

www.metla.fi/silvafennica - ISSN 0037-5330 The Finnish Society of Forest Science - The Finnish Forest Research Institute

Microsites Before and After Restoration in Managed *Picea abies* Stands in Southern Finland: Effects of Fire and Partial Cutting with Dead Wood Creation

Saara Lilja-Rothsten, Michelle de Chantal, Chris Peterson, Timo Kuuluvainen, Ilkka Vanha-Majamaa and Pasi Puttonen

Lilja-Rothsten, S., de Chantal, M., Peterson, C., Kuuluvainen, T., Vanha-Majamaa, I. & Puttonen, P. 2008. Microsites before and after restoration in managed *Picea abies* stands in southern Finland: effects of fire and partial cutting with dead wood creation. Silva Fennica 42(2): 165–176.

Different types of microsites, e.g. CWD (coarse woody debris), mounds, and uprooting pits, are important for tree regeneration and biodiversity. However, microsite diversity is greatly reduced in managed stands. We studied how restoration treatments changed microsite distribution in mature managed Picea abies stands. Four cutting treatments were used: uncut, low-CWD (5 m³ ha⁻¹ of down retention trees, DRT, and 50 m³ ha⁻¹ of standing retention trees), intermediate-CWD (as previous but leaving 30 m^3 ha⁻¹ of DRT), and high-CWD (as previous but with 60 m³ ha⁻¹ of DRT). Timber harvested from stands ranged from 108–168 m³ ha⁻¹. Half of the stands were burned, and half remained unburned. Sampling was stratified into upland and paludified biotopes within each stand. The pre-treatment microsite distributions were dominated by level ground in both biotopes; mounds and microsites on or next to CWD or a stump were slightly more abundant in the paludified than in the upland biotopes. Microsites were more diverse after cutting, with and without fire. The cutting treatment increased the relative abundances of microsites on or next to CWD. Fire consumed small diameter dead wood and flattened mounds. Microsites were more diverse in paludified than in upland biotopes. The results demonstrate that microsite diversity can rapidly be restored to structurally impoverished managed Picea stands despite a large portion of wood volume being harvested.

Keywords biodiversity, disturbance dynamics, coarse woody debris, CWD, boreal forest, managed forest, regeneration

Addresses Lilja-Rothsten, de Chantal & Kuuluvainen: University of Helsinki, Dept. of Forest Ecology, Finland; *Peterson*: Dept. of Plant Biology, University of Georgia, Athens, GA, USA; *Puttonen & Vanha-Majamaa*: The Finnish Forest Research Institute, Vantaa Unit, Finland **E-mail** saara.lilja@helsinki.fi

Received 15 August 2007 Revised 10 December 2007 Accepted 10 January 2008 Available at http://www.metla.fi/silvafennica/full/sf42/sf422165.pdf

1 Introduction

In natural forest ecosystems, disturbances, e.g. windthrow and fire, typically create legacies such as logs and stumps which increase the abundance and diversity of microsites (Beatty and Stone 1986, Peterson et al. 1990, Carlton and Bazzaz 1998, Lampainen et al. 2004). Microsites can be defined as local features of the forest floor, at a scale of centimeters to tens of centimeters, that characterise the seedling's growing environment such as substrate type, e.g. dead wood at various stages of decay or exposed mineral soil, or locations with a microclimate that differs from that of the surroundings, e.g. under a fallen crown or next to CWD (coarse woody debris). Microsite diversity is shown to be directly related to species diversity (Jonsson and Esseen 1990, Work et al. 2004) and post-disturbance regeneration (Hytteborn et al. 1987, Hörnberg et al. 1995, Lee and Sturgess 2001). The recruitment of tree seedlings crucially depends on microsites that can reduce their vulnerability to environmental extremes, competition and herbivory (Harper et al. 1965, Simard et al. 1998). In turn, microsites differ in environmental conditions (Beatty and Stone 1986, Peterson et al. 1990, Carlton and Bazzaz 1998) and differences among microsites may persist from decades to centuries and result in fine-scale vegetation patterns (Beatty 1984, Peterson and Campbell 1993).

