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Arctic tundra dendrochronology

Ph.D. thesis

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„I hereby confirm that this Ph.D. thesis “Arctic tundra dendrochronology” was elaborated independently with the usage of quoted literature and based on consultations and recommendations of my supervisor.

I agree with publishing this Ph.D. thesis according to Czech law n. 111/1998 Sb. about the universities in its current valid wording. This agreement is independent from the result of defence.

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Authors signature

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Abstract

Historically unprecedented environmental change in the Arctic ecosystems is often given into the context of its past and possible future development. In the region where instrumental meteorological observations are scarce archives need to be investigated in order to address this issues. The comprehensive synthesis one of the archives – long-live circumpolar evergreen *Juniperus communis* L. shrub is presented here. 20 individuals from southwest Greenland were investigated at the cell anatomy level to understand the ecology of the species and unhide its potential for environmental and climate reconstructions. The findings are as follows:

i) Stop of exponential cross-sectional conduit-lumen widening with increasing age is in contrast with conduit-lumen nature of trees. This indicates that shrubs do not need to saturate their water and nutrient demands via traits of classical hydraulic conductivity law but rather developed different mechanisms. Extreme weather conditions result in prostrate growth form. However, different weather factors probably influence shrub growth differently: While snow and wind act mechanically (a), temperature influences the form of growth physiologically (b). a) So long as the young shrub stem has high resilience to bend back to an upright position after snow melt and so long as it can withstand the wind during the vegetation season it most likely grows upright and the conduit-lumens widen. b) Temperature, resp. freeze-thaw events are responsible for the shrub’s preference of safety (finite size of conduit-lumens) over hydraulic efficiency, thus not allowing for more primary growth. All of these (and other) factors are apparently working together and the transition of vertical to more horizontal growth is gradual. As a consequence, the conduit-lumen sizes may not have to be further increased (due to ecophysiological restrictions possibly also must not) because water is no longer transported against gravity.

ii) Observed age/growth trend has to be taken into consideration for further employment of the wood anatomical parameter in paleoenvironmental studies. That is, shrub cell parameters can only be used for this purposes if correctly detrended. This allows for more accurate as well as longer reconstructions because youth trend was often neglected in reconstructions based on shrub annual-rings.

iii) The south-western Greenland Ice-Sheet (GrIS) melt rates reconstruction is presented for the whole 20th century. This part of GrIS is considered as the most active. According to the presented reconstruction current GrIS melt rates are not uncommon for the last century being comparable to first decades of 20th century. This finding is particularly important contribution to the debate on Atlantic meridional overturning circulation (AMOC). Too high fresh water inputs into the Northern Atlantic from GrIS melting may slow down or even stop the AMOC which would result in more continental climate in Europe. Presented results indicate that this threshold lies higher than observed current melt rates of GrIS.

Fascinating *Juniperus comunnis* species has shown to be able to address many ecological as well as environmental open questions and due to its longevity and abundant distribution has a great potential to become an important player in the Arctic research.

Key words

Juniperus communis, cell parameters, environmental reconstructions, Greenland Ice Sheet melt rates, Atlantic meridional overturning circulation

Abstrakt

Historicky bezprecedentní environmentální změny arktických ekosystémů jsou často zasazovány do kontextu jejich vývoje – minulého, ale i očekávaného budoucího. V oblastech s nedostatečnými instrumentálními meteorologickými pozorováními je nutné studovat klimatické archivy, které jsou schopny zasadit probíhající environmentální změny do kontextu minulosti. Práce předkládá syntézu jednoho takového archivu – jalovce obecného (*Juniperus communis*) – dlouhověkého cirkumpolárního keře arktické tundry. Na úrovni anatomie buňky bylo prozkoumáno 20 keřů. Kromě ekologických nároků druhu se tím odkryl i jeho potenciál pro environmentální a klimatické rekonstrukce. Mezi klíčové výsledky patří následující:

i) Zastavení exponenciálního zvětšování plochy vodivého aparátu s věkem je v rozporu s přirozeným charakterem tohoto fenoménu u stromů. To naznačuje, že keře nepotřebují zajišťovat potřeby vody a živin klasickými cestami zákonů hydraulické konduktivity ale spíše pomocí jiných mechanismů. Extrémní podmínky tedy limitují výškový vzrůst rostlin, které kvůli nim mění převládající směr svého růstu z vertikálního na horizontální. Jednotlivé projevy počasí však na vzrůst působí pravděpodobně odlišně. Zatímco sníh a vítr ovlivňují růst kmene/větví mechanicky, pak teplota spíše fyziologicky. Až do věku, kdy je mladý keř schopen ustát silný vítr ve vzpřímené pozici a jeho kmínek/větve mají dostatečnou resilienci se po odtání sněhové pokrývky opět narovnat, roste vzhůru a plocha vodivého aparátu se zvětšuje. Současně s tím teplota, resp. cykly opakovaného mrznutí a rozmrzání, způsobuje konzervativní vývoj keře, který preferuje bezpečnost (limitní velikost plochy vodivého aparátu) před hydraulickou efektivitou, čímž se brání embólii, ale tím i dalšímu výškovému růstu. Všechny tyto (ale i další) faktory jsou zřejmě dohromady zodpovědné za postupný přechod od vertikálního ke kvazihorizontálnímu růstu. Od této chvíle již není potřeba (ani to není fyziologicky možné) dále zvětšovat plochu vodivého aparátu, jelikož voda přestává být transportována proti gravitaci.

ii) Tento věkový/růstový trend je nutné uvažovat při dalším využívání růstových parametrů v paleoenvironmentálních studiích. Buněčné parametry by tedy neměly být využívány k těmto účelům, pokud nejsou správně detrendovány. To umožní nejen přesnější ale i delší rekonstrukce, protože je možné využít celý život rostlin včetně často opomíjené juvenilní fáze.

iii) Předložena je i rekonstrukce tání jihozápadní části Grónského ledovcového štítu (GrIS) během 20. st. Tato oblast je považována v rámci celého GrIS za nejaktivnější. Dle naší rekonstrukce není míra současného tání GrIS v kontextu 20. st. neobvyklá, resp. je srovnatelná s prvními dekádami 20. st. Tento poznatek je významným přispěním do debaty o Atlantické meridionální zpětné cirkulaci (AMOC). A sice, příliš velký přítok sladké studené vody do severního Atlantiku v důsledku tání GrIS může zpomalit nebo dokonce zastavit AMOC, což by způsobilo prohloubení kontinentálního charakteru evropského klimatu. Naše výsledky tak ukazují, že tato hranice leží výše, než je současná míra tání GrIS.

Jalovec obecný je fascinující arktický keř, který prokázal schopnost zodpovědět množství ekologický a environmentálních otázek. Především díky své dlouhověkosti a četnosti má obrovský potenciál stát se významných účastníkem arktického výzkumu.

Klíčová slova

jalovec obecný, buněčné parametry, environmentální rekonstrukce, míra tání Grónského ledovcového štítu, Atlantická meridionální zpětná cirkulace

Content

1. Introduction

The Arctic is a rapidly changing environment with a scarcity of long instrumental meteorological and ecological observations (ACIA, 2005). To assess predicted climate change and its impact on vegetation, appropriate archives are needed to understand past dynamics (Bradley, 1999) and predict vegetation changes in the future (Miller and Smith, 2012). An increasing number of dendrochronological studies from the Arctic portray the past and present vegetation and climate development based on growth rings from woody plants (e.g. Schmidt et al., 2006; Buchwal et al., 2013; Weijers et al., 2013; Büntgen et al., 2015; Schweingruber et al., 2013; Myers-Smith et al., 2015a). Pilot studies have shown the potential of shrubs to reconstruct glacier summer mass balance and ocean currents (Buras et al., 2012; Beil et al., 2015). All of these studies however, have solely used annual ring-width or annual shoot lengths as the main proxy (see also Myers-Smith et al., 2015b).

1.1 Potential of wood anatomy

In more temperate regions, other wood anatomical parameters such as cross-sectional conduit-lumen area or cell wall thickness have been used as climate proxies (e.g. Yasue et al., 2000; Fonti et al., 2013; Liang et al., 2013; Xu et al., 2013). The anatomy of xylem cells preserves information linked to vascular plant allometry, carbon sequestration, and ecophysiological performance, which is not available from the traditional ring-width or physical wood-density proxy parameters (Carrer et al., 2015). To maintain plant production and survival under changing environmental conditions over time, opportune adjustments in the xylem are required to succeed (Fonti et al., 2013). Among the most important roles of plant xylem tissue is the delivery of water from roots to stomata (Zimmerman, 1983). As woody plants extend their height and/or length over time, the path length of water transport increases. At the same time the resistance as well as hydraulic conductivity raises with the fourth power of conduit-lumen diameter and linearly with conduit length as physically described by the Hagen-Poiseuille formula (West et al., 1999). To prevent water deficit or embolism, trees seem to have developed an effective mechanism of xylem conduits widening from the apex downwards (Enquist, 2002; Olson et al., 2014). This mechanism was illustrated on many species of angiosperms from the tropical to the temperate zone (Olson et al., 2014) and to some extent also on gymnosperm trees in the temperate and the sub-polar zone (Anfodillo et al., 2006; Pritzkow et al., 2014). A comprehensive synthesis on the biophysical and physiological mechanisms influencing the increasing trend of conduit-lumens size of trees during ontogeny by Carrer et al. (2015) even broadens this concept.

Nonetheless, ontogeny as well as stem hydraulics of shrubs could be different from trees due to their limited height, more branching stems, or often prostrate form, wherefore the xylem anatomy may reflect different traits of development in comparison to trees. Understanding ecophysiological processes of tundra shrub growth as well as circumstances of their xylem anatomy formation may provide key insights for dealing with shrub cell parameter series, not only conduit-lumen sizes. For instance, trend analyses of shrub wood anatomy may highlight the need for detrending to account for possible age/size trends (Olson et al., 2014), to obtain more reliable climate reconstructions.

Thanks to improved methods of preparing wood-anatomical microsections (Gärtner and Schweingruber, 2013) as well as advanced digital image-analysis systems (e.g. WinCell, Regent instruments WinRHIZO Pro 2011 or ROXAS by von Arx and Carrer (2014), time series of wood-anatomical parameters can be distilled from samples in a more reliable and quicker manner. However, time series of cell anatomical parameters of shrubs from cold environments have been rarely considered so far with respect to climate (e.g. Bär et al., 2008 in Norway; Lehejček et al., 2016). Cell anatomical parameter research of shrubs was also occasionally applied in Alpine (Gärtner-Roer et al., 2013) or Arctic (Predavec and Danell, 2001) environments to address specific geomorphological or ecological issues, respectively.

To the best knowledge, Arctic tundra shrub cell parameters series have not yet been investigated to test for their suitability as paleoclimatological proxies (with the exception of Lehejček et al., 2016), even though several studies from other regions have shown that cell anatomical parameters may add information on past environmental conditions when compared to tree-rings (e.g. Schweingruber and Poschlod, 2005; Bär et al., 2008; Fonti et al., 2013; Liang et al., 2013; Xu et al., 2013).

1.2 Climate reconstructions and melt of Greenland Ice-Sheet

The Greenland Ice-Sheet (GrIS) is considered one of the most sensitive tipping elements of global climate change (Lenton et al., 2008; Hanna et al., 2011; Lenaerts et al., 2015). On the one hand, a complete melt of GrIS would result in global sea-level rise up to 7.4 m (Hanna et al., 2008). On the other hand, substantial freshwater input into the North Atlantic caused by increased GrIS meltwater runoff in a warming climate substantially weakened the Atlantic Meridional Overturning Circulation (AMOC) in model simulations (Lenton et al. 2008; Weijers 2012; Lenaerts et al., 2015). A weaker AMOC has important consequences for global climate ranging from significantly decreased temperatures in the northern hemisphere to a southward shift of the intertropical convergence zone and related to this an increased variability of the El Niño Southern Oscillation (Ganopolski and Rahmstorf, 2001; Timmermann et al., 2007).

To estimate the probability of AMOC slow-down in the 21st century, several model simulations have been undertaken – however with differing results. While Driesschaert et al. (2007) concluded that a recent halt of

AMOC is less likely, Weijers et al. (2012) found AMOC reduced by 40 % after a freshwater input of 0.1 Sverdrup (Sv) into the North Atlantic, this resulting in a surface heat loss of 80 %. A recent study by Lenaerts et al. (2015) found the contribution of GrIS to AMOC reductions in the 21st century to be low when compared to the effects of ocean surface warming and Arctic sea-ice melting. However, these authors stated themselves, that their models had not implemented ocean eddies, which were found to be important on the study of Weijers et al. (2012) to adequately simulate AMOC slow-down. Concluding, despite the progress of respective models in the last decade, there still remains uncertainty on the likelihood of AMOC slowdown at recent GrIS-melt rates.

To obtain a better understanding of GrIS-AMOC interactions and a higher confidence in thresholds of GrIS-melt, analysis of past GrIS-melt data would be of help. Based on these data an important question could be answered, namely whether recent melt rates are unprecedented. Furthermore, a better understanding of GrIS-AMOC interactions and possible consequences for global climate could be derived. The longest instrumental measurement record of melt extent for the complete GrIS covering the period 1979-2007, was provided by Abdalati (2008). According to this data GrIS recently experienced highest melt-rates since 1979. However, climate station data from Greenland show that the years around 1980 were among the coolest in the 20th century and that the decades around 1930 were warmer than today (Chylek et al., 2006; Box et al., 2009). In this context the question arises, whether recent melt rates are unprecedented or may have been stronger in the 1930ies.

To overcome the lack of long-lasting GrIS mass balance records (including melt-water runoff), a couple of respective models have been generated from meteorological data (Hanna et al., 2008; Fettweis et al., 2008; Hanna et al., 2011; Frauenfeld et al., 2011; Box, 2012). Although these models indicate good agreement with measured data and among each other, they differ temporally and with respect to absolute values of reconstructed parameters (e.g. see comparison between Hanna et al., 2011 and Box, 2012 in the latter). For instance, the reconstruction of Frauenfeld et al. (2011) indicates that recent melt rates are not unprecedented, whereas reconstructions by Hanna et al. (2011) and Box (2012) suggest recent melt to be unprecedented. Despite the high value of these reconstructions, uncertainty with respect to past GrIS-melt, possible effects on AMOC, and thresholds of freshwater input remains.

A major problem of the aforementioned reconstructions is their reliance on a rather sparse network of climate station data (or reanalysis data having similar problems), in particular for the early 20th century. Therefore, it is desirable to obtain additional, independent estimates of past GrIS-melt, in particular in regions where climate station data is lacking. Here tree-ring parameter of shrubs may serve as suitable proxies. Several studies from the Arctic and Alpine have reported significant correlations between shrub growth and summer temperatures (e.g. Blok et al., 2011; Buras et al., 2012; Lehejček et al., 2016; Myers-Smith et al., 2015a; Weijers et al., 2010, 2012) which are most important for GrIS-melt (Box et al., 2009). In 2012, Buras et al. reported the possibility to use shrubs for the reconstruction of glacier summer mass balance. Finally, shrubs are widely distributed around Greenland (Fredskild, 1996) wherefore they theoretically could be used to establish a dense network of GrIS-melt reconstructions.

The first GrIS-melt reconstruction based on growth parameters derived from shrubs growing in Kobbefjord, Southwest Greenland is presented here. The obtained reconstruction is compared against temperature based reconstructions to assess the potential of including shrubs in GrIS-melt reconstructions while it is also assessed its (un)precedent character.

2. Aims of the thesis

Growth of tundra shrubs is dynamic system with various controls. In particular, growth of cell parameters is relatively untapped source of information and therefore deep inspection is needed. Wood anatomical parameters (ring width, lumen area, cell wall thickness, lumen perimeter, lumen length and width, cell length, and the lumen length/width ratio) of evergreen Arctic shrub *Juniperus communis* L. will be therefore tested for exhibition of a particular age trend and also further inspected for its climate reconstruction potential. Many individuals of this persistent species were established well before the first continuous Arctic meteorological observations (not reliable before 1850; Brohan et al., 2006; Allan and Ansell, 2006) which makes this species attractive for paleoclimate reconstructions.

Aims of the thesis are thus as follows:

i) Detection for the particular age trend of arctic tundra shrub wood anatomical parameters which can be used for correct detrending;

ii) Suggestion of the potentially best growth parameters for climate/environmental reconstruction;

iii) Climate/environmental reconstruction itself.

Relevant parts of this thesis consist of published and submitted manuscripts of Jiří Lehejček. If not apparent than highlighted in footnotes throughout the body of this work. Mentioned papers and manuscripts are as follows.

1) **Lehejček, J.** (2015): Dwarf tundra shrubs growth as a proxy for late Holocene climate change. Czech Polar Reports 5 (2): 185-199.

2) **Lehejček, J.**, Buras, A., Svoboda, M., Wilmking, M. (2016): Wood-anatomy of *Juniperus communis*: a promising proxy for paleoclimate reconstructions in the Arctic. Polar Biology. First online: DOI: 10.1007/s00300-016-2021-z

3) Buras, A., **Lehejček, J.**, Michalová, Z., Morrissey, R., Svoboda, M., Wilmking, M. (submitted_a): Shrubs shed light on 20th century Greenland Ice Sheet melting. Geophysical Research Letters.

