Dobbert et al. Response to R1.2

Recommendation to revised version of the manuscript: Reject

Authors substantially revised their manuscript, clarified inconsistencies and they supplemented the text when this was necessary for a better understanding. However, I have still major concerns regarding methodological aspects as well as data interpretation, which need to be resolved to warrant publication.

Response to general argumentation of the authors:

“The authors are convinced that their extensive changes now justify publication in Biogeosciences, and by its a novel approach, strong methodology, unique dataset and unexpected results the paper will stimulate the discussion on our physiological understanding of arctic-alpine shrubs growth.”

I readily agree with the authors that current knowledge should be questioned and discussed to enable scientific progress. But this discussion can only take place on the basis of solidly collected data. In the following I will once again present my arguments against the publication of this manuscript in its present (revised) form, as there are methodological deficiencies that significantly affected data collection and subsequent analysis.

The authors would like to thank R1 for further constructive comments and suggestions to improve our manuscript. There were three aspects to be clarified: a) still existing doubts on accurate dendrometer measurements, b) representativeness of a dendrometer curve from a multi-stem shrub, and c) seeming mismatch of our new findings with results from (our) previous studies. We are positive that these concerns can be resolved, and we revised several parts of the manuscript, added three new figures to the supplement, and extended the interpretation of our findings, accordingly.

Response to authors' comments on my previous specific points of concern (line numbers refer to the manuscript before revision):

- Averaging of dendrometer records: Authors clarified this point and they have sufficiently complemented the methods section.
- Mounting of diameter dendrometers: The authors now give more detailed information on mounting of dendrometers. Authors add in the Materials and Methods section that the dendrometers were not mounted on bark as I previously assumed from their description (“We mounted our dendrometers on one major above-ground stem…”), but “…we removed the outer bark to place the sensor directly on the cambium.”

In this regard, I ask for clarification or elaboration on the following points:

First, please cite a study showing that dendrometers can be mounted directly on the cambial tissue without seriously affecting it. For several reasons, it is standard to mount point dendrometers on the living phloem, not on cambial tissue, which consists of a few cell layers only. Mounting on the cambium - if you can manage to do it that way - would inevitably lead to damage, mechanically or through dehydration. Furthermore, "girdling" of the phloem would block transport of carbon and hormones, which are necessary for cambium activity to occur.

Secondly, Figure A2 shows a photo of the way diameter dendrometers were assembled in this study. I admit that the resolution does not allow a clear statement, but it looks like that the diameter dendrometer was mounted directly on the stem without removing the outer bark. However, authors state in their reply that "In general, *Empetrum hermaphroditum* has a very thin bark, which is easily removed without the danger of damaging the cambium." That's fine, but I wonder, how authors could manage to mount DRO diameter dendrometers directly on the cambium. This type of dendrometer consists not only of a circular sensor head with a diameter of c. 5 mm, but also of a rectangular fixing plate to be mounted on the opposite side of the sensor head. By default this plate is c. 2 cm long and 5 mm wide. Hence, this part of the stem should also have been removed (without damaging the cambium!) to ensure that hygroscopic effects are not influencing dendrometer records.

