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

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1

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

3

4 **Running head:** *Cassiope* growth predicts arctic productivity

5

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16

17 **Abstract**

18 Question: Vascular plant productivity of arctic tundra has often been viewed as varying little
19 between years and thus being largely insensitive to the high inter-annual variation in summer
20 weather conditions. Yet, remote-sensing data and retrospective growth analyses of the
21 circumpolar dwarf shrub *Cassiope tetragona*, commonly show considerable between-year
22 variability in plant growth in response to variation in summer temperature. Given that both
23 *Cassiope* growth and vascular plant biomass production share a common environmental

2

24 driver, summer temperature, we would expect positive covariation between them. Here we
25 investigate whether this is indeed the case and if so over what spatial scale.

26 Location: Nordenskiöldland, high arctic Svalbard.

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

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

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

43

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

47

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

49

50 **Introduction**

51 The arctic climate is warming at an unprecedented rate, but with considerable heterogeneity
52 in rates of warming among and within regions (IPCC, 2014). In general, the long-term
53 positive summer temperature trend has affected plant productivity and vegetation
54 composition, leading to a greening of the Arctic (Guay et al., 2014; Ims & Ehrich, 2013; Jia,
55 Epstein, & Walker, 2009) and circumpolar increases in both tundra shrub cover (Myers-
56 Smith et al., 2011; Myers-Smith, Elmendorf, et al., 2015; Weijers, Buchwal, Blok, Loeffler,
57 & Elberling, 2017) and above-ground plant biomass (Epstein et al., 2012; Hudson & Henry,
58 2009). By contrast, extreme climatic events and winter warming may cause vegetation
59 dieback and 'arctic browning' in some regions (Phoenix & Bjerke, 2016).

60 Against the backdrop of long-term warming, there is considerable annual variability in the
61 weather yet until recently it was thought that there was little inter-annual variation in above-
62 ground tundra plant biomass production (Chapin & Shaver, 1985; Henry *et al.*, 1990; Hill &
63 Henry, 2011). Plant productivity was believed to be poorly related to weather conditions in
64 the same year (Chapin & Shaver, 1985), responding instead to time-lagged below-ground
65 resources and nutrient availability (Chapin & Shaver, 1989), which in turn are affected by
66 direct and indirect effects of warming and feedbacks (Elmendorf, Henry, Hollister, Björk,
67 Bjorkman, et al., 2012; Myers-Smith et al., 2011). This view has been challenged by
68 mounting evidence from both plot-based field studies and remote-sensing data, revealing that
69 arctic plant communities do show high between-year variability in productivity (Boelman et
70 al., 2003; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Gauthier et
71 al., 2011; Karlsen, Elvebakk, Høgda, & Grydeland, 2014; Vickers et al., 2016). Indeed, peak
72 above-ground live vascular plant biomass in high arctic Svalbard showed high variability

73 between years which was closely related to July temperature, across habitats, plant functional
74 types and species (Van der Wal & Stien, 2014). NDVI-derived estimates of plant productivity
75 in central Svalbard also showed considerable inter-annual variation, but the temporal pattern
76 of variation differed between valleys (Karlsen, Anderson, Van der Wal, & Hansen, 2018).
77 Elsewhere, annual growth of several shrub species has been found to covary with satellite-
78 derived estimates of growing season NDVI at a number of tundra sites (see for example: Blok
79 et al., 2011; Forbes, Fauria, & Zetterberg, 2010; Macias-Fauria, Forbes, Zetterberg, &
80 Kumpula, 2012; Weijers, Pape, Loeffler, & Myers-Smith, 2018). Substantial fine-scale spatial
81 heterogeneity in arctic plant productivity, even within habitats (Van der Wal & Stien, 2014),
82 has hampered earlier studies of the relationship between plant biomass production and
83 climatic variables. However, retrospective growth analysis of arctic shrubs using
84 dendroecology, the dating of annual growth rings or morphological characteristics of plant
85 stems (Myers-Smith, Hallinger, et al., 2015), allows plant growth over many years to be
86 measured from individual plants (Johnstone & Henry, 1997; Rayback & Henry, 2005;
87 Schweingruber et al., 2013; Woodcock & Bradley, 1994), so eliminating the problem of
88 confounding between temporal and spatial variation.

