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Growth Increment Patterns in the Roots of Two Alpine Forbs Growing in the Center and at the Periphery of a Snowbank

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Abstract

Snowbanks are characteristic for many alpine areas and add considerably to the great variability of growth conditions in high mountain systems. We studied the long-term (5- to 9-yr) growth response of two alpine forbs, *Pedicularis recutita* and *Cirsium spinosissimum*, to the environmental conditions in the center and at the periphery of a snowbank in the Swiss Alps. For that we analyzed the growth increments (annual rings) in the roots or rhizomes of the plants. While for both species there were no considerable size differences (number of shoots) between individuals growing in the center of the snowbank and those at the periphery, the growth patterns differed depending on species, temporal variations in growth conditions, and growth position. There were synchronous fluctuations in the width of the annual growth increments that were more pronounced in *C. spinosissimum* than in *P. recutita* and were restricted to plants growing in the center of the snowbank. These were apparently related to interannual variations in climatic conditions. In addition, *C. spinosissimum* plants growing at the periphery of the snowbank showed initially wide but strongly declining growth increments whereas plants growing in the center of the snowbank showed initially narrower but relatively stable growth increments. These patterns were only weakly reflected in *P. recutita*. Our results suggest that effects of climatic fluctuations on plant growth can be amplified in snowbanks and that there may be favorable growth conditions initially at the periphery of the snowbank that are compensated for in the center of the snowbank, in the long run, by continuously low-competition growth conditions.

Introduction

Snowbanks that form in surface depressions or at leeward slopes, respectively, add greatly to environmental heterogeneity in alpine ecosystems. Heavy snowpack exerts mechanical forces on the underlying substrate that may result in soil compaction and solifluction (Zwinger and Willard, 1996). In these areas, soils are leached and eroded more strongly by meltwater and by creeping snow, solifluction, and freeze-thaw cycles than the surrounding areas (Thorn, 1979; Komárková, 1993). Furthermore, these areas are usually acidified and nutrient poor in their centers (but see Miller, 1982). Correspondingly, soil development tends to be poor in snowbanks (Billings and Bliss, 1959) whereas, at the periphery, soil formation and productivity is increased by earlier snowmelt. In addition, the vegetation period that is already short in temperate alpine ecosystems, is further compressed by late melting snow. In the low alpine zone in the northern Alps the duration of the growth period is approximately 4 mo but may be less than 2 mo in snowbanks (Ellenberg, 1986). All these factors may restrict plant growth, and thus productivity in snowbank communities can be very low (Billings and Bliss, 1959).

On the other hand, the vegetation in snow accumulation areas is protected from hazards such as frost damage, winter desiccation, and wind pruning by constant and reliable snow cover (e.g., Billings and Bliss, 1959; Zwinger and Willard, 1996; Körner, 1999). Moreover, there are indications that competition intensity is considerably lower in the vegetation in the center of snowbanks than at the periphery (cf. Callaway et al., 2002, Olofsson et al., 2002).

Hence, plant species that grow within as well as outside snowbanks in the alpine zone are faced with contrasting growth conditions at the opposite positions in the snowmelt gradient. While the spatial pattern of snowbank formation is quite stable between years (Johnson and Billings, 1962) the differences in growth conditions along snowbank gradients may vary considerably over time as a result of between-year variation in snowfall amount and temperature regimes causing substantial fluctuations in snowpack and the duration of snow cover (cf. Billings and Bliss, 1959; Johnson and Billings, 1962; Wijk, 1986; Kudo, 1991; Kudo and Ito, 1992; Komárková, 1993; Walker et al., 1993, 1994; Stanton et al., 1994).

Several responses of plant growth and development in areas of prolonged snowpack are known, including lower mortality in *Salix herbacea* (Wijk, 1986), delayed or reduced flowering and seed production (Kudo, 1991; Chernov and Matveyeva, 1997), shifts from summergreen to semi-evergreen leaf development in some graminoids (Kudo, 1991), decreased leaf life span (Kudo, 1996) and higher shade tolerance (Onipchenko et al., 2001). However, for a meaningful assessment of the ecological constraints for plant growth and for life-history strategy in snowbank vs. nonsnowbank situations it is important to know the long-term growth responses of the plants, particularly because of the long life cycles of many alpine plants (Körner, 1999, and references therein). This includes questions on whether differences in growth conditions between snowbank and nonsnowbank areas change as the plants grow older, whether and how climatic fluctuations affect those differences and whether plants growing in snowbanks attain higher ages as a possible life-history compensation for reduced growth. Answers to these questions would help us to understand how and under which circumstances alpine perennials manage to maintain (parts of) populations under late-melting snow.

