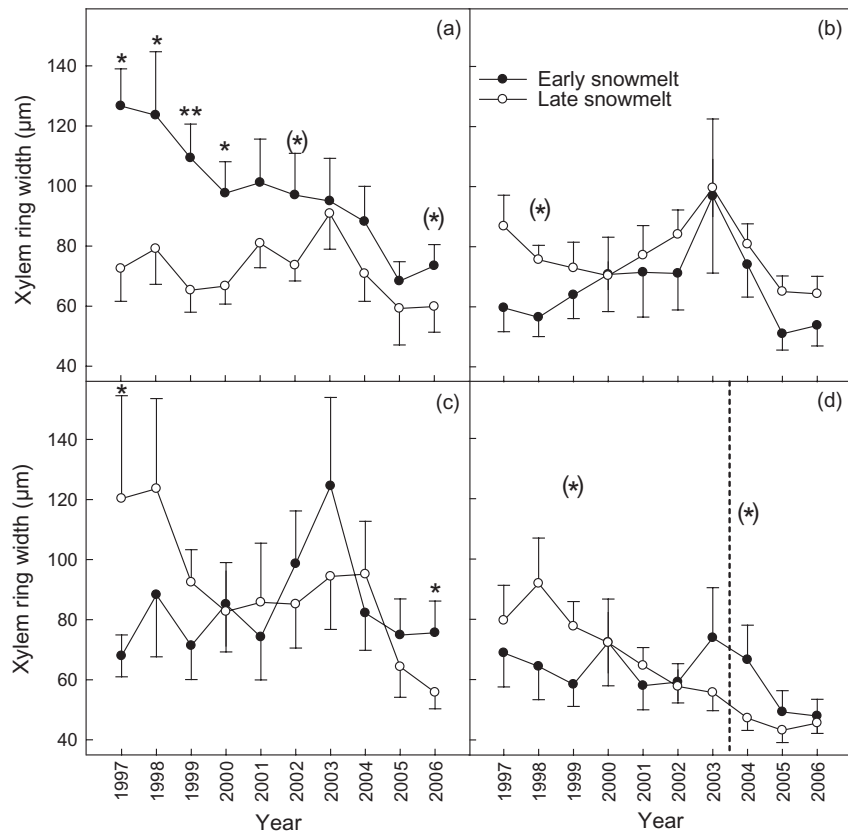


Fig. 4 Mean xylem ring width of *Vaccinium myrtillus* for the years 1997–2006 under early and late snowmelt in the four different settings: (a) elevation gradient; (b) natural snow gradient; (c) snow fence and (d) snow removal. Shown are mean values \pm 1 SE. Significance levels: ** $P < 0.01$; * $P < 0.05$; and (*) $P < 0.1$. Ring width was tested for individual years. The vertical dashed line in (d) indicates the start of the snow removal.

manipulation experiment (chi-square tests for late and early snowmelt not significant). The age distribution differed between ramets from different altitudes: most ramets were 6–10 years old at 2400 m a.s.l. and 11–15 years old at 2000 m a.s.l. ($\chi^2 = 12.9$, $df = 4$, $P = 0.012$).

Trend in xylem ring width

Across all of the sampled ramets we did not detect a trend in ring width over the last 20 years in the original data (Fig. 3a). However, ring widths of *V. myrtillus* ramets generally decrease from the centre to the margin (Figs. 1, 2). When data were corrected for this growth function, an increasing trend in growth rings over the last 20 years became apparent (Fig. 3b). The hot summer of 2003 resulted in exceptionally wide rings.

Xylem ring width and snow conditions

Ramets of *V. myrtillus* that grew at 2000 m a.s.l. showed a consistently greater xylem ring width than ramets growing at 2400 m a.s.l. ($P < 0.001$ across all years), even though this difference decreased in later years and was not significant in every single year (Fig. 4a). In the extraordinarily warm summer of 2003, plants at high

elevation (but not at low elevation) produced larger rings than in other years, indicating especially favourable growing conditions at high, but not at lower, altitudes.

Along the natural snow gradient, year rings were generally wider at sites with late snowmelt ($P < 0.01$ across all years; Fig. 4b), although the difference was only marginally significant for the individual year 1998, and was not significant for the other years. The year rings of both snow regimes showed a strong peak in 2003.

