Dwarf tundra shrubs growth as a proxy for late Holocene climate change

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Abstract

The Arctic is the most sensitive zone to climate changes and the impacts are reflected in local ecosystems. In order to extract information of the past from proxy archives the detailed knowledge of such archive is crucial. The paper summarizes modern approaches of tundra dwarf shrub research for the purposes of paleoclimatology. Dwarf tundra shrubs as still relatively untapped archive are believed to contain valuable proxy data in their annual growth increments. Field sampling, and laboratory work are reviewed in detail. Constraints of dwarf tundra shrub research are discussed as well. The relationship between climate and growth is addressed to find a link between them depending on location and species. Majority of investigations found the strongest relationship between summer temperatures and ring widths, although exceptions are not rare. Dwarf tundra shrubs can fully serve as valuable proxy archive only if those are understood. Finally, the factors influencing the length of dwarf tundra shrub life are studied in order to sample the oldest living individuals in the field. Despite the field collection should aim to sample various sizes and ages of plants to make the dataset robust, the longest living individuals which are important to prolong chronologies are usually inhabiting rather nutrient poor and undisturbed sites close to their survival limits. The paper indicates the most suitable dwarf tundra shrub research designs for the purposes of paleoclimatology. As such it can help to harvest the benefits of dendrochronology from the vast and new territories.

Key words: climate archive, lifespan, dendroclimatology, wood anatomy, the Arctic

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Introduction

Since tundra shrubs occur mainly in remote and areas (such as the Arctic or high mountains) where our understanding of climate is biased due to scarcity of direct observation (Atkinson et Gajewski 2002, Rayback et Henry 2005, Bär et al. 2006) the knowledge gained from such high-resolution archives can extend our understating of the climate in recent centuries (Woodcock et Bradley 1994). The presence of annual rings in dwarf shrubs (also called alpine/arctic dwarf shrubs) has been first documented in the beginning of the 20th century (Rosenthal 1904, Kanngiesser 1906, 1909, 1914). One of the first authors who recognized their potential for paleoecological purposes was Warren-Wilson (1964) who studied annual growth of *Salix arctica*. Since then the significance of dendroecological studies on nontree woody life forms has been growing expressively. However, many decades have passed before the first reconstructing studies (still dealing with numerous problems) could be obtained (Shaver 1986, Woodcock et Bradley 1994). Tundra shrub potential to learn more about impact of environmental/climate change started to be discussed by some authors (Büntgen et Schweingruber 2010, Hallinger et al. 2010). Studies of dwarf tundra shrubs from a dendroclimatic point of view have nevertheless received increasing attention only recently (Schmidt et al. 2006, Myers-Smith et al. 2011, Buchwal et al. 2013, Myers-Smith et al. 2015).

Potential problem of shrub research is on site identification of old individuals for collection to extend the chronology. Life span of dwarf tundra shrubs is species-specific but in general they live between ten to two hundred years maximally (for details *see* Schweingruber et Poschlod 2005). Recently, the individuals of *Juniperus communis* reaching almost 700 yrs were collected in the northern coast of Kola peninsula (Lehejček, unpublished work). The extremely short growing season, cold temperatures, and often also mineral nutrient stress in the arctic/alpine region result in extending individual life span (Ward 1982, Körner 2003). It makes those life forms convenient for paleoecological reconstructions especially in the Arctic and alpine environments where they can fill observational gaps (AICA 2005). Nonetheless, the study which evaluates the findings from different environments in order to detect the main general climate driver of shrub growth is still missing.

The investigation of dwarf tundra shrubs growth can in spite of limitations expand the current dendrochronological network into new extreme environments beyond the survival limits of trees (Büntgen et al. 2015). Therefore, the abilities of shrubs climate proxies can together with conventional tree ring research portray climate changes across most of the terrestrial world (Schweingruber 1996). It is also not without interest that shrub vegetation in certain parts of the Arctic almost doubled its extent over the last 50 years (Bunn et al. 2007). This fact shows that arctic shrubs are sensitive indicators of climate and react abruptly to changes. Moreover, the current rate of warming in the Arctic is about 0.5°C per decade which is five time faster than global average (Serreze et al. 2000, ACIA 2005). Thus, the Arctic is a great environment for studying such changes assuming that similar magnitude of shifts occurred in the past as well.

