



Methods for measuring arctic and alpine shrub growth: A review



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ABSTRACT

Shrubs have increased in abundance and dominance in arctic and alpine regions in recent decades. This often dramatic change, likely due to climate warming, has the potential to alter both the structure and function of tundra ecosystems. The analysis of shrub growth is improving our understanding of tundra vegetation dynamics and environmental changes. However, dendrochronological methods developed for trees, need to be adapted for the morphology and growth eccentricity of shrubs. Here, we review current and developing methods to measure radial and axial growth, estimate age, and assess growth dynamics in relation to environmental variables. Recent advances in sampling methods, analysis and applications have improved our ability to investigate growth and recruitment dynamics of shrubs. However, to extrapolate findings to the biome scale, future dendroecological work will require improved approaches that better address variation in growth within parts of the plant, among individuals within populations and between species.

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1. Introduction

The recent observed increases in the growth and abundance of shrubs are one of the most prominent ecological changes currently occurring in many tundra ecosystems (Sturm et al., 2001; Tape et al., 2006; Post et al., 2009; Naito and Cairns, 2011; Myers-Smith et al., 2011a; Elmendorf et al., 2012; Macias-Fauria et al., 2012). Shrubs form canopies that alter litter inputs to the soil, the tundra microclimate and therefore soil and permafrost temperatures (Myers-Smith et al., 2011a); in addition, they provide important habitat and food sources for other organisms (Kitti et al., 2009; Tape et al., 2010; Ehrich et al., 2012; Ims and Henden, 2012; Li et al., 2013). Therefore, increases in shrub cover, abundance and canopy height will alter biodiversity, soil nutrient cycling, carbon storage, water and energy exchange (Eugster et al., 2000; Sturm et al., 2001; Liston et al., 2002; Chapin et al., 2005; Sturm, 2005; Wookey et al., 2009; Blok et al., 2010). Consequently, there is a growing need to better understand the drivers of arctic and alpine shrub growth and population dynamics to improve projections of tundra vegetation change.

Shrubs provide a multi-decadal record of environmental changes in tundra ecosystems. Shrub dendrochronology, the dating of annual growth rings, has been used to reconstruct climate (e.g., Schmidt et al., 2006; Weijers et al., 2010; Rayback et al., 2012a), measure landscape-level responses to climate and disturbance (Forbes et al., 2010; Hallinger et al., 2010; Blok et al., 2011; Macias-Fauria et al., 2012; Tape et al., 2012), date landslides (Gers et al., 2001) and permafrost disturbances (Gärtner-Roer et al., 2013; Leibman et al., 2014), reconstruct glacial history (e.g., Roer et al., 2007; Owczarek, 2010; Buras et al., 2012), describe rates of isostatic rebound of shorelines (von Mörs and Bégin, 1993), assess land-use history and human impacts in tundra ecosystems (Rixen et al., 2004; Speed et al., 2011) and more. By analyzing growth over time, growth–climate relationships, aging individuals, or examining wood anatomy or wood scarring, both the timing and extent of landscape-level vegetation change or geomorphic disturbances can be determined. Much of the current shrub dendroecological literature focuses on vegetation dynamics in relation to climate, but like with tree-ring research, dendroecology extends far beyond dendroclimatology to applications across the Earth Sciences (Stoffel and Bollschweiler, 2008).

The application of dendrochronological methods requires adaptation of the standard techniques developed for tree-ring analyses (Fritts, 1976; Cook and Kairiūkštis, 1990; Schweingruber, 1996) to the

specific morphology and ecology of shrubs. Like trees, shrubs typically add a layer of wood each year, which leads to shoot and root elongation and is visible as growth rings in the cross-sections of wood. However, unlike many tree species, tundra shrubs: (1) exhibit prostrate or multi-stemmed growth forms; (2) can reproduce clonally; (3) have below-ground connections among individuals; and (4) can allocate growth to different stems both above and belowground in complex ways (reviewed below). These physiological and ecological characteristics of shrubs often confound age determination and analyses of radial and axial growth. Modified or novel approaches are thus needed for sample collection, processing, analysis, and interpretation of shrub growth from annual rings and stem increments (Fig. 1).

Shrub growth measurements have been used to: (1) quantify climate-sensitivity of growth; (2) reconstruct climate; (3) establish linkages to satellite-derived vegetation greening; (4) document advances of the shrubline ecotone; and (5) investigate landscape-level disturbances (Table 1).

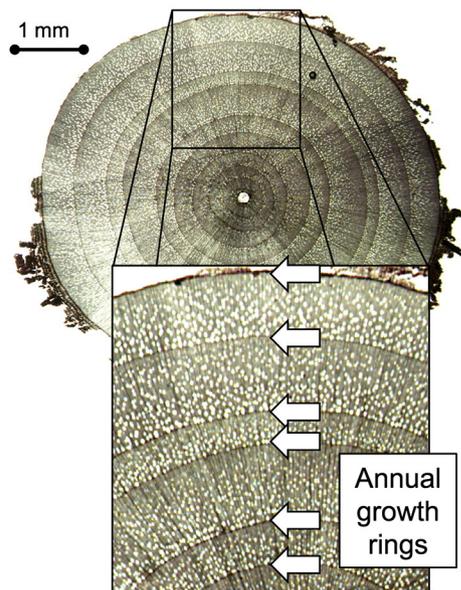
The application of dendroecological analysis to shrub species is a relatively recent advance of the last three decades (Woodcock and Bradley, 1994; Schweingruber and Poschold, 2005). As the number of studies using shrub growth measurements increases, so too, does the need for better coordination of methods to promote inter-study comparisons and the integration of data among sites and species. In this paper, we review the dendrochronological methods for the measurement and analysis of shrub growth (Fig. 2). We hope that this review can serve as a guide for future dendroecological research on tundra shrub species, stimulating further advances in this field.

2. Important botanical considerations of shrub species

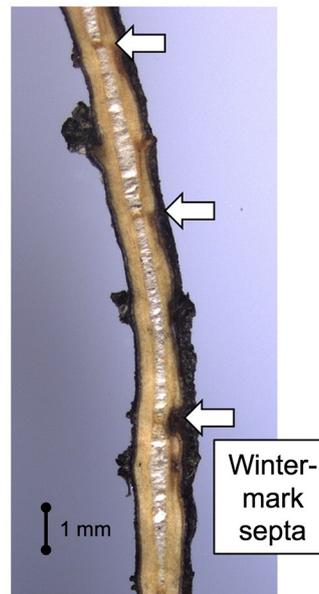
2.1. Growth form

Shrubs exhibit varied growth forms as a result of genetic differences or phenotypic plasticity in response to the growing environment (e.g., extreme cold, shade; snow cover, soil accumulation, and soil movement), which influences the interpretation of radial and axial growth measurements. Reduced apical dominance in shrubs may lead to the development of multiple stems and large clonal patches and competition or facilitation among species (interspecific), individuals of the same species (intraspecific), and stems within the same plant (e.g., self-shading; Carlsson and Callaghan, 1991; Pajunen, 2009;

a) Annual growth rings in *Salix alaxensis*



b) Annual stem increments in *Cassiope tetragona*



c) Annual Stem Increments in *Salix pulchra*

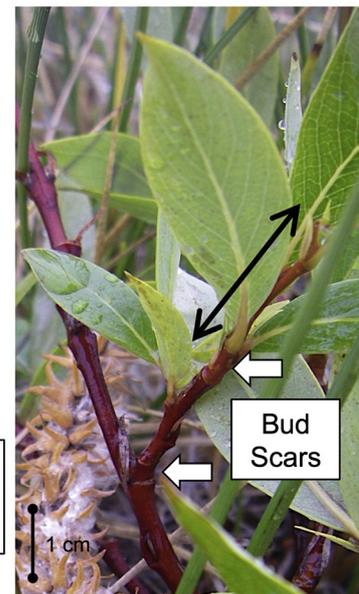


Fig. 1. Three variables that can be measured to assess annual growth dynamics: (a) radial growth (growth rings), (b) axial growth (wintermarksepta, Rozema et al., 2009), (c) and stem increments.