89 The evergreen polar dwarf shrub *Cassiope tetragona* (D. Don), Arctic bell-heather, (hereafter
90 referred to as *Cassiope*) shows well-established wave-like patterns of seasonal growth,
91 reflected in leaf lengths and distances between adjacent leaf nodes or their scars (Callaghan,
92 Carlsson, & Tyler, 1989; Johnstone & Henry, 1997; Rayback & Henry, 2006; Weijers et al.,
93 2012). These seasonal patterns allow annual growth increments of stems to be identified, with
94 the shortest internode length of each wave corresponding with the end of each growing
95 season (Johnstone & Henry 1997). Correlative and experimental studies have shown that leaf
96 and shoot growth of *Cassiope* vary considerably between years and respond positively to
97 increasing summer temperatures (Callaghan et al., 1989; Havström, Callaghan, & Jonasson,

5

98 1993; Rozema et al., 2009; Weijers, Broekman, & Rozema, 2010), although extreme winter
99 weather events may also influence summer growth (Milner, Varpe, van der Wal, & Hansen,
100 2016; Weijers et al., 2012). *Cassiope* growth chronologies also reflect summer NDVI values
101 (Weijers et al., 2018). Nonetheless, the spatial variability in patterns of annual *Cassiope*
102 growth is not well studied (but see Callaghan et al., 1989; Rayback, Lini, & Henry, 2011),
103 although it is apparent that there is strong spatial variation in plant responses to climate,
104 possibly due to variable climate sensitivity or regional differences in climatic factors such as
105 snow depth or moisture availability (Blok et al., 2015; Rayback et al., 2011). Moreover, it
106 remains untested whether retrospective growth analyses of *Cassiope* can be used as a
107 predictor of year-to-year variation in above-ground vascular plant productivity of arctic
108 tundra vegetation measured in the field.

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

121

122 **Methods**

123 *Study area*

124 The study was carried out in Nordenskiöldland, Spitsbergen, in central Svalbard (77°50'-
125 78°20' N, 15°00'-17°30' E), in the U-shaped valleys of Colesdalen, Semmeldalen and
126 Reindalen (Fig. 1a). The study area has a maritime arctic climate, with relatively mild
127 conditions compared with most other parts of the archipelago. During the period 1981-2010,
128 mean daily January and July temperatures were -12.9°C and +6.4°C, respectively
129 (Longyearbyen airport weather station). Annual mean precipitation was 186 mm, mainly
130 falling as snow between October and May and as rain between June and September. Svalbard
131 is snow covered and in darkness for much of the winter, but the short growing season has 24
132 h daylight. Snowmelt generally begins in late May.

133

134 *Retrospective analysis of Cassiope tetragona growth*

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

142 We collected *Cassiope* samples in August 2013 and 2014 from 11 sites across 3 geographic
143 areas which broadly corresponded to the Semmeldalen, Colesdalen and Reindalen valleys
144 (Fig. 1; Table 1). In our study area, the *Cassiope* zone tended to be narrow and fragmented,
145 with relatively small patches of this species growing together with the creeping dwarf shrub
146 *Salix polaris* (Wahlenb.) (Fig. 1b). In the part of Semmeldalen where biomass samples were

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147 collected (see below), *Cassiope* patches were particularly small (Fig. 1c). Samples from this
148 area therefore consisted of material pooled from 3 patches within the 2 km × 2 km biomass
149 sampling area. We classified vegetation type at each site as either *Luzula confusa* (Lindeb.) /
150 *Salix*-dominated heath (fairly flat sites with relatively deep soils and high vegetation cover)
151 or sub-ridge heath (drier, stonier sites with lower vegetation cover). The aspect of each site
152 was recorded as a bearing and grouped to the nearest cardinal or intercardinal direction.

153 Dominant *Cassiope* stems were cut at ground level and air dried. We then removed leaves
154 from main stems with live green tips and examined the stems under a dissecting microscope
155 at × 10 magnification. We used the distance between consecutive internodal minima as our
156 measure of annual growth increment (AGI). We identified leaf scars associated with these
157 internodal minima and then measured the length of stem between consecutive minima to the
158 nearest 0.1 mm precision (Aanes et al., 2002). We only included stems that could be dated
159 back as far as 1998, giving a sample size of 80 stems (5-12 (mean 7.3) stems per site; Table
160 1), comparable with sample sizes in other retrospective studies (Blok et al., 2015; Rozema et
161 al., 2009).

