

1 Age matters: Demographic senescence in the
2 moss *Polytrichastrum formosum*

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15
16 **Abstract**

- 17 1. It is known that many animal species senesce demographically, showing a decrease in survival and/or
18 fertility with age. Though there is mounting evidence for and against senescence in various flowering
19 plant species, the question of whether senescence also occurs in other plant taxa, such as mosses and
20 other bryophytes, remains unanswered.
- 21 2. We used GAMMs (generalized additive mixed models) and GLMMs (generalized linear mixed models)
22 to assess effects of age on survival, size and the monocarpic female ramets' sexual reproduction in

23 *Polytrichastrum formosum* using demographic, ramet-level data collected over 25 years in Solhomfjell
24 nature reserve, Norway.

25 3. Survival was found to be negatively correlated with ramet age, with one-year survival decreasing from
26 83% in 1-year-old to 43% in ten-year-old plants. Stem growth was positively correlated with survival but
27 accounting for it in our models did not change the relationship between age and survival qualitatively.
28 Annual growth decreased during the first years of the ramets' life but then stabilised. Sexual
29 reproduction in the monocarpic females peaked at ramet age 2–4 years but was observed at ages up to
30 13 years. The longest-living (non-reproducing) ramet died at age 14.

31 4. *Synthesis*. Our findings indicate that *Polytrichastrum formosum* ramets experience constant actuarial
32 senescence, at least in terms of survival. This finding improves our understanding of age-dependent
33 demography in mosses, as well as in plants in general. This new knowledge about moss demography
34 may also aid in management decisions for threatened species, as it can improve the precision of
35 predictions of population longevity.

36 **Keywords:** ageing; bryophyte; growth; monocarpy; mortality; ramet; survival; vital rates

37 INTRODUCTION

38 Demographic senescence, a decrease in survival and/or fertility with age, has been shown to occur in all
39 investigated mammals and birds, which are the most well-studied taxa in this regard (Jones *et al.* 2014).
40 Historically, the main focus of plant demography has been on size and/or life-cycle stage, as these are
41 considered to be accurate predictors of vital rates in many or most plants (Caswell 2001). However, recent
42 research indicates that age also matters and that there is substantial variation in how age affects vital rates
43 such as survival, reproduction and growth (Edelfeldt, Bengtsson & Dahlgren 2019; Roach & Smith 2020). In
44 some species, survival shows no significant relationship with age or may increase towards higher ages
45 (Hutchings 2010; Garcia, Dahlgren & Ehrlén 2011; Edelfeldt, Lindell & Dahlgren 2019), while other species
46 show a significant decrease in survival with age, i.e. actuarial senescence (Picó & Retana 2008; Roach,
47 Ridley & Dudycha 2009; Dahlgren *et al.* 2016). Similarly diverse relationships have been documented
48 between reproduction and age in polycarpic species (i.e. plants that are capable of sexual reproduction
49 multiple times in their life cycle): negative (Tuomi *et al.* 2013; Barks & Laird 2015), negligible (Rose, Clarke
50 & Chapman 1998; Müller *et al.* 2014), and positive (Garcia, Dahlgren & Ehrlén 2011; Tuomi *et al.* 2013). The
51 relationship between reproduction and age is not fully understood in monocarpic species (i.e. plants that
52 reproduce sexually once and then subsequently terminate growth). In general, there seems to exist a size-
53 threshold for reproduction in monocarpic species (Metcalf, Rose & Rees 2003), but some studies indicate
54 that older plants may reproduce at smaller sizes than expected due to an increased tendency of flowering
55 with advancing age (Klinkhamer, de Jong & Meelis 1987; Childs *et al.* 2003). Also, growth rates of plant
56 individuals have been shown to be affected by age in various ways (e.g. Baden *et al.* (2020)). However,
57 studies on age-based demography have predominantly been made on vascular plants (Roach & Smith
58 2020), while very little is known about the effects of age on vital rates of bryophytes (Salguero-Gómez,
59 Shefferson & Hutchings 2013).