Douhovnikoff et al., 2010; Pajunen et al., 2010). Shrubs are often defined as woody perennial plants, without a definite crown, less than 3 m high, and having multiple stems growing from the same root (FAO, 2004; Körner, 2012). However, this definition does not provide clear criteria for distinguishing shrubs from trees (Gschwantner et al., 2009), particularly when tree growth is stunted (e.g., krummholz) as is the case in many harsh environments. A variety of terms, therefore, are necessary to describe shrub growth forms (Table 2), and these different growth

forms need to be taken into account when conducting comparative dendroecological analyses.

2.2. Longevity

Many tundra shrub species can be very long lived, and have been aged as decades to centuries old (Table 3).

Table 1

Research themes and questions investigated using growth measurements in tundra shrub species.

Theme	Question	Studies	Method	Species	Timescale
Climate	1. Climate sensitivity of shrub growth	Bär et al., 2006 (2007), Rozema et al., (2009), Forbes et al. (2010), Hallinger et al. (2010), Rixen et al. (2010), Weijers et al. (2010, 2012, 2013a, b), Blok et al. (2011), Hallinger and Wilmking, (2011), Myers-Smith (2011), Buizer et al. (2012), Macias-Fauria et al. (2012)	Annual growth rings, stem increments, wintermarksepta	<i>Salix</i> spp., <i>Betula</i> spp., <i>Alnus</i> spp., <i>Juniperus</i> spp., and others	Decades to last century (1900s onward)
	2. Link shrub growth and satellite-derived vegetation greening	Forbes et al. (2010), Blok et al. (2011), Macias-Fauria et al. (2012)	Annual growth rings	<i>Salix</i> spp., <i>Betula</i> spp., <i>Alnus</i> spp.	Duration of the satellite record (1970s onward)
	3. Climate/environment reconstruction	Rayback and Henry (2005, 2006), Schmidt et al. (2006, 2010), Liang and Eckstein (2009), Rozema et al. (2009), Liang et al. (2012), Weijers et al. (2010, 2013b), Rayback et al. (2011, 2012a,b), Buras et al. (2012), Buchwal et al. (2013)	Annual growth rings, leaf scars, wintermarksepta	<i>Cassiope tetragona</i> , <i>Rhododendron</i> spp., <i>Salix</i> spp.	Decades to centuries (before the instrumental climate or environmental record)
Population dynamics	1. Pulses of recruitment 2. Changes in age distributions 3. Advance of the shrubline	Boudreau, Ropars and Harper (2010), Hallinger et al. (2010), Hallinger and Wilmking (2011), Myers-Smith (2011)	Annual growth rings	<i>Empetrum hermaphroditum</i> , <i>Salix</i> spp., <i>Betula</i> spp., <i>Alnus</i> spp., <i>Juniperus</i> spp.	Decades to last century (1900s onward)
Disturbances and landscape change	1. Landslide, permafrost, glacial history, isostatic rebound	von Mörs and Bégin (1993), Roer et al. (2007), Owczarek (2010), Buras et al. (2012), Tape et al. (2012), Gärtner-Roer et al. (2013), Gers et al. (2001), Leibman et al. (2014)	Annual growth rings	<i>Salix</i> spp., <i>Betula</i> spp., <i>Alnus</i> spp.	Half century
	2. Human disturbance	Rixen et al. (2004)	Annual growth rings, wood anatomy – scaring	<i>Vaccinium</i> spp., <i>Betula</i> spp.	Decades
	3. Herbivory	Predavec et al. (2001), Speed et al. (2011)			One decade

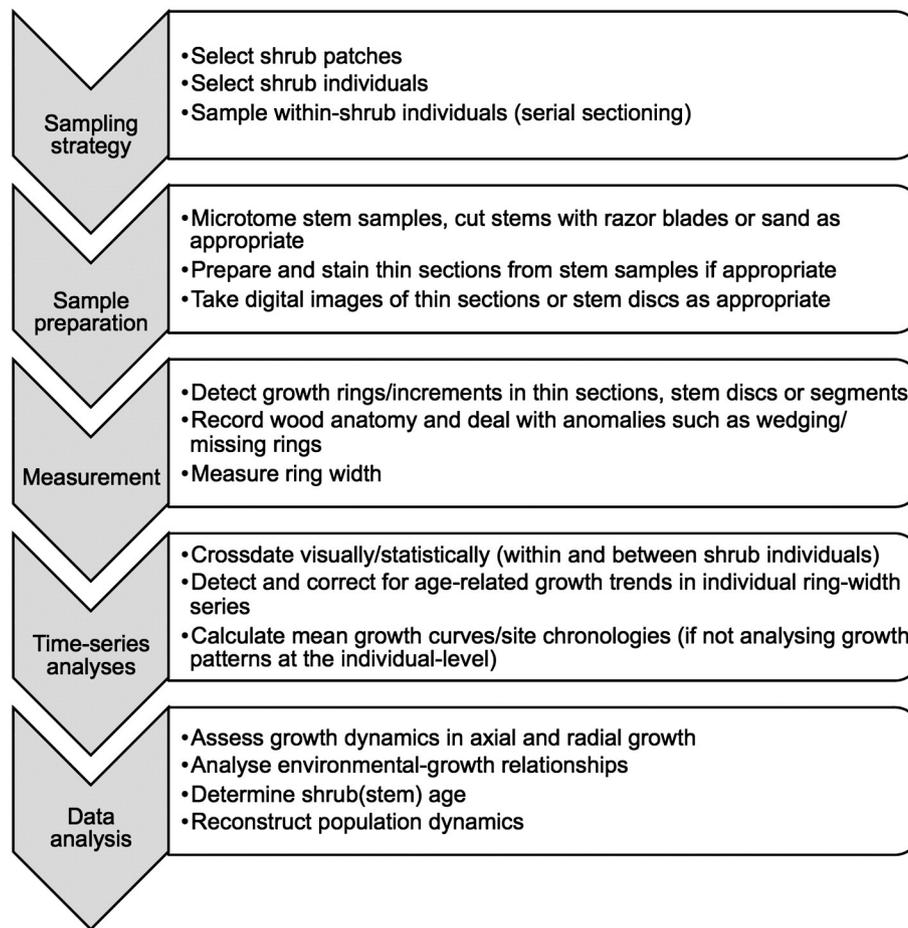


Fig. 2. A schematic overview of the steps involved in the processing of shrub growth-ring data.

Despite stem dieback induced by age, exposure or disturbance, patches of clonal shrub species continue to grow and expand for long time periods, leading some researchers to suggest that these shrubs lack age-related senescence and could be considered 'immortal' (De Witte and Stöcklin, 2010). The annual growth patterns of long-lived

shrubs contain records of the growing conditions extending back beyond the instrumental record or provide information for sites where meteorological records have not been collected (Rozema et al., 2009; Rayback et al., 2012a). However, due to stem dieback, estimating the date of establishment of shrub patches poses a significant challenge.

Table 2

Definitions of tundra shrub terminology. Descriptions of canopy heights or growth form can reflect genetic differences among species or plastic responses to the environment.

