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Can artificial introductions of diaspore fragments work as a conservation tool for maintaining populations of the rare peatmoss *Sphagnum angermanicum*?

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ABSTRACT

Species can become regionally rare when limited by the availability of suitable habitats or by limited dispersal ability. We tested if the presence of a rare bryophyte species (*Sphagnum angermanicum*) was dispersal or habitat limited and at the same time investigated the possibility of establishing new populations of this rare species. Further, we tested how propagule (fragment) size and small scale disturbances affected establishment success. All field experiments were performed by artificially transporting propagules (of various sizes) to new and old sites for the species in Sweden.

We show that *S. angermanicum* is dispersal limited on a regional scale, as no significant differences in establishment success were found between new suitable sites and old occupied sites. The larger the propagule the better was the establishment success; the best establishment success was found when transplanting whole shoots. Disturbances did not increase establishment success, in contrary, when compared to controls success was reduced by the more intensive disturbance treatments. We suggest that disturbance maybe more important for increasing direct dispersal than for making the microhabitat more advantageous for establishment. However, an intermediate disturbance, which slightly reduces the *Sphagnum*-community length increment, might also be beneficial for the establishment success of *S. angermanicum* propagules.

The reasonably high establishment success of *S. angermanicum* propagules in new suitable sites suggests that artificial introductions of fragments could be considered as an active management regime for the species if the number of localities continues to decrease.

1. Introduction

Habitat fragmentation (including habitat losses) are today one of the main threats to the long time persistence of several boreal cryptogams. The main causes of the boreal ecosystems fragmentation are human activities e.g. forestry and agriculture (Bryant et al., 1997; Östlund et al., 1997), but several fragmentation processes are caused by natural deterministic processes e.g. succession. Fragmentation results in increased distances between populations and/or patches of suitable habitats, which may result in decreased dispersal (gene flow) between populations and lower establishment potential in suitable but unoccupied sites. Further this may increase genetic drift within populations and increase the risk of local population extinction (Newman and Pilson, 1997; Groom, 1998; Saccheri et al., 1998). Inbreeding can also affect fitness

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traits such as individual longevity, sexual reproduction (frequency and viability of spores) and dispersal capacity.

The presence of many bryophytes in the landscape is limited by the lack of suitable habitats; other species are limited by a low diaspore production or inefficient diaspore dispersal ability (Longton, 1992; Söderström and Herben, 1997; Snäll et al., 2003). By performing simple artificial dispersal experiments it is possible to test if species on a regional scale are dispersal or habitat limited (Eriksson and Ehrlén, 1992; Münzbergová and Herben, 2005). If the species are able to establish at potentially suitable unoccupied habitats it can be concluded that the occurrences of the species is dispersal limited. However, identification of suitable unoccupied habitats for species is difficult. Good knowledge of the species habitat requirements is critical.

One way to conserve a viable number of populations in the long term may be to artificially introduce diaspores (sexually or asexually produced) by transplanting them to new suitable localities or to old localities where the species have disappeared. Many cryptogams have specific habitat requirements and may thus have specific local adaptations, which have been found in vascular plants (i.e. Montalvo and Ellstrand, 2001; Hufford and Mazer, 2003), but the small inter-population genetic differentiation in many bryophyte species may indicate that there is only a small genetic component in their local adaptations. Transplantation experiments have often been performed with lichens (e.g. Scheidegger et al., 1995; Zoller et al., 2000; Gilbert, 2002; Keon and Muir, 2002; Lidén et al., 2004). There are also several studies that have tested establishment success in bryophytes (e.g. Kimmerer, 1991, 2005; Kooijman et al., 1994; Li and Vitt, 1994, 1995; Geissler, 1995; Cleavitt, 2001; Sundberg and Rydin, 2002; Wiklund, 2003).

Many species are only found in disturbed habitats, usually because they need disturbances to avoid competition from superior species. Often the disturbance agent can also act as vector for the dispersal of diaspores. In boreal wetlands the establishment of new *Sphagnum* individuals from spores might be difficult or impossible in habitats already covered by matured *Sphagnum* shoots, as in a closed mire carpet (Clymo and Duckett, 1986; Sundberg and Rydin, 2002). Therefore, some kind of disturbance may be needed. In *Sphagnum* dominated wetlands large-scale disturbances are rather uncommon (e.g. fires, peat extractions and drainage), but small-scale disturbances are abundant and frequent (e.g. trampling by herbivores, tree uprooting, decaying litter and frost heaving). It has been suggested that the large-scale disturbances are of importance for colonisation of new species on a landscape level (Soro et al., 1999; Sundberg and Rydin, 2002), but for the internal population dynamics small-scale disturbances may be more important. For many bryophyte species dispersal of asexual propagules (e.g. fragments) is of major importance for maintaining the local population and for dispersal to new localities within the same region (Söderström and Jonsson, 1989; Li and Vitt, 1994; Laaka-Lindberg, 2001).