For perennial forbs that show annual rings in the roots or rhizomes (e.g., Dietz and Ullmann, 1997; Dietz and Fattorini, 2002; Dietz and Schweingruber, 2002) fluctuations in annual ring width appear to indicate variations in growth conditions (Dietz and Ullmann, 1998, Dietz and Fattorini, 2002). Gradually decreasing or increasing growth-ring

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TABLE 1

Distribution of the most abundant plant species in the snowbank gradient. Although the two common tall forbs Aconitum napellus *and* Senecio alpinus *grow everywhere in the snowbank gradient, they did not produce flowering stems in the center of the snowbank (v). These two forbs, in addition to* Alchemilla monticola*, grew to much smaller sizes in the center of the snowbank*

Center only (CS)	Periphery Only (PS)	Both
Gentiana bavarica	*Ligusticum mutellina*	*Adenostyles alliariae*
Primula elatior	*Rumex alpinus*	*Aconitum napellus* (v)
Ranunculus alpestris		*Alchemilla monticola*
Ranunculus montanus		*Cirsium spinosissimum*
Soldanella alpina		*Pedicularis recutita*
Veronica alpina		*Ranunculus aconitifolius*
		Senecio alpinus (v)

widths in successive years may reflect progressively changing growth (site) conditions (cf. Dietz and Ullmann, 1998) whereas consistent fluctuations in particular years may be indicative of chance events such as pronounced fluctuations in climatic conditions (cf. Dietz and Fattorini, 2002) or irregular management that affects plant growth only in certain years. Snowbank gradients with their extreme changes in life conditions over very short distances and periods of time represent "a natural experiment" (Körner, 1999), and in this study we have investigated ring-width patterns in two alpine forbs for a comparative analysis of growth responses in the center and at the periphery of a snowbank.

The main objectives of this study with respect to the above stated questions were (1) to find out whether there are consistent patterns in growth ring fluctuations among individuals and among species that could be related to particular climatic conditions and (2) to look for differences in longer-term growth patterns in these species, particularly as being influenced by position in- or outside the snowbank, respectively.

Methods

SPECIES

We used two polycarpic perennial forb species, *Cirsium spinosissimum* (L.) Scop. (Asteraceae) and *Pedicularis recutita* (L.) (Scrophulariaceae) which may co-occur within and outside of snowbank communities in the lower alpine zone of the northern Alps and show annual rings in persistent subterraneous plant parts. Both are semirosette plants that grow at moist sites in alpine pastures or tall-forb communities in the Alps. The spiny *C. spinosissimum* is a rather late-flowering species (July–September) whereas *P. recutita* flowers earlier, between June and August. *C. spinosissimum* develops stout and branched, perennating rootstocks. *Pedicularis recutita* develops adventitious roots originating from a stout, plagiotropic rhizome that can attain lengths of ca. 20 cm (data from Hegi, 1974, 1987).

STUDY SITE

The study area is located at the summit region of the Biet mountain south of the Sihl lake in central Switzerland (47°02′N, 8°50′E, 1900 m a.s.l.). The area belongs to the lower alpine zone of the northern margin of the Swiss Alps (the climatic timberline in this area is at ca. 1800 m a.s.l., cf. Brockmann-Jerosch, 1919). The summit area has long, cold winters and the precipitation is high (ca. 2500 mm yr^{-1}, Imhof, 1965–1978) and more or less evenly distributed throughout the year. During summer, air temperatures often rise above 20°C on sunny days (data from 2001, not shown). On average, the length of the vegetation period is 4 to 5 mo (June to October).

A tall-forb community situated at a gentle, north-facing slope was chosen (see Table 1 for species composition). This community is located directly below a ca. 10 m high calcareous cliff that delimits the community to the south (Fig. 1). During winter, snow is transported by westerly or southwesterly winds and accumulates at the north side of the cliff where it piles up several meters high. While the amount of snowdrift may vary among years a pronounced snowbank is formed in each year. Snow depth declines with distance from the cliff toward the north. This snow-depth gradient and the prolonged shading of the area by the

