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Age and growth of *Salix herbacea* L. (dwarf willow) in Alpine populations



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Abstract

Climate change affects species all over the world and puts them in danger for extinction. Environments in alpine habitats are often extreme, with high wind-exposure and snow covers most of the year, which makes the alpine species more vulnerable to climate change. It is therefore important to know time-scale of regeneration in plant populations that gives a better understanding about their reaction to the changing climate. In this study the regeneration of the clonal dwarf shrub *Salix herbacea* L. (dwarf willow) was examined in the alpine regions in Davos, Switzerland. *Salix herbacea* grows in different microhabitats, both steep slopes with high wind-exposure (ridges) and local depressions with long lasting snow cover (snow-beds). The aim of this study was to determine age of individual clones of *Salix herbacea* and also too examined if the age and growth (root diameter and average growth ring width) differ between the two microhabitats ridge and snow-bed. To investigate this, roots from *S. herbacea* were excavated from three different transects in Davos. Dendrochronological methods were used to determine age and the diameters were measured. The age of *S. herbacea* was determined to be between 12 – 43 years old and statistical analyses showed no significant difference between the ridges and snow-beds in terms of age and growth. These young clones imply a comparatively fast regeneration rate suggesting that *S. herbacea* has the ability to respond fast to a changing climate by re-colonizing.

Keywords: *Salix herbacea*, age, growth, microhabitat, dendrochronology, climate change, regeneration

1. Introduction

Climate change puts plants and animals at high risk, particularly in Alpine habitats (Beerling, 1998; Reisch *et al.*, 2007; Wijk, 1986b). When the environment changes, plants cannot migrate to a new place as easily as animals can, instead current populations may be able to express different phenotypes under new conditions (phenotypic plasticity) or, alternatively, genetically based adaptation may occur (van Kleunen & Fischer, 2005). The alpine habitat is characterized by harsh environments, such as high wind exposure and long winters, which leads to limited nutrient resources. Interactions between wind and topography create irregularities of the winter snow distribution, resulting in microhabitats with different snow melting times. Ridges (*e.g.* steep slopes) are often exposed to strong wind and remain snow-free throughout the winter or the snow melt early in spring. Snow-beds (*e.g.* depressions) on the other hand are sheltered from extreme conditions but have a short vegetation period, because the snow covers remain until late summer (Beerling, 1998; Reisch *et al.*, 2007; Wijk, 1986b). Global warming is expected to lead to longer growing seasons and lower snow cover as in ridge microhabitats and for this reason, comparing plant performance in these habitats can contribute to predictions about plant reactions to climate change.

It is important to know about the regeneration rate of plants that strongly influences their reactions to changing conditions. Fast regeneration increases the probability for evolutionary adaptation and faster re-colonization after local extinction. High longevity increases the probability for endurance of short-term environmental changes, but also slows down evolutionary adaptation. Knowing plant age in long-lived species is therefore an important first step to understand possible reactions to climate change (Brown, 1996; de Witte & Stöcklin, 2010).

The growth of woody plant shoots depends on environmental- and inherent factors; no growth occurs before the snow has melted (Wijk, 1986a). The genotypes capacity to alter the phenotype of a woody plant is a result of physiological responses to environmental change, which can leave marks in the xylem structure by influencing *e.g.* the growth ring width (growth ring thickness) or latewood density (density of growth rings produced later in the growing season). Extreme conditions, *e.g.* frost can damage the xylem cells and give permanent imprint of weakly lignified conduits inside a band of dead cell tissue (Fonti *et al.*, 2010; Jones *et al.*, 2009).

Dendrochronology is a method for the analysis of growth rings patterns and includes counting of annual growth rings. This method is a suitable way to determine age and was used to determine the “oldest living tree”, which was a 4800 years old *Pinus longaeva* found in

Nevada, USA (Schulman, 1958). It is mostly used on tree stems, but the method can also be used on shrubs and herbs with a primary root system or woody stems, as long as the growth rings are visible (Brown, 1996; de Witte & Stöcklin, 2010). Shrubs are usually younger than trees, but not always. By using dendrochronological methods an alpine dwarf shrub (*Rhododendron ferrugineum*) found in the European Alps, was determined to be 300 years old (Escaravage *et al.* 1998). This method has also been used on species in the Salicaceae family. *Salix arctica* was found to be between 31 and 59 years old (Woodcock & Bradley, 1994). The shrub *Salix pulchra* was studied in different patches and the mean age at the root collar was 33.9 years (± 13.1) at the patch- center and 27.1 years (± 12.9) at the patch- perimeter (Danby *et al.* 2011). The oldest individual in the Salicaceae family analyzed with dendrochronology is a *Salix polaris*, which was 98 years old found in Aire Valley, Svalbard (Owczarek, 2010). *Salix herbacea* has been found to be of a maximum age of 43 years using dendrochronology (Schweingruber & Poschlod, 2005). However, the highest age reported for *S. herbacea* was determined with a different method. In a study done by de Witte *et al.* (2012) the clone age of *S. herbacea* was calculated by dividing clone size by the estimated annual horizontal size growth (in situ) and the oldest clone was estimated to be at least 450 years old, while most other individuals were less than 100 years old. Further studies on growth and age of *S. herbacea* are needed to understand the regeneration better and to clarify the big age difference in the two earlier studies mention above.