The main habitat for *Sphagnum angermanicum* is intermediate fens, which are relatively short-lived. They have been suggested to persist for between 50 and 300 years (Vitt and Kuhry, 1992; Kuhry et al., 1993; Kuhry, 1997) and are thereafter replaced by poor fen habitats (Sjörs and Gunnarsson, 2002). Thus, the species must have a metapopulation dynamic not to face regional extinction if no disturbances occur. Disturbances may, however, slow down the succession and keep the mire in the suitable intermediate fen stage.

In recent field investigations it has been found that the Swedish populations of *S. angermanicum* have a clumped distribution (Gunnarsson, 2004). It can be common locally but seems to have problems with long distance dispersal (Gunnarsson, 2004). The main dispersal mode is probably by fragmentation of the gametophore. Although the species now has a low dispersal capacity the genetic structure of the Swedish populations showed only a small degree of differentiation and evidence of sexual recombination (Gunnarsson et al., 2005), suggesting that historically the species have had long distance dispersal and recombination. This study aims to investigate, firstly, if successful establishment of *Sphagnum angermanicum* fragments it is possible at new suitable localities and at the same time test if the regional occurrence of the species is dispersal or habitat limited. Further, we want to investigate what is the most successful fragment size for establishment. Finally, to test if different disturbance regimes can enhance the fragments establishment success.

2. Materials and methods

2.1. *The species*

Sphagnum angermanicum has globally an amphi-Atlantic distribution. It occurs in eastern North America from New Jersey up to southern Labrador (Maass, 1967; Phillips and Miller, 2001). Its European distribution is confined to Scandinavia (Flatberg and Moen, 1972; Gunnarsson, 2004), with a single report from Iceland (Jóhannsson, 1992). In Sweden it is only known from about 20 localities (Gunnarsson, 2004) and is classified as near threatened (NT) in the red list of Swedish species (Cronberg et al., 2005). The species is dioecious and has very rarely sporophytes (one sporophyte known from Scandinavia, specimen in TRH). Sporophyte production seems to be more common in Newfoundland (Maass, 1966, 1967). There are no specialized asexual propagules. However, *S. angermanicum* shoots probably use the capitula as the main short distance dispersal unit, as a fragile part of the stem occurs just below the capitula (ca. 0.3 cm below the shoot apex), which is easily broken when touched by e.g. cattle or moose trampling (Gunnarsson, 2004).

Sphagnum angermanicum grows typically in intermediate fens associated with *Sphagnum papillosum*, *Molinia caerulea*, *Betula nana* and *Sphagnum angustifolium* (Flatberg and Moen, 1972; Gunnarsson, 2004). The pH at sites with *S. angermanicum* ranges between 3.7 and 6.5 (mean 4.9 ± 0.6 SD) and the groundwater table varied between 4 and 50 cm (mean 17.9 cm $\pm$ 6.0 SD; Gunnarsson, 2004). At almost all Swedish *S. angermanicum* localities there were indications of small scale disturbances, usually moose trampling or irregular ground water levels (Gunnarsson, 2004).

2.2. *Site quality experiment*

In order to test if *S. angermanicum* can establish at new unoccupied sites and if the species is dispersal limited, we compared the establishment success of capitula and whole

Table 1 – Localities used in the transplantation experiment of Sphagnum angermanicum diaspores

Population number, locality	Latitude (E)	Longitude (N)	Altitude (m)
O1, Ö Vallsjön	13°22′	60°45′	400
O2, Lillbudkölen	13°23′	60°45′	420
O3, Gråbron	13°24′	60°43′	375
O4, Ö Älgsjön	13°29′	60°37′	425
N1, N Barvallhållen	13°26′	61°04′	515
N2, Barvallen	13°27′	61°04′	470
N3, WNW Gåstjärn	13°27′	61°03′	465
N4, Barvallkölen	13°27′	61°02′	460

Localities starting with O are old localities, where S. *angermanicum* was naturally present, and localities starting with N are new localities, into which it was introduced in this study.

