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Veikko Salonen

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Academic Dissertation

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PLANT COLONIZATION OF HARVESTED PEAT SURFACES

Veikko Salonen

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Revegetation of initially bare peat surfaces, created by industrial peat harvesting, was studied over the years 1984-92 at several sites in Finland. Both a field survey and a field experiment approach were used to examine influences of both biotic and abiotic factors on the rate and pattern of revegetation.

In general, the harvested peat surfaces were colonized by a low number of plant species. The dominating species were all perennials and native of nutrient-poor habitats. Substantial differences were found between sites in the rate at which the harvested surfaces were colonized by plants. Likewise, species composition of the early successional plant communities was found to vary a lot. Significant differences were found in physical and chemical characteristics of the peat substrate between sites. These differences were demonstrated to account for much of the variation in the rate of revegetation and structure of the plant communities.

Sites with a thick peat layer, and surface peat with high content of soluble phosphorus and ammonium nitrogen were likely to become densely occupied by *Eriophorum vaginatum* alone. Different grass species were likely to dominate at sites with an excess of nitrate nitrogen over ammonium nitrogen and a thin peat layer. Woody species seemed to favour sites with intermediate values of these environmental variables.

Large differences were observed in the growth in size of populations during the first five years of colonization at one study site. The rate at which different species colonized the bare peat surface was determined largely by their dispersal ability, growth rate and mode of reproduction. During the five year period, no associations were found between the three most abundant species, *Eriophorum vaginatum* and *Pinus sylvestris* with homogeneous spatial patterns and *Carex rostrata* with a clumped pattern. During the prolonged stage of colonization, the importance of competition or other interspesific interactions in directing the early succession was found to be low. However, artificial plant cover was found to facilitate establishment of three abundant species and inhibit the establishment of one.

Numbers of seeds of different species dispersed onto two newly abandoned peat harvesting sites differed substantially from those of established plant individuals of these species. The discrepancy between number of seeds and seedlings was most striking in *Betula* spp. and *Calamagrostis* spp. The relative importance of seed availability was found to be greater than that of soil quality to the rate of colonization. However, the failure of many species in establishing on the harvested peat surface, despite an abundant supply of their seeds, emphasizes the importance of substrate quality to colonization. This was also demonstrated by two separate field experiments, both with application of NPK fertilizer. In these experiments, plots with a presumably similar supply of propagules but dissimilar supply of nutrients differed significantly in terms of amount and composition of established vegetation.

Key words: Plant colonization; peat surface; substrate quality; seed availability; community structure; spatial patterns; intraspecific interactions

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List of original publications

This thesis is based on the following articles, which will be referred to in the text by their Roman numerals:

I. Salonen, V. 1987: Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. - Holarctic Ecology 10: 171-174.
https://doi.org/10.1111/j.1600-0587.1987.tb00755.x

II. Salonen, V. 1990: Early plant succession in two abandoned cut-over peatland areas. - Holarctic Ecology 13: 217-223.
https://doi.org/10.1111/j.1600-0587.1990.tb00611.x

III. Salonen, V. & Setälä, H. 1992: Plant colonization of bare peat surface - relative importance of seed availability and soil. - Ecography 15: 199-204.
https://doi.org/10.1111/j.1600-0587.1992.tb00025.x

IV. Salonen, V., Penttinen, A. & Särkkä, A. 1992: Plant colonization of a bare peat surface: population changes and spatial patterns. - Journal of Vegetation Science 3: 113-118.
https://doi.org/10.2307/3236005

V. Salonen, V. 1992: Effects of artificial plant cover on plant colonization of a bare peat surface. - Journal of Vegetation Science 3: 109-112.
https://doi.org/10.2307/3236004

VI. Salonen, V. 1992: Revegetation of harvested peat surfaces in relation to substrate quality: field survey and experiments. Manuscript.
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Contents

1. INTRODUCTION

The currently prevailing view considers succession as a complex process driven by many processes acting simultaneously (Hils & Vankat 1982, Huston & Smith 1987, Miles 1987, Walker & Chapin 1987). The relative importance of facilitation, tolerance and inhibition (Connell & Slatyer 1977), and other processes involved (e.g. competition) may vary according to environment and stage of succession. Examples of facilitation, for instance, come mainly from harsh environments and from the earliest stages of community development (Connell & Slatyer 1977, Turner 1983, Finegan 1984, Walker & Chapin 1987). Competition, in turn, is likely to play an important role in any post-colonization stage of succession (Huston & Smith 1987). Whatever the mechanisms behind the successional changes, it is individuals and populations that change. Therefore, autecological and life history characteristics of the dominating species, such as dispersal ability, growth rate, pattern of reproduction, and shade tolerance can be responsible of much of the successional changes in species composition and species' abundances throughout the process (Noble & Slatyer 1980, Sousa 1980, Hibbs 1983, Walker et al. 1986, Huston & Smith 1987).