For example, the elevated microsite structure provided by large diameter logs may protect seedlings from flooding in paludified areas (Hörnberg et al. 1997) and may offer a reduced-competition environment due to sparser vegetation (Harmon and Franklin 1989, Peterson et al. 1990). Dead wood aggregations and treefall root mounds may provide refugia against ungulate browsing (Peterson and Pickett 1995, Long et. al. 1998, Ripple and Larsen 2001, de Chantal and Granström 2007). On the other hand, burned microsites with thin humus or exposed mineral soil can greatly enhance establishment of pioneer tree species (Sarvas 1937, Vanha-Majamaa et al. 1996, Lampainen et al. 2004). Apart from being important to tree regeneration, microsites are also essential for biodiversity. Many organisms need microsites that meet specific requirements, such as critical water and light conditions (Berg et al. 1994). For example, many threatened saproxylic species depend on various types of dead wood, e.g. snags or logs, of various sizes and stages of decay (Berg et al. 1994, Jonsell et al. 1998, Siitonen 2001, Jonsell et al. 2007). Others require charred dead wood (Jonsell et al. 1998, Wikars 2002).

However, compared to natural stands, microsite diversity has decreased in Fennoscandian managed stands (Kuuluvainen and Laiho 2004). Especially lacking are microsites such as those related to CWD, under fallen crowns, and uprooting pits and mounds, mainly because dead and dying trees are generally removed during clearcutting and thinnings (Siitonen 2001) or damaged during harvesting operations (Vanha-Majamaa and Jalonen 2001, Hautala et al. 2004). In addition, an effective fire suppression policy has reduced the abundance of post-fire early-successional stands in the Fennoscandian landscape (Uotila et al. 2001), thereby decreasing the abundance of stands wherein charred dead wood microsites are abundant (Granström 2001, Vanha-Majamaa et al. 2007). A post-fire open stand structure with an abundance of dead wood is preferred by many species, many of which were previously considered to be strict old-growth specialists (Martikainen et al. 2000, Kouki et al. 2001, Similä 2002).

Although established management practices reduce the diversity of microsites, recent findings propose that silvicultural prescriptions that mimic natural disturbances can restore boreal forest structure and processes (Kouki et al. 2001, Bergeron et al. 2002, Kuuluvainen 2002, Vanha-Majamaa et al. 2007). The goal of forest restoration treatments is to change forest structures, processes, and species composition of ecosystems altered by human actions so that they are closer to those of natural forests (Bradshaw 1997). Because burned or dead wood in various stages of decay is important to biodiversity, and because the formation of a continuum of dead wood is part of succession in natural forests, the creation of CWD in managed forests is an essential goal of restoration (Siitonen 2001). Some studies show that restoration treatments enhance stand heterogeneity (Carey 2003, Lilja et al. 2005), but there is no information available about how restoration treatments actually affect microsite diversity and relative abundances and what are

their effects on ecological processes. The success of restoration treatments can only be measured in the long-term after succession has proceeded. Since forest restoration is a relatively new activity in Fennoscandia, there are no long-term results on the ecological effects of forest restoration available yet. However, even short-term effects can indicate whether restoration treatments were a step in the right direction.

Particularly the mesic types of boreal forest in Fennoscandia are characterized by small-scale variation in moisture conditions related to the topographic relief. Thus, in forestry, areas that have been delimited as one stand can actually contain several ecologically different biotopes (Vanha-Majamaa and Jalonen 2001). This patch-scale biotope variation can also affect tree regeneration and biodiversity. Indeed, paludified biotopes may act as important colonization centres and seed sources after fire (Hörnberg et al. 1995, Vanha-Majamaa and Jalonen 2001). This is because they are likely to burn more seldom and with less severity than upland biotopes due to higher soil moisture (Vanha-Majamaa and Jalonen 2001, Wallenius et al. 2004).

The aim of this study was to describe microsite distributions in managed *Picea abies* (L.) Karst stands before and shortly after restoration treatments. We hypothesised that a partial cutting treatment that extracts part of the timber and creates some dead wood would diversify microsite relative abundances. Because fire is an important disturbance factor in boreal forests, our restoration experimental setup also included a fire treatment. We asked two basic questions: 1) How do partial cutting with dead wood creation and fire change the short-term microsite distributions in managed *P. abies* stands? 2) Do the short-term changes differ between upland and paludified biotopes?

2 Material and Methods

2.1 Study Area

The study area is located in the southern boreal zone (Ahti et al. 1968) in southern Finland (61°N, 25°E). The mean annual temperature is +3.1°C and the duration of the thermal growing period is 160 days. The annual average precipitation is about 670 mm. The bedrock consists of orogenic granitoids and is covered with a thick moraine layer (Juvakka et al. 1995).

