DEMOGRAPHY AND RECRUITMENT OF SCOTs PINE ON RAISED BOGS IN EASTERN SWEDEN AND RELATIONSHIPS TO MICROHABITAT DIFFERENTIATION

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Abstract: Scots pines (Pinus sylvestris) growing on open bogs occur preferentially on hummocks and on the margin of the bogs. To assess which life history stages lead to this uneven distribution, we studied how variation in the ground-water level influences recruitment and mortality.

In a sowing experiment, the germination was high, 76% on hummocks and 66% in hollows, but it was not significantly different between the microhabitats. Seedling and juvenile pine survival was significantly lower in hollows than on hummocks. The demography of pines in three permanent plots, which represent open bogs, marginal pine forests, and their transition zone, was followed over more than 10 years. Recruitment from seeds was high in 1993 and 1994 compared to earlier surveys and was succeeded by high mortality among the recruits. Events in certain years have profound, long-term effects on the population. High mortality (ca. 60%) of the established pines in the marginal pine forest occurred in 1981. Pines growing close to the ground-water table had a lower survival probability than pines growing at a higher elevation. Differences in seedling survival seem more important than germination success in determining the uneven distribution of pines on the bog.

Key Words: distribution patterns, germination, ground-water level, mire, mortality, permanent plots, Pinus sylvestris, seedling, size distribution, survival

INTRODUCTION

Distribution patterns of tree species growing at or beyond the limit of their continuous distributions are often scattered, with small groups or individual trees spread in the border zone (Tranquillini 1979, Walter 1979, Kimmins 1987, Hennon et al. 1990). Tree distribution is limited by the availability of seeds, germination conditions, and occurrence of safe sites for the different life stages (Harper 1977, Fenner 1985). Environmental conditions that are optimal for an early life stage may be suboptimal or even fatal for a later stage (Schupp 1995) and vice versa.

Scots pine (Pinus sylvestris L.) occurs on dry and shallow soils as well as on bogs. Ombrotrophic bogs have a high and usually constant water level, low pH, and low nutrient content (Sjörs 1948, Du Rietz 1954). Scots pine lacks aerenchyma (Hesselman 1910, Metsävainio 1931) and has a shallow but very extensive root system in the uppermost 10 cm of aerated peat (Melin 1917, Kokkonen 1923, Backéus 1990, Laiho and Finér 1996). Approximately 22% of their total mass is allocated to the roots (Ohlson 1995).

Typical east Swedish bogs have a marginal forest of low pine trees gradually thinning out on the slope toward the central open bog. On the open bog, there are hummock banks oriented against the slope, some of them with small pines, and between them wet hollows usually without pines. The marginal forest, the open bog, the hummocks, and the hollows differ in degree of tree cover, in field and bottom layer composition, and in elevation above the ground-water table.

Previous studies of pine populations on Swedish mires (Ågren et al. 1983, Ågren and Zackrisson 1990) have been based on static descriptions of age and size structures. Conclusions about stand development and history in such studies are uncertain if demographic processes (e.g., recruitment and mortality) vary in intensity over time (Johnsson et al. 1994). Several observations from southern Sweden suggest that tree cover on mires has increased during the last century (Åberg 1992, Ihse et al. 1992), but the reasons for this are unknown. Earlier studies on conifer regeneration on wetlands were concerned with the germination and survival on different substrates (Hörnberg et al. 1992, Ohlsson and Zackrisson 1992, Groot and Adams 1994, St. Hilaire and Leopold 1995), but few studies related establishment and survival to ground-water level on ombrotrophic bogs.
The aim of this study was to determine reasons for the uneven distribution of pines on ombrotrophic bogs. We combined long-term (up to 15 years) population monitoring with experiments to achieve a more dynamic view of pattern and processes in the pine population. We followed recruitment and mortality in natural populations in three bog habitats: marginal forest, an intermediate transition zone, and open bog. We related the population processes to differences in vascular plant and bryophyte cover and to elevation above the ground-water table. For a more detailed understanding of the processes causing the uneven occurrence of pines on hummocks and hollows, we conducted a germination and survival experiment with seeds and juvenile plants in these two microhabitats.