In this study, the dwarf shrub *Salix herbacea* L. (dwarf willow) was analyzed. *Salix herbacea* is distributed in the arctic areas in northern regions of Europe, western Siberia and North America and also in mountainous regions of central Europe, *e.g.* the Alps (Beerling, 1998; Reisch *et al.*, 2007; Rossi *et al.*, 2005; Wijk, 1986b). This clonal, diploid ($2n = 38$), dioecious shrub belongs to the willow family (Salicaceae). *Salix herbacea* has a massive rhizome system and only short aerial stems, about 5 cm above soil surface. The clones grow horizontally in all directions and form patches (Beerling, 1998). These patches are usually under 10 cm in diameter, but sizes of 500 cm have been found (Hägberg, 2013). It is difficult to identify an individual clone out in the field, which makes it hard to locate the primary root (Reisch *et al.*, 2007; Rossi *et al.*, 2005; Wijk, 1986b).

The aim of this study was to determine age of individual clones of *Salix herbacea* L. (dwarf willow) and to investigate if the age differs between *S. herbacea* individuals growing in the two microhabitats ridge and snow-bed. The second aim was to study whether root diameter and average growth ring width of *S. herbacea* differs between the two microhabitats

ridge and snow-bed. The hypothesis is that the clones will grow better in snow-beds than in ridges because of the longer growing season.

2. Materials and methods

2.1. Study area

The study took place in Davos, Switzerland (46°48'15"N 9°50'14"E) in August 2012. Roots from *S. herbacea* were sampled from the three different transects Jakobshorn (46°46'21"N 9°50'58"E), Wannengrat (46°48'25"N 9°46'46"E) and Schwarzhorn (46°44'06"N 9°56'30"E) between 2400 – 2600 m.a.s.l. (figure 1A). These three transects is a part of a larger project conducted at the Institute for Snow and Avalanche Research in Davos, Switzerland in collaboration with the University of Konstanz, Germany and the University of Uppsala, Sweden.

Localization: First an area with *S. herbacea* was located and this area was categorized into either ridge or snow-bed depending on the areas topography. To get a random excavation site a metal ring ($\varnothing = 40$ cm) was tossed out in the located *Salix* area (figure 1C). This was done in all except one of the excavation sites in which an individual clone could be identified (figure 1D & 1E). Before excavation the coordinates were determined using a GPS (appendix I, II). Most of the excavation sites were at Jakobshorn, because this mountain was easiest to reach.

Excavation and sampling: Excavation was done with a trowel and the biggest root-parts in each area were sampled. All roots were tracked back to shoots and leaves to make sure it was *S. herbacea* (figure 1F). In total 173 roots were sampled from 10 ridges and 8 snow-beds, with 1-15 root parts sampled from each area. All roots were sampled in plastic bags, labeled with R (ridge) or S (snow-bed) and a number for each area and root (*e.g.* R1r1 means ridge no. 1 and root no. 1; appendix I). For storage and transport all roots were covered with 40 % ethanol and the plastics bag were placed in plastic boxes.

2.2. Analysis of growth rings

The sampled roots were analyzed to verify whether they were primary- or secondary roots. Primary roots have a root-shoot transition zone, also called the root collar, which corresponds to the oldest part of the individual (Schweingruber & Poschlod, 2005). Five primary roots

were selected to be cross-cut and in addition to these, one secondary root from each site (overall 16 roots) was randomly chosen to get enough data. The diameters of the selected roots were measured before cross-sections were made.

Cross-sections: Primary roots were cut near the root collar and the secondary roots were cut on their thickest part (figure 2). One drop of 99.9 % ethanol was put on the roots flat surface, to prevent curling, before 30 μm thick cross-sections were made using a microtome. Seven sections were made from each root and put on a slide with glycerol, to prevent the roots from drying out before staining (Schweingruber & Poschlod, 2005).

Staining: The glycerol on the slides was removed using distilled water. All sections were bleached with sodium hypochlorite (NaClO) and rinsed with distilled water. A mixture (1:1) of safranin (1 g dissolved in 100 ml distilled water) and astrablue (0.5 g dissolved in 100 ml tartaric acid solution) was dropped directly on the section with a pipette. The sections were rinsed thoroughly with 95 % ethanol after 2 – 3 min and covered with a cover glass. Safranin stains lignified cells red and astrablue stains unlignified cells blue (Schweingruber & Poschlod, 2005).

Age determination: All cross-sections were examined in a stereo microscope after staining and digital photos were taken. Annual growth rings in the xylem were counted to determine the age using both the stereo microscope and the digital photos (figure 3). The growth rings are shown by vessel size and frequency. In earlywood vessels are big and round, while vessels in latewood are smaller and rectangular (Schweingruber & Poschlod, 2005; Schweingruber *et al.*, 2006; figure 3). Xylem diameter was measured using a scale and the average growth ring width was calculated by dividing xylem diameter by ring number (age).

