Retrospective growth analysis of the dwarf shrub *Cassiope tetragona* allows local estimation of vascular plant productivity in high arctic Svalbard

Running head: *Cassiope* growth predicts arctic productivity

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Abstract

Question: Vascular plant productivity of arctic tundra has often been viewed as varying little between years and thus being largely insensitive to the high inter-annual variation in summer weather conditions. Yet, remote-sensing data and retrospective growth analyses of the circumpolar dwarf shrub *Cassiope tetragona,* commonly show considerable between-year variability in plant growth in response to variation in summer temperature. Given that both *Cassiope* growth and vascular plant biomass production share a common environmental driver, summer temperature, we would expect positive covariation between them. Here we investigate whether this is indeed the case and if so over what spatial scale.

Location: Nordenskiöldland, high arctic Svalbard.

Methods: We brought dendroecology and plot-based field estimation methodologies together in an empirical study using retrospective analysis of *Cassiope* growth and annual estimation of above-ground vegetation biomass production to investigate their temporal and spatial covariation, and sensitivity to summer weather conditions.

Results: Despite substantial small-scale heterogeneity, we found spatial covariation in *Cassiope* growth patterns, which weakened as distance between sampling sites increased from 0 – 25 km. Furthermore, we found a strong positive correlation between annual estimates of above-ground live vascular plant biomass and *Cassiope* shoot growth over a 12-year period at a local scale. The correlation declined with distance, likely due to increasing differences in local weather conditions.

Conclusions: We demonstrate that *Cassiope* growth can be used as a proxy for above-ground tundra vegetation productivity at the local scale. Our findings suggest that Arctic plant productivity is as sensitive to between-year variation in summer temperature as the well-established growth response of *Cassiope*. This challenges the view that tundra plant productivity varies little between years and provides a mechanistic understanding that helps reconcile field- and satellite-based annual estimation methods.

Keywords: Arctic bell-heather, *Cassiope tetragona*, arctic climate change, dendrochronology, plant–climate interaction, spatial scale, Svalbard, tundra vegetation, vascular plant productivity, vegetation biomass.

Taxon nomenclature: The Panarctic Flora (http://nhm2.uio.no/paf, accessed 11/04/18)

Introduction

The arctic climate is warming at an unprecedented rate, but with considerable heterogeneity in rates of warming among and within regions (IPCC, 2014). In general, the long-term positive summer temperature trend has affected plant productivity and vegetation composition, leading to a greening of the Arctic (Guay et al., 2014; Ims & Ehrich, 2013; Jia, Epstein, & Walker, 2009) and circumpolar increases in both tundra shrub cover (Myers-Smith et al., 2011; Myers-Smith, Elmendorf, et al., 2015; Weijers, Buchwal, Blok, Loeffler, & Elberling, 2017) and above-ground plant biomass (Epstein et al., 2012; Hudson & Henry, 2009). By contrast, extreme climatic events and winter warming may cause vegetation dieback and 'arctic browning' in some regions (Phoenix & Bjerke, 2016).

Against the backdrop of long-term warming, there is considerable annual variability in the weather yet until recently it was thought that there was little inter-annual variation in above-ground tundra plant biomass production (Chapin & Shaver, 1985; Henry *et al*., 1990; Hill &

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Henry, 2011). Plant productivity was believed to be poorly related to weather conditions in the same year (Chapin & Shaver, 1985), responding instead to time-lagged below-ground resources and nutrient availability (Chapin & Shaver, 1989), which in turn are affected by direct and indirect effects of warming and feedbacks (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Myers-Smith et al., 2011). This view has been challenged by mounting evidence from both plot-based field studies and remote-sensing data, revealing that arctic plant communities do show high between-year variability in productivity (Boelman et al., 2003; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Gauthier et al., 2011; Karlsen, Elvebakk, Høgda, & Grydeland, 2014; Vickers et al., 2016). Indeed, peak above-ground live vascular plant biomass in high arctic Svalbard showed high variability between years which was closely related to July temperature, across habitats, plant functional types and species (Van der Wal & Stien, 2014). NDVI-derived estimates of plant productivity in central Svalbard also showed considerable inter-annual variation, but the temporal pattern of variation differed between valleys (Karlsen, Anderson, Van der Wal, & Hansen, 2018). Elsewhere, annual growth of several shrub species has been found to covary with satellite-derived estimates of growing season NDVI at a number of tundra sites (see for example: Blok et al., 2011; Forbes, Fauria, & Zetterberg, 2010; Macias-Fauria, Forbes, Zetterberg, & Kumpula, 2012; Weijers, Pape, Loeffler, & Myers-Smith, 2018).Substantial fine-scale spatial heterogeneity in arctic plant productivity, even within habitats (Van der Wal & Stien, 2014), has hampered earlier studies of the relationship between plant biomass production and climatic variables. However, retrospective growth analysis of arctic shrubs using dendroecology, the dating of annual growth rings or morphological characteristics of plant stems (Myers-Smith, Hallinger, et al., 2015), allows plant growth over many years to be measured from individual plants (Johnstone & Henry, 1997; Rayback & Henry, 2005; Schweingruber et al., 2013; Woodcock & Bradley, 1994), so eliminating the problem of confounding between temporal and spatial variation.

The evergreen polar dwarf shrub *Cassiope tetragona* (D.Don), Arctic bell-heather, (hereafter referred to as *Cassiope*) shows well-established wave-like patterns of seasonal growth, reflected in leaf lengths and distances between adjacent leaf nodes or their scars (Callaghan, Carlsson, & Tyler, 1989; Johnstone & Henry, 1997; Rayback & Henry, 2006; Weijers et al., 2012). These seasonal patterns allow annual growth increments of stems to be identified, with the shortest internode length of each wave corresponding with the end of each growing season (Johnstone & Henry 1997). Correlative and experimental studies have shown that leaf

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and shoot growth of *Cassiope* vary considerably between years and respond positively to increasing summer temperatures (Callaghan et al., 1989; Havström, Callaghan, & Jonasson, 1993; Rozema et al., 2009; Weijers, Broekman, & Rozema, 2010), although extreme winter weather events may also influence summer growth (Milner, Varpe, van der Wal, & Hansen, 2016; Weijers et al., 2012). *Cassiope* growth chronologies also reflect summer NDVI values (Weijers et al., 2018). Nonetheless, the spatial variability in patterns of annual *Cassiope* growth is not well studied (but see Callaghan et al., 1989; Rayback, Lini, & Henry, 2011), although it is apparent that there is strong spatial variation in plant responses to climate, possibly due to variable climate sensitivity or regional differences in climatic factors such as snow depth or moisture availability (Blok et al., 2015; Rayback et al., 2011). Moreover, it remains untested whether retrospective growth analyses of *Cassiope* can be used as a predictor of year-to-year variation in above-ground vascular plant productivity of arctic tundra vegetation measured in the field.