Since this thesis largely depends on the above mentioned publications and manuscript, I find appropriate to give the authorship statement.

The first “review paper” has only one author and is therefore solely processed by Jiří Lehejček.

The second “wood anatomy paper” has four co-authors. The research design, field sampling, laboratory treatment, software measurements, as well as all treatments leading to master chronologies were done by Jiří Lehejček. Statistical analyses were co-authored by Jiří Lehejček and Allan Buras. Jiří Lehejček also wrote the manuscript. Allan Buras, Miroslav Svoboda, and Martin Wilmking were present at discussions on the scope and content of the manuscript. In the latter phases they helped to shape the text, clarified some possibly confusing parts, eased the flow of the text, and gave useful hints on the structure.

The third “GrIS reconstruction manuscript” has six co-authors. The research design, field sampling, laboratory treatment, and software measurements were done by Jiří Lehejček. Statistical analyses were co-authored by Allan Buras, Zuzana Michalová, and Jiří Lehejček. The manuscript was developed by Allan Buras and Jiří Lehejček. Robert Morrisey, Miroslav Svoboda, and Martin Wilmking were present at discussions on the scope and content of the manuscript. In the latter phases they helped to shape the text, clarified some possibly confusing parts, eased the flow of the text, and gave useful hints on the structure.

3. Literature review

3.1 Arctic shrubs investigations and their potential

Since tundra shrubs occur mainly in remote and uninhabited areas (such as the Arctic or high mountains) where our understanding of climate is biased due to scarcity of direct observation (e.g. Atkinson and Gajewski, 2002; Rayback and Henry, 2005; Bär et al., 2006) the knowledge gained from high-resolution archives can extend our understating of the climate in recent centuries (Woodcock and Bradley, 1994). The presence of annual rings in tundra 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 non-tree 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 and Bradley, 1994). Tundra shrub potential to learn more about impact of environmental/climate change started to be discussed by some authors (e.g. Büntgen and Schweingruber, 2010; Hallinger et al., 2010) some years ago. However, studies of tundra shrubs from a dendroclimatic point of view have received increasing attention only recently (Schmidt et al., 2006; Buchwal et al., 2014; Myers-Smith et al., 2015a; Lehejček et al., 2016).

Tundra shrubs are extremely tempting source of proxy information for their longevity and annual resolution. It makes those life forms convenient for paleoecological reconstructions especially in the Arctic and alpine environments where they can fill observational gaps (ACIA, 2005).

The investigation of 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 shrub's 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 literature review is to present comprehensive information on field, laboratory, and analytical techniques of tundra shrub research for paleoecological, especially paleoclimatological purposes. Second part of this review deals with the influence of climate and site characteristics on time span of plant's growth. The main climate drivers of tundra shrub growth are presented.

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

3.2 Field and laboratory techniques

3.2.1 Sampling

Sampling design is subordinated to research question which is challenged. However, general recommendations should be followed according to literature review.

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 and 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 and Schweingruber (2010). They also believe that a broader spatial scale of collected data help to overcome local mentioned 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.

Potential problem of shrub research is *on site* identification of old individuals for collection to extend the chronology. Life span of tundra shrubs is species-specific but in general they live between ten to two hundred years maximally (for details see Schweingruber and Poschlod, 2005). *Juniperus communis* species do not fall into this span. It can live several centuries. Recently, the individual of *Juniperus communis* having almost 700 annual rings and was collected in the northern coast of Kola peninsula (Lehejček, unpublished work). Shiyatov (oral communication in Schweingruber at Poschlod, 2005) found an individual with 840 rings in the Polar Ural. The extremely short growing season, low temperatures, and often also mineral nutrient stress in the arctic/alpine region result in extending individual life span (Ward, 1982; Körner, 2003).

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). Smaller sized species are recommended to harvest the full plant body including braches, stem, and roots. Before removing the whole plant from the soil it is appropriate to record position of the soil surface by tape (Bär et al., 2006), slope aspect, and GPS position. For plants larger than ca 20 cm it is suggested to sample only stem discs – tap root plus other along the stem if needed. 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/discs 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 and 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/sub-fossil material to extend the length of chronology (e.g. Zalatan and Gajewski, 2006; Hallinger et al., 2010; Blok et al., 2011). Kolishchuk (1990) resp. Schweingruber (personal communication) believes that not less than 10 (resp. 20) 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. This is unfortunately usually not always the case in the Arctic.

Concerning the issue of sample transportation Schweingruber and Poschlod (2005) suggest plastic zip-lock bags containing directly labelled compartments while providing detailed records on site and plant characteristics. This record should document above mentioned variables including other micro-/environmental characteristics (such as vegetation structure, inclination, altitude, occurrence of periglacial processes, or data on micro-climate; Bär et al., 2006). Since freshly harvested shrub compartment still contain water it is recommended to air dry them before packing. In case of insufficient time for drying a few drops of alcohol and raw dry rice can help to prevent mould. If alcohol is used an operator should prevent to label the bags with alcohol-based marker but rather use paper stickers and pencil. An alternative approach is to use paper bags which prevent the material from mould and fungi contamination (Hallinger, personal communication). Disadvantage of paper bags is that they often tear in pieces during logistics especially if they get wet from the moist plant material.

3.2.2 Dendrochronology – lab work

Wedging rings, missing rings or piths, frost rings, asymmetric growth including lobes or “just” extremely narrow rings (Fig. 1) are the results of the harsh environment which shrubs inhabit often also accompanied with one-sided (mechanical) stress or local death of cambium (e.g. Kolishchuk, 1990; Woodcook and Bradley, 1994; Schweingruber, 200;, Bär et al., 2006, 2007, 2008; Zalatan and Gajewski, 2006; Hallinger et al., 2010). Due to this difficulties the analysis of annual rings must undergo often more complicated procedure in comparison with regular tree ring research.

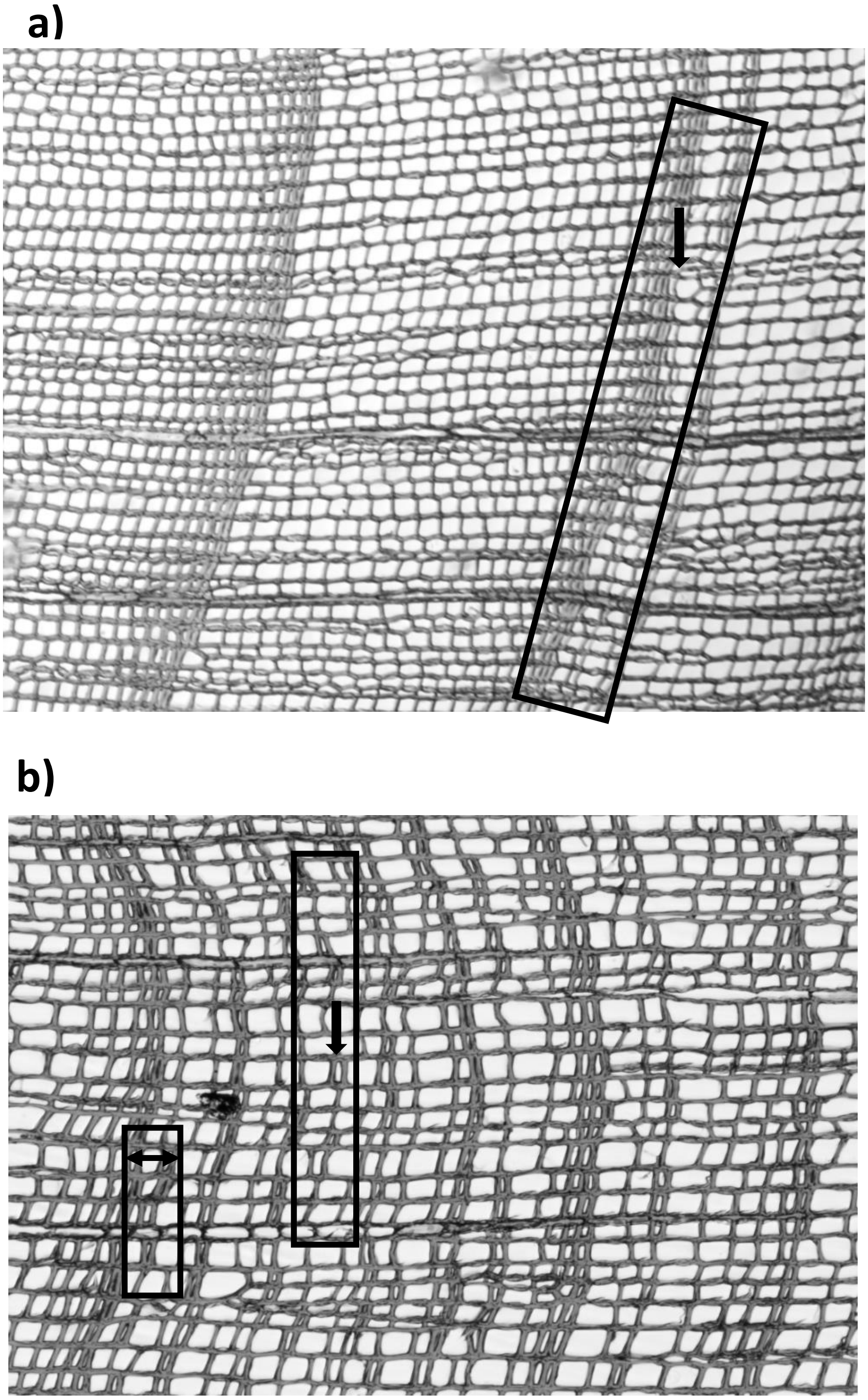

Fig. 1 Problematic areas within the microscopic thinsections (*Juniperus communis*, 100x magnification). a) wedging ring with arrow indicating the point of miss. b) extremely narrow ring consisted of two cell rows only; and ring which can be easily overlook and considered as missing because only few and sporadic latewood cells were formed.

Additional steps of analysis are sometimes 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 and Dietz, 2001). In case of relatively routine cross-dating the serial sectioning method is not required. In opposite case, between 2 and 10 thin sections equally distributed over the plant's body needs to be commonly obtained. The number depends on the degree of expected cross-dating constraints (Woodcock and Bradley, 1994).

Thinsections are made by sledge microtome knife and they are usually 10-30 µm thick (Schweingruber and Poschlod, 2005; Bär et al., 2006). Gärtner and Schweingruber (2013) suggest sticking the samples in glycerol to prevent curling and 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. Subsequently, the section is cleaned and dehydrated by increasing ethanol concentrations. Xylene is recommended for detection of remaining water (Gäertner and Schweingruber, 2013). Thin-section is afterwards conserved into resin (e.g. Canada Balsam) and permanent sample is created and micro-photographed. Such precise and high quality images can be further used for growth analyses using appropriate software (e.g. WinCell or Roxas).

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

An improvements of microsectioning

Although, these new techniques mentioned above generate perfect microsections there is still space for improvement in time efficiency and safety. Perfect microsection is important for any further wood anatomical investigations. However, less-skilled operator can get discouraged if his/her sections do not show the desirable quality quickly and may feel dizzy from exposition to xylene. To the best knowledge, the main obstacle in obtaining high quality microsections is symbolized by incorrect use of sledge microtome. Most of the problems were targeted in Gärtner and Schweingruber (2013). But even if the operator processes the microsections accordingly, tearing or decay can occur, in particular if aiming for a very thin sample. During the time I spent in laboratory I met few improvements of microsectioning which both safe time and health of the operator but are unfortunately not published yet. Here, I present two improvements which can make the operator's daily microsectioning routine faster and less hazardous.

i) Using non-break-off disposable blades

The cheap and easy-to-handle alternative to standard microtome knives are disposable "paper" break-off blades (Gärtner and Schweingruber, 2013). They present a step forward in microtome sectioning for most wood anatomical purposes – in terms of price and effectivity. Nonetheless, when cutting, the operator can decrease the quality of the sample following the lines of blade grooves even if using new, sharp blades by oblique orientation (Schneider and Gärtner, 2013; Fig. 2). In addition, the piece of treated sample suffers a loss of smooth surface which results in extra work for the operator before the piece is ready. In case the sample for microsectioning is not large enough this repeated failure of not getting the demanded quality can lead to the complete loss of the studied material and can be time consuming. Alternatively, the microsection of uneven thickness can also be the result of using blades with grooves.

Such imperfect outcomes can cause difficulties during further lab and/or image operations. First due to the narrowness of the strip microsection susceptible to twisting. This can lead to damage to the cell structure when folding back into the right position. Also the risk for the lack of space suitable for taking microphotograph in the grooved-broken or later damaged parts increases (in particular radial and tangential sections are prone because such artifact affects the information in the whole length of the section if cut parallel with tracheids or fibers). Another being the uneven thickness. Thus the outcome could possibly affect the automated measurements of cell parameters because in thicker parts of the section the shade of the cell walls artificially decreases the size of lumen areas.

An easy solution which addresses these issues presents non-break-off disposable blade with seamless surface (Fig. 2). These new kind of knives keep all the advantages of “paper” blades (e.g., price, no need to sharpen) as well as some benefits of traditional microtome knives (coherency of cutting edge). Moreover, the operator saves time as well as material thanks to less sections cut (Fig. 3).

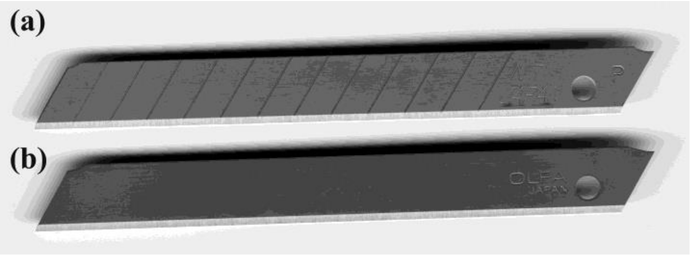

Fig. 2 Two types of disposable microtome knives (a) with grooves and (b) with seamless surface.

Fig. 3 Microsections of *Juniperus comunnis* L. (a) processed by disposable microtome knives with grooves and (b) with seamless surface.

ii) Substitution of toxic xylene (published with kind permission of Mgr. Jan Tumajer – the founder of substituents)

Xylene (dimethylbenzen) is an important aromatic hydrocarbon commonly used in the process of making permanent stained samples of both animal and plant material as a clearing or deparaffinizing agent (Premalatha et al., 2013). Its high solvency factor ensures maximum alcohol and water displacement from tissue resulting in great color stability of the sample over time. However, the over-exposition of laboratory operators to xylene evaporates can possibly lead to serious health problems (Kandyala et al., 2010). After inhalation of xylene evaporates, it is metabolised in the liver to methylhippuric acid, which is almost completely excreted into the urine during the next 24 hours (Jacobson and McLean, 2003). However, many types of health problems resulting from high xylene inhalation have been reported (e.g., depression of central nervous system; irritation of lungs, liver and kidney; gastric discomfort or vomiting) or speculated (e.g., cancer; fetus interference and contamination of breast milk; for details see the review of Kandyala et al., 2010). It also has negative environmental consequences (ATSDR, 2007).

Due to the above mentioned reasons, huge efforts were focused on introducing a xylene substitute. This brought the alternative to the process of tissue staining and stabilizing, without the negative health influences. These substitutes can be classified into 4 categories based on their chemical structure (Buesa and Peshkov, 2009; Kandyala et al., 2010). Limonene reagents are terpene extracts mainly made from orange oils by distillation of orange peel. Although they record low levels of toxicity and have a small environmental footprint, the agents have a strong odor (Miller et al., 1994), are expensive (Buesa and Peshkov, 2009), and do not perform properly with various mounting media (Kandyala et al., 2010). Aromatic hydrocarbon mixtures are not very popular, because their toxicity is almost the same as xylene. The opposite is true for alliphatic hydrocarbon mixtures lacking the aromatic cycle, which represents a very large and variable group of commonly used xylene substitutes. They are usually more expensive than xylene, but still cheaper than limonene, and odorless. Some are flammable, however there is still a huge group of alliphatic hydrocarbon mixtures with lower flammability (Kandyala et al., 2010). The last group of xylene substitutes is composed of mineral oil mixtures, which are very promising for the future. Some studies have proposed different mixtures of oils as “the best” xylene substitute for different kinds of tissue processing (Buesa and Peshkov, 2009).

An important reason for applying xylene at the end of staining procedure is to make colours of the permanent sample stable overtime (Premalatha et al., 2013). Some xylene substitutes in combination with the use of specific mounting media were criticized because of the lack of such stability, fading the colours of the tissue only few months after mounting. Some studies have focused on the comparison of color quality of histological samples processed using xylene and its substitutions, however, these were usually evaluated immediately or shortly after staining (Gubash and Milburn, 1990; Chen et al., 2010). However, xylene processed samples have recorded stable colours for centuries (Bubner, 2008), thus it is not possible to make the correct comparison of colour stability now. This uncertainty can nonetheless be overcome by detailed high-resolution microphotographs taken shortly after laboratory treatments.

We had a positive experience with isoparaffin-based DiaSolv which we used for the first time 1.5 years ago and have not seen any discoloration. It is a mixture of alliphatic hydrocarbons and their isomers (Alkene-C11-15-Iso). If used as a clearing agent, Canada balsam with refraction index similar to glass can be subsequently applied as a mounting media (Gärtner and Schweingruber, 2013).