162

163 *Vegetation biomass*

164 We estimated peak above-ground live vascular plant biomass annually in permanent plots
165 within a 2 km × 2 km area of Semmeldalen in the period 1998-2009 (12 years). Ten
166 randomly positioned plots of 25 cm × 25 cm were established at 28 sites within five distinct
167 habitat types (Van der Wal & Stien, 2014). After 5 years, sampling was restricted to three
168 habitats: dry *Salix polaris* ridge, mesic *Luzula confusa* / *S. polaris* heath with *Alopecurus*
169 *borealis* (Trin.), and wet *Dupontia fisheri* (R.Br.) dominated marsh - due to remarkably
170 similar between-year variation among habitats. Species-specific biomass estimates were

171 derived for each site by multiplying non-destructively measured shoot density within plots
172 with destructively measured shoot mass sampled around plots at peak biomass (i.e. last week
173 of July/ first week of August) outside the plots. Total above-ground live biomass in a plot
174 was estimated as the sum of the biomass of all vascular plant species present. The collected
175 biomass was largely the annual growth of vascular plants, although *S. polaris* samples
176 included woody shoot tissue, part of which would have been produced in previous years.
177 Peak plant biomass therefore equated to a field-based index of plant productivity. Full
178 methodological details and vegetation descriptions of the three habitats are provided by Van
179 der Wal & Stien (2014).

180

181 *Statistical analysis*

182 Annual *Cassiope* growth increments from the period 1998-2009 (corresponding to the period
183 over which vegetation biomass data were available) were rescaled using statistical
184 standardisation to account for individual variation in shoot length between plants, but were
185 not de-trended. Standardised increments (sAGI) had a mean of 0 and a standard deviation of
186 1 for each sampled stem. Average *Cassiope* sAGI was estimated at two spatial scales, the
187 valley level and site level (11 sites within 3 valleys), by fitting year only (valley level) or
188 year, site and their interaction (site level) as fixed effects and sample ID as a random effect in
189 a linear mixed model. Preliminary analyses of sAGI and a variance components analysis in
190 which sample was nested within site within valley and year showed that a more complex
191 random effect structure was not supported by the data. The linear mixed models were fitted
192 using the lme function in the nlme package of R, version 3.1.2 (Pinheiro *et al.*, 2015).
193 Firstly, we investigated the spatial covariation in average annual *Cassiope* growth estimated
194 by the linear mixed models at each spatial scale. At the larger between-valley scale, we used

195 model estimates to determine time series of *Cassiope* sAGIs averaged across sites within
196 valleys and correlated these between each pair of valleys from within our study area. We also
197 correlated them with growth chronologies of *Cassiope* from a study in Adventdalen (de-
198 trended residual stem growth, Blok et al., 2015), a valley to the north of our study area, and a
199 study in Endalen (standardised stem growth, Weijers et al., 2010), a side-valley off
200 Adventdalen (Fig. 1). We then related the Pearson correlation coefficients to the distance
201 between valleys. At the smaller between-site within-study area scale, we calculated the
202 correlation between time series of sAGIs for pairs of sites and related the correlation
203 coefficient to the distance between sites in each pair and to aspect and vegetation type
204 (*Luzula/Salix* heath or sub-ridge heath).

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

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

10

220

221 **Results**222 *Spatial covariation in Cassiope tetragona growth*

223 The mean annual *Cassiope* growth increment was 6.7 ± 0.1 mm (range 1.5 – 17.3 mm). There
224 were highly significant differences in average standardised annual growth increment (sAGI)
225 between years ($F_{11,869} = 43.57$, $P < 0.001$) with markedly low growth in 1999 and peaks in
226 2007 and 2009 (Fig. 2). In addition, there were minor growth troughs in 2006 and 2008. At
227 the between-valley spatial scale, these patterns were broadly consistent across our study area
228 (Fig. 2). However, the strength of the spatial covariation in temporal growth trend between
229 valleys declined with increasing distance between them ($F_{1,8} = 7.84$, $P = 0.02$; Fig. 3a). The
230 geographically closest valleys, Semmeldalen and Reindalen (7 km apart), showed high
231 correlation ($r = 0.96$, $P < 0.001$), while the lowest correlation was between Semmeldalen and
232 Endalen ($r = 0.31$, $P = 0.35$) which were over 20 km apart.

