

## Episodic but ample sporophyte production in the moss *Drepanocladus turgescens* (Bryophyta: Amblystegiaceae) in SE Sweden

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**Abstract:** In the Baltic area, the long-lived dioicous wetland moss *Drepanocladus turgescens* (T.Jensen) Broth. produces sporophytes rarely and at irregular intervals. Based on surveys of sporophyte occurrences at 13 sites in two regions in northern Gotland (Sweden) during three to five years, we ask: (1) Is sporophyte formation associated with precipitation and a precipitation index that considers the dry periods during July-August of the preceding year, when gametangia are formed and fertilization occurs? (2) Does the estimated spore output suffice for the species' long-term persistence of the (Northern) European population species? In one of the study regions, where *D. turgescens* occurs in depressions, sporophyte formation was associated with the two precipitation parameters. In the other study region, with relatively higher precipitation and exposed occurrences on a slightly sloping bedrock with very little accumulated soil, no such association existed. We suggest that this lack of weather effects results from that the exposed rock habitat requires longer continuously wet periods than the depression habitat to allow for gametangia initiation and development, and fertilisation. Average spore production for six spore capsules, from three Gotland localities was 181,000. Based on the sporophyte counts during the survey years, we estimated the total reproductive output as 411.5 million spores in 2013, and 42.5 million in 2015, in the two respective study regions. Taken together with data on haplotype patterns and considering observations on recent colonisations, we argue that such a relatively low and episodic regional spore production is sufficient to maintain global populations of long-lived species, even if these occur in specialized and geographically restricted habitats.

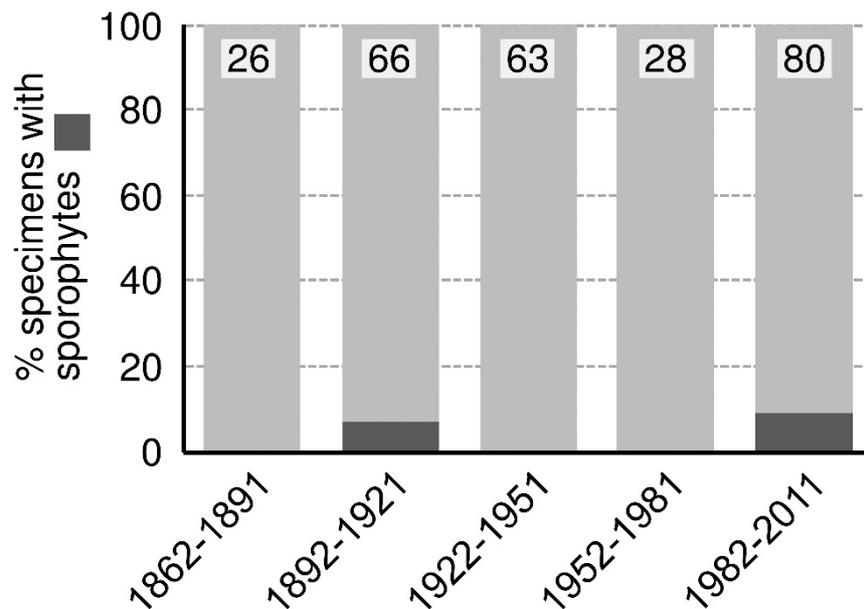
**Key words:** Episodic spore production, Habitat, Precipitation, Spore number

### Introduction

The frequency of sporophyte production in mosses varies widely among species and with the species' life histories (During 2007, Longton 1992). For example, rarity of sporophytes is more prevalent in dioicous than in monoicous species (Gammel 1950, Heegaard 2001). In a few species, sporophytes are virtually unknown, and otherwise the frequency varies from rare to common (Longton 1992). Within species, sporophyte frequency may vary among different regions or ecosystems, or temporally among years and seasons (e.g., Maciel-Silva & Pereira de Oliveira 2016, Maciel-Silva & Válio 2011, Sundberg 2002). This variation relates to weather or other environmental conditions in a number of studied species, and the environmental effects may vary among different phases of the species' life cycle (Longton 1990, Stark 2001, 2005, Sundberg 2002).