Statistical analysis: Data on the primary roots (root- and xylem diameter, age and average growth ring width) was described individually and overall median was calculated for both the primary- and secondary roots. For the secondary roots a two-sample Wilcoxon test was used to compare root traits between the two microhabitats, ridge and snow-bed, using R 2.15.2 (R Core Team, 2012). One sample from the secondary roots was removed from the dataset, because it was probably a stem and another sample was moved from secondary roots to primary roots after close examination. This left six primary roots and 14 secondary roots (eight from ridges and six from snow-beds) to be analyzed. Unfortunately not enough primary

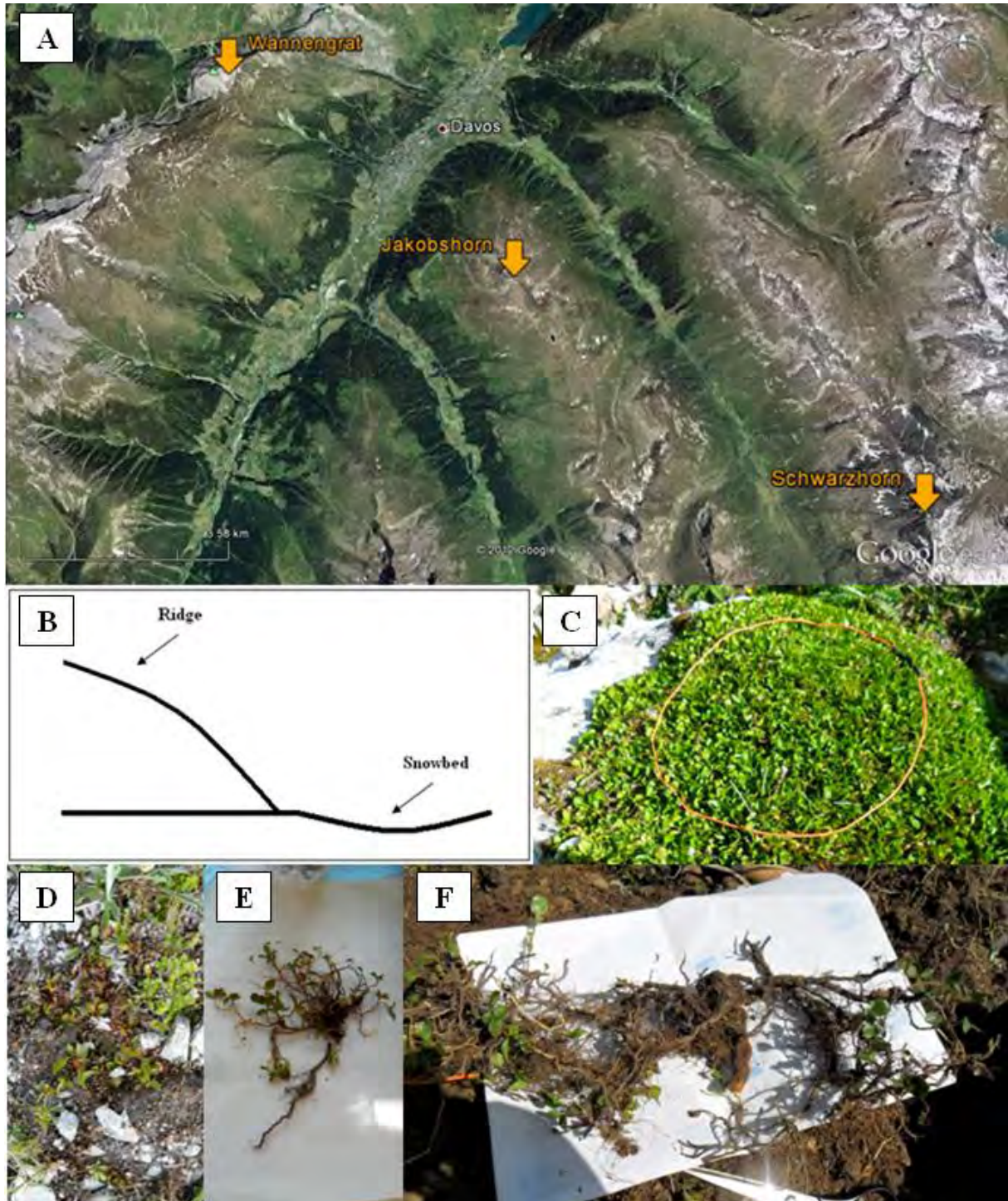


Figure 1. **A)** Map of the study area Davos, Switzerland ($46^{\circ}48'15''\text{N } 9^{\circ}50'14''\text{E}$) with the three transects Jakobshorn ($46^{\circ}46'21''\text{N } 9^{\circ}50'58''\text{E}$), Wannengrat ($46^{\circ}48'25''\text{N } 9^{\circ}46'46''\text{E}$) and Schwarzhorn ($46^{\circ}44'06''\text{N } 9^{\circ}56'30''\text{E}$). **B)** Topographic difference between ridge (steep slope) and snow-bed (depression). **C)** Metal ring with 40 cm in diameter, which determined the excavation site. **D)** The area of the clone (R10r1) that was excavated without the metal ring. **E)** Whole clone (R10r1) after excavation. **F)** Root (S6r1) with connected rhizomes, shoots and leaves.