Altogether, 24 stands (1-3 ha) located in Norway spruce (P. abies) -dominated mature managed forests on mesic site type were selected for the experiment. Most of the stands were of the Myrtillus type (MT), but five stands had also characteristics of the Oxalis Myrtillus type (OMT; Cajander 1926). The stands were of a mixed species composition, including Betula pendula, B. pubescens Roth, Populus tremula L., and Pinus sylvestris L.. In addition, Sorbus aucuparia L. and Juniperus communis L. occurred in the sapling layer. Each selected stand contained both upland and paludified upland biotopes (hereafter referred to as paludified biotopes). The upland biotopes were on mineral soil and belonged to the Vaccinium myrtillus site type (Cajander 1926). Paludified biotopes are common in mesic forests, although they are not normally distinguished in stand characteristics (Hörnberg et al. 1998; Vanha-Majamaa and Jalonen 2001). These were on peat soil, their vegetation and moisture level varied a lot, and consisted of patches of paludified Myrtillus site type and spruce mire (Laine and Vasander 1990). Although parts of the paludified biotopes were drained for forestry, patches of Sphagnum mosses still occurred. All stands were clearly managed, but their exact management history is unknown. Modern silvicultural methods, such as thinnings, have been in use in the region since the beginning of the 20th century (Juvakka et al. 1995). A more detailed land-use history is presented in Lilja et al. (2005). The average age of the stands was 80 years (range 60-100 years), the average volume was 252 m³ ha⁻¹ on the upland biotopes and 212 m³ ha⁻¹ on the paludified biotopes.

Pre- versus post-treatment	Upland biotopes			Paludified biotopes		
	G	d.f.	р	G	d.f.	р
Unburned uncut	44.64	9	< 0.001	4.38	8	>0.05
Unburned low-CWD	184.63	8	< 0.001	161.02	8	< 0.001
Unburned intermediate-CWD	182.12	8	< 0.001	126.11	9	< 0.001
Unburned high-CWD	325.13	9	< 0.001	268.43	8	< 0.001
Burned uncut	21.01	5	< 0.001	6.81	6	>0.05
Burned low-CWD	89.46	7	< 0.001	47.42	8	< 0.001
Burned intermediate-CWD	134.62	8	< 0.001	147.31	9	< 0.001
Burned high-CWD	108.24	9	< 0.001	122.05	9	< 0.001

Table 1. Log-likelihood tests (G) for differences in microsite relative abundances.

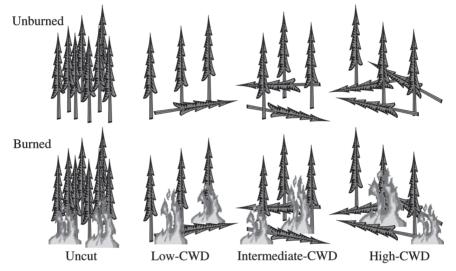


Fig. 1. Illustration of the restoration treatments with the four levels of partial cutting with dead wood creation, i.e., uncut, low-CWD (5 m³ ha⁻¹ DRT and 50 m³ ha⁻¹ SRT), intermediate-CWD (30 m³ ha⁻¹ DRT and 50 m³ ha⁻¹ SRT), and high-CWD (60 m³ ha⁻¹ DRT and 50 m³ ha⁻¹ SRT), with and without fire.

2.2 Experimental Design

Four cutting treatments were used: 1) uncut, 2) low-CWD (5 m³ ha⁻¹ of down retention trees DRT to create CWD and partial cutting leaving 50 m³ ha⁻¹ of standing retention trees SRT), 3) intermediate-CWD (similar as previous but leaving 30 m³ ha⁻¹ of DRT), and 4) high-CWD (similar as previous but with 60 m³ ha⁻¹ of DRT). Although uprootings do not occur, the creation of CWD can be thought of as emulating wind damage and the consequent microsites, as recommended by Kuuluvainen and Kalmari (2003) for the regeneration of *Picea* forests. In addition to the cutting treatment, a fire treatment was applied to half of the stands. The cutting and fire treatments were randomized among the 24 selected stands, with each combination of cutting treatment and fire being replicated three times.