Successional seres have been traditionally devided into two categories, primary and secondary (sensu Clements 1916). By definition, successions on new, previously unvegetated bare areas are primary, while all other successional seres are secondary. There are successional seres, however, which do not fall neatly into either category (Miles

1979). Succession on initially bare peat surfaces formed by peat harvesting activities gives an example of a successional sere which is somewhat intermediate in character between primary and secondary. The substrate is secondary by nature as it is composed of material formed by vegetation which existed at the place previously. A feature characteristic of primary succession is that the harvested peat surfaces are initially completely devoid of plants and of viable propagules in the soil (Curran & MacNaeidhe 1986).

Seed dispersal, seed germination, and seedling survival form the three major stages of plant colonization (Wood & Morris 1990). The rate of colonization and structure of the early successional plant community may be affected by any of these component stages. Several authors, e.g. Margalef (1968), Sousa (1984), and Vitousek & Walker (1987) have suggested that the composition of pioneer communities is determined by species' dispersal abilities and chance arrival during the initial period of colonization when competition is low. Seed dispersal can be expected to strongly affect colonization of the harvested peat surfaces since initiation of plant populations there rests on propagules available exclusively through the dispersal process.

A large gap often exists between the number of seeds dispersed into an area and the actual number of seedlings established (Sheldon 1974). A major part of that gap is due to the facts that seeds often have very strict requirements for the conditions in which they are able to germinate, and that the amount of microsites where all of these requirements are fulfilled is limited in any habitat. Seed germination is known to be highly responsive to the physical environment at the soil surface (Oomes & Elberse 1976, Winn 1985). The harvested peat surfaces offer the dispersing seeds an adverse environment in which moisture conditions can vary from one extreme (drought) to another (water-logging). In addition to water-stress, the emerged seedlings are faced with substrate conditions characterized by high acidity and low levels of nutrients essential for their growth (Lumme 1989).

An understanding of the entire process of succession implies an understanding of the dynamics of invasion (Pickett et al. 1987). With few exceptions, the soil at the beginning of secondary succession is never without propagules of some species. Egler (1954) noted that most species are present already at the outset of succession or colonize within a few years, and that this 'initial floristic composition' has lasting effects on the whole sequence. Direction of investigations to the earliest stages of succession is necessary also because the responses to disturbances are known to be most rapid then (Huston & Smith 1987).

Ten thousands of hectars of harvested peat surfaces will be formed within a few years in Finland. Revegetation of this previously non-existing habitat has not been studied. However, a few investigations of tree growth on harvested peat have been made (Kaunisto 1987 and references therein, Lumme 1989). Both field surveys and field experiments were made to obtain answers to the following main questions of this study:

1. What are the patterns and the rate at which the harvested peat surfaces with varying soil conditions are colonized by plants?
2. What are the dominating plant colonists and what life history characteristics are represented among them?
3. To what extent is the rate and pattern of colonization affected by seed availability, varying substrate conditions or interactions among species?
4. Do the early stages of plant succession on harvested peat surfaces follow any one of the known models of succession?

2. STUDY AREAS AND METHODS

The study was conducted in eight different peat harvesting areas situated in the southern part of Finland (Fig. 1). Distance between the westernmost and easternmost study areas was 360 km, whereas variation between locations of the study areas in the south-north direction was remarkably less. The amount of peat removed and thus thickness of the remaining peat layer varied a lot between and within different areas depending on, for instance, quality of the peat (e.g. ash content, rate of decomposition), stoniness of the site or chances of further reclamation. Likewise, variation between the eight areas in quantity of bare peat surfaces was high.

Sites varying in successional age (0-12 years), substrate quality and amount of established vegetation were selected in these areas to serve as study sites. Common to most sites was their location at the edge of the harvesting area. They were similarly drained and did not differ in the technique used for harvesting. The study sites had been abandoned immediately after the cessation of peat harvesting, with no disturbance from human activity except for fertilization with slurry at one site. The study areas and sites are described more exactly in each individual paper.