The general objective of the first part of the paper is to present comprehensive information on field, laboratory, and analytical techniques of dwarf tundra shrub research for paleoecological, especially paleoclimatological purposes. Second part of this review deals with the influence of climate and site characteristics on length of plant's growth.

Review question of this paper state: What are the main climate drivers of dwarf shrub growth? Is it temperature, precipitation, or season, or is it species and location-specific?

Answering these questions can help to understand signals given by growth of dwarf tundra shrubs and can significantly improve our knowledge of the past environment in remote regions.

Material and Methods for dwarf tundra shrubs investigation

Sampling

For the purposes of dendroclimatology the specific sampling design is needed for each study. Here, we provide several advices which should be followed in order to receive the strongest climate signal from our samples.

It is strongly recommended not to sample too early in the growing season, before the leaves are developed, since it is then difficult to distinguish dead individuals from living (Zalatan et Gajewski 2006).

One should also keep in mind during field sampling the potential effects of topography, microclimatology, wind conditions, snow cover (especially its relief relationships as referred in Bär et al. 2006, 2007, 2008), soil properties, moisture availability, nutrition supply, mycorrhiza symbiosis, fungal diseases, insect defoliation, browsing pressure and land-use/land-cover as stressed by Büntgen et Schweingruber (2010). They also suggest the broader spatial scale of collected samples to overcome local disturbance factors.

Concerning species selection it is important to work with the species that frequently occur in the entire study area (Bär et al. 2006) to be able to sample whole variety of different plant ages for strong master chronology development.

Sampled shrubs should be spatially distinct, and in larger cluster only one sample should be taken to prevent collection of the same genotype twice (Hallinger et al. 2010, Weijers et al. 2010). Before removing the whole plant including braches, stem, and roots from the soil it is appropriate to record position of the soil surface by tape (Bär et al. 2006), slope aspect, and GPS position. Photos of both the site as well as the whole plant should be taken for later reminder in case of later unexpected findings (Bär et al. 2006).

Since alpine as well as arctic ecosystems are fragile the investigator should concern the degree of invasiveness. Stems are examined in the great details and therefore a vast number of samples is not required. Nonetheless, one should be aware of collecting too few samples since sometimes only about one third of samples can be used for final chronology (Zalatan et Gajewski 2006, Blok et al. 2011, Zongshan et al. 2013). Most studies work with tens of samples (between 15 and 50) and the authors often collect also the dead material to extend the length of chronology (*e.g.* Zalatan et Gajewski 2006, Hallinger et al. 2010, Blok et al. 2011). Kolishchuk (1990) resp. Schweingruber (personal communication) believes that not less than 10 (resp. 30) analysed individuals can sufficiently reflect and cover the specific habitat. In general, annual growth-ring patterns can differ among shrub species (from uniform to variable growth form). This growth variation could therefore be taken into account in sampling strategy (less number of individuals with uniform growth are needed compared to individuals with variable or irregular growth form) to extract the similar strength of climatic signal. To incorporate this recommendation knowledge on ecological and anatomical aspects of the species is nevertheless required which does not have to be always the case in the Arctic.

Concerning the issue of sample transportation Schweingruber et Poschlod (2005) suggest plastic zip-lock bags containing directly labelled compartments while providing detailed records on site and plant characteristics. An alternative approach is to use paper bags which prevent the material from moulding and fungi contamination.

