

Vegetation Dynamics in a Fire Damaged Forest Area: the Response of Major Ground Vegetation Species

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Abstract

As fire is inherent to boreal forest, sustainable forest management should consider emulating this disturbance type, taking into account the natural fire regime and the historical impact of humans. Fire often removes the dominant species and reveals mineral soil, which allows new species to spread on burned areas. Variable conditions provide habitat for many different species. Fire is sometimes necessary for the retention of species which do not regenerate in the absence of fire. Fire-damaged forest stands are often salvage logged. The necessity of this procedure can be disputed, as the cleaning may decrease biodiversity, favour pioneer herbs and shrubs which are highly competitive with tree regeneration, and disturb the ecosystem's nutrient cycle. The effect of burning and post-fire cleaning was studied. Ground vegetation was investigated during three subsequent years, 2004–2006, in fire-damaged pine forest areas in North-western and South-eastern Estonia, both dry and wet site types. Fire occurred 10–12 years prior to the inventories in the first and 2–4 years in the latter. The vegetation survey took place on 2×2m squares undergoing three different treatments: Burnt and Cleaned (BC), Burnt and Uncleaned (BU) and Control (CO). Floral composition differed significantly between the treatments. Biodiversity was higher on burnt plots than in control plots in humid areas and lower in dry areas. On dry sites, *Molinia caerulea* and *Calluna vulgaris* benefit from cleaning, which may hamper pine regeneration. Prescribed burning on such sites can reduce the fire risk. On wet sites, there was no significant difference between pioneer and shade-tolerant species between cleaned and uncleaned areas. Whether cleaning after fire should be maintained as a management action therefore depends greatly on the forest site type and other circumstances, such as management objectives and surrounding stands.

Key words: fire, boreal forest, ground vegetation, succession, prescribed fire, post-fire management, salvage logging

Introduction

Fire is inherent to boreal forests (Niklasson and Granström 2000, Gromtsev 2002, Kauhanen 2002, Mallik 2003), influencing forest structure and composition throughout history in Europe during various periods of both low and high fire frequency. This changing regime is typically closely related to modifications in the intensity of human impact and practices in land use management (Hytteborn and Packham 1985, Foster et al. 1998, Wallenius et al. 2007, Summers et al. 2008) and climate (Carcaillet et al. 2007). In forests dominated by Scots pine (*Pinus sylvestris* L.) fire has in general not been stand-replacing, thus favouring the regeneration of pine (Angelstam 1998, Turner et al. 1998, Kuuluvainen et al. 2002, Ryan 2002, Hancock et al. 2005). Increasing forest management and new techniques have reduced burning as a management tool, slash-and-burn and accidental fire, minimizing the effect of fire on vegetation and forest development. It

is important for the preservation of open pine-dominated landscapes to maintain periodic fire occurrence (Engelmark et al. 1998, Kuuluvainen et al. 2002).

Forest disturbances such as windthrow and fire often create new conditions for the vegetation – exposing mineral soil, providing more light, eliminating competing species, etc. (Mallik 2003, Ilisson et al. 2006, Marozas et al. 2007). Fire also affects the soil quality, initiating nutrient release due to thermal decomposition of humus, for example (Mallik 2003). Depending on its severity, fire can remove only the upper litter layer or also damage the roots and seeds. Removal of competitive species in early successional stages allows fire-adapted species, like *Calluna vulgaris*, which regenerates fast after fire, and *Pinus sylvestris*, which needs bare mineral soil for seed germination on some forest site types, to spread (Sedlakova and Chytrý 1999, Granström 2001, Gromtsev 2002, Mallik 2003, Hille and Den Ouden 2004). All these changes in the burnt area create habitats for new species, which often leads

to increased biodiversity (Marozas et al. 2007, Davies et al. 2008, Ruokolainen and Salo 2009). Since controlled fire can also help to reduce the fire risk in forests covered with old *Calluna* shrubs (Davies et al. 2008), combined methods for prescribed burning, taking into account the forest structure, fire severity and frequency as well, should be considered as management tools (Bergeron et al. 2002, Kauhanen 2002). These would serve both the purposes of timber production and nature conservation by reducing the fire risk, favouring pine regeneration, and maintaining the high number of species. The most favourable period for pine regeneration, according to the literature review by Hancock et al. (2005), is 3–10 years after fire.

The general practice after natural or prescribed forest fire in managed stands in Estonia as well as Northern America, is to remove the burnt wood and stumps from the stand to promote tree regeneration (Lindenmayer and Noss 2006). Post-fire salvage logging is also used to reduce the loss of merchantable timber (Scgmiegelow et al. 2006, Macdonald 2007). As the cleaning is often carried out with heavy machinery, which partly removes the litter layer and shrubs, this causes an additional disturbance to the stand. Beside the physical elimination of vegetation, extended nutrients and, occasionally, seed removal, it may favour highly competitive herbs, hampering instead of facilitating tree regeneration and reducing species diversity in the ground vegetation (Lindenmayer and Noss 2006, Vanha-Majamaa et al. 2007). The effects of cleaning have not been studied extensively, although post-fire management can play an important role in directing succession towards a more diverse, fire resistant and stable timber-producing stand (Vanha-Majamaa et al. 2007).