shoots when the propagules were moved from the source population (Ö Vallsjön, O1, Table 1) into eight localities of two types; old sites where S. *angermanicum* was naturally present (including the source population) and new sites where S. *angermanicum* was absent (Table 1, Fig. 1). The transplanted diaspores were taken from several patches where S. *angermanicum* dominated the vegetation and cut into the length of capitula (top 0.3 cm of a shoot) and whole shoots (top 3 cm). Four patches (0.2×0.2 m^2) per site (five patches at population N1, Table 1) were established in August 2004 in typical S. *angermanicum* communities (cf. Gunnarsson, 2004), but where S. *angermanicum* were absent. Ten capitula and 10 shoots were regularly arranged and put into two diagonal 0.1×0.1 m^2 quadrants. Care was taken to level the top of the capitula or shoot with the rest of the living Sphagnum carpet. Number of capitula or shoots remaining visible at the top of the moss layer was registered in August 2005.

2.3. *Disturbance and fragment size experiment*

To test the effects of disturbance, fragment size and type on establishment success, we transplanted different fragments (whole shoots, capitula, stems and capitula fragments) into 20 plots (0.5×0.5 m^2) treated with different disturbance regimes. The disturbance treatments were, removing the living mosses (bare peat), mixing the top 10 cm with a hoe (mixing), intensive trampling, where all parts of the plot were trampled approximately three times (trampling), and untreated control plots (control). Five replicates of each disturbance treatment was randomly assigned among selected plots on an intermediate fen in the northern part of Barvallhållen (N1, Table 1, Fig. 1). The plots were established in September 2001 in sites that were identified as suitable but not occupied by S. *angermanicum*. The sites had a typical associated vegetation (cf. Gunnarsson, 2004), pH in the range 4.1–5.7 and a distance to ground water table ranging 5–23 cm above the ground water table.

The transplanted fragments were collected from several patches of the source population (Ö Vallsjön, O1, Table 1), cut into shoots (top 3 cm), capitula (top 0.3 cm, mean dry weight 0.63 mg ± 0.3 SD, $n = 58$), stems (the stem part below 3 cm and further 3 cm down with a mean dry weight of 0.62 mg ± 0.2 SD, $n = 25$) and capitula fragments. The capitula fragments were processed by cutting 10 normal sized capitula with a scalpel several times to create fragments of branches and stems of a mean dry weight of 0.0019 mg ± 0.0009 SD and in total an average of 320 ± 60 SD fragments per plot. The capitula fragments varied a lot in size, from parts of a leaf to a few mm long parts of a stem or a branch. The fragments were sown into four subplots (0.1×0.1 m^2 large) in the central parts of the established 0.5×0.5 m^2 plot. Ten shoots, capitula and stems were put into the growing mosses, and the capitula

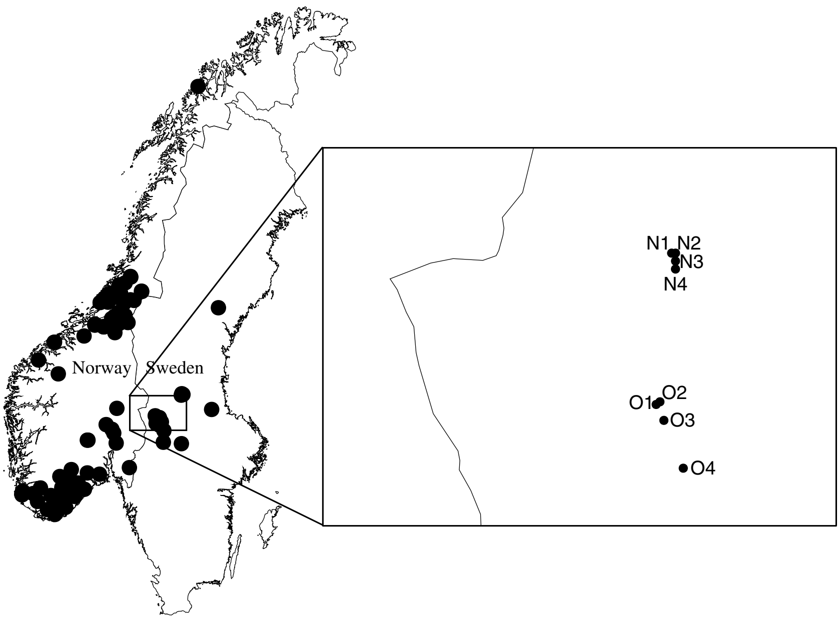

Fig. 1 – Distribution map of *Sphagnum angermanicum* in Scandinavia (after Gunnarsson, 2004) and inserted the experimental sites. N, new localities into which *S. angermanicum* was transplanted; O, old localities with *S. angermanicum* already present. Numbers refers to the localities in Table 1.

fragments were spread evenly out in the subplot. In order to measure the linear vertical length increment of the general *Sphagnum* community four cranked wires were put into each corner of the $0.5 \times 0.5\ m^2$ plots (cf. Gunnarsson and Rydin, 2000).