In this study, we aim to improve our understanding of the annual variation in above-ground vascular plant biomass production in the high Arctic by bringing together biomass estimation and retrospective analysis of annual *Cassiope* growth for a site in central Svalbard. Given that both vascular plant biomass production and *Cassiope* growth share a common environmental driver, summer temperature, we would expect positive covariation between them. However, the influence of spatial scale is unknown and, as inter-annual variation in estimated plant productivity can differ considerably between valley systems (Karlsen et al., 2018), we may also expect differences in *Cassiope* chronologies between valleys. The specific goals of our study were: 1) to investigate spatial covariation in annual *Cassiope* growth; 2) to investigate the relationship between inter-annual variability of live above-ground vascular plant biomass and growth of *Cassiope*; and 3) to consider *Cassiope* growth as a proxy for tundra vascular plant productivity.

Methods

Study area

The study was carried out in Nordenskiöldland, Spitsbergen, in central Svalbard (77°50'-78°20' N, 15°00'-17°30' E), in the U-shaped valleys of Colesdalen, Semmeldalen and Reindalen (Fig. 1a). The study area has a maritime arctic climate, with relatively mild conditions compared with most other parts of the archipelago. During the period 1981-2010, mean daily January and July temperatures were -12.9°C and +6.4°C, respectively

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(Longyearbyen airport weather station). Annual mean precipitation was 186 mm, mainly falling as snow between October and May and as rain between June and September. Svalbard is snow covered and in darkness for much of the winter, but the short growing season has 24 h daylight. Snowmelt generally begins in late May.

Retrospective analysis of Cassiope tetragona growth

Cassiope is a long-lived ericaceous dwarf shrub with a circumpolar distribution. It is one of the dominant species of the arctic tundra and is not grazed by vertebrate herbivores. It occurs on dry heaths and fell-fields, particularly in sheltered snow beds with moderate to high accumulations and late-lying snow (Callaghan et al., 1989; Johnstone & Henry, 1997). Using samples collected from across the study area, we determined annual growth of *Cassiope* dating back to 1998, for comparison with annual vascular plant biomass recorded over the same time period (see below).

We collected *Cassiope* samples in August 2013 and 2014 from 11 sites across 3 geographic areas which broadly corresponded to the Semmeldalen, Colesdalen and Reindalen valleys (Fig. 1; Table 1). In our study area, the *Cassiope* zone tended to be narrow and fragmented, with relatively small patches of this species growing together with the creeping dwarf shrub *Salix polaris* (Wahlenb.) (Fig. 1b). In the part of Semmeldalen where biomass samples were collected (see below), *Cassiope* patches were particularly small (Fig. 1c). Samples from this area therefore consisted of material pooled from 3 patches within the 2 km × 2 km biomass sampling area. We classified vegetation type at each site as either *Luzula confusa* (Lindeb.) / *Salix*-dominated heath (fairly flat sites with relatively deep soils and high vegetation cover) or sub-ridge heath (drier, stonier sites with lower vegetation cover). The aspect of each site was recorded as a bearing and grouped to the nearest cardinal or intercardinal direction.

Dominant *Cassiope* stems were cut at ground level and air dried. We then removed leaves from main stems with live green tips and examined the stems under a dissecting microscope at × 10 magnification. We used the distance between consecutive internodal minima as our measure of annual growth increment (AGI). We identified leaf scars associated with these internodal minima and then measured the length of stem between consecutive minima to the nearest 0.1 mm precision (Aanes et al., 2002). We only included stems that could be dated back as far as 1998, giving a sample size of 80 stems (5-12 (mean 7.3) stems per site; Table

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1), comparable with sample sizes in other retrospective studies (Blok et al., 2015; Rozema et al., 2009).

Vegetation biomass

We estimated peak above-ground live vascular plant biomass annually in permanent plots within a 2 km × 2 km area of Semmeldalen in the period 1998-2009 (12 years). Ten randomly positioned plots of 25 cm × 25 cm were established at 28 sites within five distinct habitat types (Van der Wal & Stien, 2014). After 5 years, sampling was restricted to three habitats: dry *Salix polaris* ridge, mesic *Luzula confusa* / *S. polaris* heath with *Alopecurus borealis* (Trin.), and wet *Dupontia fisheri* (R.Br.) dominated marsh - due to remarkably similar between-year variation among habitats. Species-specific biomass estimates were derived for each site by multiplying non-destructively measured shoot density within plots with destructively measured shoot mass sampled around plots at peak biomass (i.e. last week of July/ first week of August) outside the plots. Total above-ground live biomass in a plot was estimated as the sum of the biomass of all vascular plant species present. The collected biomass was largely the annual growth of vascular plants, although *S. polaris* samples included woody shoot tissue, part of which would have been produced in previous years. Peak plant biomass therefore equated to a field-based index of plant productivity. Full methodological details and vegetation descriptions of the three habitats are provided by Van der Wal & Stien (2014).

Statistical analysis

Annual *Cassiope* growth increments from the period 1998-2009 (corresponding to the period over which vegetation biomass data were available) were rescaled using statistical standardisation to account for individual variation in shoot length between plants, but were not de-trended. Standardised increments (sAGI) had a mean of 0 and a standard deviation of 1 for each sampled stem. Average *Cassiope* sAGI was estimated at two spatial scales, the valley level and site level (11 sites within 3 valleys), by fitting year only (valley level) or year, site and their interaction (site level) as fixed effects and sample ID as a random effect in a linear mixed model. Preliminary analyses of sAGI and a variance components analysis in which sample was nested within site within valley and year showed that a more complex random effect structure was not supported by the data. The linear mixed models were fitted using the lme function in the nlme package of R, version 3.1.2 (Pinheiro *et al.*, 2015).

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Firstly, we investigated the spatial covariation in average annual *Cassiope* growth estimated by the linear mixed models at each spatial scale. At the larger between-valley scale, we used model estimates to determine time series of *Cassiope* sAGIs averaged across sites within valleys and correlated these between each pair of valleys from within our study area. We also correlated them with growth chronologies of *Cassiope* from a study in Adventdalen (de-trended residual stem growth, Blok et al., 2015), a valley to the north of our study area, and a study in Endalen (standardised stem growth, Weijers et al., 2010), a side-valley off Adventdalen (Fig. 1). We then related the Pearson correlation coefficients to the distance between valleys. At the smaller between-site within-study area scale, we calculated the correlation between time series of sAGIs for pairs of sites and related the correlation coefficient to the distance between sites in each pair and to aspect and vegetation type (*Luzula/Salix* heath or sub-ridge heath).

