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## Reply on RC1

Svenja Dobbert et al.

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Author comment on "The application of dendrometers to alpine dwarf shrubs – a case study to investigate stem growth responses to environmental conditions" by Svenja Dobbert et al., Biogeosciences Discuss., <https://doi.org/10.5194/bg-2021-99-AC1>, 2021

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Reviewer 1

Due to considerable methodological deficiencies and a lack of physiological understanding of plant growth limitation in the alpine zone, I cannot recommend publication of this manuscript.

Authors

*The authors would like to thank Reviewer 1 for detailed and constructive input. There are two main points of concerns, a) bark, which was of course removed before measurement, and b) averaging procedure, which would have undermined the strength of our unique dataset. Both issues can be ruled out, as they were obvious misunderstandings. Moreover, we reworked the entire manuscript according to very helpful comments and further detailed suggestions (see below). As such, we addressed shortcomings in articulating the approach of our study, rewrote passages with imprecise wording, and added important arguments, references and explanations. 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. As to obvious discordance with existing literature, we clearer indicated the speculative nature of some interpretations and argue that our findings give reason to rethink certain aspects of current knowledge.*

General comments:

In this paper authors analysed the influence of environmental factors on radial growth and intra-annual growth patterns of the prostrate dwarf shrub *Empetrum nigrum* ssp. *hermaphroditum*, which is widespread in arctic and alpine ecosystems. Elevational gradients spanning 500 m were selected above treeline in a humid and continental climate region in central Norway. To determine key dates of intra-annual growth dendrometers were mounted on one major stem per plant (two regions x six samples x two region, i.e., one sample per elevation result in a total of 12 dendrometer records during four successive years). Regression and correlation analyses were applied to calculate the influence of microclimate on growth parameters. Authors found that soil moisture, solar radiation and winter conditions are the main drivers of radial stem growth of *Empetrum nigrum* ssp. *hermaphroditum*. Results of this study are unexpected, as it is generally assumed that in the temperate climatic zone growth processes at and above treeline are primarily limited by temperature during the growing season. Although authors present a unique data set of dendrometer records of an alpine shrub species together with site specific environmental data during four years, I have several major concerns regarding study design and analysis:

(i) I suppose that due to selection of only one individual per elevation, dendrometer records gathered along the elevational gradient were averaged in both regions, i.e., dendrometer data sampled along a temperature gradient of 3°C (500 m elevational gradient x 0.6 °C temperature lapse rate per 100 m elevation) were averaged to obtain a mean dendrometer series per region (n=6 per region), which were correlated with mean values of environmental variables. This averaging procedure, however, precludes a detailed and meaningful analysis of the influence of temperature on shrub growth at and above treeline (cf. comments to p. 9, line 205 and p. 10, Fig. 2).

*The reviewer is wrong assuming that the individual dendrometer curves (and associated environmental measurements) have been averaged prior to further analyses. While designing the study, we were well aware of common misconceptions regarding the utilization of, e.g., temperature data (cf. Körner & Hiltbrunner 2018) and therefor carefully chose physiologically meaningful variables without averaging, specifically to ENABLE (and not to preclude) a meaningful analysis. As focusing solely on analyses that also make sense ecologically seems so obvious and natural, we admittedly failed to state and clearly*

*describe such our approach more explicitly. Based on the reviewer's critique, we expanded on our previous statement in the Material and Methods section (lines 174/175 of the revised version):*

*"We first calculated these growth-defining parameters for each individual curve to assess the variability between sampled specimens. These values entered in the following statistical analyses individually."*

*Moreover, we included an additional statement in lines 249-252 of the revised version:*

*"For these, as well as the following statistical analysis, we used site-specific values for each sampled specimen to overcome common misconceptions regarding the utilization of, e.g., temperature data (cf. Körner & Hiltbrunner 2018), We carefully chose physiologically meaningful variables without averaging, specifically to enable a meaningful analysis (see also Löffler and Pape 2020). "*

*Throughout the manuscript, whenever data were averaged, this was done after analyses only and primarily for visual purposes, to increase readability and interpretability of the graphics and reduce the size of the final tables. We revised Figure A1 to show variability between our studied sites more clearly and conveyed a better understanding of the patterns along the elevational gradient to the reader.*

(ii) Diameter dendrometers were mounted over dead outer bark, which is a highly hygroscopic tissue. The possible influence of daily/seasonal changes in air humidity on stem diameter variations were not taken into consideration (cf. comments to p. 5, line 135).