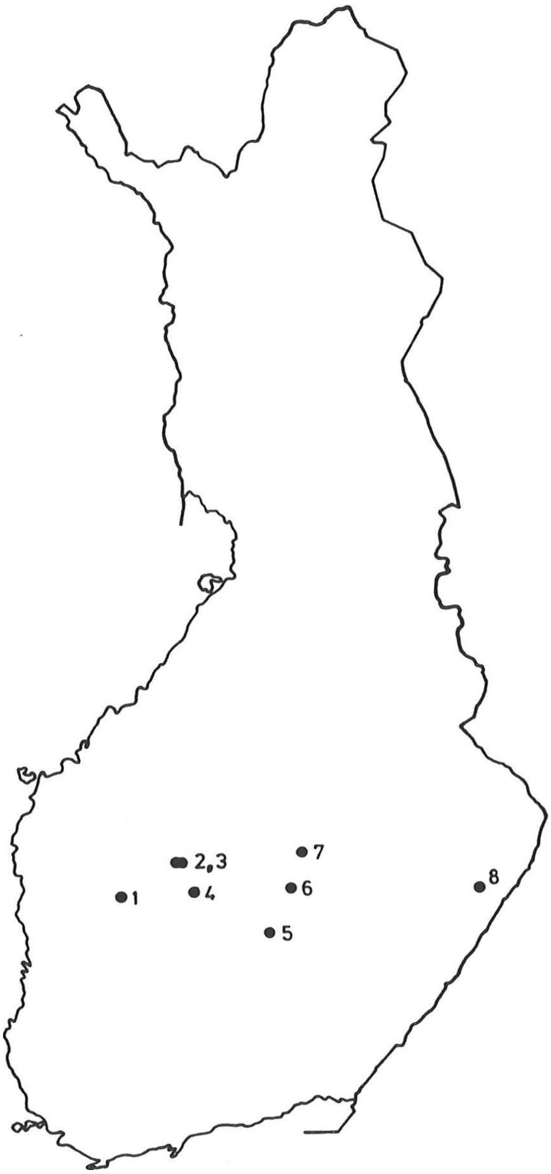

Figure 1. Names and locations of the study areas: 1= Aitoneva (Kihniö), 2= Riitasuo (Ähtäri), 3= Mustasuo (Ähtäri), 4= Lehtosuo (Keuruu), 5= Haapasuo (Leivonmäki), 6= Läyniönsuo (Hankasalmi), 7= Rastunsuo (Rautalampi), 8= Valkeasuo (Tohmajärvi).

2.1. Vegetation sampling and soil analyses (II, VI)

Each study site had been drained by ditches at intervals of 15-20 m. A 10 x 20 m plot was established in the middle of the 15-20 m wide strip for random sampling of the vegetation. The sampling was randomized by using random figures. The vegetation was analysed either by estimating the percentage cover of each species growing in 1.5 x 1.5 m squares (VI) or by harvesting the above-ground parts of the field and ground layer vegetation in 0.25 m^2 plots (II).

Soil samples were taken with a corer (area 75 cm^2, depth 10 cm) and used for analyses of amount of dry matter/volume and ash content of the peat. Soil pH, conductivity, nutrient content (water soluble NO_3-N, NH_4-N, P, K) and particle size distribution (mean particle size) were determined from samples taken from the surface peat (0-3 cm). Contents of the nitrogen compounds were measured ion-chromatographically and that of phosphorus spectrophotometrically, whilc potassium was analysed using an atomic absorption spectrophotometer. The particle size distribution was analysed with a laser diffraction method.

2.2. Analysis of population dynamics and spatial patterns (IV)

The two Cartesian coordinates were determined with 1 cm accuracy for every individual plant established during the first five years following the cessation of peat harvesting in a 10 x 25 m plot in area 3. Separated shoots or rosettes of species with vegetative growth were considered as individuals. Based on accurate yearly mappings of the established individuals, establishment of any new individuals could be reliably detected. Likewise, mortality among plants established earlier could be recorded.

Spatial point patterns formed by populations of the dominating species were analysed with Ripley's *K*-function or its transformed version *L*-function (Ripley 1981) and with the *g*-function (Stoyan et al. 1987). The so-called conditional Monte Carlo test was applied for testing associations between the dominating species. Detailed explanations of the ideas and use of these functions and tests are given in paper IV.

2.3. Seed trapping and analysis of the soil seed bank (I)

The composition of seed rains entering two peat harvesting sites (both sites in area 3), the one being abandoned since cessation of peat harvesting six years earlier and the other abandoned one year earlier, was investigated by collecting the dispersing seeds with water-filled traps during two growing seasons. The traps, each 0.20 m^2 in area, were dug to the level of the soil surface and placed in two rows in a series of five. Numbers of seeds dispersing in winter were estimated from snow samples, 0.25 m^2 each. Soil samples were taken at these sites with a corer (area 9.5 cm^2, depth 20 cm) to analyse the composition of the soil seed bank. The number of seedlings of each species growing in ten 25 m^2 plots established in the immediate vicinity of the traps was counted in two successive autumns.