Concluding; the ability to prepare microscopic samples of appropriate quality in a reasonable amount of time and cost is crucial for analysis of anatomical variations in wood. This process was greatly improved during the last decade by the invention of new types of microtomes (Gärtner et al., 2014). However, there are still some parts of the sample preparation routine which can be done more effectively. The use of knives without grooves is a small improvement without any extra cost. In contrary, the application of the xylene substitute has to be considered after examining the advantages and disadvantages of possible agents – especially demands on samples long-term stability certainty.

3.3 Cross-dating, detrending, and climate relationship

3.3.1 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 and Gajewski, 2006; Hallinger et al., 2010). Kolishchuk (1990) recommends measuring the ring widths from the periphery to the centre since the year of the harvest is usually well known.

Visual cross-dating precedes verifying by widely used computer programme COFECHA (Holmes et al., 1986). The following operations in laboratories known as serial sectioning (Kolishchuk, 1990) are focused on obtaining the complete record in case cross-dating procedure fails. Serial sectioning is applied especially on the species growing in the High Arctic environment where the growing season is short and the probability of missing rings increases. It combines findings about annual increments in different directions within the incision (1st order), in different parts of shrub (2nd order), as well as between individuals (3rd 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; Fig. 4). 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 and 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) state some interesting findings: 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 at the stem (more favourable climatic conditions) and therefore in some years cambium in the basal part of the stem is not activated at all (Kolishchuk, 1990). Such kind of statements cannot nevertheless be generalized for all tundra shrub species. For instance, Schweingruber et al. (2013) consider the longest axis of the tap root disc as the most reliable for subsequent measurements.

The value of the whole material for paleoclimatological reconstruction is dependent upon successfully cross-dating the samples (Woodcock and Bradley, 1994).

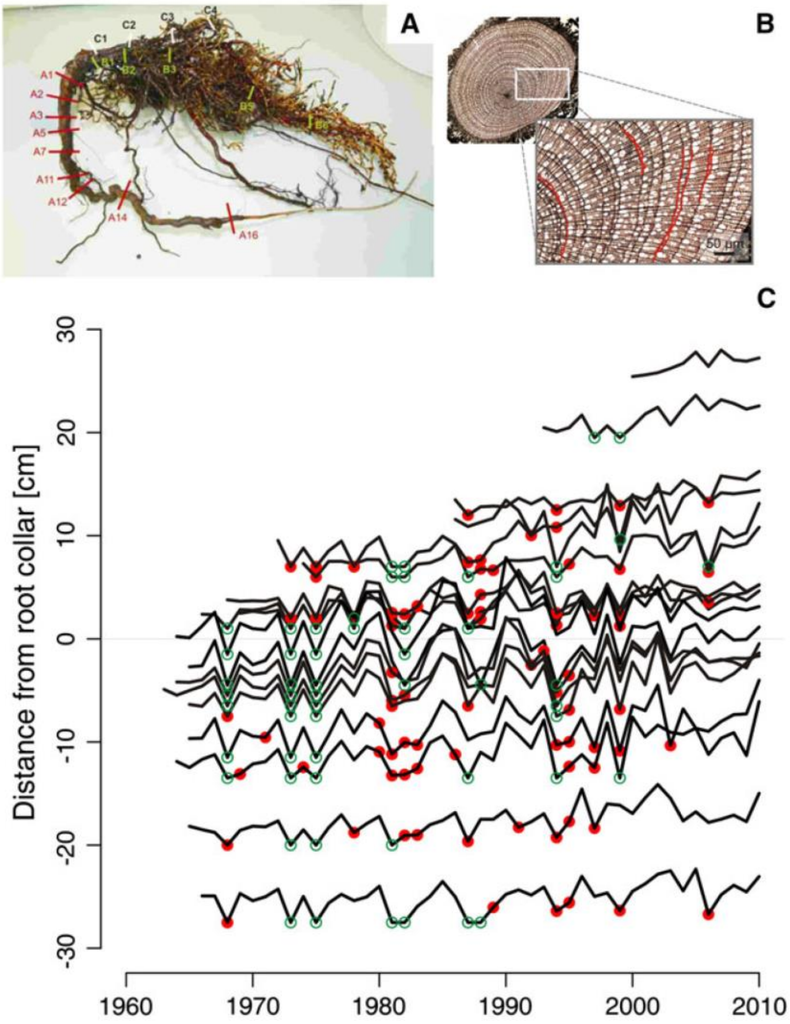

Fig. 4 Example of serial sectioning performed on *Salix polaris*:

A) - position of the sections selected for the tree ring analysis (red lines);

B) – an example of the thin sections used for tree ring measurement;

C) – the summary of cross-dated ring width measurement of a single shrub.

Adopted from Buchwal et al. (2013).

3.3.2 Detrending

Variation in the width of annual growth increments is not only caused by climatic factors but also by trends which can disturb the climatic fluctuations (e.g. uneven growth over the plant's lifetime or disturbances; Fritts, 1976). Detrending 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 al., 1990).

Such trends are generally removed by dividing the individual tree ring series by functional estimates of these trends (Weijers et al., 2010). For detrending the programmes "ARSTAN" or "R" are used most commonly (Cook, 1985; Rayback and Henry, 2005; Zalatan and Gajewski, 2006). Büntgen and Schweingruber (2010) warn of averaging measurements series from different stem sections without detrending 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).

Various detrending methods are used according to the decision of the processor. It is usually done by mean curves using a 32 year smoothing spline (Blok et al., 2011) or linear regression lines (Zalatan and Gajewski, 2006; Zongshan et al., 2013), and negative exponential curves (Blok et al., 2011; Zongshan et al., 2013) to remove intra-plant variation and 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.

It is believed that 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 which is often the case in the Arctic. 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 tundra 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 and Gajewski, 2006).

It is important to mention that so far, standard detrending methods for trees have been used for shrub chronologies as well although it has never been checked if shrubs reflect the same growth pattern as trees.

After cross-dating, standardization and creating master chronology of each particular disc 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. This applies if serial sectioning method is necessary.

3.3.3 The climate and growth relationship

There is lack of information what temperatures present the limit for cambial activity of tundra shrubs. Some studies have focused on critical temperature for cell division of conifers in cold climates (e.g. Rossi et al., 2008 or Treml et al., 2015). The authors concluded that average limiting values are around 4 - 5°C for the daily minimum temperature at 2 m height and in the soil, respectively. Körner and 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 detailed study for tundra woody life forms, however, remains for further investigations.

It is widely accepted (e.g. Fritts, 1976, Woodcock and 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 and quality. 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 tundra shrubs is not simple since this is influenced by factors like micro-climate, species (diffuse vs. ring porous), disturbances or habitats. Commonly, the correlation coefficients are lower than in similar studies using tree material. Nevertheless, significant, 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 *Rhododendr. 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 and Gajewski (2006) for *Salix alaxensis* and December, March precipitation ($r = 0,3, P < 0.05$).

3.4 Seasonal macro-climate and growth response relationship

i) 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 and 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 Table 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; Table 1).

ii) 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 (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.

iii) Summer

Many authors (e.g. Rayback and 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 and 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.

iv) Autumn

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

v) Other non-seasonal 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 tundra shrubs represent relatively untapped source for climate reconstructions in the Arctic (Schmidt et al., 2006). As it is possible to see from Table 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.

One 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 and 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 parameters can serve as a better climate proxy and provide more reliable information on paleoclimatic conditions.

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

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 recipitation
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

3.5 Constraints of tundra shrub chronology development

Büntgen and Schweingruber (2010) believe that tundra shrub annual ring research 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 tundra shrub research if they occur (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 and 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.

Suggestion may be the 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. (2016).

3.6 Micro-environmental conditions and growth response relationships

i) 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 and 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 their growth rates (Pellizzari et al., 2014). 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 and Henry, 2005). All variables should be therefore further documented to extend the 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 and 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 and Bradley, 1994) in order to obtain long and precise chronology. Although several hundred years old individuals and consequent chronologies of tundra shrubs are not rare (e.g. Hantemirov et al., 2000 or Ward, 1982) most of the species do not live longer than one or two centuries at the most (Schweingruber and 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.)

3.7 Summary of literature review

Research of tundra shrubs is still 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 the 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 and Poschlod, 2005). That is why, the 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, tundra shrubs present enormous and valuable archive not only for paleoclimatology but also for paleoenvironmental reconstructions in general. Samples of 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 ways how to extend our knowledge of remote regions paleoclimate as well as recent climate development.

4. Methods

4.1 Study site

Field work was conducted in the Kobbefjord bay (64°10´N; 51°19´E) in southwestern Greenland in August 2013 (Fig. 5).

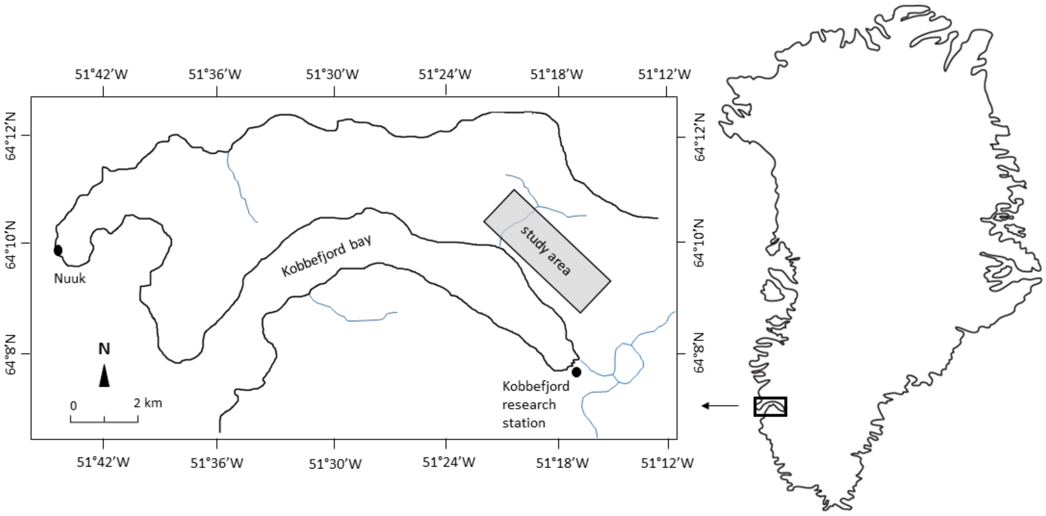

Fig. 5 Location of the sample collection in the northern part of Kobbefjord bay, Greenland.

The area is characterised by one of the oldest rock formations on the planet from the Archean eon; it consists mainly of supracrustal rocks (amphibolites and gneissic metasediments), orthogneisses in amphibolite facies, gneisses, post-tectonic granite complexes, and post-tectonic intermediate and mafic intrusions (Escher and Pulvertaft, 1995). Litosols, followed by cambisols are the prevailing soil type in the fjord (Polická, 2014). This Low Arctic region is influenced by the Northern Atlantic Ocean Current which reaches the 66° N latitude. The vicinity of the ocean provides a relatively mild climate, with a mean annual precipitation of 777 mm, mean annual temperature of -1.3 °C, and mean summer (JJA) temperature of 5.8

°C (Nuuk 4250 meteorological station; period 1981 – 2010; Cappelen, 2013).

4.2 Field sampling

For the purposes of annual ring investigation 38 living and 3 sub-fossil individuals were collected in August 2013. All samples were taken from relatively dry microsites on the northern side of the fjord with a similar aspect (SW to SE) and elevation range (between 20 and 150 m a.s.l.) on slopes with inclination between 15 - 30º. Individuals were randomly selected from a systematic grid to capture the full variety of plant ages and various sizes. Taproot discs at the soil surface were taken from each plant to maximize the number of rings. Extreme site conditions caused prostrate life forms resulting in accelerated growth at lower portions of the stem and reduced growth in upper portions of the stem, or even eccentric pith positions (Schweingruber et al., 2013) - a typically observed feature for *J. communis* (Buras and Wilmking, 2014).

4.3 Laboratory treatment

Stem discs were first cut following the longest axis to obtain cross-sections because it is the least likely to contain missing or wedging rings as a result of abnormal growth, thus, it is the most reliable for subsequent measurements (Schweingruber et al., 2013). Afterwards, the cross-sections were hand-sawed perpendicularly to tracheids, and corn starch was used to stabilize the cell walls before final cutting of the sample to prevent distortion of cellular structure (Schneider and Gärtner, 2013). From each cross-section 15 – 20 micrometers thick thinsections were obtained using a sliding lab-microtome. Sodium hypochlorite was used as bleaching agent, prior to cleaning the thinsections with water, and double-staining for 5 minutes in a 1:1 solution of Safranin and Astrablue (solution used according to

Schweingruber et al., 2013), and then washed again. Increasing ethanol concentrations were used (70%, 90%, and 98%, respectively) to dehydrate samples, Xylene was used to detect any remaining water in the samples. Finally, the samples were preserved by Canada balsam, embedded by cover glass (Schweingruber et al., 2007) and dried for at least 12 hours at 60 °C in the oven.

Images of microsections were taken using a digital camera (Canon EOS 650D) connected to a microscope (Olympus BX41) under x100 magnification, and photos were analysed using WinCell Pro 2011 software (Regent Instruments WinRHIZO Pro, 2011). Mean ring-width was measured along the longest axis of all individuals by manual path analysis using WinCell software. Due to quality of wood (e.g. rotten, twisted, reaction etc.) we were able to select only 18[a], resp. 19[b] living and 2 sub-fossil samples from above mentioned material for further cell anatomical investigations[1].

4.4 Data analysis

Mean annual increments were standardized in the software ‘R’ (R Core Team, 2015). After successful cross-dating in PAST4 software (Knibbe, 2007) the samples were visually inspected to detect possible missing rings (Schweingruber et al., 1990). Only 10 missing rings were inserted into the whole dataset of 41 samples. Those samples which also entered the cell anatomical measurements were subject of 6 missing rings insertion only (i.e. 0,24 %). After subsequent establishment of the ring width site chronology, we measured other growth parameters, including conduit-lumen area, cell wall thickness, conduit-lumen perimeter, conduit-lumen length and width, cell length, and the conduit-lumen length/width ratio, for each annual ring using WinCell areal measurements. For the detailed

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[1] Specific paragraphs of the thesis need double approach because the data were used for different purposes/publications. Therefore, if paragraphs are marked as ([a]) or ([b]), respectively, then ([a]) refers to Lehejček et al. (2016) and ([b]) refers to Buras, Lehejček et al. (submitted_a).

description of above mentioned growth parameters I refer to the WinCell manual (Regent Instruments WinRHIZO Pro, 2011) or visually to Fig. 6 bellow. In total 871,382 cells were analyzed. Cell parameters were measured for each year. Due to the low number of latewood tangential tracheid rows (typically 2-3 rows), and the limited sizes of their conduit-lumens early- and latewood was not analysed separately to obtain statistically more representative averages of wood anatomy parameters. Low numbers of latewood tangential tracheid rows were treated similarly in Seo et al. (2012). Cell parameters from each annual ring were then averaged per individual and used for further statistical analyses. All sample operations and measurements were done by the author of the thesis to keep potential subjective errors constant.

Climate data [a]

Climate data of mean monthly temperature and total monthly precipitation station data from Nuuk were downloaded from the Danish Meteorological institute (DMI; http://research.dmi.dk/data/) for the period 1890-2014. As temperature and precipitation alone may not be able to explain shrub growth variability sufficiently, the analyses of a drought index – the standardized precipitation evapotranspiration index (SPEI, Vicente-Serrano, 2010) were also included. SPEI was obtained by standardizing the balance between precipitation (i.e. water input) and potential evapotranspiration (PET, water output). PET was calculated from monthly average temperature and geographical latitude according to Thornthwaite (1948). While positive SPEI values reflect above average water supply, negative SPEI values will indicated dry conditions. To represent average conditions of the growing season climate parameters were integrated over June-July and June-July-August, respectively.

