The succession of boreal forest vegetation during ten years after slash-burning in Koli National Park, eastern Finland

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The almost complete elimination of fire from forest management practises in Scandinavia has made post-fire succession rare and, consequently, generated conservation problems. The importance of fire in conjunction with slash-and-burn cultivation has been recognised as a management strategy. It is a potential tool for managing forest structure and regeneration processes in nature reserves. In this study we observed the first decade of vegetation succession after slash-burning. Prior to the study, most trees at the study site were felled and burned. The monitoring was carried out in three burned areas of different age and an unmanaged control forest. In addition to describing the responses of different plant species and plant functional groups to fire, multivariate methods were applied to illustrate community level changes. The results indicated succession processes at each hierarchy level in the recovering community. In general, the community switched from pioneer bryophyte mass abundances to graminoid dominance within ten years. Moreover, plant diversity seemed to have increased due to slash-burning. A total of 88 plant taxa (i.e. vascular plants, bryophytes and lichens) were observed in the sample plots during the study period, as compared with the 44 taxa observed in control plots. We concluded that slash-burning is an appropriate method for mimicking natural fires, at least from a botanical perspective, and may therefore be a forest renewal practise worth considering in special areas.

Key words: boreal forest, *Calamagrostis arundinacea*, *Ceratodon purpureus*, *Epilobium angustifolium*, fire, *Mnium stellare*, multivariate methods, slash-burning, vegetation succession

Introduction

Slash-and-burn agriculture is a cultivation method of cutting living trees to clear land, burn-ing the biomass after letting it dry, and planting a crop in the ashes in an appropriate season. During past centuries slash-and-burn agriculture was an important source of livelihood for people

in Finland and Scandinavia. For example, in 1860 approximately 50% of Finland's land area was influenced by slash-and-burn cultivation (Heikinheimo 1915). During the slash-burning era (ca. from 1600 to the late 1800s), human-induced fires shaped the landscape into a mosaic of coniferous, mixed, and deciduous forests and post-fire grasslands often used as pastures. According to fire history studies conducted in Fennoscandia (e.g. Zackrisson 1977, Lehtonen *et al*. 1996), the fire frequency in Sweden and middle Finland was between 30–60 years during the period of intensive shifting-cultivation. However, most of the fires were probably due to slash-burning and other human activities (Wallenius *et al*. 2004).

The increasing value of timber was the primary reason for the cessation of this traditional cultivation technique. Unfortunately, management for efficient timber production frequently disrupts the continuity of natural and man-induced forest processes. Thus, timber production does not generate as wide a range of habitats for forest organisms as did the former management regimes. Since maximum vegetation and floristic diversity is apparently attained when a spectrum of successional communities is maintained within the landscape (e.g. Louks 1970, Heinselman 1973), the prevailing management practices may pose a threat to landscape level diversity.

In boreal ecosystems, many plant species have evolved to depend upon fire for their survival (Shafi & Yarranton 1973). Therefore, a change in the fire regime, attributed to human-caused disturbances, such as logging and climate change, may also have important impacts on biodiversity in these ecosystems. Fire is also considered as an important source of heterogeneity in the boreal forest. At many scales, continuous production and maintenance of habitat heterogeneity is generally accepted to be important for biodiversity (*sensu* Kuuluvainen 2002). Thus, management that favours the development of stands and landscape compositions and structures similar to those that characterize natural ecosystems should be favoured (*sensu* Bergeron *et al*. 2002).

The effects of wildfire on boreal forests have been studied intensively (e.g. Stickney 1986,

Halpern 1989, Schimmel & Granström 1996). In Finland, post-fire forest succession has been studied by e.g. Sarvas (1937), Lindholm & Vasander (1987), and Uotila (2004). Studies on post-fire succession, mainly concentrating on the proportions of different plant functional groups, have produced contrasting results (DeGrande *et al*. 1993, Larsen & MacDonald 1998). Moreover, to our knowledge, the early succession stage following slash-burning has not been studied in boreal ecosystems.

The primary sources of disturbance in the managed forests of Fennoscandia are wood harvesting and other silvicultural treatments, while natural disturbances are largely excluded (Kuuluvainen 2002). Since natural forests show a wide variety of disturbances of different size, severity, and repeatability, the structural differences between managed and natural forests can largely be attributed to differences in disturbance dynamics. Keeping this in mind, slash-burning might be, in association with its cultural value, a potential management method for introducing heterogeneity at stand-scale.

In this paper we present results on the vegetation development during the first ten years of succession after slash-burning on sites previously occupied by 60-year-old *Picea* forest. The study was conducted in Koli National Park, in eastern Finland. We investigated the vegetation processes at species level and among plant functional groups. In addition to describing species responses, we applied multivariate methods to create an overall picture of the early vegetation succession.

Materials and methods

Study area and experimental design

The study area is located in the Koli National Park (Salo 1997) in eastern Finland (Fig. 1). After a 55-year break, slash-and-burn cultivation was re-established in Koli National Park in 1994, when approximately one hectare of a 60-year-old managed *Picea abies* forest was burnt (Salo 1998). Naturalization of the local managed forests has since continued and additional slash-burning was carried out next to the original area
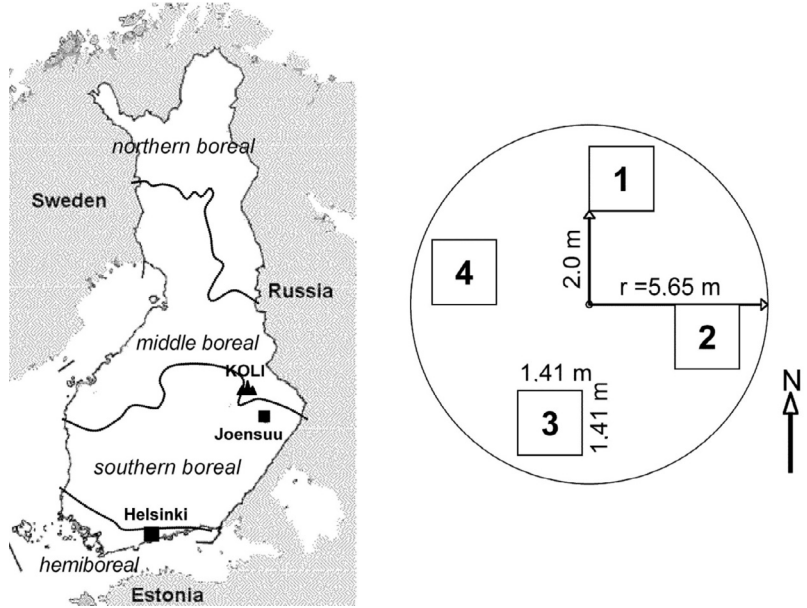
Fig. 1. Left-hand side panel: location of Koli National Park at 63°04′N and 29°52′E (Salo 1997). The boundaries between the subzones of boreal vegetation are only suggestive. Right-hand side panel: sampling design within each circular plot (Hokkanen *et al.* 2003). For details *see* Table 1.

in 1996 and 1998. The study area consists of these three areas. An adjacent 60-year-old spruce forest was used as a control. The burned sites are about of the same size, having a total area of approximately three hectares. Both the burned and the control forest were classified as *Myrtillus* type (MT) in the Finnish Forest Classification System. The Koli national Park is located in the mid-boreal vegetation zone. At Koli the growing season lasts on average for 145–160 days.