233 At the smaller spatial scale, between sites within our study area, there was no overall
234 relationship between the temporal correlation in *Cassiope* growth trend and distance between
235 sites ($F_{1,53} = 0.01$, $P = 0.91$). However, among pairs of sites with a similar aspect ($< 45^\circ$
236 difference in bearing), temporal correlation declined significantly as distance increased ($F_{1,15}$
237 = 10.63, $P = 0.005$; Fig. 3b). Furthermore, there was an interaction between vegetation type
238 and difference in aspect between sites ($F_{2,52} = 5.60$, $P = 0.006$), such that the correlation in
239 *Cassiope* growth was high between sites of the same vegetation type and similar aspect but
240 decreased with increasing difference in aspect, while there was no such effect of aspect
241 among sites that differed with respect to vegetation type. These patterns, and the apparent
242 inconsistency in strength of the relationship between distance and cross-correlation in

243 *Cassiope* growth at the valley and site scales, indicate substantial small-scale heterogeneity in
244 local growing conditions, which was averaged out at the between-valley scale.

245

246 *Temporal covariation in vegetation biomass and Cassiope growth*

247 There was obvious covariation in annual vegetation biomass in Semmeldalen and annual
248 growth of *Cassiope* in each of the valleys in our study area (Fig. 2). Within Semmeldalen,
249 there was a strong positive correlation between yearly estimates of *Cassiope* growth and
250 overall vegetation biomass across habitats ($r = 0.81$, $P = 0.001$; Fig. 4a). The correlation was
251 even stronger between average annual *Cassiope* growth and vegetation biomass within the
252 dry ridge habitat – the habitat most closely resembling the locations from which *Cassiope*
253 was sampled – although ridge biomass appeared to reach a plateau at around 27 g/m^2 ($r =$
254 0.85 , $P < 0.001$; Fig. S1a).

255 The strength of the correlation between yearly estimates of vegetation biomass and *Cassiope*
256 growth tended to decrease with increasing distance between the Semmeldalen biomass plots
257 and *Cassiope* sites (Fig. 4b). This was true for both the biomass averaged across all habitat
258 types ($r = -0.59$, $P = 0.06$) and for ridge habitat only ($r = -0.55$, $P = 0.08$; Fig. S1b).

259

260 *Cassiope growth as a proxy for vascular plant biomass*

261 Annual growth of *Cassiope*, estimated across sites, was positively correlated with July
262 temperature ($r = 0.68$, $P = 0.02$) and with summer temperature averaged across June-August
263 ($r = 0.65$, $P = 0.02$), but was not related to extreme winter weather events, indexed by rain-
264 on-snow (November-February: $r = -0.24$, $P = 0.45$; November-April: $r = -0.18$, $P = 0.57$).
265 Annual *Cassiope* growth was less tightly correlated with July temperature than vascular plant

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266 biomass across habitats ($r = 0.92$, Van der Wal & Stien, 2014). However, within
267 Semmeldalen, we found that *Cassiope* growth was a better predictor of annual vegetation
268 biomass in ridge habitat ($F_{1,10} = 26.09$, $P < 0.001$; $R^2 = 0.72$) than July temperature, which did
269 not explain any significant additional variation ($F_{1,9} = 3.06$, $P = 0.11$).

270

271 **Discussion**

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

282 Our findings support the suggestion that *Cassiope* and other vascular plants growing in
283 tundra habitats, ranging from dry *Salix/Dryas* ridge to wet *Dupontia/Eriophorum* marsh,
284 respond similarly to shared environmental conditions. A similar conclusion was reached by
285 Weijers *et al.* (2018) for two contrasting shrubs, *Cassiope* and *Salix pulchra*, in an alpine
286 tundra site in north-west Canada. In both cases, *Cassiope* and other plant species from a
287 range of habitats, showed a positive growth response to summer temperature (Van der Wal &
288 Stien, 2014; Weijers et al., 2018). This temperature response of *Cassiope* has been widely
289 reported from both the Norwegian and Canadian high Arctic (Rayback & Henry, 2006;

290 Weijers et al., 2012 and references therein). The implication of *Cassiope* being a local proxy
291 for total vascular above-ground biomass is that the great between-year variability observed in
292 *Cassiope* across the Arctic is likely to reflect a similarly widespread temporal variability in
293 the above-ground biomass of arctic tundra vegetation.

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

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

315 higher among similar sites, in terms of aspect and vegetation type. This may be due to more
316 similar moisture availability or snow conditions, with variation in snow depth influencing
317 *Cassiope* stem growth (Blok et al., 2015).