2.4. Field experiments (III, V, VI)

To study the relative importance of propagule availabity and soil quality to the rate of colonization, a field experiment was conducted in which peat was exchanged between two nearby sites (in areas 2 and 3) of similar successional age (4 years). A preceding field survey had revealed that one site (at Mustasuo) was very slowly colonized by few plant species in contrast to the other site (at Riitasuo) which was found to be colonized rapidly with several species. A 10 cm thick layer of surface peat was dug up from eight 50 x 50 cm quadrats at one site and placed in holes of similar dimensions at the other. Number of plants established in these plots and in the eight control plots were counted at the end of three successive growing seasons. Three separate soil samples were taken during one growing season from each plot for the determination of soil biota, biological activity (expressed in terms of CO_2-production) and water content. A separate 'microcosm experiment' was made to measure mineralization rates of N and C in the two type of peat soil.

A field experiment was devised in the Rastunsuo area (area 7 in Fig. 1) to test the hypothesis that the first colonists of the harvested peat surfaces promote the establishment of species arriving later by ameliorating the adverse substrate conditions. Ten pairs of 40 x 40 cm plots were located in gaps between established vegetation. The plots in each pair were randomly assigned to the test or control group. The area of each test plot was covered with 16 plastic plant imitations corresponding to a cover of 80 % of the plot area. The vegetation established in the plots was harvested and analysed after two growing seasons. Five additional pairs of plots were established to test the effects of the artificial plant cover on soil moisture and air temperature at the soil surface. Soil samples were taken from the uppermost (0-1 cm) peat layer for analyses of the soil water content and air temperatures were measured at three dates during one summer.

The influence of improved nutrient availability on vegetation establishment was studied with a field experiment at the Mustasuo area (area 3). Ten pairs of plots, 1 m^2 each, were randomly located in places with no established plants. The two plots of each pair were randomly assigned to the test or control group. The test plots were fertilized with 20 g of NPK 11-11-20 -fertilizer while no fertilizer was applied to the control plots. The numbers of plants established in the plots were counted after the first and the second growing season.

The influences of fertilization, liming and irrigation on colonization of bare peat surface were studied in an experiment conducted at two sites with the same successional age (1.5 years), one situated in Riitasuo (area 2) and the other in Mustasuo (area 3). Ten randomly located plots, each 2.4 x 9.6 m in size, were devided into eight 1.2 x 1.2 m subplots. The subplots were randomly assigned into the following treatments: 1) fertilization (F) with 25 g of NPK, 2) liming (L) with 30 g of lime, 3) watering (W) with one litre of destilled water per m^2 per week during three months, 4) F+L, 5) F+W, 6) L+W, 7) F+L+W, 8) no treatment (control, C). The numbers of plants growing in the area of a 1 m^2 square established in the middle of each plot were counted and species' above-ground dry masses were determined at the end of the first growing season.

3. RESULTS AND DISCUSSION

3.1. Rate and pattern of plant colonization

The rate at which the harvested peat surfaces were colonized by plants differed substantially between different sites. For example, two adjacent sites (one in Riitasuo and the other in Mustasuo) with the same successional age (six years) were observed to differ totally in species composition and amount of established vegetation. The Riitasuo site was colonized with 22 field layer species and eight ground layer species whereas the numbers of field and ground layer species at the Mustasuo site were eight and one, respectively. The difference in above-ground biomass of the established vegetation was over 11-fold in favour of the Riitasuo site. Many of the first species to occupy the Riitasuo site were annuals (weeds), most of which were soon replaced by perennial species. In contrast, the slowly revegetated Mustasuo site was colonized exclusively by perennials (II).

The peat harvesting activities cause marked ecological changes in the substrate. Moisture conditions in particular are greatly altered. Due to insufficient moisture no *Sphagnum* species were found on the harvested peat surfaces. Although the course of early succession at many sites was towards communities with features of bog vegetation, real bog vegetation with a ground layer dominated by *Sphagnum* will not develop unless the ground water level is much artificially raised.

A five year study of population changes at a site in Mustasuo demonstrated that the highest growth in population size was achieved by *Carex rostrata* and *Eriophorum vaginatum*, both species with good tolerance of low nutrient contents and acidity of the substrate. Also common to these two species is their ability to reproduce rapidly, either vegetatively or sexually. A drastic drop in population size was observed for *Pinus sylvestris* and a smaller one for *Betula spp.* during the five year period. The big yearly changes in population size of *Pinus* resulted mainly from fluctuations in availability of propagules from the allochtonic seed sources. Most *Pinus* seedlings were able to withstand the severity of the habitat for two or three years, whereas the vast majority of *Betula* seedlings died during the first summer.

