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Age and size at maturity in mountain and lowland populations of the expanding moss *Pogonatum dentatum*

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Abstract

The moss *Pogonatum dentatum* has expanded its distribution in Fennoscandia from mountainous areas into the lowlands. This recent expansion appears to be associated with changes in important life-history parameters in female shoots. We examined shoot age and size at first production of sex organs and mature spores in *P. dentatum* to investigate this phenomenon. Female shoots produced mature spores for the first time in the lowlands in their second year but in their third year in the mountains. However, sex organs were produced by second year plants in both areas. There was no size difference between the mountain and lowland female shoots at the time of spore production. Among mountain females reproducing for the first time, 41% of the shoots branched, making them potentially 'iteroparous'. Branching was not observed among lowland females. Male shoots showed no difference in production of sex organs, and were produced by second year shoots in both areas. Female shoots in the lowlands have earlier spore production and exhibit 'semelparous' behaviour by not producing branches. This suggests that the lowland phenotypes of *P. dentatum* are more 'invasive' than the mountain phenotypes. Earlier studies showing high rates of diaspore establishment in lowland areas also support this observation.

Introduction

Studying traits of expanding species that are associated with fitness in newly colonised and in originally occupied areas can help us understand which traits are important (Roy 1990). This may provide new insights into evolutionary potential and colonisation dynamics, as well as identifying critical life stages where management can be most effective (Sakai et al. 2001).

Variation in demographic parameters, such as age at maturity (i.e., first reproduction) and reproductive patterns should affect the age or stage structure of female and male patches. Such an effect could result if fecundity and juvenile survival depend on age, for example, and if lifetime reproductive success depends on life span and number of reproductive events (Stearns 1992). Consistent differences in these parameters between sexes or localities may provide information about the selective pressures at play (Watson 1979).

Age at maturity is closely correlated with size in organisms with indeterminate growth. The sex that makes a greater investment in reproduction ought

to be both older and larger at maturity (Melampy and Howe 1977). Studies of sexual differences in life-history traits of dioecious vascular plants have shown that females are typically older than males at maturity (Melampy and Howe 1977; Bullock and Bawa 1981; Meagher and Antonovics 1982a, b). Similar patterns are expected among dioecious bryophytes, because the female gametophore supplies the sporophyte with nutrition. It is hard to imagine any form of male investment of equal or larger magnitude than female investment in a partially parasitic sporophyte. However, Stark et al. (2000) showed that when sexual reproduction is rare (occurring in $< 3\%$ of female populations), males make a greater investment in sexual reproduction due to higher pre-fertilisation costs involved in the production of sex organs.

Information on life-history variation is urgently needed for bryophytes. There are few studies of size at maturity (Convey and Lewis Smith 1993; Rydgren et al. 1998), and those that do exist provide conflicting evidence about the existence of a reproductive threshold value (i.e., a minimum resource level or size for sexual reproduction in bryophytes). The only study of bryophytes dealing with intraspecific variation in age at maturity found differences between populations in two species but not in the third (Hedderson 1992).

The moss *Pogonatum dentatum* (Brid.) Brid. has expanded its distribution from alpine areas down into the coniferous forest region in Fennoscandia (Fagerstén 1977; Hedenäs 1983; Söderström 1992; Hassel 2000) during the second half of the 20th century. Increased availability of suitable substrate has been suggested as one explanation for the expansion (Hassel and Söderström 1999), but a shift to a more 'invasive' life strategy could be an alternative or additional explanation.

So far, studies of expanding/invasive bryophytes have dealt with: (1) regional and local rate of expansion (e.g., van der Meulen et al. 1987; Herben 1994; Stieperaere 1994; Stieperaere and Jacques 1995); (2) dispersal processes, including spore production (Hedenäs et al. 1989; Hassel and Söderström 1999), distance of diaspore transport (Hassel and Söderström 1998) and establishment (Herben et al. 1991; Hassel and Söderström 1999); (3) habitat requirements (Hedenäs et al. 1989; Herben and Söderström 1992); and (4) population structure (Hedenäs et al. 1989). No studies have dealt with differences in age and size at maturity between original sites and newly colonised areas.

The aim of this study is to establish if there are differences in life-history strategies between two contrasting areas in the expanding species *Pogonatum dentatum*. This paper focuses on (1) age and size at maturity and (2) age and stage structure of female and male patches.