Type of description	Term	Definition
Height	Tall shrub (~50 cm or greater)	High canopy height – does not necessarily denote a closed canopy growth form (e.g., <i>Alnus</i> , <i>Betula</i> and <i>Salix</i> spp.)
	Low shrub (~20–50 cm)	Intermediate canopy height between tall and dwarf/prostrate species (e.g., <i>Betula glandulosa</i> , <i>Potentilla</i> spp., some <i>Salix</i> spp.)
	Dwarf shrub (less than ~20 cm)	Short canopy height. Growth form often prostrate or decumbent (e.g., <i>Salix polaris</i> , <i>Salix arctica</i>)
Growth-form	Canopy-forming	Creates a canopy layer above the surrounding tundra
	Upright/erect (~30 cm or greater)	Vertical growth – does not necessarily denote a closed canopy growth form
	Decumbent (~5–30 cm)	Lying or growing on the ground but with erect or rising stem tips (e.g., <i>Betula nana</i> , some <i>Salix</i> spp.)
Ring and wood anatomy	Prostrate (less than ~10 cm)	Lateral growth, growing flat along the ground – lacking potential to grow vertically (e.g., <i>Salix arctica</i>)
	Reaction wood	A hypernym for tension wood (angiosperms) or compression wood (conifers), formed on one side of the stem to counteract mechanical stress and realign growth
	Partial ring	A synonym for wedging ring, a partially missing, discontinuous and incomplete ring due to failure of cambial activity
	Locally missing ring	Missing ring absent in one stem disc but present in other stem discs
	Totally missing ring	Missing ring absent in the whole plant but present in other plants of the population

Table 3

Examples of stem age estimates for the oldest individuals of a variety of shrub species growing in tundra ecosystems. Tundra shrub species can be very long lived, and these stem estimates are likely under estimates of the true age of the genetic individual that could have been expanding clonally overtime.

Species	Age (years)	Locations	References
<i>Alnus viridis</i> subsp. <i>fruticosa</i>	111	Laborovaya, YNAO, Russia	Macias-Fauria et al. (2012)
<i>Betula glandulosa</i>	82	Baker Lake, Nunavut, Canada	Lévesque, unpublished data
<i>Cassiope tetragona</i>	183	Endalen, Svalbard	Weijers et al. (2010)
<i>Juniperus nana</i>	334	Abisko, Sweden	Hallinger et al. (2010)
<i>Juniperus pingii</i> subsp. <i>wilsonii</i>	324	Nam Co, Tibet, China	Liang et al. (2012)
<i>Salix lanata</i>	99	Yuribei River, YNAO, Russia	Macias-Fauria et al. (2012)
<i>Salix arctica</i>	270	Sverdrup Pass, Ellesmere Island, Nunavut, Canada	Boulanger-Lapointe et al. (2014)
<i>Vaccinium myrtillus</i>	30	Stillberg, Switzerland	Rixen et al. (2010)

2.3. Below-ground connections

Shrubs can grow through clonal means to form large patches across the landscape. In addition to clonal growth, some shrubs (like certain trees) can transfer carbon via mycorrhizal connections between the root systems of genetically different individuals of the same species (Van Der Heijden and Horton, 2009; Deslippe and Simard, 2011), thereby extending the functional biomass beyond the individual. Due to these connections, individuals could have enhanced or reduced synchrony of growth in certain environments.

3. Sampling of individuals

The first important consideration when undertaking a dendroecological study of shrub species is how to sample individuals across the landscape. A variety of sampling designs can be used, involving subjective, systematic, or random sampling. The research question under investigation will dictate the appropriate sampling procedure (Nehrbass-Ahles et al., 2014). Subjective sampling of larger and older individuals with regular growth and dominant stems may be preferable when conducting climate reconstructions. In contrast, systematic sampling is appropriate for estimating rates of lateral expansion of shrub patches, and random or systematic sampling across environmental gradients (e.g., elevation) is required to determine age distributions, growth rates, and stem turnover.

3.1. Accounting for herbivory and human impact

Zoogenic and anthropogenic influences should be accounted for when sampling. Browsing, grazing, trampling by domestic or wild herbivores and human land-use can influence shrub growth (Hofgaard, 1997; Cairns et al., 2007; Moen, 2008; Kitti et al., 2009; Olofsson et al., 2009). Depending on the intensity of the initial impact, such disturbances can be apparent for decades or even centuries after sites are abandoned (Forbes et al., 2001). When such impacts are cryptic at ground level, it may be necessary to combine remote sensing and local knowledge from residents to determine the nature and extent of land-use and its implications for woody plant growth (Forbes et al., 2010; Kumpula et al., 2011). Land-use can be deliberately included in the sampling design to quantify the impact of human management on growth and recruitment in shrub species (Ravolainen et al., 2010, 2013; Speed et al., 2011).

4. Sampling within shrub patches and along the stem

Once the method of sampling across the landscape has been chosen, sampling within shrub patches and stem selection needs to be considered. Clonal growth of tundra shrubs obscures the identification of genetically distinct individuals in areas of continuous cover. Underground connections, observations of sex, leaf and stem morphology, or genetic markers can help to distinguish individuals (Douhovnikoff

et al., 2010). Several factors should be considered when sampling individuals for growth-ring analysis: (1) avoidance of growth deformities; (2) determination of the oldest stem; (3) identification of the root collar; (4) excavation of stems and roots; and (5) serial sectioning.

4.1. Growth deformities

To conduct climate reconstructions, sampling should avoid stems with obvious malformations, scarring or rot. Examples of growth irregularities include reaction wood (tension wood in broad-leaved and compression wood in coniferous species), missing or partial rings, frost rings, wounding or scarring due to biotic (e.g. herbivory) and abiotic factors (e.g. cryoturbation) and lobed growth form (Fig. 3, Schweingruber and Poschlod, 2005). However, excluding individuals with irregular growth will bias age estimations or other analyses requiring randomized or systematic sampling designs.

4.2. Determination of the oldest stem

Sampling the oldest stem for growth-ring analysis provides the longest record of growth; however, any age estimates based on the largest stem are only approximate, and the actual genet age may be much older (De Witte et al., 2012). It is often not possible to visually determine the oldest stem either because stem height and diameter are not correlated with stem age or the oldest stem has died and decomposed. Remotely-sensed data from repeat aerial photography or high-resolution satellite imagery can help to identify old individuals and changes in patch size overtime (Forbes et al., 2010; Myers-Smith et al., 2011b; Tape et al., 2012). However, a subjective sampling protocol is often required, such as selection of the tallest and thickest stems; and therefore, the resulting age estimates are often underestimates.

4.3. Identification of the root collar

Sampling should be conducted at or above the root collar, to determine the age of a shrub stem or the longest record of growth. Identification of the root collar mostly requires destructive harvesting of the whole shrub or several main stems. Complex shrub morphologies including adventitious roots in decumbent growth forms or buried stems can complicate identification of the root–stem interface. Specific wood-anatomical features related to cell size and presence or absence of pith generally facilitate the differentiation between stem and root tissue; however, changes in these features often evolve gradually along the root–stem interface (Schweingruber and Poschlod, 2005). To capture the maximum number of growth rings, detailed serial sectioning (see description below) can be conducted in the field and root collar identification using wood anatomy analysis can be performed in the laboratory.