The argument of e.g. Grubb (1987) and Grime (1987), that pioneers at sites poor in resources are typically long-lived, was well supported by these data: the vast majority of species colonizing the study sites and all of the dominating species were perennials. Another feature common to the dominating colonists was that they were species native of nutrient-poor habitats. These types of species compositions could result partly from the fact that the seed sources adjacent to harvested peat surfaces tend to consist of these species. However, many although not all of the dominant colonists had seeds capable of long-distance dispersion. A feature characteristic of the most successful colonists was rapid growth to maturity followed by efficient reproduction either by seed (e.g. *Eriophorum vaginatum*, *Deschampsia cespitosa*) or vegetatively (e.g. *Carex rostrata*). *Eriophorum vaginatum* and *Carex rostrata* were not found to differ in number of established individuals after five years of colonization of a site in the Mustasuo peat harvesting area suggesting that two species with substantial diffrences in dispersibility of propagules and prevailing mode of reproduction can be equally successful in colonizing the bare peat surfaces (IV).

3.2 Colonization in relation to substrate quality (II, VI)

The field survey made at several sites (VI) demonstrated that conditions following the cessation of peat harvesting can vary substantially between sites. Thickness of the peat layer above the mineral soil ranged from 11 to 124 cm, ash content of the surface peat from 3 to 25 % and pH from 4.0 to 5.4. Furthermore, manyfold differences in contents of different nutrients between sites were found. These differences clearly affected the rate and pattern of revegetation.

In a CCA-ordination of species recorded in 170 sample squares, *Eriophorum vaginatum* was located far from the other species. *Eriophorum* characteristically dominated sites with a thick peat layer, and high content of soluble phosphorus and excess of ammonium nitrogen over nitrate nitrogen in the surface peat. Grasses and most of the herbaceous species were located at the opposite end of the phosphorus/peat thickness gradient. They were also located at the nitrate nitrogen side of the nitrogen gradient. Mean particle size of the surface peat also strongly affected the ordination of species. The location of woody species and mosses in the middle part of the ordination diagram indicates that these species favoured sites with intermediate values of the measured environmental variables.

Plots fertilized with 20 g per m^2 of NPK differed significantly in the number of established plants from those without fertilization in two succesive years (paired t-test, $p<0.01$ for both years). The two types of plots also differed substantially in species composition. At the end of the first growing season, seedlings of ten species had colonized the fertilized plots while only four species were recorded in the unfertilized plots. *Epilobium angustifolium* and *Juncus alpinoarticulatus* were the dominating species of the fertilized plots while totally absent from the unfertilized plots. After two seasons, the fertilized plots were densely revegetated with mosses (*Pogonatum urnigerum, Pohlia nutans, Polytrichastrum longisetum*), but the unfertilized plots remained entirely devoid of them.

Plots fertilized with 25 g per m^2 of NPK differed significantly in biomass of vegetation established during one season from those without application of the fertilizer in two sites, one in Mustasuo and the other in Riitasuo (ANOVA, $p<0.001$ for both sites). In contrast, liming with 30 g per m^2 of dolomite lime or regular application of a small amount of distilled water did not cause significant effects on plant colonization.

A major difference in biomass of *Epilobium angustifolium* was found between the fertilized and unfertilized plots in Mustasuo. Otherwise, the plots fertilized with NPK differed only slightly in species composition from all other plots. In contrast, substantial differences were found in the species composition between the fertilized and unfertilized plots in Riitasuo. The most sriking differences between the two types of plots were found in the amount of *Calamagrostis epigejos*, three *Epilobium* species, *Gnaphalium uliginosum*, *Juncus alpinoarticulatus* and *Rorippa palustris*.

In conclusion, both the field survey and the two experiments demonstrated that plant colonization and early succession on the harvested peat surfaces can be strongly affected by the quality of the substrate. The field experiments with fertilization treatments were able to show that even a little improvement in nutrient availability can markedly influence species composition and the rate at which the bare peat surfaces becomes revegetated. These results clearly show that nutrients are insufficiently available for the growth of many of the species arriving on the peat substrate as seeds. By an application of fertilizers, NPK in particular, the revegetation process can be much accelerated. This is important from the point of landscape improvement.