At the snow fences, year rings were wider after late snowmelt in earlier years (1997–99, but only significantly in 1997; Fig. 4c), but were wider after early snowmelt in later years (from 2002 on, but only significantly in 2006).

Before the start of the snowmelt manipulations, plants that subsequently experienced later snowmelt grew slightly larger year rings (not significant in 1997–2001, marginally significant in 1999). This pattern reversed in the year before the start of the experiment. The first year of snow manipulation showed a marginally significant response in 2004 ($F = 4.41$, $P = 0.054$): year rings were wider at plots with early snowmelt. Year rings remained slightly wider in the two subsequent years after early snowmelt, but not significantly so. The warm year of 2003 resulted in (non-significant) peaks in xylem rings under early snowmelt, in both plots with snowmelt

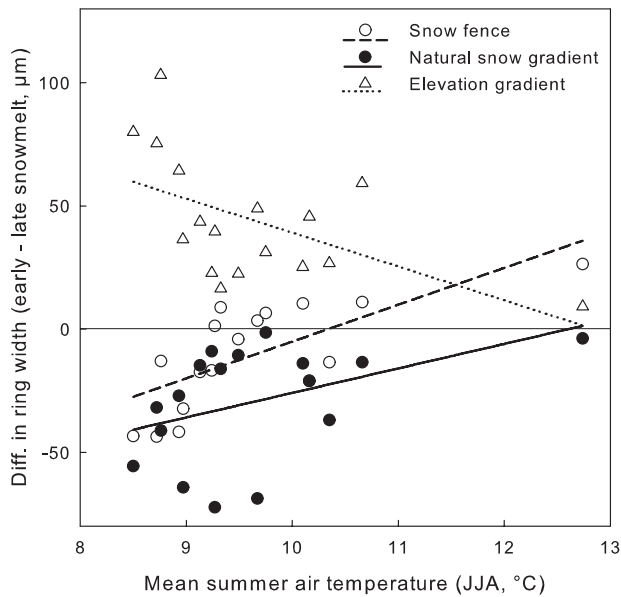


Fig. 5 Difference in mean xylem ring width between plots where the snow melts early and plots where it melts late, depending on mean summer temperatures for the 20-year period: 1987–2006. Data points above the zero line indicate better growth in early snowmelt, and those below the zero line indicate better growth in late snowmelt. The correlations are significant for the plots at the snow fences ($P = 0.009$) and the elevation gradient ($P = 0.013$), and are marginally significant for the natural gradient ($P = 0.085$).

manipulation and along the snow fences, which indicates a positive effect of early snowmelt in warm years.

The effects of elevation or snowmelt timing on year ring width of the bilberry differed between years, and depended on summer temperatures. Although year rings were generally larger at a lower elevation, this difference between high and low elevation was most pronounced in cool summers. The difference decreased with rising summer temperatures ($P = 0.013$; Fig. 5), disappearing entirely in the especially hot summer of 2003. This suggests that growing conditions at lower elevations were only markedly more favourable in years with harsh growing conditions.

Along snow fences and natural snow gradients that did not differ in altitude, but differed only in snowmelt timing, we found the opposite pattern: the colder the summers, the more negative the impact of an early snowmelt on year ring width ($P = 0.009$ and 0.085 , respectively). In warm summers, year ring growth along the snow fences was enhanced by early snowmelt, especially in 2003. Early snowmelt had positive effects on year ring growth in most summers with mean temperatures of above 9°C .

Multiple linear regression analysis indicated that the difference in xylem ring width of plants at different eleva-

tions not only depended on the summer temperature, but also on the number of frost events in spring ($t = -2.672$, $P = 0.018$; $t = 2.49$, $P = 0.023$; ns in other plot pairs). Thus, the warmer the summer and the fewer frost events there were in spring, the smaller was the difference in *V. myrtillus* growth over 400 m a.s.l. Although summer temperatures and the number of frost events were negatively related, this correlation was not significant ($P = 0.18$). Therefore, mean summer temperatures and extreme temperatures, as expressed in frost events, independently influenced the growth of these shrubs.

These results indicate that an early snowmelt can only be beneficial for bilberry growth in years with especially warm temperatures, and without spring frosts. In most years, however, early snowmelt had rather negative effects on bilberry growth, probably because it exposed plants to colder air temperatures at the start of the growing season.