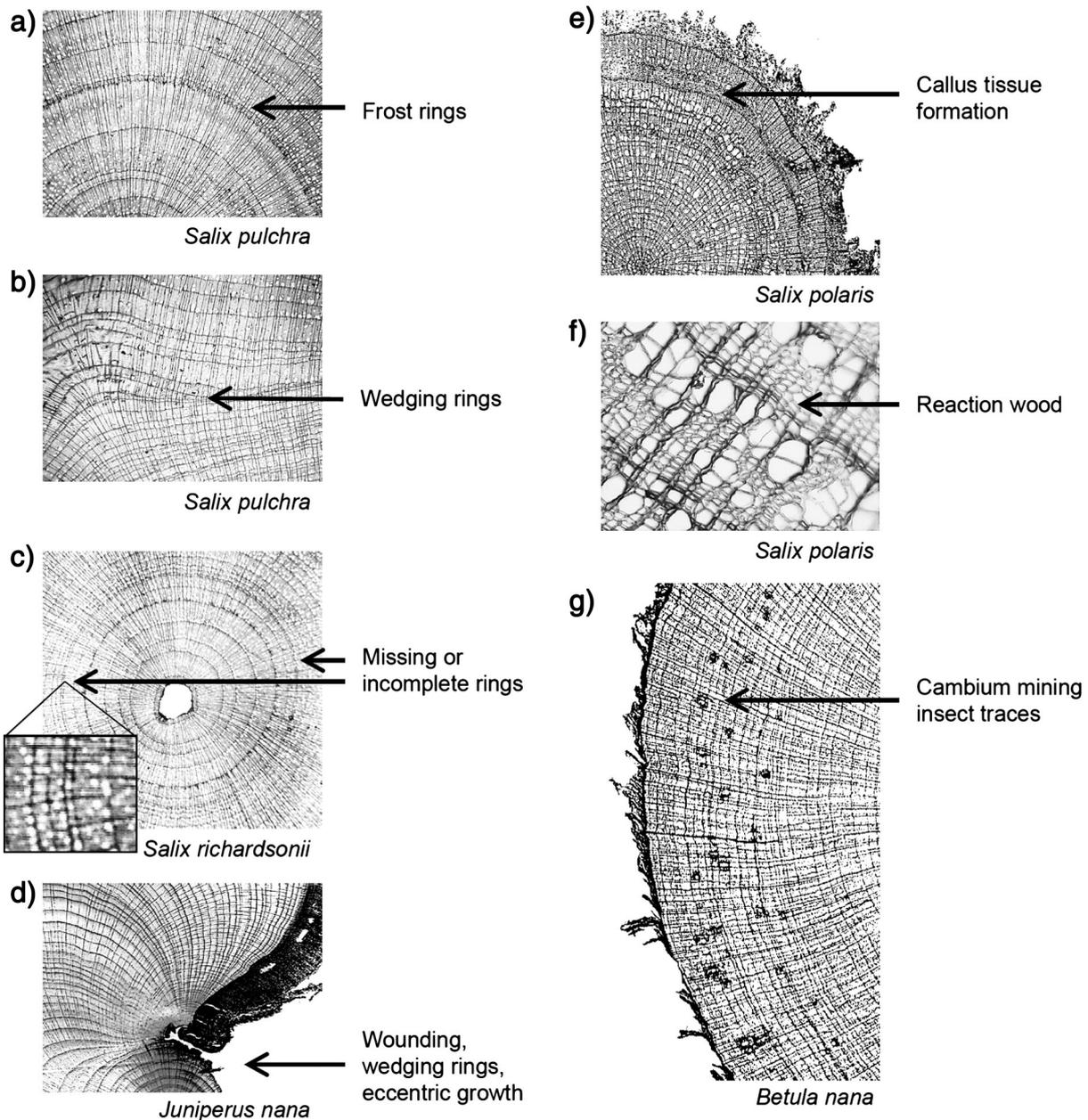


Fig. 3. Cross-sections of shrub stems illustrating (a) frost ring, (b) wedging ring, (c) missing ring, (d) wounding, (e) callus tissue formation, (f) reaction wood and (g) insect traces. Analysis of wood anatomy needs to be conducted in parallel with the measurement and crossdating of ring width series.

4.4. Stem and root excavation

To obtain the longest possible growth record in prostrate species with buried stems, excavation is often necessary (Hallinger et al., 2010; Owczarek, 2010). In trees, stem burial can lead to an abrupt decline in ring width in the affected part of the stem (Stoffel and Bollschweiler, 2008) and this same phenomenon has been observed in the shrub species *Salix pulchra*, *Betula nana* and *Betula pubescens* (Blok and Sass-Klaassen, unpublished data). Completely missing outer rings in stem segments either very close to the ground or in buried stems have been observed in *B. nana*, *Juniperus nana*, *Pinus mugo*, *Salix alaxensis* and *Salix glauca* (Wilmking et al., 2012). Where stem preservation is low, e.g., in situations where weathering, herbivory or other mechanical stresses lead to partial or total stem destruction (Hallinger et al., 2010), roots may preserve more information than stems and should be sampled together with the stem to quantify allocation across the plant.

4.5. Serial sectioning

Serial sectioning should be conducted to correct for possibly missing rings and capture variation in ring width along the stem (Fig. 4). Serial sectioning, the sampling of discs at multiple points along stems and roots, allows for very accurate age determination and the reconstruction of stem elongation rates. This approach, first applied to shrub dendrochronology by Kolishchuk (1990), has since been successfully applied to different shrub species such as *Empetrum nigrum* subsp. *hermaphroditum* (Bär et al., 2006, 2007), *J. nana* (Hallinger et al., 2010), and *Salix polaris* (Buchwal et al., 2013).

Stem discs should be marked, photographed and harvested at regular intervals along the stem and root collar. When harvesting, sections should be labeled to denote the upper and lower surfaces of each disc and their original position along the stem. We recommend sampling every 2–10 cm for slow growing species (e.g., *S. polaris*, *Salix arctica*, *Calluna vulgaris*), every 10–30 cm for moderately statured shrub species

Box 1

Wood anatomy analysis and stable isotopes.

Basic analysis of wood anatomy is necessary when measuring ring widths in shrub species for the identification of missing and partial rings; however, detailed analysis of anatomical structures is rarely used to associate growth with environmental conditions (Schweingruber and Poschlod, 2005). Wood anatomy has been used to investigate the relationship between growth and moisture in *Empetrum nigrum* subsp. *hermaphroditum* (Bär et al., 2008), rock glacier movement in *Salix helvetica* (Roer et al., 2007; Gärtner-Roer et al., 2013), and the relative frequency of scarring has been used as an index of changes in lemming populations (Predavec et al., 2001). Quantitative analysis can include measurement of the density, size and wall thickness of anatomical structures (i.e., cells, vessels and fibers in deciduous species) or growth irregularities such as reaction wood, scars or frost rings (Fig. 3). Wood density can be measured using X-ray scans of wood cores or thin sections (Schweingruber, 1988). Including wood anatomy and density into growth-ring analyses will give further insight into physiological responses of shrub growth to changing environmental conditions.

The use of stable isotopes, in addition to ring width measurements and analysis of wood anatomy, has the potential to greatly improve our ability to interpret and predict climate–growth relationships for shrub species. Stable isotopes, such as carbon, nitrogen, oxygen and hydrogen, are incorporated through biochemical processes into the physical structure of the plant, and the isotopic ratios are sensitive to environmental factors such as temperature, irradiance, soil moisture status, relative humidity and nitrogen sources (Farquhar et al., 1989; McCarroll and Loader, 2004). While stable isotope analysis of tree rings has gained prominence in dendrochronology over the past three decades (McCarroll and Loader, 2004), there are few applications to arctic and alpine shrubs.