Dendrochronology – lab work

Wedging rings, missing rings or piths, frost rings, asymmetric growth including lobes or "just" extremely narrow rings (*see* Fig. 1.) are the results of the harsh environment which dwarf shrubs inhabit often also accompanied with one-sided (mechanical) stress or local death of cambium (*e.g.* Kolishchuk 1990, Woodcook et Bradley 1994, Schweingruber 2001, Bär et al. 2006, 2007, 2008, Zalatan et Gajewski 2006, Hallinger et al. 2010). Due to this difficulties the analysis of annual rings must undergo a much more complicated procedure in comparison with regular tree ring research.

Additional steps of analysis are required to construct reliable master chronology of tundra shrubs and thus reconstruct the climate signal contained in variations of their growth (Kolishchuck 1990). The method of serial sectioning first developed by Kolishchuck (1990) facilitates the annually precise dating of each ring and it is particularly important when annual rings are poorly visible and hard to measure (Schweingruber et Dietz 2001). Commonly, between 2 and 10 thin sections equally distributed over the plant's body is obtained from the plant. The number depends on the degree of expected cross-dating constraints (Woodcock et Bradley 1994).

Stem section samples are made from compartments by sledge microtome knife and they are usually 10-30 µm thick (Schweingruber et Poschlod 2005, Bär et al. 2006). Gärtner et Schweingruber (2013) suggest sticking the samples in glycerol to prevent drying in case of long-term storing. There are also many ways of ring-visibility improvement such as highlighting by rubbing chalk, staining by Safranin and Astrablue etc. (for more *see* Schweingruber et Poschlod 2005 or Gärtner et Schweingruber 2013). Subsequently, the section is dehydrated and cleaned by ethanol, permanent slide is created and micro-photographed.

Some authors (*e.g.* Hallinger 2010, Zongshan et al. 2013) exclude from further dendrochronological analysis those discs with stem wounds, rotten wood, or extremely eccentric growth.

Chronology development

a) Cross-dating

Cross-dating is a technique that ensures each individual tree ring is assigned its exact year of formation (Speer 2010).

Annual rings are measured using sensitive digital encoder and softwares (*e.g.* WinCell, Roxas) with a precision of 0.001 mm (Zalatan et Gajewski 2006, Hallinger et al. 2010). Kolishchuk (1990) recommends measuring the ring widths from the periphery to the centre.

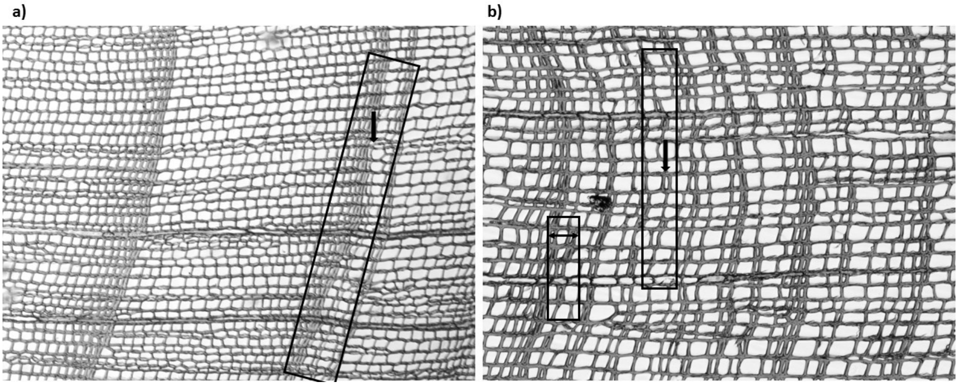

Fig. 1. Problematic areas within the microscopic sections (*Juniperus communis)*. a) wedging ring with arrow indicating the point of miss. b) extremely narrow ring consisted of two cell rows only; and ring which can be easily omitted and considered as missing because only few and sporadic latewood cells were formed - possibly distinguishable from incomplete rings or intra-annual density fluctuations using serial sectioning method.