Prior to burning, all but a few trees were felled and left to dry. In all cases burning took place in June. Fire was initiated from the edges of the slash, down-slope was preferred when it was possible. The fire destroyed all the existing vegetation and the top of the humus layer creating a slightly alkaline, nutrient-rich ash medium. After the fire had become extinct, all those trunks that had not been completely burned were gathered in several piles and re-burned.

However, the three areas were not similarly affected by the burning. The first site (burned in 1994) had a thicker residual humus layer as compared with that of the other two sites. At the third site (burned in 1998) the mineral soil had been exposed in many places and the second site (burned in 1996) was approximately intermediate between the first and third. These differences were not planned, but resulted partially from

different site conditions, such as moisture, and partially from human error. The three sites also have different topography. The first site is very flat, whereas the second site is more or less on a slope, and the third is somewhat intermediate to the first two. Different topography means differences in water movement and exposure, which potentially affect the movement of nutrients in the soil and soil temperature, respectively.

A total of 15 permanent circular plots were established in the slash-burned areas and in the control forest. The 1994 (B94), 1996 (B96) and 1998 (B98) areas and the control area received four, five, four and two plots, respectively (Table 1). These permanent plots (the same each year) were located subjectively at points considered to be representative of the areas. Each cir-

Table 1. Details considering the experimental design. *n* = number of squares sampled during the study period.

Area	Number of plots	Sampling events (yrs after fire)	*n*
B94	4	2, 3, 6, 10	64
B96	5	0, 1, 4, 8	80
B98	4	0, 2, 6	44*
Control	2	2, 6, 10	32
Total	15		220

* Only 3 plots sampled at the first event.
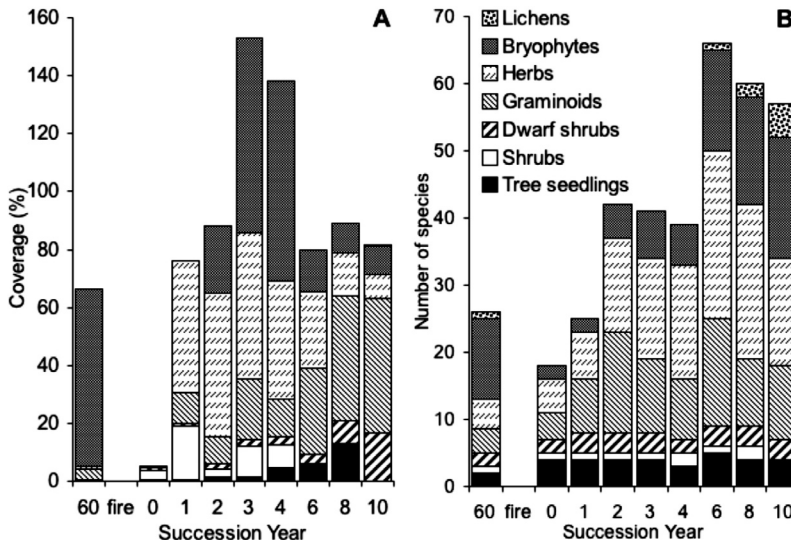
Fig. 2. — A: Coverage (%) of different plant functional groups during the first decade of vegetation succession following slash-burning. The columns represent mean coverage calculated between sample squares that were monitored for an equal time interval (sample sizes for different year groups in Table 1). — **B**: Species richness of different plant functional groups during the first decade of vegetation succession following slash-burning.

cular plot (Fig. 1) (10 m²) contained four sample squares (2 m² each), (total *n* = 220) (Table 1) (*see* Hokkanen 2003). The squares were located 2 m from the centre point of the circle in each main compass direction: North (0°), East (90°), South (180°) and West (270°). Each square was located on the right-hand side of the radius of the circle, but was in a few cases relocated when the original location had an interfering obstacle (i.e. a large rock or a tree stump) (Salo 2004). After burning, the areas were surveyed in 1994, 1996, 1997, 1998, 2000 and 2004, by the same group. Sampling normally took place from July to August.

Each sample square was inventoried for bryophytes, lichens and vascular plant species occurrence. Also the percent coverage of different plant species was estimated using the following scale: 0.1; 0.5; 1; 2; 3; 4; 5; 6; 7; 8; 9; 10; 15; 20; 25; …; 90; 93; 95; 96; 97; 98; 99; 100 (Salo 2004). The nomenclature follows Hämet-Ahti *et al.* (1998) for vascular plants and Holmåsen (1998) for bryophytes and lichens. Identification of vascular plants, bryophytes and lichens was done by Kauko Salo (Metla) and Hanna Keski-Karhu (Joensuu University).

Data analysis

In order to display the overall development and variation within all the areas, and also to compare the development between the areas, a sites × species matrix, with 220 sites (sample squares) and 88 species, was constructed from the data. The raw data was transformed with a natural logarithm function in order to make the distributions of the species descriptors more symmetrical (Legendre & Legendre 1998). According to Legendre and Legendre (1998), most multivariate methods perform better with symmetric data.

A Steinhaus similarity coefficient (designed for quantitative data and which excludes double zeroes; Legendre & Legendre 1998) was calculated for the transformed matrix in order to describe the floristic differences between different samples (years) and the different areas:

$$S_{ij} = 2W/(A + B) \qquad (1)$$

where *W* is the sum of minimum abundances of species shared by sites *i* and *j*, and *A* and *B* are the total abundance of species occurring at site *i* and *j*, respectively. We converted the similarity matrix to a dissimilarity matrix (with a square root function) in order to avoid negative eigenvalues. This matrix was further used to calculate a principal coordinates analysis (PCoA) in order to study succession at community level. The R -package (Legendre & Vaudor 1991) was used in the computations. The first three principal coordinates were used to create ordinations diagrams.
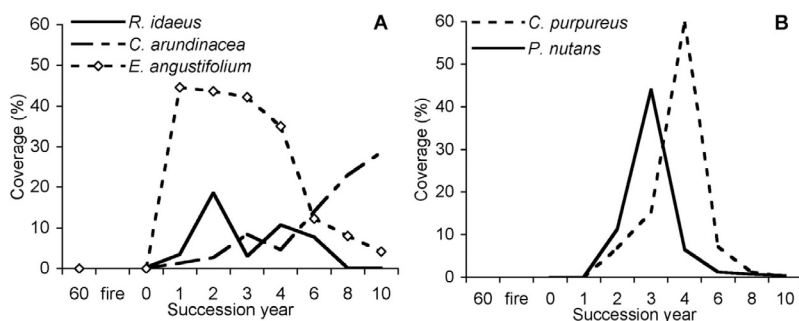
Fig. 3. Coverage of the most abundant species during the first decade of vegetation succession following slash burning. — **A**: Vascular plants. *Rubus idaeus* is a shrub, *Epilobium angustifolium* a herb and *Calamagrostis arundinacea* a graminoid. — **B**: Bryophytes (*Ceratodon purpureus* and *Pohlia nutans*). *C. arundinacea* is the only species also growing in the control plots. The values on the vertical axis represent mean coverage (%), calculated for sample squares that were monitored an equal time interval.

Results

Species richness and coverage

The plant species composition was observed to change significantly during the ten-year study period. This could be seen, for example, in the percent coverage of different plant functional groups (Fig. 2A). The species richness at the burned sites seemed also to change during the study period (Fig. 2B). Maximum species richness was apparently reached within six years after the treatment, whereafter it remained relatively constant.