Mature sporophytes produce and release spores, which in mosses are usually smaller than 20 µm and are able to disperse very far (Wilkinson *et al.* 2012). Dispersal affects not only biogeographical patterns, range expansions and (meta)population dynamics, but also processes at the gene and individual level (Clobert *et al.* 2012). Gene flow, genetic variability and population differentiation increase the resilience of species when environments change (Frankham *et al.* 2002, Williams *et al.* 2008). Dispersal capacities are thus important for addressing many topics of moss biology, including pressing conservation issues, such as predicting a species' response to climate and land-use changes (Corlett & Westcott 2013).

*Drepanocladus turgescens* (T.Jensen) Broth. is a dioicous wetland moss that is rarely reported with sporophytes (Abramova *et al.* 1961, Hedenäs 2002, Miller 1980), which is substantiated by herbarium records (Fig. 1). In Europe, specimens with sporophytes were collected at a few places during the first 25 years of the 20th century, in Northern Swedish Lappland (1 locality), on the Baltic Sea island Öland in Sweden (4), Väike-Pakri in Estonia (1), and in the surroundings of Vienna in Austria (2) (Hedenäs 2002). At the end of the 20th century, sporophytes were again encountered a few times (LH: Saaremaa, Estonia, 1989; northern Gotland, Sweden, 1996).



**Fig 1:** Sporophyte occurrence in 266 *Drepanocladus turgescens* specimens from Sweden collected between 1836 and 2011 in the holdings of the bryophyte herbarium at S, as to 30-yr periods. The figures in the upper portions of the bars are numbers of examined specimens per period.

During fieldwork for other purposes in 2011 (Hedenäs & Bisang 2015), we discovered numerous occurrences of *D. turgescens* with abundant sporophyte production on both the Swedish Baltic Sea islands Öland and Gotland. During subsequent years, we observed additional sporophyte occurrences on Gotland. This resulted in a set of twelve sporophyte-bearing sites of *D. turgescens* in two regions of Gotland, which we repeatedly re-visited three to four times between 2013 and 2018. In this paper, we explore a potential effect of weather conditions on sporophyte formation. Our first exploratory analyses, and that we did not encounter dried-out or aborted sporophytes in the spring, suggested that conditions affecting the fertilization process rather than conditions during the period of sporophyte development are critical. Hence, we here focus on a possible effect of weather conditions on water availability prior to (gametangia maturation) and during the fertilization phase. Further, we quantify the spore output during years of sporophyte production and discuss whether this could potentially be sufficient to maintain the species' current distribution in Europe.

## Material and methods

### *Study species*

*Drepanocladus turgescens* (Amblystegiaceae) forms large, a few cm up to 20 cm long, slightly and irregularly branched, turgid shoots. The species classifies as a 'perennial stayer' in the life strategy system of (During 1979, 1992). It is dioicous, has a tall seta, a cylindrical, curved, orthogonal spore capsule, and the spores are 10-17 µm

in diameter (Hedenäs 1992). Sporophytes are generally absent or rare, but during 2011–2015 we observed sporophytes at one site on the Finnish island Signilskär (Åland archipelago), and more than twenty on the two main Swedish islands in the Baltic Sea, Öland (8) and Gotland (13). In Europe, *D. turgescens* is most common in the north, in Svalbard, the Scandinavian mountain range, and in the limestone islands around the Baltic Sea. In addition, it occurs at a few isolated localities in the lowlands of Scandinavia. In Central Europe, including the Alps, its population is fragmented and declining (Hedenäs and Bisang, in press).

In lowland localities of Northern Europe, *D. turgescens* typically grows on strongly calcareous ground, in depressions that dry out periodically during summer. In mountains and in the far north it occurs also in less strongly calcareous habitats (Birks & Dransfield 1970, Hedenäs 2002), and in depressions that dry out for shorter periods than in the south. In addition, the species is relatively frequent in habitats with trickling water or along brooklets. In Scandinavia, *D. turgescens* only rarely grows in permanently wet mires.