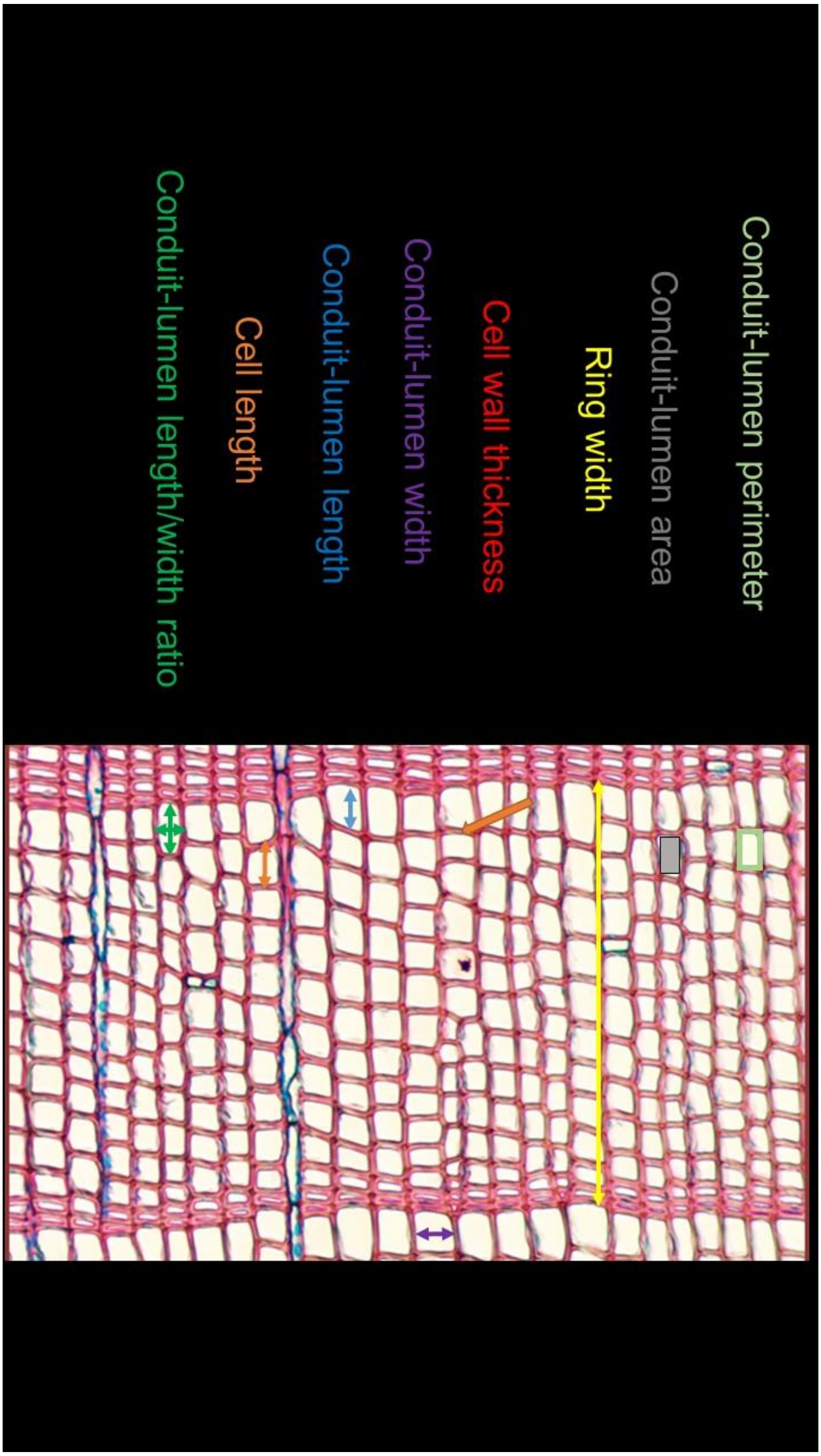


Fig. 6 Wood anatomical parameters of *Juniperus communis.*

Climate data and GrIS data [b]

Temperature data for the period 1901-2014 were extracted from CRU TS v 3.23 (Harris et al., 2013) for the grid cell closest to the shrub sampling site, i.e. 64.25° N and 51.25° E. Monthly temperatures were aggregated over different periods representative of summer temperatures. As for shrub proxies, pre-whitened summer temperature variables were also computed. In the results the focus is on temperatures averaged from June through September as they expressed highest correlations.

Annual GrIS-melt extent derived from passive microwave satellite brightness at a resolution of 25 km for the period 1979-2007 was obtained from the National Snow and Ice Data Center (Abdalati, 2008). For later comparison of the obtained GrIS-melt reconstructions with an existing one, GrIS annual runoff estimates from Hanna et al. (2008) were further extracted. Due to differing units, both data were z-transformed prior to analyses, leading to the variables annual melt anomalies (Abdalati, 2008) and annual runoff anomalies (Hanna et al., 2008). To keep the relationship among grid cells in the spatial data, the z-transformation was based on the overall average melt extent and the corresponding standard deviation. As for the proxy data described above, a pre-whitened annual melt anomaly time-series was computed.

Statistical analyses [a]

To explore whether cell parameters express trends related to cambial age (as e.g. observed for conduit-lumen area in trees, Carrer et al., 2015), each cell parameter time series were aligned according to its cambial age (i.e. each series begins at time 0) and then plotted those aligned series against cambial age. As juvenile trends were recognized in particular within the first 50 years of cambial age, the cell parameter data were detrended prior to subsequent analyses. For the detrending, the master chronology of the aligned time series was calculated using a biweight robust mean to express the overall average trend of the time series (basically a regional curve as used in the RCS method; Esper et al., 2003). Detrending was performed by fitting a polynomial function (aka ‘Spline’) to the respective master chronology of aligned cell parameter time series. For each single cell parameter time series the residuals to this average spline trend were used as detrended variables. By this, the majority of trends related to cambial age for each of the series was removed. Finally, the cambial age aligned and detrended time series were dated to their original time of harvest (i.e. series terminating in 2013 or sooner for sub-fossils). In a similar way ring-widths were detrended, i.e. using regional curve standardization (RCS). From the detrended cell parameter time series the respective master-chronologies were calculated using biweight robust-mean to reduce the influence of possible single outlier values in each year. For climate correlation purposes both standard chronology as well as the pre-whitened (i.e. removal of auto-correlation) residual chronologies were computed. Pre-whitening is important to assess high-frequency, i.e. year-to-year correlations between proxies and climate. The standard chronologies were analysed for redundant information based on the loadings of a principal component analysis (PCA). If a PCA explains most of the variance of multivariate data along the first two axes, similar loadings on those axes will indicate strong correlations among the corresponding variables (e.g. Leyer and Wesche, 2007). Exploring multivariate data for redundant information allows for reducing datasets to a minimum set of variables with differing information. This was done to simplify the overview on the examined parameters.

To quantify the representativeness of master chronologies with respect to individual growth variations, the average running correlations and Gleichläufigkeit (coefficient of coincidence abbreviated as glk, as described in Buras and Wilmking, 2015) were calculated of each shrub specimen and parameter with the respective master chronology. That is, for each individual parameter time-series, its temporary correlation and glk over 31 years with the master chronology were computed and the resulting 20 temporary correlations and glk values were averaged for the respective time-window. This procedure allows for quantifying how well each specimen on average is represented by the master chronology. This approach is used as shrubs frequently share low common variance among each other (i.e. low Rbar), which in extreme cases results in negative correlations among different ring-width measurements even from one stem-disc (Buras and Wilmking, 2014).

Master and residual chronologies of detrended cell parameters and ring-widths (RWI) were finally examined for Spearman's correlation (accounting for non-normal distribution of data) with temperature, precipitation and SPEI for the year of growth (considering January to September) and the year prior to growth (considering April to December). To express the high-frequency, i.e. year-to-year correlation strength, correlations between the residual chronologies and pre-whitened climate parameters were computed. That is, in addition to 'normal' climate correlations we also added correlation analysis considering data from which all auto-correlation has been removed. To assess the stability of climate correlations over time and thereby estimate the climate reconstruction potential of proxies, cross-calibration verification analyses were performed for climate parameters with highest correlations per proxy. That is, the period of overlapping climate and proxy data was split into two periods of equal length. For each subset period a linear regression was computed and used to predict the climate parameter of the respectively other period. Predictive skill was quantified using the reduction of error (RE) and coefficient of efficiency (CE). If RE and CE are positive for both subsets, the respective proxy is considered a valid proxy for climate reconstruction (e.g. Cook et al., 1994). All analyses were performed in 'R' (R Core Team, 2015) making use of the package 'dplR' (Bunn, 2008).

Statistical analyses [b]

Spatial relations among GrIS-melt anomalies and proxies (summer temperature and shrub growth parameters) were assessed, by computing correlation maps similar to those presented in Beil et al. (2015) for sea surface temperatures (Fig. 7). That is, for each pixel of GrIS-melt, Spearman rank correlation was computed with the respective proxy for the common overlap period (1979-2007). Similar maps using the respectively pre-whitened proxy and melt data were computed to assess high-frequency co-linearity between proxy and GrIS-melt.

For further analyses, only the selected proxies which showed meaningful spatial correlations for both correlation analyses (i.e. normal and pre-whitened data) were selected. Thus, proxies which only showed non-significant, or few and scattered weak correlations were not considered. Significantly correlated pixels ($p<0.05$) were used to generate an average regional GrIS-melt anomaly time-series for each proxy, representative of the significantly correlated area. Additionally, one average sub-area GrIS-melt anomaly time-series was computed which only covered the intersected correlation area of all meaningful proxies along the southwestern coast of Greenland from where data were obtained (Fig. 8). Furthermore, an overall GrIS-melt anomaly time-series including all grid cells was computed. The proxy-specific sub-area melt anomaly time-series were correlated against complete GrIS-melt anomaly to assess their representativeness of the whole ice-sheet. Finally, all of the obtained GrIS-melt time-series were used to build candidate transfer functions based on the respective proxy. Here, the focus is mainly on the proxy-specific sub-area melt time-series (Table 4), but results from the other two approaches (intersected area and complete GrIS) are shown for comparison as well (Tables 5 and 6).

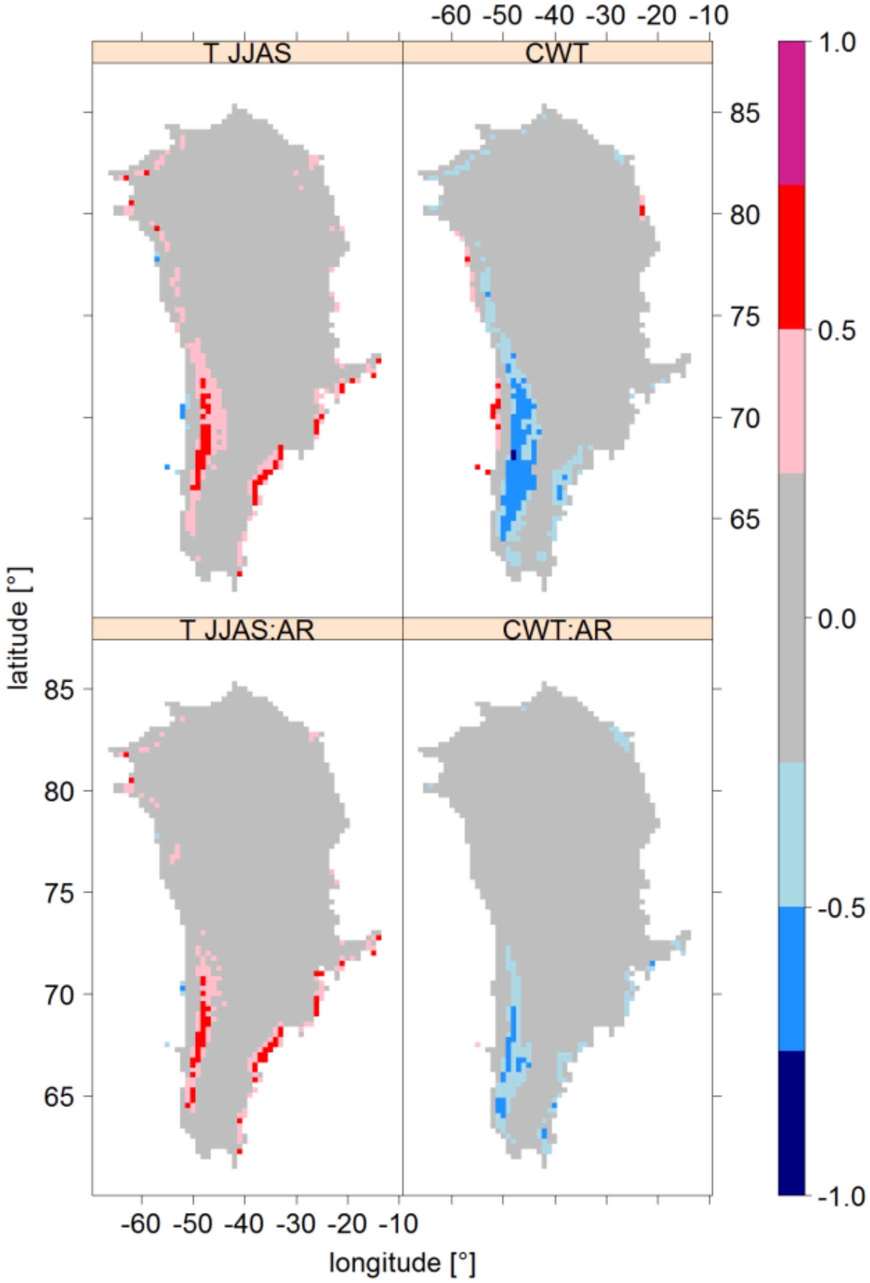


Fig. 7 Spatial GrIS-melt correlation with summer temperature (left), and cell-wall thickness (right). Grey colors refer to areas with non-significant correlations. The lower panels depict the spatial correlations of pre-whitened data.

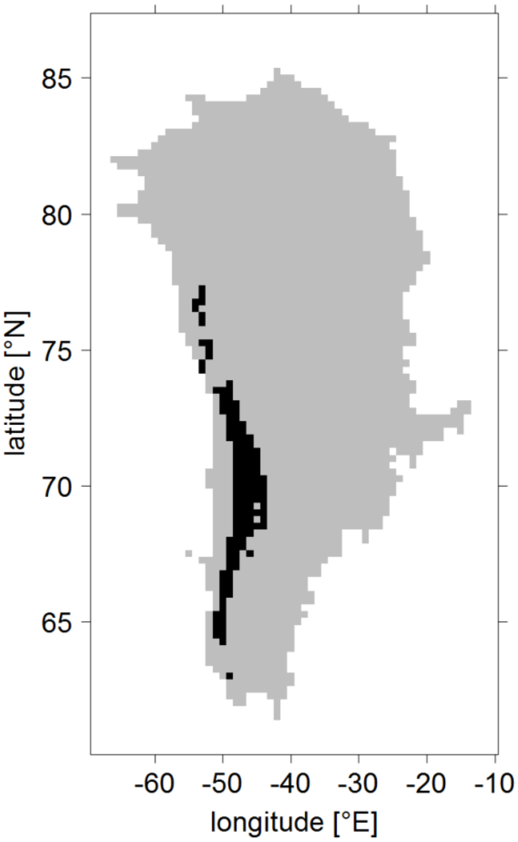


Fig. 8 Intersection of grid cells showing meaningful correlations in Fig. 7. These cells were used for all proxies to the generate transfer functions shown in Table 5.

Candidate transfer functions were computed using the reduced major axis (RMA) model. In contrast to ordinary least squares regression (OLS), RMA assumes both predictor and predictand variables to be affected by noise. Noise in this context is variability not being related to the relationship among predictor and predictand which may arise from measurement errors and variance shared with other influence factors. Although the error noise intensity is unknown for the variables, RMA seems to be a better representation of the true characteristics of the treated data in comparison to OLS, which assumes the predictor (here: climate and tree-ring parameters, respectively) to be noiseless and therefore tends to underestimate model slopes. For a detailed discussion on the treatment of noise in transfer functions, please see Kutzbach et al. (2011).

The performance of candidate transfer functions was quantified using several statistics (Table 4). First of all, the explained variance (r^2) and root mean square error (RMSE) were computed. Second, auto-correlation and normal distribution (using Shapiro-test) of model-residuals were tested, which – if revealing significant auto-correlation or non-normal distribution – would indicate invalidity of the model. Third, cross-calibration verification was performed based on the reduction of error (RE) and coefficient of efficiency (CE) as described in Cook et al. (1994). However, as RE and CE cannot be tested for statistical significance and are prone to outliers, fourthly, the bootstrapped transfer function stability test (BTFS) was applied, which bootstraps the probability of model parameters (r^2, intercept, slope) being instable over calibration and verification periods (Buras et al., submitted_b). Fifth, true collinearity between measured and modelled GrIS-melt time-series was assessed using Gleichläufigkeit (glk, Eckstein and Bauch, 1969, Buras and Wilmking, 2015) and tested for significance using sign-test (Fritts, 1976). Finally and sixth, to depict the most suited model among candidate transfer functions, Aikaike's Information Criterion (AIC; Akaike, 1976) as well as RMSE among those were compared.

Based on these six steps, the models suitable for GrIS-melt reconstruction were selected and the respective reconstructions were compared to each other (Fig. 14) as well as with the runoff-anomalies from Hanna et al. (2008; Fig. 15). For the model based on temperature, reconstruction was performed for the period of available data (1901-2012), for the model based on shrub-ring parameters, reconstruction was performed for the period with subsample signal strength (SSS) above 0.85 (Wigley et al., 1984). To obtain robust estimates of SSS, bootstrapping with 1000 iterations was used to derive explained variance (r^2) of subsample chronologies on master chronologies, i.e. SSS. All analyses were performed in ‘R’ (R Core Team, 2015) extended by the packages ‘dplR’ (Bunn et al., 2015), ‘lattice’ (Sarkar, 2008), ‘ncdf’ (Pierce, 2014), and ‘tiff’ (Urbanek, 2013).

5. Results

5.1 Wood-anatomy of *Juniperus communis*: a promising proxy for paleoclimate reconstructions in the Arctic [a]

The basic statistics of the measured parameters are given in Table 2. The PCA of cell parameters series performed very well, indicated by 70 and 16 percent (i.e. together 86 percent) of explained variance by the first two principal components, respectively. A plot of the loadings highlighted groups of strongly correlated variables (Fig. 9).