*This again revealed to be a misunderstanding: We are very aware of the effects the highly hygroscopic bark has on diameter measurements. Consequently, our dendrometers were NOT mounted over dead outer bark. We removed the outer bark before mounting the dendrometers. As we assumed this to be common knowledge and practice, we unfortunately missed to state this explicitly. To highlight this step, we included a short*

*paragraph in the Material and Methods section (lines 134-136 in the revised version):*

*"During this process, we removed the outer bark to place the sensor directly on the cambium. This ensures that hygroscopic shrinkage and swelling of dead tissues from the 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)."*

*In general, Empetrum hermaphroditum has a very thin bark, which is easily removed without the danger of damaging the cambium.*

(iii) There are numerous inconsistencies in data interpretation which need to be clarified to justify publication.

*We clarified inconsistencies in accordance with the following comments and suggestions.*

Specific comments and suggestions:

p. 1, line 15: Elevational effects on stem growth were not analysed in this study, because dendrometer records were averaged. This procedure precludes the analysis of effects of decreasing temperature with elevation on growth.

*This is not true. Actually, we expected to find growth response with elevation, hypothesized that these would be due to thermal constraints, and were surprised not to see such a coupling in the data. All our data were measured along the elevational gradient, and based on our temperature measurements at each site we see the decreasing temperature with elevation. We revised Figure A1 accordingly to show this to the reader. However, the elevational trend found in the temperature data is neither reflected in our stem diameter data, nor in the soil moisture data (see Figure A1). The decoupling of stem*

*diameter variation from the temperature trend along our elevational gradient, together with the decoupling of soil moisture from the elevational gradient, suggests that alpine temperatures are not limiting growth in our shrub species at the studied sites. Alpine ridge sites are often believed to be dry as to the wind-exposed nature. As has been shown in previous studies (e.g. Löffler 2005), soil moisture is not a limiting factor during the summer period, when plants are exposed to atmospheric summer drought. This decoupling of the soil from the atmosphere is due to a dense lichen carpet, which dries out, has no root coupling to the ground like other plants have, effectively limits descending water transport from the soil to the atmosphere, and as such reduces evaporative loss to a minimum. Along with our general novel findings on soil moisture as a strong driver of growth in *E. hermaphroditum*, 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. We added this in chapter 4.1 of the discussion section:*

*"This decoupling of stem diameter variation from the temperature trend along our elevational gradient (Fig. A1) suggests that alpine temperatures are not limiting growth in our shrub species at the studied sites. Furthermore, we found soil moisture similarly decoupled from the elevational gradient, suggesting a reduced significance of this gradient at the micro-scale, at which our near-ground environmental parameters were measured."*

*Additionally, as mentioned previously, dendrometer records were not averaged before entering into the statistical analysis (see above).*

p. 1, line 18: There are inconsistencies here: According to Table 3, onset of growth did not start before DOY 173. Furthermore, mean shoot and root temperature were below 0°C in March-April 2015-2017 and < 5°C in May 2018. How can it be possible that these correlations have come about? Please clarify.

*The dendrometer curves show stem increment in spring, before the start of the growing phase (growth initiation) (see Fig. 3). This is not defined as part of the growing phase, because it does not exceed the previous year's stem diameter and therefore cannot be seen as growth, but rather as stem recovery from the autumn/winter shrinking period during the previous year. Still, this recovery phase influences total annual growth and is possibly related to thermal conditions during winter and spring, thus reflected as such in the correlation results. Additionally, in Table 3 and Fig. 1 and 2, mean values were presented, while individual-site values entered into the analysis. We expressed this more clearly in line 251:*

*"For these, as well as the following statistical analysis, we used site-specific values for each sampled specimen..."*

*Overall, growth initiation showed a positive correlation with winter temperatures (see Fig. 6 and discussion).*

p. 1, line 19: Photosynthetic activity during winter at daily mean temperatures < -10 °C is highly speculative and rather implausible.

*Even though mean temperatures are temporarily below -10°C, higher temperatures are reached during the midday and there are short, warmer periods which experience soil thawing (see Figure 1, which we revised to include daily maximum and minimum temperatures). This is because of pronounced exposure and missing snow cover at all our studied ridge positions. We used near-ground air temperature as potential driver of plant growth, which does not directly reflect the temperature in the plant. Especially during periods of clear sky and full global radiation, canopy temperature is known to be much higher than our temperatures measured at 15 cm above ground.*

*We do not suggest that active cell growth occurs during these conditions. However, photosynthetic activity of vascular plants in late winter and under extreme conditions was reported before, and our suggestion is thus backed by the literature (e.g. Semikhatova et al., 1992; Starr and Oberbauer, 2003; Lundell et al., 2008), which we also referred to in the Discussion section.*

*Please see also below (comment regarding p. 24, line 459).*

p. 3, line 75: "caused by induced water" – unclear meaning, please reword.