### *Number of sporophytes per studied patch*

We examined in total 13 sites with sporophytes, from two regions in northern Gotland. Nine sites were located in the surroundings of the meteorological station Ar and four in the surroundings of the meteorological station Hejnum (Table 1). In these, we observed *D. turgescens* sporophytes in 2011, 2013, or 2015. We repeatedly visited all but one site between three to five times, in late spring to early summer (between 6 May and 12 June). We surveyed all Hejnum sites consecutively from 2015 to 2018, five Ar sites in 2013 and 2016–2018, and three Ar sites in 2013 and 2017–2018. At each site, we surveyed one patch. We defined a patch as a continuous occurrence of *D. turgescens* in a periodically wet depression, with a distance between neighbouring ramets of up to a maximum of 1 m. We estimated the patch size to the nearest 1 m<sup>2</sup>, or to the nearest 0.25 m<sup>2</sup> for patches smaller than 1 m<sup>2</sup>; 0.25 m<sup>2</sup> indicates a patch size of up to this area. We estimated sporophyte numbers in each patch in 2013 and 2015 by counting capsules. In patches with more than ca. 100 capsules, we counted sporophytes in at least two plots of 10 x 10 cm<sup>2</sup>, using a frame with a cm-grid, within each of the distinguishable capsule-bearing sub-patch areas. We then estimated the total sporophyte number in the patch based on these counts and the area of the sub-patches in relation to the total patch size.

**Tab 1:** Study sites on northern Gotland, Sweden: **ACRONYM:** Site, Lat., Long. (S reg. no. for collected vouchers).

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#### *Closest to Ar meteorological station:*

**BUN:** Bunge, near limestone kiln W of Bunn, 57.8527°N, 18.9744°E; **HAU1:** Fleringe, ca. 400 m SW of Hau farm, 57.8922°N, 18.9777°E (B184253, B196890, B237271); **HAU2:** Fleringe, ca. 700 m SW of Hau farm, 57.8881°N, 18.9742°E (B184254, B196892, B23763); **KYR1:** Fleringe, W end of Kyrkgatmyr, S side, 57.8890°N, 18.9581°E (B196895, B237272); **KYR2:** Fleringe, middle of Kyrkgatmyr, S side, 57.8892°N, 18.9589°E (B196894, B236513); **LAR:** Lärbro, ca. 800 m SW of Stora Ire, 57.7782°N, 18.8589°E (B196928); **STR:** Bunge, ca. 500 m E of Strå, 57.8791°N, 19.0071°E (B184252, B196888, B237635); **TVA1:** Fleringe, ca. 1.6 km WSW of Tväringsmyr, 57.8702°N, 18.9199°E (B196905); **TVA2:** Fleringe, ca. 1.6 km WSW of Tväringsmyr, 57.8702°N, 18.9186°E (B196906).

#### *Closest to Hejnum meteorological station:*

**HEJ1:** Hejnum, Hejnum hällar, 1.5 km NE of Graute, 57.6778°N, 18.6596°E (B222088, B238801); **HEJ2:** Hejnum, Hejnum hällar, 1.5 km NE of Graute, 57.6782°N, 18.6592°E (B222089, B238802); **HEJ3:** Hejnum, Hejnum hällar, 1.5 km NE of Graute, 57.6787°N, 18.6617°E (B222091, B238803); **HEJ4:** Hejnum, Hejnum hällar, 1.5 km NE of Graute, 57.6782°N, 18.6641°E (B222092, B238804).

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### *Relationship between sporophyte production and habitat wetness*

In *D. turgescens* sex organs mature, and fertilization takes place during late summer, from the second half of August (Arnell 1875), and embryos develop into sporophytes in the following late spring to early summer (own observations). Based on preliminary exploratory analyses and the lack of observed dried-out capsules in late spring, we argue that conditions affecting the initiation and development of sexual organs and the fertilization process are likely to be critical for sporophyte occurrence. We therefore investigated the effect of the precipitation and its temporal distribution during July–August in the year before the sporophyte observations.

