



ORIGINAL ARTICLE

High frequency growth variability of White spruce clones does not differ from non-clonal trees at Alaskan treelines



Martin Wilmking^{a,*}, Allan Buras^{a,1,2}, Pascal Eusemann^{a,3}, Martin Schnittler^a, Mario Trouillier^a, David Würth^a, Jelena Lange^a, Marieke van der Maaten-Theunissen^{a,b}, Glenn Patrick Juday^b

^a Institute of Botany and Landscape Ecology, University Greifswald, Soldmannstr. 15, 17487 Greifswald, Germany

^b Professor Emeritus of Forest Ecology, School of Natural Resources and Extension, University of Alaska Fairbanks, 99775, USA

ARTICLE INFO

Keywords:

Picea glauca
Reproduction
Dendroclimatology
Dendroecology

ABSTRACT

Northern and elevational treelines are classic sites for dendroclimatological studies. At these marginal sites only one climate parameter is usually considered growth limiting and trees from these sites are therefore used to reconstruct that parameter back in time. Marginal sites are also those sites within a species range, where clonal reproduction is most frequent. Clonal growth can ensure plant species survival and growth under stressful conditions or if the environmental conditions do not allow sexual reproduction, e.g. by layering, by stems resprouting after damage, or through the exchange of resources between different clone ramets ("stems"). We literally stumbled across clonal and non-clonal growth forms of White spruce growing intermingled with each other at two Alaskan treeline sites. The two growth forms could not be distinguished a priori in the field. After sampling and detection of clones we thus asked whether clonal ramets and non-clonally grown trees (singletons) showed similar growth patterns. Clones were identified by identical multilocus genotypes in a SSR microsatellite genotyping analysis and radial growth was analyzed using traditional tree ring width methods. High-frequency growth patterns were very similar between singletons and clonal ramets in Alaskan treeline White spruce, thus posing no problem in including both reproductive strategies in a classic dendroclimatological investigation.

1. Introduction

Treelines represent impressive examples of clearly visible edges of a species' geographical distribution, where usually one environmental factor is considered growth limiting. Often this factor is inferred to be climatic and in the case of northern and elevational treelines, is generally known or suspected to be growing season temperature (Holtmeier, 2009; Körner, 1998, 2012). Treeline systems are often assumed to react strongly and directly to climate change, and in fact the climate sensitivity of treelines and treeline advance in reaction to climate warming is well documented (Lloyd and Fastie, 2002; Esper and Schweingruber, 2004; Wilmking et al., 2004; Harsch et al., 2009). Treelines have thus been extensively used to reconstruct past climatic dynamics using tree rings (e.g. ring width, density, isotopes) as climate archives (Esper, 2002; Grudd, 2008; Grudd et al., 2002; Helama et al., 2009; Linderholm and Gunnarson, 2005; Lindholm et al., 2014; McCarroll et al., 2013; Porter et al., 2013, 2014).

As an ecological question, much research has been conducted on treeline dynamics and the processes that govern treeline formation (for an extensive review see Körner, 2012). Many treeline systems include upright single trees as well as krummholz and tree islands, the latter being generally clonally in origin (Holtmeier, 2009). Clonality in trees is often associated with stressful or disturbed habitats, because it enhances a genotype's probability of survival in such habitats by producing multiple descendants of a single zygote (Eriksson and Jerling, 1990) and may increase the quality of the micro-environment by facilitation effects (Scott and Hansell, 2002; Holtmeier and Broll, 2010). Clonality also enhances a plant's ability to regenerate from damage (Peterson and Jones, 1997) and allows more efficient foraging for resources and sharing of resources among several connected ramets (Hutchings and De Kroon, 1994). Therefore, clonality generally increases towards the edge of a species' geographical distribution range (Klimešová and Doležal, 2011; Silvertown, 2008), where species-specific stress is typically higher.

* Corresponding author.

E-mail address: wilmking@uni-greifswald.de (M. Wilmking).

¹ These authors contributed equally to the work.

² Currently at: Professorship of Ecoclimatology, Technische Universität München, Hans-Carl-von-Carlowitz Platz 2, 85354 Freising, Germany.

³ Currently at: Johann Heinrich von Thünen-Institute of Forest Genetics, Eberswalder Chaussee 3a, 15377 Waldsiedersdorf, Germany.

In northern Alaska, a region where temperatures have been rising faster than almost anywhere else on the globe during recent decades (Bekryaev et al., 2010; Walsh et al., 2014), treelines are formed mainly by White spruce (*Picea glauca* (Moench) Voss). White spruce normally regenerates through sexual reproduction via seeds. The species can also reproduce vegetatively through layering, resulting in at least temporarily connected ramets, which might affect radial growth patterns through resource exchange between them. Clonal growth forms in White spruce treelines have been shown to exist in the northern Canadian lowlands, usually associated with continuous permafrost conditions (Walker et al., 2012; Scott and Hansell, 2002). There, clonal growth forms can make up a considerable proportion of a population's individual trees at the tundra-treeline ecotone (Walker et al., 2012). During a study focusing on population genetics at Alaskan treelines, we found clonal growth in White spruce at several upland, non-permafrost locations in northern and Interior Alaska, classic sites for dendroclimatological investigations. At these sites, clonal and non-clonal growth forms co-exist under the same environmental conditions and we therefore asked the basic but important question: Do the two differing reproductive strategies result in similar growth patterns?