MATERIALS AND METHODS

Study Sites

The main study site is Ryggmossen, a typical east Swedish raised bog ca. 25 km NW of Uppsala (60°03' N, 17°20' E) at an altitude of ca. 60 m above sea level. Because of the high conservation value of Ryggmossen, a second bog, Åkerlänna Römosse, situated ca. 21 km NW of Uppsala (60°01' N, 17°22' E) at an altitude of ca. 45 m above sea level was chosen for the experimental studies. The precipitation in both areas is ca. 600 mm per year. The bogs have the same developmental history; they were ancient lakes that became choked with fen vegetation and were eventually dominated by Sphagnum species (Eriksson 1912, Du Rietz and Nannfeldt 1925). Åkerlänna Römosse has, like Ryggmossen, a marginal pine forest and a central open bog, but here the lagg fen was drained in the beginning of this century, and peat has been extracted from parts of the marginal pine forest. However, the open bog shows no signs of influence from draining. For further details about the vegetation and the developmental history of Ryggmossen, see Du Rietz (1950) and Hällingbäck and Sjörs (1990); for Åkerlänna Römosse, see Eriksson (1912) and Sjörs (1948). The ground-water level on Ryggmossen was monitored by Rydin (1986) during the period 1981–84.

Germination and Survival of Sown and Planted Pines

To study how the different environmental conditions in hummocks and hollows affect pine establishment, we conducted an experiment in which seed germination and survival of seedling and juvenile pines were tested in both hummocks and hollows. On 28 June 1993, ten plots in hummocks and ten plots in hollows were established on the open part of Åkerlänna Rö-

mosse. The plots were placed on distinct hummocks or in hollows, large enough for a 50 x 60 cm plot and with a homogeneous Sphagnum cover. The hummock plots were dominated by Sphagnum fuscum (Schimp.) Klinggr. and small amounts of Calluna vulgaris (L.) Hull. Empetrum nigrum L. or Eriophorum vaginatum L. were present in a few of the plots. The hollow plots were in lawn communities (sensus Sjörs 1948) dominated by Sphagnum cuspidatum Hoffm., and in the field layer, Eriophorum vaginatum dominated. The hummock plots were significantly higher above the ground-water table than the hollow plots (32.2 cm ± 5.2 s.d. and 11.5 cm ± 1.8 s.d. (t = 12.1, P < 0.001), respectively).

Each plot was divided into 10 x 10 cm subplots. In 15 subplots, a juvenile pine (one-year-old and bare rooted) was planted, and in 12 alternate subplots, three seeds were sown (i.e., 36 seeds per plot). The roots of the juvenile pines were washed with distilled water to remove excessive nutrients. Both the seeds and the juvenile pines had northern Uppland provenance, and they were grown at Lugnets nursery, Bålsta, Uppland. The seeds were quality-controlled with a viability of ca. 95 %.

The plots were examined five times in 1993: June 28, July 14 and 22, August 13, and October 20; twice in 1994: June 18 and November 7; and again on August 24 1995. At each examination, the mortality of the juveniles and the mortality of the seedlings were recorded. Since only one seed per habitat type germinated after August 13, the cumulative number of seeds that had germinated on that day was used as a basis for the mortality calculations. A large part of the seedlings disappeared, these seedlings were considered as dead in the mortality analysis. Comparison between hummocks and hollows of percent germination was made by t-test, and comparison of mortality of juveniles and seedlings over time was made with repeated measurements ANOVA (SAS Institute Inc. 1989, Scheiner 1993) after arcsin transformation.

Pine Demography

Three permanent plots (10 x 10 m) were selectively established in three different habitats on Ryggmossen: on the open bog, in the transition zone, and in the marginal pine forest. The open bog plot was situated in an area with scattered pines, the few pines that grow there are rarely more than 0.5 m tall. Pines in the marginal pine forest are usually not more than 10 m tall. The forest has about 1000 stems / ha with a diameter > 10 cm at ground level. In the transition zone, no pines have a diameter > 10 cm, but there are many