We downloaded precipitation data for the two meteorological stations Ar (57.9168°N, 18.9569°E) and Hejnum (57.6954°N, 18.6377°E) from the Swedish Meteorological and Hydrological Institute (SMHI; <https://opendata-download-metobs.smhi.se/explore/?parameter=3>; accessed 1 April 2018). These stations are located close to the two respective study regions with occurrences of *D. turgescens* sporophytes. For each year prior to the field observations and for the two meteorological stations separately, we computed the total precipitation amount for July and August. We also calculated a Precipitation Index (PI) that takes into account the number of days without precipitation. Successive dry days increase the likelihood that patches dry out (Stark 2005), which impedes successful fertilization. PI is the total amount of precipitation during July and August

(P, mm) divided with the number of days during July and August with at least 1 mm precipitation (A) minus the number of days with <1 mm precipitation (B):  $PI = P / (A - B)$ . (A - B) was negative for all study years, indicating fewer rainy than dry days during this period. A more strongly negative PI for a certain year indicates more favourable moisture conditions, (i. e., relatively few dry days that counteract the moistening effect of precipitation).

### *Spore counts and spore output estimates*

We estimated spore numbers per capsule in six capsules, two from each of three specimens collected in the study regions on Gotland (Bunge, E of Strå, 57.8791° N, 19.0071° E, 2011; S, reg. no. B184252; Fleringe, Kyrkgatmyr, 57.8892° N, 18.9589° E, 2013; S, reg. no. B196894; Hejnum, Hejnum hållar, 57.6782° N, 18.6592° E, 2015; S, reg. no. B222089). We selected ripe, but undehisced capsules, and made all spore counts on 30 October 2018.

Under a dissecting scope, we opened each capsule separately in 5 ml deionized water with a minute amount of detergent to facilitate spore clump disintegration. We first shook the water-spore-capsule wall mixture for 30 sek on a Vortex Genie® 2 (Scientific Industries) at a shaking speed of 3.5. We then examined the mixture under the dissecting scope, picked out capsule wall pieces clean of spores, and ‘crushed’ remaining visible spore clumps with a fine pair of forceps. We shook the mixture for another 30 + 60 sek on the Vortex to disperse the spores thoroughly in the water. Immediately thereafter, we took a 1 ml subsample and placed this in a Gridded Sedgewick Rafter (Wildco®, Model #1801-G20), with a 1 ml cell volume. The counting chamber has a 20 x 50 square grid, and thus each grid cell has a volume of 1 µl. We counted spore numbers in ten randomly selected (www.random.org; accessed 29 October 2018) grid cells, and multiplied the mean spore number per grid cell with 5000 to estimate the total spore number per capsule.