2. Material and methods

2.1. Study species

Picea glauca (Moench) Voss (White spruce) is one of the signature tree species of the North American boreal forest. It occurs across the entire continent from Newfoundland and Labrador in the east to Alaska in the west, forming the northern treeline in the western part of North America (Lloyd et al., 2005; Payette and Filion, 1985). Its vertical distribution ranges from sea level to 1520 m (Burns and Honkala, 1990), often forming the elevational treeline. The species is widely used in forestry in Canada and the United States and is one of the most important commercial species in the North American boreal forest (Burns and Honkala, 1990).

2.2. Study areas and sample collection

We established two study areas at White spruce treeline in Alaska, at classic dendroclimatological sampling sites at the presumably temperature limited range edge of that species (Fig. 1), one at northern

Table 1
Description of study sites.

	BRT	BRF	ART	ARF
Latitude	67.95	67.95	63.74	63.72
Longitude	−149.74	−149.75	−149.01	−149.01
Elevation [m a.s.l.]	923	876	1008	802
n individual stems	358	470	313	380
n singletons analyzed (sample depth of the singleton chronology)	34	110	113	168
n clones	23	27	10	10
n clonal ramets analyzed (sample depth of the clonal chronology)	64	59	13	2

Latitude, longitude and elevation refer to the center point of each plot. “n individual stems” is the total number of visual tree-like structures or individual stems in the plot (clone ramets or singletons), “n singletons analyzed” is the number of singletons used in the analyses (= sample depth of singleton chronology), “n clones” is the total number of clones (comprised of several ramets each) in the respective plot and “n clonal ramets analyzed” is the total number of ramets (belonging to different clones) which we analyzed in a respective plot.

treeline in the Central Brooks Range (67°56'N, 149°44'W) (BR) and one at elevational treeline in the Alaska Range (Denali National Park and Preserve, 63°43'N, 149°00'W) (AR). Growing on south-facing slopes, White spruce forms the local treeline at an elevation of about 960 m and 1050 m a.s.l., at the two sites respectively, undisturbed by human activity. Due to the southern exposure, soils at both sites are usually completely unfrozen during the summer down to the bedrock (pers. observation during numerous field campaigns and measurements over three years with soil temperature loggers). Within each area, we selected two plots of roughly one ha each of nearly monospecific White spruce stands including the current upper limit of the treeline ecotone (treeline plot, T) and closed canopy forest areas below (forest plot, F). The two plots bordered each other in the Brooks Range, while in the Alaska Range the two plots were separated by about 1 km of nearly flat terrain. This set-up resulted in four plots, two in each study area (Brooks Range treeline, BRT; Brooks Range forest, BRF; Alaska Range treeline, ART; Alaska Range forest, ARF). Needles for DNA extraction were collected from all living trees inside the plots, dried and stored on silica gel. Tree height and, if the tree was tall enough, diameter at breast height (dbh) were recorded from all trees and saplings using a Suunto PM-5 clinometer and a measuring tape. Tree cores were collected from all trees with a dbh larger than 5 cm, usually two cores were taken perpendicular to each other as low as possible to the ground.

2.3. Genotyping

Dry needles were powdered in a Retsch ball mill MM301 (Retsch, Germany). Approximately 70 mg of needle tissue was used for DNA extraction with the Invisorb Spin Plant Mini Kit (Stratag, Birkenfeld, Germany) following the manufacturer's protocol. DNA concentration was measured with NanoDrop Lite (Thermo Fisher Scientific, Waltham, MA, USA), adjusted to 5 ng and used as template DNA for microsatellite analysis in three different multiplex reactions (Eusemann et al., 2014). Clones were determined by identification of identical multilocus genotypes (MLG) using GenAEx 6 (Peakall and Smouse, 2006). To account for scoring errors (see Schnittler and Eusemann, 2010) we allowed a threshold of two deviating loci within an MLG, i.e. a putative clone. As genetic diversity measures we calculated clonal diversity $R = (G-1)/(N-1)$ with G being the number of genotypes and N the number of sampled trees and its opposite parameter, clonality $C = 1-R$ (Dorken and Eckert, 2001), as well as the proportion of clonally derived trees within the stand. Probability of Identity (PID) was calculated using GenAEx 6, and null allele frequencies were calculated using GenePop'007 (Rousset, 2008). Apart from the clonality estimations, all population genetic