Shoot length

The shoot length of *V. myrtillus* in 2006 was greater after early snowmelt when analysed across all plot types (mean values \pm SE, $F = 4.255$, $P = 0.045$). When plot types were analysed separately, shoot length was greater after early snowmelt in the natural snow gradient (mean values \pm SE), along the snow fences (mean values \pm SE) and in the snow manipulation experiment (mean values \pm SE); however, shoot length was only significantly increased in the snow manipulation experiment ($F = 5.441$, $P = 0.018$). The correlation between shoot length and ring width was marginally significant ($P = 0.068$).

Community responses

Most of the species studied at our study site showed clear preferences for plots with either early or late snowmelt along the natural snowmelt gradient (Fig. 6). Typical ridge species such as lichens (mainly of the genera *Cladonia* and *Cetraria*) and *Loiseleuria procumbens* were more abundant in plots with early snowmelt, whereas snowbed species like *Soldanella pusilla* and *Ligusticum mutellina* were more frequent at snow-rich, late-melting sites.

Similar patterns were found at the sites where the snow fences had caused snow accumulation in the last 30 winters: the abundance of ridge species was higher and that of snowbed species lower where snow melted early, although the pattern was not statistically significant.

At the snow manipulation experiment, no difference in species abundances between plots with different snowmelt treatments was apparent after three years of manipulations.

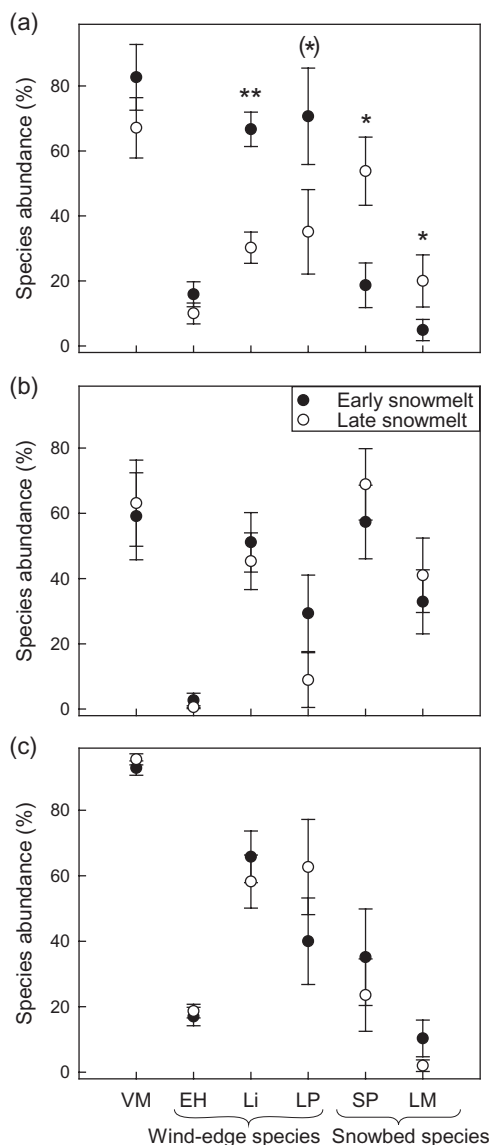


Fig. 6 Abundance of key species (i.e., dominant or indicative of snow conditions) in three snow regime types: (a) natural snow gradient; (b) snow fence and (c) snow removal. Species included are: the dominant *Vaccinium myrtillus* (VM); the indicator species for ridges (thin snow cover), lichens (Li), *Loiseleuria procumbens* (LP) and (to a lesser extent) *Empetrum nigrum* (EH); and the snowbed species *Soldanella pusilla* (SP) and *Ligusticum mutellina* (LM). Values shown are means \pm 1 SE. Significance levels: (*) $P < 0.1$; (*) $P < 0.05$; (**) $P < 0.01$.

Discussion

Xylem ring width

Like tree rings, the year rings of dwarf shrubs are indicators of annual plant growth, and thus reflect the environmental conditions plants experience at specific sites. Although the xylem rings of the dwarf shrub

V. myrtillus and similar species are very small, they are distinct enough to allow for proper year ring analysis. Therefore, these plants can be used as archives to study, for example, population biology and responses to specific growing conditions over past years or decades (Dietz & Ullmann 1998; Rayback 1998; Rixen et al. 2004).

