Ann. Bot. Fennici 35: 197–201
Helsinki 20 November 1998
ISSN 0003-3847

Seed and spore banks of two boreal mires

Sinikka Jauhiainen

Jauhiainen, S., Department of Forest Ecology, P.O. Box 24, Helsinki, FIN-00014 University of Helsinki, Finland

Received 22 May 1998, accepted 25 August 1998

The importance of the seed bank as a regenerative strategy in disturbed mires and the viability of seeds and spores in peat stratigraphy on two drained mires were studied prior to restoration. Most of the seedlings developed from the surface sample but still viable seeds occurred in the deepest layer sampled (50 cm). Germination from seeds, however, remained low. Six species of vascular plants: *Betula pubescens* Ehrh., *Eriophorum vaginatum* L., *Rubus chamaemorus* L., *Vaccinium myrtillus* L., *V. uliginosum* L., and *Andromeda polifolia* L. with a maximum of 367 seedlings per m^2 germinated. The regenerative strategy of these plants seems to be vegetative expansion from adventitious roots and buried propagules rather than germination from seeds. It was found, however, that some seeds in the peat profile may preserve their viability for centuries.

Key words: peatland, regeneration, restoration, seed bank

INTRODUCTION

Large-scale drainage during recent decades has reduced the areas of undisturbed mires in Finland (e.g., Aapala *et al.* 1995). The succession of mire vegetation after drainage has developed towards forest floor vegetation (Laine *et al.* 1994). Some drained mires, however, have been unsuited to forest growth and remained disturbed. Some of these mires, and those belonging to key biotopes or threatened site types were chosen for the restoration program, which started in Finland in 1994. Some may be restored as buffer zones to diminish the effects of peatland forestry on waterways (Laine *et al.* 1997). The effort at active restoration is to re-establish the mire plant communities present before drainage. It is important to know what is the condition of seed banks in peat in the succession towards mire vegetation after restoration.

It has been found that seed banks play quite an important role in regeneration of plant communities in habitats such as marshes (Van der Valk & Davis 1978, Smith & Kadlec 1985, ter Heerdt & Drost 1994), shorelines and flooding areas (Nicholson & Keddy 1983, Schneider & Sharitz 1988, McDonald 1993, Jutila 1994) and cut over peatlands (Salonen 1992). Seed banks of peatlands such as bogs and fens have attracted less interest and studies on these habitats are rare (Moore & Wein 1977, McGraw 1987).

The objectives were to study (1) the potential of seed and spore banks to provide the bases for mire vegetation development after the restoration, and (2) at what depth in peat deposit viable seeds are still found.

MATERIAL AND METHODS

Study sites

The study sites are located about 60 km north-east of Tampere in southern Finland. The minerotrophic Konilampi mire site, later called the fen site, is located on northern part of Hanhisuo mire, (61°48´N, 24°17´E, 155 m a.s.l.). It has a radiocarbon age of 3 220 ± 100 BP (Hel-3858) at a depth of 45–50 cm. At present it supports a pine-dominated stand (*Pinus sylvestris* L.) with some spruce (*Picea abies* (L.) Karsten) and birch (*Betula pubescens* Ehrh. and *B. pendula* Roth). The average age of the pines is 85 years. The dwarf shrub layer consists mostly of *Ledum palustre* L., *Vaccinium uliginosum* L.*, Vaccinium myrtillus* L. and *Betula nana* L. The area was drained in 1955, and ditch maintenance carried out in 1965 and 1988 (Ekola & Päivänen 1991).

The ombrotrophic Viheriäisenneva mire, later called the bog site, (61°51´N, 21°14´E, 160 m a.s.l.) has a radiocarbon age of 680 ± 90 BP (Hel-3863) at a depth of 45–50 cm. It was nearly treeless in 1950, but developed a young pine stand after drainage operations which took place between 1955 and 1988 and planting of pine seedlings in 1966. The dwarf shrub layer consists of *Calluna vulgaris* (L.) Hull, *Empetrum nigrum* L. and *Vaccinium uliginosum* and the lichen/moss layer is dominated by *Cladonia* species and some ombrotrophic species of *Sphagnum.*

The area belongs to the eccentric raised bog region (Ruuhijärvi 1983) of the southern boreal coniferous forest zone (Ahti *et al.* 1968). Mean annual precipitation in the area is 709 mm, mean daily temperature in July is 15.3°C and in January –8.9°C. The effective temperature sum using a +5°C threshold is 1 060 degree days per year (according to the Finnish Meteorological Institute, Juupajoki station, between 1961 and 1990).