R1 is right, that measurements on the cambium are hard to be implemented. We rephrased our text accordingly to avoid further misunderstandings. So far, to our knowledge, the use of dendrometers for the study of stem physiological activity (including growth) has been restricted to trees. Mounting dendrometers for the first time to dwarf shrub stems was a challenging task and indeed led to several ideas and potential technical solutions to be tested. Our dendrometer project initially started in 2008, many years before the here referred study period. During a test period, we developed the study design in different alpine regions. We invested in trials over several years to a) choose the best sensor type, b) find the final best option of mounting the dendrometers onto the shrub stems, and c) to proof that we measure active physiological activity (cambial activity) instead of passive swelling and shrinking of dead tissue. All the dendrometers included in our recent manuscript were running for at least one year before the start of the study period in 2015, to ensure that they produce meaningful data and that growth of the sampled plants is not impaired by the dendrometer mounted to the stem (added in the manuscript: "To ensure that the dendrometers run properly and produce exploitable data unaffected by the mounting of the dendrometers and bark removal, we tested the study design for several years, before selecting data series for our analysis."). As such, some stems were too young, and too soft and thin and died as a result of the "surgery", some stems suffered from the intervention (e.g. leaf loss). In both cases dendrometers were mounted to another specimen and the biased data were not used for analyses. Overall, branch structure and tissue properties of *Empetrum hermaphroditum* proved to be well suited for the installation and proper functioning of the chosen sensor type. From the reviewer's comment we assume that the procedure of mounting the dendrometers itself needs some clarification. We think that our new supplement figure A will help the readers follow our methodological and technical procedure based on the terminology used in our text. We removed dead outer bark material (periderm) directly where the sensor and the fixing plate were placed (the reviewer´s description of the sensor is accurate). As such, we ensured close contact of the dendrometer with the stem and minimized the effects of hygroscopic shrinkage and swelling of the dead outer bark on the final records (e.g. Oberhuber et al., 2020). Our overall aim was to get as close to the living tissue as possible. We made sure not to remove more protective bark material than necessary, and we tried to avoid damaging the living tissue (see anatomical structure in micro-slice picture in our new Fig. A). We are aware that removing the bark might be accompanied by a small wound to the stem. If we had any indication suggesting that continued life and growth were affected during our trial phase, we removed the specimen from the dataset, and mounted the dendrometer at another specimen. As such, the twelve specimens on which our recent manuscript is based, are actually part of a much more comprehensive study.

In general, the procedure we replicated on shrubs is common practice in trees (e.g. Oberhuber et al., 2020; Wang et al., 2020; Grams et al., 2021). However, the process of removing the dead outer bark was greatly facilitated by the unique anatomy of *E. hermaphroditum* in comparison to trees: Our shrubs are characterized by a thin but clearly pronounced living tissue, and selective removal of the outer bark is easy and can be done without the use of special equipment or cutting (new Fig. A). In most cases, parts of the successive periderms of the rhytidome probably down to the outer phellem were easily removed with the outer bark, when the stem was moistened before the “surgery”, as suggested by the anatomical structure shown in Fig. A. Usually, the procedure was not accompanied by any leaking fluids from the plant, proving that the living tissue was not damaged. In comparison to similar interventions on tree stems, removing the outer bark on our shrubs was, on the one hand, easy to handle as to the papery structure of the bark, but on the other hand, also tricky to see with bare eyes as to its micro-scale structure.

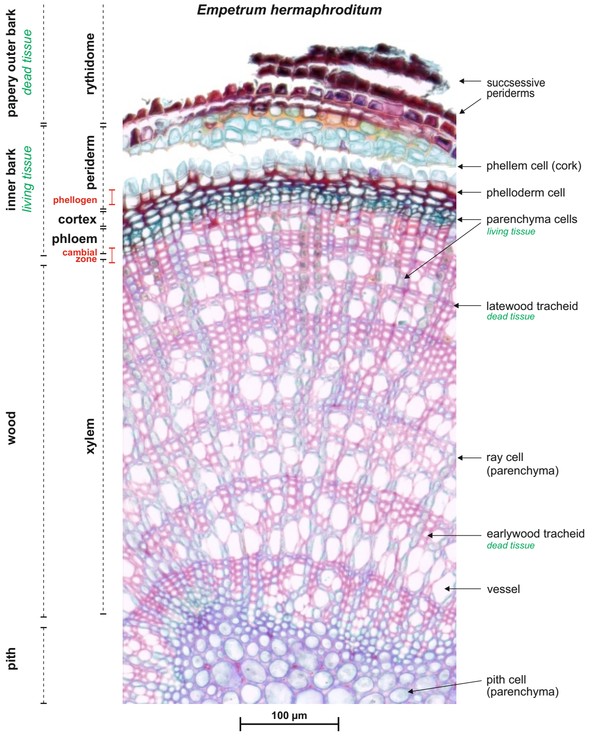


Figure A: Radial micro-slide of a stem from *Empertum nigrum* ssp. *hermaphroditum* (1:1000 magnification). The outermost layers of the papery outer bark, which repeat the successive pattern of the shown periderm, got lost while cutting. In our dendrometer approach, we removed the outer layers of the bark, most likely down to the phellogen. As shown here, the loose bark structure allows removal without severe damage of the inner tissue. We aimed at mounting our dendrometer sensor as close to the still protected cambial zone, to achieve data on physiologically active stem diameter variability such as growth, excluding swelling and shrinking of the passive outer bark tissue.