*This addition was removed here to improve clarity.*

p. 3, line 78: "inter-annual" or "intra-annual" – please check.

*We checked this and the correct term here is intra-annual.*

p. 3, line 84: Dendrometers used in this study record stem diameter variations, whereas point dendrometers record radial stem variations. Please correct.

*The term point dendrometer is not uniformly defined in literature and by manufacturers. Usually, it refers to dendrometers which measure stem variations at one (radius) or two (diameter) points, to distinguish them from band dendrometers, which measure stem circumference. We measured stem diameter, and our dendrometers are called point dendrometers by the manufacturer (probably because of their technical principle, which allows mounting them to measure radial variations). We fully agree, that the term point dendrometer might be confusing here and therefore removed it throughout the text.*

p. 3, line 88: Please explain meaning of "mechanistic adaptation".

*We here used the term "mechanistic adaptation" to distinguish our measuring (physiological) approach from the methods commonly used in dendroanatomy, which focuses on structures and anatomical signatures. However, since this term is probably not clear to all readers, we here changed it to "growth patterns", which reflects the main objective of our work more accurately.*

p. 4, line 108: Please indicate that sites at 900 and 1000 m asl are (natural?) treeline sites. Has the elevation of the tree line been influenced by humans? Are study sites selected along the elevational gradient influenced e.g., by grazing?

*Furthermore, it is quite important to indicate slope and exposure of all study sites, as well as plant structure (height) of selected shrubs, because all these factors affect temperature that the plants experience (cf. Körner 2021).*

*The sites at 900 and 1000 m a.s.l. are all alpine sites (without trees), but they are near-treeline, which is found at ~800 m a.s.l. in the oceanic study region and at ~1000 m a.s.l. in the continental study region). We included these aspects in the text (lines 108-111 of the revised version)*

*"..., in accordance with the tree line in this region, which is located at about 750 to 800 m a.s.l.. In the continental region, we used 1000, 1100, 1200, 1300, 1400, and 1500 m a.s.l.. Here, the tree line is situated slightly higher, at about 1000 m a.s.l. (Röbner et al., 2008; Röbner and Löffler, 2007). Thus, all of our studied sites were located above the tree line."*

*The treeline in Scandinavia has indeed been influenced by humans over long periods of time. Recently, only very extensive sheep herding is practiced, and *E. hermaphroditum* is usually not affected by grazing (see Weijers and Löffler, 2020), a fact which we included in chapter 2.2 Species and Specimens. For more information on climate and human influence on the treeline in the study regions, please also see Röbner and Löffler, 2007 and Röbner et al., 2008, now cited in line 110 of the revised text.*

*As suggested, we included height of the plants in Figure A1. Slope and exposure were not included, since they were naturally identical at the ridge positions with slope =  $\sim 0^\circ$ , which indicates no exposure.*

p. 4, line 114: Please indicate mean height of shrub-canopy along elevational gradients.



*We included mean height of shrubs, lichens, mosses, graminoids, and forbs at the studied sites in a revised version of Figure A1.*

p. 5, line 128: DRO-dendrometers measure stem diameter variations and therefore are different from point dendrometers. To avoid misunderstanding, please correct.

*We agree that the term point dendrometer might be misleading and removed it from the entire text (see above).*

p. 5, line 135: Please consider that the "daily mean approach" yields time series of daily stem diameter variations, which include both water- and growth-induced diameter changes. Several authors found that bark is a highly hygroscopic tissue (e.g., Ilek et al. 2016, Gall et al. 2002). Therefore, stem diameter changes recorded by dendrometers mounted on dead outer bark as in this study may be affected by evaporation and absorption of water from the bark tissue. Dead outer bark should be (completely) removed to reduce hygroscopic shrinkage and swelling of dead tissues on dendrometer records. To be able to unequivocally relate stem diameter fluctuations to environmental parameters and accurately determine stem water deficit, hygroscopic processes must be taken into account even when dendrometers were mounted over even thin dead outer bark layers (cf. Oberhuber et al. 2020). Therefore, authors need to demonstrate the lack of influence of changes in diurnal and seasonal air humidity on changes in stem diameter. Because hygroscopic effects could partly explain unexpected climate-growth relationships found in this study (i.e., influence of winter freezing conditions, soil moisture availability, solar radiation) I suggest adding records of daily (seasonal) changes of relative air humidity within study regions.

*Our dendrometers were not mounted on dead bark (see our comment above). Rather, the bark was removed before mounting the dendrometer. We are aware of the problems caused by placing the dendrometer on top of the bark and included a short text in the Material and Methods section, citing the suggested literature:*

*"During this process, we removed the outer bark to placed the sensor directly on the cambium. This ensures that hygroscopic shrinkage and swelling of dead tissues from the 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)."*

p. 5, line 144f: The phrases "...hydrological processes", and "reversible shrinking and swelling associated with the stem water deficit" are unclear, please reword.