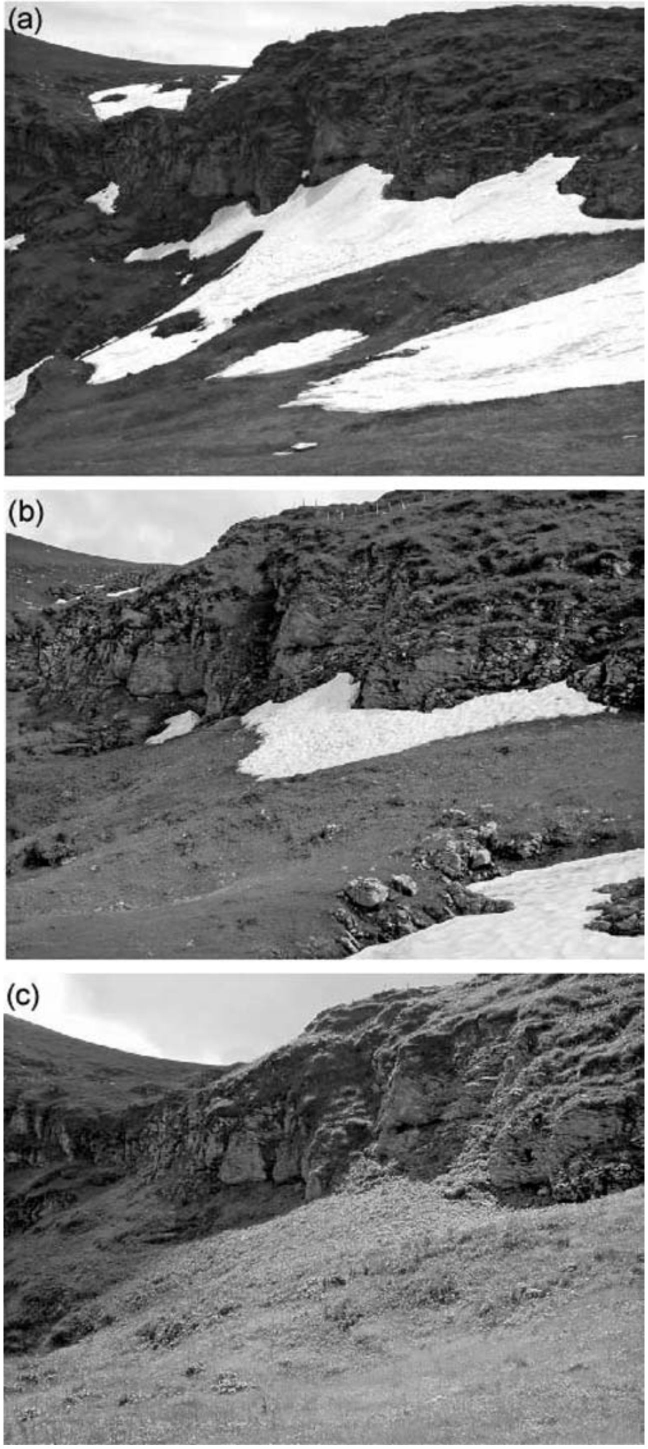

FIGURE 1. The snowbank site on 15 June 2002 (a), after a hot early summer week, on 22 June 2002 (b), and on 28 July 2002 (c). In (b) the central snowbank area is still covered by snow of 1 to 2 m depth. At that time the snow bank had an extent of 45 m (parallel to the cliff) × 10 m. Minor snow cover was partly left at the periphery of the snowbank on 15 June (a) but was gone in that zone on 22 June (b).

cliff, in spring, as compared to the more distant area results in a snowbank gradient of vegetation initiation. The distant zone of the community surveyed (periphery of the snowbank, PS; $\geq$15 m from the cliff) is normally largely snow-free at the beginning of June whereas the proximal parts of the community (center of the snowbank, CS; $\leq$6 m from the cliff) may be covered by snow up to mid or even end of July. In addition, in CS, temporary snow cover that may occur as early as September in some years is of longer duration. CS represents an early snowbank community (sensu Johnson and Billings, 1962) with a vegetation period of at most three months. In the snowbank area the soil is shallow ($<$10 cm) while it reaches 15 to 20 cm depth at the periphery.

Many of the more abundant plant species occur along the whole snowbank gradient but there are also several species that differentiate between the opposite ends of the gradient (Table 1). Both *C. spinosissimum* and *P. recutita* were more scattered in PS than in CS. At the end of July 2002 the vegetation was still low in CS (mean vegetation height 10–20 cm) whereas in PS the mean vegetation height was 40 to 60 cm. Furthermore, cover of higher plants in CS was comparatively low (but there was considerable moss cover) whereas vegetation cover was close to 100% in PS.