To clarify the mounting process in the manuscript we specified:

> *"We mounted our dendrometers on one major above-ground stem horizontal to the ground surface on randomly chosen specimens, which were as close to the assumed root collar as possible. During this technical process, we removed the dead outer bark to place the sensor as close to the living tissue as possible, following a common practice for dendrometer measurements of trees (e.g. Oberhuber et al., 2020; Wang et al., 2020; Grams et al., 2021). This ensures that hygroscopic shrinkage and swelling of dead tissues from the outer bark do not influence the diameter measurements. Such processes have been previously addressed in trees (Zweifel and Häsler, 2000; Gall et al., 2002; Ilek et al., 2016), and comparative studies revealed a complex interplay of xylem as well as phloem growth and pressure induced size changes, which simultaneously affect radial stem change and are thus captured by the dendrometers (Turcotte et al., 2011; Zweifel et al., 2014b; Oberhuber et al., 2020)."*

To further highlight our findings regarding water induced shrinking and swelling and growth, we would like to present a closer look at our raw data in a new supplement figure (Fig. B). Here, we show that stem diameter changes during winter and spring are clearly coupled with soil moisture as well as soil freezing and thawing effects, suggesting that we indeed measured effects of active physiological stem shrinking and swelling. During the main growing phase however, our dendrometers captured a clear phase of stem increment, independent on available soil moisture, which we interpreted as growth.