The establishment success of the diaspores in the plots was monitored after 9, 12, 24, 36 and finally after 48 months. The number of visible capitula formed by the different propagule types at the top of the moss surface was scored and transformed into establishment success by calculating the frequency of the transplanted fragments (for capitula fragments the average value 320). The length increment of the *Sphagnum* community was measured with a ruler to the nearest mm after 9, 12, and 24 months.

2.4. *Data analysis*

In order to test the effect of site quality on establishment success we used nested Quasi-likelihood models (locality nested within locality type) using S-PLUS 3.0, since the distributions of the response variables (shoot and capitula establishment frequencies) was Poisson distributed. An analysis of deviance was used to identify the significance of the independent factors. As the scale parameter is often under or over dispersed, the *F*-statistics were used (Crawley, 2002). The effects of habitat disturbance treatments on establishment success were tested for each registration period with the non-parametric Kruskal–Wallis test in Minitab 14.

3. Results

3.1. *Site quality experiment*

After 12 months the establishment success of capitula and shoots did not differ between old and new sites. There was, however, a large variation between localities (Fig. 2; Table 2). The establishment success of capitula was lower (mean frequency = 0.24) than the success of whole shoots (mean frequency = 0.52; Fig. 2). There was a positive relationship between high shoot establishment and high capitula

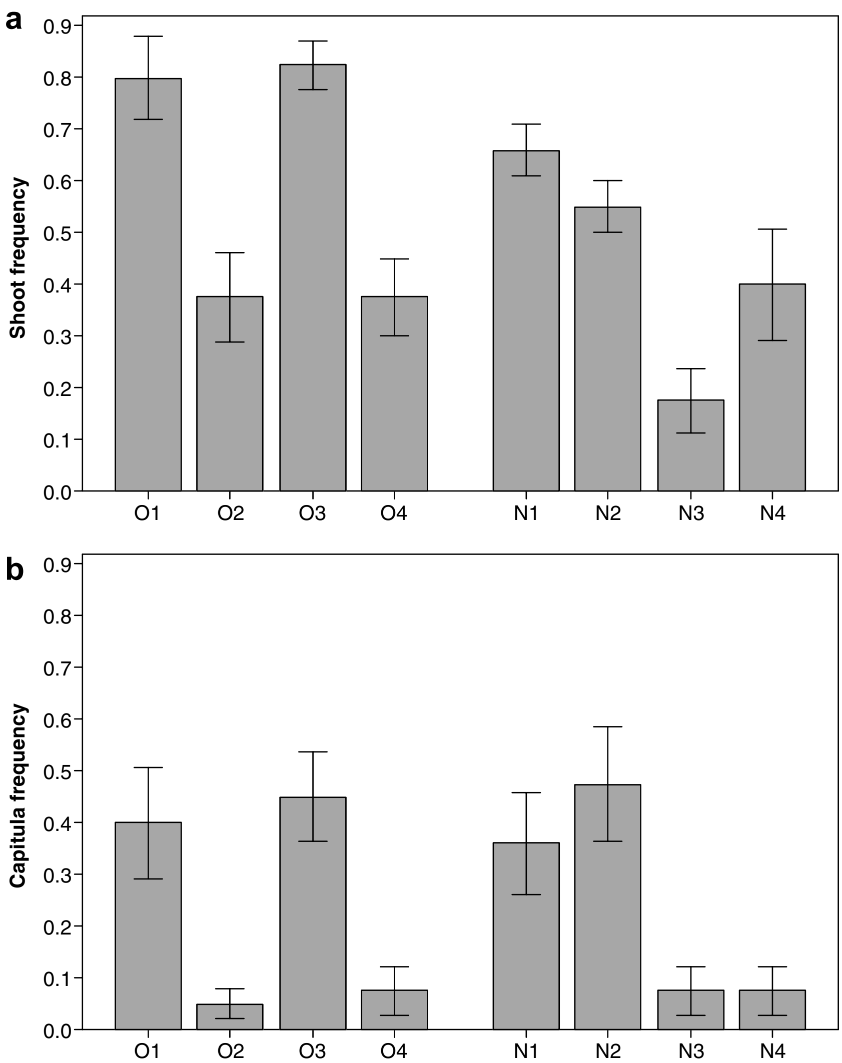

Fig. 2 – Establishment success (frequency of transplanted diaspores) of *Sphagnum angermanicum* shoots (a) and capitula (b) survival after one year in old (O) and new (N) localities (numbers refers to the localities in Table 1).