A total of 88 plant taxa were recorded during the study period in the sample squares on the slash-burned areas (Table 2). These taxa included 18 (20%) bryophytes, 5 (5.6%) lichens, 5 (5.6%) pteridophytes, 32 (36 %) herbs, 19 (21%) graminoids, 3 (3.4%) dwarf shrubs, 1 (1%) shrub and 5 (5.6%) trees. The differences in the proportions have to be considered with caution, however, since the sample size in the year groups was different. Only nine additional species were observed in the control plots. These species included mainly bryophytes (such as *Barbilophozia*, *Calypoegia*, *Ptilidium*, *Rhizomnium* and *Rhytidiadelphus*), *Oxalis acetosella* and *Alnus incana*. 33 (38%) of the species observed in the slash-burned areas were also present in the control plots.

Vegetation succession was primarily initiated by *Epilobium angustifolium*, which colonized the area immediately after slash-burning and remained the dominant field layer plant for the following six years; it was also the most abundant vascular plant in this study (Fig. 3A). It also had the lowest spatial variation among the widely distributed pioneers. *Rubus idaeus* seedlings also became established directly after burning and its relative coverage reached relatively high values within two years (Fig. 3A).

The primary pioneer bryophytes *Pohlia nutans* and *Ceratodon purpureus* were the most abundant ground layer plants in this study (Fig. 3B). *P. nutans* had its peak abundance three years after burning and disappeared almost as rapidly as it appeared. High abundances of *C. purpureus* occurred the following year, after which it disappeared in the same way as *P. nutans*.

The last species to dominate the system during the study period was *Calamagrostis arundinacea* (Fig. 3A). Its abundance increased steadily throughout the study period gaining dominance in the community after six years. After ten years it was still the dominant plant in the community. However, it was already negatively affected by spruce.

The colonization of trees began with the sprouting recovery of birch species (*Betula* spp., including *Betula pendula* and *Betula pubescens*) and *Sorbus aucuparia* (Fig. 4a). Establishment of *Pinus sylvestris* seedlings was also observed directly after burning. The abundance of pine fluctuated through the study period and did not reach relevant coverage, although the established seedlings started to grow faster within ten years. *Picea abies* (Fig. 4a) was observed throughout

Table 2. A list of observed taxa in order of increasing abundance. The values indicate average percent coverage. p = present (coverage < 1%).

Species	\ 0	\ 1	\ 2	\ 3	\ 4	\ 6	\ 8	\ 10	Control
Bryophyta									
Aulacomnium palustre						p	p	p	p
Barbilophozia barbata			p			p	p	p	
Barbilophozia lycopodioides									p
Brachythecium spp.				p		p	2	3	1
Calypogeia mulleriana									p
Ceratodon purpureus			7	15	60	7	1	p	
Chiloscyphus profundus						p	p	p	
Dicranum majus								p	p
Dicranum polysetum				p		p	p	1	1
Dicranum scoparium					p	p	p	p	2
Hylocomium splendens				p		p	p	p	17
Marcanthia polymorpha			p		p	p	p	p	
Mnium stellare		p							
Plagiothecium dendriculatum						p	p	p	p
Plagiothecium laetum	p								p
Pleurozium schreberi				p	p	p	p	p	39
Pohlia nutans	p	11	44	7	1	1		p	
Polytrichum commune									p
Polytrichum juniperinum		p	5	8	2	6	6	5	
Ptilidium ciliare									p
Ptilidium pulcherrinum									p
Ptilium crista-castrensis								p	1
Rhizomnium punctatum									p
Rhodobryum roseum							p		p
Rhytidiadelphus triquetrus									p
Sphagnum angustifolium								p	p
Dwarf shrubs									
Calluna vulgaris		p	p	1		1	1	4	
Vaccinium myrtillus	p	1	p	1	2	1	2	1	11
Vaccinium vitis-idaea	p	p	p	1	1	1	1	3	p
Graminoids									
Agrostis capillaris	p	p	p	4	1	2	1	4	
Anthoxanthum odoratum		p	p	p		p		p	
Calamagrostis arundinacea	p	1	3	8	5	14	23	29	1
Calamagrostis epigejos								p	
Calamagrostis purpurea		p			p	p	p		
Carex canescens		p	1	p		p		p	
Carex digitata		p	p	p	1	p	1	p	p
Carex nigra			p			p			
Carex ovalis		p	1	1		p			
Carex pallescens						2		p	
Deschampsia cespitosa		p	p	2	p	1	p		
Deschampsia flexuosa	p	p	1	2	1	3	11	11	2
Luzula pilosa			p	p		p		p	
Luzula multiflora	p	9	3	4	5	6	7	3	p
Melica nutans			p		p	p	p		p
Phleum pratense			p	p		p	p		
Poa pratensis						p	1	1	
Secale cereale		p	p						
Herbs									
Angelica sylvestris							p		
Cerastium fontanum						p			

Continued

Table 2. Continued.