The term 'maturity' in bryophytes can be defined in two ways. The haploid shoot (gametophore), constituting the dominant phase of the bryophyte life cycle, can be termed 'mature' at the age or stage it produces female (archegonium) or male (antheridium) sex organs for the first time. Alternatively, by including the sporophyte in the maternal life cycle, 'maturity' of a female shoot (a gametophore with an attached sporophyte) may be defined as the age or stage at which spores are first produced. This paper examines both types of female maturity, referred to as G-maturity (gametophore) and S-maturity (sporophyte). We also define a 'population' as a group of patches occupying a limited area, and a 'patch' as a cluster of shoots that can consist of one or more individuals/genets. A 'shoot' or 'gametophore' or 'ramet' is potentially independent, but may be connected with nearby shoots by underground rhizoids, while a 'branch' is an aboveground innovation on a shoot.

Materials and methods

Study species

Pogonatum dentatum (Bryophyta: Polytrichaceae) is dioecious and shoots rarely live longer than 4 years. Gametophore size varies from just a few millimetres in juvenile plants up to about 2 cm in adults. In both mountain and lowland localities, females and males often form distinct patches with little mixing of sexes. The growth of patches can take place by underground rhizoid wicks (cf. Wiggelsworth 1947) or by establishment of gametophore fragments. The haploid gametophore life cycle starts either with a spore (sexual reproduction) or an asexually produced fragment (e.g., leaf, detached branch, part of stem), both forming a filamentous protonema from which one or several gametophores develop. The diploid zygote develops into a sporophyte that is apically attached to

the female gametophore, and produces haploid spores by meiosis. Production of an archegonium terminates growth of the gametophore, unless a branch is produced. Single female shoots of Polytrichaceae are usually 'semelparous' (Wyatt and Derda 1997), although they are potentially 'iteroparous' if they produce branches, which can then produce a new archegonium. Male shoots are more commonly 'iteroparous' and can continue growth from the same growing point after producing sex organs (Schofield 1985).

Study area

Populations were sampled from two areas in northern Sweden (Figure 1). The mountain area is in the alpine region at Stekenjokk (65°05′ N, 14°30′ E, altitude 800 m), on a mountain heath above the tree limit. The lowland area is in the boreal region at Junsele (63°45′ N, 17°15′ E, altitude 300 m), in spruce forest. Annual precipitation, mean July temperature and length of growing season are 1000–1100 mm, 8 °C and 110–120 days in the mountain area compared to 600–700 mm, 12 °C and 150–160 days in the lowland area (National Atlas of Sweden 1995).

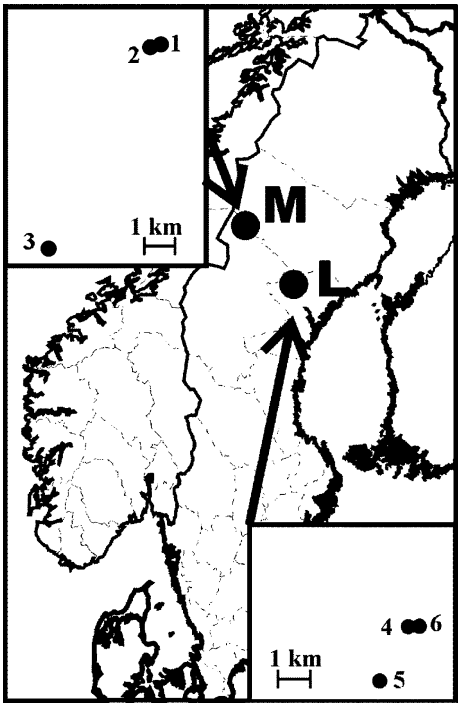

Figure 1. Map of Scandinavia indicating the study areas, L and M, which represent lowland (Junsele) and mountain (Stekenjokk) areas, respectively. The small maps indicate the distance between the studied populations (1–6) within each area.

Sampling

Populations were sampled from disturbed soil. In the mountain localities the main disturbance factors are wind and frost heave. The lowland populations were sampled from forest roads affected by man-made disturbance. The samples were collected in early September 1999, when most sporophytes in both areas were fully developed with their capsules still intact. Three populations were sampled from each area. Detailed information on the population area, patch size and altitude is provided in Table 1.

One male and one female patch were sampled from populations 1, 3, 4 and 6. Patches varied in the sampled populations, with some being unisexual (mixed with immature shoots), and others with both sexes growing together. The samples were 10 cm in diameter and taken from unisexual patches with fertile males and sporophyte-bearing females. Thus the age and stage structure is based on female and male patches that had reached maturity. One population from each area (2 and 5) was more intensively studied, with female and male shoots being sampled from five different patches. The distance between two patches was at least 1 m, but not more than 15 m. All samples were kept cool until they were placed in a freezer on return to the laboratory. For analysis, a 2×2 cm area was randomly selected from the circular 10 cm diameter patch.