DATA COLLECTION

On 27 September 2001, 40 individuals per species were randomly chosen and carefully excavated, 20 each from the central snowbank area mentioned above and from the periphery. In many cases it was only possible to collect fragments of the rootstock (*C. spinosissimum*) or the rhizome system (*P. recutita*) from the shallow soil above the bedrock. Yet, care was taken to obtain the presumably oldest subterraneous plant parts. For some individuals, it could not be determined whether the oldest roots or rhizome fragments were obtained and whether rotten parts of the rootstock or rhizomes would have been older than the oldest plant parts collected. However, as we were mainly interested in ring width patterns, it does not pose a serious problem for our study that we could only estimate plant age. As a size parameter, the number of shoots was counted per individual.

In the laboratory, the main roots or rhizomes were cut using a sledge microtome to produce thin cuttings (ca. 30 μm). Main roots were cut near to the proximal end to avoid missing growth rings (Schweingruber and Dietz, 2001). The rhizomes were scrutinized to identify the oldest parts and these were used for the cuttings. Cross sections of the roots or rhizomes were stained with Phloroglucinol/HCl (causing reddish coloring of the cell walls of vessels and of lignified parenchyma cells) and examined under a dissecting microscope (Leica MZ 8). The cross sections were photographed with a digital camera (Nikon CoolPix 990, resolution at 2048 × 1536 pixels) and transferred to the computer for image processing and analysis.

The secondary xylem was analyzed for the presence and pattern of growth rings formed by earlywood (large vessels) that alternate with latewood (small vessels) in concentric rings. If growth rings were present their number was counted and the ring widths were measured manually by using linear measurement tools in a technical drawing and image-processing program (Deneba Canvas 7 for Windows, cf. Fig. 2). Three separate radii were analyzed for each individual to account for tangential variation in growth ring width and the means of the three measurements were used as the width of the respective growth rings.

Due to central root rot in many individuals or occasional aberrant xylem patterns only half of the individuals could be used for the analyses.

ANALYSIS

We tested whether growth ring widths were significantly different in particular years from the values expected for a purely ontogenetic trend. Just testing for exceptionally wide or narrow growth rings would yield trivial results if growth rings change consistently in width with increasing age because of ontogenetic reasons or changes in habitat conditions as was the case in our study. For example, if growth ring widths decrease monotonously with age the oldest growth rings may be evaluated as significantly wide while the youngest ones may appear significantly narrow. This result would probably not reflect any climatic or other environmental influence underlying fluctuations in growth ring width. Therefore, for each individual, a "distinctness" score D was calculated for the ring width of each year, that equals the sum of the differences in ring width to the previous and the following year that are not explained by the general changes over time:

$$D_0 = (W_{-1} - W_0) - (W_0 - W_1), \qquad (1)$$

where W denotes the ring width and the indices (0, –1, 1) indicate the year for which the distinctness score is calculated and the previous and following year, respectively. Distinctness scores were not calculated for marginal years (i.e. 2000 and the earliest year with sufficiently high sample size [$n \geq 7$] to be included in the analysis) because these cannot be compared with both a previous and a following year.

All calculations (including computation of the D scores) were done with standardized growth ring widths to bring all values to compatible units from a normal distribution with a mean of zero and a standard deviation of one. A permutation test was used to test whether particularly wide or narrow growth rings were significantly overrepresented in specific years. In the null model particularly wide or narrow growth rings are expected to occur with equal probability in every year, so that random patterns should emerge if several individuals are compared. To test for deviation from this null model the D scores for each year were summed over all individuals separately for each species and position in the snowbank gradient and the sums were divided by the number of individuals to obtain a mean score for the given year. Each of these scores was compared with a distribution of 999 scores obtained from the same data set but with the ring width values randomly reshuffled within individuals (null distribution). Significant deviations were detected by comparison of the observed scores with the scores of the null distribution (Manly, 1999). As different years were tested simultaneously Bonferroni adjustment was used (see Table 3).

Results

Cirsium spinosissimum and *Pedicularis recutita* showed a non-significant trend for a higher number of shoots per individual in the peripheral zone than in the snowbank center (Mann-Whitney U-Test, $P \geq 0.19$; see Table 2). Both species showed clearly demarcated growth rings in almost all individuals (see Fig. 2). For both species, the mean age of the oldest analyzable roots or rhizomes did not differ significantly between individuals from PS and CS (Mann-Whitney U-Test, $P \geq 0.32$). On average, individuals of *C. spinosissimum* showed 10 growth rings in the oldest parts of the roots and, therefore, appeared to be older than individuals of *P. recutita* which on average had only five or six growth rings in the oldest parts of the rhizomes (Table 2).