Thickness of the remaining peat layer, amount of phosphorus and nitrogen in the surface peat, the balance between the two soluble compounds of nitrogen, ash content and mean particle size of the surface peat were able to explain much of the variation between sites in revegetation. *Eriophorum vaginatum* can be expected to dominate the early successional vegetation at sites with a thick peat layer and high contents of phosphorus and ammonium nitrogen. Sites with a thin peat layer and high content of nitrate nitrogen are likely to become dominated by grasses and weeds. *Deschampsia cespitosa* seemed to favour sites with a high ash content, while *Calamagrostis* species were more abundant at sites with a lower ash content.

3.3. Colonization in relation to propagule availability (I)

A total of 419 living diaspores m^{-2} in one year and 2559 m^{-2} in the next were caught in traps placed in the site where peat harvesting had ceased 6 to 7 years earlier. The number of living diaspores trapped in the site with a successional age of one to two years was 134 and 2107, respectively. The large difference between the two years results mainly from the high number of propagules of *Betula* spp. and *Calamagrostis* spp. dispersed to both sites in the latter year. For *Betula* spp. that year was a 'mast year' (sensu Harper 1977). The two sites differed only slightly in the species composition of the seed rain, whereas marked differences were found in the numbers of diaspores of some species.

Up to the end of the second year of study, 37 seedlings m^{-2} on average had established in the site with the higher successional age. 99.5 % of these seedlings were those of *Eriophorum vaginatum*, which was the dominating species of the vegetation established on that site. Much fewer *Eriophorum* seedlings, but substantially more seedlings of *Pinus sylvestris*, had established in the other site, where the average density of all plants was 1.3 m^{-2}. Thus, a striking difference existed between the number of propagules dispersed and seedlings established in both sites.

Numbers of suitable microsites offered in these two sites proved to be more or less limited for all species. The discrepancy between the number of diaspores and seedlings was especially notable in *Betula* spp.: no *Betula* seedlings were found in one site and only two seedlings grew in the other although ca. 1880 and 1930 *Betula* spp. propagules m^{-2} were trapped in these sites, respectively. No safe sites for *Calamagrostis* spp., a taxon well represented in the seed rain, existed in these two particular sites. The harvested peat surfaces of these two sites clearly favoured species native of peat substrate more than other species. The unsuccesful species were those not adapted to tolerate some of the characteristic features of the harvested peat substrate: acidity, low supply of nutrients, drought or occasional deficit of oxygen during periods of excess water. These data thus clearly demonstrated that it is not only the availability of propagules but also the quality of the substrate that determines the structure of the early successional plant community.

3.4. Relative importance of propagule availability and substrate quality to colonization (III)

The relative importance of seed availability was found to be higher than that of soil quality to plant colonization of two former peat harvesting sites. All plots (irrespective of origin and quality of the subtrate) at one site (Mustasuo) were slowly colonized by few (7 in total) plant species, while all plots at the other site (Riitasuo) were rapidly colonized by more numerous (16) species. After three growing seasons, plant biomass in plots with peat dug up from Mustasuo and transplanted in Riitasuo was more than 900-fold compared with that in plots with the same kind of soil in Mustasuo. Correspondingly, plant biomass in plots with peat native of Riitasuo and transplanted in Mustasuo was 340 times less than that in plots with the same kind of peat in Riitasuo. At the Mustasuo site, plant biomass was significantly higher in the transplanted plots compared with the native plots (Mann-Whitney U-test, $p<0.05$), while only a slight difference in favour of the latter was found between the two types of plot at the Riitasuo site.

It can be concluded that the difference in amount and composition of adjacent vegetation and thus in supply of propagules was the major factor behind the substantial difference in the rate of colonization between the two sites. Despite differences in certain biotic and abiotic soil characteristics, such as microbial activity, ash content, particle size distribution and contents of nutrients required by plants for growth, soil quality was only a minor factor affecting colonization. However, much larger differences in substrate quality accomplished experimentally by a fertilization treatment caused significant impacts on the rate and pattern of colonization.

3.5. Colonization in relation to other species (IV, V)

The spatial point patterns of the three most abundant species, *Carex rostrata, Eriophorum vaginatum* and *Pinus sylvestris*, colonizing a 10 x 25 m plot of initially bare peat surface in a period of five years, were found to be independent of each other. Of the three species, *Carex rostrata* had a clearly clumped spatial pattern, while the two others had a homogeneous pattern. The spatial pattern of both *Eriophorum* and *Pinus* did not vary between places with *Carex* and those without *Carex* suggesting that the establishment of *Eriophorum* and *Pinus* was by no means affected by *Carex*. The density of the mainly vegetatively produced *Carex* shoots in the clumps was apparently too low for interspecific interactions to occur.