Secondly, we investigated the temporal covariation in the annual growth of *Cassiope* and annual peak above-ground live vascular plant biomass, hereafter referred to as vegetation biomass. Annual average vegetation biomass was estimated across all habitat types, and within the dry ridge habitat only, using linear mixed models as described in Van der Wal & Stien (2014). We calculated the correlation between the average *Cassiope* sAGI time series from Semmeldalen sites and the average yearly vegetation biomass in Semmeldalen estimated across all habitats and for dry ridge habitat only. We related the strength of the correlation to distance between sites using data from all 11 *Cassiope* sites.

Finally, we considered the potential usefulness of *Cassiope* as a proxy by which arctic vascular plant productivity could be estimated. We created linear regression models of annual average across-habitat vegetation biomass and dry ridge biomass in response to average sAGI, across sites and for the Semmeldalen sites only whilst accounting for summer and winter weather conditions (mean daily June-August temperature, mean daily July temperature, precipitation falling in November-February as rain-on-snow and November-April rain-on-snow) by fitting these terms as covariates in the model.

Results

Spatial covariation in Cassiope tetragona growth

The mean annual *Cassiope* growth increment was 6.7 ± 0.1 mm (range $1.5 – 17.3$ mm). There were highly significant differences in average standardised annual growth increment (sAGI)

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between years ($F_{11,869} = 43.57$, $P < 0.001$) with markedly low growth in 1999 and peaks in 2007 and 2009 (Fig. 2). In addition, there were minor growth troughs in 2006 and 2008. At the between-valley spatial scale, these patterns were broadly consistent across our study area (Fig. 2). However, the strength of the spatial covariation in temporal growth trend between valleys declined with increasing distance between them ($F_{1,8} = 7.84$, $P = 0.02$; Fig. 3a). The geographically closest valleys, Semmeldalen and Reindalen (7 km apart), showed high correlation ($r = 0.96$, $P < 0.001$), while the lowest correlation was between Semmeldalen and Endalen ($r = 0.31$, $P = 0.35$) which were over 20 km apart.

At the smaller spatial scale, between sites within our study area, there was no overall relationship between the temporal correlation in *Cassiope* growth trend and distance between sites ($F_{1,53} = 0.01$, $P = 0.91$). However, among pairs of sites with a similar aspect ($< 45°$ difference in bearing), temporal correlation declined significantly as distance increased ($F_{1,15} = 10.63$, $P = 0.005$; Fig. 3b). Furthermore, there was an interaction between vegetation type and difference in aspect between sites ($F_{2,52} = 5.60$, $P = 0.006$), such that the correlation in *Cassiope* growth was high between sites of the same vegetation type and similar aspect but decreased with increasing difference in aspect, while there was no such effect of aspect among sites that differed with respect to vegetation type. These patterns, and the apparent inconsistency in strength of the relationship between distance and cross-correlation in *Cassiope* growth at the valley and site scales, indicate substantial small-scale heterogeneity in local growing conditions, which was averaged out at the between-valley scale.

Temporal covariation in vegetation biomass and Cassiope growth

There was obvious covariation in annual vegetation biomass in Semmeldalen and annual growth of *Cassiope* in each of the valleys in our study area (Fig. 2). Within Semmeldalen, there was a strong positive correlation between yearly estimates of *Cassiope* growth and overall vegetation biomass across habitats ($r = 0.81$, $P = 0.001$; Fig. 4a). The correlation was even stronger between average annual *Cassiope* growth and vegetation biomass within the dry ridge habitat – the habitat most closely resembling the locations from which *Cassiope* was sampled – although ridge biomass appeared to reach a plateau at around 27 g/m^2 ($r = 0.85$, $P < 0.001$; Fig. S1a).

The strength of the correlation between yearly estimates of vegetation biomass and *Cassiope* growth tended to decrease with increasing distance between the Semmeldalen biomass plots

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and *Cassiope* sites (Fig. 4b). This was true for both the biomass averaged across all habitat types ($r = -0.59$, $P = 0.06$) and for ridge habitat only ($r = -0.55$, $P = 0.08$; Fig. S1b).

Cassiope growth as a proxy for vascular plant biomass

Annual growth of *Cassiope*, estimated across sites, was positively correlated with July temperature ($r = 0.68$, $P = 0.02$) and with summer temperature averaged across June-August ($r = 0.65$, $P = 0.02$), but was not related to extreme winter weather events, indexed by rain-on-snow (November-February: $r = -0.24$, $P = 0.45$; November-April: $r = -0.18$, $P = 0.57$). Annual *Cassiope* growth was less tightly correlated with July temperature than vascular plant biomass across habitats ($r = 0.92$, Van der Wal & Stien, 2014). However, within Semmeldalen, we found that *Cassiope* growth was a better predictor of annual vegetation biomass in ridge habitat ($F_{1,10} = 26.09$, $P < 0.001$; $R^2 = 0.72$) than July temperature, which did not explain any significant additional variation ($F_{1,9} = 3.06$, $P = 0.11$).

Discussion

Our study of tundra vegetation in high arctic Svalbard has shown a strong positive correlation between estimates of annual growth of the dwarf shrub *Cassiope tetragona* and annual peak vascular plant biomass over a 12-year period. Furthermore, we found evidence of spatial covariation in *Cassiope* growth between valleys, including the widespread presence of extreme marker years (Weijers et al., 2010). However, the strength of covariation declined as distance between sampling sites increased, likely due to between-valley differences in growing conditions. Possible causes of local summer temperature differences between valleys within the same year include a gradient of oceanic influence and associated cloudiness, spatial differences in snow-pack characteristics with effects on growing season length, and the influence and duration of sea ice cover (Karlsen et al., 2018).

Our findings support the suggestion that *Cassiope* and other vascular plants growing in tundra habitats, ranging from dry *Salix*/*Dryas* ridge to wet *Dupontia*/*Eriophorum* marsh, respond similarly to shared environmental conditions. A similar conclusion was reached by Weijers *et al.* (2018) for two contrasting shrubs, *Cassiope* and *Salix pulchra*, in an alpine tundra site in north-west Canada. In both cases, *Cassiope* and other plant species from a range of habitats, showed a positive growth response to summer temperature (Van der Wal & Stien, 2014; Weijers et al., 2018). This temperature response of *Cassiope* has been widely

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reported from both the Norwegian and Canadian high Arctic (Rayback & Henry, 2006; Weijers et al., 2012 and references therein). The implication of *Cassiope* being a local proxy for total vascular above-ground biomass is that the great between-year variability observed in *Cassiope* across the Arctic is likely to reflect a similarly widespread temporal variability in the above-ground biomass of arctic tundra vegetation.

Although not studied here, a range of factors may lead to subtle differences in realised annual growth of *Cassiope* and the wider vascular plant community, including differential susceptibility to herbivore impacts. For example, biomass in ridge habitat showed limited variation between the years 2004-2007 and 2009, despite variability in *Cassiope* growth (Fig. S1a) and summer temperature (Van der Wal & Stien, 2014). Ridge habitat experiences relatively high grazing pressure (Van der Wal et al., 2000), particularly during winter when snow depth tends to be lower than in other habitats. By contrast, *Cassiope* tends to be avoided by grazers (Havström et al., 1993), so may represent a better indicator of variability in plant productivity between years.