*For clarity, we reworded this sentence as follows:*

*"To separate GRO from water-related expansion and contraction of the stem, we first excluded reversible shrinking and swelling associated with stem water fluctuations from the original data using the approach proposed by Zweifel (2016)."*

*The term "stem water fluctuations" now better describes what we meant here.*

p. 5, line 146: I suggest adding "the final growth curve", which was used to determine relationships between stem growth and environmental variables.

*This must be a misunderstanding possibly due to inconsiderate wording. "The final growth curve" does not refer to one individual curve, but rather to the final curves for each individual specimen. All of these curves were used to determine relationships between stem growth and environmental variables. We reworded this in the text:*

*"... the final growth curves were derived from the original measured data..."*

*Additionally, we included the described cumulative curves in Figure 3.*

p. 6, line 169-174: Sentence starting with "Buchwal et al. (2013)...." and the following sentence belong to discussion section.

*We disagree. This sentence belongs to the explanation of our methodical approach regarding the specimens that did not experience any growth, and is therefore important at this point.*

p. 6, line 174: Please explain "non-growing seasons" or reword.

*We reworded this sentence:*

*"We did not calculate growing seasons for these years, and the analyses proceeded separately"*

p. 6, lines 184ff: Please add manufacturer of soil moisture and radiation sensors. Furthermore, was the radiation sensor mounted on an open site or below "canopy".

*Our loggers as well as all temperature, soil moisture and global radiation sensors were manufactured by ONSET which is indicated in the text (p. 7, line 196), Furthermore, the global radiation sensor was mounted close to the plant and was not affected by the canopy. We edited the text accordingly:*

*"Additionally, we measured the shoot zone global radiation ( $W/m^2$ ) at 1 cm above the ground surface in close proximity to the plant (hereafter GRSZ) using ONSET's HOBO type S-LIB-M003 silicon pyranometer ( $\pm 10 W/m^2$  accuracy). We made sure that those measurements were not affected by the canopy."*

p. 7, Figure 1: I suggest showing not only daily mean values of shoot and root zone temperatures but also daily mean maxima and minimum temperatures.

*We revised Figure 1 to include daily mean maximum and minimum temperatures.*

p. 8, Legend of Table 1: "inter-stem variability" or "site variability"? Please check.

*"Site variability" is the more accurate wording here. Was changed accordingly.*

p. 9, line 205: Has the abbreviation GDD10 been explained before?

*GDD10 stands for the number of days with shoot zone temperature > 10 (growing degree days). The abbreviation is explained in Table 3. For clarity, we added the explanation here as well.*

p. 9, lines 202-211: This paragraph belongs to results section.

*We disagree. This paragraph describes our collected data (Material).*

p. 9, line 205: Do authors have any explanation why temperatures vary only slightly between sites? Along an elevational gradient spanning 500 m (900 to 1400 m asl and 1000 to 1500 m asl) and taking a temperature lapse rate of 0.6 °C per 100 m elevation

into account, a temperature difference of 3 °C between the lowest and highest study site is to be expected. Furthermore, also soil moisture shows low variability although selected study regions belong to the humid and continental climate zone. Please discuss these findings.

*There is a clear elevational temperature gradient (see our previous comment regarding p.1, line 15), both for near-ground air and soil temperatures, but the difference between the lowest and highest study sites is on average slightly lower than proposed by the linearly regressed adiabatic lapse rate, here. We expanded Figure A1 to include the environmental conditions along the elevational gradient. The reasons are daily variations in the adiabatic lapse rate induced by nocturnal inversions, and variations over specific weather phenomena and seasonality (e.g. Löffler et al. 2006; Pape et al. 2009; Wundram et al. 2010). We included this in line 216. In general, our results highlight that the measured near-ground conditions follow common patterns of ambient air temperature measured at standard heights (e.g. 2 m above ground) only partially.*

*Soil moisture shows no elevational gradient and overall low short- and medium-term variability, but there is a strong seasonality in the soil moisture data, with clear indication of winter frost droughts at the alpine ridges. All studied alpine ridges from oceanic and continental climate regions had similar patterns along the elevational gradient. We used this above discussed finding to explain missing elevational relations of growth and soil moisture (see our previous comment regarding p.1, line 15: Alpine ridge sites are often believed to be dry as to the wind-exposed nature. As has been shown in previous studies (e.g. Löffler 2005), soil moisture is not a limiting factor during the summer period, when plants are exposed to atmospheric summer drought, and this decoupling of the soil from the atmosphere is due to a dense lichen carpet, which dries out, has no root coupling to the ground like other plants have, effectively limits descending water transport from the soil to the atmosphere, and as such reduces evaporative loss to a minimum. Along with our general novel findings on soil moisture as a strong driver of growth in *E. hermaphroditum*, 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.)*

p. 9, lines 220ff: This sentence belongs to discussion section.