Table 1. Characteristics of populations of *P. dentatum* sampled in the lowland and mountain areas.

Population	Pop. area (m)	Max. patch size (cm)	No. of patches	Altitude (m)
1 mountain	18×12	40×40	12	822
2 mountain	36×15	150×150	20+	814
3 mountain	16×4	40×40	8	868
4 lowland	70×4	40×40	20+	371
5 lowland	47×5	Continuous	1	290
6 lowland	19×3	20×20	15	353

Measurements

From the 2×2 cm sample all shoots were removed, washed and sorted by age and sex. The sex of immature shoots (without gametangia) could not be determined, but mature shoots of the opposite sex in the samples were almost absent, so all immature shoots from a sample were assumed to be of the same sex.

Shoots of the Polytrichaceae have a segmented appearance due to regular variation in leaf length, and these segments have been shown to represent annual growth increments (Longton and Greene 1967; Watson 1975, Figure 2). Age was determined by counting shoot growth segments. Shoots from male patches were recorded as in their first year (0-year-old) when only one growth increment was seen, in their second year (1-year-old) for two growth increments and so on. The ages of female shoots were determined in the same way, but they were also classified by stage classes (Figure 2) because shoots of the same age can be in different developmental stages. The following stages were recognised; ST, immature shoot without sex organs; F, female shoot which has produced sex organs, fertilised or not, but without elongated seta; and S, female shoot which is fertilised and has an elongated seta and swollen capsule. Before weighing, the shoots were dried at 70 °C for 24 h and sporophytes detached from the female gametophores by cutting the seta just above the foot.

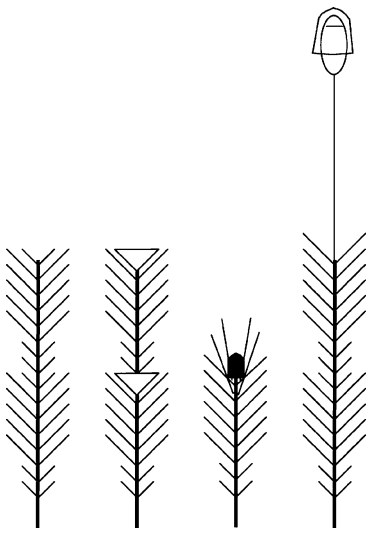

Figure 2. Schematic illustration of some of the age and stage classes. From the left: third year immature (ST2), third year male (M2), second year fertilised female with calyptra (F1) and third year female fully developed sporophyte (S2).

Statistical analyses

Differences in weight at maturity between the mountain and lowland areas for females and males were tested using nested analysis of variance (ANOVA), SPSS release 10.0.7. The dependent variable was gametophore size at maturity (G), the fixed factor was area (A, with two levels, mountain and lowland) and the random factor population (P, with six levels, populations 1–6) nested within area. Thus we analysed the following linear model:

$$G_{ijk} = \mu + A_i + P(A)_{j(i)} + e_{ijk},$$

where μ is the overall mean gametophore size, e is the error term, and the subscripts i, j and k refer to the area, population and shoot, respectively. A similar model was used to test for differences between populations 2 and 5 (random factor) with patch (1–10) as a random factor nested within populations. In the analyses we compared male shoots of age class 1 for both areas, and females in stage class S (i.e., second year lowland females and third year mountain females, cf. results).

To test for the existence of a threshold size for production of female gametophore sex organs (archegonia), we used a logit regression analysis (Jongman et al. 1995). Our data only allowed us to test immature second year females against archegonia-producing second year females from the mountains, as we had only four shoots of the latter category from the lowland area.

To test for differences in growth rates, we regressed gametophore size on age and then tested for heterogeneity in regression slopes (Underwood 1997). We computed separate regressions for female and male gametophore size before and after the production of sex organs (archegonia and antheridia) and between the lowland and mountain areas.

A t-test for independent samples was used to test for differences in mean female gametophore weight between branching and non-branching shoots (SPSS release 10.0.7). A $R \times C$ test of independence was used to test for similarity of male age structure between lowland and mountains (Sokal and Rohlf 1995).

Results

Age at maturity

Most female shoots reached G-maturity during their second year in both mountain and lowland areas (Figure 3). Our observations suggest, however, that while archegonia were produced in the spring in the lowlands, their production was delayed until summer in the mountains.

In the lowlands, 95% of the second year female shoots were in the S-stage (Figure 3b). There were only four shoots with unfertilised archegonia that remained in the F-stage. As there were no third year or older females (Figure 3b), it seems that most or all female shoots in the lowlands had completed their entire life cycle in 2 years. In contrast, no second year female reached the S-stage in the mountains (Figure 3a). Nearly all mountain females (96%) produced spores for the first time when they were in their third year.