Topographic complexity creates a mosaic of microclimates which are especially diverse at high latitudes and are likely to influence shrub growth differently (Armbruster, Rae, & Edwards, 2007). Both the timing of the spring green-up and estimated plant productivity in Svalbard show high variability between years and at the scale of individual valleys (Karlsen et al., 2018, 2014). This is likely to contribute to the spatial decline in covariation of *Cassiope* growth observed with increasing distance. At local scales, Van der Wal and Stien (2014) showed substantial fine-scale spatial heterogeneity in peak plant biomass within and between habitats. This was mirrored in our study by high within- and between-site variability in *Cassiope* growth, likely to be partly due to small-scale heterogeneity in micro-topography and winter snow depth (Armbruster et al., 2007; Opedal, Armbruster, & Graae, 2015). Indeed, when accounting for aspect, patterns observed at the between-valley level were also revealed at the spatial scale of sites within valleys. Correlation in *Cassiope* growth was higher among similar sites, in terms of aspect and vegetation type. This may be due to more similar moisture availability or snow conditions, with variation in snow depth influencing *Cassiope* stem growth (Blok et al., 2015).

Dendrochronological analyses of the dwarf shrub *Cassiope tetragona* commonly report considerable between-year variability in growth and sensitivity to a variety of climatic variables, including summer temperature, throughout the Arctic (e.g. Callaghan et al., 1989;

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Johnstone & Henry, 1997; Rayback & Henry, 2005; Rayback et al., 2011; Rozema et al., 2009). Some studies use this feature for historical reconstruction of past climate (Rayback & Henry, 2006; Weijers et al., 2010). Yet, while year-to-year variation in *Cassiope* is accepted as the norm, this does not hold for vascular plant productivity of tundra vegetation as a whole (Chapin & Shaver, 1985; Henry et al., 1990; Hill & Henry, 2011). We demonstrate that between-year variation in *Cassiope* growth was strongly correlated with between-year variation in vascular plant biomass of the tundra vegetation in our study system. As such *Cassiope* growth may be a useful local proxy for vegetation productivity, although predictive power declines with distance from where *Cassiope* is sampled. Given the strength of the relationship between *Cassiope* growth and vegetation productivity in our study, and the consistently reported between-year variability in *Cassiope* growth and sensitivity to summer temperature across the Arctic, it may be expected that plant productivity in many parts of the Arctic is equally sensitive to between-year variation in summer conditions. Wider-scale field calibration would help to understand the generality of this result. The observed declining spatial covariation in annual *Cassiope* growth, as well as the waning covariation between above-ground vascular plant biomass and *Cassiope* growth, point to local summer weather conditions influencing plant growth. Our key finding that retrospective growth analysis captures local vascular plant productivity suggests that integrating dendroecology with satellite-based measurements can be an efficient approach to studying and understanding spatio-temporal patterns of tundra productivity.

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Authors' contributions

RvdW and AS conceived and designed the study and collected samples; JMM conducted the retrospective growth analysis and carried out the statistical analyses with input from AS; JMM led the writing of the manuscript with significant contributions from RvdW and AS. All authors contributed to the interpretation of analyses, critically reviewed the draft manuscript and approved the final manuscript for publication.

References

Aanes, R., Sæther, B.-E., Smith, F. M., Cooper, E. J., Wookey, P. A., & Øritsland, N. A. (2002). The Arctic Oscillation predicts effects of climate change in two trophic levels in a high-arctic ecosystem. *Ecology Letters*, *5*, 445–453.

Armbruster, W. S., Rae, D., & Edwards, M. E. (2007). Topographic complexity and biotic response to high-latitude climate change: variance is as important as the mean. In A. H. H. J.B. Ørbæk, R. Kallenborn, I. Tombre, E.N. Hegseth, S. Falk-Petersen (Ed.), *Arctic-Alpine Ecosystems and People in a Changing Environment* (pp. 105–122). Berlin: Springer Verlag.

Blok, D., Weijers, S., Welker, J. M., Cooper, E. J., Michelsen, A., Löffler, J., & Elberling, B. (2015). Deepened winter snow increases stem growth and alters stem δ13C and δ15N in evergreen dwarf shrub *Cassiope tetragona* in higharctic Svalbard tundra. *Environmental Research Letters*, *10*, 44008.

Blok, D., Sass-Klaassen, U., Schaepman-Strub, G., Heijmans, M.M.P.D., Sauren, P. & Berendse, F. (2011). What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences*, *8*, 1169-1179.

Boelman, N. T., Stieglitz, M., Rueth, H. M., Sommerkorn, M., Griffin, K. L., Shaver, G. R., & Gamon, J. A. (2003). Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia*, *135*, 414–421. https://doi.org/10.1007/s00442-003-1198-3

Callaghan, T. V, Carlsson, B. A., & Tyler, N. J. C. (1989). Historical records of climate-related growth in Cassiope tetragona from the Arctic. *Journal of Ecology*, *77*, 823–837.

Chapin, F. S., & Shaver, G. R. (1985). Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, *66*, 564–576.

Chapin, F. S., & Shaver, G. R. (1989). Differences in growth and nutrient use among arctic plant growth forms. *Functional Ecology*, *3*, 73–80.

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., … Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, *15*, 164–175.

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N.,

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Cooper, E. J., … Wipf, S. (2012). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, *2*, 453–457. https://doi.org/10.1038/nclimate1465

Epstein, H. E., Raynolds, M. K., Walker, D. A., Bhatt, U. S., Tucker, C. J., & Pinzon, J. E. (2012). Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental Research Letters*, *7*, 15506. https://doi.org/10.1088/1748-9326/7/1/015506

Forbes, B.C., Macias-Fauria, M. & Zetterberg, P. 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology*, *16*, 1542-1554.

Gauthier, G., Berteaux, D., Bety, J., Tarroux, A., Therrien, J. F., McKinnon, L., … Cadieux, M. C. (2011). The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. *Ecoscience*, *18*, 223–235.

Guay, K. C., Beck, P. S. A., Berner, L. T., Goetz, S. J., Baccini, A., & Buermann, W. (2014). Vegetation productivity patterns at high northern latitudes: a multi-sensor satellite data assessment. *Global Change Biology*, *20*, 3147–3158.

Havström, M., Callaghan, T. V, & Jonasson, S. (1993). Differential growth responses of *Cassiope tetragona*, an arctic dwarf-shrub, to environmental perturbations among three contrasting high-and subarctic sites. *Oikos*, *66*, 389–402.