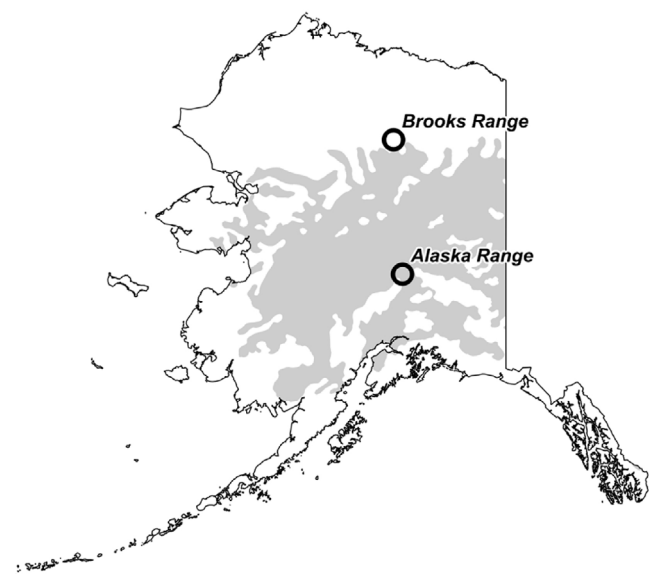


Fig. 1. Location of the study sites, grey shading indicating the range of White spruce in Alaska (Little, 1971). The Brooks Range site represents the northern treeline, while the Alaska Range site is an elevational treeline.