Species	Succession year								Control
	0	1	2	3	4	6	8	10	
Cirsium palustre		p			p	1	p		
Convallaria majalis							p		
Dactylorhiza maculata							p		
Epilobium angustifolium	p	45	44	42	35	12	8	4	
Epilobium montanum		p							
Erigeron acer						p			
Fragaria vesca						p			
Galeopsis bifida			1	p	p	2	p	p	
Galium uliginosum						p			
Geranium sylvaticum				p	p	p	p	p	p
Gnaphalium sylvaticum					p	p	p	p	
Goodyera repens							p		
Hieracium sp.				p		p	p	p	
Maianthemum bifolium	p	p	3	6	p	4	1	1	1
Melampyrum pratense				p		p	1	1	p
Melampyrum sylvaticum			p		3	6	2	2	p
Oxalis acetosella									p
Potentilla erecta			p	p		p	p	p	
Rhinanthus serotinus								p	
Rubus arcticus			p		p	p	p	p	p
Rubus saxatilis			p	p	p	p	p		p
Rumex axetosella			1	p	p	p			
Solidago virgaurea					p				
Solidago canadensis							p		
Stellaria palustris						p			
Taraxacum officinale	p	p	p	p	p	p	p		
Trientalis europaea				p	p	p	p	p	
Veronica officinalis	p	p	p	p	2	1	2	p	
Viola canina			p	p	p	p	p	p	
Viola mirabilis			p		p	p	p		
Viola riviniana	p	p	p	p	p	p	p	p	
Lichens									
Cetraria pinastri								p	p
Cladina arbuscula							p	p	
Cladina stellare								p	
Cladonia cornuta								p	
Cladonia deformis						p	p	p	p
Pteridophyta									
Dryopteris carthusiana						p	p	p	p
Equisetum sylvaticum	p	p			p	p			
Gymnocarpium dryopteris			p	p		p		p	p
Lycopodium clavatum				p		p	p	p	
Selaginella selaginoides								p	
Shrubs									
Rubus idaeus	p	3	19	3	11	8	p	p	
Trees									
Alnus incana									p
Betula sp.	p	p	p	p	p	3	3	1	2
Picea abies	p	p	p	p	p	1	2	11	p
Pinus sylvestris	p	p	p	p		p	p	p	p
Prunus padus						p			
Salix caprea						p		p	
Sorbus aucuparia	p	p	p	1	1	p	1	1	p
Total number of species	19	26	42	41	40	68	59	60	42
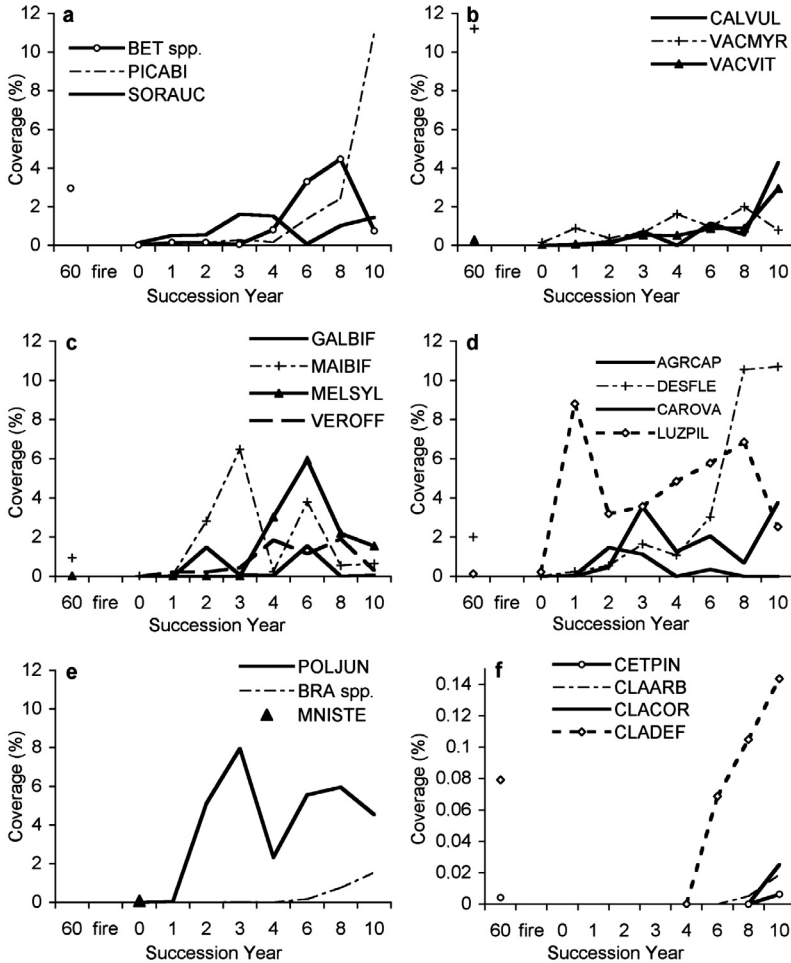
Fig. 4. Cover of selected species in different plant functional groups during the first decade of vegetation succession following slash-burning: (**a**) tree seedlings, (**b**) dwarf shrubs, (**c**) herbs, (**d**) graminoids, (**e**) bryophytes, and (**f**) lichens. Abbreviations: *Betula* spp. (BET spp.), *Picea abies* (PICABI), *Sorbus aucuparia* (SORAUC), *Calluna vulgaris* (CALVUL), *Vaccinium myrtillus* (VACMYR), *Vaccinium vitis-idaea* (VACVIT), *Galeopsis bifida* (GALBIF), *Maianthemum bifolium* (MAIBIF), *Melampyrum sylvaticum* (MELSYL), *Veronica officinalis* (VEROFF), *Agrostis capillaris* (AGRCAP), *Deschampsia flexuosa* (DESFLE), *Carex ovalis* (CAROVA), *Luzula pilosa* (LUZPIL), *Brachythecium* spp. (BRA spp.), *Polytrichum juniperinum* (POLJUN), *Cetraria pinastri* (CETPIN), *Cladina arbuscula* (CLAARB), *Cladonia cornuta* (CLACOR), and *Cladonia deformis* (CLADEF). The values on the vertical axis represent mean percent coverage, calculated for sample squares that have been monitored for an equal time interval.

the study period and, as the established seedlings increased in size, it started seriously to shadow the non-woody community within ten years.

Vaccinium myrtillus and *Vaccinium vitis-idaea* (Fig. 4b) both sprouted from roots after fire. Nevertheless, they seemed to recover at a relatively slow rate. Regeneration of *Calluna vulgaris* (Fig. 4b) seemed to be relatively similar to that of *V. vitis-idaea*, although it is not clear whether it sprouted or regenerated via seeds. Its

occurrence clearly showed high spatial variation, being restricted to dryer patches.

The species turnover of herbs was relatively similar to those of mosses, except that herb species generally had wider temporal distributions. After the dominance of *Epilobium angustifolium* was relaxed after four to six years, other herbs became established in the community, although they were still heavily suppressed by *Rubus idaeus*. Other early successional herb spe-

cies in the community included *Galeopsis bifida*, *Maianthemum bifolium*, *Melampyrum sylvaticum*, *Veronica officinalis* (Fig. 4c), *Rubus saxatilis*, *Cirsim palustre*, *Potentilla erecta*, *Melampyrum pratense* and *Geranium sylvaticum* (Table 2).

The graminoid succession started from grasses regenerating via subterranean organs, followed by sedges and seed-dispersed grasses. *Luzula pilosa* (Fig. 4d) recovered immediately after burning and became relatively abundant the following growing season; it was present throughout the study period, even in the control areas. *Deschampsia flexuosa* regenerated slowly during the first six years. It did not reach a clear peak during the study period and it is possible that *D. flexuosa* continued to increase in abundance even after ten years (Fig. 4d). After all, it was still present in the control areas in relatively high numbers. *Agrostis capillaris* was present throughout the study period and showed no decline in abundance even ten years after burning (Fig. 4d).

Colonization and peak abundance differed clearly between the pioneer moss species. The first species in the chronological series was *Mnium stellare*, which was only observed one year after burning (Table 2). The second pioneer was *Pohlia nutans* (Fig. 3B) and the third *Ceratodon purpureus* (Fig. 3B). Like *C. purpureus*, *Polytrichum juniperinum* (Fig. 4e) colonized the area within two years after burning and was still strongly present after ten years. Species characteristic of later succession (i.e. *Aulacomnium palustre* (Table 2) and *Brachythecium* (Fig. 4e) and *Plagiothecium* species) entered the recovering community within five to six years. Interestingly, even the late successional species, which made a major contribution to the ground coverage in the control areas, *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum polysetum*, and *Dicranum scoparium* were already present after six years (Table 2). Lichens (i.e. *Cladonia deformis* and *Cladina rangiferina*) were also found to establish within four to six years, although they were only observed with very low abundances (Fig. 4f).

The ordination diagrams displayed a clear but diffuse temporal post-fire development in vegetation composition. The data points were organized along a strong gradient, resulting in a clear arch (Fig. 5A). Furthermore, variation within squares sampled the same year seemed to decrease during the study period. The variation, observed in the first summer following slash-burning, was approximately twice as great as in the following year. This is expected on the basis of succession theory. The high variation in years '1' and '4' may also have been due to a greater within area variation in B96, as compared to the other areas (B94 and B98). Moreover, the control area was clearly separated from the burned areas, indicating a significant difference between initial and later succession.

As the different slash-burned areas were not always sampled during the same events, the average difference between the areas was examined (Fig. 5C and D). The arrangement of the centroids for sample squares within each area revealed a few sources of variation observed in Fig. 5A and B. Although the overall development seemed to be relatively similar and the position of centroids for different years was relatively logical in the three burned areas, there were some peculiar differences. Firstly, year '2' in B94 and B98 differed remarkably from each other. Also the year '6' differed between the two areas, the variation being much lower, however. Secondly, the three areas seemed to develop at a different rate, although the relative difference between the areas was hard to judge. Roughly stated, development was apparently more rapid in B98, as compared to B94.