60 Besides ageing, bryophyte mortality is brought about by a large number of factors (Økland 1995),
61 exemplified by various disturbance agents such as burial in leaf litter (Halvorsen 2012), desiccation (Watson
62 1975; During 1979; Pedersen, Hanslin & Bakken 2001) and amensalism, i.e. deprivation of light by burial in
63 carpets of larger plants (Økland 1995; Halvorsen 2012). This implies that size may be an important driver of
64 bryophyte survival, which indeed has been demonstrated for some species. For example, ramet size was
65 found to be positively correlated with survival in *Hylocomium splendens* (Økland 1995). However, a few
66 studies also suggest that age plays a significant part in determining survival of bryophytes. Thus, in a study
67 of six closely related moss species of the family Polytrichaceae, Watson (1979) found that adult ramet
68 survival decreased with age until levelling off in the oldest age classes. Pohjamo and Laaka-Lindberg (2004)
69 attributed low survival of tall stems of a liverwort to senescence. Observations suggesting adult survival
70 that is independent of age has also been reported for some bryophyte species (During & ter Horst 1985). It
71 is worth noting, however, that none of these studies in which age-related relationships have been inferred,
72 are based on long-term data. The longest-lasting of these observational field studies lasted for less than
73 three years (During & ter Horst 1985) and age distributions were inferred from indirect measures, such as
74 seasonally induced variation in leaf morphology (Watson 1979). Long-term studies of bryophyte survival in
75 which individuals are followed throughout their life spans are so far lacking, and we are not aware of any
76 studies assessing effects of age on the reproduction of bryophytes. In general, the effect of age on
77 bryophyte growth is also poorly understood, although decreasing annual segment lengths with age has
78 been reported in a study of *Polytrichum alpestre* (Longton 1979).

79 Current evolutionary theories of demographic senescence predict that early-life separation between
80 somatic and germ cell lines in an organism will be associated with an age-related increase in mortality (and
81 possibly decreased fertility) after reaching sexual maturity (Hamilton 1966; Kirkwood 2017). Plants do have
82 this separation between cell lines, but it is currently unclear exactly when the separation takes place.
83 However, research on angiosperms has shown that early-life separation is possible (Lanfear 2018). In
84 angiosperms (and most other vascular plants), the diploid sporophyte is the longer- and free-living

85 generation, while it is the haploid gametophyte that has this role in bryophytes. It is currently unknown
86 whether this difference may influence eventual age-related senescence in this group.

87 The main aim of this study is to assess to what extent the demography of *Polytrichastrum formosum* ramets
88 is age dependent. More specifically, we assessed the question of whether *P. formosum* ramets experience
89 demographic senescence in terms of negative correlations between age and the vital rates survival,
90 reproduction, and growth. We present analyses of data on ramets of *P. formosum* collected over a twenty-
91 five-year period between 1994 and 2019 in fifteen permanent plots in Solhomfjell nature reserve, Norway.
92 As the length of the study period exceeds the maximum recorded lifespan for the ramets followed during
93 the study by a factor of two, these data are well suited for the purpose. Three hypotheses are evaluated: 1)
94 the effect of age on survival and stem growth of ramets is positive early in life and negative later in life; 2)
95 the effect of stem growth rate of ramets on its survival is positive, which may mask some of the effects of
96 age; and 3) in this monocarpic species, sexual reproduction of female ramets peaks in specific age interval.

97 METHODS

98 STUDY SPECIES

99 *Polytrichastrum formosum* (Hedw.) G.L.Sm. is a dioecious, acrocarpous moss of the family Polytrichaceae
100 which forms extensive, often 50–200 mm tall, dense turfs (Andersen *et al.* 1976). Females are monocarpic
101 and terminate after producing a sporophyte, while males are polycarpic (Touw & Rubers 1989). The species
102 is common in the temperate zones of the Northern Hemisphere, on moist, mildly acidic, humus-rich soils
103 (Touw & Rubers 1989). Accordingly, *P. formosum* is commonly found in forests on boulders or on the
104 ground, and it also occurs on well-drained moorland and lowland heath (Touw & Rubers 1989).

105 Gametophytes of *Polytrichastrum formosum* grow throughout their life span, and older parts form
106 underground rhizomes. They can reproduce asexually by regeneration from fragments or by a branching
107 and eventual separation (During 1990). These clonal processes can result in moss cushions of genetically

108 identical ramets that are either independent, or sometimes connected via rhizomes (van Groenendael & de
109 Kroon 1990). Other moss cushions can be genetically diverse and consist of multiple genets (Van der Velde
110 *et al.* 2001). Typically, regeneration from fragments has been found to be of negligible importance for the
111 survival of local populations of this species, whereas branching of the subterranean rhizome is the main
112 process by which new ramets arise (Van der Velde *et al.* 2001). Sexual reproduction serves long-distance
113 dispersal but is thought to have limited impact on local population dynamics (Van der Velde, Van de Zande
114 & Bijlsma 2001).