Table 2 – Summary of a Quasi-likelihood model for the establishment success of shoot and capitula for different types of localities (old or new) and localities nested within type

Source	Shoot frequency			Capitula frequency		
	df	ms	F-value	df	ms	F-value
Type	1	15.0	2.48 n.s.	1	0.070	0.013n.s.
Locality (type)	6	22.3	10.5***	6	17.3	6.54***
Residual	25	2.13		25	2.65	

n.s., $p > 0.05$.
*** $p < 0.001$.

establishment. Localities with high capitula establishment also had high shoot establishment (Fig. 2).

3.2. *Disturbance and fragment size experiment*

The establishment success after 9 months was very low for stems and capitula fragments. For the stems two plots had developed two capitula each (total establishment frequency 0.02 after 9 months), but these capitula disappeared after the first summer (until October 2002). Capitula fragments had higher establishment success, 11 establishments after 9 months, but because of the high number of propagules sown the total establishment frequency became lower (total frequency of 1.70×10^{-3}). Most established capitula fragments disappeared during the first summer and only two were still present in October 2002 (Fig. 3). Only a few capitula fragments were present until 2005 when 10 established capitula were found. Similar temporal patterns were found also for shoots and capitula, but with a much higher establishment success (total frequency in October 2002 of 0.61 and 0.19, respectively). There was a reduction in numbers of capitula and shoots found in the treatments after the first summer and thereafter a slight recovery until the last registration (Fig. 3).

Since the number of establishments were low for stems, and capitula fragments no further statistical tests were run on these data. For capitula we found no significant treatment effects on establishment success, but for the whole shoots we found significant effects after the first summer (Table 3, Fig. 3a). This was mainly explained by the high disappearance of shoots during the first summer in the bare peat and the mixing treatments. At the last registration several new capitula were found in these treatments (Fig. 3a) probably as an effect of several dividing capitula.

The length increment of the *Sphagnum* community differed between the treatments, where the bare peat and the mixing treatments resulted initially in a compaction, but produced a slight increment later on (Fig. 4). Meanwhile, the control and the trampling treatments had similar length increment (20–30 mm increment in two years, Fig. 4). The relation between the accumulated length increment until November 2003 and the establishment success of shoots (Fig. 5) shows that the plots with the lowest length increment (bad growing conditions in the bare peat and mixing plots) had low establishment success and that the plots with the highest length increment also had rather low success (Fig. 5). The highest shoot establishment success was found at intermediate length increments (10–20 mm length increment) of the *Sphagnum* community (Fig. 5).

4. Discussion and conclusion

If the number of localities of *S. angermanicum* in Sweden decreases from the currently 20 known localities, which is above the threshold (<10 localities) for classification as threatened (IUCN, 2001), it may be necessary to manage the populations or we risk losing this species from the country. It can be concluded that it was, with reasonably good precision, possible to identify suitable habitats for the species based on the knowledge of its habitat requirements, e.g. accompanying species, pH demands and distance to ground water table (Flatberg and Moen, 1972; Gunnarsson, 2004) and it was possible to introduce the species to new localities without applying any disturbance treatment. The establishment success rates of whole shoots and capitula differed between sites but were generally high compared to smaller fragments and to spore germination success for other *Sphagnum* species or mosses (Li and Vitt, 1994, 1995; Dalen and Söderström, 1999; Hassel and Söderström, 1999; Sundberg and Rydin, 2002). Together this suggests that it is possible to maintain or increase the number of populations of the species by artificial introduction using large sized fragments.