## **Results**

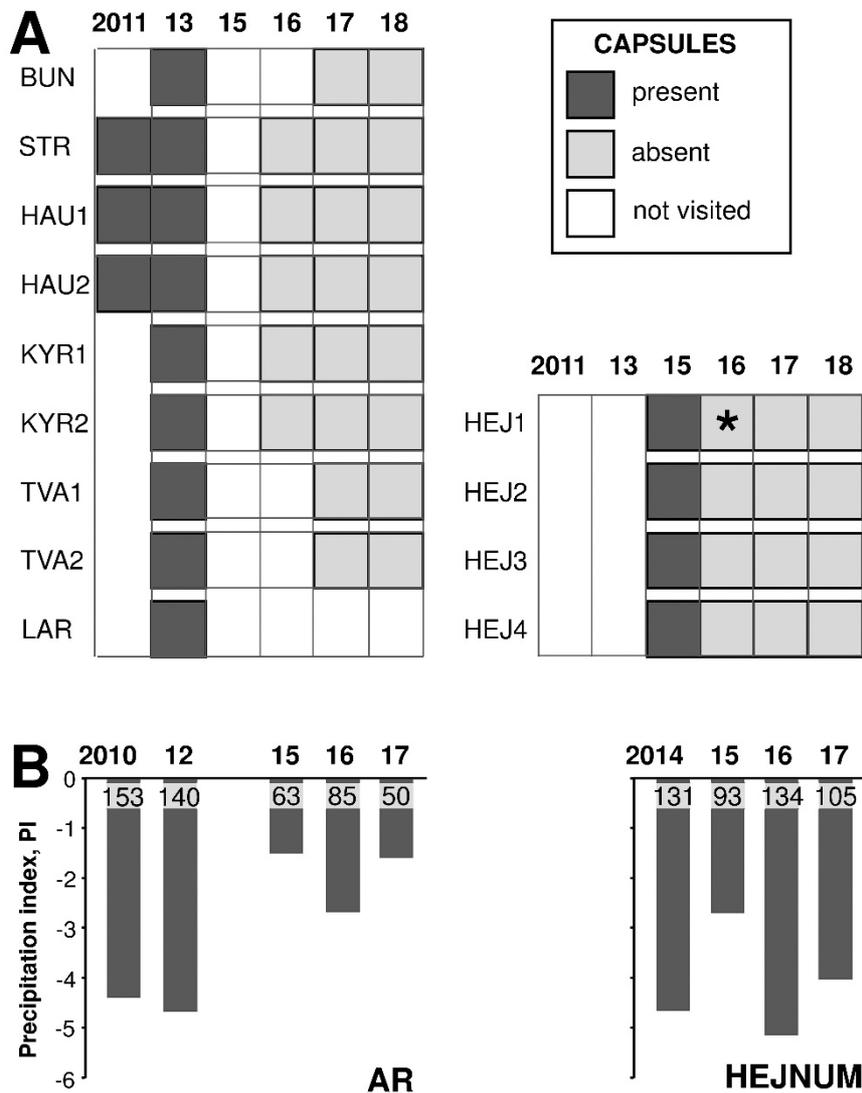
### *Number of sporophytes produced*

Out of 13 patches with observed sporophyte production during at least one year (Fig. 2, Table 1), we monitored 12 during 3-4 years between 2013 and 2018. In three of these sites, we had encountered sporophytes already in 2011, but we did not perform any counts in that year.

During 2013, the estimated sporophyte production in the studied sites of the Ar region was 2,274 (Table 2). It varied from 11 to 1,898 sporophytes per patch, with 83% of the capsules in one single patch (STR, Table 1). Estimated sporophyte density ranged from 0.7 to 38 sporophytes per m<sup>2</sup> patch area. The estimated sporophyte production in the Hejnum region in 2015 was 235 sporophytes (Table 2), varying from 23 to 100 sporophytes per patch. Sporophyte density was between 11 and 320 sporophytes per m<sup>2</sup>. We found the highest density in a small patch of 0.25 m<sup>2</sup>.

**Tab 2:** Observations of patch size, *Drepanocladus turgescens* cover, and total numbers of sporophytes at *D. turgescens* patches in 2013 or 2015; sporophyte numbers based on field counts (see Material and Methods). Site acronyms are explained in Table 1.

Site acronym	Observation date	Patch size, m <sup>2</sup>	<i>D. turgescens</i> cover, %	Total no. of sporophytes
<b>STR</b>	11 May 2013	50	20	1898
<b>HAU1</b>	11 May 2013	14	20	22
<b>HAU2</b>	11 May 2013	30	10	84
<b>KYR1</b>	11 May 2013	40	15	91
<b>KYR2</b>	12 May 2013	78	10	74
<b>BUN</b>	12 May 2013	22	5	11
<b>TVA1</b>	12 May 2013	12	10	21
<b>TVA2</b>	12 May 2013	142	10	62
<b>LAR</b>	13 May 2013	16	10	11
<b>HEJ1</b>	16 May 2015	3	70	32
<b>HEJ2</b>	16 May 2015	0.25	70	23
<b>HEJ3</b>	16 May 2015	1	70	100
<b>HEJ4</b>	16 May 2015	0.25	70	80



**Fig 2:** (A) Observations of *Drepanocladus turgescens* sporophytes at 13 sites on northern Gotland between 2011 and 2018. Dark grey, sporophytes present; light grey, sporophytes absent; white, site not surveyed. (B) Precipitation index (PI) and total precipitation in July and August (mm, base of bars) in the years preceding the survey years. Acronyms for the sites are explained in Table 1.

### *Sporophyte production and habitat wetness*

Sporophyte occurrence per patch and year is depicted in Fig. 2A. Figure 2B displays the PI and total precipitation (mm) for July plus August, for the years prior to the sporophyte survey. Total precipitation was considerably higher in Hejnum than in Ar from 2015 to 2017 (147 to 210%). PI and precipitation amount co-varied with the presence of sporophytes in the following year in Ar, but not in Hejnum.