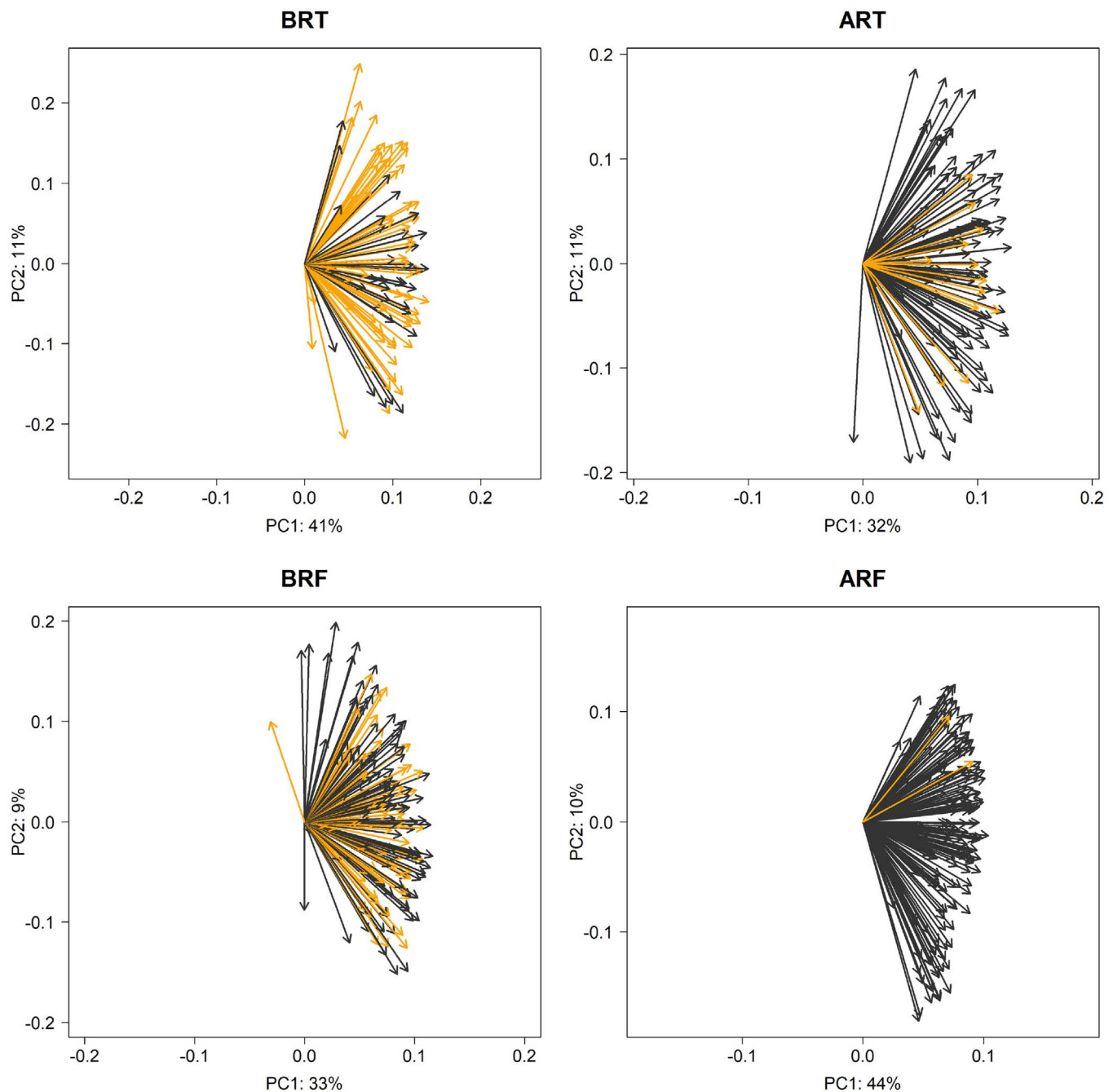


Fig. 2. PCGA (Principal Component Gradient Analysis) is not able to differentiate between clonal ramets (orange) and singletons (black) suggesting similar growth patterns independent of reproductive strategy. Each arrow represents one individual tree or clonal ramet. Also visible is the high percentage of clonal ramets in the BRT site, the climatically most stressful site at northern treeline. Axes numbers reflect the amount of variance explained by the respective principal component. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

calculations were performed on a genet basis, i.e. after exclusion of clonal duplicates from the data set. Percental clonal growth was defined as the number of ramets belonging to clones at a site versus the total amount of stems/ramets at that site. Non-clonally grown stems were called “singletons”.

2.4. Tree-ring analysis

All tree cores were air dried and then glued transverse side up onto wooden sample holders. Surfaces were prepared with either a core-microtome (WSL, Switzerland; Gärtner and Nievergelt, 2010) or by progressively finer sanding until cellular structures became visible. Tree cores were then either measured for ring width using a LINTAB 5 table

(1/1000 mm resolution) and the TSAPWin Software (Frank Rinn, Heidelberg, Germany), or scanned on a flatbed scanner (Epson Perfection V700 Photo) with 3200 dpi and subsequently measured using CoReRecorder (v. 7.7, Cybis Elektronik & Data AB, Sweden) with 1/1000 mm precision. Crossdating was done visually using CDendro (v. 7.7, Cybis Elektronik & Data AB, Sweden) and verified using COFECHA and the dplR package (Bunn, 2008) of the R programming software v. 3.1.1 (R Foundation for Statistical Computing). To reduce effects of different age cohorts, we restricted our analyses to all trees that had established until 1976. We chose 1976 as it demarcates an important year with respect to the shift of a locally important climate mode, i.e. the Pacific Decadal Oscillation (Ohse et al., 2012). We also used subsets of trees (e.g. all trees established before 1947, another shift