To reduce redundant information the data set was simplified based on PCA loadings to ring-width index (RWI), cell wall thickness (CWT), and conduit-lumen area (LA). Master chronologies of these three parameters are shown in Fig. 10. Moving window correlation and Gleichläufigkeit indicate a fair representation of each single parameter time-series ($cor > 0.27$, $glk > 0.58$) with low fluctuations over time (Fig. 11).

LA and CWT aligned by cambial age expressed cambial age trends common to all of the series (Fig. 12). A steep positive trend for LA was observed in the first 50 years. An opposite trend comparable to LA with respect to temporal behaviour was seen for CWT.

For all three considered proxies significant climate correlations were found (Fig. 13). Particularly (early) summer temperatures (June-July and June-July-August) and (early) summer SPEI showed strong correlations. That is, ring-width and conduit-lumen area correlated positively to summer temperatures but negatively to SPEI, whereas cell wall thickness showed negative correlations with summer temperatures and positive correlations with SPEI. Assessing the stability of the proxy-climate relationships – and thus the potential of proxies for climate reconstruction – using cross-calibration verification analyses resulted in unstable transfer functions for ring-widths and conduit-lumen area, but stable transfer functions for cell wall thickness (Table 3).

Table 2 Series intercorrelations (Rbar), average mean sensitivities, mean values, and standard deviations (σ) of analysed wood anatomical parameters.

Parameter	Rbar	mean sensitivity	average ± sd
Ring width (μm)	*0.17*	*0.33*	*245 ± 70*
Lumen area (μm²)	*0.19*	*0.15*	*128 ± 17*
Lumen length (μm)	*0.15*	*0.11*	*12 ± 1*
Lumen width (μm)	*0.15*	*0.07*	*11 ± 1*
Averaged Cell Wall thickness (μm)	*0.03*	*0.05*	*2.78 ± 0.15*
Cell Length (μm)	*0.17*	*0.07*	*17 ± 1*
Lumen Perimeter (μm)	*0.19*	*0.08*	*45 ± 3*
Lumen Form coefficient	*0.23*	*0.03*	*0.70 ± 0.02*
Lumen L/W-ratio	*0.04*	*0.11*	*1.2 ± 0.1*

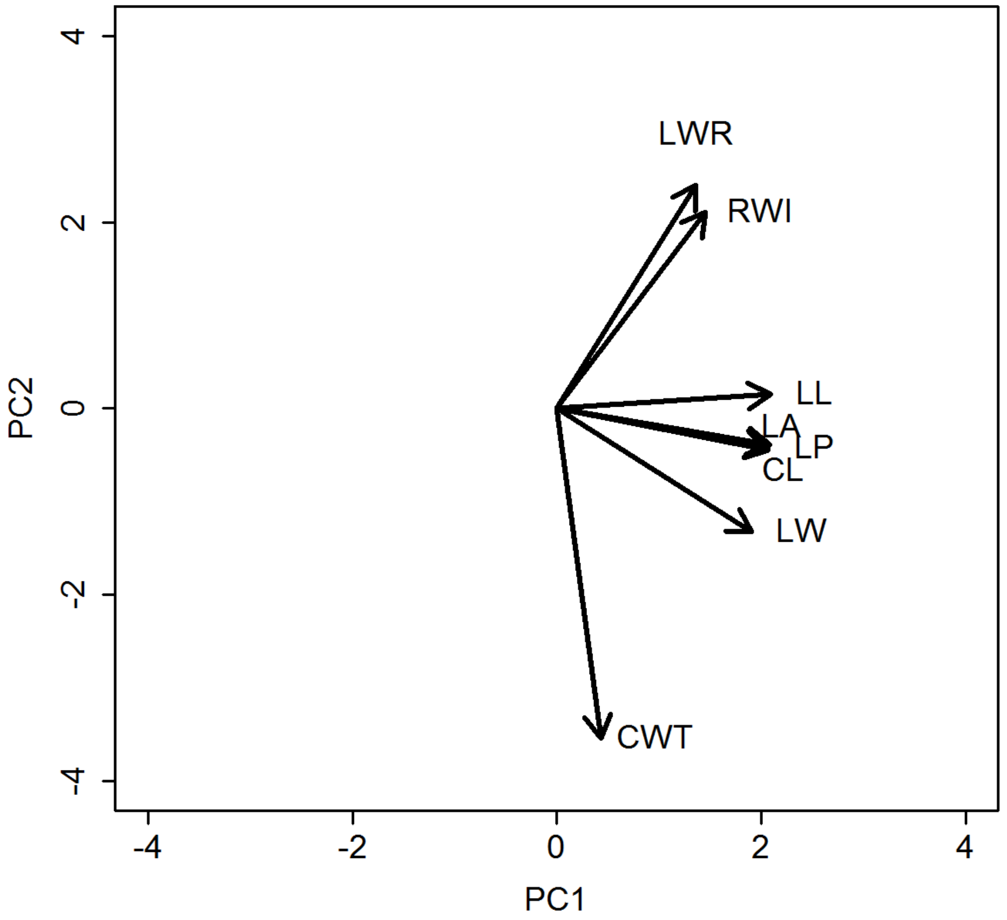


Fig. 9 Loadings of a Principal Component Analysis over wood anatomy parameters indicate high positive correlations among conduit-lumen Area (LA), conduit-lumen Perimeter (LP), conduit-lumen Length (LL), conduit-lumen Width (LW), and Cell Length (CL). Ring-width index (RWI) and conduit-lumen Length Width ratio (LWR) are positively correlated with each other and negatively with Cell Wall Thickness (CWT). RWI, LWR, and CWT are weakly correlated with the other variables.

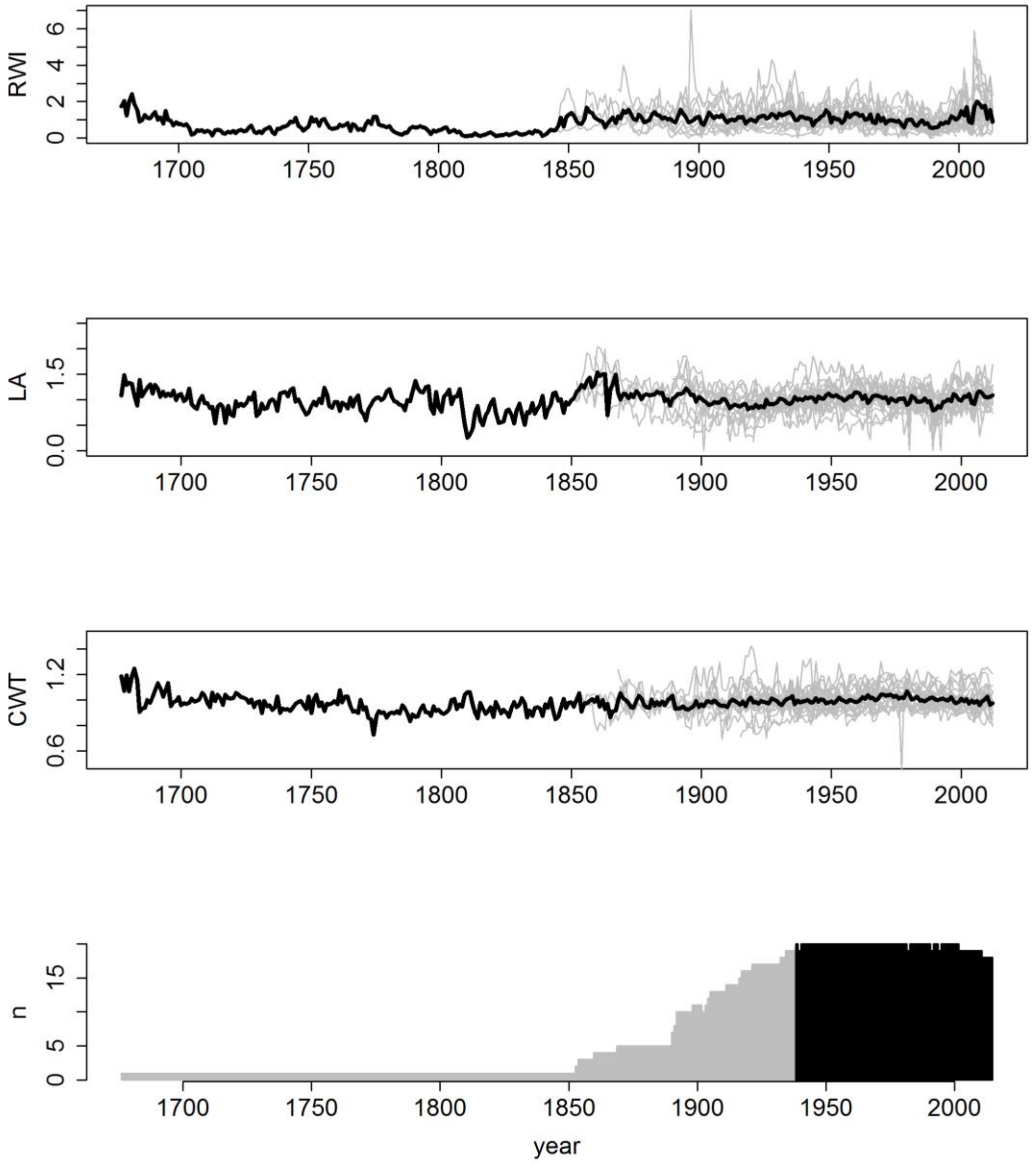


Fig. 10 Master chronologies and single time series of RWI, LA and CWT plotted along with sample size. In all further analyses, only the period of common interval, i.e. 1937-2012 (black bars in the lowest panel) was considered.

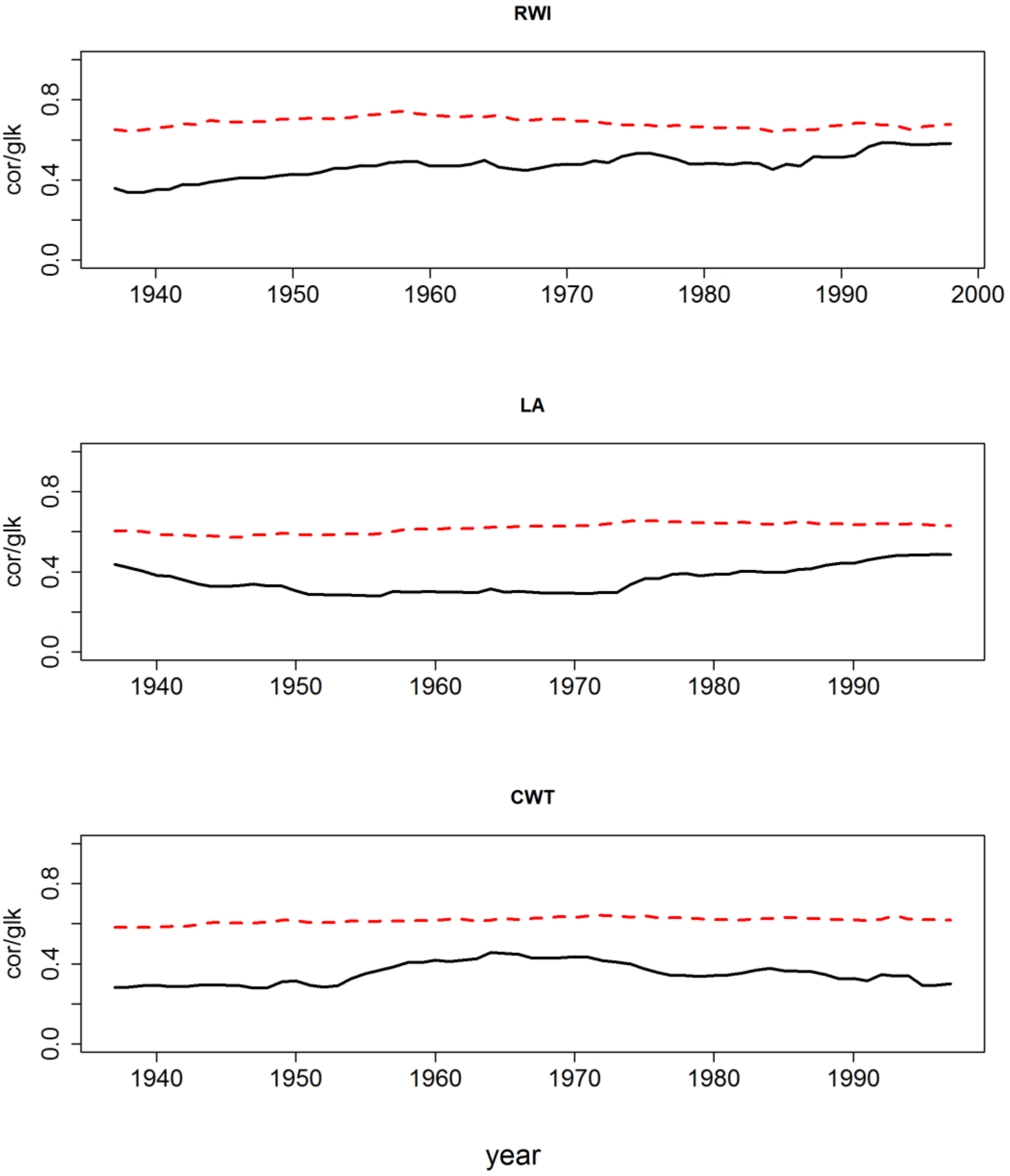


Fig. 11 Average running glk (red dashed) and correlation (black solid) of single series with the master chronology for each proxy considered (RWI, LA, CWT) using moving window of 31 years indicated fairly stable representativeness over time.

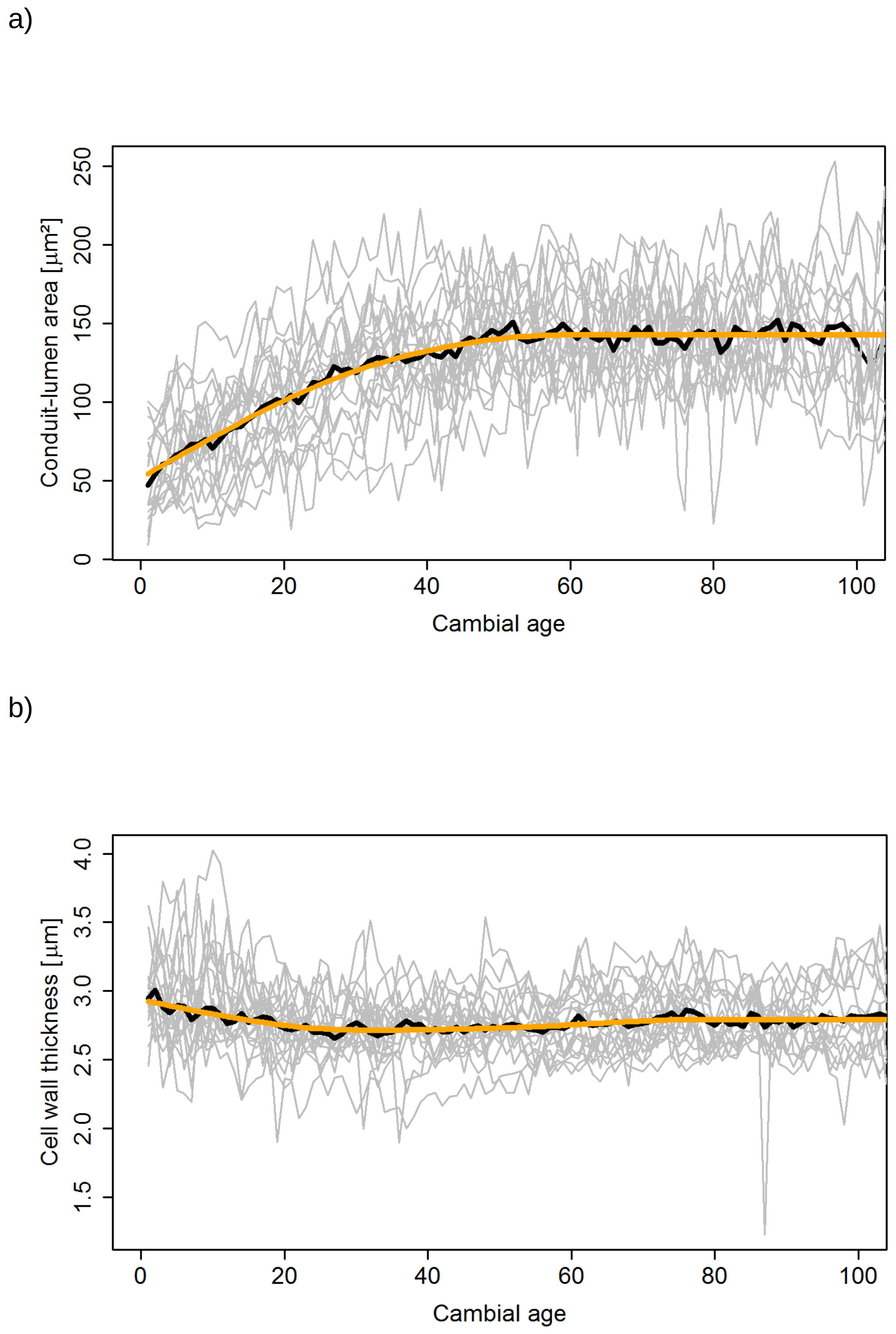
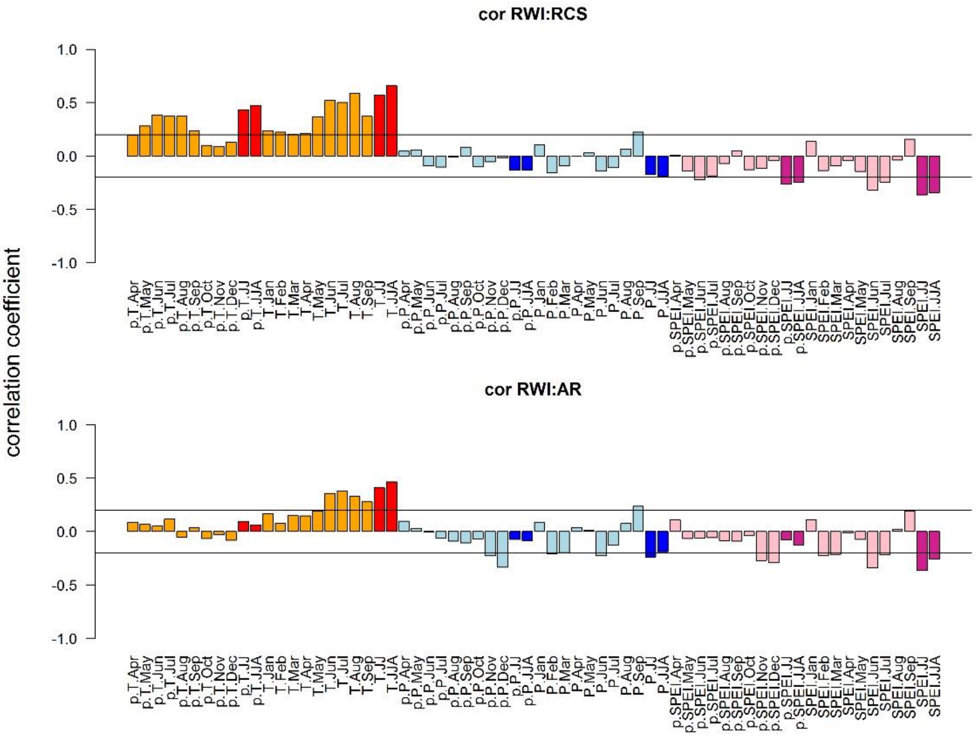