For both species and both sites growth ring width decreased with calendar year and reached minimum values in 2000 (Fig. 3). Apart from this general trend there were considerable fluctuations in growth ring width between individuals within species and among successive years. While most of these fluctuations do not depart from random patterns there are a few exceptions (distinctness values, Table 3). In the center of the snowbank, for both species, the growth ring width of 1998 was consistently greater than the adjoining growth rings from 1997 and 1999, respectively (see Fig. 3). However, in the peripheral zone, there was only a weak trend for a positive deviation of the 1998 ring width in *C. spinosissimum* and no such deviation could be found in *P. recutita* (Fig. 3, Table 3). Conversely, the growth ring width of 1999 tended to

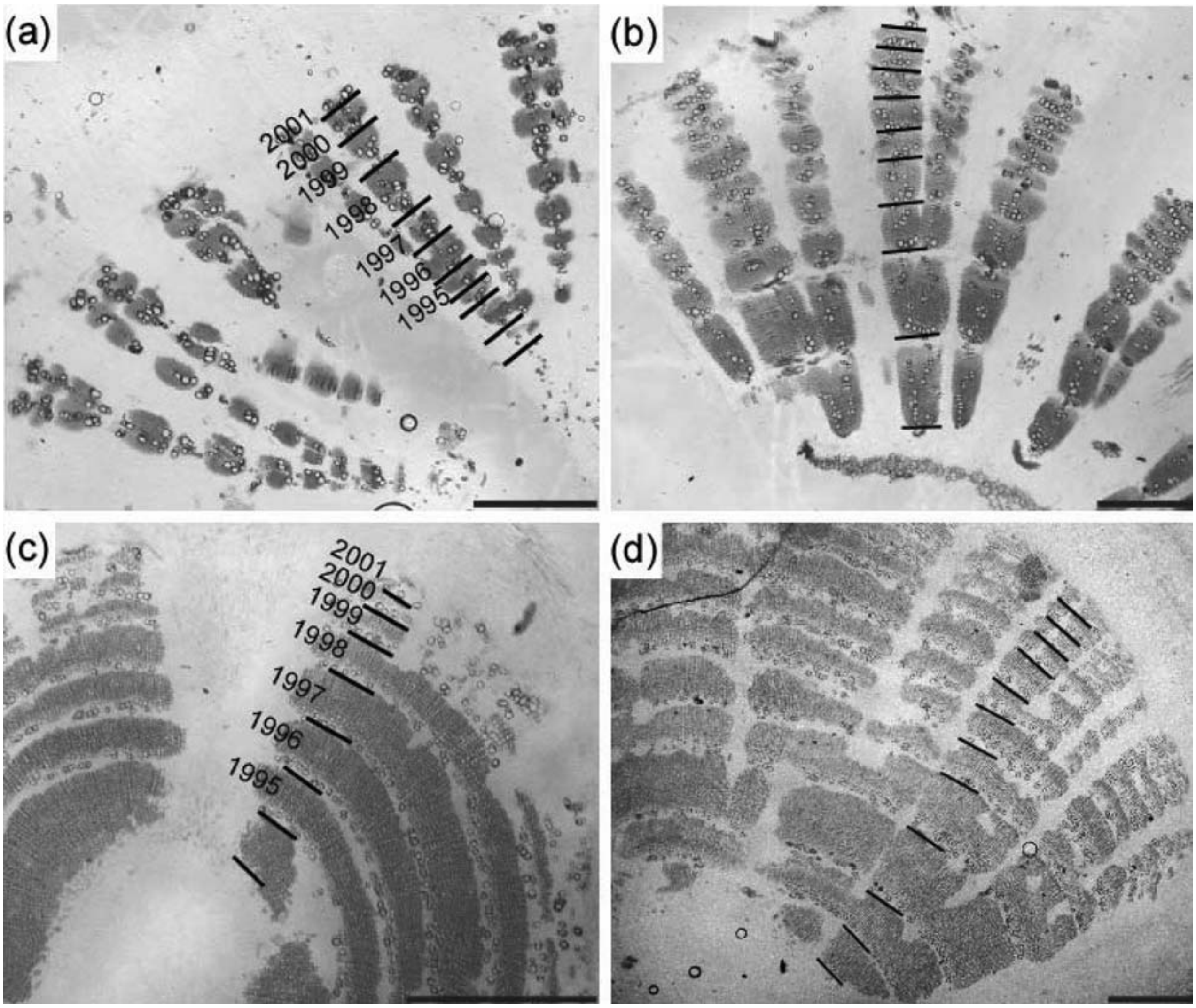

FIGURE 2. Patterns of growth rings in the secondary root xylem of Cirsium spinosissimum *(a, b) and* Pedicularis recutita *(c, d). The samples in (a) and (c) were collected in the center of the snowbank whereas the samples in (b) and (d) were obtained from the periphery of the snowbank. The markers along the xylem radii denote transition from latewood of the previous growing period to earlywood of the following one. The distance between consecutive markers represents the width of the enclosed growth ring. The horizontal bars indicate 1 mm.*

be particularly narrow in *C. spinosissimum* in CS. There was also a significant deviation of the 1995 growth ring width in *P. recutita* from CS, which, however, is not reflected in the *C. spinosissimum* data series.

While comparisons of growth ring width among calendar years may indicate fluctuations in plant growth due to variations in growth conditions among years, for analysis of ontogenetic changes in growth or changes in the microsite conditions during plant life it is necessary to compare growth rings that were formed at consecutive plant ages. Corresponding results are shown in Figure 4. In *C. spinosissimum* the development of growth ring width with age was clearly different at the opposite sides of the snowbank gradient. In the plants growing in CS growth ring width remained fairly constant during the first 6 yr, measuring about 500 µm, and decreased steadily afterwards (the two most recent growth rings averaged at 300 µm). Conversely, starting at an average of 1400 µm, growth ring width declined considerably during the first five years in the plants