318 Dendrochronological analyses of the dwarf shrub *Cassiope tetragona* commonly report
319 considerable between-year variability in growth and sensitivity to a variety of climatic
320 variables, including summer temperature, throughout the Arctic (e.g. Callaghan et al., 1989;
321 Johnstone & Henry, 1997; Rayback & Henry, 2005; Rayback et al., 2011; Rozema et al.,
322 2009). Some studies use this feature for historical reconstruction of past climate (Rayback &
323 Henry, 2006; Weijers et al., 2010). Yet, while year-to-year variation in *Cassiope* is accepted
324 as the norm, this does not hold for vascular plant productivity of tundra vegetation as a whole
325 (Chapin & Shaver, 1985; Henry et al., 1990; Hill & Henry, 2011). We demonstrate that
326 between-year variation in *Cassiope* growth was strongly correlated with between-year
327 variation in vascular plant biomass of the tundra vegetation in our study system. As such
328 *Cassiope* growth may be a useful local proxy for vegetation productivity, although predictive
329 power declines with distance from where *Cassiope* is sampled. Given the strength of the
330 relationship between *Cassiope* growth and vegetation productivity in our study, and the
331 consistently reported between-year variability in *Cassiope* growth and sensitivity to summer
332 temperature across the Arctic, it may be expected that plant productivity in many parts of the
333 Arctic is equally sensitive to between-year variation in summer conditions. Wider-scale field
334 calibration would help to understand the generality of this result. The observed declining
335 spatial covariation in annual *Cassiope* growth, as well as the waning covariation between
336 above-ground vascular plant biomass and *Cassiope* growth, point to local summer weather
337 conditions influencing plant growth. Our key finding that retrospective growth analysis
338 captures local vascular plant productivity suggests that integrating dendroecology with

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339 satellite-based measurements can be an efficient approach to studying and understanding
340 spatio-temporal patterns of tundra productivity.

341

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346

347 **Authors' contributions**

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

353

354 **Data accessibility**

355 Data will be archived in the Dryad Digital Repository.

356

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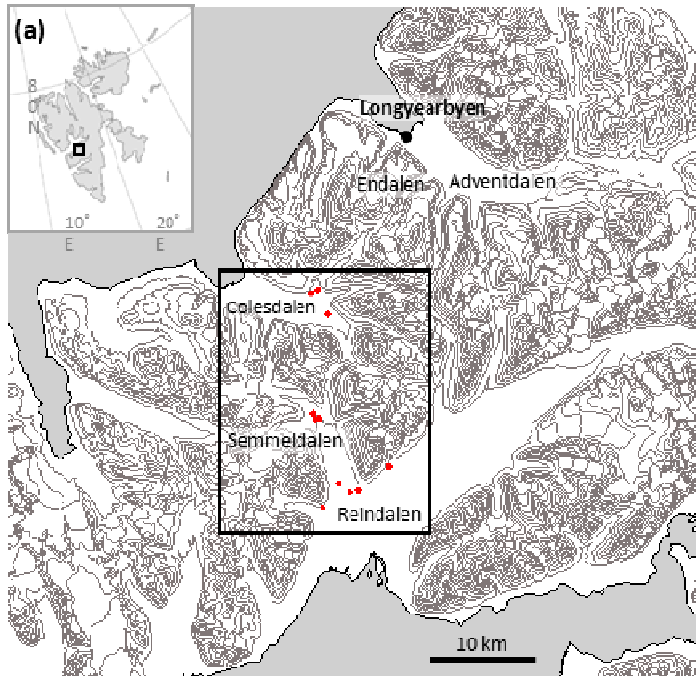
507 **Table 1.** Number of *Cassiope tetragona* samples from each site within each of three valleys
508 in Nordenskiöldland, Svalbard (see Fig. 1), together with mean annual growth increment
509 (AGI) \pm SE.

Valley	Site					Total n	Mean AGI (mm)
	1	2	3	4	5		
Colesdalen	5	9	8			22	7.21 \pm 0.44
Reindalen	6	6	8	6	7	33	6.65 \pm 0.33
Semmeldalen	12	7	6			25	6.17 \pm 0.36