Henry, G. H. R., Svoboda, J., & Freedman, B. (1990). Standing crop and net production of sedge meadows of an ungrazed polar desert oasis. *Canadian Journal of Botany*, *68*, 2660–2667. https://doi.org/10.1139/b90-336

Hill, G. B., & Henry, G. H. R. (2011). Responses of High Arctic wet sedge tundra to climate warming since 1980. *Global Change Biology*, *17*, 276–287. https://doi.org/10.1111/j.1365-2486.2010.02244.x

Hudson, J. M. G., & Henry, G. H. R. (2009). Increased plant biomass in a High Arctic heath community from 1981 to 2008. *Ecology*, *90*, 2657–2663. https://doi.org/10.1890/09-0102.1

Ims, R. A., & Ehrich, D. (2013). Terrestrial ecosystems. In H. Meltofte (Ed.), *Arctic biodiversity assessment: status and trends in Arctic biodiversity* (pp. 384–440). Akureyri, Iceland: CAFF (Conservation of Arctic Flora and Fauna).

IPCC. (2014). *Climate change 2014: Impacts, Adaptation and Vulnerability. Working Group II Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* (C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, … L. L. White, Eds.). Cambridge, UK & New York, USA: Cambridge University Press.

Jia, G. S. J., Epstein, H. E., & Walker, D. A. (2009). Vegetation greening in the Canadian arctic related to decadal warming. *Journal of Environmental Monitoring*, *11*, 2231–2238.

Johnstone, J. F., & Henry, G. H. R. (1997). Retrospective analysis of growth and reproduction in *Cassiope tetragona* and relations to climate in the Canadian high arctic. *Arctic and Alpine Research*, *29*, 459–469.

Karlsen, S. R., Anderson, H. B., Van der Wal, R., & Hansen, B. B. (2018). A new NDVI measure that overcomes data sparsity in cloud-covered regions predicts annual variation in ground-based estimates of high arctic plant productivity. *Environmental Research Letters*, *1*, 25011. https://doi.org/10.1088/1748-9326/aa9f75

Karlsen, S. R., Elvebakk, A., Høgda, K., & Grydeland, T. (2014). Spatial and temporal variability in the onset of the growing season on Svalbard, arctic Norway — measured by MODIS-NDVI satellite data. *Remote Sensing*, *6*, 8088–8106. https://doi.org/10.3390/rs6098088

Macias-Fauria, M., Forbes, B.C., Zetterberg, P. & Kumpula, T. (2012). Eurasian Arctic greening reveals teleconnections and the potential for structurally novel ecosystems. *Nature Climate Change*, *2*, 613-618.

Milner, J. M., Varpe, Ø., van der Wal, R., & Hansen, B. B. (2016). Experimental icing affects growth, mortality, and flowering in a high Arctic dwarf shrub. *Ecology and Evolution*, *6*, 2139–2148. https://doi.org/10.1002/ece3.2023

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S. A., Wilmking, M., Hallinger, M., Blok, D., … Vellend, M. (2015). Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, *5*, 887–891. https://doi.org/10.1038/NCLIMATE2697

Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., … Hik, D. S. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, *6*, 45509. https://doi.org/10.1088/1748-

14

9326/6/4/045509

Myers-Smith, I. H., Hallinger, M., Blok, D., Sass-Klaassen, U., Rayback, S. A., Weijers, S., … Wilmking, M. (2015). Methods for measuring arctic and alpine shrub growth: A review. *Earth-Science Reviews*, *140*, 1–13. https://doi.org/10.1016/j.earscirev.2014.10.004

Opedal, Ø. H., Armbruster, W. S., & Graae, B. J. (2015). Linking small-scale topography with microclimate, plant species diversity and intra-specific trait variation in an alpine landscape. *Plant Ecology & Diversity*, *8*, 305–315.

Phoenix, G. K., & Bjerke, J. W. (2016). Arctic browning: extreme events and trends reversing arctic greening. *Global Change Biology*, *22*, 2960–2962. https://doi.org/10.1111/gcb.13261

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2015). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-120.

Rayback, S. A., & Henry, G. H. R. (2005). Dendrochronological potential of the Arctic dwarf-shrub Cassiope tetragona. *Tree-Ring Research*, *61*, 43–53.

Rayback, S. A., & Henry, G. H. R. (2006). Reconstruction of summer temperature for a Canadian high arctic site from retrospective analysis of the dwarf shrub, Cassiope tetragona. *Arctic, Antarctic, and Alpine Research*, *38*, 228–238.

Rayback, S. A., Lini, A., & Henry, G. H. R. (2011). Spatial variability of the dominant climate signal in Cassiope tetragona from sites in Arctic Canada. *Arctic*, *64*, 98–114. https://doi.org/10.14430/arctic4083

Rozema, J., Weijers, S., Broekman, R., Blokker, P., Buizer, B., Werleman, C., … Cooper, E. J. (2009). Annual growth of Cassiope tetragona as a proxy for Arctic climate: developing correlative and experimental transfer functions to reconstruct past summer temperature on a millennial time scale. *Global Change Biology*, *15*, 1703–1715. https://doi.org/10.1111/j.1365-2486.2009.01858.x

Schweingruber, F. H., Hellmann, L., Tegel, W., Braun, S., Nievergelt, D., & Buentgen, U. (2013). Evaluating the wood anatomical and dendroecological potential of Arctic dwarf shrub communities. *IAWA JOURNAL*, *34*, 485–497. https://doi.org/10.1163/22941932-00000039

Van der Wal, R., Irvine, J., Stien, A., Shepherd, N., & Albon, S. D. (2000). Faecal avoidance

15

and the risk of infection by nematodes in a natural population of reindeer. *Oecologia*, *124*, 19–25. https://doi.org/10.1007/s004420050020

Van der Wal, R., & Stien, A. (2014). High-arctic plants like it hot: A long-term investigation of between-year variability in plant biomass. *Ecology*, *95*, 3414–3427.

Vickers, H., Høgda, K. A., Solbø, S., Karlsen, S. R., Tømmervik, H., Aanes, R., & Hansen, B. B. (2016). Changes in greening in the high Arctic: insights from a 30 year AVHRR max NDVI dataset for Svalbard. *Environmental Research Letters*, *11*, 105004. https://doi.org/10.1088/1748-9326/11/10/105004

Weijers, S., Alsos, I. G., Eidesen, P. B., Broekman, R., Loonen, M. J. J. E., & Rozema, J. (2012). No divergence in *Cassiope tetragona*: persistence of growth response along a latitudinal temperature gradient and under multi-year experimental warming. *Annals of Botany*, *110*, 653–665. https://doi.org/10.1093/aob/mcs123

Weijers, S., Broekman, R., & Rozema, J. (2010). Dendrochronology in the High Arctic: July air temperatures reconstructed from annual shoot length growth of the circumarctic dwarf shrub *Cassiope tetragona*. *Quaternary Science Reviews*, *29*, 3831–3842. https://doi.org/10.1016/j.quascirev.2010.09.003

Weijers, S., Buchwal, A., Blok, D., Loeffler, J., & Elberling, B. (2017). High Arctic summer warming tracked by increased Cassiope tetragona growth in the world's northernmost polar desert. *Global Change Biology*, *23*, 5006–5020. https://doi.org/10.1111/gcb.13747

Weijers, S., Pape, R., Loeffler, J., & Myers-Smith, I. H. (2018). Contrasting shrub species respond to early summer temperatures leading to correspondence of shrub growth patterns. *Environmental Research Letters*, *13*, 34005. https://doi.org/10.1088/1748-9326/aaa5b8

Woodcock, H., & Bradley, R. S. (1994). *Salix arctica* (Pall.): Its potential for dendroclimatological studies in the High Arctic. *Dendrochronologia*, *12*, 11–22.

