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Age analysis helps to estimate plant performance on ski pistes

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Abstract

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Age structure and growth performance of a dwarf shrub, *Vaccinium myrtillus* L., and a perennial herb, *Potentilla aurea* L. em. Willd., were studied on and beside two ski pistes in the Swiss Alps. The age of *V. myrtillus* ramets and *P. aurea* plants was determined by counting annual xylem rings at the shoot base. Biomass and shoot length of both species were measured. *Vaccinium myrtillus* ramets were significantly younger on ski pistes than in control plots. *Potentilla aurea* plants, however, showed no difference in age structure on and beside the pistes. Biomass and height of *V. myrtillus* ramets were considerably lower on the pistes than beside. The biomass of *P. aurea* plants was higher on the pistes. The growth form of *P. aurea* plants was short and compact on the pistes and long and outspread beside the pistes. The results indicate that the dwarf shrub *V. myrtillus* responds negatively in growth performance and age to the disturbance and stress on ski pistes. *Potentilla aurea*, however, might react to the changed environmental conditions and/or profit by decreased competition with dwarf shrubs on the pistes. The year ring analysis of the herb and the dwarf shrub proved to be a valuable tool for investigating population structures and thus helped to improve the understanding of plant performance on ski pistes.

Key words: Alpine environment, annual rings, plant chronology, growth form, *Vaccinium myrtillus*, *Potentilla aurea*.

Introduction

Ski pistes cover almost 1% of the Alps' surface in Switzerland (Seilbahnen 2001). Environmental changes on ski pistes can be caused by ground-levelling in summer (Bayfield 1996, Urbanska 1997), by skiers and snow-grooming vehicles in winter and, rapidly increasing, by the production of artificial snow (Kammer and Hegg 1990, Newesely 1997, Rixen et al. 2003). On most pistes, the vegetation cover is less dense,

and the proportion of unvegetated ground is higher than beside the pistes (Pröbstl 1990). Woody plants, e.g. dwarf shrubs, are usually more negatively affected by mechanical disturbance than other ecological groups like herbs. However, we only know a few details about these changes in vegetation composition.

Depending on the traits of the plant species, we may expect different responses to the stressful conditions on the ski pistes. If mostly the regeneration of a plant is affected, a population would consist mainly of old and no or few young individuals (Schaal 1978). A cause for this may, for example, be overgrazing that inhibits recruitment from seedlings (Crisp and Lange 1976). On the other hand, if mainly the survival and, to a lesser extent, the regeneration is negatively affected, a population may contain mostly younger plants. This may be the case e.g. when frequent disturbance enables extensive recruitment from seedlings (Dietz and Ullmann 1998).

In forest ecosystems, it is common practice to determine the age of trees and to relate it to the tree's growth performance (Schweingruber 1988, 1996). Recently, approximately 84% of Central European dicotyledonous plants in subalpine and alpine zones have been reported to show countable growth rings (Schweingruber and Dietz 2001b). In herbs the rings have proved, in many cases, to be caused by annual growth (Dietz and Ullmann 1997, Dietz and Fattorini 2002). *Potentilla erecta* has been reported to show clear demarcations, and growth rings in individuals with known age could be verified as annual (Dietz and Ullmann 1997). *Vaccinium myrtillus* (bilberry) as a dwarf shrub species from a seasonal climate is as likely to show annual rings as any other shrub or tree in this climate (Hegi 1995, Steiner 1999). Plant chronology has successfully been applied to reconstruct the colonisation by alien plant species (Dietz and Ullmann 1998, Dietz et al. 1999, Dietz 2002, Dietz and Schweingruber 2002) or the colonisation of glacier forefields (Münch 2001, Schwarz 2001). Although annual rings of dwarf shrubs have been known for a long time (Rosenthal 1904), these have hardly ever been analysed (Steiner 1999).

In this study, the plant chronology is used to investigate the age distribution and growth of plants on ski pistes. This information could otherwise only be obtained by labour- and time-intensive monitoring of ski pistes (Fattorini 2001). We studied the annual rings and growth parameters of a dwarf shrub (*Vaccinium myrtillus* L.) and a herb (*Potentilla aurea* L. em. Willd.) in order to estimate their past and present growing conditions. Our work addresses the following questions: What is the age structure of these two alpine plant species? Does the age distribution and growth performance of the plants display favourable or disadvantageous environmental conditions beside or on ski pistes? The growth responses of *V. myrtillus* and *P. aurea* may depend on whether they are directly negatively affected by, or whether they can react to different environmental conditions. They might also be indirectly positively affected if another competitive species is suppressed. Thus, we will finally discuss the role of disturbance, stress and competition for the age distributions of *V. myrtillus* and *P. aurea*.