Most of our ramets were 6–15 years old, and many were more than 20 years old, which is in line with comparable studies (Hegi 1995; Rixen et al. 2004). This allowed us to analyse the last 10–20 years of growth. The fact that year ring widths decreased with age was not a problem in the analysis, as we generally compared plot types with similar age distributions. There may have been a bias towards older plants, and, thus, smaller rings at lower elevations in the comparison between altitudes. However, this would mean that we underestimated the difference in growth response between altitudes. It is likely that this difference would have been even more distinct had the age distribution at high and low elevation been even more similar.

The detrended growth ring data show a clear increase in growth over the last 20 years, and are therefore comparable with data from treeline trees: radial tree growth of *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine treeline has also increased in recent decades (Rolland et al. 1998). *V. myrtillus* showed especially wide growth rings in the hot summer of 2003. Apparently, the positive effects of the high temperatures outweighed the negative effects of heat-related drought. Whereas plants (trees) at lower elevations suffered from drought in Switzerland in 2003 (Dobbertin & Rigling 2006), there seem to be no indications that bilberry experienced drought stress in that year at the treeline or above it.

The finding that ramets of *V. myrtillus* showed wider year rings at low elevation than at high elevation is not surprising, as temperatures are higher and the growing season longer at lower elevations. Interestingly, however, this difference in growth ring widths disappeared in years with warm summer temperatures. Similar findings, i.e., decreasing growth differences along altitudinal gradients in warmer years, were found in treeline trees in the Alps (Paulsen et al. 2000). There are two possible explanations for this finding. First, at the high elevation site, low temperatures might normally be the limiting factor for plant growth, but in warm summers without frosts, the temperature might exceed this threshold. In cooler summers, however, the limitation by growing season temperatures may be relatively more important at high elevations than at low elevations. Second, heat-related drought might even reduce plant growth at low elevation in warm years.

Within the same elevation, growth rings were larger under later snowmelt along the natural gradient,

although the growing season was shorter on those plots. A possible explanation is that a longer lasting snow cover protects plants better from harsh conditions in spring and early summer. This view is supported by the finding that late snowmelt along the natural snow gradient and the snow fence was only beneficial in cold, but not in warm, summers (Fig. 5). Direct positive effects of late snowmelt on plants were also detected by Wipf (2006), who found enhanced shoot growth of several shrub species including *V. myrtillus* in plots with experimentally postponed snowmelt. This finding was attributed to protection from frost damage by snow. Inouye (2000) pointed out that early stages in the annual plant life cycle in early summer are especially at risk because just after bud break, young leaves and flower buds are particularly vulnerable to frost damage, whereas they become less frost-susceptible during the summer (see also Ulmer 1937; Tolvanen 1997; Taschler et al. 2004). The longer lasting snow cover may not only influence plants directly, but might have changed site properties, such as soil nutrient content or water availability (Stanton et al. 1994; van der Wal et al. 2000; Rixen et al. 2003; Hiller et al. 2005). Protection from frost and more favourable growing conditions might easily outweigh the potential negative effect of a shortened growing season. Summer frost may be frequent or even increase in a warmer climate because more extreme temperature regimes are expected in parts of the world (Inouye 2000; Martin et al. 2010). Therefore, we may not assume that adverse effects of frosts in Arctic and alpine environments will decrease in a warmer climate.

Shoot length

The new shoots of *V. myrtillus* grew longer in 2006 in early melting than in late melting snow removal plots. This finding to some extent supports the results of the ring width analysis. In the two previous years, 2004 and 2005, however, shoots were longer in late melting plots (Wipf 2006). The reason for the different findings may be differences in temperatures between years. Temperatures in 2006 after snowmelt were warm, and only one mild frost event occurred. In the two previous years, post snowmelt temperatures dropped several times below freezing, which caused frost damage on the plants that were free of snow and had already started flushing leaves (Wipf 2006). Different effects of snow manipulations in different years might also explain inconsistent results in several previous studies in alpine and Arctic settings (e.g., Walker et al. 1999; van der Wal et al. 2000; Walker et al. 2001; Stinson 2004; Wahren et al. 2005; Dorrepaal et al. 2006; Wipf & Rixen 2010 [this issue]).