Visual cross-dating precedes verifying by widely used computer programme COFECHA (Holmes et al. 1986). Width of annual rings should be measured on every disc in several direction separated from each other by at least 90° (Hallinger et al. 2010) while directions with minimum number of discontinuous rings or scars are preferred (Bär et al. 2006). The following operations in laboratories known as serial sectioning (Kolishchuk 1990) are focused on obtaining the complete record. It combines findings about annual increments in different directions within the incision (1^{st} order), in different parts of shrub (2^{nd} order), as well as between individuals (3^{rd} order) in order to detect missing rings and prepare samples for cross-dating (Schweingruber et al. 1990) to receive master chronology (Bär et al. 2006). Cross-dated ring-width series of samples from the same stem height are averaged and compared to those from other heights within the same individual to check for wedging or missing rings (Blok et al. 2011). In case of missing ring detection in chronology such should be artificially inserted with the lowest possible increment assigned (Bär et al. 2006). To be considered as a missing ring Woodcock et Bradley (1994) suggest rather conservative criteria: 1) it has to be clearly identified in at least two other samples; 2) be narrow in the samples in which it appeared.

Hallinger et al. (2010) note some findings gained during serial sectioning of *Junniperus nana*. They state that the largest diameter of the stem does not always contain the most number of years. Often the outermost ring at the stem base does not refer to the last year of the growth, and simultaneously, there is many missing rings at the root collar. The possible reason for this fact may be age-related move of phytohormones higher up, resp. downward in the stem (*e.g.* cytokinins, resp. auxins) and therefore in particular years cambium in the basal part of the stem might not activated at all (Kolishchuk 1990, Wilmking et al. 2012). This could also explain the fact that some dwarf shrub species at high latitudes do not show any visible radial growth trend (Schmidt et al. 2006) with wider stem near the surface. Limitation of the stem base growth due to the low close-to-ground temperatures might also be the case of above mentioned if the dwarf shrub is not in prostrate form or has very low sizes which rules this effect out since such conditions therefore influence the whole plant body uniformly. The value of the whole material for paleoclimatological renconstruction is dependent upon successfully cross-dating the samples (Woodcock et Bradley 1994).

b) Removal of age trend - standardization

Variation in the width of annual growth increments is not only caused by climatic factors but also by long term trends which can disturb the climatic fluctuations (*e.g.* uneven growth over the plant's lifetime, Fritts 1976). Standardization is removing of non-climatic growth trends from the annual growth increments series. It allows the resultant standardized values of particular plants to be averaged together into master chronology (Cook et Kairiukstis 1990).

Such trends are generally removed by dividing the individual tree ring series by functional estimates of these trends (Weijers et al. 2010). For standardization the program ARSTAN is used most commonly (Cook 1985, Rayback et Henry 2005, Zalatan et Gajewski 2006). Therefore, Büntgen et Schweingruber (2010) warn of averaging measurements series from different stem sections without standardisation the stem-height-curves first (done *e.g.* by Bär et al. 2006, 2007 or Hallinger et al. 2010) otherwise it artificially increases the relevance of juvenile growth phases because upper stem sections experience longer period of growth then those close to root collar because the cambial activity starts from the top (Kolishchuk 1990).

It is done by mean curves using a 32 year smoothing spline (Blok et al. 2011) or linear regression lines (Zalatan et Gajewski 2006, Zongshan et al. 2013) and negative exponential curves (Blok et al. 2011, Zongshan et al. 2013) to remove intra-plant variation and age related as well as other long term growth trends. In addition, the master chronology (using *e.g.* biweight robust mean) of the aligned time series from one disc is calculated to express the overall average trend of the time series (regional curve as used *e.g.* in the RCS method; Esper et al. 2003). Detrending can be performed by fitting a polynomial function (*e.g.* aka 'Spline') to the respective master chronology of aligned series. For each serie the residual to this average spline trend can be used as detrended variable. Such operations should lead to removal of the most of the growth related trends and low-frequency signals. Alternatively, the ring-width data can be standardized using a horizontal mean detrending to preserve the low-frequency variability in the data.