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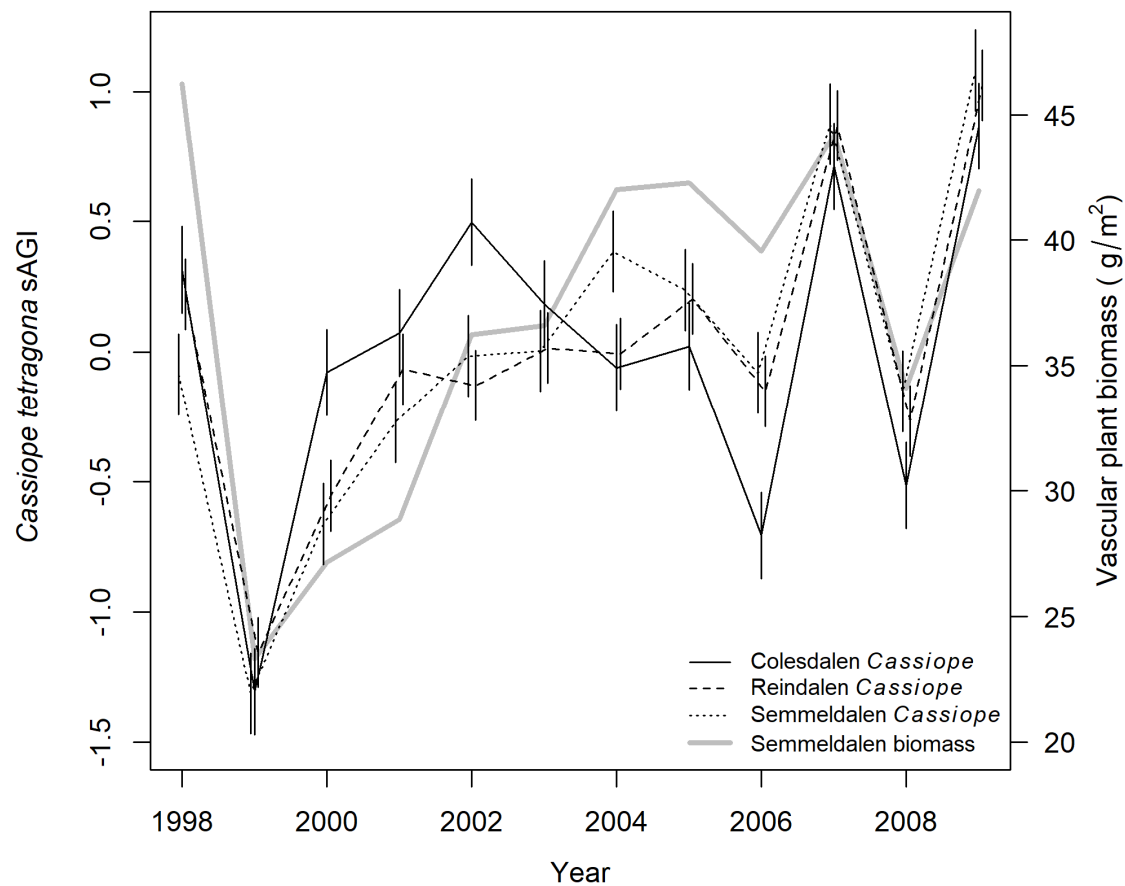
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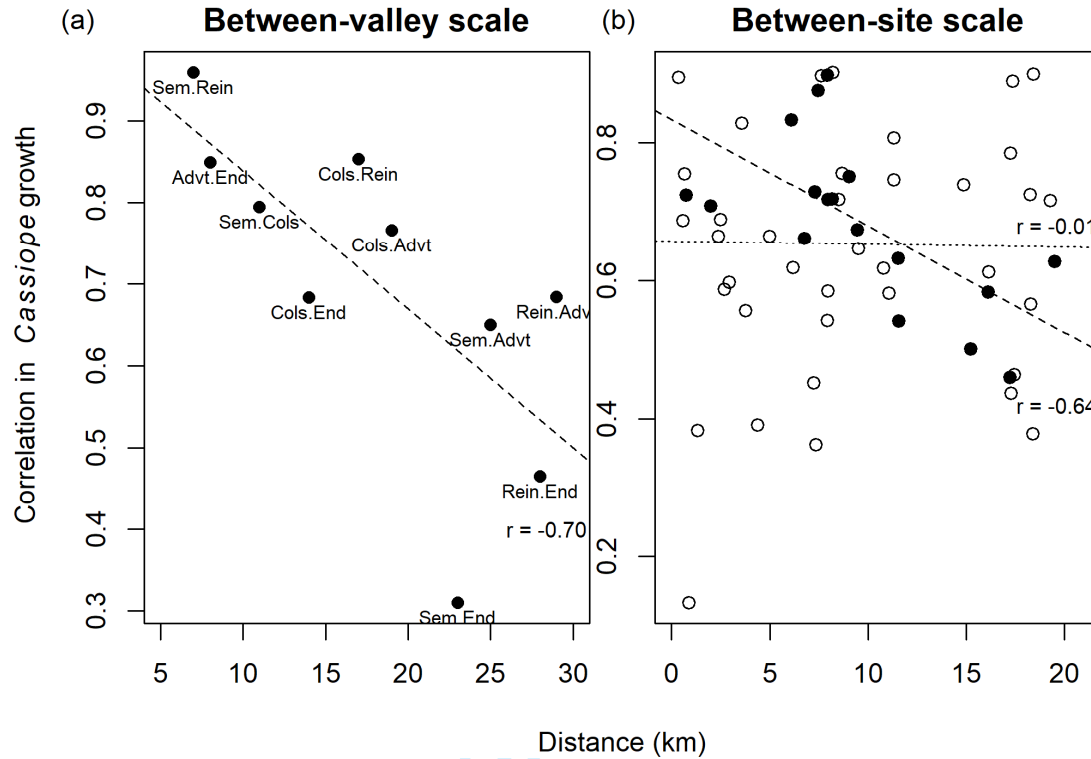
513 **Figure 1.** (a) Topographic map of the Nordenskiöldland study area (black box) on high arctic
514 Svalbard (inset) in relation to other places referred to in the text. Red points indicate the
515 *Cassiope tetragona* sampling sites in the three main valleys of the study area. (b) Reindalen
516 sampling area showing fragmented *Cassiope* zone in foreground and to left in *Luzula/Salix*-
517 dominated heath. (c) Small *Cassiope* patch typical of sub-ridge heath in Semmeldalen.