Sampling

Peat samples were collected prior to rewetting in September 1994 using an auger of 8.3 × 8.4 × 100 cm. Nine cores from both sites to a depth of 50 cm were taken; the distance between sampling points varied from 10 to 12 meters. Above-ground parts of plants were removed with scissors. The cores were divided into the following sections: the upper 20 cm was cut into four 5 cm slices and the lower 20 to 50 cm into three 10 cm slices. Samples were stored in the cold room (+5°C) over the winter.

Germination test

The germination experiment was started on 18 April 1995 in the university greenhouse in Helsinki. Each peat sample was mixed with pure quartz sand in a ratio by volume of 3:1.5 (peat:sand) in order to increase the movement of water and to prevent the pure peat becoming compacted. The mixture of peat and sand formed a two cm thick layer on plastic trays the bottoms of which were perforated. A little quartz sand was strewn on the surface of the mixture to make it lighter in colour. Trays were placed in a random order on the greenhouse table and irrigated.

The set of trays was covered with thin, white gauze which prevented adventitious wind-dispersed seeds coming from outside the greenhouse. The samples were continually kept moist by watering with tap water when necessary, usually every other day. Minimum and maximum temperatures were recorded during the experiment with a thermometer placed between the trays. On a few warm days in May the temperature in the greenhouse rose to over 40°C. The table with the set of trays were then surrounded by black plastic curtains to reduce heating due to direct sunlight. Daytime temperatures later varied between 22 and 35°C, while night temperatures varied between 15 and 18°C. No special illumination program was arranged. Day and night lengths were 15 and 9 hours at the beginning of the experiment (mid April) and 18 and 6 hours at the end of the experiment (mid July).

Germination recording

Germination was recorded weekly for twelve weeks. Any plants which started to grow from old branches or dormant buds were removed to avoid confusion with those which germinated from seed. Only seed and spore-germinated plants were carefully recorded and identified. After six-weeks growing period seedlings and sporelings were removed and replanted into small trays. The peat layer in each germination tray was turned over and germination was allowed to proceed for another six weeks. Plants were grown to a size which enabled identification. Some of the plants germinated, especially mosses, remained very small and necessitated microscopic identification by using cell structure. The botanical nomenclature for vascular plants follows Hämet-Ahti *et al.* (1986) and for mosses Koponen *et al.* (1977).

RESULTS AND DISCUSSION

Germination from vegetative propagules started as soon as the samples were placed in the greenhouse. On the second day there were already signs of *Eriophorum vaginatum* in some of the trays. During the first week more *Eriophorum*, *Vaccinium uliginosum* and *Rubus chamaemorus* initiated. *Empetrum nigrum* emerged on the third week. After the turnover of the samples, propagules of *V. uliginosum* and *E. nigrum* germinated. All these were picked out in order to avoid confusion with the coming seed germinations. The number of germinants initiated from seeds and spores remained small. On the fen site, 21 seeds and 18 spores (i.e. 18 tiny cushions of bryophytes appeared, where the number of individuals was uncountable) germinated from 63 samples. These represented 5 species of vascular plants: *Betula pubescens, Eriophorum vaginatum, Rubus chamaemorus, Vaccinium myrtillus* and *V. uliginosum*, and 4 species of bryophytes: *Sphagnum angustifolium, S. balticum, S. russowii* and *Warnstorfia exannulata,* (Table 1). On the bog site, 17 seeds and 8 spores germinated, representing 3 species of vascular plants (*Andromeda polifolia, Eriophorum vaginatum, Vaccinium uliginosum*) and 4 species of bryophytes (*Polytrichum strictum, Sphagnum fuscum, S. magellanicum, Wanstorfia exannulata*; Table 1). All these species were found in the present vegetation of the sites.

In forest vegetation, seeds of *Vaccinium myrtillus* and *V. vitis-idae* have been reported to germinate poorly (Ahti 1980), however in this study seeds of *V. myrtillus* gave high germination. These seeds as well as *V. uliginosum* might benefit from a day length of 15–18 hours which was during the experiment. Giba *et al.* (1993 and 1995) have found that *V. myrtillus* needs several days of white light for germination. On the other hand high temperatures on a few days in greenhouse might influence germination of the other species adversly.