Age related trends of tundra shrubs ring widths do not differ from trees if the canopy is closed. Such series are characterised by early suppressed growth followed by a relatively sharp growth increase and subsequent decline (*e.g.* Forbes et al. 2010). On contrary, the age trends are very difficult to generalize if canopy does not close. Most commonly, they are declining (*e.g.* Blok et al. 2011, Rixen et al. 2010, Weijers et al. 2010), sometimes are not evident (Buchwal et al. 2013) and often also not consistent (Hallinger et al. 2010, Tape et al. 2012). Selection of appropriate detrending method for removing particular age trends is therefore crucial for successful paleoclimate reconstructions using dwarf shrubs ring-width series.

The series which do not show appropriate correlation with the master chronology can be excluded from the site chronologies (Zongshan et al. 2013). Residual standardised chronology retained without the influence of the previous year growth on the growth of next year (Cook et al. 1990) can be used for subsequent analysis (Zalatan et Gajewski 2006).

c) Further data treatment

After cross-dating, standardization and creating master chronology of each particular disc of all series are usually averaged within the whole stem (Bär et al. 2006, 2007, Hallinger et al. 2010, Blok et al. 2011) to obtain comparable growth estimates. Subsequently, also all individuals of one site type are averaged in order to receive master chronology.

The climate and growth relationship

There is lack of information what temperatures present the limit for cambial activity of dwarf shrubs. Very few relevant studies have focused on critical temperature for cell division of conifers in cold climates (*e.g.* Rossi et al. 2008). The authors concluded that average limiting values are around 4-5°C for the daily minimum temperature at 2 m height. Körner et Paulsen (2004) defined the limit for growing season as the time period of ten days air temperature means higher than 0°C. Ten days interval is the minimum duration for vessel development and lignification (Suzuki et al. 1996). Such study for prostrate woody life forms, however, remains for further investigations.

It is widely accepted (*e.g.* Fritts 1976, Woodcock et Bradley 1994, Bär et al. 2008, Weijers et al. 2010) that climate conditions preceding and during the growing season influence the growth. To find which climate variables are the most important for plant growth it is crucial to have climate data from nearby meteorological station which cover at least a part of shrub's lifespan or to use extrapolated climate data *e.g.* from the Climatic Research Unit. Subsequent statistical analyses highly depend on particular meteorological data availability. The more detailed the observations are the finer scale can be used for finding climate-growth relationship. To generalize the common strength of climate response in the tree rings of dwarf shrubs is not simple since this is influenced by factors like micro-climate, species (diffuse vs. ring porous), or habitats. Commonly, the correlation coefficients are lower than in similar studies using tree material but significant, highly correlating and over whole period stable results have been reported. Following list can give an impression on the wide variety of results concerning both strength of correlations and variables: Buchwal et al. (2013) for *Salix polaris* and mean JJA temperatures ($r = 0.70$, $P < 0.01$); Zhongshan et al. (2013) for *Rhododendron przewalskii* and April, July temperatures ($r = 0.326$, $P < 0.05$); Hallinger et al. (2010) for *Juniperus nana* and June + July temperatures ($r = 0.4$, $P < 0.05$); Blok et al. (2011) for *Salix pulchra* and early summer temperature ($r = 0.73$, $P < 0.01$); Zalatan et Gajewski (2006) for *Salix alaxensis* and December, March precipitation ($r = 0.3$, $P < 0.05$).