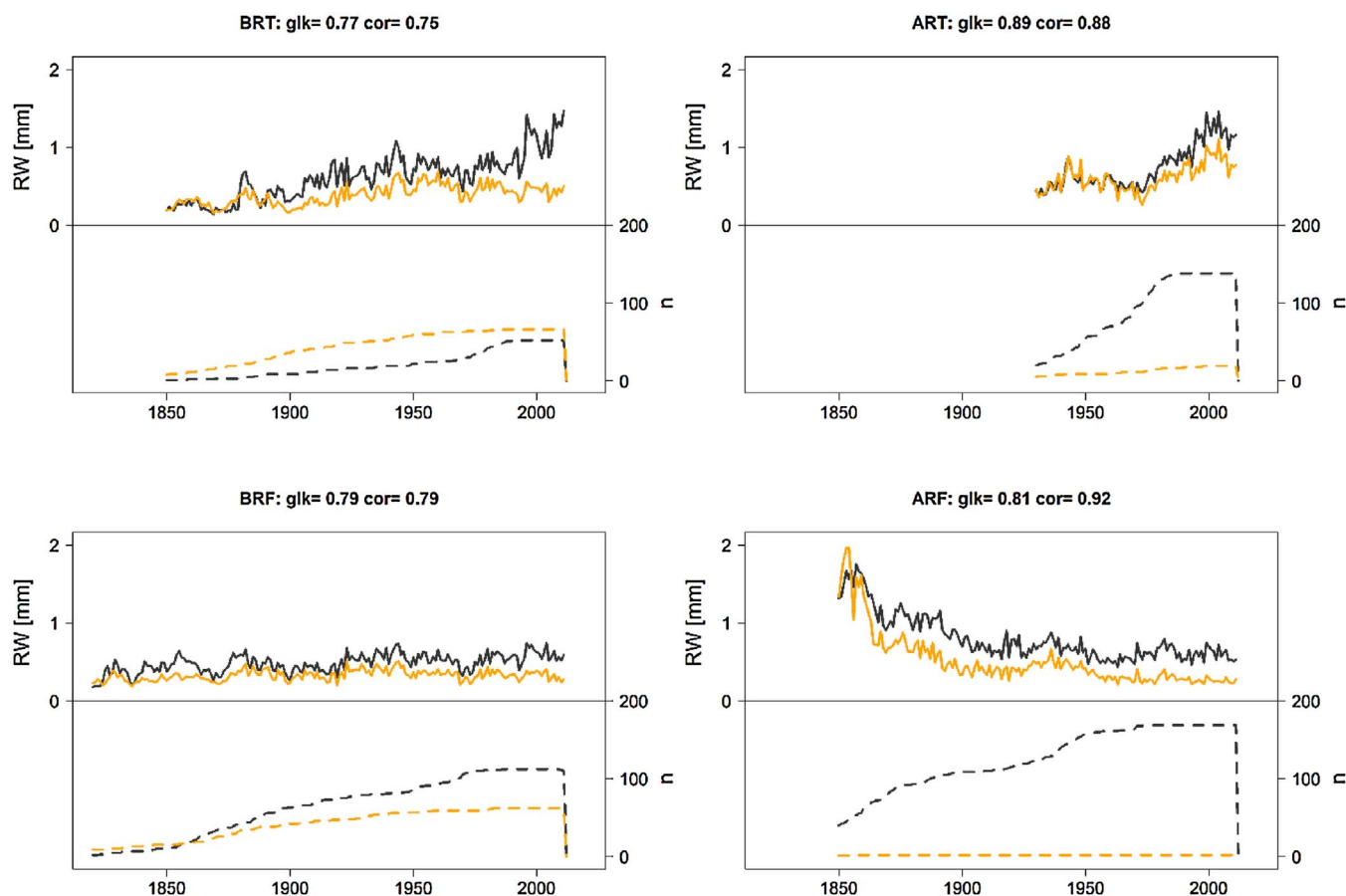


Fig. 3. Singletons (black curve) generally outperform clone ramets (orange curve) in terms of absolute radial growth, but high-frequency growth variability is very similar. Sample sizes delineated by dashed lines and right y-axis. Glk: Gleichläufigkeit, cor: Pearson correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the PDO) and all trees in the analyses, but the results were always very similar. Raw ring width was individually detrended using a 50-year cubic smoothing spline with 50% frequency cut-off (dplR-package, Bunn, 2008) for visualizing and comparing the growth patterns of the two groups (clonal vs. seed-derived ramets/stems) over time. Detrended ring-widths were used in a Principal Component Gradient Analysis (PCGA, Buras et al., 2016) to explore whether clone ramets and singletons expressed specific and differing growth variability. For the PCGA, detrended ring-widths were variance-scaled and only the common overlap period was considered in the analysis, i.e. the period from 1976 to 2012. To compare absolute growth (represented by raw ring-widths) as well as detrended growth between clone ramets and singletons, we computed respective master chronologies per site using a biweight robust mean. Gleichläufigkeit (Eckstein and Bauch, 1969; Buras and Wilmking, 2015) and (Pearson) correlations between master chronologies were computed per site, reflecting growth similarity between ramets and singletons. We repeated all analyses with BAI, the results were similar and we opted to only present the raw and RWI chronologies.

3. Results and discussion

In the field, we were unable to distinguish clonal ramets from singletons. Only the genetic analyses showed a higher frequency of clonal growth towards the range margins of White spruce. Clonality is generally higher in the northern treeline (Brooks Range) than the Central Alaska elevational treeline site (Denali NP). Within each site, clonality is generally higher in treeline versus forest plots (Table 1).

The pattern of higher clonality in more stressful habitats is consistent with the literature (Klimešová and Doležal, 2011; Silvertown,

2008; Honnay and Bossuyt, 2005). Although clonal growth forms have not been extensively documented in White spruce, clonality can be high in White spruce stands on permafrost soils, such as in the northern Canadian lowlands close to Churchill, Manitoba (Scott and Hansell, 2002) or the Mackenzie delta (Walker et al., 2012). Our analysis appears to be one of the first, if not the first, to show White spruce clones on upland, non-permafrost soils. We can only speculate about the mechanism, but layering, or ingrowth of low hanging branches, seems the main mechanism responsible. Since layering results, at least for a period of time, in a connection of the different ramets facilitating resource exchange between them, radial growth patterns might be affected by clonality.

Our PCGA-analysis has shown, however, that growth patterns of clone ramets and singletons could not be separated (Fig. 2). At all four sampling plots, the range of clone ramet growth variability is well within the spectrum of growth variability of the singletons (but notice the low sample size in ARF). This suggests that climate-growth relationships of clone ramets and singletons do not differ systematically, since PCGA-gradients have been reported to reflect gradients of climate-growth relationships (Buras et al., 2016). While singletons generally outperform single clone ramets in terms of absolute radial growth (Fig. 3), the detrended time series of ring width show virtually no difference between clonal ramet and singleton growth chronologies (Fig. 4). We also tested subsets of data related to different PDO phases, the results (not shown) are the same: The similarity in growth forms is consistent through time and across different PDO phases. Gleichläufigkeit between the two chronologies per plot was high and varied between 0.77 and 0.89 for the raw ring width and 0.80 and 0.86 for the detrended chronologies. Correlation between the two chronologies per plot was high as well, and varied between 0.75 and 0.92 for the raw