115 **STUDY SITE**

116 The study was carried out in Solhomfjell nature reserve, Norway (8°48–51'E, 58°57'N; 350–480 m a.s.l.).
117 The study site is a reference area for monitoring boreal forests and consists of unmanaged Norway spruce
118 (*Picea abies*) forests with field-layer vegetation dominated by European bilberry (*Vaccinium myrtillus*). A
119 detailed description of the study site is given by Økland and Eilertsen (1993).

120 A total of 200 permanent vegetation plots, 1 m² each, were placed using a restricted random procedure
121 along eight transect lines in 1988 (Økland & Eilertsen 1993). The distance between adjacent transects is 2
122 km or less, and no between-plot distance is less than 3 m. For this study, 14 subplots, 25 × 25 cm each,
123 were censused over the years 1994–2019. A minimum of eight *P. formosum* ramets had to be observed at
124 census in a specific year for the subplot to be included or retained in the study. If more than 50 ramets
125 were observed in a subplot, the subplot's "active area" was reduced by a standardised procedure until the
126 number of ramets no longer exceeded 25.

127 **MONITORING**

128 All *P. formosum* ramets that were observed in the active area of each subplot in any year 1994–2019 were
129 tagged using PVC rings created from HAMA plastic beads (Malte Haaning Plastics Co., Nykøbing Mors,
130 Denmark) with an outer diameter of 4.5 mm and an inner diameter of 2.5 mm. Each ring was sliced into ca.
131 1 mm tall sections and a slit was provided to allow the rings to be applied to moss stems using two pincers.

132 Ramets were tagged every year by applying a new ring a few millimetres below the apex. This tagging
133 method has been used for studies of *Hylocomium splendens* over thirty years (Økland 1995). In contrast to
134 other tagging methods (e.g. pins inserted into the substrate next to shoots (Hobbs & Pritchard 1987) and
135 strings tied around the stem at a fixed distance from the apex (Watson 1975)), comparative observations of
136 tagged shoots inside and untagged shoots outside the subplot border over the 25-year study period show
137 no indications of effects of this tagging method on *P. formosum* ramets, e.g. by attracting herbivores or
138 directly affecting growth and/or survival.