The mean volume of wood that was harvested from the stands was $168 \text{ m}^3 \text{ ha}^{-1}$ with low-CWD, $145 \text{ m}^3 \text{ ha}^{-1}$ with intermediate-CWD and 108 m^3 ha⁻¹ with high-CWD (Table 1). The harvestings were carried out in winter 2002 (February and March) using conventional forestry machinery which cut the branches from the stems and spread the logging residues evenly on the forest floor. However, branches were not removed from the stems of down retention trees (Fig. 1). The burnings were carried out in summer 2002 (June to

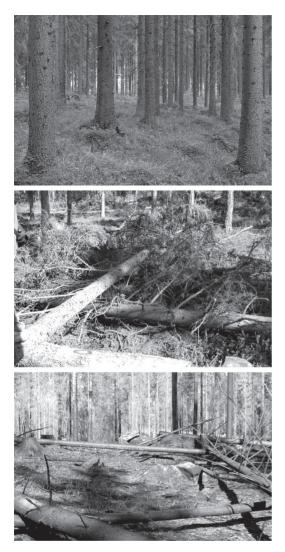


Fig. 2. An example of microsites before and after restoration cutting and burning on an upland part of a stand. Top: before restoration treatments; Center: unburned high-CWD; Bottom: burned high-CWD. (Photos Erkki Oksanen and Saara Lilja)

August) using the traditional Finnish prescribed burning technique (Lemberg and Puttonen 2003). In this method, the ignition lines form a circle around the stand and the burning front advances partly against the wind, which decreases the risk of fire escape. In addition, extra ignition lines were lit inside the circle, but these ignition lines did not cross the sample plots.

2.3 Assessments

For sampling, 30×50 m sample plots were placed randomly in each stand on both the upland and paludified biotopes, for a total of 48 sample plots. Each plot included a 5 m buffer zone, so that inventories were carried out in the central 20×40 m area. Pre-treatment inventories were done during summer 2001 and post-treatment inventories in autumn 2003. Microsite relative abundances were determined by recording microsite type at points every 20 cm along three parallel equally spaced 40 m lines in each plot, for a total of 600 points per plot. The microsites were defined using the characteristics of the forest floor at point scale. The recorded microsite classes were: 1) level ground (relatively flat ground with no other discernible characteristic), 2) mound (>20 cm rise from surrounding average ground level), 3) depression (>20 cm drop from surrounding average ground level), 4) on CWD, 5) next to CWD (≤ 15 cm away), 6) on or next to a stump (≤ 15 cm away), 7) under a fallen tree crown, 8) on logging waste, and 9) uprooting spot or exposed soil, and 10) on a stone. The origin of mounds and depressions was not readily identifiable anymore.

2.4 Statistical Analyses

The pre- and post-treatment relative abundances of microsites, i.e. the distributions of random points among microsite types, were compared for each treatment using a log-likelihood test value:

$$G = 2\sum_{i=1}^{k} o_i \ln \frac{o_i}{e_i}$$
(1)

where k is the number of microsite classes, and o_i and e_i are the observed and expected frequencies in class i, respectively. The expected distribution is the average between pre- and post-treatment frequencies; thus the null hypothesis is no change in among-microsite frequencies. The tests were performed using only stands that were inventoried both pre- and post-treatment. As the test requires that microsite classes have both pre- and post-treatment expected frequencies that are at least one, microsite classes had to be deleted in some cases. A second requirement of the test is

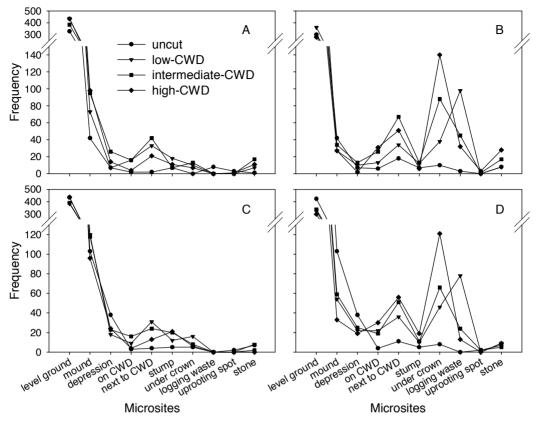


Fig. 3. Relative frequency abundances of microsites in stands restored using the cutting treatment without fire: A) pre- and B) post-treatment in upland biotopes, and C) pre- and D) post-treatment in paludified biotopes. Note the different break intervals on the Y-scale.

that not more than 25% of microsites have an expected frequency less than 5 (Ott 2000); when that requirement was not fulfilled, microsites with an expected frequency smaller than 5 were combined into one category for the test (burned uncut stands in both biotopes)

3 Results

3.1 Pre-Treatment Conditions

The pre-treatment distribution of microsites differed significantly between upland and paludified biotopes, although it was rather uniform among stands within each biotope. In both biotopes, the pre-treatment microsite distribution was dominated by level ground (Fig. 3A, C, and 4A, C). The main differences between biotopes were due to mounds, depressions, and microsites on or next to CWD or a stump being slightly more abundant in the paludified than in the upland biotopes (Fig. 3A, C, and 4A, C).