Discussion

Seasonal macro-climate and growth response relationship

a) Winter

Cold winters which are responsible for root injuries are among the most limiting factors of shrub growth (Pederson et al. 2004). They are often accompanied by delayed snow melt resulting in shortened vegetation season and possibly reducing early wood formation (Vaganov et al. 1999, Schmidt et al. 2006, Pellizzari et al. 2014). Warm period within winter can also cause significant damage when the plant loses its frost resistance and is therefore sensitive to upcoming extreme cold events as discussed *e.g.* in Zongshan et al. (2013). Also Sturm et al. (2001) believe that winter snow cover plays crucial role in shrub expansion due to enhanced nutrient supply in the harsh Arctic environment. Zalatan et Gajewski (2006) consider winter as crucial season (for *Salix alaxensis* in western Canadian Arctic) as well but their findings are different. They found a correlation between high winter precipitation associated with enhanced soil moisture during the growing season. Locality of their investigation is, nevertheless very continental (*see* Appendix 1.). Therefore, the effect of precipitation is such an important factor of growth compare to more oceanic areas where soil moisture is not an issue (*e.g.* Zongshan et al. 2013).

b) Spring

Climate in spring can influence the growth as well. Early and warm spring can extend the length of the growing season and enhances earlywood formation (*see* Schmidt et al. 2006, Zongshan et al. 2013). Schmidt et al. (2006) are among a few authors who consider early spring climate conditions at their research site as the most important factor for shrub growth. They found out a correlation between late snow melt and narrow growth rings indicating deteriorated growth conditions. This was observed especially from the 1960s onward when the climate in northeast Greenland has become more oceanic as a consequence of diminishing sea ice. In this case the changes are nevertheless locally driven. This might be the reason why Schmidt et al. (2006) presented growth chronology signal with poor annual increments in recent decades in contrast to general trend.

c) Summer

Many authors (*e.g.* Rayback et Henry 2005, Bär et al. 2008, Hallinger et al. 2010, Weijers et al. 2010) report summer temperatures as the most important growth influencing factor. Warm summers are the most often described as crucial factors for enhanced growth. Nonetheless, higher summer temperatures do not have to necessarily lead to proportionally wider ring widths, especially on south facing slopes which may suffer from drought as stressed by Bär et al. (2008).

Rayback et Henry (2005) also found a negative correlation between growth and Arctic Oscillation (AO) which brings summer cyclones to the Arctic accompanied with bellow average temperatures and above average precipitation to the influenced regions. They reported higher values of $\delta^{18}O$ in *Cassiopea tetragona* samples from western Canadian Arctic in years with enhanced AO causing worse growth of investigated plants. That indirectly corresponds to often reported findings that high summer temperatures favour shrub growth.

d) Autumn

Autumn as a post-vegetation period is not believed to have a strong relationship to shrub growth in any reviewed study.

e) Other non-seasonals effects

Sometimes it is believed that the previous growing season can have a stronger impact on current year's growth than the actual season (Fritts 1976). The later studies generally disagree with this idea by reporting a relatively strong correlation between current year's growth and temperatures (*e.g.* Buchwal et al. 2013). However, such conclusions do not have to necessarily be in contradiction with Fritts (1976) while it is not difficult to find a correlation between annual growth increments of two subsequent years due to relatively gradual climatic fluctuations. Recently, Weijers et al. (2010) observed the effect of previous year's September precipitation on *Casiope tetragona* growth explained by late-summer drought and snow protection against frost damage by the end of the month. Previous year effect should, however, be only considered as trigger if proper standardisation is applied and autocorrelation is removed.

Investigations of dwarf tundra shrubs represent relatively untapped source for climate reconstructions in the Arctic (Schmidt et al. 2006). As it is possible to *see* from Appendix 1. this archive conserves often different proxy information of past climate. Only if such variations and specifics are described and understood we can have a full profit from this vast resource.

We should therefore be aware of generalized conclusions. Climate related growth responses of every species at particular locality should be interpreted independently concerning local climate with consideration of site specifics both on micro and macro-spatial scale. There is also lack of studies working with other growth parameters than widths of growth rings (*e.g.* lumen areas, lumen perimeters, cell wall thicknesses). Recent progress in preparation of permanent micro-sections (Gärtner et Schweingruber 2013) enabled to take into consideration the cell sizes, cell wall thicknesses, vessel sizes, or cell or ray density. It can expose new directions of shrub research. In region where plant growth has to overcome that many obstacles such parameter can serve as a better climate proxy and provide more reliable information on paleoclimatic conditions.