Discussion

Major changes were evident in the initial secondary forest succession following slash-burning. These changes were observed on different scales; from individual species to the overall composition of the plant community.

Community level patterns

The site ordination accounted for 29% of the total variation in species composition (Fig. 5).

Species responses to slash-burning

Generally, plant species differ in their ability to respond to fires of different depth of penetration.
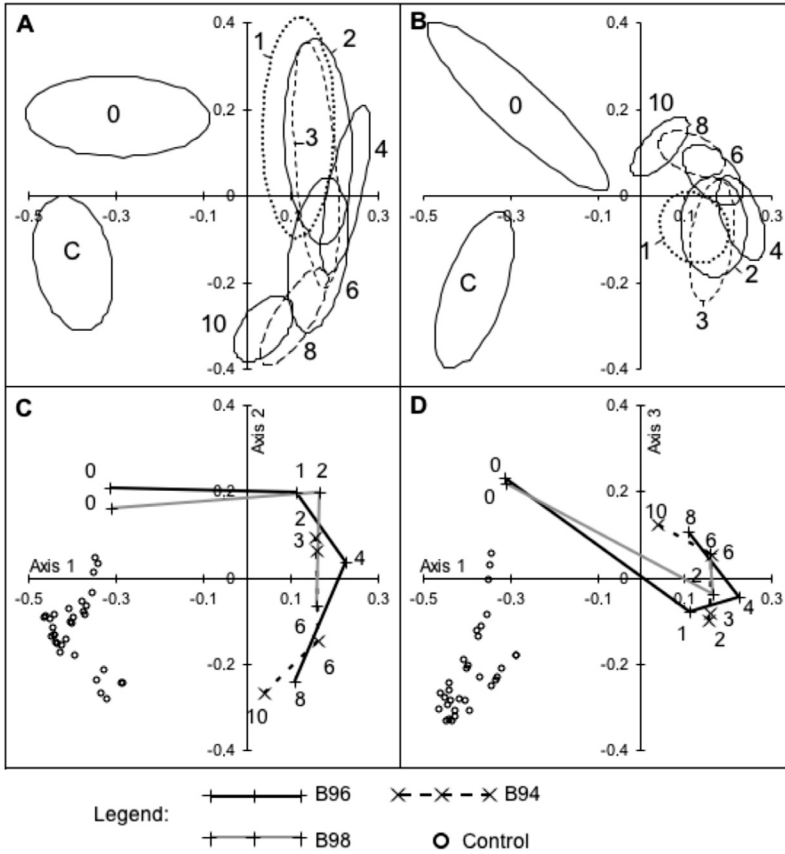
Fig. 5. Four PCoA diagrams, which display the vegetation succession within the study area (*n* = 220) (**A**, **B**) and differences between the three slash-burned areas (**C**, **D**). — **A** and **C**: axes 1 and 2. — **B** and **D**: axes 1 and 3. The ellipses in A and B represent 95% concentration ellipses for sample squares that had been sampled in the same year. The numbers indicate succession year, and C indicates the control (60 years old).

These differences are principally due to variation in the position of seeds and rhizomes in the soil and to the colonizing habit of the plant (Schimmel & Granström 1996). Our results showed a considerable difference in species responses to slash-burning, according to their life form and regeneration strategy.

The first species to stand out in the post-fire succession was *Epilobium angustifolium*. It is known to rapidly colonize deforested areas (Lindholm & Vasander 1987, Granström & Schimmel 1993), even over great distances (Archibold 1980, Solbreck & Anderson 1986). *E. angustifolium* was not growing in the control plots and, because it does not store seeds in the soil (Grime *et al.* 1981, Granström 1986), it colonized the area via dispersed seeds, as reported by Schimmel and Granström (1996). It could thus be considered an invader strategist (Rowe 1983, Sirois 1995). After an initial rapid proliferation, its stature decreases, flowering declines, and the seedling density is reduced (Turner *et al.*

1997). Such a decline was observed four years after burning. Moreover, the observed response curve of fireweed was strikingly similar to that reported by Stickney (1986).

The second dominant colonizer among vascular plants was *Rubus idaeus*. This shrub is locally important in areas subjected to deforesting disturbance (Whitney 1984). It is relatively intolerant to shading and its growth is thus associated with large breaks in the forest canopy. During its short occupancy it produces a long-lived seed bank ready for activation following disturbance (Whitney 1978). It could be classified, on the basis of its regeneration strategy, as an evader (Rowe 1983). Because of its relatively tall stature, in comparison to other non-woody vascular plants, its decline was not a consequence of shading in *Vaccinium myrtillus*-type habitats. The most probable explanation for its decline was increasing competition with grasses for soil nutrients and water. Our observations are in conflict with those of Lindholm and Vasander

(1987), who reported that *R. idaeus* was present even 120 years after prescribed burning. This difference may be due to habitat factors.

The third dominant vascular plant was *Calamagrostis arundinacea*. This grass sprouts from survived underground rhizomes (Novak *et al*. 2001). According to Turner *et al*. (1997) seed dispersal is not important for the reinvasion of this genus. *C. arundinacea* may thus be an endurer strategist (Rowe 1983). This species regenerated relatively slowly, probably due to competition with *E. angustifolium*. It gained dominance in the community after six years, and remained the dominant species until the end of the study period, without any signs of decline.

In the herb succession *Maianthemum bifolium* was apparently replaced by *Melampyrum sylvaticum*, but there was probably no causal relationship between these two species. Interestingly, these herbs are considered to be forest species. *M. bifolium* is a small, shade tolerant ground layer plant indicative of fertile habitats, and *M. sylvaticum* is a hemiparasite, usually found in spruce forests but it can also be encountered in meadows. *Maianthemum* species are considered endurers (Sirois 1995), since they regenerate from buried roots. *M. sylvaticum*, on the other hand, has a weak root system and relatively heavy, animal-dispersed seeds. *Melampyrum* species have been found already during the next year following a ground fire (Schimmel 1993), indicating relatively effective dispersal in spite of heavy seeds. In the present case, however, *M. sylvaticum* was not observed until the second year after burning, indicating that colonization occurred through dispersed or resident seeds. *Veronica officinalis* was observed to recover immediately after burning. It is often encountered on clear-cut areas, but not in the understorey of spruce forests. It may thus have regenerated from a buried seed bank. *Galeopsis bifida* is a clear invader strategist (Rowe 1983). It is most commonly encountered on disused land, clear-cut areas, and other open habitats free of taller vegetation. It probably colonized the area via seeds within a few years after burning, and disappeared within ten years.

Luzula pilosa differs from the other graminoids in its regeneration strategy. It can be classified as an evader (Rowe 1983), since it mainly recovers from the surviving seed bank (Schimmel 1993). However, its seeds cannot germinate unless the humus layer is reduced (Granström 1986), e.g. by a severe fire. Recovery from underground rhizomes is also possible if the fire has not been too severe. This seemed to be the case, at least locally. The bimodal abundance curve we found in our study may be a combination of individuals with a different recovery mode. *Carex ovalis*, like other sedges, seemed to be an invader strategist (Rowe 1983). It was rapidly outcompeted by regenerating grasses. *Agrostis capillaris* can also be considered an invader (Sirois 1995).