Calluna vulgaris was quite abundant in the vegetation of the bog site, but did not germinate

Table 1. Mean (range) number of seedlings and sporelings per m^2 at two mire sites in Finland.

	Andromeda polifolia	*Betula pubescens*	*Eriophorum vaginatum*	*Rubus chamaemorus*	*Vaccinium myrtillus*	*Vaccinium uliginosum*	*Polytrichum strictum*
Fen site							
0– 5	–	31.8 (0–143)	47.8 (0–287)	–	63.7 (0–287)	95.6 (0–287)	–
5–10	–	–	–	31.8 (0–143)	–	–	–
10–15	–	–	–	–	15.9 (0–143)	–	–
15–20	–	–	–	–	–	–	–
20–30	–	–	–	–	–	–	–
30–40	–	–	–	–	–	–	–
40–50	–	–	–	–	31.8 (0–287)	15.9 (0–143)	–
Bog site							
0– 5	15.9 (0–143)	–	15.9 (0–143)	–	–	–	47.8 (0–143)
5–10	–	–	–	–	–	–	31.8 (0–143)
10–15	–	–	–	–	–	15.9 (0–143)	–
15–20	–	–	–	–	–	15.9 (0–143)	15.9 (0–143)
20–30	–	–	–	–	–	31.8 (0–143)	15.9 (0–143)
30–40	–	–	–	–	–	–	–
40–50	31.8 (0–143)	–	–	–	–	31.8 (0–143)	–

	Sphagnum angustifolium	*Sphagnum balticum*	*Sphagnum fuscum*	*Sphagnum magellanicum*	*Sphagnum russowii*	*Warnstorfia exannulata*
Fen site						
0– 5	15.9 (0–143)	15.9 (0–143)	–	–	31.8 (0–143)	63.7 (0–287)
5–10	–	–	–	–	15.9 (0–143)	47.8 (0–143)
10–15	–	15.9 (0–143)	–	–	–	15.9 (0–143)
15–20	–	31.8 (0–287)	–	–	31.8 (0–143)	–
20–30	–	–	–	–	–	–
30–40	–	–	–	–	–	–
40–50	–	–	–	–	–	–
Bog site						
0– 5	–	–	31.8 (0–287)	15.9 (0–143)	–	15.9 (0–143)
5–10	–	–	47.8 (0–143)	15.9 (0–143)	–	–
10–15	–	–	–	–	–	–
15–20	–	–	–	–	–	–
20–30	–	–	–	–	–	–
30–40	–	–	–	–	–	–
40–50	–	–	–	–	–	–

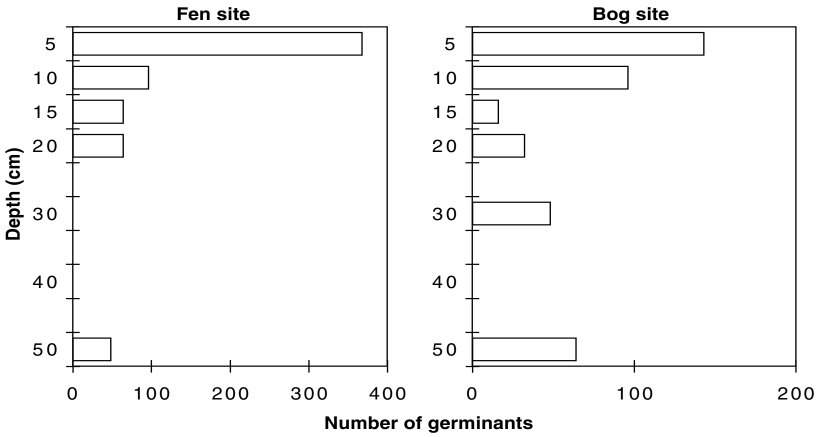

Fig. 1. Depth profile of germinated seeds and spores at two mire sites in Finland.

from this seed bank. According to Helsper and Klerken (1984) low pH of the substrate might reduce germination of *Calluna.* The soil cores in this study site had a pH of 3.4. The other important reason might be the simultaneous occurrence of *Cladonia* species in the vegetation. Hobbs (1985) reported that *Cladonia* strongly inhibits the germination of *Calluna* seeds.

No conifer seeds germinated in this study, although at the fen site there is a pine-spruce stand that produces seeds.