The application of stable isotope analysis in many shrub species is a challenge due to narrow annual growth rings; however, species with annual stem increments such as *Cassiope* spp. provide ample sampling material. Previous studies based on stable isotope ratio time series derived from *Cassiope tetragona* and *Cassiope mertensiana* investigated plant–climate relationships and successfully reconstructed past climate (Welker et al., 2005; Rayback et al., 2012a, b). However, recent findings suggest that secondary growth influences the climate signal in annual stem length increments in *Cassiope* spp., and only the first ring layer and pith of each annual fragment should be used for isotopic analysis (Weijers et al., 2013a). Therefore, stable isotope analysis needs to be conducted with care, incorporating high precision sampling within growth increments, and taking into account the variation in isotopic signature of wood across the growing season.

(e.g., *S. pulchra*, *J. nana*), or every 50–100 cm for investigations in large-statured species (e.g., *P. mugo*, *Alnus viridis*). Fresh samples should be stored in paper bags at a cool, dry place to prevent rot.

5. Sample preparation

Sample preparation for growth-ring analysis of shrub species differs from the methods most often used with tree species. Like with tree

species, ring widths of fast-growing shrubs can be measured from cores or discs using a sliding stage or image analysis software. The visibility of ring boundaries and cell structure can be enhanced either by sanding with progressively finer grit sandpaper (large diameters) or by shaving stem sections with a razor blade (small diameters). The contrast between cell walls and lumen can be further enhanced by staining solutions (see below) and subsequently rubbing chalk onto the prepared surface. However, thin sectioning is required to measure the rings and analyze wood anatomy in shrub species with narrow rings (Schweingruber et al., 2011).

5.1. Thin sectioning

Thin sectioning allows for measurement of ring widths and detailed wood anatomy analysis, which is a rarely tapped source of information on the ecology of tundra ecosystems (Gärtner and Schweingruber, 2013). In brief, thin-sectioning consists of the preparation of thin stem cross sections (8–30 µm) using a sliding microtome, enabling the detection and measurement of narrow growth rings either directly under a light microscope or from digital images taken from the sections. Before sectioning, samples can be boiled or soaked in water to rehydrate desiccated tissue. If necessarily, staining solutions (e.g., 1% Safranin solution, dark soya sauce, ink, or florescence) can be used to enhance differentiation between rings and lignified or non-lignified cells (Lussier et al., 2004; Schweingruber et al., 2006). Sections can be mounted on slides using water or mounting media and can be backlit to enhance ring visibility. We recommend taking high resolution photographs or scans of thin sections including a reference scale. When necessary, images should be modified to enhance contrast, saturation or sharpness before measurements are performed using image analysis software.

6. Growth-ring measurements

After sample preparation, ring widths can be measured, stem ages can be estimated and wood-anatomical characteristics can be examined. However, when undertaking dendroecological measurements on shrub species, a number of considerations must be taken into account. Shrub growth form, age, environmental conditions, and exposure to disturbance interact to determine the formation or lack of growth rings and their eccentricity (Fig. 3). Non-uniform cambial activity around the stem circumference may cause partial (wedging) or missing rings (Fig. 3, Schweingruber and Poschlod, 2005). Like with trees, shrub measurements need to account for growth irregularities, but the appropriate methods differ as the growth irregularities are often greater in tundra shrub species growing in extreme environments.

6.1. Ring width measurements

Measurements along multiple radii extending from the center of the stem cross section towards the cambium are required to account for growth irregularities (Fig. 5, Buras and Wilmking, 2014). Measuring two to four radii per disc is usually sufficient in tall shrubs with upright growth forms (e.g., *S. pulchra*, *Betula glandulosa*), but up to eight radii may be needed for prostrate shrubs (e.g., *J. nana*, *S. arctica*). All radii from one disc should be crossdated to assign the correct calendar year to each ring based on matching patterns of ring development before these data are further analyzed (Fritts, 1976; Stokes and Smiley, 1996). Crossdating serial sections ring-width series from can be used to identify missing rings at the base of the stem (Figs. 4 and 6, Wilmking et al., 2012).

6.2. Crossdating

Crossdating ring-width series is the process of matching ring width pattern between different measurement series with the goal to obtain correctly dated series. Crossdating is a hierarchical process that

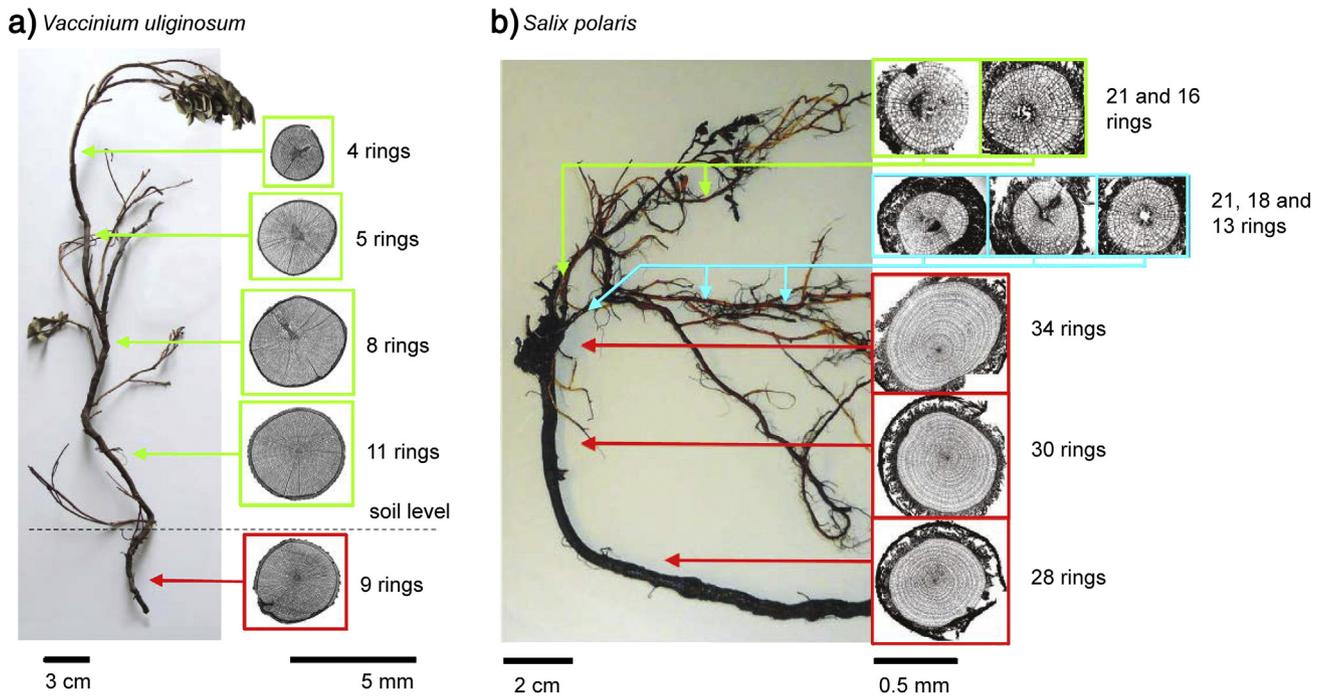


Fig. 4. Serial sectioning can facilitate the identification of missing outer rings and the oldest part of the plant. These examples of *Vaccinium uliginosum* and *Salix polaris* illustrate the difficulty distinguishing the oldest part of the plant in the field.

compares radii, serial sections, stems within individuals, and individuals within a population. Crossdating can be conducted on raw or detrended growth series depending on the analytical approach. It is an iterative process involving the identification of marker or pointer years, e.g. extremely narrow or wide rings and/or specific wood-anatomical features. Crossdating should be conducted visually, based on comparison of ring-width series and can then be verified by statistical techniques.