Fig. 12 Age trends in cell parameters. a) conduit-lumen area, and b) cell wall thickness. Solid thick black line represents the average over all series, solid thick orange line represents a fitted polynomial function.

a)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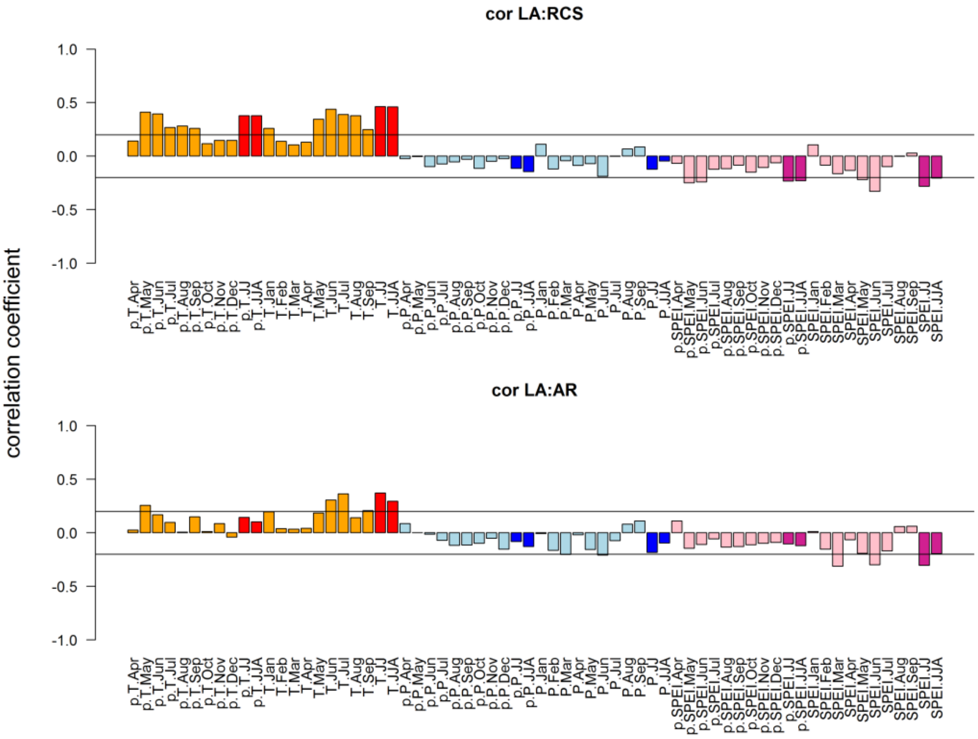
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c)

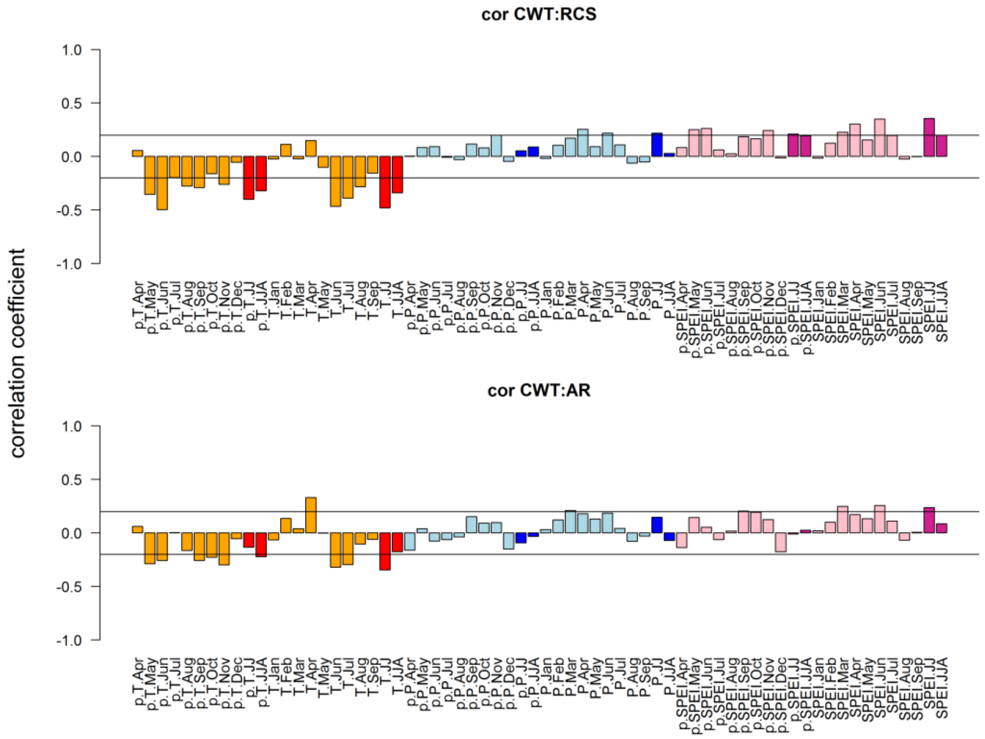

Fig. 13 Climate correlations of RWI, LA, and CWT with temperature (monthly: orange and seasonally: red, left bars), precipitation (monthly: light-blue, seasonally: blue, mid bars), and SPEI (monthly: pink, seasonally: violet, right bars). p depicts months and seasons prior to the year of growth. The horizontal lines indicate the significance level of $p < 0.05$. Upper panels represent climate correlations with standard chronologies (RCS), lower panels with residual chronologies (AR). a) correlations with ring-width chronologies, b) correlations with conduit-lumen area chronologies, and c) correlations with cell wall thickness chronologies.

Table 3 Cross-calibration verification statistics considering summer temperature (ST) and summer SPEI (SS) for RWI, LA, and CWT. Positive reduction of error (RE) and coefficient of efficiency (CE) values indicate good predictive skills of transfer functions and are highlighted in bold.

	period	R cal	R^2 cal	R ver	R^2 ver	RE	CE
RWI-ST	1937-1974	*0.508*	*0.258*	*0.731*	*0.534*	*0.369*	*0.362*
	1975-2012	*0.731*	*0.534*	*0.508*	*0.258*	*-0.120*	*-0.167*
RWI-SS	1937-1974	*-0.402*	*0.162*	*-0.389*	*0.151*	*0.108*	*0.099*
	1975-2012	*-0.389*	*0.151*	*-0.402*	*0.162*	*-0.090*	*-0.136*
LA-ST	1937-1974	*0.330*	*0.109*	*0.571*	*0.326*	*0.164*	*-0.037*
	1975-2012	*0.571*	*0.326*	*0.330*	*0.109*	*-0.096*	*-0.887*
LA-SS	1937-1974	*-0.330*	*0.109*	*-0.226*	*0.051*	*0.076*	*-0.145*
	1975-2012	*-0.226*	*0.051*	*-0.330*	*0.109*	*0.167*	*-0.434*
CWT-ST	1937-1974	*-0.478*	*0.229*	*-0.481*	*0.232*	***0.229***	***0.228***
	1975-2012	*-0.481*	*0.232*	*-0.478*	*0.229*	***0.226***	***0.225***
CWT-SS	1937-1974	*0.440*	*0.193*	*0.283*	*0.080*	***0.052***	***0.050***
	1975-2012	*0.283*	*0.080*	*0.440*	*0.193*	***0.167***	***0.166***

5.2 Shrubs shed light on 20th century Greenland Ice Sheet melting [b]

Two of the considered climate and shrub proxies showed meaningful correlations with GrIS-melt anomaly (Fig. 7). Correlations were weaker but nonetheless significant for pre-whitened data indicating similar spatial patterns although of lower extent. While summer temperatures generally were positively correlated, shrub cell-wall thickness mostly correlated negatively. The areas of significant correlations were roughly 184,000 km² and 154,000 km² for cell-wall thickness and summer temperature, respectively. Areas of correlations calculated for pre-whitened data reduced to 105,000 km² for cell-wall thickness and 110,000 km² for summer temperature.

Spearman rank-correlation and Gleichläufigkeit between sub-area and complete GrIS-melt anomaly time series showed good agreement for both (for summer temperature r = 0.92 and glk = 0.92, for cell-wall thickness r = 0.86 and glk = 0.89). Comparing the GrIS-melt transfer functions based on summer temperature (M:ST) and cell-wall-thickness (M:CWT), M:CWT appeared to a slightly better predictor of regional GrIS-melt (Table 4). While M:CWT passed all stability tests, M:ST had higher RMSE and AIC and did not pass sign-test. Similar analyses restricted to the intersected area of meaningful correlations (Fig. 8) resulted in worse performance of M:ST, with M:CWT performing comparably well and passing all tests but sign-test (Table 5). If considering complete GrIS-melt anomaly time-series both proxies performed worse in comparison to sub-area based models, with M:ST being the better proxy and passing all tests but sign-test. Here, M:CWT failed for RE and CE (Table 6). Thus, M:CWT appeared to be a valid predictor of local GrIS-melt.

Subsample signal strength of the cell-wall thickness chronology was above 0.85 until 1904, indicating the ability of M:CWT to reconstruct GrIS-melt anomaly back until then without losing much of explained variance. A comparison of reconstructed GrIS-melt anomaly based on either cell-wall thickness (R:CWT) or summer temperature (R:ST; Fig. 14), revealed a general offset among both and periodically differing long-term trends ($r = 0.50$, $p < 0.001$).

The GrIS-runoff anomaly series from Hanna et al. (2008) showed moderate agreement with the overall GrIS-melt anomaly ($r = 0.69$, *glk = 0.74*, Fig. 15 upper panel). ST and CWT based melt anomaly time-series expressed slightly higher and lower correlations respectively (ST: $r = 0.74$, *glk = 0.74*; CWT: $r = 0.62$, *glk = 0.63*; Fig. 15 second panel from above). Correlations between the complete Hanna et al. (2008) runoff reconstructions and R:ST and R:CWT respectively were comparably lower and lowest for ST (ST: $r = 0.43$, *glk = 0.75*; CWT: $r = 0.54$, *glk = 0.63*; lower panels Fig. 15).

Table 4 Performance of the candidate GrIS-melt anomaly transfer functions. Columns from left to right show the predictor variables, adjusted r², Gleichläufigkeit (* means sign-test was significant) maximum value of absolute auto-correlation of residuals (ACF; both non-significant), Shapiro-test p-value testing for normal distribution of residuals, root mean square error as proportion of the lowest value (RMSE), the difference of Akaike's Information Criterion (AIC) to the lowest value, reduction of error (RE), coefficient of efficiency (CE), and the minimum p-values from bootstrapped transfer function stability test. The respectively best values are highlighted in bold, values in italics indicate that the respective tests were passed.

Model	r² adj.	glk	ACF max |r|	Shapiro p-value	RMSE [%]
M:ST	**0.44**	0.71	*0.30*	*0.09*	112
M:CWT	0.42	***0.79****	***0.26***	***0.64***	**100**

Model	Δ AIC	RE I/II	CE I/II	BTFS p-value
M:ST	2.2	*0.37/0.47*	***0.18/0.37***	*0.169*
M:CWT	**0**	***0.53/0.46***	*0.18/0.17*	***0.19***

Table 5 Performance of the candidate GrIS melt-anomaly transfer functions representative of the area shown in Fig. 8. Columns from left to right show the predictor variables, adjusted r^2, Gleichläufigkeit (* means sign-test was significant) maximum value of absolute auto-correlation of residuals (ACF; both non-significant), Shapiro-test p-value testing for normal distribution of residuals, root mean square error as proportion of the lowest value (RMSE), the difference of Akaike's Information Criterion (AIC) to the lowest value, reduction of error (RE), coefficient of efficiency (CE), and the minimum p-values from bootstrapped transfer function stability test. The respectively best values are highlighted in bold. Values in italics indicate that the respective tests were passed.

Proxy	r^2 adj.	glk	ACF max |r|	Shapiro p-value	RMSE [%]
T JJAS	0.32	0.64	***0.26***	*0.06*	120
CWT	**0.42**	**0.75**	*0.35*	***0.31***	**100**

Proxy	Δ AIC	RE I/II	CE I/II	BTFS p-value
T JJAS	4.72	*0.37/0.29*	-0.12/-0.05	*0.20*
CWT	**0**	***0.55/0.43***	***0.21/0.16***	***0.22***

Table 6 Performance of the candidate GrIS melt-anomaly transfer functions representative of the whole ice-sheet. Columns from left to right show the predictor variables, adjusted r², Gleichläufigkeit (* means sign-test was significant) maximum value of absolute auto-correlation of residuals (ACF; both non-significant), Shapiro-test p-value testing for normal distribution of residuals, root mean square error as proportion of the lowest value (RMSE), the difference of Akaike's Information Criterion (AIC) to the lowest value, reduction of error (RE), coefficient of efficiency (CE), and the minimum p-values from bootstrapped transfer function stability test. The respectively best values are highlighted in bold. Values in italics indicate that the respective tests were passed.