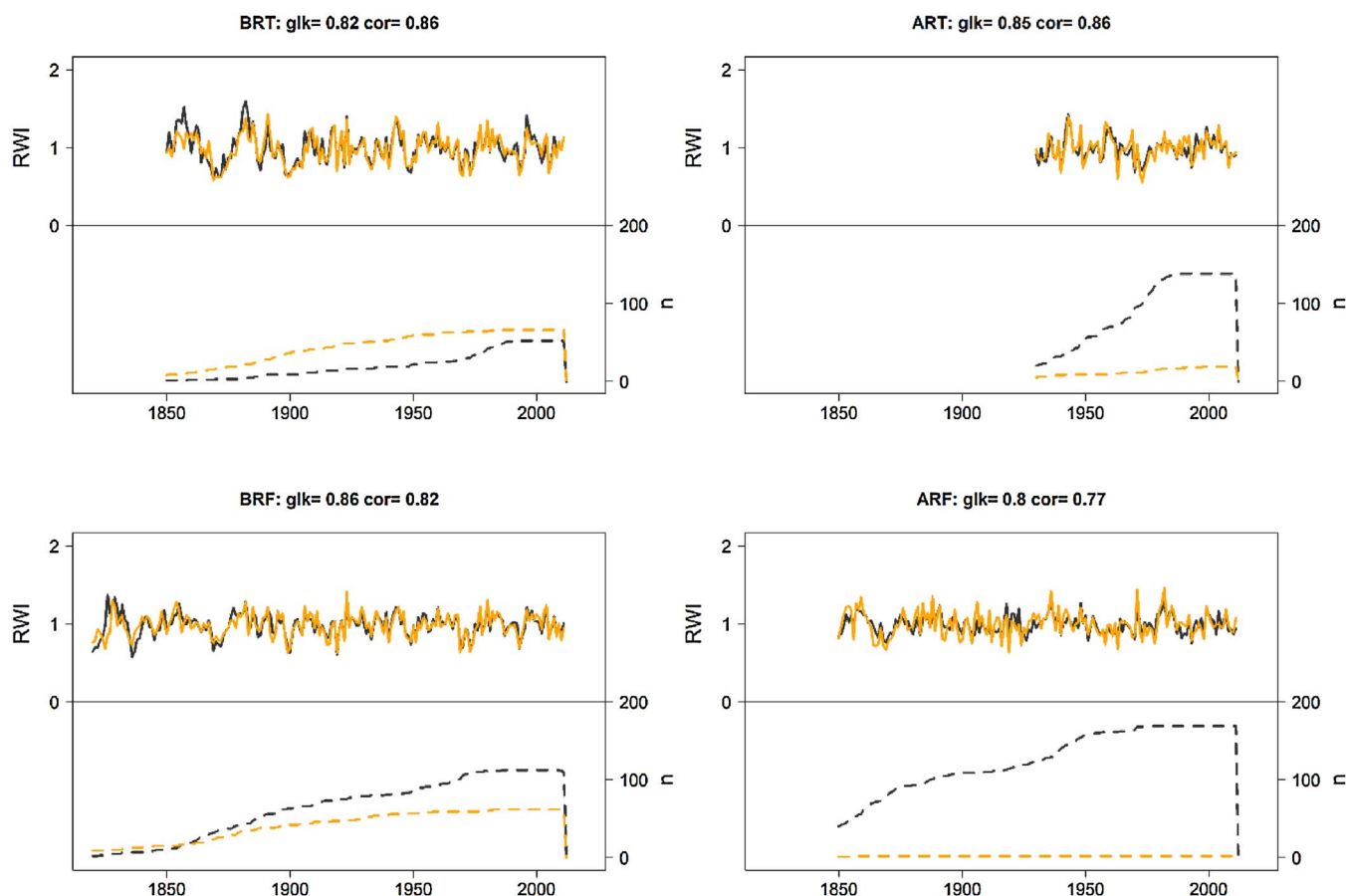


Fig. 4. High-frequency growth variability of clonal ramets (orange curve) is very similar to that of singletons (black curve) White spruce in every plot, shown here 50-year spline detrended data. Sample sizes delineated by dashed lines and right y-axis. Glk: Gleichläufigkeit, cor: Pearson correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ring width and 0.77 and 0.86 for the detrended chronologies.

While it is beyond this study to speculate about the generally higher absolute radial growth in the singletons when compared to the clone ramets, clearly, in terms of growth variability over time, clonal ramets and the non-clonally grown singletons safely can be regarded as similar.