that grew in the peripheral zone and levelled off at 300 to 400 µm in the fifth and following growth periods. Hence, if plants of comparable ages are compared, growth rings were wider in the PS plants in the first growing seasons but in the following years this pattern reversed and the rings of the fifth or sixth growth period were narrower in the PS plants than those of the CS plants (Fig. 4). For the most recent years there was no difference in growth ring width among PS and CS plants.

In *P. recutita* there were stronger fluctuations in growth ring width in the CS-plants than in PS-plants that obstruct clear patterns. There were no clear differences in the growth ring development among sites and the patterns were only weakly similar to that of *C. spinosissimum* (Fig. 4).

TABLE 2

Number of shoots and number of growth rings (age) of the oldest roots or rhizome fragments, respectively, for individuals of Cirsium spinosissimum *and* Pedicularis recutita *sampled in the center or the peripheral area of the snowbank. Shown are median values (1st, 3rd quartile) for shoot number and means (±1 S.D.) for the number of growth rings*

	Cirsium spinosissimum		*Pedicularis recutita*	
	Center	Periphery	Center	Periphery
No of shoots per indv.	2 (1, 2)	2 (1, 3)	3 (2, 7)	5 (4, 7)
Number of growth rings	10.7 (±3.0)	9.3 (±3.9)	6.4 (±2.8)	5.2 (±2.7)

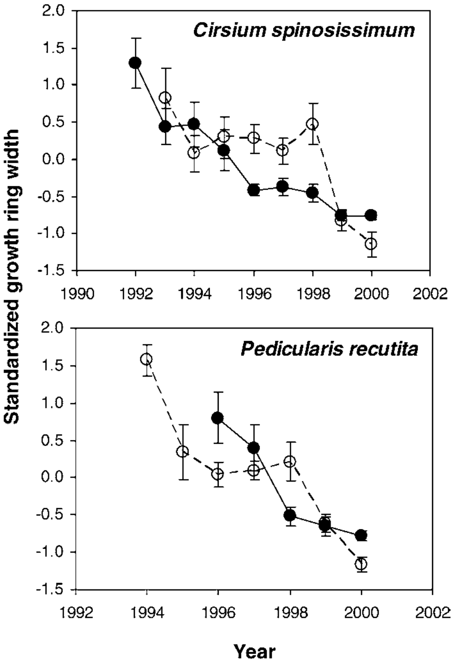

FIGURE 3. Standardized growth ring widths (mean ± 1 S.E.) in the secondary xylem of Cirsium spinosissimum *and* Pedicularis recutita *in relation to the calendar year. Open circles/dashed lines indicate samples obtained from the snowbank center; filled circles/solid lines denote samples collected from the peripheral zone. See text for further information.*

Discussion

Our results give no clear indication whether the life-span of the two forb species varies with position in the snowbank gradient. There is just a weak tendency in our data that plants in CS grow older than those in PS despite their comparatively low growth increments. However, this tendency is consistent with observations on the prostrate dwarf willow *Salix herbacea* growing along a snowbed gradient. In the area with the shortest snow-free period shoot growth of *S. herbacea* was lower but shoot age was higher than in the area with early-melting snow (Wijk, 1986). Wijk (1986) attributed the higher mortality of *S. herbacea* at the more productive periphery of snowbeds to higher competition intensity and herbivore damage by insects.