Proxy	r² adj.	glk	ACF max |r|	Shapiro p-value	RMSE [%]
T JJAS	**0.31**	0.71	*0.29*	*0.10*	**100**
CWT	0.25	**0.75**	***0.25***	***0.80***	109

Proxy	Δ AIC	RE I/II	CE I/II	BTFS p-value
T JJAS	**0**	***0.12/0.32***	***0.06/0.28***	***0.17***
CWT	3.59	0.25/-0.17	0.19/-0.23	*0.10*

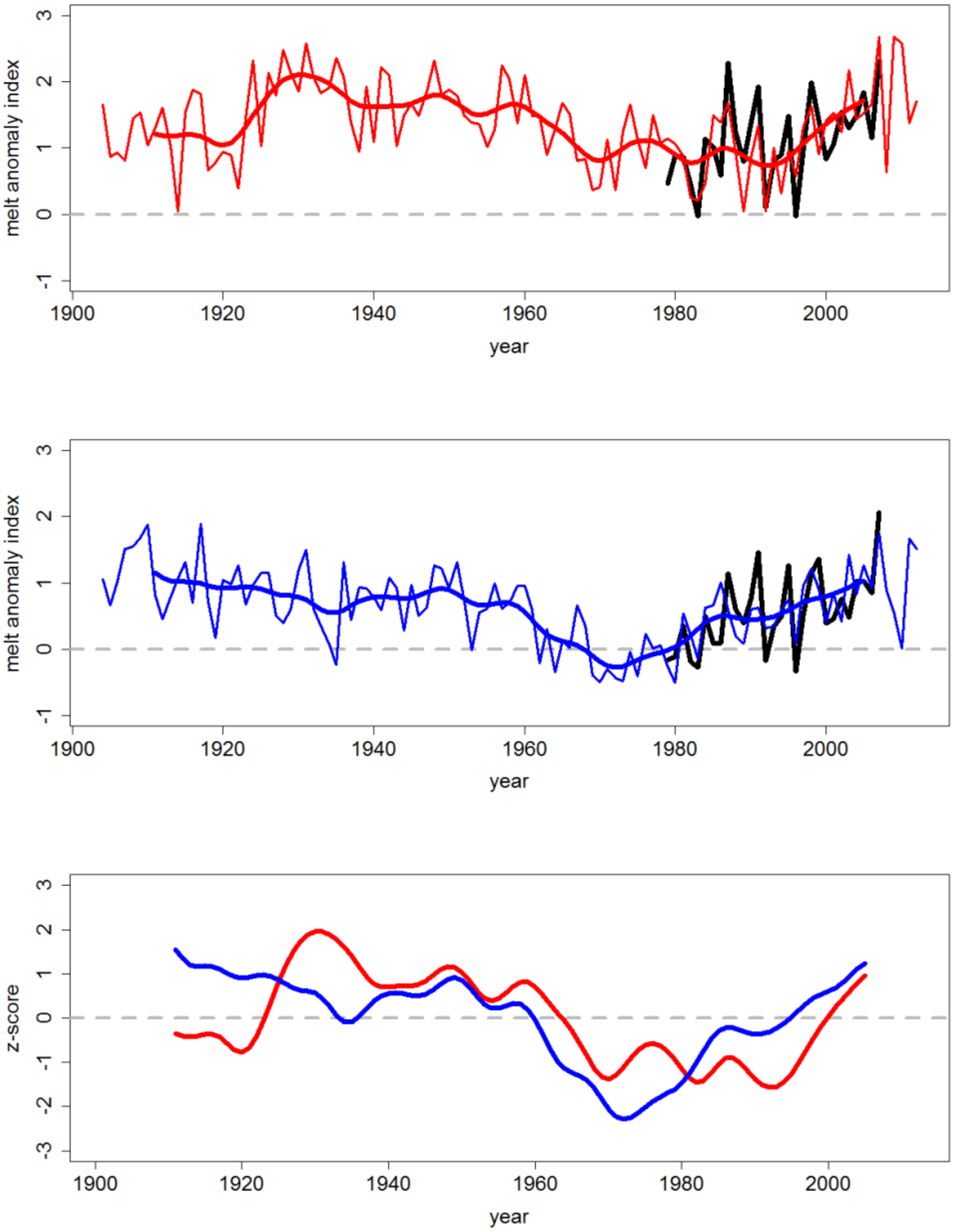

Fig. 14 Comparison between the temperature based reconstruction (upper panel, red) and the cell-wall thickness based reconstruction (middle panel, blue) of GrIS-melt extent index plotted at annual resolution together with 15 year Gaussian filtered values. To ease their comparison, z-transformed 15 year Gauss-filtered values are shown in the lower panel.

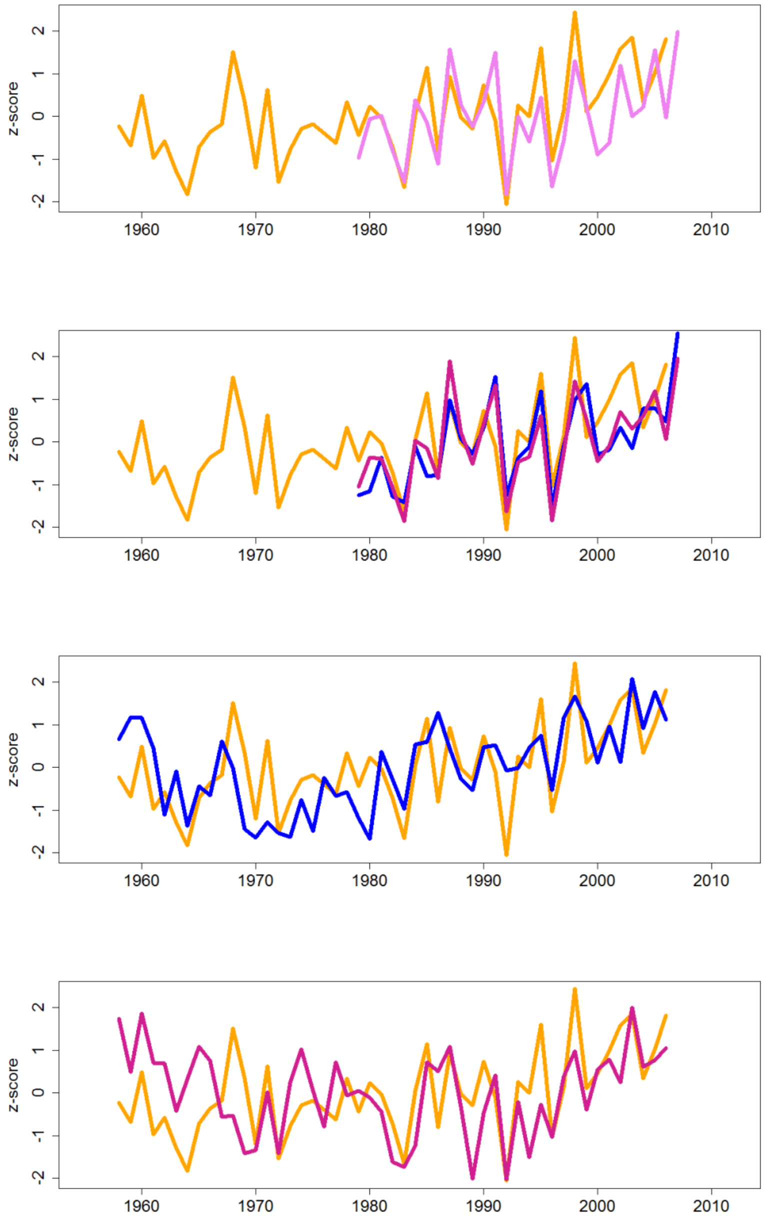

Fig. 15 From top to bottom: Comparison between reconstructed GrIS-runoff from Hanna et al. (2008) in orange with 1) total GrIS-melt anomaly index in pink, 2) GrIS-melt anomaly time-series of the pixels being significantly correlated with cell-wall thickness in blue and summer temperature in violet, 3) GrIS-melt anomaly index as reconstructed from cell-wall thickness in blue, and 4) GrIS-melt anomaly index as reconstructed from summer temperatures in violet. Please note that the variables were z-transformed to allow for visual comparison.

6. Discussion

6.1 Discussion on age trend of arctic tundra shrub, detrending, and suggestion of the potentially best growth parameters for climate/environmental reconstructions [a]

A successful analysis and test of wood anatomical parameters from *J. communis* shrubs for climate sensitivity in Lehejček et al. (2016) represents the first study of this sort from the polar zone to date.

Comparably small absolute values for wood anatomical parameters (RWI, LA, and CWT) are in agreement with the general assumption of narrow and embolism resistant conduits in cold environments (Olano et al., 2013; Olson et al., 2014; Kozakiewicz and Życzkowski, 2015). From the investigated parameters only detrended cell wall thickness seems to be a suitable climate proxy. Altogether age trends were found for cell wall thickness and conduit-lumen area which is an important ecophysiological finding of the study. These results support the use of the widely distributed and long-lived *J. communis* shrub in the Arctic for the purposes of paleoclimatological reconstructions.

The question of detrending

Trends were observed for all analysed wood anatomical parameters. The trends observed for conduit-lumen area in the first 50 years are comparable to conduit-lumen area trends observed for trees. There, conduit-lumen area trends are explained by an increasing distance to the apex, i.e. the lumen area is adjusted to fit the hydraulic conductivity needed for water transport through a longer stem (Carrer et al., 2015). This result should be considered in further shrub wood anatomy studies, because proper accounting for the ontogenetic development of biological proxies is of paramount importance when using their time series for climate and environmental reconstruction (Carrer et al., 2015).

The employed detrending was based on the average trends that the cell parameter time series expressed, which seems to be the most appropriate, as it reflects the average trends of the examined population. A somewhat similar procedure in tree ring sciences is called “regional curve standardization” (RCS) and is generally used to better conserve low frequency trends in the proxy time series (Esper et al., 2003). Here it allowed to use the whole length of the chronology, as shrub chronologies are usually shorter than tree ring chronologies. We recommend this approach because it leads to a better applicability of the available data than simply leaving out the sample parts containing the “youth trend” (Liang et al., 2013).

Trends

i) Conduit-lumen area

The finding of conduit-lumen area increase in the first 50 years of a shrubs life is in line with the generally accepted pattern of initial enlargement of conduit-lumen area with increasing height/cambial age (e.g. Anfodillo et al., 2006; Olson et al., 2014; Pritzkow et al., 2014; Carrer et al., 2015). However, after the first ca. 50 years the conduit-lumen size seems to reach a plateau and do not show any further increase. Similar trends for trees were first described by Sanio (1872). Nevertheless, recent research has shown continuous increase of conduit-lumen size throughout ontogeny (Anfodillo et al., 2013; Enquist, 2003; Fonti et al., 2013; Olson and Rossel, 2013), basically showing that the higher a tree gets, the larger conduit-lumen area at lower stem height is necessary. Since in general low temperatures, high wind speeds, and long-lying deep snow cover (which induce a down-bending of shrub stems) are most likely main limiting factors for height growth in these cold environments (e.g. Petit et al., 2011), we believe that the different nature of trees versus prostrate shrub conduits may be caused by the prostrate growth form of shrubs. Since the struggle for light hardly is an issue for Arctic shrubs, most likely severe weather conditions limit upright growth and result in the maximum height of a stem at a certain point where the stem bends from a vertical position to a more or less horizontal one. Different weather factors probably influence shrub growth differently: While snow and wind act mechanically (i), temperature influences the form of growth physiologically (ii). i) As long as the young shrub stem has high resilience to bend back to an upright position after snow melt and as long as it can withstand the wind during the vegetation season it most likely grows upright. ii) Temperature, resp. freeze-thaw events are responsible for the shrub's preference of safety (finite size of conduit-lumens) over hydraulic efficiency, thus reducing primary growth (Davis et al., 1999; Rossi et al., 2008; Petit et al., 2011). All of these (and other) factors are apparently working together and the transition of vertical to more horizontal growth is gradual. As a consequence, conduit-lumen size may not have to be further increased (due to ecophysiological restrictions possibly also must not) because water is no longer transported against gravity. This interpretation is supported by Darcy's Law which describes the flow of fluids through a porous medium (Darcy, 1856). While hydraulic conductivity remains constant in the plants body during stem elongation, the rate of flow is influenced only by the ratio $\delta H/\delta L$, where δH is the height difference and δL the longitudinal difference (distance from the root-collar to the shoot tip). δL raises steadily from the shrub establishment but δH reaches a peak value at the maximal height of the stem, i.e. the point from which the shrub does not grow vertically but rather horizontally or even downslope with the help of gravity. This interpretation seems logical taking differing hydraulic architecture between shrub- and tree-like form of *J. communis* (Beikircher and Mayr, 2008) and between shrubs and trees in general into consideration.

ii) Cell wall thickness

The observed opposite trend of decreasing cell wall thickness with increasing age in comparison to conduit-lumen area has been attributed by Zobel and Buijtenen (1989) to enhanced mechanical support function of trees needed particularly in the initial stages of plant development. Prostrate shrubs may react similarly until they reach maximal height, which then would result in levelling out the decreasing trends of CWT values. This assumption should however be verified by appropriately designed sampling, i.e. detailed recording of stem shape and growth direction with respect to the stem anatomy.

iii) Climate correlations

For each of the proxies considered, significant correlations with climate parameters were found. While ring-width and conduit-lumen area were positively correlated with summer temperatures and negatively correlated with June precipitation and summer SPEI, cell wall thickness showed an opposite behaviour. Although temperature correlations generally were stronger, precipitation and SPEI correlations were significant. Thus, under relatively drier conditions juniper expressed larger ring-widths, increased conduit-lumen areas, but decreased cell wall thickness.

Positive correlations between ring-width and summer temperature has frequently been observed for Arctic and sub-Arctic regions (e.g. Wilson, 1957; Havström et al., 1995; Rayback and Henry, 2005, 2006; Bär et al., 2008; Rozema et al., 2009; Hallinger et al., 2010; Hantemirov et al., 2011; Blok et al., 2011; Weijers et al., 2010, 2012; Buchwal et al., 2013; Myers-Smith et al., 2015a), however the negative correlation with June precipitation and summer SPEI was less often observed. It may be due to the fact the juniper is a thermophyllic species and generally prefers very well drained, warm soils. For example, Polická (2014) reported that soils under juniper stands were dryer and had a lower water holding capacity compared to other shrub sites. Since SPEI is the result of a calculation using both temperature and precipitation, a negative SPEI correlation may be mainly due to positive correlations with temperature or negative correlations with precipitation, or a combination of both. Also, the observed correlations may have another reason, as high SPEI values (and thus low ring-widths) probably coincide with more frequent cloud cover in the growing season, leading to a lower amount of photo-assimilates due to reduced rates of photosynthesis. Due to the lack of sunshine hour data from the investigated field-site, its influence on the examined parameters was not possible to test.

The observed correlations between conduit-lumen area and climate parameters are in line with correlations reported by Eilmann et al. (2009). They found Scots Pine (*Pinus sylvestris*) radial conduit-lumen diameter to increase with drought. However, in their study Scots Pine ring-width expressed negative correlation with drought, which is not the case for juniper ring-width at respective site in Greenland. Eilmann et al. (2009) explained increased conduit-lumen area as a compensation for reduced conducting area due to lower ring-width under drought. This explanation contrasts correlations observed for ring-widths in presented case. In addition, other studies have reported negative correlations between drought and conduit-lumen area of coniferous trees (e.g. Jenkins, 1975; Sterck et al., 2008). Also, it remains questionable here to compare different species since the conducting area is also a function of sapwood area which may differ substantially. Thus, the physiological explanation for the observed correlations remains still open.

Eilmann et al. (2009) and Martin-Benito et al. (2013) also reported lower cell wall thickness under drier conditions, which fits the observed negative correlations between cell wall thickness and summer temperature and positive correlations with SPEI in presented case. Eilmann et al. (2009) explained this phenomenon as strategy to build a more effective water conducting system (higher conduit-lumen diameter) with lower construction costs (lower cell wall thickness) under dry conditions due to the reduced amount of photo-assimilates. According to Jones (1998) carbon uptake is reduced under dry conditions due to stomatal closure and Wiley and Helliker (2012) claim that trees allocate more carbon to reserves, which theoretically could explain thinner cell walls under dry conditions as observed and presented above. However, negative correlations between ring-width and SPEI suggest that juniper actually benefits from drier conditions, possibly due to a higher availability of photo-assimilates under sunny conditions (see above). Concluding, it remains open to explain why juniper in Kobbefjord increases cell wall thickness with increasing water availability or decreasing temperatures in summer. In this context, we suggest investigating stable carbon isotopes or manipulative experiments, which possibly allow for assessing whether juniper in Kobbefjord actually suffers from dry conditions or not.

The lack of a physiological understanding is caused also by the unexplored ecology of the species in the Arctic. Despite these knowledge gaps, the analyses indicated that *J. communis* shrub wood-anatomical parameters may act as valuable climate proxies in Arctic environments. Although the climate correlations observed for ring-widths were stronger if compared to cell-anatomical parameters, they seem to be obscured by additional noise varying over time as indicated by unstable cross-calibration verification analyses. In contrast, cell wall thickness expressed stable climate-proxy relationships over the investigated period. A possible explanation for this may be related to moth outbreaks which recently have been reported for Southwestern Greenland (Young et al., 2016). The observed moth outbreaks had significant effects on deciduous shrubs due to defoliation of those, this leading to narrower rings. However, it is less likely that moths forage on juniper needles, wherefore the latter may benefit from moth outbreaks due to reduced competition with weakened adjacent deciduous shrubs. Young et al. (2016) reported a severe moth outbreak in 2005, after which juniper in Kobbefjord showed increased ring-widths for 4-5 years, while cell wall thickness showed no apparent change. Thus it seems possible, that ring-widths are positively affected by moth outbreaks, this explaining their unstable relationship with climate parameters, as moth outbreaks also have been reported earlier in time (Young et al., 2016).

Taking into consideration presented results, climate/environmental reconstructions based on wood-anatomical proxies of *J. communis* are possible if datasets with an appropriate sample replication and long record are available. As reported earlier (e.g. Schweingruber and Poschlod, 2005) and documented here, junipers are long-lived and possibly provide the longest time-series of annual ring properties in the Arctic. Altogether, this makes juniper a species of high interest for climate reconstruction in the Arctic.

6.2 Discussion on usage of the growth parameters for reconstruction and the climate/environmental reconstruction itself [b]

Interpretation of GrIS-melt reconstructions

The presented results in Buras et al. (submitted_a) indicate shrub cell-wall thickness to be a valuable predictor for GrIS-melt. Regarding regional transfer functions (Tables 4 and 5) cell-wall thickness performed slightly better in comparison to summer temperature, which frequently has been used – partly in combination with other proxies – to reconstruct variables related to GrIS-melt (e.g. Hanna et al., 2008, 2011; Box et al., 2009; Box, 2013; Fettweis et al., 2011; Frauenfeld et al., 2011). These findings are supported by other studies showing the ability of tree-rings (e.g. Watson and Luckman, 2004; Laroque and Smith, 2005; Wood et al., 2011) and shrub-rings (Buras et al., 2012) to reconstruct variables related to glacier melt. To the best knowledge, the reconstruction shown in Buras el al. (submitted_a) is the first GrIS-melt reconstruction derived from dendrochronological data.