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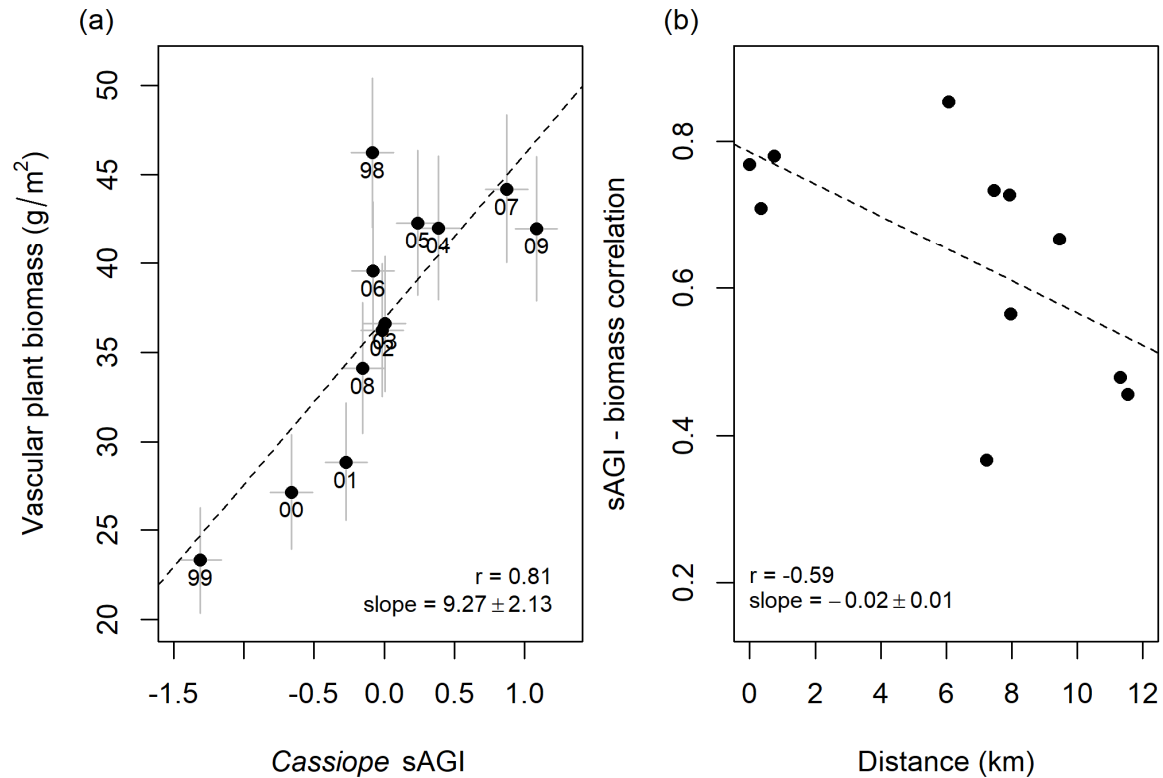
518
 519 **Figure 2.** Temporal patterns in standardised annual growth increments (sAGI) of *Cassiope*
 520 *tetragona* estimated for each of three valley areas in the Nordenskiöldland study area,
 521 Svalbard, over the period 1998-2009 (black lines) and total above-ground live vascular plant
 522 biomass in Semmeldalen, estimated over the same time period (grey line). Plots of the sAGI
 523 are offset slightly between areas to allow error bars (± 1 SE) to be distinguished.