Supplementary Material

Fig. S1. (a) Relationship between annual *Cassiope tetragona* growth increments from Semmeldalen and total annual above-ground live biomass of dry ridge heath in Semmeldalen; (b) correlations from (a) in relation to distance between *Cassiope* sites and dry ridge biomass plots.

Appendix 1. Annual increments of *Cassiope tetragona* collected in Nordenskiöldland study area, high arctic Svalbard.

Appendix 2. Annual estimates of above-ground live vascular plant biomass from Semmeldalen, high arctic Svarlbard & weather co-variates.

Table 1. Number of *Cassiope tetragona* samples from each site within each of three valleys in Nordenskiöldland, Svalbard (see Fig. 1), together with mean annual growth increment (AGI) ± SE.

|			Site				Mean
Valley	**1**	**2**	**3**	**4**	**5**	**Total n**	**AGI (mm)**
Colesdalen	5	9	8			22	7.21 ± 0.44
Reindalen	6	6	8	6	7	33	6.65 ± 0.33
Semmeldalen	12	7	6			25	6.17 ± 0.36
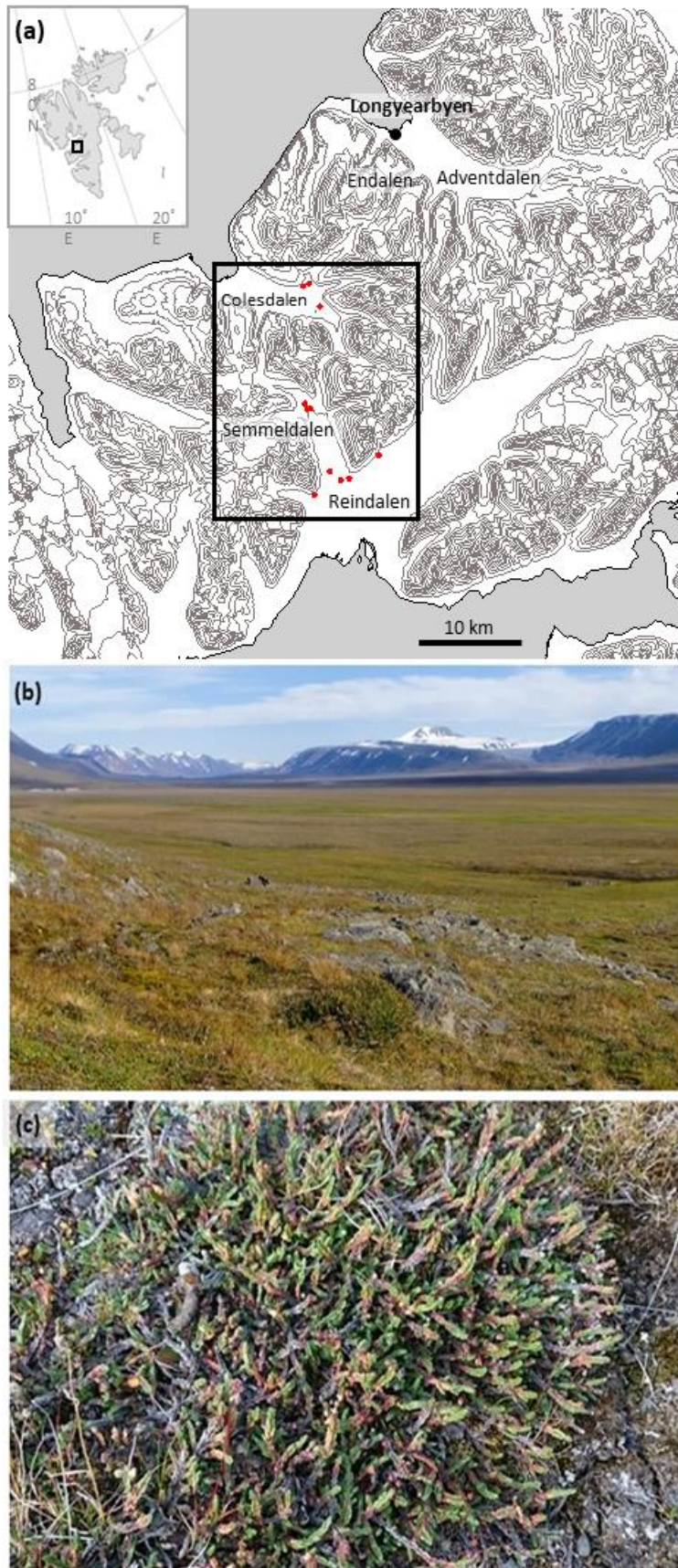
Figure 1. (a) Topographic map of the Nordenskiöldland study area (black box) on high arctic Svalbard (inset) in relation to other places referred to in the text. Red points indicate the *Cassiope tetragona* sampling sites in the three main valleys of the study area. (b) Reindalen sampling area showing fragmented *Cassiope* zone in foreground and to left in *Luzula*/*Salix*-dominated heath. (c) Small *Cassiope* patch typical of sub-ridge heath in Semmeldalen.