This study addresses the dynamics of the ground vegetation after fire. Depending on post-fire treatments, nutrient availability (Skre et al. 1998) and the amount of light reaching the ground vary. Management should be applied according to the use of the forest after burning – forest managed for timber production or for conservation (Wallenius et al. 2002, Mallik 2003) – to create proper conditions for the desired biome.

The main aim of the study is to explore the effect of fire and human disturbance to ground vegetation dynamics. We expect (1) shade-tolerant species to be more abundant on the burnt and uncleaned plots and shade-intolerant species to dominate on burnt and cleaned plots, (2) fire-adapted species to have greater coverage on burnt plots, (3) the composition of major species gradually to revert to a species composition similar to the pre-fire period and (4) the number of species to be highest on burnt and uncleaned plots.

Materials and methods

Study areas

The study was carried out on two different sites: Vihterpalu (59°13' N 23°49' E), situated in North-western Estonia and Naha (58°11' N 27°25' E) situated in South-eastern Estonia. Estonia belongs to the hemiboreal vegetation zone (Ahti *et al.* 1968), the average temperature being +5.2 °C. The coldest month is February, at –5.7 °C and the warmest is July at +16.4 °C. The average precipitation is 550–650 mm. There are about 200 fires per year with an average size of 3.7 ha (1992–2006), of which less than one percent is caused by natural factors (Yearbook Forest 2007).

Vihterpalu stands belong to the *Vaccinium uliginosum* and *Calluna* site types (Löhmus 1984) with sandy and dry soils. Ditching has been carried out to lower the water level. Fire disturbance is frequent on these sites. Fire occurred in Vihterpalu in 1992, when the forest was 52 years old. The Naha stands belong to the transitional and raised bog site types (Löhmus 1984) with a peat layer of about 30 cm. Fire occurred in 2002, when the forest was 36 years old. Both sites were covered with pure *Pinus sylvestris* forest from natural regeneration. Productivity in these forests was low and the trees were in the lower quality classes. No thinning had been carried out, although the first thinning is usually done when the forest is about 30 years old.

Fire intensity varied within and between the sample plots, creating patches with different damage levels, and leaving some scattered trees alive. At Vihterpalu, the entire organic layer was consumed, leaving mostly base sand. At Naha, the wet peat layer protected the organic soil from high severity levels.

Research design

In 2002, 15 permanent study plots (20×40 m) were established on fire-damaged and untouched control areas for ground vegetation measurements (9 at Vihterpalu and 6 at Naha). Measurements were carried out in the summers of 2004–2006. Three types of plot were set up: (I) control (CO), 5 plots; (II) burnt and uncleaned (BU), 5 plots – trees were left on the plot after the fire; (III) burnt and cleaned (BC), 5 plots – plots were cleaned after fire (Table 1). One Naha control plot was excluded from the analyses due to different site type. At Vihterpalu, the cleaning was carried out with a bulldozer, piling up the burned stumps and stems. At Naha, the burned stems were cut and removed. Since the treatments were carried out differently, their effects on ground vegetation development after fire may be divergent.

Ten 2×2 metre sample squares were placed along the central transect (40 m) on each plot at 2-metre in-

Table 1. Differentiation of 14 study plots at Naha and Vihterpalu between 4 different forest site types and 3 different treatments. Each plot contained ten 2×2 m vegetation squares

Study site	Plots of Vihterpalu			Plots of Naha		
	BU	BC	CO	BU	BC	CO
Transitional (mesotrophic) bog				2	1	1
Raised (oligotrophic) bog					1	
<i>Vaccinium uliginosum</i>	2	2				
<i>Calluna vulgaris</i>	1	1	3			

Treatment abbreviations: BU, burnt and uncleaned; BC, burnt and cleaned; CO, control

tervals (Figure 1). The coverage (%) of herbs, mosses and lichens in each sample quadrat was determined.

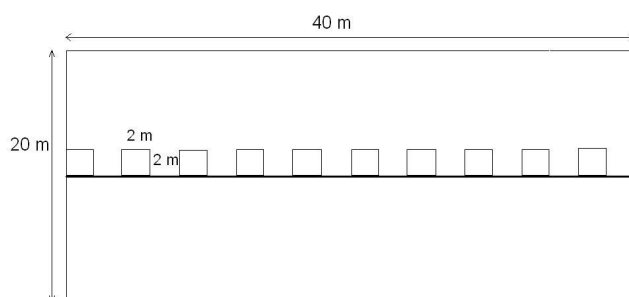


Figure 1. Layout of the sample squares along the central transect on plots

Data analysis

Sørensen’s similarity index (Roberts 1986) was calculated to enable comparison of floristic composition within and between plots of the same and divergent treatments.