Before establishing new populations, a number of questions need to be considered. Firstly, how many populations are needed? For a species like *S. angermanicum* that seems to have very little regional dynamic (metapopulation dynamic), the number of localities must be high enough that local stochastic and deterministic extinction do not cause the species to decrease to a thresholds, under which long time survival is unsure. Secondly, which localities should be maintained to get the highest possible survival rate? Here there is a choice between trying to increase the populations at already occupied sites, reintroduction to previously occupied site, or introduction to new localities. If the reasons for decline or disappearance from old localities are known and reversible, a reintroduction may be best, but if the reasons are unknown or irreversible, it may be better to try to introduce a population to a new locality without predictable threats; this may cause an ethical dilemma especially if it has to be introduced to new regions. Thirdly, we need to know the genetic structure among populations to decide which populations propagules should be sampled from for artificial introduction. In the case of *S. angermanicum* all Swedish populations are genetically quite similar (Gunnarsson et al., 2005), thus the choice of source populations may be less important and the genetic part of the local adaptation may be small. However, the more abundant Norwegian populations may be considered as source populations for the introduction. These popu-

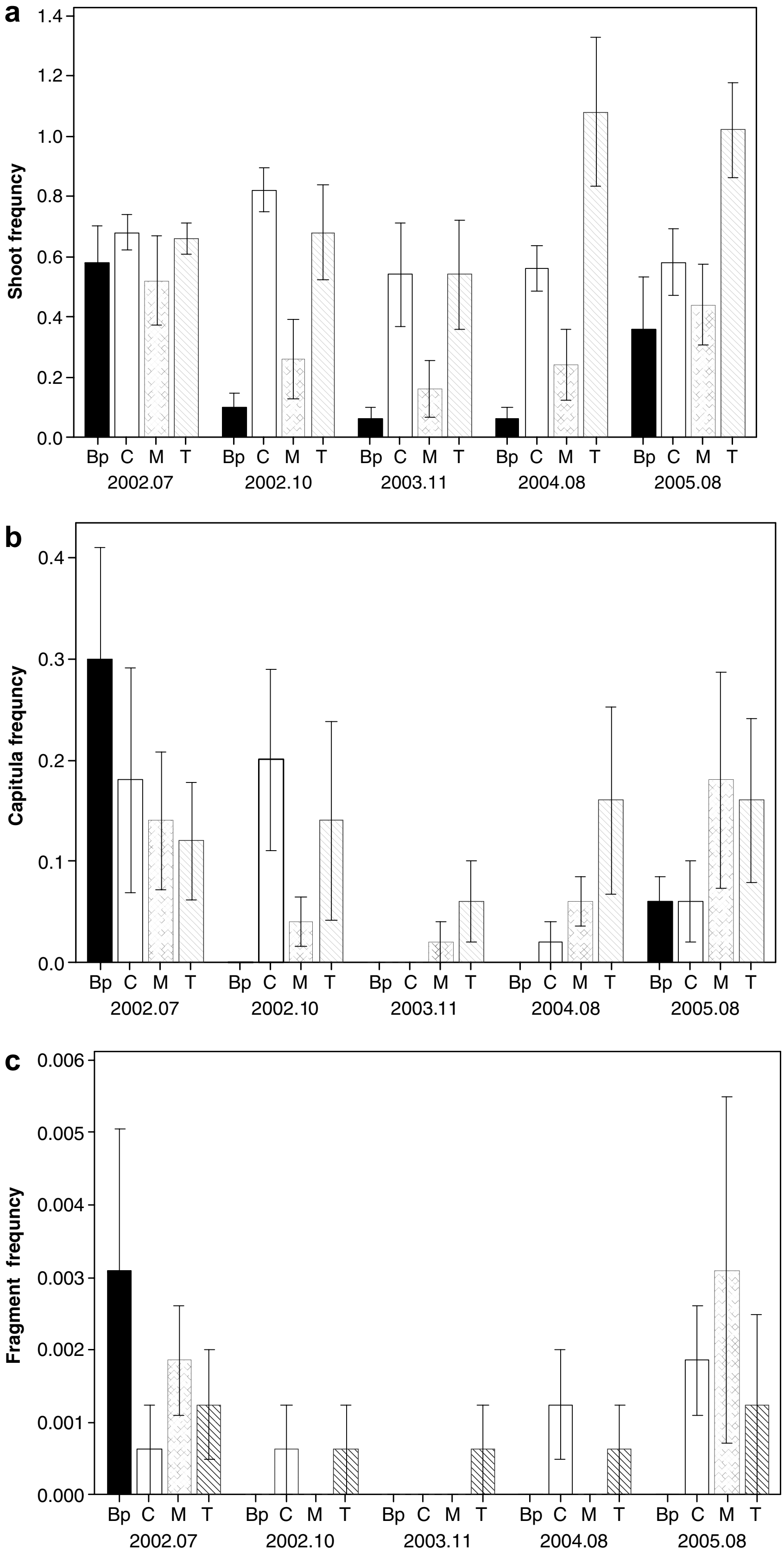

Fig. 3 – Establishment success (frequency of the transplanted propagules) of different fragment sizes, whole shoots (a), capitula (b) and capitula fragments (c) from the start of the experiment in October 2001 until August 2005. Note the different scales on the *Y*-axis. Treatments are bare peat (Bp), control (C), mixing (M) and trampling (T).