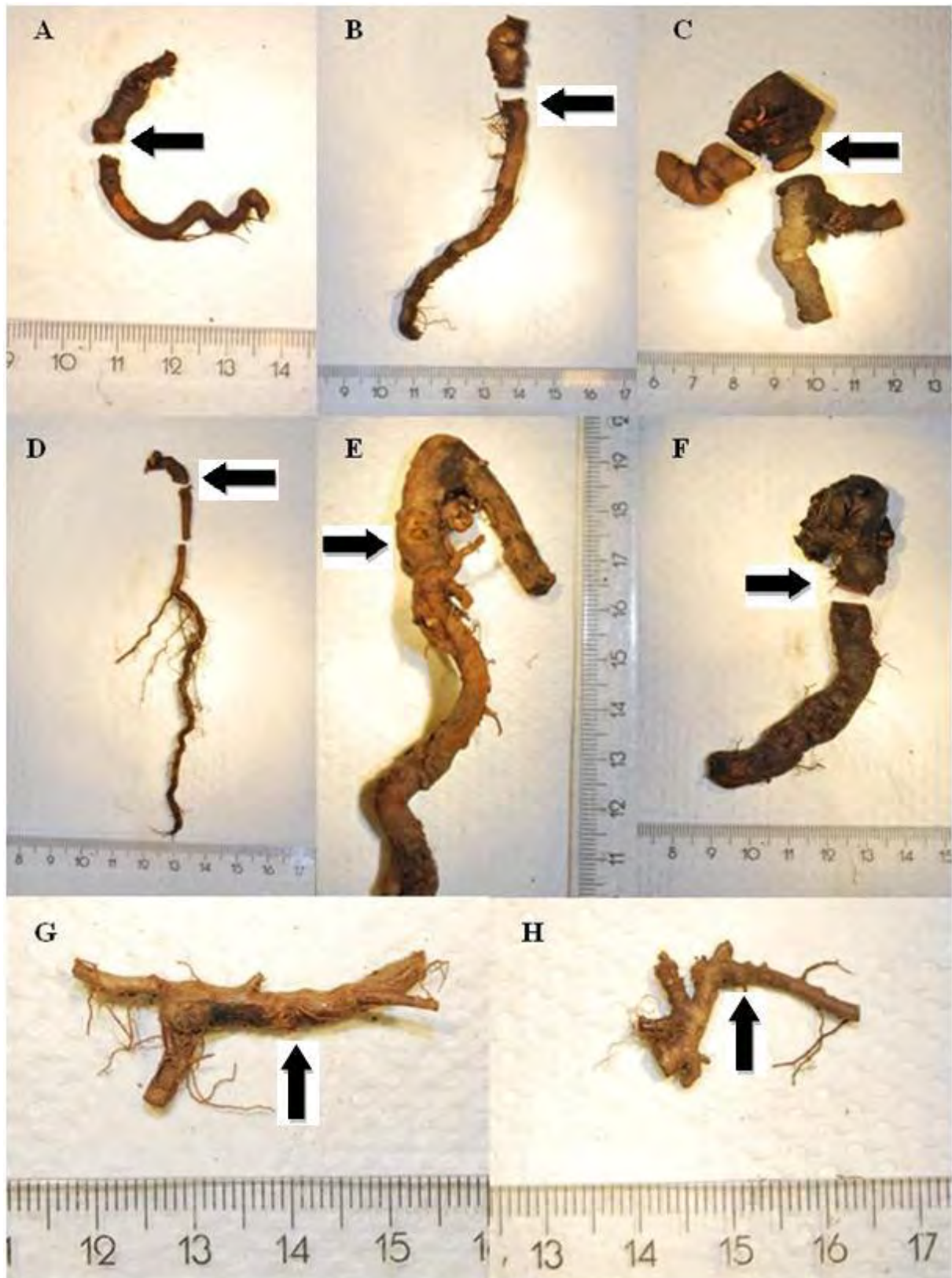


Figure 2. Primary roots (A-F) and secondary roots (G-H) of *Salix herbacea*. **A)** individual R2r1 with root collar. **B)** individual R6r1 with root collar. **C)** individual R9r1 with location of cross-section. **D)** individual R10r1 with root collar. **E)** individual S3r3 with location of cross-section. **F)** individual S6r1 with location of cross-section. **G)** individual R1r2 with location of cross-section. **H)** individual S2r4 with location of cross-section.