Material and Methods

Species

We selected two species frequently occurring in the alpine environment and on ski pistes and showing distinct growth rings: The bilberry (*Vaccinium myrtillus* L., Ericaceae), a dwarf shrub, and the golden cinquefoil (*Potentilla aurea* L. em. Willd., Rosaceae), a herb. *Vaccinium myrtillus* is a clonal, deciduous dwarf shrub with a maxi-

Tab. 1. Characterisation of the four study plots.

Plot	Elevation (m a.s.l.)	Aspect (°)	Slope (°)	Years of snow production	Years since levelling
Site 1 – piste	2205	250	22	7	0
Site 1 – control	2205	230	27	0	0
Site 2 – piste	2040	267	18	0	25
Site 2 – control	2035	280	17	0	0

Plot	Bare ground (%)	Annual above-ground biomass prod. (g m ⁻²)	Average veg. height (cm)	No. of <i>P. aurea</i> plants per m ²	No. of <i>V. myrt.</i> ramets per m ²
Site 1 – piste	7	222	6.8	3.8	30.9
Site 1 – control	5	193	19.8	3.1	58.6
Site 2 – piste	15	67	5.5	25.7	10.2
Site 2 – control	1	403	36.2	1.9	80.4

num height of approximately 50 cm (Grime et al. 1988, Hegi 1995). A single clone can easily cover several m². The species is largely confined to acidic soils in the boreal and subalpine zone and has a Euro-Siberian distribution but also occurs in East Asia and North America. *Potentilla aurea* is a semi-rosette hemicryptophyte from the sub-alpine-alpine zone of southern and central European mountains (Ellenberg 1988).

Study sites and sampling procedure

Our study sites were located at two ski pistes in the Jakobshorn ski resort in Davos, Switzerland (Site 1: 46°46'26N, 9°50'13E. Site 2: 46°47'09N, 9°50'16E). At each site we chose two plots, one on the piste and one beside the piste at a similar elevation and with a similar aspect and slope steepness (Tab. 1). On one piste, the ground had been machine-graded 25 years ago; on the other piste, artificial snow has been applied for seven years. The sites were mostly influenced by the ski piste treatments as they were only moderately and rarely grazed by cattle. Furthermore, there were no indications for herbivory by deer or grouse. The vegetation consisted of species from alpine dwarf shrub heaths and alpine Matgras swards (Nardetum, Ellenberg 1988). The most frequent dwarf shrubs, among other *Vaccinium* species, were *Vaccinium myrtillus*, *Juniperus nana* and *Rhododendron ferrugineum*. The percentage of bare ground and the annual above-ground biomass production (Tab. 1) were determined when vegetation relevés at each plot were performed (Wipf et al. 2002). The vegetation height was measured with a Styrofoam plate on a pole at ten random locations per plot. The density of the target species was counted at 10 × 1 m² per plot and calculated to the mean number of plants/ramets per m² (Tab. 1).

At each of the four plots, we collected 30–35 ramets of *V. myrtillus* plants and 30–35 *P. aurea* plants in August 2000. The sampling followed a grid with an area of 10 × 20 m, where each sampling point on the grid was at least two meters away from the next one so as to obtain independent samples. At each point, the nearest plant of each species