In both the mountains and lowlands, nearly all second year male shoots had produced antheridia. Only 5 out of 322 second year male shoots investigated in this study were immature. We cannot exclude the possibility, however, that some or all of these immature shoots were female.

Size at maturity

Mean female and male shoot sizes at G-maturity were in the same range for both areas (Table 2). Lowland females tended to be slightly larger than mountain females, but this was not statistically tested due to a limited number of lowland females in the F-stage (Table 2). The nested ANOVA showed no significant differences in female shoot size at S-maturity between the mountain and lowland areas ($p = 0.858$, Table 3). The differences among populations within areas were, however, highly significant ($p = 0.000$, Table 3). These differences can also be seen in Figure 4, which shows that most of the variation was among populations within areas. The nested ANOVA between patches within mountain population 2 and lowland population 5 showed no significant difference between populations, but a significant effect of patches (Table 3). The same results were found for the size of male shoots at G-maturity, with most of the variation expressed at the population and patch level (Table 3).

The logit regression analysis did not show a significant effect of size when testing for a threshold size for production of female sex organs (archegonia) in the mountains ($p = 0.248$).

The regression analysis of male shoot size showed a linear increase with age in both areas (Table 4). There was no reduction in growth rate after production of antheridia from second year to third year compared with the growth rate from first year to second year (Table 4). The male growth rate from first year to third year was, however, significantly higher in the mountains than in the lowland area (Table 4).

Female shoots in the mountain area did not show reduced growth after production of archegonia from the second year to third year compared with the growth rate from first year to second year (Table 4), but the growth rate was significantly

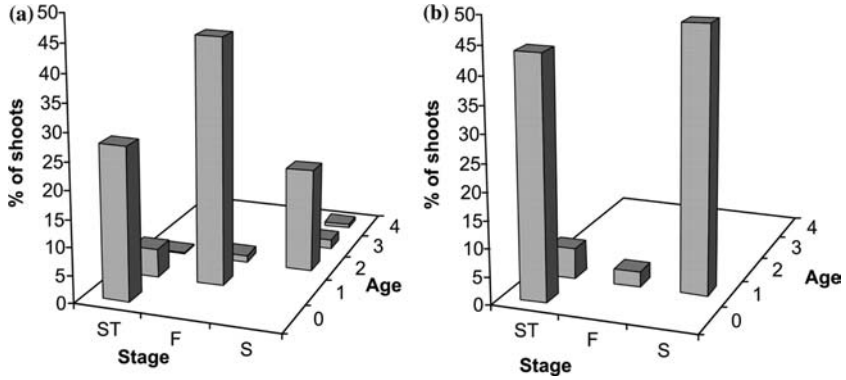

Figure 3. Percentage of female shoots distributed on age and stage classes, combined data for all (a) mountain populations and (b) lowland populations. Age 0 corresponds to first year, age 1 to second year and so on. For explanation of stage classes see text.

Table 2. Mean size (mg) at maturity for female and male shoots in the mountain and lowland areas.

	Size (mg ± sd)	
	Mountain	Lowland
Female (S-maturity)	1.30 ± 0.48 (n = 58)	1.50 ± 0.48 (n = 69)
Female (G-maturity)	0.86 ± 0.31 (n = 110)	1.06 ± 0.38 (n = 4)
Male (G-maturity)	0.91 ± 0.40 (n = 194)	0.97 ± 0.36 (n = 123)

Table 3. Effects of area (mountains versus lowlands) and population-nested-within-area on female and male shoot weight (mg) at S- and G-maturity, respectively.

Source	df	Female shoot weight		Male shoot weight	
		MS	P	MS	P
Area	1	0.005	0.858	0.025	0.875
Pop (area)	4	0.223	0.000	1.268	0.000
Pop	1	0.327	0.082	0.499	0.243
Patch (pop)	8	0.096	0.000	0.371	0.000

And effects of population (2 and 5) and patch nested-within-population on female and male shoot weight (mg) at S- and G-maturity, respectively. Both analysed by nested ANOVA. Shoot weight was *ln* transformed before the analyses.

higher for female shoots from the lowlands compared with the mountains from first year to second year (ST0 to F1/S1, Table 4). There was also a significant difference between female and male shoots in the lowlands from first year to second year, with females having a higher growth rate, but there was no significant difference in the mountains between females and males at this age interval (Table 4).

Production of branches

Females in the lowlands did not produce branches after S-maturity, while 41% did in the mountains. Mountain females with branches were significantly (p = 0.002) heavier (1.53 ± 0.58 mg) than those without branches (1.14 ± 0.31 mg).