Community responses

The species abundances along the natural snow gradient were in line with common phytosociological knowledge (Ellenberg 1988; Körner 2003; Tveraabak 2004): areas with long-lying snow cover were characterized by snowbed species such as *Soldanella pusilla* and *Ligusticum mutellina*, whereas windswept areas with early snowmelt were dominated by lichens and the Alpine azalea *Loiseleuria procumbens*. Species abundances after 30 years of moderate snow cover changes along the snow fences started to show similar tendencies, although they were not yet significant.

Nearly all snow manipulation experiments showed changes in species composition after approximately one or two decades (e.g., Scott & Rouse 1995; Walker et al. 1999; Seastedt & Vaccaro 2001; Wahren et al. 2005). In extreme cases, large snow accumulations behind snow fences caused considerable die-off of the dominating species, which favoured a rapid turnover of the vegetation composition (Bell & Bliss 1979; Smith et al. 1995; Walker et al. 1999; Welch et al. 2005). Although having received less attention than warming temperatures, our findings indicate that snow cover may be the primary driver of future Arctic and alpine vegetation change.

Conclusions

- Xylem ring width analysis of the shrub *V. myrtillus* provided a valuable tool to investigate growth across elevation and snow gradients.
- Detrended growth ring data showed an increasing trend over the last 20 years, especially in the extraordinarily hot summer of 2003.
- Xylem ring width was greater in plots with late snowmelt than in plots with early snowmelt along the natural snowmelt gradient. However, this was only true in years with relatively cold summers. This result indicates that beneficial effects of early snowmelt for shrub growth, i.e., prolonging the growing season, may be offset by, for example, frost events in years with cold summers. Such frost events may continue to happen in a future climate with enhanced temperature extremes.
- Growth rings were larger at lower elevation than at higher elevation, but only in years with relatively cold summers. In warm years, no difference in growth between high and low elevation could be detected, probably because temperature is not limiting for growth in these conditions.
- A number of plant species showed a clear preference for either late or early snowmelt along the snowmelt gradient. After 30 years of snow manipulation at the snow fences, species abundance started to change

according to the snow preference of specific species. This result shows how strongly snow characteristics shape species abundance in Arctic and alpine habitats.