Biodiversity was calculated using the coverage data per species and the total coverage. We used both the Shannon-Wiener index (Began et al. 1996) and the Simpson index (Simpson 1949) for purposes of comparison. Pielou’s species evenness (Pielou 1966) was determined to check for extreme cases. The paired Student t-Test was used to test for differences in the Shannon biodiversity indices within treatments (Halpern 1989).

Twenty-one species were selected for further analysis according to a minimum of 5% average coverage. The cover of mosses at Vihterpalu in 2004 was not measured. As the forest site type on one sample plot at Naha turned out to differ fundamentally from those on the other plots, ground vegetation measurements from this plot were excluded from the analysis (Table 1). Data were analysed using the ‘Mixed’ GLM procedure in SAS (Release 9.1) to test whether and how the different stand properties determine the species coverage in the stand and Multiple ANOVA (Statgraphics, Centurion XV, Statpoint Inc.) to test annual and treatment effects for 14 species in detail. Cover data was arcsine - transformed using equation 1.

$$C_t = \arcsin \sqrt{\frac{C}{100}} \tag{1}$$

where C_t is the transformed value of coverage and C is the coverage.

A Sørensen similarity index of 0.33 indicates that Naha and Vihterpalu have rather divergent floristic compositions, a finding confirmed by the ‘Mixed’ procedure. The results for both areas are thus presented separately.

Results

A total of 61 different species of ground vegetation were registered over the three years of measurements (Appendix 1). The Naha sample plots contained 31 species and those at Vihterpalu 44. Of these, 14 species were common to both areas. Most of these common species had significantly different coverage between areas (the ‘Mixed’ procedure).

The similarity was considerably higher between plots undergoing the same treatment than between plots with different treatments. While these differences are more obvious at Naha than Vihterpalu (Table 2), the species composition in the undisturbed control plots was generally different from the disturbed plots. Comparison between years at Naha reveals that subsequent years were more similar than non-subsequent years.

Different biodiversity indices (Shannon-Wiener and Simpson, Table 3) calculated for each treatment, averaging the values of the sample quadrates, showed that the plots which were left untouched after burning showed greater biodiversity levels with more spe-

Naha	BC	BU	CO	Vihterpalu	BC	BU	CO
BC	0.40–0.74			BC	0.43–0.91		
BU	0.30–0.63	0.67–0.95		BU	0.25–0.88	0.40–0.71	
CO	0–0.22	0–0.32	0.44–0.72	CO	0.09–0.58	0.09–0.56	0.33–0.71

Table 2. Ranges of Sørensen’s similarity index values within and between different plot treatments

Treatment abbreviations: BU, burnt and uncleaned; BC, burnt and cleaned; CO, control

Table 3. The Shannon-Wiener and Simpson biodiversity indices and Pielou's evenness index, average ± standard deviation of vegetation squares per treatment. As mosses were not investigated at Vihterpalu in 2004, the data for this year have not been incorporated into the biodiversity calculations

District	Treatment	No. of years	No. of squares	Shannon-Wiener index (H')	Simpson index (D)	Pielou's evenness index (E)
Naha	BC	3	20	<i>0.83 ± 0.35</i>	<i>0.54 ± 0.23</i>	<i>0.57 ± 0.26</i>
Naha	BU	3	20	<i>1.01 ± 0.39</i>	<i>0.50 ± 0.20</i>	<i>0.55 ± 0.20</i>
Naha	CO	3	10	<i>0.78 ± 0.26</i>	<i>0.57 ± 0.15</i>	<i>0.54 ± 0.21</i>
Vihterpalu	BC	2	30	<i>0.77 ± 0.35</i>	<i>0.57 ± 0.20</i>	<i>0.52 ± 0.29</i>
Vihterpalu	BU	2	30	<i>0.79 ± 0.37</i>	<i>0.55 ± 0.22</i>	<i>0.64 ± 0.45</i>
Vihterpalu	CO	2	30	<i>0.89 ± 0.39</i>	<i>0.50 ± 0.21</i>	<i>0.66 ± 0.35</i>

Treatment abbreviations: BU, burnt and uncleaned; BC, burnt and cleaned; CO, control. Bold and italic values represent the highest and second-highest diversity levels respectively.

cies in both areas than burnt and cleaned plots. However, the differences are not that clear at Vihterpalu. At recently-damaged Naha, the disturbed plots had higher species diversity than the undisturbed plots, whereas at Vihterpalu, where fire occurred over a decade before the first inventories, the undisturbed plots were more diverse. Analysis of the biodiversity indices at plot level revealed the same picture. The Pielou's evenness index varied considerably within treatments, especially in the Vihterpalu sample plots.