Crossdating will allow for the identification of partial rings, and locally (missing within parts of the plant) or completely (missing within the plant but present in other individuals in the same population) missing rings (Fig. 3), which occur much more frequently in tundra shrub species growing in harsh growing environments. Identification of missing rings or combination of partial rings to create dated annual growth series should be conducted when wood anatomical features suggest irregular growth. Changes made to ring width series during crossdating should be carefully documented so that methods are repeatable, and that records of missing or partial rings can be incorporated into dendroecological analyses. Many resources are available describing the visual and statistical techniques available for crossdating in trees that can also be applied to shrubs (e.g., Schweingruber, 1988, 1996). Once the data have been properly measured and crossdated, the range of data analysis techniques is vast.

7. Stem-increment measurements

Repeated stem-increment measurements are another useful means for assessing growth in many shrub species. Non-destructive sampling can be conducted by measuring annual growth each year in the field, or stem harvesting can be conducted and growth increment can be measured using bud scars or wood anatomical features from longitudinal sections (i.e., wintermarksepta), or reconstructed using several dated stem sections along an individual stem (Hallinger et al., 2010). Stem increments can be correlated with various climate variables (Rayback and Henry, 2005, 2006; Wipf et al., 2009; Weijers et al., 2010, 2012, 2013b) and disturbances such as herbivory (Ravolainen et al., 2013). Stem-increment data are subject to many of the same constraints as growth-ring measurements and can be treated in much

the same way during data analysis. However, there are some additional factors that should be considered, such as the best method of stem-increment measurement for a given species and the potential high variation in growth among stems of the same plant.

There are a variety of methods used to measure stem increments among different tundra shrub species. Annual growth is visible as the distance between scars of winter buds in *Salix* and *Vaccinium* spp. (Fig. 1), or as patterns of leaf length or leaf scars in *Cassiope* spp. (Callaghan et al., 1989; Havström et al., 1993, 1995; Johnstone and Henry, 1997; Rayback and Henry, 2006; Rayback et al., 2011, 2012a,b; Weijers et al., 2012, 2013a) or *E. nigrum* subsp. *hermaphroditum* (Buizer et al., 2012). These features often remain visible for several years and allow for measurements of past growth increments along a stem; however, the visibility of older scars varies among individuals and species.

Inter-annual growth of *Cassiope tetragona* can also be measured using wintermarksepta (Rozema et al., 2009; Weijers et al., 2010, 2012, 2013a, b). Wintermarksepta are dark bands in the pith, which are visible in longitudinal stem sections that are formed at the end of the growing season. Wintermarksepta correlate well with leaf node scar measurements in *C. tetragona* (Weijers et al., 2012), but have not yet been observed in other heather species (Rayback, unpublished data; Weijers, unpublished data).

Annual stem increments are often variable among stems and this measure does not necessarily provide a good integrator of growth for the plant or shrub vegetation community as a whole. Variability in annual increments between stems on the same individual is very high for *Salix* species (Johnstone, University of Saskatchewan, unpublished data) and high rates of stem dieback and turnover have been observed in species such as *Vaccinium myrtillus* (Rixen et al., 2010). Shoot length has been found to decrease with age (e.g., *V. myrtillus*, *Vaccinium uliginosum* and *Salix herbacea*), with the longest increments occurring on lateral shoots from old buds and on first-year ramets (Wijk, 1986). Differential responses of primary and secondary growth to warming, fertilization and shading have been observed in the dwarf shrub species *C. tetragona*, *Empetrum hermaphroditum* and *B. nana* in Abisko, Sweden (Campioli et al., 2012a), and differential responses of stem increment

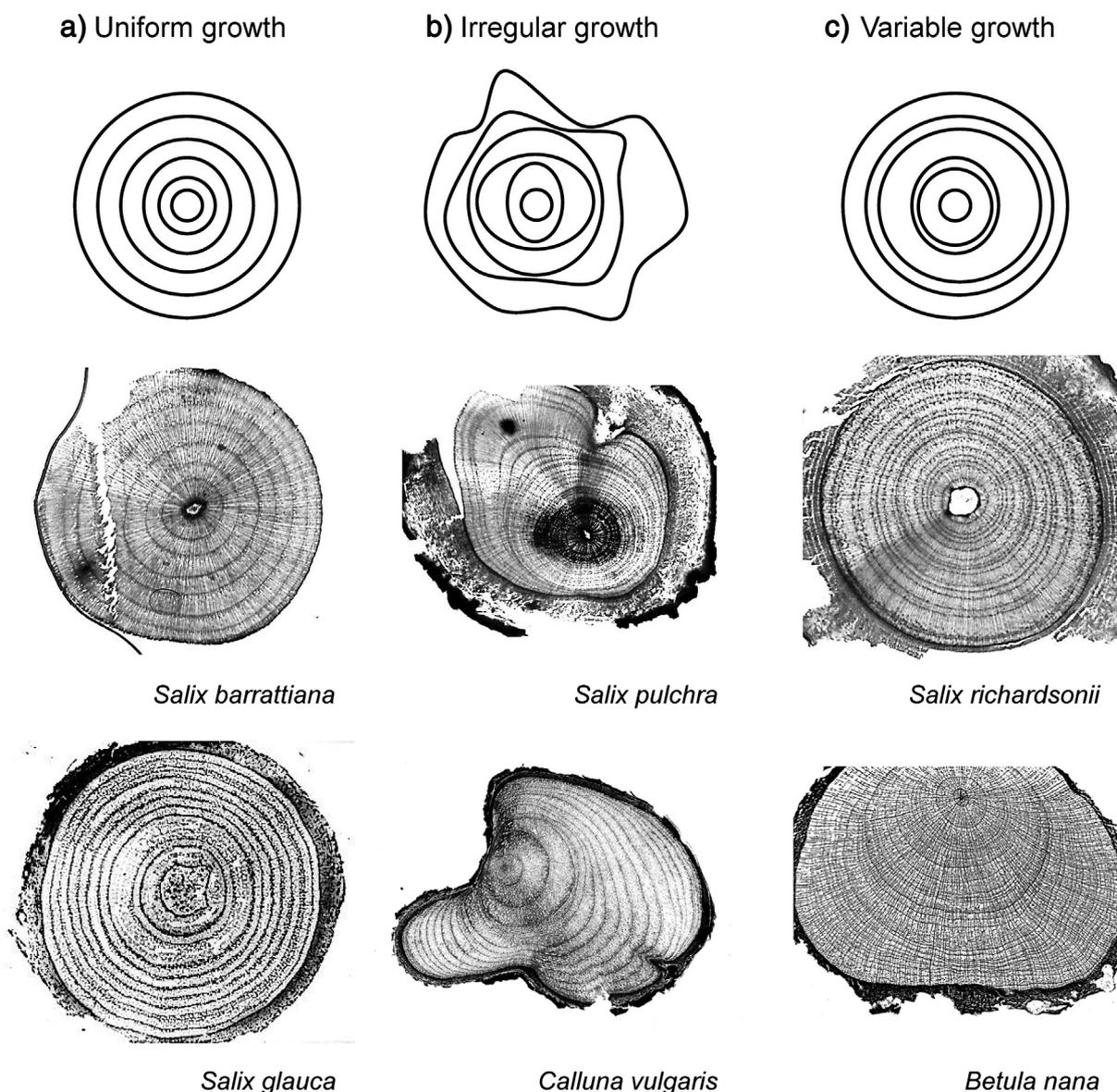


Fig. 5. Annual growth-ring patterns can differ dramatically, with rings having (a) uniform, (b) irregular, or (c) variable growth. This growth variation could reflect the ecology of the plant and will influence the interpretation of growth climate analyses.

growth and above ground biomass to soil warming were observed in the species *V. myrtillus*, *Vaccinium gaultherioides* and *E. hermaphroditum* in the Swiss Alps (Anadon-Rosell et al., 2014). Consequently, variability, turnover, age-growth dependency and competition among stems, individuals, and species should be considered when measuring stem elongation over multiple years, as this can limit the potential for correlation with climate or other environmental variables. Few studies compare lateral and axial growth measurements for the same shrub individuals (e.g., Shaver, 1986; Bret-Harte et al., 2002; Hallinger et al., 2010; Campioli et al., 2012b), and this is a much needed next step for the field to identify whether both measurements are good proxies for the overall growth of the plant for the shrub species under investigation.