524



525

526 **Figure 3.** Correlation in temporal patterns of annual growth of *Cassiope tetragona* at two
 527 spatial scales. (a) Between-valley scale in relation to distance between them; data for
 528 Semmeldalen (Sem), Colesdalen (Cols) and Reindalen (Rein) from this study, Adventdalen
 529 (Advnt) data from Blok *et al.* (2015) and Endalen (End) data from Weijers *et al.* (2010;
 530 reported in Blok *et al.*, 2015). (b) Between-site scale in relation to distance between sites
 531 within our Nordenskiöldland study area, Svalbard, for all site-pairs (open points, dotted fitted
 532 line). Black points and dashed fitted line are for pairs of sites with a similar aspect.



533

534 **Figure 4.** (a) Relationship between annual estimates of standardised *Cassiope tetragona*
 535 growth increments (sAGI) in the Semmeldalen sites and total above-ground live vascular
 536 plant biomass in Semmeldalen, estimated across all habitat types. Points are labelled by year.
 537 (b) Correlation between temporal *Cassiope tetragona* growth trends (sAGI) and total above-
 538 ground vascular plant biomass in relation to distance between *Cassiope* sites and the biomass
 539 plots in Semmeldalen, with biomass estimated across all habitat types.

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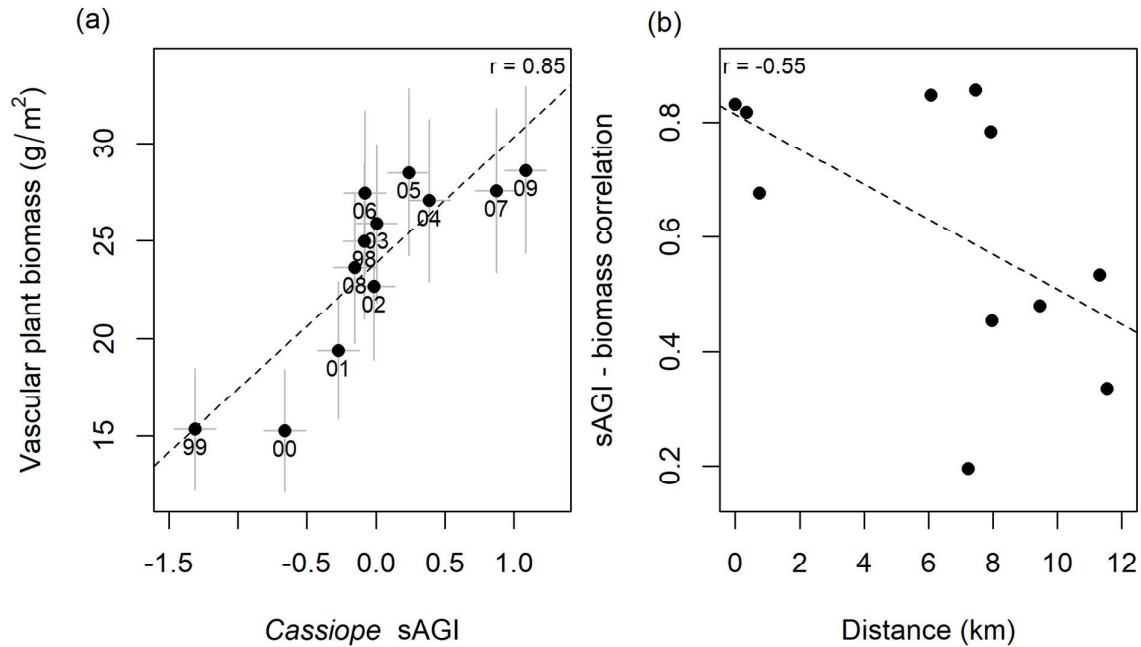


Figure S1. (a) Relationship between annual estimates of standardised *Cassiope tetragona* growth increments (sAGI) in the Semmeldalen sites and total above-ground live vascular plant biomass estimated across the dry ridge habitat in Semmeldalen. Points are labelled by year. (b) Correlation between temporal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