*We disagree. This sentence explains why and how we included estimated times of snow coverage into our analyses, even though we did not measure snow directly.*

p. 10, Figure 2: It is quite surprising that mean monthly shoot and root zone temperatures reach similar maxima (around 8-10 °C) during the supposed main growing season (June-September). This is most likely an effect of averaging temperature records along the elevational gradient or selection of sites showing different slope and/or exposure. The extended elevational transect would be an ideal study design to investigate the influence of shoot and root zone temperatures on growth of this dwarf shrub. Unfortunately, limited sample size (one dendrometer record per elevation) precludes any analysis in this regard.

*Shoot and root zone temperatures follow similar patterns throughout the year (see Figure 1), which is why maxima are reached at similar times. However, the absolute values (see y-axis scale) are of course different. To make this more visible, we aligned Figure 2a and 2b, showing both graphs with the same y-axis scale. We agree that an extended elevational gradient should principally better address the thermal limits of shrub growth at its upper alpine distribution. Here, we will have further data from additional dendrometers which we have already installed (not included here due to shorter time series). We disagree that the analysis of the elevational growth gradient was limited by the sample size, here. Actually, our result regarding the elevational gradient was that there was no thermally driven growth gradient. However, we agree that the study design could be expanded to include, for example, sites representing the thermal limit of the species.*

p. 11, line 245: "with the daily growth for each season" – Stem growth does not occur during all seasons (cf. Fig. 3)? Please clarify meaning of "daily growth" in this respect.

*To clarify, we changed "daily growth for each season" to "daily stem change for each season". This is consistent throughout the text: We defined growth in chapter 2.4 Analysis of Seasonal Growth Patterns as "growth-induced irreversible stem expansion".*

p. 11, Table 2: Please explain inverse relationship between growth cessation and total annual growth: the later growth stops during the year, the lower the annual increment?

*Please keep in mind here, that Table 2 presents the results of a multiple partial regression. As such, the resulting coefficients represent the relationship between the dependent variable (total annual growth) and each independent variable, while controlling for all other variables. The contribution of growth cessation to the model (see Table 2) was very low, indicating an overall low influence of growth cessation on total annual*

*growth, which we indicate in the results section. Because of this role within the full model, such a conclusion is not reasonable from this result.*

*As discussed in detail in the discussion (chapter 4.4 Growth Initiation and Cessation): Growth cessation was related to soil moisture and temperature, yet we could not identify a threshold. Peak growth usually occurred early during the growing season, indicating a lesser role of the late growing season for total annual growth.*

*In the discussion we included a short additional statement to clarify that our results highlight the complexity of such relations rather than support the assumption that total growth is directly linked to growing season length:*

*"Overall, our results regarding growth timing demonstrated the complexity of these processes and we cannot confirm a clear relation of growing season length and overall growth (Rammig et al., 2010; Blok et al., 2011; Prislán et al., 2019)."*

Also add explanation of abbreviation "Part" in legend.

*"Part" is not an abbreviation here. It is statistical terminology and stands for Part correlation, which is also sometimes referred to as semipartial correlation, which was added for clarity (Table 2). For interpretation: The semipartial can also be viewed as the decrease in  $R^2$  that results from removing the independent variable from the model.*

p. 14, Figure 3: Determination of stem water deficit is most likely influenced by bark hygroscopicity (see comments to p. 5, line 135). I suggest removing Figure 3d. Furthermore, is "stem diameter variability" or are "stem radial variations" depicted in Figure 3b. In Table 4 values of "stem radial growth" are shown. Please clarify and be consistent in using "stem diameter variations" or "stem radial variations" throughout the text.

*Bark hygrosopicity should not be an issue, since we have removed the outer bark before mounting the dendrometers (see above). We therefore did not remove Figure 3d. Figure 3b depicts stem diameter variability, as stated in the Figure (y-axis) and the legend: "Averaged measured daily stem diameter variability and Gompertz models fitted to zero growth curves."*

*Additionally, we changed "stem radial variations" in Table 4 to "stem diameter variation". In general, we used stem variation throughout the text to distinguish between the directly measured variations and growth, which we defined in chapter 2.4 Analysis of Seasonal Growth Patterns: "total annual growth, defined as growth-induced irreversible stem expansion (GRO)".*

p. 15, Table 4: Please check value of "stem radial growth" in 2017, which amounts to "1485".