### *Number of spores produced*

Spore number per studied spore capsule varied between 116,500-348,000, with a mean of 181,000 spores per capsule (Appendix 1). Based on the sporophyte counts in 2013 from the Ar region and 2015 from the Hejnum region, this results in an annual total reproductive output in northern Gotland of 411.5 and 42.5 million spores, respectively.

## Discussion

We noted sporadic but partly extensive sporophyte formation in the wetland moss *D. turgescens* that was regionally associated with moisture conditions during the summer months preceding the capsule observations. Reproductive output in terms of spore numbers was considerable during years with sporophyte production.

### *Sporophyte production and habitat wetness*

Gametangia formation and fertilisation in bryophytes were associated with rainfall or patch hydration in several studies from different climatic areas (Maciel-Silva & Pereira de Oliveira 2016, Maciel-Silva & Valio 2011, Pereira *et al.* 2016, Stark 2005, Sundberg 2002). For *D. turgescens*, we found that sporophyte occurrence was related to wetness during the period of gametangia formation and fertilization in the Ar area. This held true for both wetness measures, i.e. the total precipitation and the precipitation index (PI) for July and August during the year prior to sporophyte maturation (Fig. 2). Beyond summer rainfall amount, PI takes also into account the relative numbers of days with and without precipitation. Consecutive dry days will lead to patch dehydration (Stark 2005), which may result in drought stress during gametangia formation, or may inhibit spermatozoid movement. Although moss antheridia, sperms and embryonic sporophytes have been shown in laboratory experiments to be tolerant to desiccation under certain conditions of dehydration (Döbbeler 2017, Shortlidge *et al.* 2012, Stark & Brinda 2015), it is expected that extended periods of substrate drought negatively impact the development of gametangia, sporophytes, as well as sperm motility.

In the Hejnum region, sporophyte occurrence was unrelated to precipitation data in the previous year (Fig. 2). The *D. turgescens* sites' topography and habitat differ between the Ar and Hejnum regions, which may explain this discrepancy. Sundberg (2002) showed that *Sphagnum* reproduction in different habitats may respond differently to similar weather conditions. The precipitation in Hejnum is 1.5-2 times higher than in Ar. Intuitively we would therefore expect sporophyte production during some years when patches in the Ar area are too dry. However, the patches in Hejnum occur on gently sloping, exposed rock (Fig. 3A), whereas those in Ar are either located in periodically wet depressions (Fig. 3B) or bordering *Cladium* fens, which in turn occupy very large depressions that stay wet or moist during long periods (Fig. 3C). At the Hejnum sites, water likely seeps over the rocks during rain showers and accumulates briefly in very shallow depressions or disappears into narrow vegetation strips along fissures. At the AR sites, on the other hand, water accumulates from rain falling directly into the depressions inhabited by *D. turgescens* or water moves into the depressions from the immediate surroundings. We suggest that the Hejnum sites, on exposed rock with at most very little or no soil, are more sensitive to dry spells than the Ar sites, where water evaporates more slowly from the depressions after rainfall. To explore this possibility further, detailed monitoring of patch moisture with data loggers during the period critical for gametangia formation and fertilization is required.

Sporophytes number per patch varied between 11 and 100, except for a single patch with almost 1,900 capsules. The predominance of patches with relatively few sporophytes agrees with our observations from Öland, Åland, and Estonia. The outstanding patch at STR in the Ar region was situated at the margin of a *Cladium* fen (Fig. 3C). However, similarly sized patches at KYR1 and KYR2 also bordered a *Cladium* fen, so fen proximity cannot be the only explanation for the high sporophyte number at this site.

Weather conditions can influence different stages of bryophyte reproduction, possibly depending on the habitat and involving different mechanisms (Sundberg 2002). Both extended droughts and heavy rainfalls may cause widespread sporophyte abortion during some years, which severely reduces the number of mature sporophytes (Stark 2001). Fertilization occurs during late summer in *D. turgescens*. With one exception (Fig. 2), we never observed aborted

sporophytes from the previous year during 2016 to 2018. We could have missed abortions during the embryonic stage of the sporophyte (Stark 2002). Such abortions would also have resulted from unsuitable conditions around the time of fertilization, which was the period we scored for effects on sporophyte formation. Later sporophyte abortion would be expected if weather parameters from autumn to the following spring, rather than during late summer, would be critical in explaining mature sporophyte presence.