Patch structure

The total numbers of female shoots from the 2 × 2 cm samples were 308 in the mountain area and 144 in the lowland area. Of these, 85 and 63, respectively, were in the first year (age class 0). The mean female density in the patches was 5.2 and 11.0 shoots/cm^2 in the lowland and mountain areas, respectively.

Female shoots were as old as in their fifth year. Second year shoots were, however, most frequent in both areas (Figure 3). No third-, fourth- or fifth-year shoots were found in the lowland area (Figure 3b).

In lowland patches females in the combined age and stage classes ST0 and S1 were most frequent in early September, but in the mountain area classes ST0, F1 and S2 dominated (Figure 3).

The total numbers of male shoots from the 2 × 2-cm samples were 398 in the mountains and 179 in the lowlands, of which 53 and 20, respectively, were in the first year. The mean male density within patches was 6.4 and 14.2 shoots/cm^2 in the lowlands and mountains, respectively.

Male shoots were found as old as in their fifth year in the mountains and fourth year in the lowlands. Age structure among males differed significantly between the mountain and the

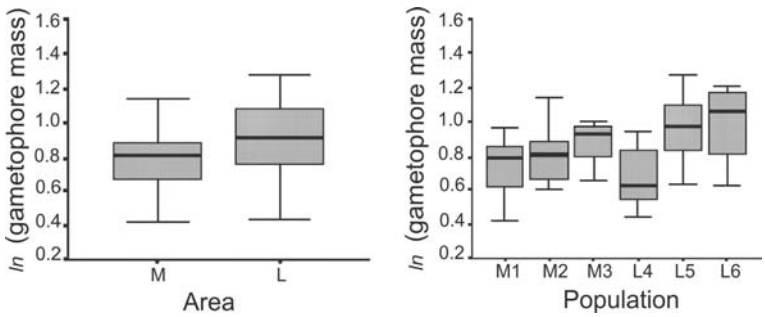

Figure 4. Boxplot showing the variation in female gametophore mass (*ln* mg) within the mountains (M) and lowlands (L) and for populations 1–6.

Table 4. Pairwise comparisons of growth rate among groups of shoots by testing if within-group linear regressions of size against time/age have homogeneous slopes.

Sex, area	Age interval (year)	*n*	*b* (slope)	SS_{reg}	SS_{res}	*p*-Value
Male, lowland	First–second	143	0.214***	0.786	4.877	$p > 0.75$
Male, lowland	Second–third	155	0.223***	1.262	4.856	
Male, mountain	First–second	247	0.281***	3.279	8.704	$p > 0.75$
Male, mountain	Second–third	300	0.275***	5.201	10.632	
Male, lowland	First–third	175	0.219***	2.457	5.604	$p < 0.05$
Male, mountain	First–third	353	0.278***	11.636	11.626	
Female, mountain	First–second	195	0.216***	2.228	3.982	$p > 0.75$
Female, mountain	Second–third	168	0.208***	1.648	4.796	
Female, mountain	First–second	195	0.216***	2.228	3.982	$p < 0.001$
Female, lowland	First–second	136	0.393***	5.212	5.719	
Female, lowland	First–second	136	0.393***	5.212	5.719	$p < 0.001$
Male, lowland	First–second	143	0.214***	0.786	4.877	
Female, mountain	First–second	195	0.216***	2.228	3.982	$p > 0.05$
Male, mountain	First–second	247	0.281***	3.279	8.704	

*** $p < 0.001$

lowland areas ($G = 28.447 > \chi^2_{0.05(4)} = 9.488$). A stepwise expansion of a two-way table showed that there was no difference in age structure between lowlands and mountains among first years (age 0) and second years (age 1, $p > 0.05$), but in the mountains there were more shoots than expected among third-, fourth- and fifth-years (age 2, 3 and 4, Figure 5).

Discussion

Differences in life-history traits are most obvious between mountain and lowland females, with lowland females growing faster, producing spores a year earlier, and not producing branches. These factors probably enhance the differences in patch structure between mountain and lowland areas. The difference in patch structure is not as clear for males, although there are more males in the three oldest mountain age classes compared with the lowland patches. These differences could be due to environmental effects or evolutionary processes. The current study does not allow us to discriminate between these two explanations. Hopefully this matter can be resolved by reciprocal transplant experiments and genetic studies currently in progress. The following discussion attempts to explain the observed patterns.