Deschampsia flexuosa, together with the dwarf shrubs *Vaccinium vitis-idaea* and *Vaccinium myrtillus*, is considered to be one of the most abundant understorey species in north European boreal forests (Kielland-Lund 1981, Reinikainen *et al*. 2000). It is one of the vascular plants characterising early succession after clear cuttings. *D. flexuosa* can be classified as an endurer or invader, depending on the conditions. It regenerates from buried rhizomes after an intermediately severe fire, but it is killed in more severe fires (Schimmel & Granström 1996). It does not have a preserved seed bank (Granström 1986, Schimmel & Granström 1996) and its recovery is therefore probably mediated through local sprouting, prolific flowering of the survived individuals (Schimmel & Granström 1996), and seed dispersal from the adjacent forest.

The dwarf-shrubs *Vaccinium vitis-idaea* and *Vaccinium myrtillus* can be classified as endurers (Sirois 1995, Schimmel & Granström 1996), since they recover from buried roots after fire. However, regeneration of these species was slow in this study as compared with their regeneration after less severe wildfires (Schimmel & Granström 1996) and prescribed burning (Lindholm & Vasander 1987). This was most probably due to shading and resource competition with faster-growing herbs and graminoids. Their abundance started to increase within ten years. This could be connected to increasing tree seedling cover. However, *V. vitis-idaea* favours drier, pine-dominated forests and it is not maintained in the community for a long period of time. On the other hand, *V. myrtillus* is a characteristic plant of the prevailing mesic forest communities in the area.

Heather (*Calluna vulgaris*) is known to be well adapted to withstand fire (Gimingham 1972). According to Schimmel (1993), the post fire recovery of heather is initiated from a preserved seed bank. It is thus an evader strategist, although it may also recover from rhizomes in similar circumstances as *Luzula pilosa*. However, it may be more sensitive to heat than *L. pilosa*, since *C. vulgaris* was not observed during the same year the slash was burned. The colonization of *C. vulgaris* is possibly favoured by an increase in the soil calcium content after fire (Uotila 2004).

Our findings, regarding the shift from herb to grass dominance in early succession, are partially in conflict with those of many other studies (summarized by Rego *et al*. 1991), which state that the cover of herbs and grasses increases significantly during the first years after a fire, before being dominated by the increasing cover of sprouting shrubs, and finally the trees. However, habitat characteristics may have had a major impact on the course of succession.

Within ten years the community started to be strongly affected by the presence of spruce (*Picea abies*) seedlings (Niklasson 2002). Sirois (1995) considers Scots pine (*Pinus sylvestris*) and spruce to be evaders (Rowe 1983), due to their above ground seed bank in their canopy. Scotch pine is also particularly tolerant against forest fires (Kolström & Kellomäki 1993). In the present case, the adjacent forest provided the slash-burned areas with a plentiful supply of propagules. High numbers of spruce seedlings were in fact observed, but the number of pine seedlings remained low. As deep organic layers are poor seedbeds for a variety of species including forest trees (Zasada *et al*. 1992), humus-consuming fires are beneficial to tree seedling establishment (Ahlgren 1959, Schimmel 1993). However, pine seedling survival is reported as being affected by ground vegetation cover (Johnsson 1999). Pine seedling establishment is also more sensitive to site conditions than that of spruce (Johnsson 1999). Therefore, spruce may be more tolerant against herbaceous competition and may also not need as severe a fire as pine to recover.

Two deciduous trees, *Sorbus aucuparia* and *Betula* spp., were observed to sprout from underground buds almost immediately after burning.

Among the boreal forest tree species, sprouting is known to be the most pronounced in birch (Uemura *et al*. 1990). However, new seedlings managed poorly in the dense, recovering vegetation. The decline observed in the abundance of birch can also be explained by the growth of individual trees. The coverage of young trees that had grown tall enough for their canopy to exit the shrub layer was not estimated.

The three most abundant pioneer bryophytes, characteristically present on charred surfaces (Sarvas 1937, Crum 1979), *Pohlia nutans*, *Ceratodon purpureus* and *Polytrichum juniperinum* formed a clear succession sequence. They colonized burned areas via dispersed spores and could be classified as invaders (Rowe 1983), since they were present only a short time during the course of succession. Many authors have reported that *Polytrichum* spp. and *C. purpureus* are dominant bryophytes in early post fire succession (e.g. Sarvas 1937, Black & Bliss 1978, Schimmel 1993). It appears that *Polytrichum* spp. and *C. purpureus* become well established if the burned surface consists of a rather compact layer of surface-charred, mor humus or exposed mineral soil (Schimmel & Granström 1996). There are also reports indicating that *C. purpureus* starts to become overtopped and shaded out by *Polytrichum* species after a few years. Our results supported these findings. Sarvas (1937) reported that *C. purpureus* is replaced by *P. nutans*, but our results indicated that the situation is the opposite.

Pleurocarpous mosses, such as *Pleurozium schreberi*, *Hylocomium splendens*, *Brachythecium* spp. (several species), and *Plagiothecium* spp. (several species), which were the predominant species in the control plots, colonized the areas between three to six years after burning. Their recovery was very slow and they did not reach high abundances during the study period. These species favour closed habitats and according to Schimmel and Granström (1996), pleurocarpous mosses and fruticose lichens (classified as "avoiders" by Novak *et al*. 2001) are totally dominant in understorey vegetation, but are virtually absent in burned plots at least during the first five years. Normally these species do not achieve dominance until approximately 30 years after fire, and in the meantime *Polytrichum* spp.

and *C. purpureus* are dominant (Sarvas 1937, Black & Bliss 1978, Schimmel 1993).

Lichens were the last to arrive at the fire area. The first lichen species (*Cladonia deformis*) was observed not until six years after burning. After wildfires, lichens are known to regenerate vegetatively from surviving or partially burned thallus fragments. However, the fact that lichens appeared as small, randomly scattered tiny patches would seem to indicate recovery from dispersed spores. According to Sarvas (1937), *C. deformis* is expected to recover within five years after a fire, and the re-establishment of *Cladina* species takes approximately ten years. Ground lichens are not, in general, typical plants of mesic, spruce-dominated forests (Esseen *et al.* 1997, Uotila 2004), which explained their low diversity in this study.

As concluded by Schimmel (1993), bryophyte flora best fits the classical mode of succession, with species replacing each other in sequence. However, trees also have a clear replacement pattern. Some replacement can also occur within herbs and graminoids, but this is not as clear as with mosses and trees. Actually, a more realistic picture of species replacement patterns could be obtained by considering herbs and graminoids together. Stickney (1986) reported that a well developed ground surface bryophyte layer occurred extensively after a severe wildfire, and it did not appear as an initial stage but developed concurrently with the vascular component. These and other findings concerning sequential establishment of different moss species led to the conclusion that a successional process is operating at the bryophyte level at the ground surface parallel to the development of the vascular vegetation. Our results clearly supported these ideas.

Species richness

Our results showed an increase in plant species richness during the six-year period after slash-burning. Although almost 40% of the plant species were also present in the control plots, 55 new species were encountered in the burned plots. This result supported the view that plant species richness increases (Trabaud & Lepart 1980, Armour *et al.* 1984) following fire. Vas-

cular plant diversity seemed to be greater in comparison to bryophyte richness at least during the first decade. Respectively, bryophyte species richness was greater in the 60-year-old control forest. This pattern was most probably due to increased competition and shading by fewer and bigger plant individuals (i.e. *Calamagrostis arundinacea* and *Picea abies*).