**Fig 3:** *Drepanocladus turgescens* habitats with found sporophytes from the two study regions Hejnum and Ar on northern Gotland. (A) Gently sloping rock with very little soil at the Hejnum site HEJ3. (B) Small depression at the Ar site HAU1. (C) *Cladium* fen margin at the AR site STR. Site abbreviations as in Table 1. Photos by L. Hedenäs (A, B) and I. Bisang (C).

Finally, other factors than the wetness *per se* may be responsible for the differences in sporophyte formation between the Hejnum and Ar regions. Temperature, light intensity, and photoperiod have been shown to influence sex organ initiation (Chopra & Bhatla 1983, Hohe *et al.* 2002), and gametophyte size or spatial distribution of sex organ may affect sporophyte production (Rydgren & Økland 2002). Such factors and their role in realized sexual reproduction in *D. turgescens* deserve further attention.

#### *Significance of spore output*

The estimated average of 181,000 spores per *D. turgescens* capsule compares to numbers per capsule in other ground-living pleurocarpous mosses, such as *Brachythecium rutabulum* (Hedw.) Schimp. and *Pleurozium schreberi* (Brid.) Mitt. (Longton 1997). The wide variation in spore numbers per capsule, 116,500-348,000, is also consistent with finds in other studies, where the variation has been associated with capsule size variation (Sundberg & Rydin 1998).

During successful years of realised sexual reproduction, *D. turgescens* produces at most 40-400 million spores from the study patches on northern Gotland. These are maximum values for these patches, since all observed sporophytes are unlikely to mature. During our survey periods in the spring, some of the counted capsules had not yet reached maturity. Nevertheless, we have reasons to believe that the total spore output in the Baltic Sea area during the survey years was higher than these figures. First, our study sites are obviously a sample of the total sporophytic population in the area. We did not re-visit all Gotland sites with known sporophyte occurrences, and we could not systematically screen all additional *D. turgescens* localities on Gotland and other Baltic areas with potential sporophyte production. Secondly, we encountered sporophytes at other places around the Baltic Sea during the survey years, in 2011 and 2015 at several sites on Öland and in 2013 at one on Signilskär (Åland archipelago). At the latter site, we also noticed sporophytes in the related *Drepanocladus trifarius* (F.Weber & D.Mohr) Broth. in a habitat similar to that of *D. turgescens*. *Drepanocladus trifarius* is another wetland moss that rarely produces capsules (Bisang *et al.* 2014). We presume that suitable conditions for sporophyte production occurred widely in the Baltic area during these years and that total reproductive output in *D. turgescens* was considerable in the area.

Many terrestrial pleurocarpous mosses are ‘perennial stayers’ sensu During (1979, 1992), characterized by prevailing clonal expansion, long life span and relatively low reproductive effort. Compared to poor competitors like, e.g., *Orthodontium lineare* Schwägr. (‘colonist’ life strategy), total spore output in *D. turgescens* is low. *Orthodontium lineare* produced altogether 3.5 billion spores during one year in only twelve sites in southern Sweden (Hedenäs *et al.* 1989). In *Diselium nudum* (Dicks.) Brid. with an ‘annual shuttle’ life strategy, a single large colony may produce 125-175 million spores annually (Lönnell *et al.* 2012). For *D. turgescens* the question is whether the erratic and over time relatively low spore output is sufficient to maintain its European population, including an adequate intraspecific genetic variation (Hedenäs 2016), and to allow colonization of appropriate unfilled habitats. On Gotland, for example, the species occurs also in relatively recent wheel-tracks on alvar-ground, which implies that, currently, colonization takes place now and then. In open terrain, and over relatively short distances, this could be accomplished by wind-blown apical buds that detach easily from the shoots (Hedenäs 1992). Indirect evidence from haplotype variation in *D. turgescens* suggests that the species can establish at suitable localities far from extant occurrences, evidently resulting from spore dispersal. The haplotypes of two populations that occur in land rise areas (Åland, Finland; Gästrikland, Sweden) that have been available for colonization for at most 250-500 years, agree with a colonization by spores from localities further south in the Baltic Sea region (Hedenäs 2014). We conclude that episodic sporophyte production and a relatively low spore output suffice to maintain the European and, considering the similar sporophyte frequency in North American *D. turgescens* (Miller 1980), probably its global population. Our observations on *D. turgescens* can probably be extrapolated to other long-lived perennial mosses with rare or very