Females of the expanding species *P. dentatum* produce mature spores in their second year in recently colonised lowland habitat and in their third year in the original mountain habitat. This fits with the prediction that selection should reduce age at maturity in a growing population towards its physiological minimum (Cole 1954; Lewontin 1965). Accelerated S-maturity in the lowland area can be explained by an increased probability of juveniles surviving to maturity (Bell 1980) or by a higher fitness in lowland ancestors because they produce spores earlier and start reproducing sooner (Cole 1954; Lewontin 1965). The timing of spore dispersal is the same in both areas, occurring during late autumn and early spring, depending on weather conditions. The exact timing of spore germination is not known, but a field sowing

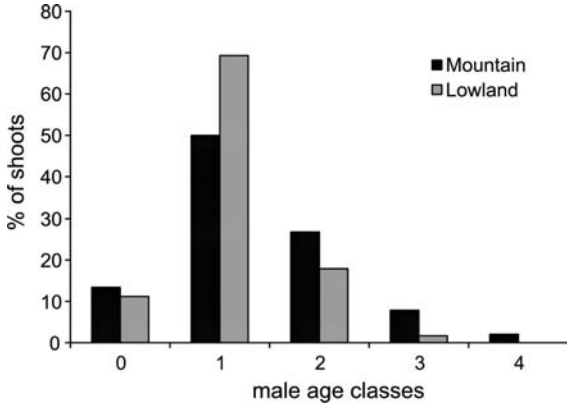

Figure 5. Percentage of male shoots distributed among age classes in the mountain and lowland areas. Age 0 corresponds to first year, age 1 to second year and so on.

experiment in the lowlands (Hassel and Söderström 1999) showed that it probably occurs in spring or early summer, because immature shoots are found in the autumn. At the end of the following growing season the lowland shoots develop mature spores ready for dispersal, whereas female shoots in the mountains are still in the F-stage. We cannot rule out the possibility that environmental constraints in the mountains, such as a shorter growth period after fertilisation or a colder climate, contribute to delays in gametangial development in mountain females as compared to lowland females. Thus the earlier S-maturity in the lowland area could be explained by faster growth under more favourable environmental conditions. Hedderson (1992) found delayed maturity (defined as formation of a sporophyte and production of antheridia) in both females and males in populations of *Polytrichum commune* Hedw. and *Polytrichum juniperinum* Hedw. from an upland site compared to populations from two lowland sites. Hedderson (1992) explained this as a result of differences in selective pressures between the sites, with the upland site more stable and the lowland site in an early stage of succession. In the lowlands, we found that sex organs are produced in spring (Hassel 2000), while in the mountains they are produced during the summer, indicating that both sexes are producing sex organs as early as possible. So the relatively small difference in time of archegonium production translates into a 1-year difference in time of production of mature spores. A critical stage in the development of the sporophyte is spore formation, which coincides with the swelling of the capsule and which requires translocation of resources from the gametophore to the sporophyte (Proctor 1977). Hancock and Brassard (1974) found high mortality of immature sporophytes during winter in the moss *Buxbaumia aphylla* Hedw. in Newfoundland with spore formation delayed until after the winter. This mechanism could be a way of minimising resource loss, and could apply to *P. dentatum* in the mountains.

Another interesting aspect of female age and size at maturity is the production of branches only in the mountains. A possible explanation for this may be that the plants are using different strategies in resource allocation to sexual and asexual reproduction, with lowland plants (genets) allocating most of their resources to sexual reproduction and mountain plants dividing their resources between sexual and asexual reproduction. The production of branches makes the mountain female shoots potentially 'iteroparous'. Iteroparity is favoured in situations where mortality at the immature stage exceeds adult mortality, whereas semelparity is favoured when adult mortality exceeds mortality at the immature stage (Charnov and Schaffer 1973). Establishment rates from spores can be used as a rough estimate of immature mortality, since this seems to be a critical stage in the life cycle of many bryophytes (Longton 1997). Using sowing experiments, Hassel and Söderström (1999, 2003) showed that establishment from *P. dentatum* spores was common in the lowlands but very rare in the mountains. This suggests that the selective pressure on timing of first reproduction is different in the two areas. Delayed reproduction is a way to compensate for high mortality at the immature stage, if mortality decreases with age (Stearns 1992). Other factors that may amplify differences between lowland and mountain populations are that the lowland populations occupy habitats in early successional stages and newly available habitats are not likely to re-occur at the same site within the lifetime of the population. In contrast, mountain populations experience a continuous series of small disturbances as a result of frost and wind exposure and thus over time have more-or-less continuous access to new patches in an area.

Both sexes showed large variations in size at maturity between patches within populations. This variation could be caused by environmental heterogeneity among the patches, either through genetic differentiation with selection as the main evolutionary force (e.g., Såstad et al. 1999), or through environmental effects on the phenotype (phenotypic plasticity).