*Here, "." was missing. Stem radial growth in 2017 was 14.85.*

p. 15, line 285f, Figure 4: All 25 environmental parameters explained total annual growth? How is this to be explained? Not all relationships are statistically significant.

*This refers to the results of the regression model, which included all environmental parameters and was indeed able to explain annual growth to a very large extent: "Together, all 25 chosen micro-environmental parameters (Table 3) were able to explain the total annual growth to a very large extent, even though not all parameters contributed significantly." Further analysis and a breakdown of the contribution of each variable follows.*

p. 16, line 291f: "main growing phase during spring" – see comment to p. 1, line 18 (no spring growth according to Table 3). Please clarify.



*Mean growth initiation is indeed not in spring, but as suggested by the standard deviation, variability between years and specimens was high, with many individual specimens starting growth in spring or early summer. Additionally, some specimens started stem increment in spring, which was not termed growth here, because we defined growth as irreversible stem expansion following Zweifel (2016). We assume that this early stem increment might be related to refilling processes rather than formation of new xylem and cambial growth (see Mayr et al., 2006) and included this in chapter 2.4 Analysis of Seasonal Growth Patterns.*

*To avoid confusion, we reworded the phrase:*

*"Comparisons of seasons also showed that micro-environmental influences had strong explanatory power during spring, when many of the plants started stem increment."*

p. 16, line 296: Is "R" Pearson correlation coefficient? If yes, change to "r" throughout the manuscript.

*We changed "R" to "r" when we refer to Pearson's correlation coefficient throughout the text.*

p. 16, line 298: Influence of soil moisture availability on "growth processes" throughout "all four seasons" is highly speculative because (i) leaf water potentials were not determined, (ii) mean values of soil moisture given in Fig. 1 are not indicating drought stress during the growing season in both study regions, and (iii) most alpine plants have a small fraction of deep roots reaching up to 1 m depth. Furthermore, which "growth processes" were influenced throughout the year?

*The influence of soil moisture on growth is strongly emphasized by our results, which are presented here. The soils from our study regions are usually only about 30 – 35 cm deep (solid bedrock below), and we found maximum root density at about 5 – 20 cm. As such, deep roots can be ruled out here. Moreover, our measurements of the soil water content in 15 cm depth indicate that our soils in both climate regions are not experiencing any*

*summer drought (see above), but they are nonetheless influenced by drought during the winter months, caused by intensive soil freezing. During such winter periods, intensive soil frosts may severely limit water uptake and might result in frost drought. Our chain of arguments here is that an evergreen alpine species at the ridges, which is not covered by snow during the winter, is temporarily exposed to solar radiation and results in transpiration losses. The activated photosystem of the plant will deliver carbohydrates during the cold months (frost protection, reserve fabrics), being of advantage to an evergreen species, e.g. to grow better after a mild but sunny winter and spring. In reverse, if frozen ground limits water uptake, temporary snow cover and cloudy weather limit winter metabolism and little reserve fabrics have been accumulated during the previous season, growth will be limited during the current season. Altogether, our findings are quite unexpected on a first glance, but turn to be sound when taking all the different aspects into consideration. We discussed our above chain of arguments in details in the Discussion section (see below), being aware of the partly speculative nature of the interpretation of our statistical analysis. As such, we again argue that our findings give reason to rethink certain aspects of current knowledge based on our novel physiological records on stem diameter variations.*

p. 16, line 300: Sentence starting with "This result..." belongs to discussion section.

*We moved this sentence to the discussion section (chapter 4.4 Growth Initiation and Cessation).*

p. 18, Figure 5: It is highly surprising that Pearson correlation coefficients between "radial stem diameter and micro-environmental data" are almost all highly significant throughout the year including lag phases extending from three days to one year. Did authors check for normal distribution of data? Furthermore, Deslauriers et al. (2007) suggested including only the main period of growth to assess relationships between environmental variables and dendrometer data. Therefore, to determine climate-growth relationships, only the most linear growth phase should be considered, i.e. correlations should be calculated for e.g. the period  $\pm 14$  days around the inflection point of the Gompertz model. Furthermore, to determine environmental influences on growth, radial stem increments extracted from dendrometer records according to e.g. Zweifel (2016) should be used in the correlation analysis rather than "daily values of stem variability" (which include reversible shrinking and swelling of the bark). Figure 5a: "Correlation with mean values": which mean values, annual means? Please add and also indicate meaning of significance symbols in legend.