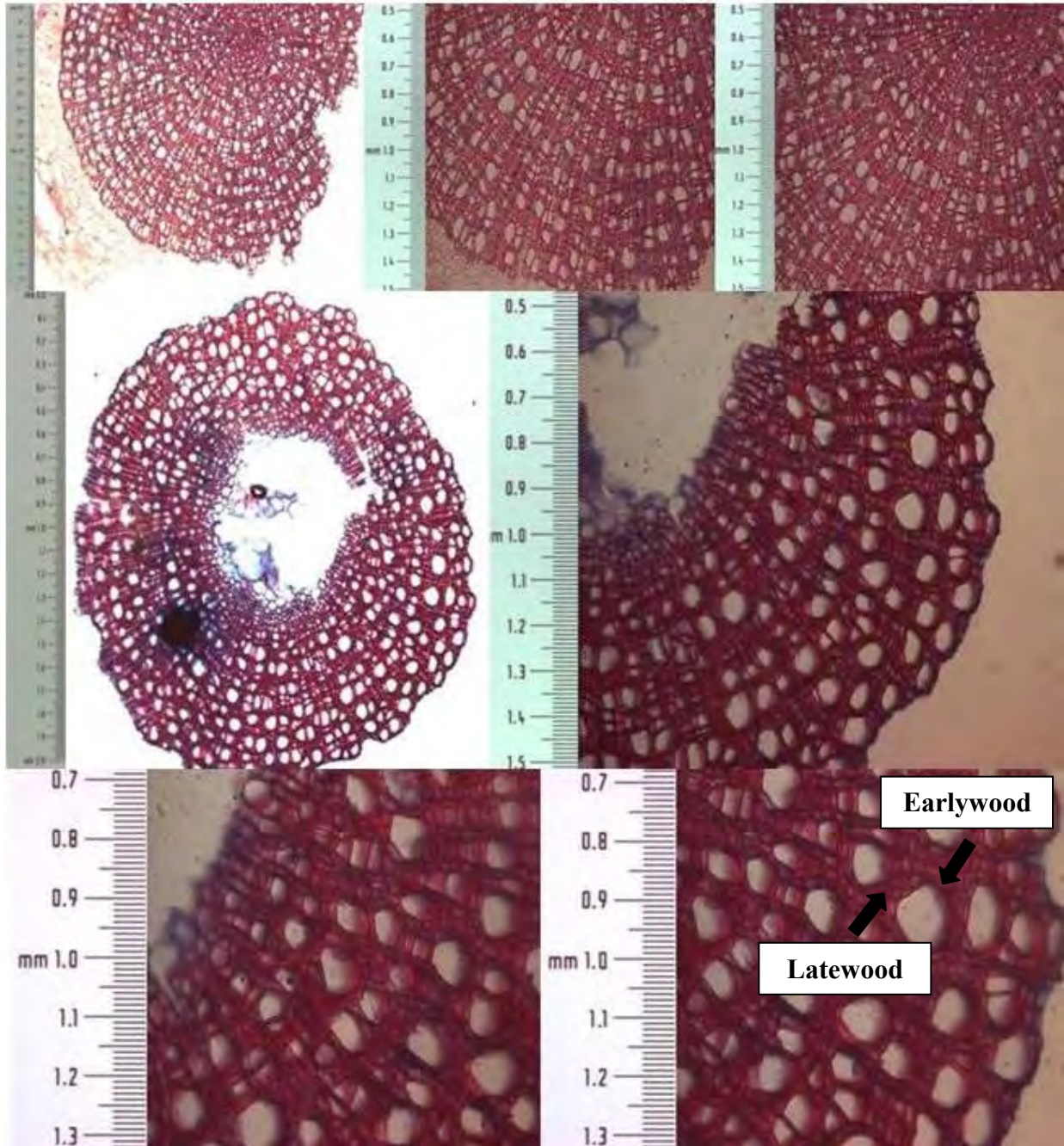


Figure 3. Digital photos of cross-sections of *Salix herbacea* roots investigated in a stereo microscope in three different enlargements: 5x lens, 10x lens and 16x lens. Growth rings are visible as large, round vessels (earlywood) and small, rectangular vessels (latewood). **A-C)** individual R10r1 (5x and 10x, respectively). **D-E)** individual R4r8 (5x and 10 x, respectively). **F-G)** individual R4r8 (16x), demonstrating the location of one earlywood- and latewood vessel.

roots were found and as a result it was only possible to compare the secondary roots between the two microhabitats.

3. Results

3.1. Primary roots

From the six primary roots three had a clear root collar, one had a hook and two were partly above ground with rhizomes growing in different directions (figure 2). The age of the primary roots were between 12 – 43 years (appendix III, table 1). Four of them were sampled in ridges with the ages of 12, 19, 26 and 43 years. The other two were sampled in snow-beds with the ages of 28 and 34 years. The two oldest primary roots (34 and 43 years) were the two roots that were partly above ground with rhizomes growing in different directions and these two were also the thickest roots, with a root diameter of 13.3 mm respectively 16.7 mm and a xylem diameter of 6.1 mm respectively 7.5 mm. The primary roots average growth ring widths were between 79 – 180 μm , with a median value of 142 μm .

Table 1. Median and range for root diameter (mm), xylem diameter (mm), age (years) and average growth ring width (μm) in primary- and secondary roots of *Salix herbacea*.

	Primary roots	Secondary roots
Median root diameter (mm)	9.80	2.38
Median xylem diameter (mm)	3.84	1.31
Median age (years)	27	9.5
Median growth ring width (μm)	142.18	138.45
Range root diameter (mm)	3.90 – 16.70	1.63 – 6.10
Range xylem diameter (mm)	1.39 – 7.46	0.71 – 2.70
Range age (years)	12 – 43	6 – 24
Range growth ring width (μm)	79.21 – 179.84	85.82 – 151.32

3.2. Secondary roots

The secondary roots were between 6 – 24 years old (appendix III, table 1). The eight roots from ridges were between 6 – 24 years old with a median of 10 years and the six roots from snow-beds were between 8 – 11 years old with a median of 9.5 years; however this difference was not statistically significant ($W = 26.5$ and $p = 0.7940$; figure 4). The root diameter (median value of 2.69 mm in ridges and 2.20 mm in snow-beds), xylem diameter (median value of 1.28 mm in ridges and 1.34 mm in snow-beds) and the average growth ring width

(median value of 126.55 μm in ridges and 147.67 μm in snow-beds) did not differ significantly between roots collected from ridges and snow-beds ($W = 21$ and $p = 0.7546$, $W = 29$ and $p = 0.5728$, $W = 10$ and $p = 0.0813$, respectively).