Changes in biodiversity at Naha and Vihterpalu during the inventory years were divergent (Figure 2). At Naha (2a), the diversity either peaked or increased during this period. Only in the control plot the last

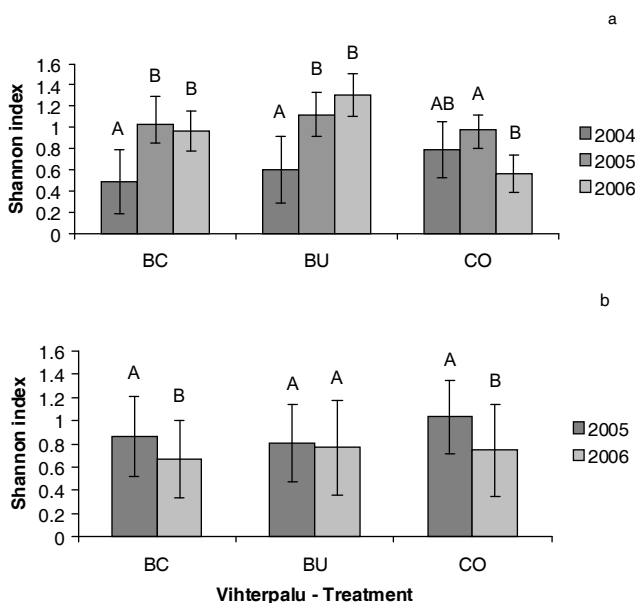


Figure 2. The Shannon-Wiener index – average of permanent sample plots per treatment and year for Naha (a) and Vihterpalu (b). Error bars show standard deviation. Statistically significant differences denoted by different letters above bars (paired Student t-Test, P<0.05)

year did show the least diverse species composition. At Vihterpalu (2b), diversity decreased in the burnt and cleaned plots, although this trend can be observed for control plots as well. The differences between both treatments are clearer at Naha, shortly after the fire, than at Vihterpalu.

Plot treatment revealed statistically significant differences for all main species coverage, whereas observation years revealed significant differences only for six species (three at Naha and three at Vihterpalu) (Tables 4 and 5). In Vihterpalu all the three species were mosses.

Table 4. The significance levels of Multiple ANOVA analysis of major species for year, treatment and interactions at Naha

	Year	Treatment	Interaction
<i>Chamaedaphne calyculata</i>	< 0.0001	< 0.0001	0.0053
<i>Eriophorum vaginatum</i>	< 0.0001	< 0.0001	0.0022
<i>Ledum palustre</i>	0.0924	< 0.0001	0.2255
<i>Pleurozium schreberi</i>	0.1068	< 0.0001	0.0821
<i>Polytrichum commune</i>	0.1013	< 0.0001	0.5033
<i>Sphagnum</i> spp.	0.0101	< 0.0001	< 0.0001
<i>Vaccinium uliginosum</i>	0.3589	< 0.0001	0.2830

Table 5. The significance levels of Multiple ANOVA analysis of major species for year, treatment and interactions at Vihterpalu

	Year	Treatment	Interaction
<i>Calamagrostis epigeios</i>	0.0977	0.0003	0.5537
<i>Calluna vulgaris</i>	0.5850	< 0.0001	0.9612
<i>Dicranum polysetum</i>	< 0.0001	< 0.0001	< 0.0001
<i>Dicranum scoparium</i>	< 0.0001	< 0.0001	< 0.0001
<i>Molinia caerulea</i>	0.6734	0.0001	0.7468
<i>Pleurozium schreberi</i>	0.3065	< 0.0001	0.7500
<i>Polytrichum juniperinum</i>	0.0002	< 0.0001	0.0080
<i>Vaccinium vitis-idaea</i>	0.7981	< 0.0001	0.3668

At Naha three species – *Eriophorum vaginatum*, *Ledum palustre*, *Polytrichum commune* – increased their coverage after fire, whereas the coverage was greater on uncleaned than on cleaned plots. *Ledum palustre* was not found on cleaned plots (Table 6).

Fire decreased the coverage of *Chamaedaphne calyculata*, *Pleurozium schreberi*, *Sphagnum* spp. and *Vaccinium uliginosum*. *Sphagnum* spp. was the only species group among these four that was able to subsist on cleaned plots and have even greater coverage there than on uncleaned plots.

Table 6. Mean values of transformed total coverage data of major Naha species by treatment and statistically significant difference (denoted by different letters showing homogeneous groups)

	CO	BU	BC
<i>Chamaedaphne</i>			
<i>calyculata</i>	0.2177 A	0.1930 A	0.0000 B
<i>Eriophorum vaginatum</i>	0.1690 A	0.3968 B	0.2238 A
<i>Ledum palustre</i>	0.0905 A	0.1894 B	0.0000 C
<i>Pleurozium schreberi</i>	0.5468 A	0.0023 B	0.0000 B
<i>Polytrichum commune</i>	0.0811 A	0.8816 B	0.6174 C
<i>Sphagnum</i> spp.	0.8355 A	0.2173 B	0.2816 B
<i>Vaccinium uliginosum</i>	0.1489 A	0.0690 B	0.0000 C

Treatment abbreviations: BU, burnt and uncleaned; BC, burnt and cleaned; CO, control

Three bog species – *Chamaedaphne calyculata*, *Eriophorum vaginatum*, *Sphagnum* spp. – produced significant differences for the observation years with the coverage of all these species increasing (Table 7).