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References

- Bell K.L. & Bliss L.C. 1979. Autecology of *Kobresia bellardii*—why winter snow accumulation limits local distribution. *Ecological Monographs* 49, 377–402.
- Billings W.D. & Bliss L.C. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology* 40, 388–397.
- Dietz H. & Ullmann I. 1998. Ecological application of “herbchronology”: comparative stand age structure analysis of the invasive plant *Bunias orientalis* L. *Annals of Botany* 82, 471–480.
- Dobbertin M. & Rigling A. 2006. Pine mistletoe (*Viscum album* ssp. *austriacum*) contributes to Scots pine (*Pinus sylvestris*) mortality in the Rhone valley of Switzerland. *Forest Pathology* 36, 309–322.
- Dormann C.F. & Woodin S.J. 2002. Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology* 16, 4–17.
- Dorrepaal E., Aerts R., Cornelissen J.H.C., Van Logtestijn R.S.P. & Callaghan T.V. 2006. Sphagnum modifies climate-change impacts on subarctic vascular bog plants. *Functional Ecology* 20, 31–41.
- Ellenberg H. 1988. *Vegetation ecology of Central Europe*. 4th edn. Cambridge: Cambridge University Press.
- Esper J., Cook E.R., Krusic P.J., Peters K. & Schweingruber F.H. 2003. Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies. *Tree-Ring Research* 59, 81–98.
- Friedel H. 1961. Schneedeckendauer und Vegetationsverteilungen im Gelände. (Snow cover duration and vegetation patterns in alpine terrain.) *Mitteilungen der Forstlichen Bundesversuchsanstalt Mariabrunn (Wien)* 59, 317–369.
- Galen C. & Stanton M.L. 1993. Short-term responses of alpine buttercups to experimental manipulations of growing season length. *Ecology* 74, 1052–1058.
- Galen C. & Stanton M.L. 1995. Responses of snowbed plant species to changes in growing-season length. *Ecology* 76, 1546–1557.
- Hegi G. 1995. *Illustrierte Flora von Mitteleuropa. (Illustrated flora of Central Europe.)* Berlin: Blackwell Scientific Publishers.
- Hiller B., Nuebel A., Broll G. & Holtmeier F.K. 2005. Snowbeds on silicate rocks in the Upper Engadine (Central Alps, Switzerland)—pedogenesis and interactions among soil, vegetation, and snow cover. *Arctic Antarctic and Alpine Research* 37, 465–476.
- Inouye D.W. 2000. The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters* 3, 457–463.
- Jonas T., Rixen C., Sturm M. & Stoeckli V. 2008. How alpine plant growth is linked to snow cover and climate variability. *Journal of Geophysical Research—Biogeosciences* 113, G03013, doi: 10.1029/2007JG000680.
- Jones H.G., Pomeroy J.W., Walker D.A. & Hoham R.W. 2001. *Snow ecology*. Cambridge: Cambridge University Press.
- Knowles N., Dettinger M.D. & Cayan D.R. 2006. Trends in snowfall versus rainfall in the western United States. *Journal of Climate* 19, 4545–4559.
- Körner C. 2003. *Alpine plant life*. 2nd ed. Berlin: Springer.
- Laternser M. & Schneebeli M. 2003. Long-term snow climate trends of the Swiss Alps (1931–99). *International Journal of Climatology* 23, 733–750.
- Martin M., Gavazov K., Körner C., Hättenschwiler S. & Rixen C. 2010. Reduced early growing season freezing resistance in alpine treeline plants under elevated atmospheric CO₂. *Global Change Biology* 16, 1057–1070.
- Myneni R.B., Keeling C.D., Tucker C.J., Asrar G. & Nemani R.R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386, 698–702.
- OcCC Consortium 2007. *Klimaänderung und die Schweiz 2050. (Climate change and Switzerland 2050.)* Bern: Advisory Body on Climate Change/Proclim—Forum for Climate and Global Change.
- Paulsen J., Weber U.M. & Korner C. 2000. Tree growth near treeline: abrupt or gradual reduction with altitude? *Arctic Antarctic and Alpine Research* 32, 14–20.
- Rasband W.S. 2006. ImageJ 1.36b. Bethesda, MD: US National Institutes of Health. Accessed on the internet at <http://rsb.info.nih.gov/ij> in 2006.
- Rayback S.A. 1998. A dendrogeomorphological analysis of snow avalanches in the Colorado Front Range, USA. *Physical Geography* 19, 502–515.
- Rixen C., Casteller A., Schweingruber F.H. & Stoeckli V. 2004. Age analysis helps to estimate plant performance on ski pistes. *Botanica Helvetica* 114, 127–138.
- Rixen C., Freppaz M., Stoeckli V., Huovinen C., Huovinen K. & Wipf S. 2008. Altered snow density and chemistry change soil nitrogen mineralization and plant growth. *Arctic Antarctic and Alpine Research* 40, 568–575.
- Rixen C., Stoeckli V. & Ammann W. 2003. Does artificial snow production affect soil and vegetation of ski pistes? A review. *Perspectives in Plant Ecology Evolution and Systematics* 5, 219–230.
- Rixen C., Stoeckli V., Huovinen C. & Huovinen K. 2001. The phenology of four subalpine herbs in relation to snow cover characteristics. In A.J. Dolman et al. (eds.): *Soil-vegetation-atmosphere transfer schemes and large-scale hydrological models. Proceedings of an international symposium (Symposium S5) held during the Sixth Scientific Assembly of the International Association of Hydrological Sciences (IAHS) at*