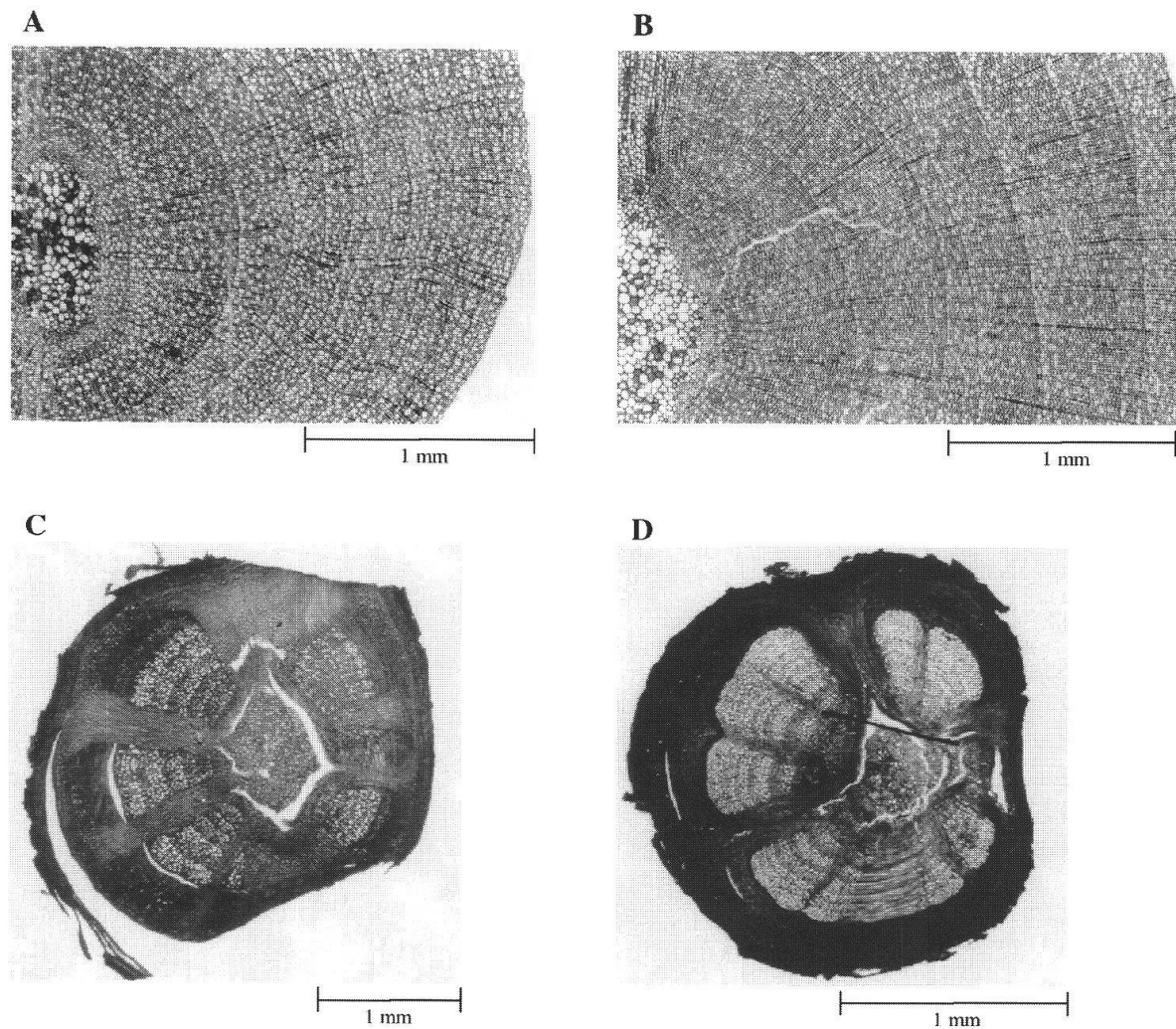


Fig. 1. Photographs of cross sections of *Vaccinium myrtillus* (A, B) and of *Potentilla aurea* (C, D). The *V. myrtillus* plants were 17 (A) and 12 (B) years and the *P. aurea* plants six (C) and approximately seven (D) years old.

was sampled. The ramets of *V. myrtillus* were cut two centimeters below the soil surface. If branches were growing very closely together, the tallest ramet of a group was chosen. *Potentilla aurea* plants were sampled including their main root if possible. The plants were stored in 40% alcohol at 5°C prior to the analysis.

Estimates of plant age and growth

We counted the annual rings of *Vaccinium myrtillus* at the base of each ramet in episcopic light under a binocular microscope (Iseli and Schweingruber 1989, Schweingruber 2001a). The ring boundaries were clearly marked in almost all ramets (Fig. 1). We assume that the error of the counts was not higher than one or two years in most specimens. In three old specimens the growth rings were very narrow, possibly leading to a greater error.

The *Potentilla aurea* plants were cut at the base of the shoots where plants are oldest, and the annual rings were mostly clearly marked (Dietz and Fattorini 2002). Unlike most other perennials, the proximate end of the main root of *P. aurea* was not the most suitable region for the ring analysis (Schweingruber and Dietz 2001b). From the base of the shoots, microscopic cross-sections 15–30 μm thick were made with a sledge microtome after the plant tissue was hardened in 95% alcohol (Schweingruber and Dietz 2001b). The annual rings were counted under a microscope with normal or polarised light. The ring boundaries were clearly marked in most plants and not visible in only one case. We assume that the error of the counts usually did not exceed one year.

To estimate the growth performance of *Vaccinium myrtillus*, we measured the ramet length and, after 48 hours of drying at 60°C, the dry weight without leaves. On each individual plant of *P. aurea*, we measured the plant length (total and separately for root and shoot without leaves) and the biomass (total and separately for root and shoot; only above-ground measures are reported here). Additionally, the diameter of the shoot base was measured for both species but is not reported here because it was highly correlated with biomass and shoot length ($P < 0.001$).