Constraints of dwarf tundra chronology development

Büntgen et Schweingruber (2010) believe that dwarf shrub annual ring research with accompanied serial sectioning has a great potential in accurate dating of events using extremely slow growing individuals. They also believe that serial sectioning is able to overcome often mentioned constraints of dwarf shrub research (missing or wedging ring, lobes *etc.*). But they are aware of averaging radii of different stem heights from the same individuals due to rather different development.

Nevertheless many authors found strong correlation values between growth and climate in their studies even when "simply" averaging after removing age-related growth trends (*e.g.* Bär et al. 2006, 2007, Hallinger et al. 2010). To obtain higher levels of certainty and reliability Büntgen et Schweingruber (2010) suggest individual standardization of measurement radii from different stem heights before averaging measurements at the shrub level. Kolishchuk (1990) offers an alternative approach by averaging only three or four neighbouring sections from the top to the basal part of the trunk starting with the disc where a ring occurs at first.

We suggest to focus on other growth (cell) parameters which were documented to serve as climate proxies in trees such as cell radial diameter (Xu et al. 2013) or cell wall thickness (Yasue et al. 2000). Dealing with such parameters can help to overcome the problem of relying on one information only (ring width) which can be rather problematic in the Arctic/alpine climate zone. In contrary, averaging many individual cell parameters per annual ring can deliver more robust results. The obstacle of tapering of wood anatomical elements towards stem apex (for trees discussed *e.g.* in Carrer et al. 2015) can be overcome by appropriate designed detrending which is described in Lehejček et al. (in revision).

Micro-environmental conditions and growth response relationships

Soil moisture and nutrients

Soil moisture availability is by some authors not believed to be a limiting growth factor throughout the year even in the continental areas (Löffler 2005). It is assumed that the plants have adequate supply with melt water especially during the early growing season (Bär et al. 2007). In contrary, Schweingruber et Poschlod (2005) reported often discontinuous or even false rings occurring in plants from dry areas growing in shallow soils. They suggested to sample plants from the sites with intermediate soil moisture and poorer nutrient availability which enables the longest life span and does not present stress factor for shrubs, yet.

Site conditions are imprinted in the shrubs (*e.g.* occurrence of frost rings, earlywood/latewood portions) and growth rates (Pellizzari et al. 2014). Such site differences are often caused by resource partitioning (water, nutrients, or photosynthases) which can easily modify the plant's growth response according to environmental conditions (Rayback et Henry 2005). All variables should be therefore further documented to extend our knowledge about micro-climate and growth relationship in order to separate climate driven growth responses from locally disturbing factors as well as to find the longest living individuals.

In general, shrubs achieve the maximum age in the deteriorated climate conditions (Bär et al. 2006) close to their survival limits where their sensitivity to climate variations is also enhanced. It is important to stress that finding the oldest individual has no relevance if it is not possible to compile the chronology of its growth due to extremely narrow rings, too many missing rings, or other factors. Woodcock et Bradley (1994) reported increasing amount of missing ring with the shrub age. It implicates the need of collection of variously old samples from a range of micro-environment (Woodcock et Bradley 1994) in order to obtain long and precise chronology. Although several hundred years old individuals and consequent chronologies of dwarf shrubs are not rare (*e.g.* Hantemirov et al. 2000 or Ward 1982 for junipers) most of the species are do not live longer than one or two centuries at the most (Schweingruber et Poschlod 2005). Chronologies originating from such material therefor usually cover only tens of years or first century. Nonetheless, in the conditions of the Arctic with the scarcity of meteorological stations containing only limited and short records even such chronologies can help to understand past climate and/or other variables connected to climate change (*e.g.* glacier melt, period of snow cover *etc.*)

Conclusion

Research on dwarf tundra shrubs is immature and has to surmount many difficulties. Not only problems with anatomy of plants growing in the harsh environments but often also the correlation of master chronology with climate is weaker than the one from nearby tree chronologies (*e.g.* Zongshan et al. 2013). Such investigations can nevertheless extend usage of dendroecological studies into new climatic zones and therefore might help to understand future environmental changes, their drivers and impacts in the arctic and alpine ecosystems.