In contrast, some evidence of the ability of interspecific interactions to structure the early successional plant community was gained from an experimental study, in which plots covered densely with artificial plants differed significantly in the number of established seedlings from those with no cover after two seasons (paired t-test, $p<0.05$). The artificial plants promoted the establishment of *Betula, Salix phylicifolia* and *Deschampsia cespitosa,* but inhibited the establishment of *Epilobium angustifolium* significantly. Water content in the uppermost peat layer was significantly higher in the plots covered with the artificial plants, and air temperature on the level of the peat surface was significantly higher in plots without the artificial cover. Seed germination can be highly dependent on both of these environmental factors.

4. CONCLUSIONS

The harvested peat surfaces were found to vary substantially both in terms of physical and chemical properties of the substrate and in the rate and pattern of plant colonization. Despite variation in site conditions, a generalization can be made that the harvested peat surfaces form a severe habitat characterized by a high intensity of stress. Individual responses of the colonizing species to different stress factors (drought, water-logging, deficit of oxygen, acidity, shortage of nutrients) structured the early successional plant communities.

These data revealed certain attributes characterizing successful colonists of the harvested peat surfaces. The studied sites were mainly colonized by species native of peatlands and other nutrient-poor habitats. Based on the classification by Grime (1977, 1987) of three primary strategies in plants, the dominant colonists of harvested peat surfaces belong to the group of stress-tolerants. Some of the species colonizing the less unproductive peat surfaces fall into the category of stress-tolerant competitors.

Both propagule availability and soil quality were found to strongly influence the initiation and subsequent growth of populations on the harvested peat surfaces. Although the results of one experiment suggest that propagule availability is more important than soil quality for the rate of revegetation, they do not deny the importance of physical and chemical properties of the substrate demonstrated by other experiments. Very clearly, the colonization by plants of harvested peat surfaces is much of an interplay between these two basic factors. The initiation of each plant population definitely depends on the allochthonous propagules i.e. propagules dispersed to the site from elsewhere. Soil quality, in turn, can determine which of the species present in the seed rain are present also as established plants. Soil quality also strongly affects plant growth and survival and thus efficiency of the autocthonic seed production.

Success in colonizing the bare peat surfaces is determined largely by the life history characteristics of species. Among traits with the strongest effect on successful establishment and population growth are dispersal ability, growth rate, pattern of reproduction, and tolerance of the hostility of the substrate. The earliest stage of plant succession on the harvested peat surfaces appeared to be driven mainly by life history processes, while the importance of other processes with competitive, facilitative, and inhibitive interactions among species was less. The observed facilitation in establishment of three abundant species by artificial plants suggests, however, that facilitative interactions among species colonizing the harvested peat surfaces are possible; real plants might as well ameliorate the adverse site conditions in ways similar to those by the artificial plants and thus facilitate the establishment of species arriving later. The dense growth of *Polytrichum* species observed at some of the study sites can be expected to lead to inhibitive interactions between the mosses and the later arriving species. Competitive interactions are likely to increasingly affect the structure of the plant communities along with time.

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Selostus

Kasvillisuuden uusiutuminen turvetuotannosta vapautuneilla suonpohjilla

Kasvisukkession alkua, etenkin kasvien kolonisaatiovaihetta, tutkittiin vv. 1984-92 kahdeksalla turvetuotantoalueella ja näiden yli 20:llä turpeennoston jälkeen hylätyllä alueella Keski-Suomessa. Turpeennoston päättyessä täysin kasvipeitteettömien ja myös vailla maaperän siemenpankkia olevien suonpohjien kasvittumisnopeutta ja -tapaa ja näihin vaikuttavia bioottisia ja abioottisia tekijöitä selvitettiin sekä kenttätutkimusten että kenttäkokeiden avulla. Erityisesti tutkittiin kasvien elinhistoriallisten ominaisuuksien (esim. leviämiskyky, kasvutapa ja -nopeus, lisääntymistapa ja -nopeus, elinikä), siementarjonnan, lajien välisten interaktioiden ja kasvualustan ominaisuuksien vaikutusta kasvittumiseen.