4. Conclusions

We found clones of White spruce growing mixed with non-clonal White spruce at typical treeline sites in two Alaskan mountain ranges. Clone frequency increased towards climatically more stressful sites: More clones occurred at northern than elevational treeline sites and generally there were more clones at local treeline than in a forest site below. While singletons generally outperformed single clone ramets in terms of absolute radial growth, high-frequency growth variability of clones and non-clonal trees was very similar thus posing no problem in including chronologies from both reproductive strategies in a classic dendroclimatological investigation.

Acknowledgements

This study was supported by DFG EU 132/1-1 and DFG WI 2680/8-1. Data were analyzed and paper was written within the Research Training Group RESPONSE (DFG RTG 2010).

References

- Bekryaev, R.V., Polyakov, I.V., Alexeev, V.A., 2010. Role of polar amplification in long-term surface air temperature variations and modern arctic warming. *J. Clim.* 23, 3888–3906.

- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124.
- Buras, A., Wilmking, M., 2015. Correcting the calculation of Gleichläufigkeit. *Dendrochronologia* 34, 29–30.
- Buras, A., van der Maaten-Theunissen, M., van der Maaten, E., Ahlgrimm, S., Hermann, P., Simard, S., Heinrich, I., Helle, G., Unterseher, M., Schnittler, M., Eusemann, P., Wilmking, M., 2016. Tuning the voices of a choir: detecting ecological gradients in time-series populations. *PLoS One* 11, e0158346.
- Silvics of North America: 1. Conifers. In: Burns, R.M., Honkala, B.H. (Eds.), *Agriculture Handbook 654*. U.S. Department of Agriculture, Forest Service, Washington, DC.
- Dorken, M., Eckert, C.G., 2001. Severely reduced sexual reproduction in northern populations of a clonal plant, *Decodon verticillatus* (Lythraceae). *J. Ecol.* 89, 339–350.
- Eckstein, D., Bauch, J., 1969. Beitrag zur Rationalisierung eines dendrologischen Verfahrens und zur Analyse seiner Aussagesicherheit. *Forstwissenschaftliches Zentralblatt* 88, 230–250.
- Eriksson, O., Jerling, L., 1990. Hierarchical selection and risk spreading in clonal plants. In: van Groenendael, J., de Croon, H. (Eds.), *Clonal Growth in Plants: Regulation and Function*. SPB Academic Publishing, Den Haag, pp. 79–94.
- Esper, J., Schweingruber, F.H., 2004. Large-scale treeline changes recorded in Siberia. *Geophys. Res. Lett.* 31, L06202.
- Esper, J., 2002. Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science* 295, 2250–2253.
- Eusemann, P., Herzig, P., Kieß, M., Ahlgrimm, S., Herrmann, P., Wilmking, M., Schnittler, M., 2014. Three microsatellite multiplex PCR assays allowing high resolution genotyping of White spruce, *Picea glauca*. *Silvae Genetica* 63, 230–234.
- Gärtner, H., Nievergelt, D., 2010. The core-microtome: a new tool for surface preparation on cores and time series analysis of varying cell parameters. *Dendrochronologia* 28, 85–92.
- Grudd, H., Briffa, K.R., Karlén, W., Bartholin, T.S., Jones, P.D., Kromer, B., 2002. A 7400-year tree-ring chronology in northern Swedish Lapland: natural climatic variability expressed on annual to millennial timescales. *The Holocene* 12, 657–665.
- Grudd, H., 2008. Torneträsk tree-ring width and density ad 500–2004: a test of climatic sensitivity and a new 1500-year reconstruction of north Fennoscandian summers. *Clim. Dyn.* 31, 843–857.
- Harsch, M.A., Hulme, P.E., McGlone, M.S., Duncan, R.P., 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol. Lett.* 12, 1040–1049.
- Helama, S., Timonen, M., Holopainen, J., Ogurtsov, M.G., Mielikäinen, K., Eronen, M., Lindholm, M., Meriläinen, J., 2009. Summer temperature variations in Lapland