8. Standardization and chronology development

Dendrochronological methods involve standardization of ring width or stem-increment series and the building of chronologies that summarize the growth of multiple individuals of the same species at a site. Before analyzing growth measurements from shrub species, several

factors should be considered: (1) age-related growth trends; (2) method of detrending; and (3) variation in growth along the stem.

8.1. Age-related growth trends

Detrending of ring width series is used to account for ontogenetic trends (Fritts, 1976; Cook and Kairiūkštis, 1990). As shrub species age, there may be a decline in the width of radial growth with the increase in stem diameter (Fig. 6), or constant/increasing growth with greater biomass as the shrub individual is able to access greater resources. Narrow or completely missing rings are often observed in samples from older individuals (Wilmking et al., 2012). Age-related trends (most often declines, but also increases) in ring width or shoot length have been found in tall *Salix* spp. (Blok et al., 2011; Tape et al., 2012) and dwarf shrub species such as *C. tetragona* (Weijers et al., 2010, 2012, 2013b) or *V. myrtillus* (Rixen et al., 2010). However, no consistent age-related trends in ring width have been found for individuals of *J. nana* in Northern Sweden (Hallinger et al., 2010), *Salix* spp. in the Yukon Territory (Myers-Smith, 2011) or *A. viridis* subsp. *crispa* in interior Alaska

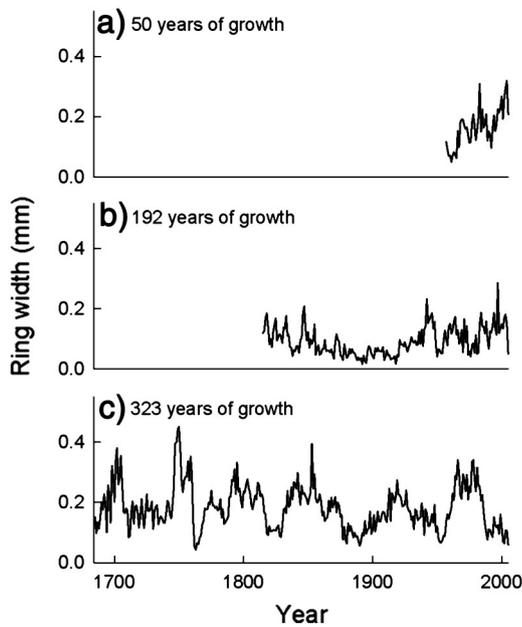


Fig. 6. Not all shrub species exhibit age-related growth trends such as the commonly observed negative exponential growth trend in trees. This is likely due to variable allocation of resources for growth to different stems overtime. Here, the annual growth of three *Juniperus nana* individuals from Northern Sweden is displayed representing different life stages (323, 192 and 50 years of age). The ring width series (a) is an average of four height levels (with two radii each); if this individual was to be included into a chronology, separate detrending of the different height levels might be appropriate to make sure that no artificial growth increase (trend distortion) towards the end of the ring width curve is occurring. The two lower ring width series (b, c) are each averages of two radii of the lowest sampling height level on the main shrub stem. In (b), a decrease of growth is followed by an increase after half of the shrub's lifespan. In (c), no clear trend can be denoted. Note that periods of strong growth can still occur at ages of more than 300 years (c).

(Tape et al., 2012). In cases where age-related growth trends are not evident, traditional detrending methods might not be appropriate.

8.2. Method of detrending

Detrending should be conducted with caution so as not to obscure actual trends in the environmental factor of interest or create artificial results (Fig. 7). When shrub growth exhibits an age trend, the choice of trend line and method of the ring width index calculation during standardization can strongly influence the results (Fig. 7). Negative exponential, flexible spline or linear relationships have been used in the detrending of tall shrub species (Forbes et al., 2010; Hallinger et al., 2010; Blok et al., 2011), and for wintermarksepta measurements of *C. tetragona* (Weijers et al., 2010, 2012, 2013b). If age-related growth trends are not apparent, detrending of ring width series using these methods is not appropriate and standardization alone will suffice.

8.3. Variation in growth along the stem

Ring widths in trees typically increase towards the tip of the stem (Krause and Eckstein, 1992), but this is not necessarily the case in shrub species (e.g., *J. nana*, *S. glauca*, *C. vulgaris*, *A. viridis*; Hallinger and Wilmking, 2011; Hallinger, Wilmking and Buras, unpublished data). Since ring widths do vary among different parts of the stem, we recommend standardizing the individual stem-level series gained from serial sectioning prior to averaging and integrate growth patterns along the stem or root (Büntgen and Schweingruber, 2010; Hallinger and Wilmking, 2011). The resulting growth series will better summarize the overall trends in growth across the entire plant. After standardization and summarization of radii, stem sections and stems within individuals, population-level chronologies can be built and/or statistical analyses conducted.

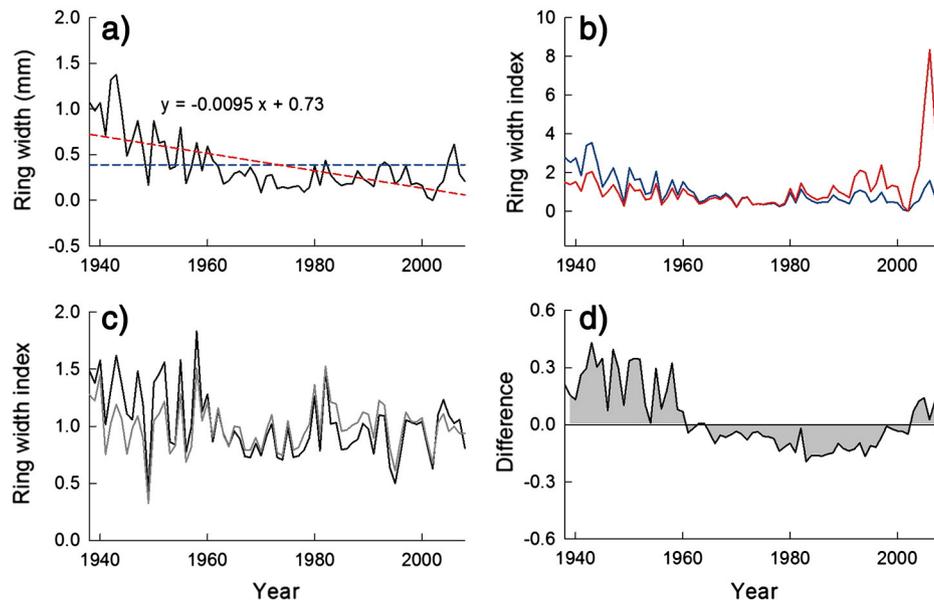


Fig. 7. Care needs to be taken when removing age-related growth trends (detrending). The choice of the detrending method can strongly influence the resulting standardized ring-width series, leading to over- or under-estimation of growth, and therefore can substantially influence the results of statistical analyses of growth relationships overtime. In dendrochronology, a detrended or standardized growth series is referred to as the ring width index (see y axis in plots b and c). Deliberate detrending of an individual ring width series of *Alnus viridis* subsp. *fruticosa* with a straight line with either a horizontal slope (indicating no age-related ring width trend; a, blue) or a negative slope (indicating a linear decreasing trend in ring width with age; a, red) leads to either an overestimation of the ring width index in the earlier part of the record (b, blue) or an overestimate of the most recent years of growth (b, red). At the chronology level, the use of two different detrending methods: (1) negative straight lines and dividing actual growth by estimated growth (c, dark gray) and (2) horizontal lines and subtracting actual by estimated growth after a power transformation (c, light gray) results in pronounced differences in the growth trends between the resulting chronologies in this example of 10 individuals (d).