SYNCHRONOUS FLUCTUATIONS IN GROWTH RING WIDTH

In CS both species developed particularly wide growth rings in 1998, probably as a result of exceptionally favorable growth conditions in that year. This is supported by climatic data of the SMA MeteoSchweiz (1998) showing that the higher altitudes in the Alps received record excess temperatures in February 1998. High temperatures or low precipitation in the early months of the year prevented the accumulation of much snow in the northern Alps. These conditions were likely to prevent the development of a substantial snowbank in 1998 and probably allowed plant growth in CS to commence rather early. The same pattern of a positive deviation of the 1998 growth ring width was also found in two further unrelated alpine species, *Trifolium thalii* and *Lotus alpinus*, that were sampled from a restoration experiment in the alpine belt of the Jakobshorn Mountain (2596 m a.s.l.) near Davos, Switzerland (46°47′N, 9°49′E, Dietz and Fattorini, 2002). Both studies also correspond to each other in that the 1999 growth rings that were formed in a year with record amounts of snow in early spring (SMA MeteoSchweiz, 1999) tend to be particularly narrow.

TABLE 3

*Year-specific mean distinctness scores of growth ring width (mean D) and significance of their deviation from mean scores of the null distribution (*P *values). Data are only shown if the sample size for calculation of the D scores was ≥7. Values in brackets are levels of significance resulting from Bonferroni adjustment*

	Cirsium spinosissimum				*Pedicularis recutita*			
	Snowbank		Periphery		Snowbank		Periphery	
Year	Mean D	*P* (0.008)	Mean D	*P* (0.008)	Mean D	*P* (0.01)	Mean D	*P* (0.017)
1994	0.78	0.093	−0.11	0.827	—	—	—	—
1995	−0.23	0.611	0.19	0.532	1.74	<0.001	—	—
1996	−0.15	0.780	0.58	0.072	0.32	0.492	—	—
1997	0.53	0.248	−0.12	0.689	0.07	0.88	−0.51	0.369
1998	−1.66	<0.001	−0.23	0.449	−0.95	0.04	0.78	0.165
1999	0.97	0.032	0.3	0.320	0.27	0.549	0.01	0.885

However, indications for increased growth in 1998 were only weak in *C. spinosissimum* and *P. recutita* that grew at the periphery of the snowbank. In an alpine snow depth gradient on Niwot Ridge, Colorado, Walker et al. (1994) observed that the variation of phytomass in the snowbank community was most sensitive to date of snow release whereas that of the adjoining wet or moist meadows were most sensitive to soil moisture of the current season. It therefore seems that in areas with increased snowpack climatic fluctuations that predominantly affect the melting date of snow are transformed into more pronounced variations in plant growth in snowbanks than outside these areas.

LONG-TERM GROWTH TRAJECTORIES

The contrasting developmental patterns in growth ring width in CS as compared to PS that were obvious in *C. spinosissimum*, suggest that

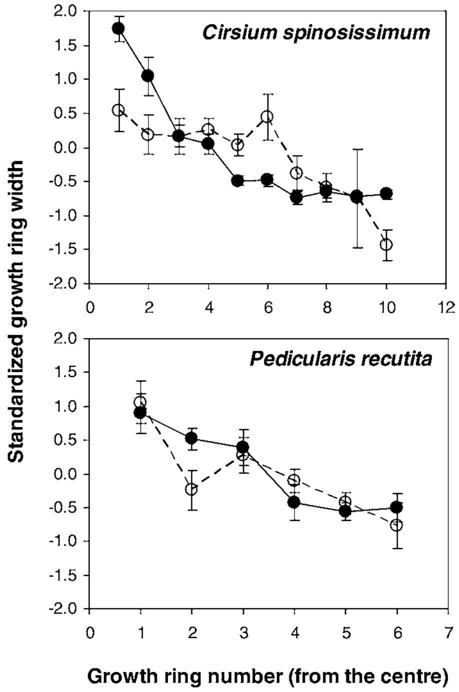

FIGURE 4. Standardized growth ring widths (mean ± 1 S.E.) in the secondary xylem of Cirsium spinosissimum *and* Pedicularis recutita *in relation to root or rhizome age, respectively. Open circles/dashed lines indicate samples obtained from the center of the snowbank; filled circles/solid lines denote samples collected from the margins of the snowbank. See text for further information.*