- Maastricht, The Netherlands, from 18 to 27 July 2001. Pp. 359–362. Wallingford, UK: International Association of Hydrological Sciences.
- Rolland C., Petitcolas V. & Michalet R. 1998. Changes in radial tree growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750. *Trees—Structure and Function* 13, 40–53.
- Schöb C., Kammer P.M., Choler P. & Veit H. 2008. Small-scale plant species distribution in snowbeds and its sensitivity to climate change. *Plant Ecology* 200, 91–104.
- Schweingruber F.H. & Poschold P. 2005. Growth rings in herbs and shrubs: life span, age determination and stem anatomy. *Forest Snow and Landscape Research* 79, 195–415.
- Scott P.A. & Rouse W.R. 1995. Impacts of increased winter snow cover on upland tundra vegetation—a case example. *Climate Research* 5, 25–30.
- Seastedt T.R. & Vaccaro L. 2001. Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, USA. *Arctic, Antarctic, and Alpine Research* 33, 100–106.
- Shabanov N.V., Zhou L.M., Knyazikhin Y., Myneni R.B. & Tucker C.J. 2002. Analysis of interannual changes in northern vegetation activity observed in AVHRR data from 1981 to 1994. *IEEE Transactions on Geoscience and Remote Sensing* 40, 115–130.
- Smith B., Mark A.F. & Wilson J.B. 1995. A functional analysis of New Zealand alpine vegetation: variation in canopy roughness and functional diversity in response to an experimental wind barrier. *Functional Ecology* 9, 904–912.
- Solomon S., Qin D., Manning M., Chen Z., Marquis M., Averyt K.B., Tignor M. & Miller H.L. Jr. (eds.) 2007. *Climate change 2007. The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- Stanton M.L., Rejmanek M. & Galen C. 1994. Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, USA. *Arctic and Alpine Research* 26, 364–374.
- Starr G., Oberbauer S.F. & Pop E.W. 2000. Effects of lengthened growing season and soil warming on the phenology and physiology of *Polygonum bistorta*. *Global Change Biology* 6, 357–369.
- Stinson K.A. 2004. Natural selection favors rapid reproductive phenology in *Potentilla pulcherrima* (Rosaceae) at opposite ends of a subalpine snowmelt gradient. *American Journal of Botany* 91, 531–539.
- Sturm M., McFadden J.P., Liston G.E., Chapin F.S. III, Racine C.H. & Holmgren J. 2001. Snow–shrub interactions in Arctic tundra: a hypothesis with climatic implications. *Journal of Climate* 14, 336–344.
- Symon C., Arris L. & Heal B. (eds.) 2005. *Arctic climate impact assessment*. Cambridge: Cambridge University Press.
- Tape K., Sturm M. & Racine C. 2006. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology* 12, 686–702.
- Taschler D., Beikircher B. & Neuner G. 2004. Frost resistance and ice nucleation in leaves of five woody timberline species measured in situ during shoot expansion. *Tree Physiology* 24, 331–337.
- Tolvanen A. 1997. Recovery of the bilberry (*Vaccinium myrtillus* L.) from artificial spring and summer frost. *Plant Ecology* 130, 35–39.
- Tveraabak L.U. 2004. Atlantic heath vegetation at its northern fringe in central and northern Norway. *Phytocoenologia* 34, 5–31.
- Ulmer W. 1937. Über den Jahresgang der Frosthärte einiger immergrüner Arten der alpinen Stufe, sowie der Zirbe und Fichte. (Seasonal cycle of frost hardiness of some evergreen species in the alpine zone, including stone pine and spruce.) *Jahrbücher für wissenschaftliche Botanik* 84, 553–592.
- van der Wal R., Madan N., van Lieshout S., Dormann C., Langvatn R. & Albon S.D. 2000. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia* 123, 108–115.
- Wahren C.H.A., Walker M.D. & Bret-Harte M.S. 2005. Vegetation responses in Alaskan Arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* 11, 537–552.
- Walker D.A., Billings W.D. & De Moolenaar J.G. 2001. Snow–vegetation interactions in tundra environments. In H.G. Jones et al. (eds.): *Snow ecology*. Pp. 266–324. Cambridge: Cambridge University Press.
- Walker M.D., Walker D.A., Welker J.M., Arft A.M., Bardsley T., Brooks P.D., Fahnestock J.T., Jones M.H., Losleben M., Parsons A.N., Seastedt T.R. & Turner P.L. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in Arctic and alpine tundra. *Hydrological Processes* 13, 2315–2330.
- Welch D., Scott D. & Thompson D.B.A. 2005. Changes in the composition of *Carex bigelowii*–*Racomitrium lanuginosum* moss heath on Glas Maol, Scotland, in response to sheep grazing and snow fencing. *Biological Conservation* 122, 621–631.
- Wipf S. 2006. *Winter climate change in tundra ecosystems: the importance of snow cover*. PhD thesis, Institute of Environmental Sciences, University of Zurich.
- Wipf S. & Rixen C. 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Research* 29, doi: 10.1111/j.1751-8369.2010.00153.x.
- Wipf S., Rixen C. & Mulder C.P.H. 2006. Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. *Global Change Biology* 12, 1496–1506.
- Wipf S., Stoeckli V. & Bebi P. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change* 94, 105–121.
- Zhou L.M., Tucker C.J., Kaufmann R.K., Slayback D., Shabanov N.V. & Myneni R.B. 2001. Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research—Atmospheres* 106, 20 069–20 083.