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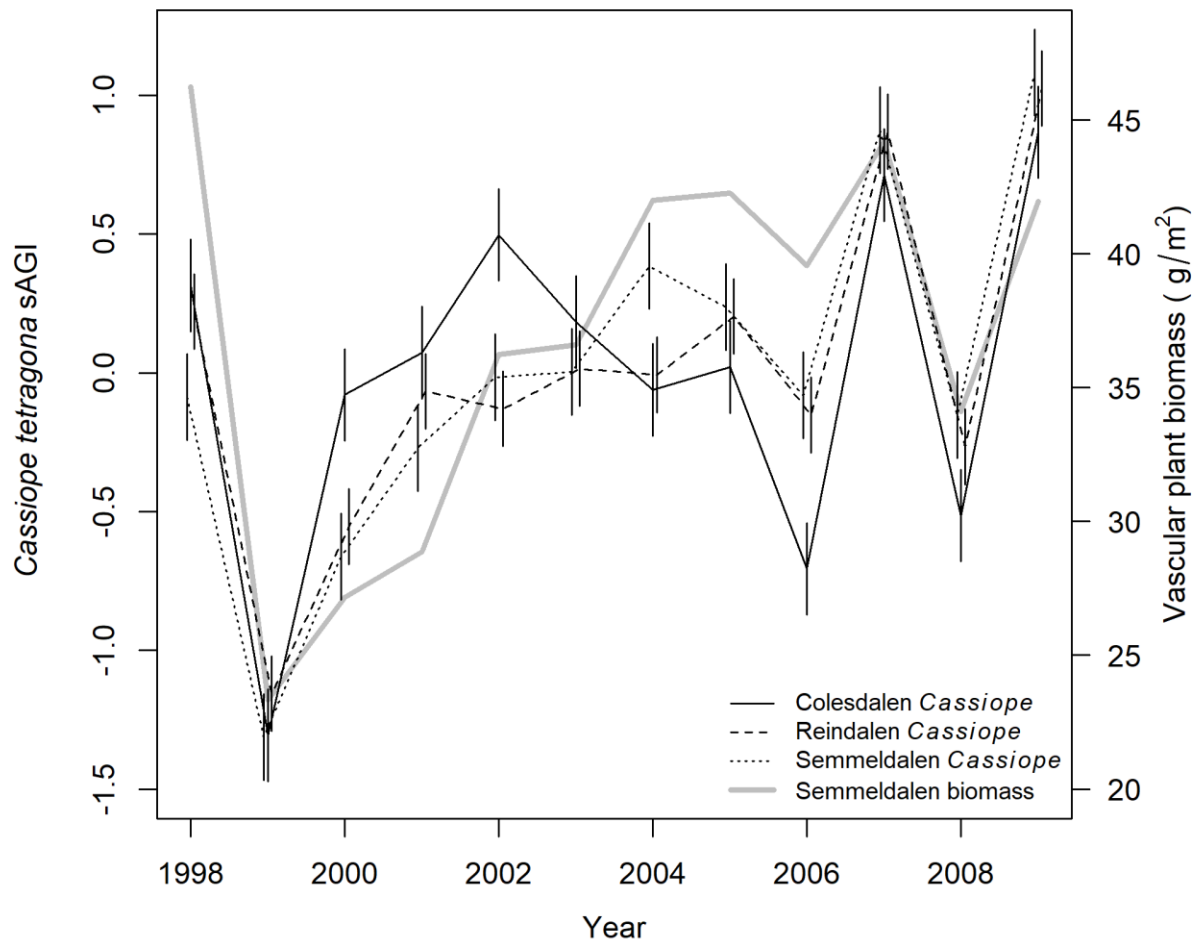
Figure 2. Temporal patterns in standardised annual growth increments (sAGI) of *Cassiope tetragona* estimated for each of three valley areas in the Nordenskiöldland study area, Svalbard, over the period 1998-2009 (black lines) and total above-ground live vascular plant biomass in Semmeldalen, estimated over the same time period (grey line). Plots of the sAGI are offset slightly between areas to allow error bars (±1 SE) to be distinguished.
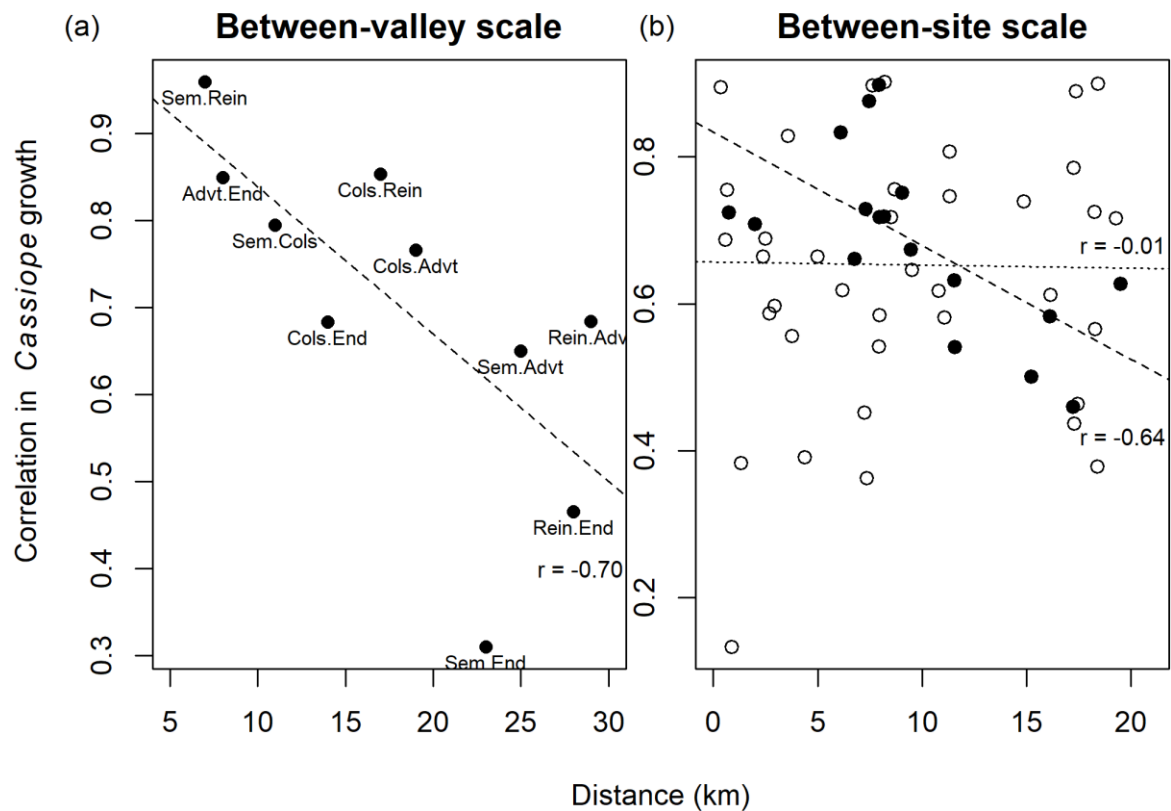
Figure 3. Correlation in temporal patterns of annual growth of *Cassiope tetragona* at two spatial scales. (a) Between-valley scale in relation to distance between them; data for Semmeldalen (Sem), Colesdalen (Cols) and Reindalen (Rein) from this study, Adventdalen (Advnt) data from Blok *et al*. (2015) and Endalen (End) data from Weijers *et al*. (2010; reported in Blok et *al*., 2015). (b) Between-site scale in relation to distance between sites within our Nordenskiöldland study area, Svalbard, for all site-pairs (open points, dotted fitted line). Black points and dashed fitted line are for pairs of sites with a similar aspect.
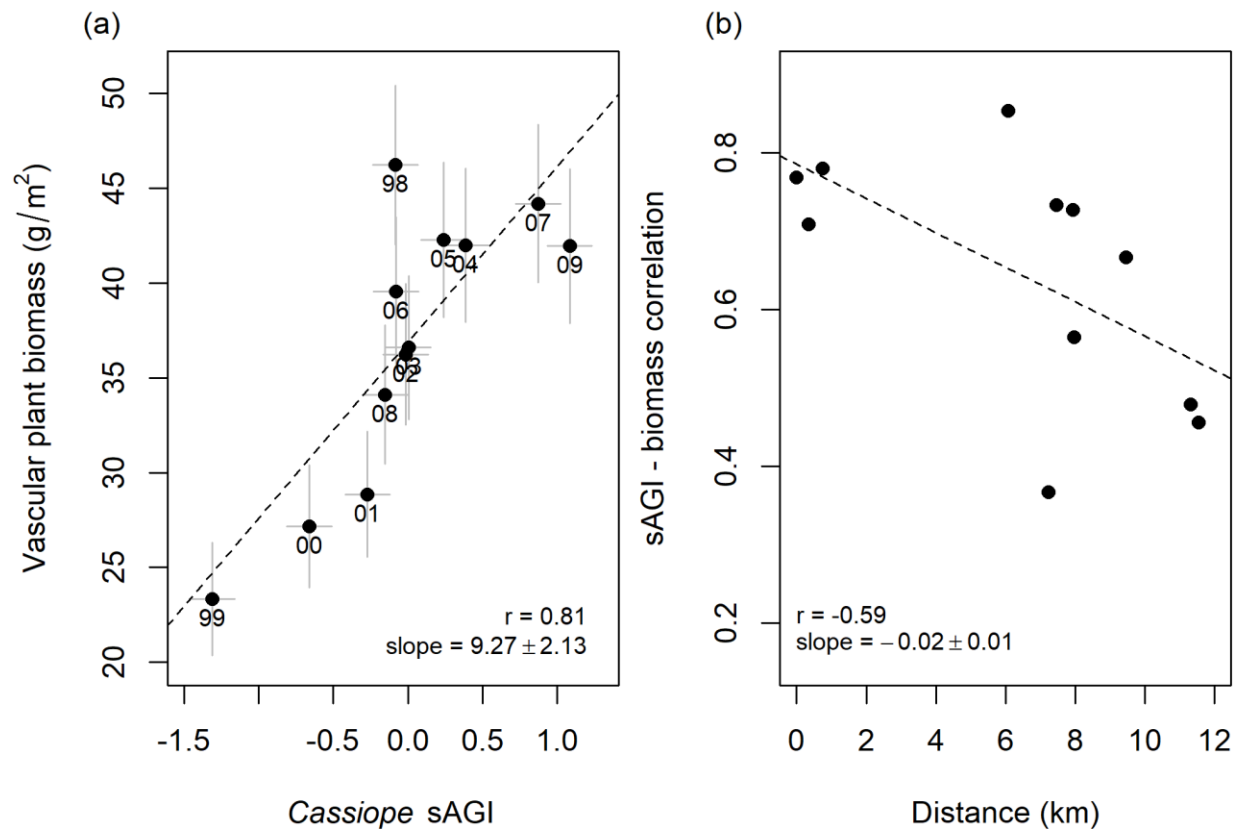
Figure 4. (a) Relationship between annual estimates of standardised *Cassiope tetragona* growth increments (sAGI) in the Semmeldalen sites and total above-ground live vascular plant biomass in Semmeldalen, estimated across all habitat types. Points are labelled by year. (b) Correlation between temporal *Cassiope tetragona* growth trends (sAGI) and total above-ground vascular plant biomass in relation to distance between *Cassiope* sites and the biomass plots in Semmeldalen, with biomass estimated across all habitat types.