Studies investigating post fire species diversity have reported contrasting results. According to Turner *et al.* (1997), overall species richness increases during the first five years of post-fire succession. Ruuhijärvi *et al.* (1985) found that plant species richness increases up to 14 years after prescribed burning, and Lindholm and Vasander (1987) reported maximum species richness 15 years after burning (*see* also Uotila 2004). Moreover, vascular plant richness is found to be greatest in early succession, and bryophyte and lichen diversity in late succession (Rees & Juday 2002, Waide *et al.* 1999). The opposite view states that the initial post-fire plant community is primarily composed of surviving individuals (Armour *et al.* 1984, Lyon & Stickney 1976). Furthermore, Rego *et al.* (1991) found community diversity and the number of species to be only slightly altered by fire. Hence, the regeneration of trees, coupled with the rapid resurgence of most shrub species from underground parts, has consequently led to the view of succession in boreal ecosystems as a cyclic process involving little overall floristic variation, despite major environmental changes resulting from fire (Viereck & Schandelmeier 1980).

Our findings supported the view of Trabaud and Lepart (1980), who stated that new species appear progressively on the microsites opened up by the fire and gradually increase the species diversity and richness. These species then gradually decline as the pre-fire community re-establishes on the site. According to Trabaud and Lepart (1980), the length of time for this to occur varies according to the pre-fire community and the characteristics of the fire.

Community level patterns

Our results indicated a significant change in community composition following slash-burn-

ing. According to the site ordination, the permanent sample squares differed considerably between the burned and control areas. Although there was variation between the experimental areas, the overall pattern was relatively clear. The differences in vegetation development between the three areas may have been due to differences in fire intensity and site topography. There was also a continual, although diffuse, succession sequence appearing in the ordination diagrams (Fig. 5). Succession seemed to be initially very rapid, and then slowing down as time elapsed. However, the recovering community was not even close to the surrounding forest with respect to the species composition within ten years after burning. The succession sequence was realized through the replacement of invasive, fast growing pioneers with more competitive species that were finally replaced by late succession species with high shade and low nutrient level tolerance. One possible explanation for the observed pattern might have been a change in the availability of soil nutrients after burning.

As with species richness, different views have been proposed considering the patterns of community composition following fire. For example, Rego *et al.* (1991) found plant frequency composition to be only slightly affected by fire, while cover composition was initially reduced for many species, but recovered within four to six years. They concluded that other factors are much more important than fire in regulating understorey vegetation. This agrees with Trabaud and Lepart's (1980) conclusion that fire does not dramatically alter species composition, and that pre-fire composition is a major factor in the initial stages in postfire succession (Armour *et al.* 1984, Stickney 1986). Moreover, Reich *et al.* (2001) did not detect any systematic differences in vascular plant nor bryophyte community composition between post-logged and post-fire stands. In contrast, other studies have reported that fire influences vegetation succession (Annila 1993, Novak *et al.* 2001). Buried or immigrant seeds are found to contribute as much to rapid re-vegetation as does vegetative reproduction after destructive burning (Lutz 1956, Heinselman 1973).

Conclusions

The vegetation succession following slash-burning of a boreal forest consisted of a recognizable replacement sequence of plant species. These species were generally the same reported to be the most important in a recovering community after a wildfire or after prescribed burning. Moreover, as the effects of slash-burning on the local flora seemed to be similar to those reported for natural fires, we found slash-burning to be a nature-mimicking forest restoration method, well suitable for special areas such as nature reserves, in order to increase local heterogeneity. However, this conclusion is relevant only for plants and lichens. Moreover, since the fire regimes of natural forests are largely unknown, our conclusions are only applicable to those anthropogenic forests dating back to the slash-burning era.

References

Ahlgren, C. E. 1959: Some effects of fire on forest reproduction in northeastern Minnesota. — *J. For.* 57: 194–200.

Annila, E. 1993: Fire increases biodiversity of forest ecosystem. — *Finnish Forest Research Institute. Research Papers* 462: 19–23.

Archibold, O. W. 1980: Seed input into a postfire site in northern Saskatchewan. — *Can. J. For. Res.* 10: 129–134.

Armour, C. D., Bunting, S. C. & Neuenschwander, L. F. 1984: Fire intensity effects on the understory in ponderosa pine forests. — *J. Range Manage.* 37: 44–49.

Bergeron, Y., Leduc, A., Harvey, B. D. & Gauthier, S. 2002: Natural fire regime: a guide for sustainable management of the Canadian boreal forest. — *Silva Fennica* 36: 81–95.

Black, R. A. & Bliss, L. C. 1978: Recovery sequence of *Picea mariana–Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. — *Can. J. Bot.* 56: 2020–2030.

Crum, H. 1979: Mosses of the great Great Lakes forest. — *Contribution University of Michigan Herbarium* 10. Ann. Arbor., Michigan.

DeGrande, L., Gagnon, D. & Bergeron, Y. 1993: Changes in the understory of Canadian southern boreal forest after fire. — *J. Veg. Sci.* 4: 803–810.

Esseen, P. A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997:

Boreal forests. — *Ecological Bulletins* (Stockholm) 46: 16–47.

Gimingham, C. H. 1972: *Ecology of heathlands*. — Chapman and Hall, London.

Granström, A. 1986: *Seed banks in forest soil and their role in vegetation succession after disturbance*. — Ph.D. thesis, Swedish University of Agricultural Sciences. Umeå.

Granström, A. & Schimmel, J. 1993: Heat effects on seeds and rhizomes of a selection of boreal forest plants and potential reaction to fire. — *Oecologia* 94: 307–313.

Grime, J. P., Mason, G., Curtis, A. V., Rodman, J., Band, S. R., Mowforth, M. A. G., Neal, A. M. & Shaw, S. 1981: A comparative of germination characteristics in a local flora. — *J. Ecol*. 69: 1017–1059.

Halpern, C. B. 1989: Early succession patterns of forest species: Introduction of life history traits and disturbance. — *Ecology* 70: 704–720.

Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P. (eds.) 1998: *Retkeilykasvio*, 3rd ed. — Luonnontieteellinen keskusmuseo, Kasvimuseo, Helsinki.

Heikinheimo, O. 1915: Kaskiviljelyn vaikutus Suomen metsiin. — *Acta. Forestalia Fennica* 4: 1–264.

Heinselman, M. L. 1973: Fire in virgin forests of the Boundary Waters Canoe Area, Minnesota. — *Quarter. Res*. 3: 329–382.

Hokkanen, P. J. 2003: Vascular plant communities in boreal herb-rich forests in Koli, eastern Finland. — *Ann. Bot. Fennici* 40: 153–176.

Hokkanen, P. J., Salo, K. & Paatelainen, H. 2003: Avainbiotooppien kasvillisuus Kolin kansallispuistossa. — *Metsäntutkimuslaitoksen tiedonantoja* 893: 1–71.

Holmåsen, I. 1998: *Lavar och mossor,* 4th ed. — Stenström Interpublishing AB.

Johnsson, B. 1999: Stand establishment and early growth of planted *Pinus sylvestris* and *Picea abies* related to microsite conditions. — *Scand. J. For. Res*. 14: 425–440.

Kielland-Lund, J. 1981: Die Waldgesellschaften SO-Nordwegens. — *Phytoecologia* 9: 53–250.

Kolström, T. & Kellomäki, T. 1993: Tree survival in wildfires. — *Silva Fennica* 27: 277–281.

Kuuluvainen, T. 2002: Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. — *Silva Fennica* 36: 97–125.