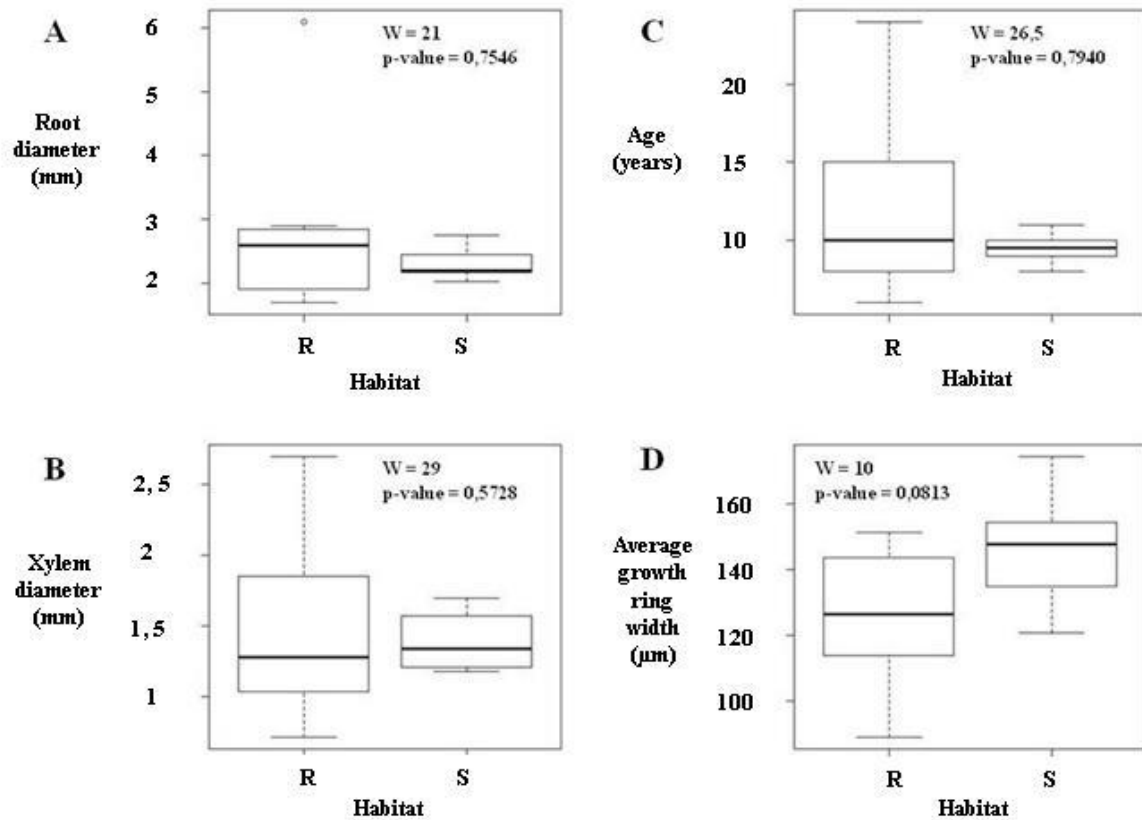


Figure 4. Root traits and age of *Salix herbacea* in the two microhabitats ridges (R) and snow-beds (S) in the Swiss Alps. **A)** Root diameter (mm). **B)** Xylem diameter (mm). **C)** Age (years). **D)** Average growth ring width (μm).

4. Discussion

The aim was to determine the age of *Salix herbacea* and the two oldest primary roots found in this study were 34 and 43 years old; these were also the thickest roots. No significant difference could be found between individuals of *S. herbacea* in the two microhabitats in terms of age, root- and xylem diameter and average growth ring width. In other words no evidence was found that individual clones of *S. herbacea* growing in snow beds or ridges differ in age. However, the sample size of the analyzed roots was small, which limits the possibility to detect differences. At the same time the variation in age, diameter (xylem and root) and average growth ring width, within each microhabitat appeared large, especially in ridges.

The results from the analyzed secondary roots indicate that the snow melting time does not have that much influence on the growth of *S. herbacea*, since no difference between ridge and snow-bed were found. Snow-beds have a shorter growing season as a result of the long lasting snow covers, but at the same time ridges are exposed to more wind and dramatic temperature changes. These results imply that ridges and snow-beds probably are equally stressful habitats, but due to different factors.