Statistical analysis

Data were analyzed in SPSS 10.0.5 (SPSS 1999). Differences in age distribution between plots were analysed with Chi-square tests of association. Biomass and shoot length were analysed by means of Analysis of Variance (ANOVA). The age of the plants was included in the analysis as a covariate (Tab. 2). Further explanatory variables in the ANOVA included “site” (site 1 or site 2), “piste” (piste plot or control plot) and all two- and three-way interactions. Since the factors “machine-grading” and “artificial snow” were not replicated in this study, they could not be analysed separately, but were combined in the factor “piste”. The response variables in the ANOVA were ln-transformed to achieve homogeneity of variance and normal distribution of error.

Results

Vaccinium myrtillus

The *Vaccinium myrtillus* plants growing beside the ski pistes showed a broader age distribution than the plants from the pistes (Fig. 2, $\chi^2 = 58.6$, df 7, $P < 0.001$). While on the pistes plants were generally younger than 15 years, plants beside pistes were up to 45 years old. Although the two sites differed significantly as plants were older at site 1 ($\chi^2 = 16.0$, df 7, $P = 0.025$), the difference between the piste and the control plots at the two sites was similar.

The biomass and the shoot length were significantly lower on the pistes than on the control plots (Fig. 3A,B, Fig. 4A,B, Tab. 2). The factor “piste” was significant after ‘plant age’ was taken into account in the statistical analysis (Tab. 2) which indicated that differences in standing biomass and shoot length cannot only be explained by different plant age. Furthermore, plants of the same age showed lower values in the growth parameters biomass and shoot length on the pistes than beside the pistes (Fig. 3A,B). Biomass differed between the two sites, but no significant interactions between “site” and “piste” were found (Tab. 2). This indicated that the differences between

Tab. 2. Effects of ski pistes on growth parameters in *Vaccinium myrtillus* and *Potentilla aurea*. ANOVA's on biomass and shoot length (all ln-transformed), with P values: (*) P < 0.1; * P < 0.05; ** P < 0.01; *** P < 0.001.

Vaccinium myrtillus

Source	ln (shoot biomass)			ln (shoot length)		
	df	ms	F	df	ms	F
Age	1	35.438	97.396 ***	1	6.825	145.208 ***
Site	1	13.355	36.705 ***	1	3.241	68.959 ***
Piste	1	24.125	66.302 ***	1	5.921	125.972 ***
Site*Age	1	0.509	1.400	1	0.514	10.938 **
Piste*Age	1	0.124	0.342	1	0.359	7.630 **
Site*Piste	1	0.672	1.847	1	0.808	17.182 ***
Site*Piste*Age	1	0.755	2.074	1	0.103	2.183
Residual	131	0.364		131	0.047	
Total	139			139		

Potentilla aurea

Source	ln (above-ground shoot biomass)			ln (shoot length)		
	df	ms	F	df	ms	F
Age	1	11.417	11.469 ***	1	2.955	13.127 ***
Site	1	0.930	0.935	1	4.578	20.339 ***
Piste	1	5.717	5.743 *	1	8.863	39.375 ***
Site*Age	1	3.124	3.139 (*)	1	0.020	0.088
Piste*Age	1	4.065	4.083 *	1	1.111	4.936 *
Site*Piste	1	1.124	1.129	1	3.302	14.668 ***
Site*Piste*Age	1	7.326	7.359 **	1	0.343	1.525
Residual	130	0.995		130	0.225	
Total	138			138		

piste and control did not differ between sites. Shoot length, on the other hand, differed significantly between sites, and the interaction between “site” and “piste” was significant too, because the difference between piste and control was greater at site 2 than at site 1 (Tab. 2, Fig. 3A,B).

Potentilla aurea

The age distribution of *Potentilla aurea* plants did not differ between piste and control plots ($\chi^2 = 2.45$, df 3, P = 0.48) but between the two sites ($\chi^2 = 29.6$, df 3, P < 0.001; Fig. 2). The median age of *P. aurea* was six and the maximum age 13 years.