Table 7. Mean values of transformed coverage data of major Naha vegetation species by observation year and statistically significant difference (denoted by different letters showing homogeneous groups)

	2004	2005	2006
<i>Chamaedaphne calyculata</i>	0.0762 A	0.1554 B	0.1790 B
<i>Eriophorum vaginatum</i>	0.0786 A	0.2514 B	0.4596 C
<i>Ledum palustre</i>	0.0735 A	0.1213 B	0.0850 AB
<i>Pleurozium schreberi</i>	0.1578 A	0.2062 B	0.1851 AB
<i>Polytrichum commune</i>	0.4745 A	0.5472 AB	0.5584 B
<i>Sphagnum</i> spp.	0.3759 A	0.4621 B	0.4964 B
<i>Vaccinium uliginosum</i>	0.0691 A	0.0903 A	0.0584 A

At Vihterpalu three species – *Calamagrostis epigeios*, *Calluna vulgaris*, *Polytrichum juniperinum* – increased their coverage after fire (Table 8). All these three, except *Calamagrostis epigeios*, had greater coverage on cleaned than uncleaned plots. *Calamagrostis epigeios* was absent on control plots and appeared only after fire and the coverage of *Polytrichum juniperinum* on the control plots was very low.

Fire decreased the coverage of four species – *Dicranum polysetum*, *Dicranum scoparium*, *Pleurozium schreberi*, and *Vaccinium vitis-idaea*, whereas all these species except *Vaccinium vitis-idaea* disappeared from cleaned plots.

The coverage of *Molinia caerulea* was not affected by the fire, as the coverage values of the control and burnt and uncleaned plots are not significantly

Table 8. Mean values of transformed coverage data of Vihterpalu vegetation species by treatment and statistically significant difference (denoted by different letters showing homogeneous groups)

	CO	BU	BC
<i>Calamagrostis epigeios</i>	0.0000 A	0.0515 B	0.0311 B
<i>Calluna vulgaris</i>	0.0618 A	0.5013 B	0.5920 C
<i>Dicranum polysetum</i>	0.1708 A	0.0063 B	0.0000 B
<i>Dicranum scoparium</i>	0.2079 A	0.0093 B	0.0000 B
<i>Molinia caerulea</i>	0.0089 A	0.0061 A	0.0600 B
<i>Pleurozium schreberi</i>	0.7794 A	0.0457 B	0.0000 B
<i>Polytrichum juniperinum</i>	0.0011 A	0.5694 B	0.6625 B
<i>Vaccinium vitis-idaea</i>	0.2632 A	0.1643 B	0.0634 C

Treatment abbreviations: BU, burnt and uncleaned; BC, burnt and cleaned; CO, control

different. *Molinia caerulea* has the greatest coverage on burnt and cleaned plots.

Three mosses – *Dicranum polysetum*, *Dicranum scoparium*, and *Polytrichum juniperinum* – produced significant differences for the observation years with *Dicranum scoparium* coverage increasing significantly in one year (Table 9).

Table 9. Mean values of transformed coverage data of Vihterpalu vegetation main species by observation year and statistically significant difference (denoted by different letters showing homogeneous groups). Mosses were not investigated in 2004

	2004	2005	2006
<i>Calamagrostis epigeios</i>	0.0189 A	0.0203 A	0.0433 A
<i>Calluna vulgaris</i>	0.3866 A	0.3613 A	0.4073 A
<i>Dicranum polysetum</i>		0.1181 A	0.0000 B
<i>Dicranum scoparium</i>		0.0223 A	0.1225 B
<i>Molinia caerulea</i>	0.0311 A	0.0191 A	0.0248 A
<i>Pleurozium schreberi</i>		0.2575 A	0.2926 A
<i>Polytrichum juniperinum</i>		0.4847 A	0.3373 B
<i>Vaccinium vitis-idaea</i>	0.1677 A	0.1726 A	0.1506 A

Discussion

Forestry practices have undergone rapid development over the last 50 years, forests now being managed more sustainably, in addition to timber production and protection of biodiversity and environment rising in importance. Managing forest for multiple purposes needs combined methods which are focused on the specific habitats of different species (including endangered species) and also takes the time of harvest, weather and previous management measures

used in the area to emulate the natural disturbance regime into consideration (Angelstam 1998, Bergeron et al. 2002, Pennanen 2002, Ryan 2002, Wallenius et al. 2002, Macdonald 2007). Management should also consider the frequency of fire, which may increase (Päätaalo 1998, Carcaillet et al. 2007) or decrease depending on location (Flannigan et al. 1998) with climate change. Combined methods allow traditional species to stay in their habitat and provide suitable habitat for other species (Franklin et al. 2002, Haeussler et al. 2002).