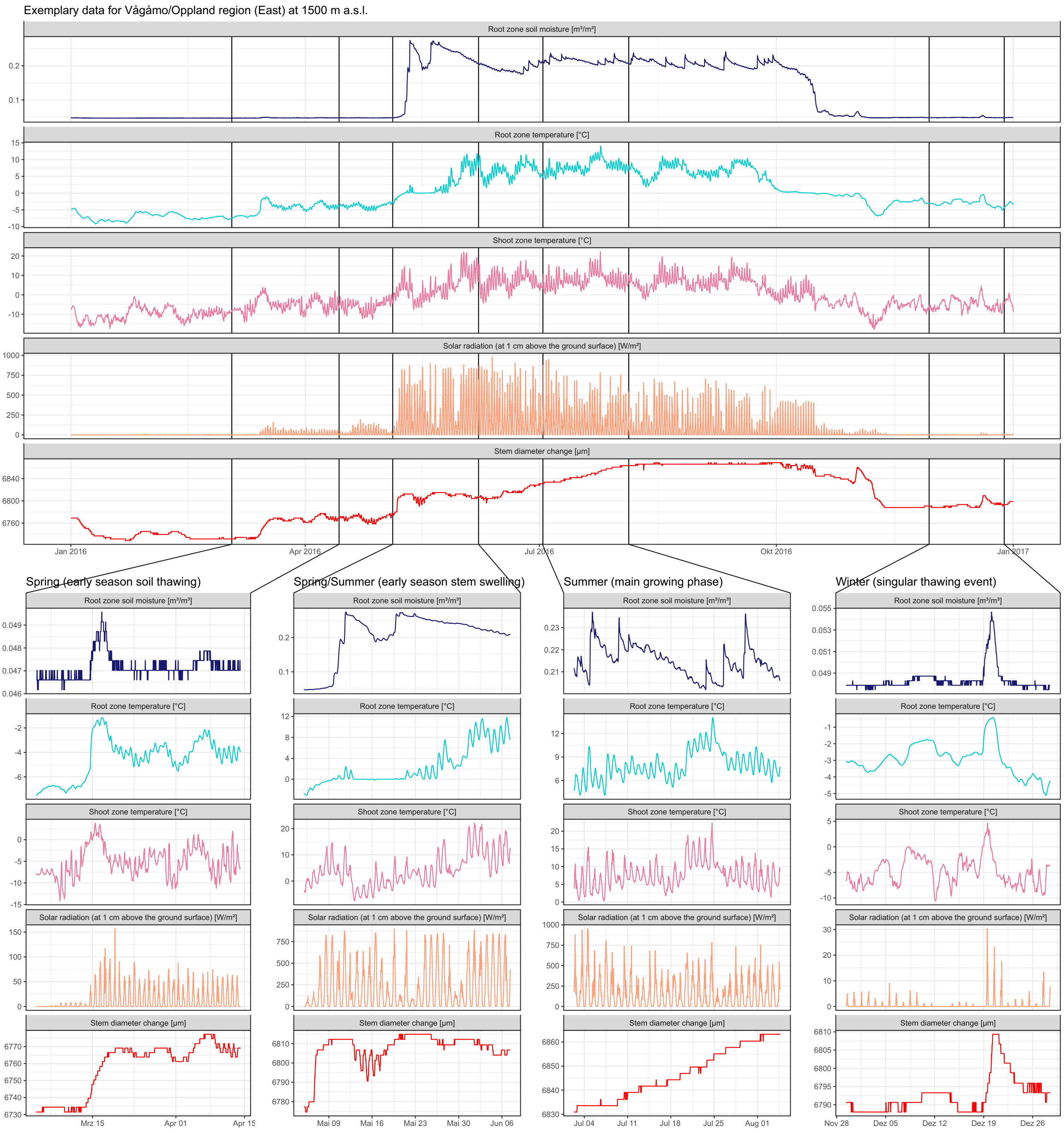


Figure B: Raw data for one exemplary specimen from the Vågå/Innlandet region at 1500 m a.s.l. Here, we present hourly data of stem diameter changes and the respective micro-environmental conditions. The four sections show important phases of the annual stem diameter variability and their relation to the micro-environment in detail. Coupling of soil moisture and stem diameter during the winter and spring months, when water induced stem swelling and shrinking occurs, and decoupling during the main growing phase is clearly evident. Additionally, the direct response of stem diameter to singular soil thawing events in winter is clearly visible in the curves.

- Limited sample size, i.e., one dendrometer record per plant and elevation: In their reply to this major issue, authors argumented that “Actually, our result regarding the elevational gradient was that there was no thermally driven growth gradient.”

The presentation of unexpected results is not an argument in favour of the small sample size.

Furthermore, dendroecological studies on *E. hermaphroditum*, which two of the authors of this manuscript co-authored (Löffler was co-author in all papers cited below), revealed high intra-plant growth variability and authors also pointed out the necessity of a high number of samples for determining radial growth of the dwarf shrub under study.

Main points of previous dendroecological (i.e., tree ring) studies:

Bär et al. (2006) found that “***E. hermaphroditum*** **shows highly individual growth histories**. Thus, cross-dating of growth curves is restricted to several radii within an individual and to mean curves of individuals growing at the same micro-site. Wedging rings and missing rings as well as eccentricity and asymmetric geometry of the stem constrict the synchronisation of growth curves.”

Bär et al. (2007) pointed out that “For a proper synchronization of the growth rings, serial sectioning was applied **in order to deal with the high internal growth variability and the high proportion of discontinuous rings.”**

Bär et al. (2008) stated in their last sentence: “Hence**, carefully synchronized and well replicated ring-width series of dwarf shrubs** from alpine regions can be used as sensitive indicators for reconstructing past climate in vast regions beyond the polar and alpine tree limits.”

Furthermore, in lines 336ff of the study under review authors state that “In contrast to the oceanic-continental gradient, our study showed **high inter-plant growth variability** (Fig. A1 and Fig. A3), which has been previously described in E. hermaphroditum (Bär et al., 2008) and could be a result **of the nanoscale of internal growth variability within the multi-stemmed plant itself** (Bär et al., 2007).”

Therefore, it seems to be quite obvious that a single point measurement (or diameter record in this case) does not represent radial growth (and hence intra-annual growth patterns derived from it) of a multi-stemmed shrub at a given elevation. Extremely low growth rates (< 100 µm) are likely to increase the uncertainties of a “single measurement”.