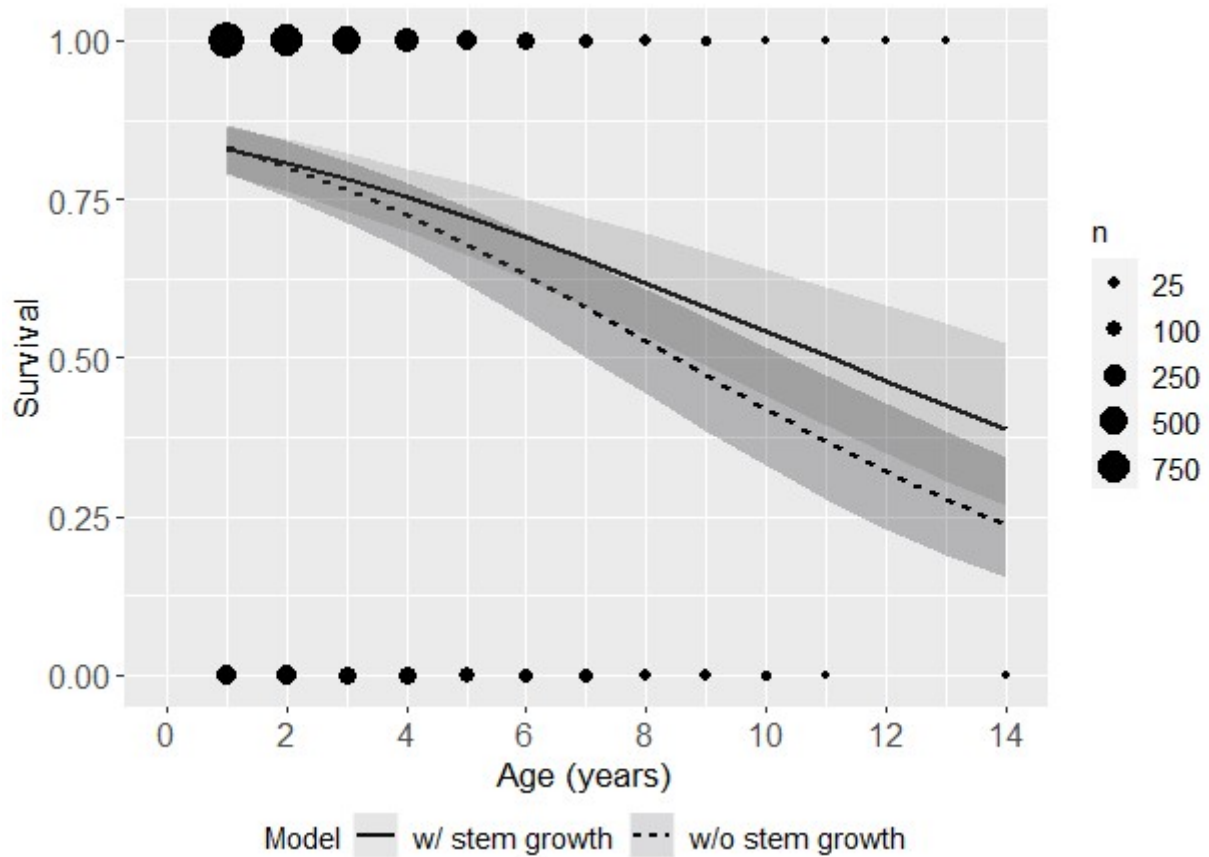
139 A total of 2,434 ramets were followed during the study period, of which the year of appearance was known
140 for 1,343 ramets. These were used in our analyses. Out of these, 107 female ramets reproduced sexually
141 and subsequently terminated, while 885 ramets terminated for other reasons. At each census, the ramets'
142 stem growth since the previous census was measured. A ramet was considered as terminated (dead) if it
143 was observed with negligible stem growth (< 1 mm) since the previous census and little or no green parts
144 were left on the stem. Fifteen ramets recorded as terminated at one census were found to have
145 regenerated (resumed stem growth) at the next census and thus re-entered the census. The yearly stem
146 growth, hereafter referred to just as "stem growth", was used as a proxy for size in analyses of survival; the
147 full length of the entire green part of stems was not measured. Female ramets were identified by their
148 sporophytes and ramets with male structures were rare, so the sex of most ramets was therefore unknown.

149 **ANALYSES AND MODELLING**

150 Stem growth and survival were modelled using thin-plate spline regressions and the package 'gamm4'
151 (Wood & Scheipl 2017) in *R* (version 3.6.1). This type of generalized additive mixed model (GAMM) enabled
152 identification of possible nonmonotonic age trajectories of both stem growth and survival without
153 assuming specific functional relationships. In GAMMs describing survival, a logit link function and a
154 binomial error distribution were used. When modelling stem growth as a function of age, an identity link
155 function and a Gaussian error distribution were used. Average survival differed among plots (Fig. S1). To

156 account for this variation, and for the repeated measurements of ramets, random intercepts for years,
157 plots and individual ramets were included. Average survival was also found to decrease over the study
158 period, but accounting for this decrease did not affect the estimated age trajectory (Table S1). To limit
159 model complexity, the number of basis functions were limited to 4–6 depending on the model in question.
160 All models were fitted both excluding and including sexually reproducing females, as well as to sexually
161 reproducing females only. Unless stated otherwise only models excluding sexually reproducing female
162 ramets are reported in the results while all other models are presented in the supplementary material.

163 Age-dependent survival GAMMs showed linear tendencies regardless of whether stem growth was
164 included or not (this did not, however, hold true for models for sexually reproducing females). Accordingly,
165 we used generalized linear mixed models (GLMMs) for the age-dependent survival models excluding
166 sexually reproducing females. Models of survival were fitted both including and excluding stem growth as a
167 covariate to assess if observed effects of age were affected by a potential correlation between age and
168 stem growth.