The use of timber is also growing in these times of growing energy need. This means that dead trees, snags and stumps are often removed from the forest to produce heat or electricity (Macdonald 2007). At the same time, dead wood must be considered as a part of the energy and matter flux of the ecosystem and its biodiversity component, providing heterogeneous landscapes, various microhabitats, and shade and light (Cooper-Ellis et al. 1999, Clinton and Baker 2000, Wallenius et al. 2002, Mallik 2003, Lindenmayer and Noss 2006, Macdonald 2007). Piles of dead wood can also provide a refuge for some species which otherwise might be replaced by light-demanding species (Angelstam 1998, de Chantal and Granström 2007). Fire often provides such sites by creating patches of burnt and unburnt vegetation, which can be occupied by various species (Vanha-Majamaa et al. 2007, Ruokolainen and Salo 2009), an effect also confirmed in our research, with biodiversity being highest on burnt and uncleaned plots.

Disturbance often reveals bare soil, providing regeneration conditions for various species. This generally results in a large number of species on disturbed areas (Jonsson and Esseen 1998, Ilisson et al. 2006, Marozas et al. 2007), with some being eliminated by competition over time. The decline in number of species immediately after fire due to destruction or removal of vegetation is followed by more species after a few years, with a succeeding decrease (Cooper-Ellis et al. 1999, Ilisson et al. 2006, Vanha-Majamaa et al. 2007). This trend was observed at Naha, where the diversity of species was higher and increasing during the inventory years, whereas at Vihterpalu, where the fire occurred ten years earlier, the succession was in its advanced stage with species diversity starting to decrease. Our research confirmed the successional changes in moss coverage in Vihterpalu with *Dicranum polysetum* and *Pleurozium schreberi* coverage decreasing and *Polytrichum juniperinum*, a pioneer species, increasing (Gloaguen 1990, Jonsson and Esseen 1998, Marozas et al. 2007).

For some species in our study, like *Pinus sylvestris* and *Calamagrostis epigeios*, natural regeneration

by fire can be a prerequisite on some forest site types (Päätaalo 1998, Gromtsev 2002, Hancock et al. 2005), as an abundance of *Vaccinium* species or *Calluna* can hamper seed germination (Mallik 2003). Our research showed that severe disturbance of burned plots after fire (salvage logging) physically removed most shrubs and herbs like *Chamaedaphne calyculata* and *Ledum palustre* entirely. The coverage-decreasing effect of constant wear, trampling and removal of above-ground plant parts has been confirmed by many authors (Hytteborn et al. 1985, Turner et al. 1999, Wallenius et al. 2002, Macdonald 2007, Marozas et al. 2007). The double-disturbance effects of fire and cleaning were probably the reason why only some shade-intolerant species, like *Calluna vulgaris*, *Molinia caerulea* and *Polytrichum juniperinum*, were able to regenerate after fire on burnt and cleaned plots. The abundance of *Calluna vulgaris* was probably caused by rapid vegetative regeneration and the heat effect which encourages seed germination (Sedlakova and Chytry 1999). *Calluna* is able to restore its coverage on burnt patches with good light conditions within two to four years (Sedlakova and Chytry 1999, Marozas et al. 2007), whereas *Vaccinium* species require five to six years (Marozas et al. 2007). This allows *Calluna* to dominate in early succession. *Vaccinium* species are also able to resprout after fire, but the survival of rhizomes and roots depends on the severity of the fire (Turner et al. 1998, Turner et al. 1999, Macdonald 2007). Severe fires, which remove a thick layer of humus, may result in lower species diversity (Wallenius et al. 2002, Macdonald 2007), whereas the highest species diversity maintains itself under moderate disturbance conditions (Mallik 2003) in which divergent conditions are provided. Moderate disturbances are also suitable for *Pinus sylvestris* regeneration, as some seed trees remain (Hille and Den Ouden 2004).

Fire severity and frequency depends on the fuel load on the ground (Päätaalo 1998, Baeza 2006). Harvesting, which is sometimes proposed as a management measure mimicking fire, causes hardly any serious damage to understory vegetation and does not consume the organic layer (Franklin et al. 2002, Hart and Chen 2008). That is why prescribed burning should also be used, as the management measure most comparable to natural fire disturbance (Mallik 2003, Pitkänen et al. 2003). Using prescribed burning also reduces the risk of natural fire (Päätaalo 1998, Davies et al. 2008), which may cause considerable damage to property.

If prescribed burning is not an option for more sustainable management, other methods should be considered. Clear-cutting is the most often suggested harvesting way of copying fire (Bergeron et al.