The biomass of *P. aurea* was significantly higher on pistes than on control plots (Fig. 4C,D, Tab. 2). The highly significant three-way interaction between “site”, “piste” and “age” (Tab. 2) was caused by the poor growth of older plants on the control plot of site 1 (Fig. 3C,D). Despite the higher biomass production on the pistes, the shoot length of *P. aurea* was significantly lower on the pistes (Fig. 3C,D, Fig. 4C,D, Tab. 2). This indicated that *P. aurea* grew more compactly with thick and short shoots on the

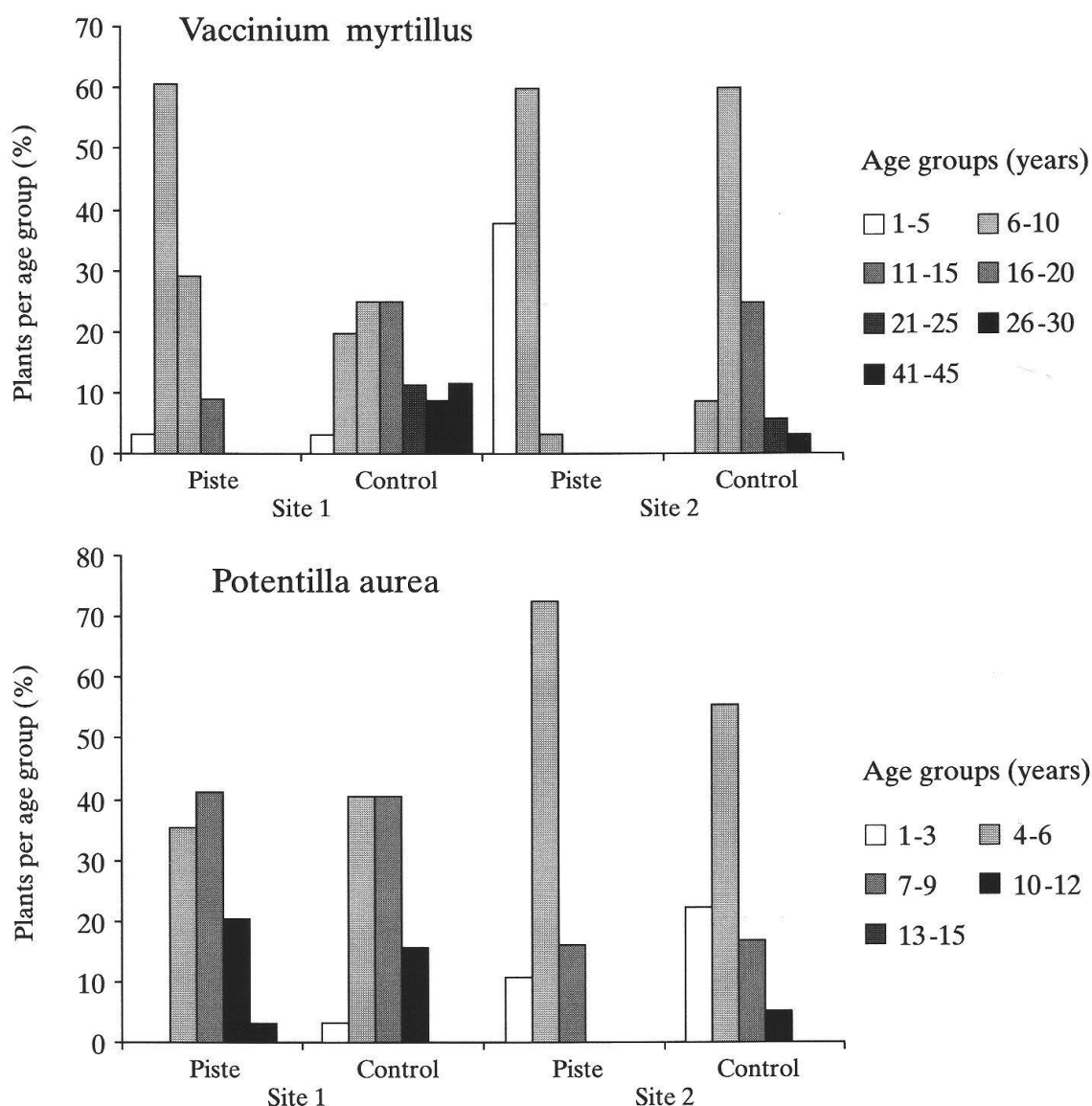


Fig. 2. Age distribution of *Vaccinium myrtillus* and *Potentilla aurea* at the two study sites, based on 30–35 plants per plot.

pistes and more outspread with thin and long shoots beside the pistes which was consistent with our observations. The highly significant interaction for shoot length between “site” and “piste” (Tab. 2) was caused by the high values on the control plot of site 2 (Fig. 3C,D, Fig. 4C,D) where *P. aurea* grew in a high and dense dwarf shrub vegetation (Tab. 1).