Suonpohjien kasvittumisnopeudessa, kuten myös sukkession alkuvaiheessa olevan kasvillisuuden lajikoostumuksessa, esiintyi suurta alueiden välistä vaihtelua. Kasvittumisnopeuden ja -tavan havaittiin riippuvan alueiden välisestä vaihtelusta kasvualustojen fysikaalis-kemiallisissa ominaisuuksissa. Sekä kenttätutkimukset että -kokeet osoittivat kasvittumisen riippuvan etenkin ravinteiden määrästä suonpohjan pintaturpeessa. Erityisen selvänä turpeen ravinnetalouden merkitys tuli esiin kenttäkokeessa, jossa NPK-lannoitettujen koeruutujen kasvillisuuden maanpäällinen biomassa oli yhden kasvukauden jälkeen noin 1000-4500 -kertainen luontaisesti kasvittuneisiin kontrolliruutuihin verrattuna. Luontaiseen kasvittumisnopeuteen ja kasvillisuuden lajikoostumukseen vaikuttivat selvästi myös pintaturpeen keskimääräinen partikkelikoko ja jäljelle jätetyn turvekerroksen paksuus. Tupasvilla oli yleensä valtalajina alueilla, joiden jäljelle jäänyt turvekerros oli paksu, pintaturpeesta mitatun liukoisen fosforin määrä mahdollisimman suuri ja ammoniumtypen osuus kokonaistypestä nitraattityppeä korkeampi. Useat heinäkasvit esiintyivät valtalajeina ohutturpeisilla alueilla, joilla pintaturpeen liukoinen typpi esiintyi pääasiassa nitraattityppenä.

Turpeennoston päättyessä kasvipeitteettömien ja vailla maaperän siemenpankkia olevien turvepintojen kasvittuminen ei voi käynnistyä ilman ulkopuolelta tulevia siemeniä ym. leviäimiä. Tarjolla olevien siementen maaran vaikutus kasvittumisnopeuteen oli kasvualustan laatua suurempi kenttäkokeessa, jossa luontaisesti nopeasti kasvittuvan alueen pintaturvetta siirrettiin hitaasti kasvittuvalle alueelle ja päinvastoin. Toisaalta alueelle tulevan 'siemensateen' ja sukkession alkuvaiheen kasviyhteisön välillä havaittiin suuri määrällinen ja lajistollinen epätasapaino. Monet leviäiminä turvepinnoille saapuneista lajeista eivät esiintyneet kasviyhteisöissä lainkaan ja monen muun lajin yksilömäärät olivat mitättömiä siementarjontaan verrattuna. Kasvualustan ominaisuuksien merkitys turvepinnoille siemeninä saapuneiden lajien menestymiselle oli näin ollen myös suuri.

Alueella, missä kasvittumista seurattiin yksilökohtaisen tarkasti viiden ensimmäisen vuoden ajan, havaittiin suuria lajien välisiä eroja populaatioiden kasvunopeudessa. Erot populaatiokoon muutosnopeuksissa johtuivat paljolti alueita kolonisoivien lajien erilaisista elinhistoriallisista ja autekologisista ominaisuuksista. Parhaiten menestyivät vähäravinteisella ja happamalla kasvualustalla viihtyvät lajit, joilla on hyvä leviämiskyky ja jotka kykenevät lisääntymään nopeasti joko suvullisesti tai suvuttomasti. Kasvillisuuden valtalajeja muilla luontaisesti kasvittuneilla tutkimusalueilla olivat tupasvilla, heinät (hietakastikka, korpikastikka, nurmilauha) ja puuvartiset kasvit (koivut, mänty, kiiltopaju). Kasvillisuuden pohjakerroksen valtalajeja olivat nuokkuvarstasammal ja karhunsammalet. Rahkasammalia ei esiintynyt millään tutkimusalueella. Tutkimusalueiden kasvillisuudelle oli luonteenomaista vähälajisuus.

Kasvittumisen hitaudesta johtuen erilaiset sukkession kulkuun vaikuttavat kasviyksilöiden väliset interaktiot olivat hyvin vähäisiä alueella, missä kasvillisuuden kehittymistä seurattiin tarkasti viiden ensimmäisen kasvukauden ajan. Kolmen valtalajin (mänty, pullosara, tupasvilla) välillä ei havaittu minkäänlaista assosiaatiota. Männyn ja tupasvillan tilajakauma oli homogeeninen, pullosaran puolestaan voimakkaasti klusteroitunut. Kenttäkokeella havaittu keinotekoisen kasvipeitteen positiivinen vaikutus kolmen ja negatiivinen vaikutus yhden lajin kolonisoitumiseen kuitenkin osoitti, että kasviyksilöiden välisillä interaktioilla voi myöhemmin, populaatioiden tihetessä, olla huomattava merkitys sukkession kululle.

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ORIGINAL PAPERS

I

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IV

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V

EFFECTS OF ARTIFICIAL PLANT COVER ON PLANT COLONIZATION OF A BARE PEAT SURFACE

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Revegetation of harvested peat surfaces in relation to substrate quality: field survey and experiments

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