8.4. Chronology development

Classical dendroecological analysis is an adaptation of time series analysis, where population-level chronologies are built to compare growth patterns over time. Chronologies are dimensionless indices of standardized growth data summarized among individuals. A growth chronology represents the variation in growth for any one year compared to the summarized growth across the time series. Many resources explain how to build chronologies in the tree-ring literature (Fritts, 1976; Schweingruber, 1988, 1996; Cook and Kairiūkštis, 1990) and various statistical packages exist for the standardization of growth data and the development of chronologies. Chronology development is only one potential analysis framework for shrub growth data and hierarchical statistical approaches nesting the growth of individuals within sites such as linear mixed models and Bayesian analyses are growing in popularity in the literature (see below). Regardless of the statistical approach, analysis of shrubring and stem increment data should be undertaken carefully taking into account the eccentricities of shrub growth.

9. Growth analyses

The number of different analyses that are being conducted with dendroecological data continues to increase, from dendrochronological studies investigating growth–climate relationships, ecological analyses of the sensitivity of growth to environmental factors, to explorations of recruitment rates and range expansion using age distribution data (Table 1). Patterns of inter-annual growth contain unique information on how tundra shrub species grow overtime and under different ecological conditions (Fig. 5). Growth varies with climate (e.g., Forbes et al., 2010), herbivory (e.g., Speed et al., 2011), competition for resources, site-specific variation in soil moisture, nutrients or microtopography (e.g., Macias-Fauria et al., 2012; Tape et al., 2012), among plant communities (Schmidt et al., 2010; Boulanger-Lapointe and Lévesque, unpublished data), or with reproductive effort overtime (Koenig and Knops, 1998). The appropriate data analysis technique will vary with the question under investigation, sampling strategy employed, and data collection methods, as discussed above. We are only now beginning to explore some of the different statistical options available for the testing of dendroecological research questions (see Box 1).

9.1. Dendroclimatic analysis

Dendroclimatic analysis, using site-level chronologies, has been used to document positive climate relationships between growing season temperatures and/or precipitation and growth in large-statured shrub species such as *J. nana* (Hallinger et al., 2010; Buras et al., 2012), *Salix lanata* and *A. viridis* subsp. *fruticosa* (Forbes et al., 2010; Macias-Fauria et al., 2012), *Salix lapponum* L. and *S. glauca* L. (Buras et al., 2012) or *S. pulchra* and *B. nana* (Blok et al., 2011), and in dwarf shrub species such as *C. tetragona* (Weijers et al., 2010, 2012, 2013b; Rayback et al., 2012a), *V. myrtillus* (Rixen et al., 2010) and *C. vulgaris* (Beil and Hallinger, pers. comm.). These analyses quantify the summarized climate responses of all individuals from a given site, but are less able to explore the variation in synchrony of growth and climate response among individuals.

Hierarchical statistical models and model comparisons, rather than chronologies, can alternatively be used for the analysis of growth rings (Schmidt et al., 2006, 2010; Ettinger et al., 2011; Speed et al., 2011), testing the ecological basis for the variability in growth between individuals. Synchronized growth between individuals at a site suggests that a large-scale factor such as regional climate is controlling growth (e.g. Bär et al., 2008; Macias-Fauria et al., 2012). In contrast, variable patterns of inter-annual growth between individuals suggest the importance of smaller-scale processes (e.g., interspecific competition or herbivory; Speed et al., 2011; Speed et al., 2013) or the modulation of regional

factors through local conditions (e.g., variation in soil moisture, nutrient availability or microtopography, Tape et al., 2012). These methods provide appropriate frameworks for the analysis of ecological questions using hierarchical sampling designs of individuals within a given site or treatment and across multiple sites or treatments within a landscape.

9.2. Growth trends

Dendroclimatic analyses of growth are typically conducted on standardized growth data, providing an index of relative inter-annual growth. In contrast, analyzing raw measured ring widths, rather than standardized data, can give important insights into shrub growth trends, patch dynamics and the drivers of change overtime. For example, annual growth rings of expanding patches of *A. viridis* subsp. *fruticosa* on the North Slope of Alaska were wider and more closely tracked spring and summer temperatures than stable patches (Tape et al., 2012). The long-term radial and vertical growth of *J. nana* in the Swedish mountains followed long-term trends of growing season temperatures (Hallinger et al., 2010; Hallinger and Wilmking, 2011). In addition, variation or trends in growth can be used to explore the impacts of herbivory by ptarmigan (Tape et al., 2010), ungulates and small rodents (Predavec et al., 2001; Ravolainen, et al., 2013). The raw record of growth provides different information than that which can be obtained from analyses using typical dendrochronological techniques, though extracting a growth trend is challenging (Bowman et al., 2013).

9.3. Shrub age and age distributions

Age and age distributions of long-lived plants give insights into past and present population and range dynamics. Recruitment rates can indicate whether populations are stable, increasing or decreasing over time (Boulanger-Lapointe et al., 2014), and the age distributions of tundra tree and shrub individuals at a given site can provide insight into range boundary dynamics (Danby and Hik, 2007; Mamet and Kershaw, 2012). For example, an expanding population could have greater numbers of younger individuals as a result of new recruitment beyond the range edge (Jump et al., 2009; Hallinger et al., 2010). In comparison, stable or contracting range edges could have greater numbers of older individuals when compared to the centre of the range (Trant et al., 2011). To date, only a few studies have explored shrub population dynamics using shrub age distributions, and this is a high priority area for future research (Table 1). However, using age distributions alone to infer population responses to changing environmental conditions can produce conflicting results unless disturbances and mortality events are taken into account (Trant, unpublished data). In order to address population dynamics at the landscape scale, much greater sampling efforts are required to identify pulses of recruitment and the climate sensitivity of recruitment patterns (Büntgen et al., in revision).

10. Conclusions

The analysis of the growth of shrub species has applications across the Earth Sciences and requires a multidisciplinary approach involving plant physiology and anatomy, ecology, climatology, geomorphology, and statistical design. Recent advances in sampling methods, analysis and applications, reviewed here, have improved our ability to investigate the dynamics of shrub growth and recruitment in tundra ecosystems. However, new advances are required to adequately deal with: (1) clonal growth and patch dynamics; (2) variation in growth among parts of the plant and among individuals; and (3) the scaling of individual-based sampling to understand changes at the landscape or biome scale.

To explore the full potential of dendroecology, the field will require new approaches. Creative exploration of dendroecological methods and data analysis will provide new avenues to explore previously unanswered questions in tundra ecosystems, such as how below-ground

connections mediate growth among different individuals or how biomass allocation changes in response to environmental drivers. The entire plant community could be better integrated into investigations of shrub growth responses to climate and other ecological drivers (Büntgen et al., in revision), and the similarities and differences among controls on growth and recruitment could be better explored to improve our understanding of the proliferation of shrub species in tundra ecosystems.

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