Discussion

The year rings were helpful markers for determining the age of our study plants. The maximum ramet age in *Vaccinium myrtillus* exceeded previous findings by other stu-

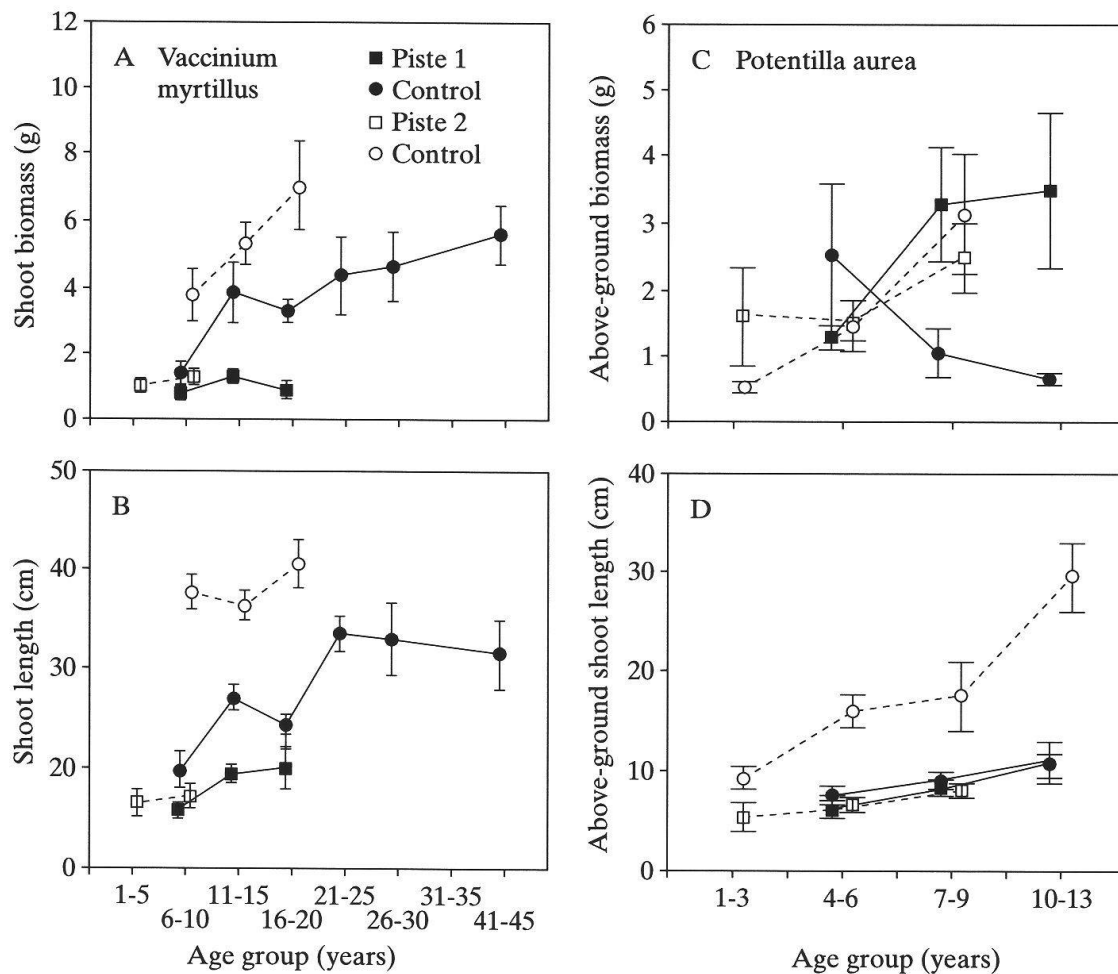


Fig. 3. Growth parameters (mean \pm SE) of age groups of *Vaccinium myrtillus* (A, B) and *Potentilla aurea* (C, D). *Vaccinium myrtillus*: shoot biomass (A) and shoot length (B). *Potentilla aurea*: above-ground biomass (C) and above-ground shoot length (D).

dies. While Hegi (1995) and Steiner (1999) describe maximum ages of 29 years and 34 years, respectively, we found some ramets with more than 40 annual rings. As we cut ramets of *V. myrtillus* at the soil surface, below-ground parts of the plants are likely to be older. In alpine environments, even 100-year old dwarf shrubs, e.g. *Loiseleuria procumbens*, could be found (Schweingruber and Dietz 2001a). The maximum ages of different alpine herb species reached 20–43 years in the study of Schweingruber and Dietz (2001b) according to year ring analysis. *Potentilla aurea* in our study was considerably younger, nonetheless, reaching a maximum age of 13 years.