Table 3 – Summary of Kruskal–Wallis test statistics (H) on the disturbance treatment effect on establishment success of shoots and capitula measured at different times from July 2002 until August 2004

Time	Shoot frequency			Capitula frequency		
	df	Kruskal–Wallis *H*	*p*-Value	df	Kruskal–Wallis *H*	*p*-Value
July 2002	3	0.82	0.85	3	2.3	0.52
October 2002	3	12	0.007	3	6.2	0.10
November 2003	3	9.7	0.021	3	4.2	0.24
August 2004	3	13	0.004	3	6.0	0.11
August 2005	3	8.0	0.046	3	1.7	0.65

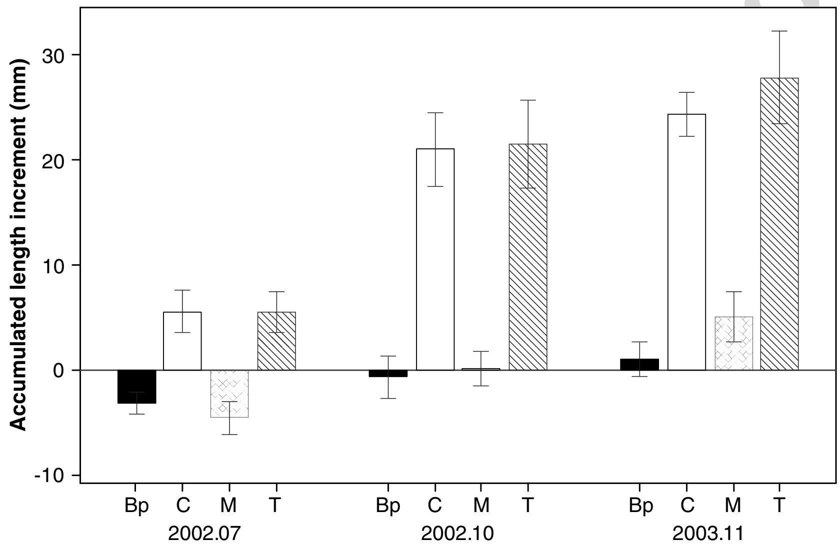

Fig. 4 – Accumulated vertical *Sphagnum* length increment, from October 2001 until November 2003, in the different treated plots: bare peat (Bp), control (C), mixing (M) and trampling (T).

lations may have a larger genetic diversity, but may not have the same degree of local adaptation (Montalvo and Ellstrand, 2001; Hufford and Mazer, 2003).

This study indicates that the occurrence of *S. angermanicum* in the region is dispersal limited, as there was no difference in establishment success in localities without *S. angermanicum* and in localities with the species (Table 2). Dispersal limitation has been found in many rare cryptogams (Longton, 1992; Snäll et al., 2003; Lidén et al., 2004). For *S. angermanicum* the lack of sexual reproduction (no sporophyte production) seems to be the main reason for the limited distribution as spores are considered to be responsible for long distance dispersal in bryophytes (Longton and Shuster, 1983; Kimmerer, 1994; Söderström and Herben, 1997; Laaka-Lindberg, 2001). The low genetic diversity in each population may be one of the causes of low sexual output, perhaps an effect of local inbreeding depressions, which can effect the sexual cycle (Reed and Frankham, 2001), resulting in a reduced sporophyte production in bryophytes. Both male and female individuals have been observed in several Norwegian populations, but no sporophytes have been found, so the lack of sexual reproduction may not be caused by a skewed sex ratio (Flatberg, 2002, and pers. comm.). Short distance dispersal by fragmentation, for *S. angermanicum* by breaking off the capitula, may assure maintenance of populations in the core area, but is obviously insufficient for long distance dispersal. Moreover, there are several suitable unoccupied habitats for *S. angermanicum* in the region and in many parts of mid boreal Sweden (Sjörs and Gunnarsson, 2002), which could be potential new habitats for the species if it eventually starts to dis-