2002). To preserve biodiversity and avoid the risk of an altered water regime and increased wind velocity, however, shelterwood or salvage cutting, which can be compared with moderate disturbance, should be considered instead of clear-cutting, leaving some dead trees for biodiversity purposes (Hannerz and Hanell 1997, Macdonald 2007, Roberts and Zhu 2002, Vanha-Majamaa et al. 2007). Since a clear-cut area is more readily subject to temperature fluctuations and erosion, restoring the nutrient cycle may take longer (Hannerz and Hanell 1997). This again may lead to a delay in forest regeneration.

Conclusion

Combined forest management methods are required to encourage tree regeneration, and at the same time preserve biodiversity, reduce fire risk and provide rapid regeneration and nutrient cycling. Knowledge of ground vegetation species and their reaction to fire makes it easier to make the decision.

Moderate disturbance of peatlands often creates advantageous conditions for bog species with removing fire-sensible vegetation, like mosses, and thereby lowering transpiration. In dry areas however removal of ground vegetation allows light-demanding species to spread (*Calamagrostis epigeios* in Vihterpalu).

Cleaning wet site types has the predictable effect of optimising pine regeneration, whereas on dry site types it favours highly competitive species like *Molinia caerulea* and *Calluna vulgaris*, which hamper the regeneration of pine and possibly hardwoods which are desired to reduce fire risk. For dry areas, prescribed burning for reducing species competition and fire risk could be suggested, like moderate disturbance (salvage logging with retention areas for wet site types), as this avoids severe disturbance to the forest floor and ensures an undamaged seed bank.

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Appendix 1. List of species and their coverage (%) in the annual surveys in areas with different disturbance regimes at Naha (a) and Vihterpalu (b)

(a) Naha	Control (coverage, %)			Burnt and uncleaned (coverage, %)			Burnt and cleaned (coverage, %)		
	2004	2005	2006	2004	2005	2006	2004	2005	2006
<i>Sphagnum</i> sp.	69.50	49.80	46.05	1.03	10.45	12.08	0.98	13.25	20.80
<i>Pleurozium schreberi</i>	22.80	35.00	29.00	0.10					
<i>Vaccinium myrtillus</i>	5.75	8.80	8.00						
<i>Vaccinium uliginosum</i>	3.65	5.50	3.25	1.35	1.95	3.03			
<i>Chamaedaphne calyculata</i>	1.50	7.90	10.05	2.08	5.35	9.13			
<i>Dicranum polysetum</i>	0.95	6.10	4.10	0.03					
<i>Ledum palustre</i>	0.85	2.55	0.35	3.85	6.68	7.13			
<i>Eriophorum vaginatum</i>	0.75	4.80	10.10	2.88	13.50	40.00	0.33	6.18	25.08
<i>Polytrichum commune</i>	0.75	2.10	2.15	55.00	60.40	63.00	26.35	38.50	41.25
<i>Vaccinium vitis-idaea</i>	0.35	5.20	5.15	0.23	1.38	2.10			
<i>Hylocomium splendens</i>	0.10								
<i>Calluna vulgaris</i>	0.05			0.40	1.98	2.25	0.03	0.30	0.60
<i>Dicranum scoparium</i>	0.05								
<i>Melampyrum sylvaticum</i>	0.35			0.05	0.18		0.03	0.05	0.03
<i>Ptilium crista-castrensis</i>	0.20		1.00						
<i>Epilobium angustifolium</i>				0.18	0.15	0.08	0.30	2.18	0.55
<i>Rubus chamaemorus</i>				0.05	0.50	0.55			
<i>Calamagrostis arundinacea</i>				0.03			0.08		
<i>Oxycoccus palustris</i>				0.03					
<i>Typha latifolia</i>				0.03			0.08	0.03	
<i>Carex</i> sp.							0.48	1.30	5.53
<i>Agrostis capillaris</i>							0.08	0.95	0.05
<i>Epilobium adenocaulon</i>							0.08	0.05	
<i>Taraxacum officinale</i>							0.08	0.05	
<i>Juncus effuses</i>							0.05	0.10	0.50
<i>Phleum pratense</i>							0.05	0.03	
<i>Impatiens noli-tangere</i>							0.05		
<i>Scirpus sylvaticus</i>							0.03	0.48	1.10
<i>Rubus idaeus</i>								0.30	0.03
<i>Impatiens parviflora</i>								0.10	
<i>Epilobium montanum</i>								0.03	3.05
(b) Vihterpalu									
<i>Vaccinium vitis-idaea</i>	12.27	16.08	8.39	11.27	6.35	7.00	0.50	1.18	2.83
<i>Calluna vulgaris</i>	1.63	0.78	1.74	27.50	27.50	33.20	34.53	32.27	39.00
<i>Molinia caerulea</i>	0.33	0.18		0.37			1.27	1.33	3.70
<i>Betula</i> sp.	0.23								
<i>Vaccinium myrtillus</i>	0.10	0.07	0.68						
<i>Deschampsia flexuosa</i>	0.07			0.03					
<i>Pleurozium schreberi</i>	47.98		51.30	0.23		2.33			
<i>Dicranum polysetum</i>	13.92			0.10					
<i>Cladina rangiferina</i>	2.08			0.03					
<i>Dicranum scoparium</i>	0.83	17.00		0.07	0.33				
<i>Cladina mitis</i>	0.70	1.45		0.02					
<i>Hylocomium splendens</i>	0.47	0.34							
<i>Cladonia fimbriata</i>	0.22			0.23	0.00				
<i>Ledum palustre</i>	0.17	0.08							
<i>Lycopodium annotinum</i>	0.17								
<i>Cirriphyllum piliferum</i>	0.15								
<i>Cladonia coniocraea</i>	0.08			0.15					
<i>Cladonia deformis</i>	0.07			0.02					
<i>Cladonia stellaris</i>	0.07								
<i>Dicranum montanum</i>	0.07								
<i>Cetraria islandica</i>	0.05								
<i>Cladonia cornuta</i>	0.05			0.28					
<i>Carex</i> sp.	0.03			0.13	0.75	1.00	0.62		0.10
<i>Eurhynchium angustirete</i>	0.03			0.13					
<i>Cladonia gracilis</i>	0.02			0.07					
<i>Polytrichum juniperinum</i>	0.02			45.07	20.00	46.35			
<i>Ptilium crista-castrensis</i>	0.02								
<i>Empetrum nigrum</i>	0.02								
<i>Cladonia cenotea</i>	0.00								
<i>Rhytidiadelphus triquetrus</i>	0.00			0.02					
<i>Epilobium angustifolium</i>				0.67	0.20	0.68	0.43	0.38	0.04
<i>Calamagrostis epigeios</i>				0.53	0.48	3.18	0.13	0.25	2.33
<i>Calamagrostis arundinacea</i>				0.20		2.33			
<i>Luzula multiflora</i>				0.03					
<i>Stereocaulon</i> sp.				2.65					
<i>Agrostis capillaris</i>				0.05	0.34				
<i>Orthotrichum speciosum</i>				0.02					
<i>Physconia enteroxantha</i>				0.02					
<i>Racomitrium canescens</i>						0.34	0.33		
<i>Potentilla erecta</i>							0.13		
<i>Senecio</i> sp.							0.10		
<i>Populus</i> sp.							0.07		