This large variation in gametophore size is also the main reason we did not observe a threshold size for the production of archegonia in mountain females. This result agrees with Convey and Lewis Smith (1993, Polytrichaceae) but not with Rydgren et al. (1998, *Hylocomium splendens* (Hedw.) Schimp.) and Stark et al. (2001, *Syntrichia caninervis* Mitt.). The dependence on a certain minimum size for sexual reproduction in phanerogams is well established (Samson and Werk 1986; Shipley and Dion 1992; Schmid et al. 1995), although exceptions exist (e.g., Rees and Crawley 1989).

The recent expansion of *P. dentatum* into the lowlands seems to be associated with changes in important life-history parameters. The main differences are between female shoots from the two areas. Females in the lowlands exhibit 'semelparous' behaviour, while 41% of the mountain females show potential 'iteroparity' with the production of branches. This, together with high rates of establishment from diaspores in the lowlands, suggests that lowland phenotypes of *P. dentatum* are more 'invasive' than mountain phenotypes. Whether these differences in life-history parameters are due to evolutionary processes or environmental effects is uncertain, and should be investigated further by transplant experiments.

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References

Bell G. 1980. The cost of reproduction and their consequences. Am. Nat. 116: 45–76.

Bullock S.H. and Bawa K.S. 1981. Sexual dimorphism and the annual flowering pattern in *Jacartia dolichaula* (D. Smith) Woodson (Caricaceae) in a Costa Rican rain forest. Ecology 62: 1494–1504.

Charnov E.L. and Schaffer W.M. 1973. Life history consequences of natural selection: Cole's result revisited. Am. Nat. 107: 791–793.

Cole L.C. 1954. The population consequences of life history phenomena. Q. Rev. Biol. 29: 103–137.

Convey P. and Lewis Smith R.I. 1993. Investment in sexual reproduction by Antarctic mosses. Oikos 68: 293–302.

Fagerstén R. 1977. New records of *Pogonatum dentatum* (Musci, Polytrichaceae) for Finland. Memoranda Societatis Fauna et Flora Fennicae 55: 73–76.

Hancock J.A. and Brassard G.R. 1974. Phenology, sporophyte production, and life history of *Buxbaumia aphylla* in Newfoundland, Canada. Bryologist 77: 501–513.

Hassel K. 2000. Bryophyte profiles 2. *Pogonatum dentatum* (Brid.) Brid. (Bryopsida: Polytrichaceae). J. Bryol. 22: 55–60.

Hassel K. and Söderström L. 1998. The presence of *Pogonatum dentatum* (Brid.) Brid. in roadside diaspore banks in Sweden. Lindbergia 23: 113–118.

Hassel K. and Söderström L. 1999. Spore germination in the laboratory and spore establishment in the field in *Pogonatum dentatum* (Brid.) Brid. Lindbergia 24: 3–10.

Hassel K. and Söderström L. 2003. Life history variation of *Pogonatum dentatum* (Brid.) Brid. in contrasting habitats. J. Hattori Bot. Lab. 93: 215–222.

Hedderson T.A.J. 1992. Studies on life history evolution in mosses; constraints, tradeoffs and local adaptation. Ph.D. Dissertation, University of Reading.

Hedenäs L. 1983. *Pogonatum dentatum* – en norrlandsmossa på väg söderut. Svensk Botanisk Tidskrift 77: 147–150.

Hedenäs L., Herben T., Rydin H. and Söderström L. 1989. Ecology of the invading moss species *Orthodontium lineare* in Sweden: spatial distribution and population structure. Holarctic Ecol. 12: 163–172.

Herben T. 1994. The role of reproduction for persistence of bryophyte populations in transient and stable habitats. J. Hattori Bot. Lab. 76: 115–126.

Herben T., Rydin H. and Söderström L. 1991. Spore establishment probability and the persistence of the fugitive invading moss, *Orthodontium lineare*: a spatial simulation model. Oikos 60: 215–221.

Herben T. and Söderström L. 1992. Which habitat parameters are most important for the persistence of a bryophyte species on patchy, temporary substrates? Biol. Conserv. 59: 121–126.

Jongman R.H.G., ter Braak C.J.F. and van Tongeren O.F.R. 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge.

Lewontin R.C. 1965. Selection for colonizing ability. In: Baker H.G. and Stebbins G.L. (eds), The Genetics of Colonizing Species. Academic Press, New York.

Longton R.E. 1997. Reproductive biology and life-history strategies. Adv. Bryol. 6: 65–101.

Longton R.E. and Greene S.W. 1967. The growth and reproduction of *Polytrichum alpestre* Hoppe on South Georgia. Philos. Trans. R. Soc. Lond. Ser. B 252: 295–322.