Since most viable seeds are concentrated in the upper few centimeters of the soil (Harper 1977) in most of the earlier seed-bank studies only the upper layers of soils have been sampled, rarely to the depth where no more germination can occur. Van der Valk and Davis (1979) sampled *Carex* communities in prairie marshes in Iowa and found 1 141 viable seeds m^{-2} at a depth of 35 cm. The age of the seeds at that depth was not reported. McGraw (1987) sampled a *Sphagnum* bog in the Appalachian mountains to a depth of 45 cm and found still-viable seeds in the deepest sample.

In this study, most of the seedlings also emerged from the surface samples (0–5 and 5–10 cm) (Fig. 1). However, on both sites the samples from 40–50 cm produced two species of vascular plant; *Vaccinium myrtillus* and *V. uliginosum* at the fen site and *Andromeda polifolia* and *V. uliginosum* at the bog site. Bryophytes germinated from samples at depths of 20 cm and 10 cm at the fen site and the bog site respectively.

Cool, dark and anaerobic conditions with slow microbial activity are beneficial for seed survival (Ødum 1965). In peatlands anaerobic conditions increase with increasing depth, and decomposition in the buried layers slows down. These conditions might be optimal for seed survival (Clymo 1965, 1978, McGraw 1987, 1991). The sterility of very acid *Sphagnum* peat may also account for seed longevity (Leck 1989).

In mires the main reproduction strategy seems to be vegetative growth. Van der Valk and Davis (1979) suggested that a more appropriate term for wetland seed banks would be "propagule banks". This is corroborated by results of Sastroumo (1981), who found that seeds are less important than turions in the process of lake colonization. Clymo and Duckett (1986) and Poschlod and Pfadenhauer (1989) found several *Sphagnum* species regenerating vegetatively from almost all their parts, although from the depths they appeared to be brown and dead. In the present study several vascular plants — typical peatland species — started vigorously from old fragments.

CONCLUSIONS

The results show that the potential of seed and spore banks to contribute to the regeneration of mire vegetation after restoration is rather poor, and vegetative growth seems to be a more important reproduction strategy. It was found also that species diversity, seed production and thus germination on peatlands differ greatly from those of marshes and other wetlands. However, seeds buried in peat deposition may survive over centuries.

Acknowledgements: I am grateful to Jukka Laine, Ph.D. and Harri Vasander, Ph.D. for valuable comments on the manuscript. This study was financially supported by the Graduate School of Forest Ecology, Universities of Helsinki and Joensuu.

REFERENCES

Aapala, K., Lindholm, T. & Heikkilä, R. 1995: Protected mires in Finland. — In: Moen, A. (ed.), Regional variation and conservation of mire ecosystems. Gunneria 70: 205–220.

Ahti, T. 1980: Vaccinium myrtillus L. Mustikka. — In: Jalas, J. (ed.), Suuri Kasvikirja III: 296–304. Otava, Helsinki.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — Ann. Bot. Fennici 5: 169–211.

Clymo, R. S. 1965: Experiments on breakdown of Sphagnum in two bogs. — J. Ecol. 53: 747–758.

Clymo, R. S. 1978: A model of peat bog growth. — In: Heal, O.W. & Perkins, D.F. (eds.), Ecological studies 27: 187–223. Springer-Verlag, Berlin.

Clymo,R. S. & Duckett, J. G. 1986: Regeneration of Sphagnum. — New Phytologist 102: 589–614.

Ekola, E. & Päivänen, J. 1991: Suometsätieteen laitoksen pysyvät koealat Hyytiälän ympäristön ojitetuilla soilla. Metsänhoidolliset koealat ja kasvukoealat. — Helsingin yliopiston suometsätieteen laitoksen julkaisuja 10: 1–112.

Giba, Z., Grubiòic D. & Konjevic, R. 1993: The effect of white light, growth regulators and temperature on the germination of blueberry (Vaccinium myrtillus L.) seeds. — Seed Sci. Technol. 21: 521–529.

Giba, Z., Grubiòic D. & Konjevic, R. 1995: The involvement of phytochrome in light-induced germination of blueberry (Vaccinium myrtillus L.) seeds. — Seed Sci. Technol. 23: 11–19.

Harper, J. L.1977: Population biology of plants. — Acad. Press, London. 892 pp.

Helsper, H. P. G. & Klerken, G. A. M. 1984: Germination of Calluna vulgaris (L.) Hull in vitro under different pH conditions. — Acta Bot. Neerlandica 33: 347–353.