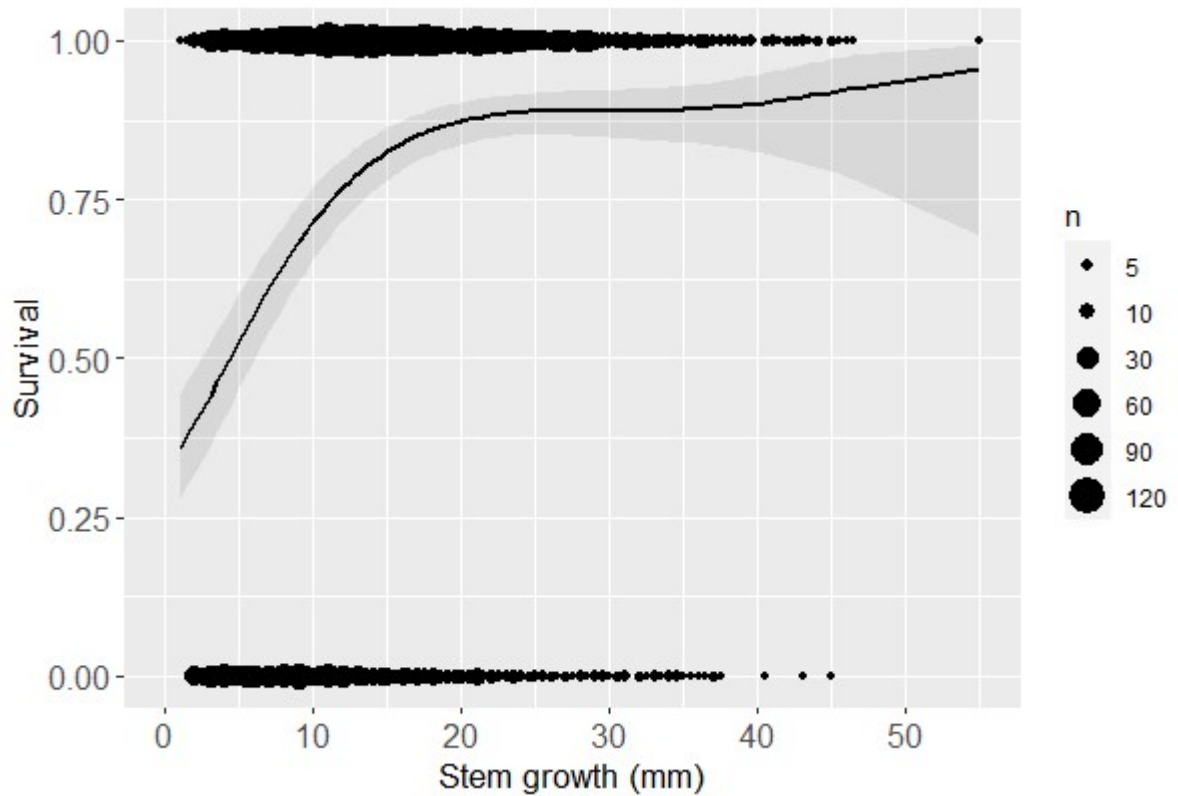


170

171 Fig. 1 Survival probability of *Polytrichastrum formosum* ramets over one-year periods as a function of age, with (slope = -0.15, $z = -$
 172 7.02, $p < 0.001$, $n = 3872$) and without (slope = -0.21, $z = -10.23$, $p < 0.001$, $n = 3872$) stem growth since the previous census as a
 173 covariate in the model. For the model including stem growth, the presented relationship applies to ramets with stem growth equal
 174 to the overall mean ($15.1 \text{ mm}\cdot\text{yr}^{-1}$). Sexually reproducing females are not included in the models. The shaded bands indicate 95 %
 175 confidence intervals. n is the number of observations.

176 Survival decreased almost linearly with age (Fig. 1, Table S1). One-year-old ramets had ca. 83 % chance of
 177 surviving to the next year in both models, while 10-year-old ramets had a survival probability of 44 % when
 178 stem growth was not accounted for and 54 % when it was. The mean age at termination was 3.4 years
 179 (median = 3 years) and the longest recorded lifespan was 14 years.