Addressing the limited sample size along the elevational gradient, there seems to remain a misunderstanding. We agree that the sample size is too small to make any overall assumptions about the elevational gradient. Therefore, in our manuscript we do not consider the results regarding the elevational gradient among main results of our study. Instead, we would like to highlight here that we found surprisingly similar annual growth patterns and statistically significant response patterns to the micro-environment in twelve individually sampled plants from differing sites along an elevational gradient (see manuscript):

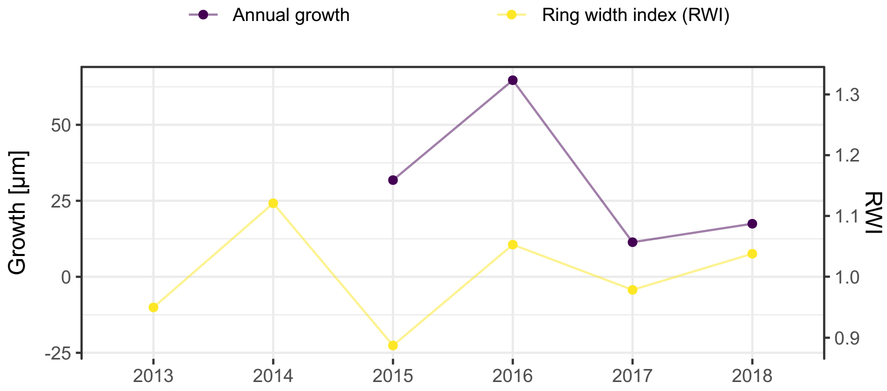
> *"These conditions varied comparatively little between the study regions (Fig. 2 and Fig. A1), and led to very similar seasonal growth patterns and timing of growth (Fig. A6) ...".*

We would like to highlight here that our approach is fundamentally different from traditional measurement methods for shrub growth in that we are observing site-specific processes of stem diameter change, while the ring-width-approach from previous studies looks at the results of these processes (ring widths). The traditional approach is usually presented with a larger sample size and does not include variability between micro-sites or individual specimen. Here, we focus on fine-scale patterns instead, which we found surprisingly synchronized, due to the similarities of the environmental conditions, which are a result of the topographical position. Our sampled specimens seem to be uniquely affected by these specific micro-environmental conditions found at the sampled ridge positions. Here, further comparative studies are necessary, to clarify how growth patterns might differ in a heterogeneous alpine environment e.g. along topographic gradients. We are currently working on these questions within our research project. However, the findings presented here already highlight the strength of the measuring approach in identifying common fine-scale patterns across sites. Also, dendrometer measurements on trees have proven that meaningful results can be drawn from comparatively small sample sizes per species (e.g. Duchesne et al., 2012 (n = 3); Liu et al., 2019 (n = 11); van der Maaten et al., 2018 (n = 5)).

High inter-plant growth variability holds true, as seen from the magnitude of observed growth varied between sites. Overall patterns, including winter stem shrinking and summer growth, however, were found to be similar in the majority of sampled specimens. Such patterns have not been discussed previously in literature, and they cannot be derived using traditional sampling methods, including the ring-width approach used by Bär et al. (2006, 2007, 2008). Here, it is important to distinguish between growth derived from wood anatomical traits (growth rings), and the growth processes measured by dendrometers. A comparative study would further validate our dendrometer approach. We therefore simultaneously sampled several specimens from the same positions studied with our dendrometers and conducted micro-slice based anatomical measurements on growth rings, using the same approach from our earlier studies on *E. hermaphroditum* (Bär et al. 2006). We are currently working on a study attempting such a comparison, and first results suggest that the radial growth measured by our dendrometers is indeed mirrored in the wood anatomy data (see Fig. C).

We are aware of the intra-plant variability, which might affect our results. However, the fact that we were able to derive meaningful growth curves, which followed similar patterns from 12 individual specimens suggests that these patterns represent an important aspect of shrub growth. Additionally, our ring-width data presented in the new Fig. C was derived from multiple stems (following Bär et al., 2006 and 2007). Here, high synchrony with the stem diameter change derived from the dendrometer data further validates the approach.