rare sporophyte production and with wide continental or global distributions, such as *Calliergon megalophyllum* Mikut., *Calliergonella lindbergii* (Mitt.) Hedenäs, *Dichelyma capillaceum* (Dicks.) Myrin, *Entodon concinnus* (De Not.) Paris, *Hamatocaulis vernicosus* (Mitt.) Hedenäs, *Rhytidium rugosum* (Hedw.) Kindb., and *Sarmentypnum trichophyllum* (Warnst.) Hedenäs. Several of these grow in special habitats with restricted distributions. We therefore suggest that widespread long-lived perennial mosses with specialised habitat requirements can maintain genetic diversity and persist in the long term, also when sporophyte production is rare and erratic.

#### *Future perspectives*

The available data suggest that the levels of sexual reproduction and spore dispersal have so far been sufficient for the long-term survival of the European *D. turgescens* population, but the ongoing climate change may alter this. A recent increase in fertility in British *Lunularia cruciata* (L.) Lindb. (Blackstock 2018), altered growth and reproductive performance of *Polytrichastrum alpinum* (Hedw.) G.L.Smith on the Antarctic Peninsula (Shortlidge *et al.* 2017), and bryophyte distribution shifts in mountain areas (Bergamini *et al.* 2009, Patiño *et al.* 2016), were suggested to result from climate change. They indicate that a changed climate will influence the performance of many bryophyte species. We argue that the negative influence will probably be strongest for species that grow in habitats that are close to what bryophytes can tolerate in the long-term in terms of temperature, low precipitation or low humidity, factors that negatively affect bryophyte growth (Proctor 2011). High temperatures and lowered water levels will be especially crucial for wetland species (Glime 2011) like *D. turgescens*. The species occurs at many sites on the alvar of Öland and on Gotland in habitats with limited water availability, not only during the fertilisation period. At some of the surveyed sites, we observed considerable decreases in patch size or cover of *D. turgescens* between years with and without sporophytes. Climate models forecast that spring and summer precipitation will increase on Gotland until the end of the 21st century (Persson *et al.* 2015), suggesting more favourable conditions for *D. turgescens* growth and sexual reproduction. Concurrently, a predicted temperature increase will counteract the higher precipitation and lead to generally drier conditions, longer drought periods during summer, and increased evaporation. This will negatively affect both the abundance and fertility of *D. turgescens*.

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**Appendix 1.** Spore counts in the ten 1 µl cells of the Gridded Sedgewick Rafter, and estimated spore numbers per capsule. Two spore capsules were studied for each of three specimens. Further information on the origin of the specimens is provided in the text. Mean numbers of spores (with standard deviations) and estimated spore numbers per capsule are provided in the bottom of the table.

Specimen (S reg. no) and capsule number (1 or 2)						
	B222089		B184252		B196894	
	1	2	1	2	1	2
Grid cell 1	34	19	24	27	21	46
Grid cell 2	24	25	11	47	31	65
Grid cell 3	22	19	21	34	29	91
Grid cell 4	27	22	25	42	41	72
Grid cell 5	29	25	15	46	36	72
Grid cell 6	21	30	46	45	41	89
Grid cell 7	14	25	26	45	33	74
Grid cell 8	33	16	27	39	26	58
Grid cell 9	26	26	33	56	27	71
Grid cell 10	22	26	19	48	30	58
Mean (S.D.)	25.2 (6.0)	23.3 (4.2)	24.7 (9.8)	42.9 (8.0)	31.5 (6.4)	69.6 (13.8)
Spores/capsule	126,000	116,500	123,500	214,500	157,500	348,000

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