As GrIS-melt is most pronounced in Southwest Greenland (Abdalati and Steffen, 1997; Fettweis, 2007), the presented new reconstruction allows for additional insights into the past of GrIS melting as it contrasts existing reconstructions. For the period prior to 1940 prominent differences between the two presented reconstructions were observed (Fig. 14). While R:ST – similar to other temperature based reconstructions (e.g. Hanna et al., 2011; Box, 2012) – indicated a peak melt around 1930, R:CWT showed lower melt around this period if compared to the early 20th century. From 1940 through 1970, both reconstructions describe qualitatively similar patterns, though minor differences were observed. From 1970 through the early 1990ies R:ST indicated melt below average but with no clear trend followed by a sharp increase to recent melt rates. In contrast, cell-wall thickness showed a steadily increasing melt from 1970 onwards to recent date. Possible reasons for observed differences are discussed in the next section.

Although the two reconstructions draw a different picture of past GrIS-melt, they agree in content that recent melt rates are in the same order as for certain periods in the first half of the 20th century. As both reconstructions represent areas which fairly well represent overall GrIS-melt, these findings suggest that recent GrIS-melt – though being high – are not unprecedented. This statement is supported by the reconstruction by Frauenfeld et al. (2011) but contrasts the reconstructions by Hanna et al. (2011) and Box (2013) who found recent melt rates unprecedented.

Why do shrubs cell-walls correlate with GrIS?

At the first instance, one may be surprised to find shrubs cell-walls with an average thickness of 2.78 µm correlating with GrIS-melt data representative of 184,000 km². Similar to Buras et al. (2012) it is obvious that there is no direct mechanistic link between shrub cell-wall thickness and GrIS-melt. The mechanisms behind the observed correlations are most likely dependencies of both variables to a similar set of climate parameters. GrIS-melt is affected by various influence factors, of which air temperature appears to be most influential (Box et al., 2009). However, other factors such as incoming solar radiation, surface albedo (affected by precipitation), cloud cover, atmospheric moisture, and wind conditions were reported to significantly affect GrIS-melt (Hock, 2003; Box, 2012; Frauenfeld et al., 2011). On the other hand, shrub growth is also affected by a multitude of influence factors. Several studies have shown dependencies to growing season temperature, precipitation, or drought indices (e.g. Blok et al., 2011; Buras et al., 2012; Myers-Smith et al., 2015a; Weijers et al., 2010, 2012; Lehejček et al., 2016). As plant growth strictly depends on photosynthesis, shrub growth further is affected by the amount of solar radiation received within the growing season.

GrIS-melt mainly occurs throughout the growing season (June through August; Abdalati and Steffen, 1997) which conditions likely are mirrored in shrub-ring parameters. Even though shrubs experience local climate conditions, based on Fig. 7 it appears that this local climate is representative for regional GrIS-melt in summer. Box et al. (2009 and Fig. 7 therein) have reported similar spatial correlation patterns with coastal climate station data.

For coastal regions however correlations between GrIS-melt and proxies considered here were non-significant (Fig. 7). One reason for this may be that these regions on average experience melt from April through October (Abdalati and Steffen, 1997), a period which at its margins is not representative for shrub growth. However, correlations with temperatures averaged over different seasons did not show increasing correlation coefficients for coastal regions (not shown). Another possible reason is increasing noise in the satellite data caused by an increasing contribution of bare rock and tundra towards coastal areas (Fettweis et al., 2011). Concluding, it appears that the shrub data presented here share some of the influence factors of GrIS-melt, in particular temperature, precipitation, and solar radiation.

As integrating information related to three climate parameters being relevant for GrIS-melt, we believe shrubs are a powerful respective proxy. This possibly explains the differences observed between R:ST and R:CWT as described above. Summer precipitation and cloud cover data from Nuuk indicate relatively drier and less cloudy conditions for the first half of the 20th century (Fig. 8). Less precipitation probably means less snowfall on top of the interior ice sheet in summer, this resulting in increased melting due to the lower albedo of old snow and glacier ice (e.g. Ettema et al., 2009). At the same, less cloud cover means more incoming solar radiation. Both effects in combination may lead to increased melt of GrIS, which is not reflected by summer temperatures alone. But as reported above, shrubs and GrIS are likely to react on these parameters in addition to their temperature sensitivity, this possibly explaining, why R:CWT indicates higher melt rates in the early 20th century in comparison to R:ST and other existing reconstructions (Hanna et al., 2011; Box, 2012).

Reliability of reconstructions

Despite the differences observed between the two presented reconstructions, tests for assessing the stability of transfer functions over time were supportive for both models (Table 4). A comparison of these reconstructions to the runoff reconstruction by Hanna et al. (2008) showed moderate agreement for both. The differences among reconstructions can be explained by noise specific to each of the used proxies in addition to a differing spatial relevance (whole ice-sheet in Hanna et al., 2008 vs. southwestern Greenland in this case). Nevertheless the long-term trend of Hanna et al. (2008) runoff and cell-wall thickness based GrIS-melt matched fairly well which was captured to a lower extent by the temperature based reconstruction (Fig. 15).

To avoid possible misinterpretations, it is important to stress that presented results do not question the value of summer temperatures as GrIS-melt predictors. Several studies have shown strong correlations between networks of climate station data and GrIS-melt (e.g. Hanna et al., 2008, 2011; Frauenfeld et al., 2011). Probably, when used in a network, site-specific noise of temperature data is efficiently accounted for, this leading to higher explanatory power of respective models. In addition, when comparing the two GrIS-melt reconstructions shown in Buras et al. (submitted_a), one has to recall, that they are representative of different areas (Fig. 7). Therefore, the absolute melt-anomalies for the cell-wall thickness based reconstruction in general are lower, which is explained by the fact that it also includes grid cells farther off the coast. Significant transfer functions were also found for two common areas, however with lower performance quality (Tables 5 and 6), that is why the interpretation was focused on the regional proxy-specific reconstructions.

Even though the M:CWT passed all tests, it is worth stressing, that shrubs are affected by influence factors which are not related to GrIS-melt, indicated by 58 percent of unexplained variance in the transfer function. Relevant influence factors are competition, disturbance, and ontogenetic trends of growth parameters. While ontogenetic trends of cell-wall thickness are believed to be successfully removed using RCS-detrending, competition and disturbance are not easily accounted for. A possible cause of disturbance and competition affecting shrub performance in Kobbefjord is moth outbreaks. Young et al. (2016) have reported a severe moth outbreak in Western Greenland in the year 2005 and another weaker one in 1981 (see also Fox et al., 1987 cited in Young et al., 2016), leading to strong herbivory pressure on deciduous shrubs. Being a coniferous shrub, juniper probably is not negatively affected by moth outbreaks, but might in contrast benefit due to reduced competition for resources (as discussed in chapter 6.1). Identification of the respective effects (growth release) in presented data caused by moth outbreaks may explain why ring-widths – which possibly are affected stronger by moth outbreaks – were not significantly correlated with GrIS-melt in contrast to the findings shown by Buras et al. (2012). To address such kind of uncertainties and support the reliability in presented reconstruction the subsample signal strength was used, which indicated only minor loss of reconstructions skill back until 1904 (Wigley et al., 1984).

6.3 Implications and possible scenarios for future research

i) GrIS-melt reconstructions

A possibility to increase the predictive power of the presented cell-wall thickness based transfer function is acquisition of additional samples. It is widely accepted, that individual noise is evened out more efficiently in master chronologies derived from larger sample sizes (e.g. Wigley et al., 1984; Carrer, 2011). Due to the high time consumption of wood anatomy measurements and nature conservation concerns, ‘only’ 21 wood anatomy time-series were considered. Nevertheless, the possibility of increasing melt estimate precision, when acquiring additional samples in future studies, should be mentioned. Due to recent software developments which allow for faster analyses of wood-anatomy parameters (ROXAS; von Arx, 2014), larger sample sizes seem to be feasible for future studies.

If acquiring additional samples from several sites, the probability of possible site specific factors (such as moth outbreaks) influencing GrIS-melt reconstructions becomes lower. Furthermore, a respective sampling network, will possibly allow for reconstruction of GrIS-melt representative for a larger area of the ice-sheet. Corresponding climate station network reconstructions of GrIS related variables already exist (e.g. Hanna et al., 2008; Frauenfeld et al., 2011). Theoretically, additional shrub-proxy data could also be combined with temperature data to fill gaps in areas not covered well by climate stations. For the case of *Juniperus communis* ssp. *nana*, additional sites are abundant but restricted to the southern half of Greenland (Fredskild, 1996). For northern Greenland, *Cassiope tetragona* which is long-lived and showed strong correlations with summer temperatures on Svalbard may be a suitable alternative (Weijers et al., 2010, 2012).

Finally, emphasizing the fact, that it was not found meaningful to perform spatial melt correlations for ring-widths although cell-wall thickness was shown to be a valid proxy. Ring-widths have earlier been used to successfully explore for correlations with glacier-melt related variables (Watson and Luckman, 2004; Laroque and Smith, 2005; Wood et al., 2011; Buras et al., 2012), but to the best knowledge no study has investigated for relationships with other wood-anatomy parameters. Based on presented findings, it is therefore proposed to consider wood anatomy parameters in future studies aiming at glacier melt reconstructions from growth rings of woody perennials.

ii) environmental North Atlantic/circumpolar network of *J. communis*

Spatially restricted pilot studies have shown the potential of shrubs to reconstruct snow regime, summer temperature, glacier summer mass balance and ocean currents (Buras et al., 2012; Beil et al., 2015) the phenomena extremely tied to and influenced by global climate development. Unfortunately, almost nothing is known about the climate/environmental sensitivity of shrubs from different synoptic zones, manifested e.g. by degree of climate continentality. If this understood, the systematic access to whole regional or even circumpolar reconstructions and prognosis can become open.

Wood anatomy of woody perennial Arctic tundra shrubs can complete and strengthen other Arctic archives such as ice cores or lake/marine sediments. Moreover, tundra shrubs are more evenly distributed in the Arctic tundra then glaciers or lakes. They also live closer to the ocean which is the most important climate driver of the region. *Juniperus communis* is one of the species with circumpolar distribution having the longest time span between all Arctic tundra shrubs.

This pilot one-site wood anatomical study investigating this Arctic species has shown specie's enormous and yet untapped potential for paleo-environmental/climatic research including the potential ability to date disturbance events (Lehejček et al., 2016). Although past and current environmental changes are imprinted in the juniper growth parameters, growth trends and disturbance events can cover its reconstructive capital. While the topic of age trend removal was already successfully solved in abovementioned study, influence of disturbances on Arctic juniper growth parameters is still underinvestigated.

During the year 2017 my focus will direct on already collected material from Kobbefjord, Greenland and Kola peninsula, Norway (unpublished dataset). Both localities have experienced the disturbance growth affecting events. Kobbefjord vegetation has been attacked by moth outbreaks - at least two events are documented in the last 50 years (Lehejček et al., 2016). Vegetation in north-western Kola is strongly affected by (mainly) sulphur dioxide pollution from Russian Severonikel smelter complex since 1969 (Barcan, 2002). Annual-rings from Kobbefjord show instable climate correlations over time indicated by poor results of cross-calibration verification analyses possibly caused by after-disturbance growth release. Similarly, the climate signal in the annual-rings from Kola is lost after the construction of smelter. At the same time cell-parameters in Kobbefjord case indicated no apparent response on moth outbreak. Kola data were not processed with this respect yet. Nonetheless, it seems realistic and promising that Arctic junipers store the information on both climate and disturbances to certain extend independently.

Disturbing effect of soil erosion on juniper growth from north Iceland will be studied subsequently as well. This should not only help to better understand how juniper reacts on another disturbance agent but also verify and specify dating of soil erosion occurrence in the region – so far only documented in Icelandic Sagas. Dating the event as well as better understanding the process can support the restoration efforts of Soil

Conservation Service of Iceland because common juniper which often grows at stony and almost bare land is the only surviving woody species of affected area. As such can become part of the solution or even a frontier in mitigation the biggest Icelandic environmental problem.

Above mentioned triple approach to “disturbances vs. juniper growth” issue will allow for better understanding the most of the possible disturbance events influences in the Arctic (defoliation, pollution, and soil erosion) resulting in the phenomena of growth releases and growth suppressions. Based on this disturbance synthesis of *Juniperus communis* plus already presented concept of the growth trends detrending we can distil specie’s real contribution to nature of global change thanks to ability to distinguish between various growth influencing factors.

Therefor it will become possible to build functional North Atlantic juniper network which will consist of 7 localities. Besides already mentioned (Kobbefjord, Greenland and Kola peninsula, Norway) collected by the author of this Ph.D. thesis four others were acquisitioned by Landscape Ecology Group from Greifswald University (Finse, Norway; Kevo, Finland; Abisko, Sweden; and Ural, Russia). The last seventh locality will be sampled in north Iceland during the summer 2017. Wide distribution of localities surrounding the North Atlantic as well as its climatic representativeness for the region influenced by North Atlantic oceanic system (e.g. represented by AMOC) is a crucial precondition for successful intercontinental reconstruction. Such network setting actually offers unique opportunity to test the effect of continentality on the shrub growth and ask the research question: “Does the local climate overrule the global climatic effect in juniper growth parameters?” Only if this is understood, broader intercontinental environmental reconstruction focusing also on identification of climate threshold triggers in the Northern Atlantic may become possible. Better understanding of North Atlantic nature and future scenarios projection should be feasible via wood anatomy of *Juniperus communis*.

A logic further step would be to test the possibility to extract the advantageous circumpolar distribution of *J. communis*. In summer 2017 the additional juniper samples will be collected in Denali National Park, Alaska. As this locality is not affected by North Atlantic climate the cross-dating and finding common signal may be a challenge. Nevertheless, in case the compatibility of those datasets is proved and the systems do not show to be too different to generalize, the road to circumpolar environmental reconstructions based on juniper wood anatomy gets open.

iii) Combination of different archives

Initial attempts to link shrub series with lake sediment record offers solid basis to invest more time in this approach. Linking those two archives in the Arctic is rather innovative, but also very useful for complementing individual records. The tops (most recent layers) of lake sediments are usually disturbed by organisms, water mass movements, or problematic extraction and therefore mostly not easy to interpret. That is why the record from annual rings of dwarf shrubs is beneficial extension.

Lake sediments from five lakes from Kobbefjord, Greenland as well as northern Kola peninsula, Norway were drilled and thus material for this multi-proxy approach is available. Lake sediment cores were analyzed extensively while combining: litological (grain-size composition), petrophysical (magnetic susceptibility), geochemical (determination of basic lithophile elements, organic and anorganic carbon, sulphur, and nitrogen), and biological proxy (biostratigraphy of diatoms) methods. Climatic and environmental variability is thus verified by a number of approaches. For determination of the time development of sedimentation appropriate dating methods were applied (AMS radiocarbon dating, and 210Pb for the youngest parts of sediments accumulated in last centuries). The results from Greenland indicate that lake basins are subject of sedimentation for ca 800 years while those from Kola peninsula reach up to 5,000 years of development.

Next step is to merge those two archives into one reconstruction of regional environmental development.

7. Conclusions

This thesis provides the comprehensive insight into the wood anatomy of *J. communis* and its potential for climate reconstructions in the Arctic.

Age trends were detected in time series of conduit-lumen area as well as cell wall thickness suggesting the necessity for detrending (to diminish trends related to ontogeny) prior to use of these anatomical time series as environmental proxies. Compared to trees, the prostrate form of *J. communis* does not exhibit the general conduit-lumen size increase over the whole lifetime of the plant, but its conduit-lumens stop to increase in size, in case of this study after about 50 years. This might be caused by combination of extreme climate and physiological adaptation on freeze-thaw events resulting in prostrate growth. To what extent this is a general pattern for other sites and prostrate shrubs species remains the question for further research.

Of the tested growth parameters, only standardised cell wall thickness passed cross-calibration verification tests and showed stable significant correlations with summer temperatures and SPEI. This makes *J. communis* a very promising proxy for climatic reconstructions in particular with respect to its abundancy and longevity. Based on this findings several research questions will have to be answered by further shrub wood-anatomical studies. Such investigations should namely test the relevance of presented recommendations for other shrub species (e.g. diffuse- or ring-porous shrub species), as well as variations across different sites and habitats, and ecological gradients. This study also presents many important physiological questions concerning the nature of cell anatomy of tundra shrubs, which should be tackled in upcoming research.

The shrub-wood anatomy based reconstruction of Greenland Ice Sheet melt anomalies is also presented here for the first time. The reconstruction suggests that recent melt rates yet are in the order of maximum 20th century values. Shrub growth related parameters were shown to be valid proxies for gaining additional insights on past GrIS-melt dynamics. Based on these findings, the establishment of a shrub network across Greenland may possibly allow for the acquisition of GrIS-melt proxies being independent from the frequently used meteorological variables. Combination of shrub and meteorological based proxies within a joint network may allow for increasing the precision GrIS-melt reconstructions to obtain a better understanding of past GrIS-melt dynamics and possible impacts on the Atlantic Meridional Overturning Circulation.

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Electronic Supplementary Material

An integral component of this Ph.D. thesis is CD with complete text and figures of the work.