ДИНАМИКА РАСТИТЕЛЬНОСТИ В ПОВРЕЖДЕННЫХ ПОЖАРОМ ЛЕСАХ: РЕАКЦИЯ ДОМИНАНТНЫХ ВИДОВ НАДПОЧВЕННОЙ РАСТИТЕЛЬНОСТИ

К. Парро, К. Кёстер, К. Йыгисте и Ф. Водде

Резюме

Поскольку пожары свойственны бореальному лесу, для экологически устойчивого лесоводства необходимо изучать тип этого повреждения, принимая во внимание естественный режим пожаров и историческое воздействие людей. Пожар часто уничтожает доминирующие виды растительности и обнажает минеральную почву, позволяя новым видам растений распространяться на выжженных площадях. Измененные условия обеспечивают среду обитания для многих видов растительности. Иногда пожар необходим для сохранения видов растений, которые могут возобновляться только после пожара. Часто производится очистка древостоев от поврежденных пожаром деревьев. Необходимость этой процедуры спорна, поскольку такая очистка может уменьшить биологическое разнообразие и способствовать развитию пионерных видов трав и кустов, которые в силу своей высокой конкурентоспособности препятствуют возобновлению древесных пород и нарушают цикл питательных веществ в экосистеме. Был изучен эффект выжигания и послепожарной очистки древостоев. Надпочвенная растительность исследовалась на протяжении трех лет (2004–2006 гг.) в поврежденных пожаром сосновых древостоях Северо-западной и Юго-восточной Эстонии. Древостои располагались на территориях как сухого, так и влажного типов. На момент исследования на данной территории первый пожар был зарегистрирован 10–12 лет назад и последний – 2–4 года назад. Анализ растительности проводился на квадратах площадью 2Ч2 м на трех разных участках: Выжженный и Очищенный (ВО), Выжженный и Неочищенный (ВН) и Контроль (К). Участки значительно отличался по флористическому составу. Биологическое разнообразие на выжженных участках было выше, чем на контрольных участках влажных территорий и ниже - на сухих территориях. На сухих территориях послепожарная очистка способствовала распространению *Molinia caerulea* и *Calluna vulgaris*, что возможно препятствовало возобновлению сосны. Плановое сжигание на таких территориях может уменьшить пожароопасность. На влажных территориях не было отмечено никакого существенного различия между видами-пионерами и теневыносливыми видами на очищенных и неочищенных участках. Поддерживать ли очистку древостоя после пожара, как хозяйственную меру, строго зависит от типа лесного участка, и других обстоятельств, таких как, хозяйственная цель и окружающие древостои.

Ключевые слова: пожар, бореальные лес, надпочвенная растительность, смена растительности, плановое сжигание, послепожарное лесоводство, вывоз поврежденных пожаром деревьев