Hobbs, R. J. 1985: The persistence of Cladonia patches in closed heathland stands. — Lichenologist 17: 103–110.

Hämet-Ahti, L., Suominen, J., Ulvinen, T., Uotila, P. & Vuokko, S. (eds.) 1986: Retkeilykasvio. 3. painos — Suomen Luonnonsuojelun Tuki ry., Helsinki. 598 pp.

Koponen, T., Isoviita, P. & Lammes, T. 1977: The bryophytes of Finland: An annotated checklist. — Flora Fennica 6: 1–77.

Jutila, H. 1994: Kosteikkojen siemenpankit. — Luonnon Tutkija 4: 128–134.

Laine, J., Minkkinen, K., Puhalainen, A. & Jauhiainen, S. 1994: Effect of forest drainage on the carbon balance of peatland ecosystems. — In: Kanninen, M. & Heikinheimo, P. (eds), The Finnish Research Programme on Climate Change. Second Progress Report: 310–316. Painatuskeskus, Helsinki 1995.

Laine, J., Minkkinen, K., Sinisalo, J., Savolainen, I. & Martikainen, P. J. 1997: Greenhouse impact of a mire after drainage for forestry. — In: Trettin, C., Jurgensen, M., Grigal, D., Gale, M. & Jeglum, J. (eds.), Northern forested wetlands: ecology and management: 437–447. Lewis Publ., Boca Raton-New York, London, Tokyo.

Leck, M. A. 1989: Wetland seed banks. — In: Leck, M. A., Parker, V. T. & Simpson, R. L.(eds.), Ecology of soil seed banks: 283–305. Acad. Press, San Diego.

McDonald A. W. 1993: The role of seedbank and sown seeds in the restoration of an English flood-meadow. — J. Veg. Sci 4: 395–400.

McGraw, J. B. 1987: Seed-bank properties of an Appalachian Sphagnum bog and a model of the depth distribution of viable seeds. — Can. J. Bot. 65: 2028–2035.

McGraw, J. B., Vavrek, M. C. & Bennington, C. C. 1991: Ecological genetic variation in seed banks I. Establishment of a time transect. — J.Ecol. 79: 617–625.

Moore, J. M.& Wein, R. W. 1977: Viable seed populations by soil depth and potential site recolonization after disturbance. — Can. J. Bot. 55: 2408–2412.

Nicholson, A & Keddy, P. A. 1983: The depth profile of a shoreline seed bank in Matchedash Lake, Ontario. — Can. J. Bot. 61: 3293–3296.

Ødum, S. 1965: Germination of ancient seeds; floristical observation and experiments with archaeologically dated soil samples. — Dan. Bot. Ark. 24: 1–70.

Poschlod, P. & Pfadenhauer, J. 1989: Regeneration vegetativer Sprobteilchen von Torfmoosen. Eine vergleichende Studie an neun Sphagnum-Arten. — Telma 19: 77–88.

Ruuhijärvi, R. 1983: The Finnish mire types and their regional distribution. — In: Core, A. J. P. (ed.), Mires: swamp, bog, fen and moor. 4B. Regional studies: 47–67. Elsevier, Amsterdam.

Salonen, V. 1992: Plant colonization of harvested peat surfaces. — Biol. Res. Rep. Univ. Jyväskylä 29: 1–29.

Sastroutomo, S. S. 1981: Turion formation, dormancy and germination of curley pondweed, Potamogeton crispus L. — Aq. Bot. 10: 161–173.

Schneider, R. L. & Sharitz, R. R. 1988: Hydrochory: A critical influence in regeneration of a bald cypress-water tupelo forest. — Ecology 69: 1055–1063.

Smith, L. M. & Kadlec, J.A. 1985: The effects of disturbance on marsh seed banks. — Can. J. Bot. 63: 2133–2137.

ter Heerdt, G. N. J. & Drost, H. J. 1994: Potential for the development of marsh vegetation from the seed bank after a drawdown. — Biol. Conserv. 67: 1–11.

Van der Valk, A. G. & Davies, C. B. 1978: The role of seedbanks in the vegetation dynamics in prairie glacial marshes. — Ecology 59: 322–335.

Van der Valk, A. G. & Davis, C. B. 1979: A reconstruction of the recent vegetational history of a prairie marsh, Eagle Lake, Iowa, from its seed bank. — Aq. Bot. 6: 29–51.