Our results show the importance of knowledge about plant age for interpreting growth performance. Knowing biomass or plant height alone may be misleading when causes for growth performance are interpreted. It may not be possible to distinguish whether biomass is low because growth is decreased or because plants are young. In our study we could show that standing biomass of the dwarf shrub *Vaccinium myrtillus* is low on ski pistes not only because plants are younger but also because growth is decreased.

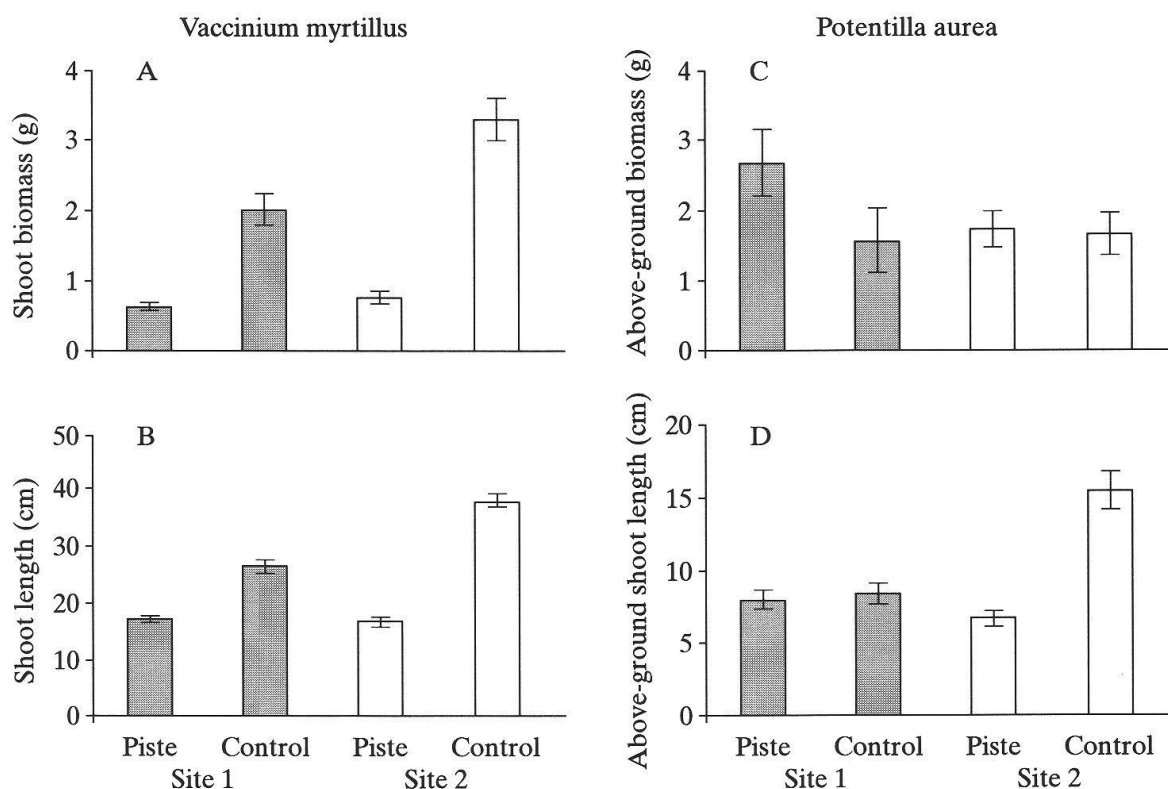


Fig. 4. Growth characteristics (mean \pm SE) of *Vaccinium myrtillus* (A, B) and *Potentilla aurea* (C, D) at the two sites on and beside the pistes. *Vaccinium myrtillus*: shoot biomass (A) and shoot length (B). *Potentilla aurea*: above-ground biomass (C) and above-ground shoot length (D).

We used the age analysis trying to reconstruct the past and present growing conditions of the analysed species. For *V. myrtillus* the growth characteristics were relatively clear as on both ski pistes plants were significantly younger than off-piste. However, the causes for this might be slightly different on the two studied pistes because one had been levelled 25 years before the study while the other has been receiving artificial snow for seven years. Because these two factors were confounded in our study, we can only estimate the causes for the low age of *V. myrtillus* on the ski pistes. On the non-levelled piste, we expect that the mechanical disturbance and stress through snow-grooming vehicles and skiers caused a decrease in the survival rate of ramets. The plants may have been injured when the snow was compacted during piste preparation or when people have skied on a thin snow cover in early or late winter (Rixen 2002). Other stress factors that have to be considered under a compacted snow cover are severe soil frost through an increased thermal conductivity or oxygen depletion through a decreased permeability of the snow cover (Cernusca et al. 1990, Rixen 2002). Tolvanen et al. (1992) have shown that ramets of *V. myrtillus* had a decreased survival rate when branches were clipped off (Tolvanen 1994, 1997), which is likely to be similar to stress factors on ski pistes. Artificial snow seems to mitigate some of the stress factors on ski pistes like mechanical damage or soil frost (Cernusca et al. 1990, Rixen 2002), on the other hand, it shortens the vegetation period by a delayed