microsite conditions did not only differ between CS and PS but developed quite distinctly at the opposite ends of the snowbank gradient. While CS plants maintained rather constant and comparatively narrow growth ring widths during the first years of life, growth ring width decreased steadily afterwards, indicating that growth conditions have deteriorated or plants have increasingly turned senescent. In contrast, in PS plants, initially wide growth rings declined strongly in the first years of growth but the width remained fairly constant in the fifth and the following growth periods. These disparate growth-ring patterns suggest that the trajectory of changing site conditions were different in CS and PS. Apparently, in CS growth conditions were rather restricted from the beginning of plant growth, probably because of the shallow soil and the short growth period. On the other hand, growth conditions at the microsite scale do not appear to change systematically over short time periods in this area, maintaining plant growth on a rather low but constant level for several years before growth ring width declines. The most likely explanation for this situation is persistently low interspecific competition in CS resulting from the low abundance or weak performance of tall forbs (cf. Table 1). In contrast, sites with early snowmelt support the most luxuriant plant growth and may also be characterized by strong competitive interactions (Stanton et al., 1994; Walker et al., 1995). In PS growth conditions were clearly more favorable, particularly in the first years of growth when seedling establishment probably took advantage of higher resource availability after some (small-scale) disturbance. In later years, however, increasing competition by neighboring tall forbs (mostly large individuals of *Alchemilla monticola, Adenostyles alliariae,* and *Rumex alpinus*, cf. Table 1) seem to have increasingly restricted growth of *C. spinosissimum* to levels even lower than that of most CS plants.

It is a frequent pattern that plant cover in areas with strongly reduced resource availability as in snowbanks is low (with cryptogamous cover being high in some places) (Billings and Bliss, 1959; Kudo and Ito, 1992; Walker et al., 1995) and competition intensity may also be correspondingly low (cf. Callaway et al., 2002; Olofsson et al., 2002) whereas the reverse is true for the rather resource-rich and earlier-melting periphery of snowbanks (e.g., Stanton et al., 1994). The patterns of growth rings in the study species reflect these different growth conditions well and provide additional information on the likely trajectory of growth conditions at the microsite scale starting at the point of time when the individual plants germinated or established themselves.

Our results suggest that growth of both, *P. recutita* and *C. spinosissimum* is not strongly reduced by the snowbank conditions, at least not in the long run of the perennials' life. Rather, the more stable growth conditions in CS may provide compensation for restricted growth in the early years of plant life as compared to the situation at the periphery of the snowbanks. As a consequence, differences in size were small among plants of both *P. recutita* and *C. spinosissimum* growing at the opposite ends of the snowbank gradient, especially if compared with size differences of the more competitive but apparently less stress-tolerant co-occurring tall forbs that were strongly suffering from the snowbank conditions but formed the dominant canopy layer of the vegetation at the periphery of the snowbank. As indicated by the fluctuations in growth ring width in CS, plants growing in snowbanks may particularly profit from occasionally warm or dry spells that prevent heavy snowpack and allow to commence growth early. Consequently, they can probably take advantage of this "window of opportunity" as the density of possible competitors is low in snowbanks. However, in face of global warming, an increasing frequency or intensity of mild winters may tip the balance between species distributions such as to allow increasing expansion of tall competitors into diminishing snowbanks, at least in the low alpine zones. Changed composition of well known communities may be the result (see also Keller et al., 2000).

In conclusion, while the age structure did not seem to differ between the subpopulations at the opposite ends of the snowbank gradient our results suggest that there were both variable influences of climatic fluctuations and differences in growth conditions between the center and the periphery of the snowbank that resulted in corresponding variations in plant growth as preserved in the patterns of annual ring width in alpine *Cirsium spinosissimum* and *Pedicularis recutita*. Furthermore, there were disparate trends in the sequences of growth ring width in plants sampled at the opposite ends of the snowbank gradient, suggesting that the development of growth conditions was quite different in the center and at the periphery of the snowbank. The patterns observed in this case study can only suggest the possible causes of growth fluctuations in plants growing along snowbank gradients. However, our reconstructive approach generates testable hypotheses on important mechanisms and growth responses in the vegetation of alpine snowbank areas.

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