Determining age in Alpine dwarf shrubs is difficult, because the root-shoot transition zone can be deep below the surface in older plants. Schweingruber and Poschlod (2005) found a 30 year old shoot of the alpine species *Gentiana punctata* 25 cm below the surface. The transition zone is sometimes impossible to detect when the shoot is below the surface because it forms adventitious roots and in addition, it is hard to see from the outside if it is a shoot or a root (Schweingruber & Poschlod, 2005; Schweingruber *et al.*, 2006). It is therefore possible that more than six of the 173 sampled roots were primary roots, but due to the difficulties to locate the transition zone some of them may have been missed during the analysis. Another difficulty with determining age are possibly discontinuous growth rings, caused by climatic conditions (*e.g.* cold summers), mechanical stress or limitations in growth space for the root- and branch systems, that could make it harder to get accurate age estimation (Hakkarainen *et al.*, 2005; Kuivinen & Lawson, 1982; Owczarek, 2010).

The oldest individual in this study was 43 years old, which is the same age found by Schweingruber & Poschlod (2005) using the same method. However, de Witte *et al.* (2012) reported a much older clone with an age between 450 – 520 years with a different method. In this method they assumed that the clone would grow a certain distance from the center per year and with this clone size the age was calculated. From all clone sizes de Witte *et al.* (2012) found, 96,4 % were calculated to be less than 100 years old, but the distance between each sample was 76 cm, thus our finding of younger (and most likely smaller) clones is not inconsistent with the results of de Witte *et al.* (2012). Indeed, in a study conducted by Häggberg (2013) at the same site near Davos, Switzerland, a large number of small clones were detected (38 % sampled in ridge and 49 % sampled in snow-bed were 10 cm or smaller). Häggberg (2013) also found a few larger clones, with a size up to 5 m that are probably much older, but the great majority of the clones were small. These small clones imply a relatively young age and together with the young ages from this study it is likely that *S. herbacea* has a faster regeneration rate than previously assumed. *Salix herbacea* may therefore have the capacity to respond comparatively fast to changing environments; this would allow the species to re-colonize quickly and potentially undergo evolutionary adaptation.

5. Conclusion

The age and growth of *Salix herbacea* was not found to differ between ridge and snow-bed. This indicates that the regeneration in both microhabitats is equally fast. All clones in this study were relatively young, between 12 – 43 years old, which implies fast regeneration. This is an advantage for *S. herbacea* regarding changing climate, due to the increased potential for response.

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Appendix

I. Table over locals: Number of roots collected at each local, showing the local transects, coordinates, elevation, collection date and stem-density (table 2).

Table 2. The different locals (R = ridge, S = snow- bed) with number, number of collected root-parts at each local, which transect (J = Jakobshorn, W = Wannengrat, S = Schwarzhorn), the coordinates (in degrees, minutes and seconds) where the excavation took place, elevation (m.a.s.l) and the collection date (when the excavation took place).

Local	No. of collected		Coordinates	Elevation	
	root – parts	Transect		(m.a.s.l)	Collection date
			46°46.337' N		
R1	3	J	9°50.996' E	2519	13 August 2012
			46°46.483' N		
R2	13	J	9°51.102' E	2533	15 August 2012
			46°45.891' N		
R3	10	J	9°51.289' E	2491	17 August 2012
			46°46.127' N		
R4	13	J	9°51.129' E	2561	20 August 2012
			46°45.932' N		
R5	9	J	9°51.233' E	2490	20 August 2012
			46°46.398' N		
R6	7	J	9°51.152' E	2442	21 August 2012
			46°48.500' N		
R7	15	W	9°47.493' E	2376	22 August 2012
			46°44.278' N		
R8	12	S	9°57.740' E	2451	23 August 2012
			46°46.239' N		
R9	1	J	9°51.493' E	2408	28 August 2012
			46°46.314' N		
R10	1	J	9°51.001' E	2549	13 August 2012
			46°46.321' N		
S1	10	J	9°51.008' E	2538	14 August 2012
			46°46.486' N		
S2	14	J	9°51.092' E	2525	15 August 2012
			46°45.892' N		
S3	10	J	9°51.297' E	2483	17 August 2012
			46°46.133' N		
S4	8	J	9°51.070' E	2518	20 August 2012
			46°45.919' N		
S5	8	J	9°51.208' E	2475	20 August 2012

			46°46.373' N		
S6	10	J	9°51.179' E	2421	21 August 2012
			46°48.499' N		
S7	14	W	9°47.488' E	2374	22 August 2012
			46°44.276' N		
S8	10	S	9°57.774' E	2446	23 August 2012
<hr/>					
Sum: 173					
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II. Maps of transects: Three maps with the location of each excavation site from the three transects: Jakobshorn, Wannengrat and Schwarzhorn (figure 5).