snowmelt (Stoeckli and Rixen 2000, Rixen et al. 2001, Keller et al. 2003) and, hence, imposes another stress factor on ski pistes. On the levelled piste where *V. myrtillus* had to recover from total removal 25 years ago, the re-colonisation has to be considered as well. This re-colonisation could have happened from ramet parts that were left in the soil or from seeds. However, the oldest ramet at this site was eleven years old. This could mean that 14 years had passed after levelling before the first dwarf shrubs re-colonised the area or that ramets at this site had a high turnover rate. The results are supported by other studies that found vegetation re-growth at alpine graded sites to be slow (Urbanska 1997, Fattorini 2001).

The lower above-ground biomass and shoot length of *V. myrtillus* on the ski pistes was not only a trait caused by young plants because ramets of the same age also showed this tendency. This indicates that the growing conditions on both ski pistes are less favourable than off-piste due to the stressful conditions explained above. Although the two pistes together with their control plots differed in many of the parameters measured, the differences between piste and control of most growth parameters did not differ significantly between sites. This suggests that the degree of stress to *V. myrtillus* on either piste type may be similar.

In contrast to *V. myrtillus*, the environmental conditions on the ski pistes did not seem to influence the age distribution of *P. aurea*. Possibly, the disturbance on ski pistes could not affect a herbaceous hemicryptophyte like *P. aurea* as much as it did the shrubby *V. myrtillus*. However, the growth forms of *P. aurea* were quite different between piste and off-piste plants given that piste plants grew rather compactly with short but thick shoots while off-piste plants grew more loosely and outspread with long but thin shoots. Beyond that, the mean biomass was higher on ski pistes. This might show that *P. aurea* is able to adapt its growth strategy to the changed environmental conditions. However, there might also be an indirect effect of a decreased competition by *V. myrtillus*. It seems plausible that *P. aurea* profits by the ski piste treatments, because the higher growing competitor is suppressed.

The age analysis of *P. aurea* and *V. myrtillus*, but also of other alpine perennial plants, offers a valuable tool to investigate aspects of plant population biology in alpine habitats in general and on ski pistes in particular. It helped to improve our understanding of plant performance under disturbance on ski pistes. Furthermore, age analysis may allow the detailed analysis e.g. of the re-colonisation of levelled ski pistes and the estimation of the plants' fitness in a specific environment. Further applications may also include studies on plant migration due to climate change, plant responses to changes in land use or responses to melting of permafrost or glacier regions.

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Zusammenfassung

Die Altersstruktur und Wachstumsleistung von Heidelbeere, *Vaccinium myrtillus* L. und Gold-Fingerkraut, *Potentilla aurea* L. em. Willd. wurden auf und neben zwei Skipisten in den Schweizer Alpen untersucht. Das Alter von Heidelbeer-Rameten und Fingerkraut-Pflanzen wurde durch Zählen der jährlichen Xylemringe an der Sprossbasis bestimmt. Als Wachstumsparameter wurden Biomasse und Sprosslängen von beiden

Arten gemessen. Die Rameten der Heidelbeere waren signifikant jünger auf Skipisten als auf Kontrollplots. Das Fingerkraut dagegen zeigte keine Unterschiede in der Altersstruktur auf und neben Skipisten. Die Biomasse und Höhe der Heidelbeere war erheblich geringer auf Pisten als neben Pisten. Die Biomasse von Fingerkraut-Pflanzen war höher auf den Skipisten. Vor allem aber waren die Wuchsformen beim Fingerkraut unterschiedlich: auf Skipisten waren Pflanzen niedrig und kompakt, neben den Pisten hatten sie lange und dünne Sprosse. Die Ergebnisse zeigen, dass die Heidelbeere mit reduziertem Wachstum auf die Stressfaktoren auf den Skipisten reagiert und dort weniger alt wird. Das Gold-Fingerkraut hingegen kann anscheinend auf die veränderten Umweltbedingungen reagieren und profitiert möglicherweise gar von geringerer Konkurrenz durch Zwergsträucher auf den Pisten. Die Altersanalyse bewährte sich als wertvolle Methode zur Analyse von Populationsstrukturen und half somit die Wuchsleistung von Pflanzen auf Skipisten besser zu verstehen.

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