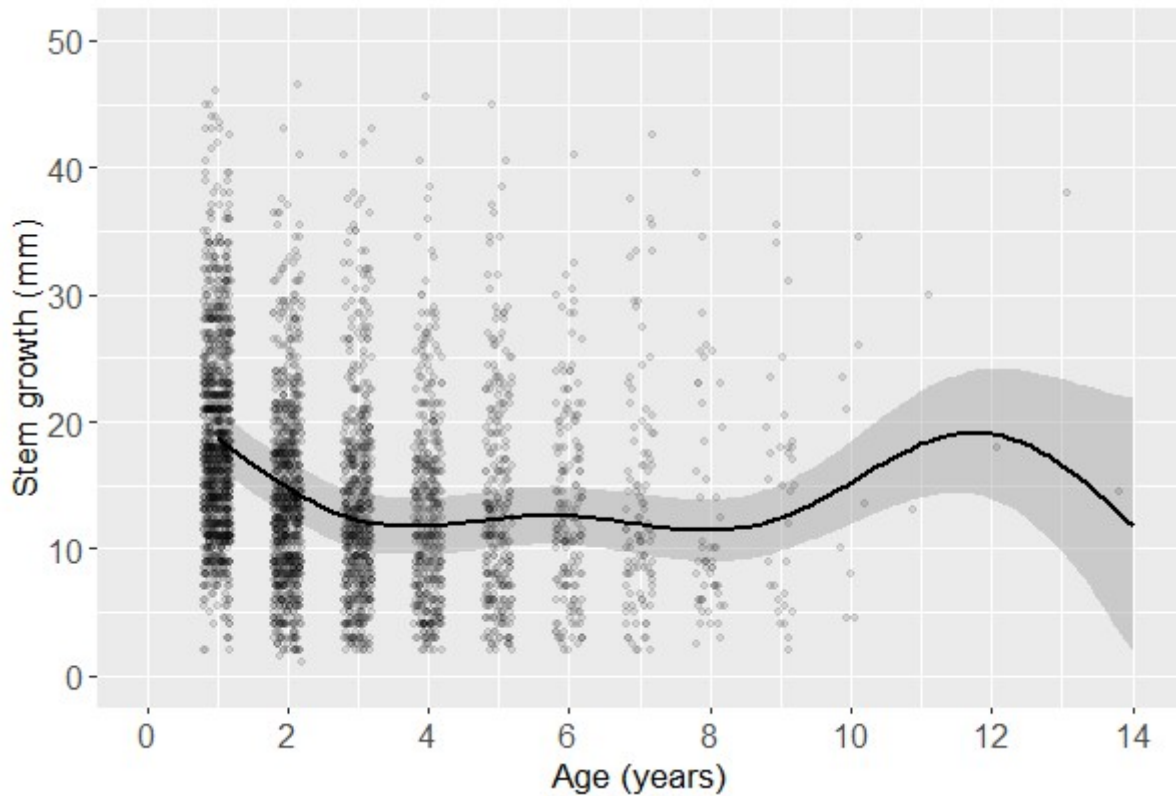
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181

182 *Fig. 2* Survival probability from one year to the next of *Polytrichastrum formosum* ramets as a function of size (stem growth during
 183 the last year), modelled using a generalized additive mixed model (estimated degrees of freedom = 2.69, $\chi^2 = 252.1$, $p < 0.001$, $n =$
 184 3836). Sexually reproducing females are not included in the model. The shaded band indicate the 95 % confidence interval. n is the
 185 number of observations.

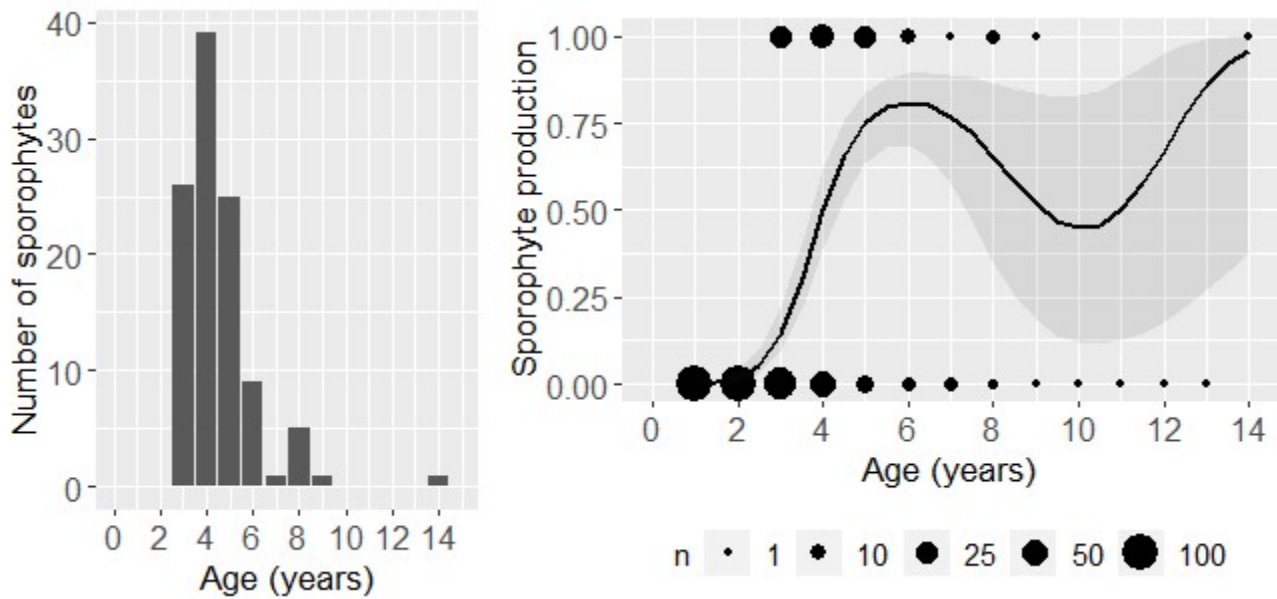
186 Survival was positively correlated with stem growth, with ramets growing 5 mm and 20 mm having 53 %
 187 and 87 % chance of survival to the next year, respectively (Fig. 2). Survival levelled off towards high stem
 188 growth rates, thus a ramet growing 40 mm in one year had a 90 % survival probability. A ramet with a
 189 yearly stem growth equal to the average across all ages (15.1 mm) had an 83 % chance of survival to the
 190 next census.