Meagher T.R. and Antonovics J. 1982a. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: life history studies. Ecology 63: 1690–1700.

Meagher T.R. and Antonovics J. 1982b. Life history variation in dioecious plant populations: a case study of *Chamaelirium luteum*. In: Dingle H. and Hegmann J.P. (eds), Evolution and Genetics of Life Histories. Springer-Verlag, New York, pp. 139–154.

Melampy M.N. and Howe H.F. 1977. Sex ratio in the tropical tree *Triplaris americana* (Polygonaceae). Evolution 31: 867–872.

National Atlas of Sweden. 1995. Climate, Lakes and Rivers. Sveriges Nationalatlas Förlag, Stockholm.

Proctor M.C.F. 1977. Evidence on the carbon nutrition of moss sporophytes from $^{14}CO_2$ uptake and the subsequent movement of labelled assimilate. J. Bryol. 9: 375–386.

Rees M. and Crawley M.J. 1989. Growth, reproduction and population dynamics. Funct. Ecol. 3: 645–653.

Roy J. 1990. In search of the characteristics of plant invaders. In: di Castri F., Hansen A.J. and Debussche M. (eds), Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers, Dordrecht, pp. 335–352.

Rydgren K., Økland R.H. and Økland T. 1998. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. 4. Effects of experimental fine-scale disturbance. Oikos 82: 5–19.

Sakai A.K., Allendorf F.W., Holt J.S., Lodge D.M., Molofsky J., With K.A., Baughman S., Cabin R.J., Cohen J.E., Ellstrand N.C., McCauley D.E., O'Neil P., Parker I.M., Thompson J.N. and Weller S.G. 2001. The population biology of invasive species. Ann. Rev. Ecol. Syst. 32: 305–332.

Samson D.A. and Werk K.S. 1986. Size-dependent effects in the analysis of reproductive effort in plants. Am. Nat. 127: 667–680.

Såstad S.M., Pedersen B. and Digre K. 1999. Habitat-specific genetic effects on growth rate and morphology across pH and water-level gradients within a population of the moss *Sphagnum angustifolium* (Sphagnaceae). Am. J. Bot. 86: 1687–1698.

Schmid B., Bazzaz F.A. and Weiner J. 1995. Size dependence of sexual reproduction and of clonal growth in 2 perennial plants. Can. J. Bot. 73: 1831–1837.

Schofield W.B. 1985. Introduction to Bryology. Macmillan Publishing Company, New York.

Shipley B. and Dion J. 1992. The allometry of seed production in herbaceous angiosperms. Am. Nat. 139: 467–483.

Söderström L. 1992. Invasion and range expansions and contractions of bryophytes. In: Bates J.W. and Farmer A.M. (eds), Bryophytes and Lichens in a Changing Environment. Oxford, Clarendon Press, pp. 130–157.

Sokal R.R. and Rohlf F.J. 1995. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Company, New York.

Stark L., McLetchie N. and Mishler B. 2001. Sex expression and sex dimorphism in sporophytic populations of the desert moss *Syntrichia caninervis*. Plant Ecol. 157: 183–196.

Stark L.R., Mishler B.D. and McLetchie D.N. 2000. The cost of realized sexual reproduction: assessing patterns of reproductive allocation and sporophyte abortion in a desert moss. Am. J. Bot. 87: 1599–1608.

Stearns S.C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Stieperaere H. 1994. *Lophocolea semiteres* (Lehm.) Mitt. in Belgium and The Netherlands, another antipodal bryophyte spreading on the European continent. Lindbergia 19: 29–36.

Stieperaere H. and Jacques E. 1995. The spread of *Orthodontium lineare* and *Campylopus introflexus* in Belgium. Belg. J. Bot. 128: 117–123.

Underwood A.J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge.

van der Meulen F., van der Hagen H. and Kruijsen B. 1987. *Campylopus introflexus*. Invasion of a moss in Dutch coastal dunes. Proc. Koninklijke Nederlandse Akad. Wetenschappen Ser. C-Biol. Med. Sci. 90: 73–80.

Watson M.A. 1975. Annual periodicity of incremental growth in the moss *Polytrichum commune*. Bryologist 78: 414–422.

Watson M.A. 1979. Age structure and mortality within a group of closely related mosses. Ecology 60: 988–997.

Wiggelsworth G. 1947. Reproduction in *Polytrichum commune* L. and the significance of the rhizoid system. Trans. Br. Bryol. Soc. 1: 4–13.

Wyatt R. and Derda G.S. 1997. Population biology of the Polytrichaceae. Adv. Bryol. 6: 265–296.