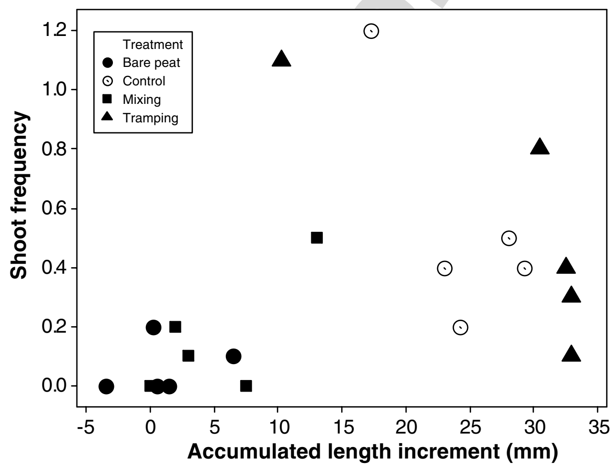

Fig. 5 – Shoot frequency in November 2003 in relation to the accumulated vertical length increment until November 2003 given the different treatments.

perse again or considered as candidate sites for artificial introduction.

Establishment from small fragments (capitula fragments) is probably much more sensitive to the environment and to seasonal variation in temperature and moisture conditions (Li and Vitt, 1995; Wiklund, 2003) than larger fragments, and therefore small fragments have a lower establishment success. However, it is still in the same range as establishment success from spores (Hassel and Söderström, 1999; Sundberg and Rydin, 2002). In the first year the weather conditions were extraordinary with a great deal precipitation in June (134 mm compared to the normal 74 mm measured at the closest weather station Malung, 45 km south from the experimental site, SMHI, 2002a). These high precipitation levels may have resulted in some of the loosely attached fragments being washed away, partly explaining the low number of fragments re-found. Late summer (August and September) 2003 was drier than normal (SMHI, 2002b,c), which can explain the disappearance of fragments in the bare peat treatment until October 2002 (Fig. 3), but as the *Sphagnum* carpet at the site never completely dried out (personal observation), a large part survived in the plots with more intact *Sphagnum* vegetation (Fig. 3). The following years had normal climatic conditions, except for a high amount of precipitation in August 2004 (SMHI, 2004), but at this time all remaining shoots were firmly attached to the substrate. In conclusion, establishment success might have been higher if performed in a year with more normal climatic conditions.

The size of the transplanted unit is an important factor in obtaining a resource effective transplantation strategy of rare species. One way to increase the establishment success may be to transplant larger patches of the species in sizes from one to several dm^2, but transplanting such large patches may reduce the vigour of the source population and for that reason be considered unsuitable. Perhaps the best strategy would be to use capitula fragments as transplant units. They could easily be picked directly in field from the source population. This would have minimal effects on the source populations and still having high establishment success at the new locality. Shoots from which capitula have been taken will regenerate by producing new capitula from side-branches, which will not be the case when using whole shoots as transplanting units.

The part of the fragment that was used for transplantation also affected the establishment success. In our study the top 3 cm performed better than the stems (3–6 cm part). The decreasing establishment success with depth was also found by Rochefort et al. (2003) in regeneration experiments on cutover peatlands, but with the difference that the reduction in regeneration was observed for fragments below 6 cm for the majority of the species and some species were viable even at a lower depth. Nevertheless, our low establishment success of stem fragments may be explained by the short time available for them to induce regeneration of a growing meristem before being overgrown by the surrounding *Sphagnum* community.

There were no significant positive effects of local microhabitat disturbances on establishment success. In contrary there were reductions in establishment success in the mixing and the bare peat treatments. This was not as expected, since we always observed disturbances at sites with *S. angermanicum* (Gunnarsson, 2004). However, the influence of disturbance (trampling by animals or water-actions) on the populations may not enhance the establishment success, but may be important for increasing shoot fragmentation and local dispersal. Intermediate levels of disturbance, which reduce the length increment of the *Sphagnum* community, may, however, be beneficial for establishment by reducing the competition from the already present *Sphagnum* community and enhancing establishment of the less competitive *S. angermanicum* fragments. In addition, the disturbance may also be important for keeping the habitat in the intermediate fen stage, slowing down the succession to the poor fen stage, allowing *S. angermanicum* to remain at the same locality without dispersing to new sites.

It is important to monitor the long time survival of the introduced propagules when managing newly established populations. In cases of low survival, as in the case of *Marchesinia mackaii* (Geissler, 1995), it must be considered whether repeated attempts to introduce the species should be performed or if the locality should be abandoned as a non-suitable site. An optimal and cost effective situation would be a situation with high establishment success after only one introduction attempt, enhancing the species chance of long time survival in the country.

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