191

192 *Fig. 3* Stem growth since previous census of *Polytrichastrum formosum* ramets as a function of ramet age, modelled using a
 193 generalized additive mixed model (estimated degrees of freedom = 4.73, $F = 150.7$, $p < 0.001$, $n = 3905$). Sexually reproducing
 194 females are not included in the model. The shaded band indicates the 95 % confidence interval. Points indicate individual
 195 measurements and are jittered horizontally to limit overlap.

196 Average annual stem growth decreased over the first four years from ca. 19 mm to 12 mm and then
 197 levelled off (Fig. 3). The tendency to increased stem growth observed for ramets 10 years or older was
 198 based upon very few observations. Stem growth of sexually reproducing females followed largely the same
 199 pattern (Fig. S2).



200

201 Fig. 4 Left panel: The number of sporophyte-bearing ramets observed during the study period (1995–2019) as a function of ramet
 202 age. Right panel: Probability of producing a sporophyte as a function of age (estimated degrees of freedom = 2.89, $\chi^2 = 92.23$, $p <$
 203 0.001, $n = 483$) for female *Polytrichastrum formosum* ramets that were observed to reproduce during the study. The shaded band
 204 indicates a 95 % confidence interval. n is the number of observations.

205 Sporophytes were predominantly found on three to five year-old female ramets (accounting for 84 % of all
 206 sporophyte-bearing ramets); 36 % were four years old (Fig. 4 Left panel). No sporophytes were observed on
 207 ramets aged two years or younger (Fig. 4 Left & Right panel). The number of observed sporophytes per year
 208 ranged from 0 to 12 (mean = 5.35 for each year in which sporophytes were observed). No sporophyte was
 209 observed in the years 1995–97, 2007 and 2019.

210 DISCUSSION

211 In this uniquely long-term ramet-based study of a monocarpic moss we found a clear negative correlation
 212 between age and survival, suggesting actuarial senescence. While stem growth also affected survival, its
 213 inclusion in the survival model did not significantly influence the age trajectory. Annual stem growth was
 214 negatively correlated to age for young ramets. As expected, sexually reproducing females had a different
 215 survival age trajectory compared to other ramets, with the occurrence of sexual reproduction (and

216 termination) in females being centred around ages 3–5 years. These patterns of survival, growth and
217 reproduction suggest that age may matter and has to be taken into account for a full understanding of the
218 demography and life history of at least some bryophytes.

219 The negative correlation between survival and age indicates actuarial senescence in *P. formosum*,
220 corroborating findings by Watson (1979), who found similar relationships in a few *Polytrichum* and
221 *Polytrichastrum* species. Similar age-related decreases in survival have been observed in several species of
222 flowering plants, including grasses (Canfield 1957) as well as non-grass monocot (Dahlgren *et al.* 2016) and
223 dicot (Roach, Ridley & Dudycha 2009) herbs. However, it also seems that many flowering plant species do
224 not experience actuarial senescence (Dahlgren & Roach 2017) – their survival and reproduction show no
225 significant negative correlation with age – which may indicate that more studies are needed to sort out
226 general patterns of age trajectories of survival also in bryophytes. Knowing these patterns also for
227 bryophytes will give us a better understanding of senescence in plants in general and may be important for
228 proper management of threatened species, as it has been found that not accounting for age can cause
229 imprecise population projections for plants (Chu & Adler 2014; Edelfeldt, Bengtsson & Dahlgren 2019).