According to reviewed literature higher summer temperature are believed to be the most positively influencing the shrub growth. Ring width can be regarded as a variable integrating temperature conditions during the main growing season at particular localities. However, special cases where local setting can eliminate climate effect of growing season are reported. Therefore, deep knowledge of local environment is fundamental.

The longest life spans of tundra shrubs are usually achieved at sites with an intermediate level of soil moisture with rather limited nutrient supply, and at undisturbed sites (Schweingruber et Poschlod 2005). That is why detailed reconnaissance of the field is crucial to obtain the longest possible chronology. The field sampling should not concentrate only on the oldest plants since their growth becomes deteriorated with age but should aim on population age diversity to strengthen and make the climate signal more reliable over the whole chronology.

Despite many successes achieved with tundra shrub ring width investigations the further studies should focus also on other growth parameter (lumen areas, lumen perimeters, cell wall thicknesses *etc.*) to strengthen the climate/growth correlation.

In spite of outlined constrains, dwarf tundra shrubs present enormous and valuable archive not only for paleoclimatology but also for paleoecological reconstructions. Samples of dwarf tundra shrubs provide high-resolution year-to-year information on climate variation based on annual rings. Yet, such detailed record is not very long, reaching only first centuries and it is therefore crucial to involve in research other proxy archives giving longer but less precise records such as lake sediment or ice cores. This is nowadays one of the few ways how to extend our knowledge of remote regions paleoclimate as well as recent climate development.

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Author	Species	Locality	Altitude (m a.s.l.)	Mean monthly low and high temperature (°C)	Precipitation (mm / year)	Degree of continentality	Mean annual growth increment (mm / year)	Crucial season responsible for enhaced growth	Primary reason	Secondary reason
Zongshan et al. (2013)	*Rhododendr. przewalskii*	Western Sichuan, China	4050	-8 / 12.6	600 - 1000	oceanic	0.5	April, July	temperature	N/A
Bär et al. (2006, 2007, 2008)	*Empetrum hermaph.*	Central Norwegian Scandes	1000 - - 1600	N/A	300 - 400	moderate	0.07 – 0.11	June - August	temperature	heat sums
Hallinger et al. (2010)	*Juniperus nana*	Northern Swedish Scandes	770 - - 1100	-6 / 15	310	continental	0.11 – 0.32	summer	temperature	N/A
Weijers et al. (2010)	*Casiopea tetragona*	Longyearbyen, Svalbard	50	-15.3 / 5.9	271	continental	N/A	July; September	temperature	previous year precipitation
Blok et al. (2011)	*Salix pulchra*	NE Siberia	11	-33.9 / 10.6	210	continental	N/A	17th June - - 19th July	temperature	N/A
Schmidt et al. (2006)	*Salix arctica*	Zackenberg, NE Greenland	0-600	-22.4 / 3.7	180	very continental	0,12	early spring	snow cover extend	N/A
Zalatan et Gajewski (2006)	*Salix alaxensis*	Victoria Island, Canada	35	- 28.6 / 9.2	162	very continental	0.76	December - - March	precipitation	N/A
Woodcock et Bradley (1994)	*Salix arctica*	Northern Ellesmere Island	15	-33 / 3.5	154	very continental	0.08	N/A	N/A	N/A

Appendix 1.
Summary of the selected findings and observations hold on dwarf tundra shrubs. Mean monthly low and high temperatures indicate the mean temperature of the coldest and the warmest month, respectively.