A Ring width index and dendrometer data



B Mean summer temperatures (June, July, August)

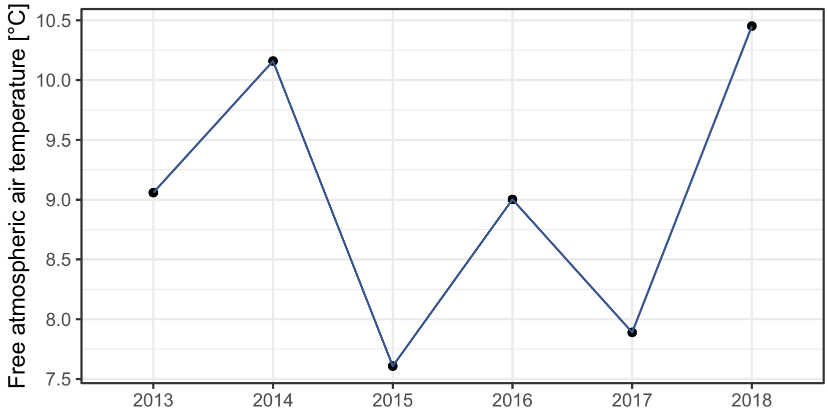


Fig. C: Comparison of annual growth measured using dendrometers (see Material and Methods), and ring width derived by measuring annual growth rings of 12 specimens from similar positions on exposed ridges, presented here as ring width index (RWI). Ring width was measured from multiple micro-slices per specimen (following Bär et al., 2006) (A), (B) shows free atmospheric air temperatures measured at 2 m above ground in both study regions. Such temperature data is commonly used for comparison of climate-growth relationships in dendroecological studies. With this figure we aimed to reproduce previous studies (Bär et al., 2006 and 2007) for comparison with our dendrometer measurements.

- Frost drought as a major determinant of shrub growth: In their reply authors state that "we here show that frost droughts during winter are obviously restricting our shrub species, and that this phenomenon is similarly represented along all alpine ridges despite elevational and regional climate differences."

If frost drought in late winter is a major issue, which significantly affects growth of *E. hermaphroditum*, how can it be that at the same time this shrub species "remains photosynthetically active during the snow-free period" (see lines 18ff)? As a result of freezing temperatures water transport is either severely reduced or completely interrupted – this would certainly impair carbon assimilation. I would also expect that stomata are closed to prevent excessive water loss as long as soils are frozen. Authors are also stating in their reply that "intensive soil freezing" occurs during winter months. Therefore, please show data or cite a paper that supports your interpretation, i.e., relevant carbon assimilation is possible during periods when soils are frozen.

Furthermore, did authors observe any leave damages caused by frost drought, i.e., browning and subsequent shedding of leaves in spring, which would indicate that severe drought stress occurred during winter (lines 344ff: "..and frost-triggered droughts might result in tissue damage caused by an internal water deficit.") . If winter drought is an important issue for this shrub species as suggested by authors, I would expect that at least at the highest elevation and in the more continental study region signs of frost drought are clearly visible.

We did indeed observe the described effects of frost drought, i.e., browning and subsequent shedding of leaves in spring in several cases after harsh, cold and stormy winters, but usually the plants at the ridges were affected only partially (we did not observe entirely dead specimens). Such effects did not follow the expected patterns suggested by the reviewer. Instead, lower alpine elevation sites had strongest indications (in East and West), and this observation match stronger protective icing effects with elevation and the reverse effects of inversion weather conditions, with the lowest temperatures at the low-alpine ridges (Löffler et al. 2006).

In general, we agree that stomata would be closed to prevent excessive water loss as long as soils are frozen. However, if our evergreen species is forced to photosynthetic activity during clear sunny weather conditions in the winter months, this means that in order to effectively use the relatively high radiation measured during this time, the stomata will open for CO_2 intake and transpiration loss. This will make the plant highly dependent on the availability of liquid water from the roots and vulnerable to drought frost damage, when ground frost is severe. The strong dependency of stem diameter variability on liquid water availability is clearly visible in our raw data (see new Fig. B): During the winter months stem increment is clearly coupled with soil moisture and individual thawing events.

As such, we expanded on the text to further explain and strengthen our interpretation of the observed results during the winter months:

> *"Our findings regarding seasonally differentiated response to near ground environmental conditions (Fig. 5) highlight the importance of winter conditions for early growth. This indicates that for our sampled evergreen species at the chosen sites, which experienced only short periods of snow cover that otherwise would be likely to influence the growth response, the degree to which photosynthetic activity was energetically effective in synthesizing carbohydrates during the winter months was especially important. Such continued activity was found in E. hermaphroditum, as well as several other evergreen shrub species before (e.g. Bienau et al., 2014; Wyka and Oleksyn, 2014; Blok et al., 2015). Photosynthetic activity is forced due to exposure to high solar radiation reaching the evergreen plants at the ridge positions where a protective snow cover is missing. This causes continued water transport under extreme temperatures, increasing the risk of cavitation (Tyree and Sperry, 1989; Venn and Green, 2018). Long and severe ground frosts might limit access to soil moisture, and frost-triggered droughts might thus result in tissue damage caused by an internal water deficit (Mayr et al., 2006). However, E. hermaphroditum at our studied sites proved mostly frost hardy, drought tolerant and highly adapted to these*