230 The fact that we find indications of actuarial senescence in ramets does not mean that the same is
231 necessarily the case for genets; that is, the genetic individual potentially consisting of multiple ramets.
232 Theoretical models indicate that both genets (Gardner & Mangel 1997) and ramets (Orive 1995) of plants
233 can escape senescence under some circumstances, due to the modular nature and/or decoupling of size
234 and age generally found in clonal species (Kroon & Groenendael 1997). Due to long life spans of genets and
235 unclear relatedness of ramets, demographic studies of genets of clonal plants are essentially lacking
236 (Dahlgren & Roach 2017). However, molecular techniques, such as those applied by Ally, Ritland and Otto
237 (2010), offer promising opportunities for studies of genets, which may grant us a better understanding of
238 how clonality is related to senescence.

239 Despite not notably affecting the relationship between age and survival, stem growth appeared to have a
240 positive effect on survival, in accordance with our expectation. Although survival in some species of moss
241 has been found to be mostly independent of size (During & ter Horst 1985), the long-term study of
242 *Hylocomium splendens* by Økland (1995) indicated a strong size-dependent effect on almost all vital rates,
243 including branching and survival. Size is typically also positively correlated to high vital rates in herbaceous
244 vascular plants (e.g. Solbrig (1981), Aarssen and Jordan (2001)). However, this correlation may be brought
245 about by other factors than size as such. A high stem growth rate may simply be indicative of a ramet's
246 vitality and a sign of the amounts of resources available to it; potentially making stem growth an indicator
247 of higher survival probabilities rather than the cause of it. Regardless of which is the cause, and which is the
248 effect, stem growth was an important predictor of survival of this moss. This strongly motivates taking
249 measures of size, together with age, into account in future demographic research on bryophytes.

250 The decrease of stem growth rate in the first few years of a ramet's life could indicate senescence.
251 However, this decrease is followed by a plateau and field observations (D.W. Tholstrup & R. Halvorsen,
252 personal observation) indicated that most ramets stayed connected to the parental plant for the first
253 couple of years. These observations could indicate rapid initial growth being facilitated by the connection
254 to other ramets, which has been observed to occur in other species (e.g. *Populus grandidentata* (Zahner &
255 DeByle 1965)). Thus, age itself is unlikely to drive this pattern in stem growth.

256 Sporophyte production peaked at ramet ages of 3–5 years. Since sexual reproduction takes place the year
257 before sporophytes mature, the reproductive events peaked at 2–4 years of age. Such relatively “early”
258 sexual reproduction in relation to the possible life span of ramets is in agreement with findings by Metcalf,
259 Rose and Rees (2003), showing that monocarpic plants follow a simple ‘law of diminishing returns’
260 according to which reproduction takes place once the pay-off from reproduction exceeds the gain from
261 continued survival. Thus, reproduction should take place as soon as enough resources are available for
262 supporting, in the case of mosses, a sporophyte.

263 We conclude that *Polytrichastrum formosum* ramets appear to experience demographic senescence.
264 However, more studies are necessary to understand how ageing generally affects mosses and other
265 bryophytes, as well as the causes that drive these effects. Long-term individual-based studies are of
266 particular value in cases like this, when age cannot be inferred precisely from morphology. In addition,
267 future studies that identify genets will contribute greatly to a better understanding of ageing, not only in *P.*
268 *formosum* but in plants in general. Based on our results, we recommend age to be considered in future
269 demographic studies of mosses, as well as in other instances when demographic models are used for
270 population projections.

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275 constructive comments on our manuscript from the editor and two anonymous reviewers.

276 **DATA AVAILABILITY STATEMENT**

277 Data available from the Dryad Digital Repository:

278 <https://datadryad.org/stash/share/r3OHJ2p920TdVVaAj2jy95WeEBZs7DIikuwMBs5XXe8> (Tholstrup,
279 Halvorsen & Dahlgren 2021).

280 **AUTHOR'S CONTRIBUTION**

281 RH designed and conducted the fieldwork; DWT, JPD and RH conceived the ideas; DWT analysed the data
282 and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval
283 for publication.

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