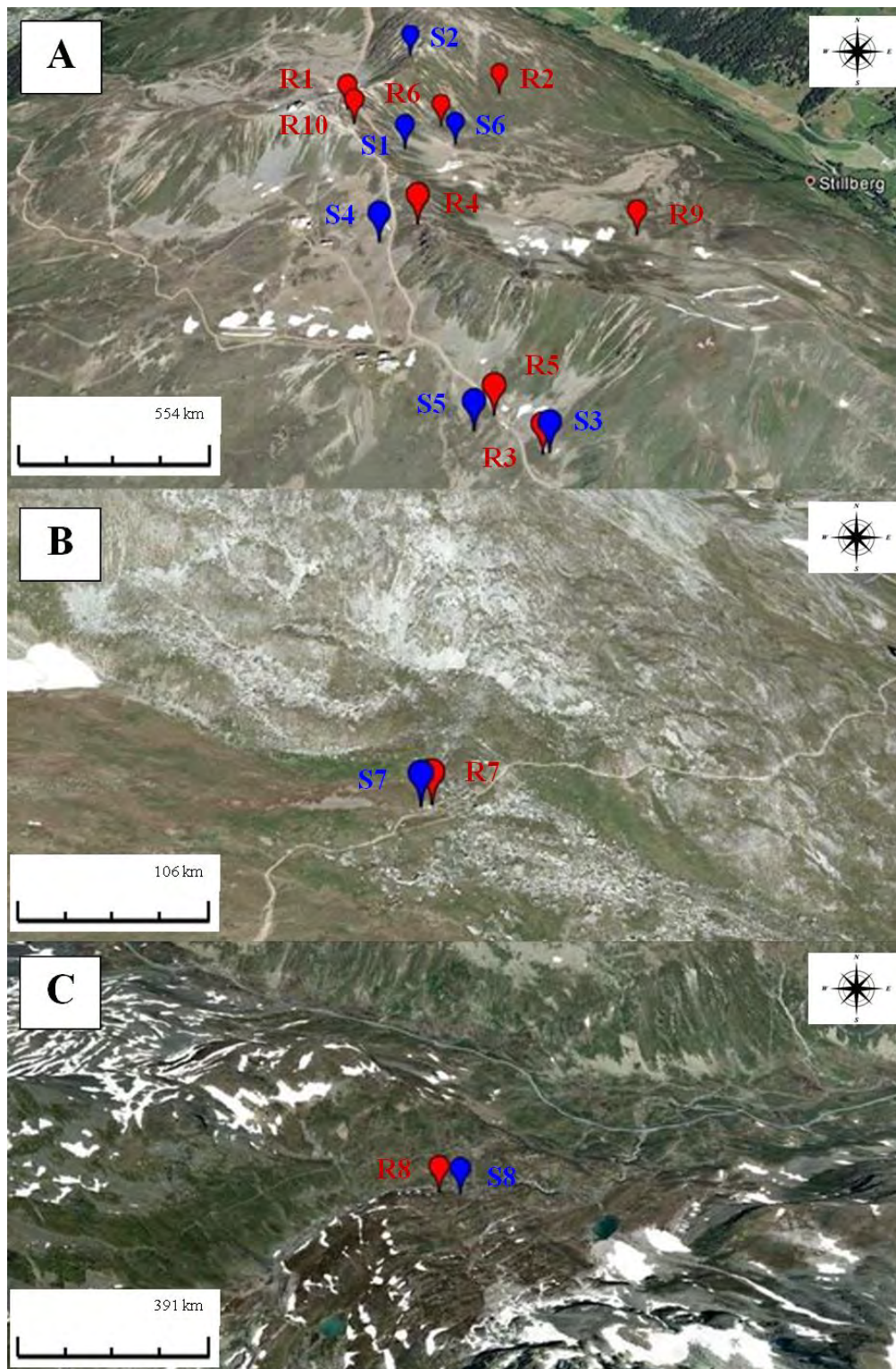


Figure 5. A) Map over the excavation site in Jakobshorn, showing the location of R1-R6, R9-R10 and S1-S6. B) Map over the excavation site in Wannengrat, showing the location of R7 and S7. C) Map over the excavation site in Schwarzhorn, showing the location of R8 and S8. In all three pictures the red dots represent ridges and the blue dots represent snow-beds.

III. Tables over examined roots: Table over individual primary roots respectively secondary roots showing root diameter (mm), xylem diameter (mm), age (years) and average growth ring width (μm ; table 3 & 4).

Table 3. Primary roots diameter (root- and xylem in mm), age (years) and average growth ring width (μm) in *Salix herbacea*.

Name	Root diameter (mm)	Xylem diameter (mm)	Age (years)	Average growth ring width (μm)
R2r1	4.92	1.50	19	79.21
R6r1	8.98	3.80	26	145.99
R9r1	16.70	7.46	43	173.44
R10r1	3.90	1.39	12	115.92
S3r3	10.61	3.87	28	138.36
S6r1	13.26	6.11	34	179.84

Table 4. Secondary roots diameters (root- and xylem in mm), age (years) and average growth ring width (μm) in *Salix herbacea*.

Name	Root diameter (mm)	Xylem diameter (mm)	Age (years)	Average growth ring width (μm)
R1r1	6.10	2.70	24	112.59
R2r3	2.47	1.29	11	117.51
R3r7	1.69	1.27	9	141.31
R4r8	2.79	1.17	8	145.90
R5r2	2.07	0.71	8	89.03
R6r6	2.89	2.08	18	115.39
R7r12	2.71	1.63	12	135.58
R8r3	1.75	0.91	6	151.32
S1r1	2.22	1.33	9	147.86
S2r4	2.75	1.57	9	174.44
S4r6	2.17	1.70	11	154.40
S5r6	1.63	0.77	9	85.82
S6r10	2.02	1.18	8	147.49
S7r6	2.44	1.21	10	120.94
S8r10	2.18	1.35	10	134.81