*We agree that our results are quite surprising. The data are normally distributed. We chose not to reduce the data to the growing season, and rather include each season*

*separately, because in our case there is important information to be gained for example from the stem shrinking observed during autumn and winter, which is not included in the growing phase, and which is also not included in "radial stem increments". Figure 5a refers to the whole year (as opposed to the seasons). Legend was changed. To convey this reasoning more clearly to the reader, we included a short statement in the Material and Methods section:*

*"Here, we chose to include the complete dendrometer series, rather than reducing the data to the main growing season (Deslauriers et al., 2007), to capture seasonal stem shrinking and swelling throughout the year."*

p. 20ff: The discussion sections needs to be substantially revised based on comments given above. Extended speculative data interpretations should be avoided.

*We revised the discussion section based on all the detailed constructive comments.*

p. 20, line 322: Sub-heading is not appropriate – please reword.

*We reworded the heading of chapter 4.1 ("Intra-annual growth patterns") to "Intra-annual patterns of stem change".*

p. 20, lines 324 and 330: Topographical effects on growth of *Empetrum* were not analysed in this study, because all sites were located on exposed ridge positions.

*It is true that we did not analyze topographical effects on growth in this study. Here, we refer to topography to highlight the fact that the studied exposed ridge positions are characterized by unique micro-environmental conditions (which we describe in the text). These conditions are a result of fine-scale topography within the studied regions, which*

*distinguishes the ridge positions from their nearest environment. We clarified this in the text:*

*"In this study, we demonstrated that our focus species *Empetrum hermaphroditum* displayed distinct annual growth patterns in response to near-ground environmental drivers and in close accordance with distinct conditions caused by the local topographical characteristics of the studied wind-blown ridge positions. These unique micro-environmental conditions are a feature of the heterogeneous topography that characterizes alpine terrain (Scherrer and Körner, 2011) and are thus distinctly different from the surroundings. They include high exposure to global radiation and very little, temporary snow cover during the winter months, associated with very low temperatures (Wundram et al., 2010)"*

p. 20, line 335: "intra-plant growth variability" – in Fig. A1 and A3 inter-plant variability is shown, please check wording.

*Checked. "intra-plant growth variability" was changed to "inter-plant growth variability".*

p. 20, line 329: "very similar seasonal growth patterns" – In Fig. A4 I see large differences in stem diameter changes between regions in 2015 and 2018. Please clarify.

*That is true. Stem diameter changes vary in amplitude, yet, the seasonal pattern (shrinking during autumn and winter, growth during summer) and timing of the phases is surprisingly similar. We added the aspect of timing in the text ("... and led to very similar seasonal growth patterns and timing of growth (Fig. A4), ...")*

p. 22, line 386f: "negative correlation between stem diameter variation and number of snow-free days" – "stem diameter variation" is different from stem growth; please clarify.

*Throughout the whole text, we refer to stem growth as defined in the Material and Method section (“...defined as growth-induced irreversible stem expansion (GRO)”), which is based on Zweifel (2016). Stem diameter variation includes all measured stem changes. These terms are used accordingly throughout the whole text.*

p. 22, line 391: “to prepare for the following winter” – Why preparing for winter period? Please explain in more detail.

*We revised this sentence:*

*“In accordance with Buchwal et al. (2013), we assumed that during years of no apparent radial growth, dwarf shrubs might prioritize growth in the more protected and long-living belowground segments, instead of investing in the more vulnerable shoots.”*

p. 22, line 408f: Regarding importance of soil moisture availability for growth, see comment to p. 16, line 298.

*As above, the key role of soil moisture in influencing growth processes is surprising and as such novel to the literature. Here, we carefully argue along with our strong statistical results acknowledging generally accepted physiological mechanisms. Our studied sites experience strong seasonality in water availability due to extreme winter conditions. The relation of growth and soil moisture availability, rather than temperatures is one of the key findings presented here. We revised the text accordingly:*

*“This highlights a key role of the extreme winter temperatures, causing frost drought and consequent water stress even if soil water contents are usually sufficiently high during summer (Tranquilini, 1982; Mayr et al., 2006).”*

p. 22, line 413f: Onset of budbreak and plant growth in spring in the alpine zone is generally related to increase in temperature and photoperiod. A relationship between photosynthetic activity and growth onset is mere speculation and not substantiated by any previous study in the scientific literature (cf. Körner 2021).