Supplementary Material
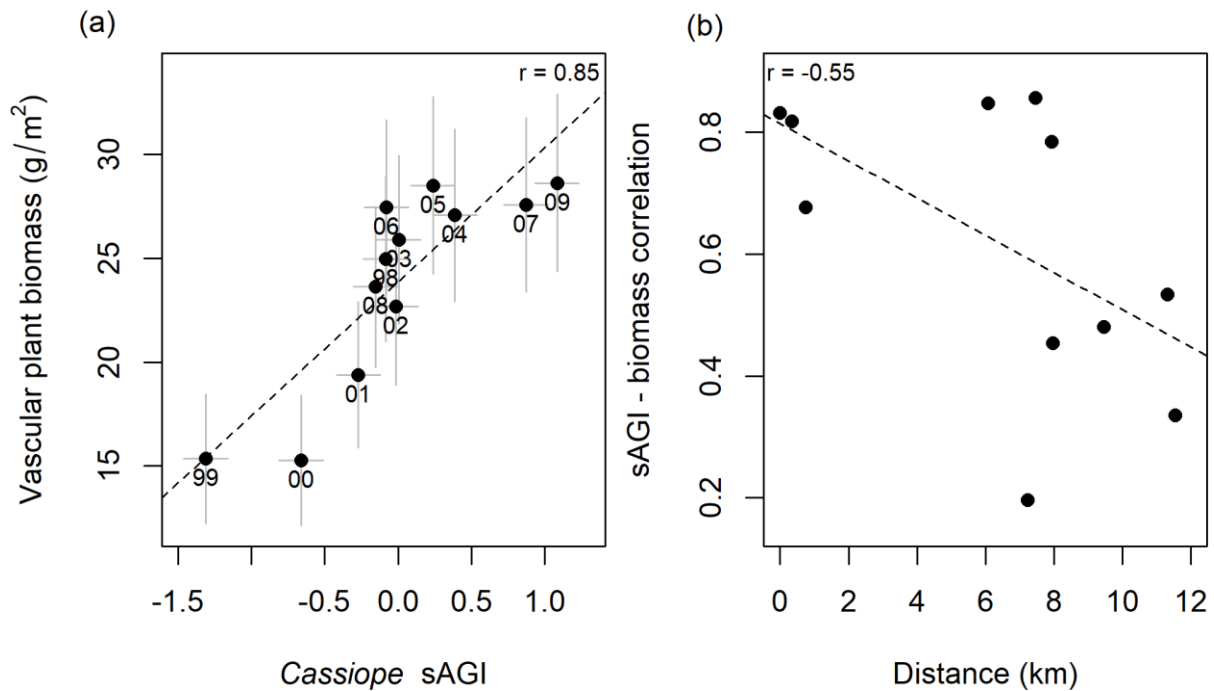
Figure S1. (a) Relationship between annual estimates of standardised *Cassiope tetragona* growth increments (sAGI) in the Semmeldalen sites and total above-ground live vascular plant biomass estimated across the dry ridge habitat in Semmeldalen. Points are labelled by year. (b) Correlation between temporal *Cassiope tetragona* growth trends (sAGI) and total above-ground vascular plant biomass in relation to distance between *Cassiope* sites and the biomass plots in Semmeldalen, with biomass estimated across the dry ridge habitat.