- during the Medieval Warm Period and the Little Ice Age relative to natural instability of thermohaline circulation on multi-decadal and multi-centennial scales. *J. Quat. Sci.* 24, 450–456.
- Holtmeier, F.K., Broll, G., 2010. Wind as an ecological agent at treelines in North America, the Alps, and the European Subarctic. *Phys. Geogr.* 31, 203–233.
- Holtmeier, F.K., 2009. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Springer, Netherlands.
- Honnay, O., Bossuyt, B., 2005. Prolonged clonal growth: escape route or route to extinction? *Oikos* 108, 427–432.
- Hutchings, M.J., De Kroon, H., 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. *Adv. Ecol. Res.* 25, 159–238.
- Körner, C., 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115, 445–459.
- Körner, C., 2012. *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits*. Springer, Basel.
- Klimešová, J., Doležal, J., 2011. Are clonal plants more frequent in cold environments than elsewhere? *Plant Ecol. Divers.* 4, 373–378.
- Linderholm, H.W., Gunnarson, B.E., 2005. Summer temperature variability in Central Scandinavia during the last 3600 years. *Geografiska Annaler Ser. A Phys. Geogr.* 87, 231–241.
- Lindholm, M., Ogurtsov, M.G., Jalkanen, R., Gunnarson, B.E., Aalto, T., 2014. Six temperature proxies of Scots pine from the interior of northern Fennoscandia combined in three frequency ranges. *J. Climatol.* 18, 578761.
- Little, E.L., 1971. *Atlas of United States trees. Conifers and Important Hardwoods*, vol 1 U.S. Department of Agriculture Miscellaneous Publication 1146, 9 p., 200 maps.
- Lloyd, A.H., Fastie, C.L., 2002. Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Clim. Change* 52, 481–509.
- Lloyd, A.H., Wilson, A.E., Fastie, C.L., Landis, R.M., 2005. Population dynamics of black spruce and White spruce near the arctic tree line in the southern Brooks Range, Alaska. *Can. J. For. Res.* 35, 2073–2081.
- McCarroll, D., Loader, N.J., Jalkanen, R., Gagen, M.H., Grudd, H., Gunnarson, B.E., Kirchhefer, A.J., Friedrich, M., Linderholm, H.W., Lindholm, M., Boettger, T., Los, S.O., Remmele, S., Kononov, Y.M., Yamazaki, Y.H., Young, G.H.F., Zorita, E., 2013. A 1200-year multiproxy record of tree growth and summer temperature at the northern pine forest limit of Europe. *The Holocene* 23, 471–484.
- Ohse, B., Jansen, F., Wilmking, M., 2012. Do limiting factors at Alaskan treelines shift with climatic regimes? *Environ. Res. Lett.* 7, 015505.
- Payette, S., Filion, L., 1985. White spruce expansion at the tree line and recent climatic changes. *Can. J. For. Res.* 15, 241–251.
- Peakall, R., Smouse, P.E., 2006. GENALEX 6: genetic analysis in excel: population genetic software for teaching and research. *Mol. Ecol. Notes* 6, 288–295.
- Peterson, C.J., Jones, R.H., 1997. Clonality in woody plants: a review and comparison with clonal herbs. In: de Kroon, H., van Groenendaal, J. (Eds.), *The Ecology and Evolution of Clonal Plants*. Backhuys Publishers, Leiden, pp. 263–289.
- Porter, T.J., Pisaric, M.F.J., Kokelj, S.V., deMontigny, P., 2013. A ring-width-based reconstruction of June–July minimum temperatures since AD1245 from White spruce stands in the Mackenzie Delta region, northwestern Canada. *Quat. Res.* 80, 167–179.
- Porter, T.J., Pisaric, M.F.J., Field, R.D., Kokelj, S.V., Edwards, T.W.D., deMontigny, P., Healy, R., LeGrande, A.N., 2014. Spring-summer temperatures since AD 1780 reconstructed from stable oxygen isotope ratios in White spruce tree-rings from the Mackenzie Delta, northwestern Canada. *Clim. Dyn.* 42, 771–785.
- Rousset, F., 2008. Genepop'007: a complete re-implementation of the Genepop software for Windows and Linux. *Mol. Ecol. Resources* 8, 103–106.
- Schnittler, M., Eusemann, P., 2010. Consequences of genotyping errors for estimation of clonality – a case study from *Populus euphratica* Oliv (Salicaceae). *Evol. Ecol.* 24, 1417–1432.
- Scott, P.A., Hansell, R.I.C., 2002. Development of White spruce tree islands in the shrub zone of the forest-tundra. *Arctic* 55, 238–246.
- Silvertown, J., 2008. The evolutionary maintenance of sex: evidence from the ecological distribution of asexual reproduction in clonal plants. *Int. J. Plant Sci.* 169, 157–168.
- Walker, X., Henry, G.H.R., McLeod, K., Hofgaard, A., 2012. Reproduction and seedling establishment of *Picea glauca* across the northernmost forest-tundra region in Canada. *Global Change Biol.* 18, 3202–3211.
- Walsh, J., Wuebbles, D., Hayhoe, K., Kossin, J., Kunkel, K., Stephens, G., Thorne, P., Vose, R., Wehner, M., Willis, J., Anderson, D., Doney, S., Feely, R., Hennon, P., Kharin, V., Knutson, T., Landerer, F., Lenton, T., Kennedy, J., Somerville, R., 2014. Ch. 2: our changing climate. In: Melillo, J.M., Richmond, T.C., Yohe, G.W. (Eds.), *Climate Change Impacts in the United States: The Third National Climate Assessment*. U.S. Global Change Research Program, pp. 19–67.
- Wilmking, M., Juday, G.P., Barber, V.A., Zald, H.S.J., 2004. Recent climate warming forces contrasting growth responses of White spruce at treeline in Alaska through temperature thresholds. *Global Change Biol.* 10, 1724–1736.