*We agree that the interpretation of our statistical finding on the growth relationship to photosynthetic activity is speculation. We here propose a kind of nano-scale effect of soil thawing caused by radiation and respective heat transfer into the upper soil layer, which we assume to be in turn related to growth onset:*

*"Under snow free conditions, it is likely that in our study design global radiation is directly linked to soil thawing close to the soil surface, which was previously linked to growth onset (Descals et al., 2020)."*

*In our study design such effects were best captured by radiation sensors, since soil temperatures and soil moisture were measured at 15 cm below ground, and air temperature 15 cm above ground, respectively.*

p. 23, lines 418-440: Speculative discussion should be condensed. Regarding frost induced stem shrinkage in the literature please see and cite Zweifel and Häsler (2000) and King et al. (2013). Furthermore, regarding importance of carbon assimilation for growth onset and soil moisture availability for growth cessation, it is well known that in alpine plants no critical depletion of carbohydrates occurs in the seasonal cycle, and in temperate climate zones alpine plants initiate winter bud formation tightly coupled to the photoperiod, respectively (cf. Körner 2021).

*Zweifel and Häsler propose a mechanism of bark dehydration, which is responsible for winter shrinking, however, since we removed the bark, this is not the case for our data (see above). However, we revised our text on frost induced stem shrinkage and included more literature on similar effects in trees:*

*"In trees, radial stem shrinkage has been related to sap flow and tree water content*

*(Zweifel et al., 2006; Tian et al., 2019). When temperatures sink below approximately  $-5^{\circ}\text{C}$ , extra-cellular water begins to freeze inducing the osmotic withdrawal of intra-cellular water and thus cell and ultimately stem shrinkage (Zweifel et al., 2000; King et al., 2013)."*

*Regarding depletion of carbohydrates, we propose an early-season carbon surplus caused by photosynthetic activity in winter and early spring. In general, through such processes carbon assimilation may be greater or lower than demand for plant functions, resulting in periods of carbon surplus and deficit, respectively (e.g. Martínez-Vilalta et al., 2016). There's never a critical depletion of non-structural carbohydrates (NSC), but still diminished resources at or shortly after snowmelt and, thus, at the onset of the growing season - due to respiratory consumption during winter (Körner 2021). A surplus of NSC, gained by photosynthetic activity in late winter/spring due to high solar irradiance is, thus, likely to be beneficial for growth throughout the growing period. We included this statement in line of the revised text:*

*"In general, carbon assimilation may be greater or lower than demand for plant functions, resulting in periods of carbon surplus and deficit, respectively (e.g. Martínez-Vilalta et al., 2016). There's never a critical depletion of carbohydrates in alpine plants, but still diminished resources at or shortly after snowmelt and, thus, at the onset of the growing season - due to respiratory consumption during winter (Körner 2021). A surplus of carbohydrates, gained by photosynthetic activity in late winter/spring due to high solar irradiance is, thus, likely to be beneficial for growth throughout the growing period."*

p. 24, line 459: "photosynthetic activity throughout the year" – It is highly implausible for photosynthesis to occur throughout the year, i.e. at mean temperatures below  $-10^{\circ}\text{C}$  (Table 1, Fig. 1).

*This is discussed in detail above (see comments on p. 1, line 19 and p. 22, line 413): Even though mean temperatures are below  $-10^{\circ}\text{C}$ , higher temperatures are reached during the midday and there are short, warmer periods which experience soil thawing (see Figure 1, which we revised to include daily maximum and minimum temperatures). This is because of the high exposure and missing snow cover at our studied positions. Additionally, we used near-ground air temperature as potential driver of plant growth, which does not directly reflect the temperature in the plant. Especially during periods of clear sky and full global radiation, canopy temperature is known to be much higher than our temperatures measured at 15 cm above ground.*

*We do not suggest that active cell growth occurs during these conditions. However, photosynthetic activity of vascular plants in late winter and under extreme conditions was reported before and our suggestion is thus backed by the literature (e.g., Starr and Oberbauer, 2003; Lundell et al., 2008; Semikhatova et al., 1992, also cited in the Discussion section).*

p. 24, lines 475ff: Climate warming has caused an increase in growth of shrubs in arctic and alpine ecosystems. I would assume that a further rise in temperature would primarily promote the spread of shrubs (and trees) in these temperature limited ecosystems rather than impair it.

*This is a common assumption in literature (e.g. Chapin et al., 2005; Post et al., 2019). In recent years, however, the spreading trend of shrubs in these ecosystems and the respective greening has been recognized as highly heterogeneous and complex, with the direction of change is still poorly understood (e.g. Elemendorf et al., 2012; Abott et al., 2016; Nielsen et al., 2017; Macias-Fauria et al., 2020). Thus, our view of temperature-growth relations is challenged. Competition might play a role here. Our results for *E. hermaphroditum* do most likely not apply to other species, but they suggest that at ridge positions, *E. hermaphroditum* growth might be limited with temperature increase, with important implications for species composition within these ecosystems.*

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*Additionally included references in the revised version:*

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Please also note the supplement to this comment:

<https://bg.copernicus.org/preprints/bg-2021-99/bg-2021-99-AC1-supplement.pdf>