Larsen, C. P. S. & MacDonald, M. G. 1998: An 840-year record of fire and vegetation in boreal white spruce forest. — *Ecology* 79: 106–118.

Legendre, P. & Legendre, L. 1998: *Numerical ecology*, 2nd English ed. — Elsevier, Amsterdam.

Legendre, P. & Vaudor, A. 1991: *The R-package*: *Multidimensional analysis, spatial analysis*. — Département de Sciences biologiques, Université de Montréal, Montréal, available on the web at http://www.bio.umontreal.ca/casgrain/en/labo/R/index.html.

Lehtonen, H., Huttunen, P. & Zetterberg, P. 1996: Influence of man on forest fire frequency in North Karelia, Finland, as evidenced by fire scars on Scotch pine. — *Ann. Bot. Fennici* 33: 257–263.

Lindholm, T. & Vasander, H. 1987: Vegetation and stand development of mesic forest after prescribed burning. — *Silva Fennica* 21: 259–278.

Louks, O. L. 1970: Evolution of diversity, efficiency, and community stability. — *Am. Zool*. 10: 17–25.

Lutz, H. J. 1956: Ecological effects of forest fires in the interior of Alaska. — *Tech. Bull. U.S. Dep. Agr*. 1133: 1–121.

Lyon, L. J. & Stickney, P. F. 1976: Early vegetation succession following Rocky Mountain wildfires. — *Tall Timbers Fire Ecol. Conf. Proc*. 14: 355–373.

Niklasson, M. 2002: A comparison of three age determination methods for suppressed Norway spruce: implications for age structure analysis. — *For. Ecol. Manage*. 161: 279–288.

Novak, S., Kershaw, P. G. & Kershaw, L. J. 2001: Plant diversity and cover after wildfire on anthropogenically disturbed and undisturbed sites in subarctic upland *Picea mariana* forest. — *Arctic* 55: 269–280.

Rees, D. C. & Juday, G. P. 2002: Plant species diversity on logged versus burned sites in central Alaska. — *For. Ecol. Manage*. 155: 291–302.

Rego, F. C., Buntin, S. C. & da Silva, J. M. 1991: Changes in understory vegetation following prescribed fire in maritime pine forests. — *For. Ecol. Manage*. 41: 21–31.

Reich, P. B., Bakken, P., Carlson, D., Frelich, L. E., Friedman, S. K. & Grigal, D. F. 2001: Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. — *Ecology* 82: 2731–2748.

Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I. & Hotanen, J.-P. (eds.) 2000: *Kasvit muuttuvassa metsäluonnossa [Changes in the frequency and abundance of forest and mire plants in Finland since 1950]*. — Kustannusosakeyhtiö Tammi, Helsinki. [In Finnish with English summary].

Rowe, J. S. 1983. Concepts of fire effects on plant individuals and species. — In: Wein, R. W. & McLean, D. A. (eds.), *The role of fire in northern circumpolar ecosystems*: 135–154. John Wiley, New York, New York, USA.

Ruuhijärvi, R., Lindholm, T. & Vasander, H. 1985: *Mustikkatyypin metsän ravinnetalouden ja kasvillisuuden rakenteen kehitys kulotuksen jälkeen [The development of nutrient dynamics and vegetation structure in a Vaccinium myrtillus -type forest after prescribed burning]*. — Helsingin yliopiston kasvitieteen laitos. [In Finnish with English summary].

Salo, K. 1997: Nature of Koli National Park. — In: Solberg, B. & Miina, S. (eds.), *Conflict management and public participation in land management*: 257–263. EFI Proceedings no. 14.

Salo, K. 1998: Kolin kansallispuisto kehittyy monipuoliseksi tutkimus- ja retkeilyalueeksi. — *Metsäntutkimuslaitoksen tiedonantoja* 718: 59–61.

Salo, K. 2004: Kasvisukkessio huhtakaskialueilla Kolin kansallispuitossa. — *Metsäntutkimuslaitoksen tiedonantoja* 915: 47–52.

Sarvas, R. 1937: Havaintoja kasvillisuuden kehityksestä Pohjoissuomen kuloalueilla. — *Silva Fennica* 44: 32–64.

Schimmel, J. 1993: *On fire. Fire behaviour, fuel succession, and vegetation processes to fire in the Swedish boreal forest*. — Ph.D. thesis, Swedish University of Agricultural Sciences, Department of Forest Vegetation Ecology, Umeå, Sweden.

Schimmel, J. & Granström, A. 1996: Fire severity and vegetation response in the boreal Swedish forest. — *Ecology* 77: 1436–1450.

Shafi, M. I. & Yarranton, G. A. 1973: Vegetational heterogeneity during a secondary (postfire) succession. — *Can. J. Bot.* 51: 73–90.

Sirois, L. 1995: Initial phase of postfire forest regeneration in two lichen woodlands of northern Québec. — *Ecoscience* 2: 177–183.

Solbreck, C. & Andersson, D. 1986: Vertical distribution of fireweed, *Epilobium angustifolium*, seeds in the air. — *Can. J. Bot.* 65: 2177–2178.

Stickney, P. F. 1986: *First decade plant succession following the Sundance forest fire, northern Idaho*. — U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. INT-197.

Trabaud, L. & Lepart, J. 1980: Diversity and stability in garrigue ecosystems after fire. — *Vegetatio* 43: 49–57.

Turner, M. G., Romme, W. H., Gardner, R. H. & Hargrove, W. W. 1997: Effects of fire size and pattern on early succession in Yellowstone National Park. — *Ecol. Monogr.* 67: 411–433.

Uemura, S., Tsuda, S. & Hasegawa, S. 1990: Effects of fire on the vegetation of Siberian taiga predominated by *Larix dahurica*. — *Can. J. For. Res.* 20: 547–553.

Uotila, A. 2004: *Vegetation patterns in managed and seminatural boreal forests in eastern Finland and Russian Karelia*. — Ph.D. thesis. University of Joensuu, Faculty of Forestry.

Viereck, L. A. & Schandelmeier, L. A. 1980: *Effects of fire in Alaska and adjacent Canada — a literature review*. — Bureau of Land Management, Alaska. Technical Report 6.

Waide, R. B., Willing, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P. & Parmenter, R. 1999: The relationship between productivity and species richness. — *Annu. Rev. Ecol. Syst.* 30: 257–300.

Wallenius, T. H., Kuuluvainen, T. & Vanha-Majamaa, I. 2004: Fire history in relation to site type and vegetation in Vienansalo wilderness in eastern Fennoscandia, Russia. — *Can. J. For. Res.* 34: 1400–1409.

Whitney, G. G. 1978: *A demographic analysis of Rubus idaeus* L. *and Rubus pubescens* Raf.*: The reproductive traits and population dynamics of two temporally isolated members of the genus Rubus*. — Ph.D. thesis, Yale University, New Haven, Ct.

Whitney, G. G. 1984: The reproductive biology of raspberry and plant-pollinator community structure. — *Am. J. Bot.* 71: 887–894.

Zackrisson, O. 1977: Influence of forest fires on the North Swedish boreal forest. — *Oikos* 29: 22–32.

Zasada, J. C., Sharik, T. L. & Nygren, M. 1992: The reproductive process in boreal forest trees. — In: Shugart, H. H., Leemars, R. & Bonan, G. B. (eds.), *A systems analysis of the global boreal forest*: 85–125. Cambridge University Press, New York.