> *conditions (Carlquist, 1989; Hacke et al., 2001), with winter stem diameter change closely linked to soil moisture availability and singular thawing events, suggesting that the sampled specimens were able to utilize available liquid water even under extreme conditions (new Fig. B*).”*

A clearer understanding of the stem anatomy of *E. hermaphroditum* might also be of help here, which is why we included the following in chapter 2.2 Species and Specimen:

> *“The species belongs to the Empetraceae family of heathlike shrubs. Its stem anatomy was described by Carlquist (1989) and is characterized by a narrow vessel diameter, which can be interpreted as a form of adaptation to drought or physiological drought due to cold as it impedes embolism formation. In general, the family is known to match extreme environments by adapting stem anatomy (Carlquist, 1989).”*

This highlights the adaptive capability of species of the Empetraceae family, including adaption of stem anatomy to winter drought caused by soil freezing.

- A clarification is needed as to why in a previous dendroecological study co-authored by Pape and Löffler contradictory results regarding growth limitation of *hermaphroditum* by climate factors were found. Bär et al. (2008) reported that “This study indicates that mean summer (June–August) temperatures determine the width of the growth rings of *Empetrum hermaphroditum* irrespective of topoclimate.”

It is highly implausible that determination of climate-growth relationships based on dendroecological techniques (inter-annual) vs. dendrometer records (intra-annual) lead to such contrary results as reported in this study. Please clarify and discuss this issue in a revision.

Both studies (Bär et al., 2008 and our present study) do not only differ in the deployed technical approach. Instead, the previous study used a different dataset, which is only partly comparable to the one used here. For instance, the samples presented in our new paper were taken from two, instead of one, study regions, spanning a much wider environmental gradient. At the same time, we restricted our sampled sites to exposed ridge positions in the new dendrometer study, which experience very similar micro-site conditions, regardless of the regional climate signal. We discuss this in details in the first paragraph of the discussion section. Soil moisture is one of the key factors determining these micro-conditions (mainly due to snow distribution). Because such fine-scale soil moisture measurements were not included in the study from 2008, their effects could not be assessed. As such, the results of both studies as a whole might suggest that while temperatures play a key role in determining growth processes, on a micro-scale soil moisture and snow conditions might be more important within a topographically heterogeneous environment, especially at positions where snow drift plays a major role. We are currently exploring this topographical variability to be presented in future publications.

In general, we considered comparability of our dendrometer approach to previous study designs for several years, which is why we also collected ring width data at our studied sites. We included some of this data in the new figure C and are currently working on a comparative study. In the manuscript we included a short discussion of the figure and its implications in the discussion section:

> *"Thus, in our studied alpine environment, we cannot confirm high temperatures as the main general driver of shrub growth, as was assumed in several previous studies (i.e., Elmendorf et al., 2012; Hollesen et al., 2015; Ackerman et al., 2017; Weijers et al., 2018b).*
>
> *Such previous studies commonly used free atmospheric air temperature measured at 2 m above ground and ring width measurements (e.g. Bär et al. 2007 and 2008). A direct comparison of annual growth derived from our dendrometer measurements and such ring width measurements at the studied sites revealed high synchrony (Fig. C*). Here, the ring width data was linked to summer temperature as well, suggesting that the assumed temperature-growth relation holds partly true at our sampled sites (Fig. C*). Dendrometer data have the potential to reveal much deeper insights into complex functional aspects of growth, and in combination with on-site environmental data might help rethinking climate growth relations. Further studies are necessary here to fully explore how dendrometer measurements compare to traditional measurement methods and which additional information can be gained. Still, the comparative data presented in Fig. C* clearly shows that both have the potential to reveal important aspects of stem variability and growth."*

*Figure numbers will be adjusted in the final revised version of the manuscript.

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