3.2 Effect of Cutting Treatment and Fire on Microsite Distributions

The cutting treatment without fire significantly changed the post-treatment distributions of microsites compared to the pre-treatment ones, except in uncut stands in paludified biotopes (Table 1). Especially, the relative abundances of microsites on or next to CWD or a stump, under a fallen crown, and on logging waste increased (Fig. 3),

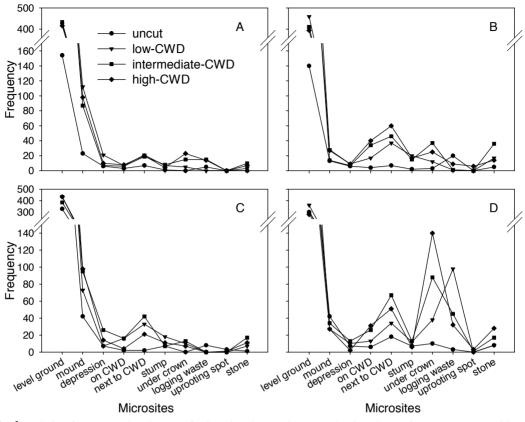


Fig. 4. Relative frequency abundances of microsites in stands restored using the cutting treatment combined with fire: A) pre- and B) post-treatment in upland biotopes, and C) pre- and D) post-treatment in paludified biotopes. Note the different break intervals on the Y-scale.

which is obviously a consequence of the cutting treatment. Due to these increases, there were fewer microsites on level ground, mounds, and depressions (Fig. 3). Although no restoration treatment was applied to unburned uncut stands, their post-treatment microsite distribution in upland biotopes changed compared to the pretreatment one (Table 1), due to the dynamic nature of forests that includes a continuum of dead wood formation, for example.

The burning outcome differed according to biotope. Stands in the paludified biotopes burned unevenly such that portions were left unburned as opposed to stands in the upland biotopes where the burning was more uniform. The burning result was also patchy in uncut stands, obviously because of the low amount of forest floor fuels.

The cutting treatment combined with fire

also changed the post-treatment distributions of microsites, except in uncut stands in paludified biotopes (Table 1). The relative abundance of level ground microsites decreased slightly in most burned stands except with low-CWD which had a gain. At the same time, the relative abundance of mounds decreased by at least half in all burned stands (Fig. 4). The relative abundances of microsites on or next to CWD or a stump, under a crown and on stones increased. Although the relative abundance of microsites under a crown increased, the increase was less than in unburned stands as fire destroyed part of the crowns. In contrast to unburned stands, burned stands had a lower relative abundance of microsites on logging waste which was also consumed by the fire, especially with intermediate- and high-CWD in upland biotopes (Fig. 3 and 4).

4 Discussion

4.1 Pre-Treatment Patterns

In our study, microsite distribution in managed Picea forests, i.e. the pre-treatment condition, was dominated by level ground. A likely cause is the long-lasting utilization and intensive management of forests in southern Finland, as reflected by the low amount of CWD in the pre-treatment managed stands, which consisted mainly of logging waste (Lilja et al. 2005). Kuuluvainen and Laiho (2004) compared P. sylvestris -dominated stands in southern Finland and Russian Karelia and concluded that the long lasting forest utilization had decreased microsite diversity and increased the share of level ground. However, after natural disturbance such as windthrow, the proportion of level ground decreases (Beatty 1984, Peterson and Campbell 1993, Kuuluvainen and Kalmari 2003). Despite being dominated by level ground, the pre-treatment microsite distribution was more varied in paludified than in upland biotopes, as would be expected where a saturated substrate decreases tree stability (Everham and Brokaw 1996) and promotes tree fall disturbances (Hautala and Vanha-Majamaa 2007), especially in shallow-rooted P. abies forests (Konôpka 2001). Both mounds and CWD-related microsites, such as microsites on or next to CWD or a stump, were more abundant in the paludifed than in the upland biotopes. Hörnberg et al. (1997) reported that mounds, which are often overgrown remnants of dead wood, are typical for old-growth swamp forests. Also, the long fire intervals in paludified Picea stands should allow for the long-term accumulation of dead wood from single-tree mortality (Hörnberg et al. 1995). This may explain partly the greater abundance of mounds in the paludified portions of stands. However, before restoration treatments, stands in both the upland and paludified biotopes lacked CWD-related microsites compared to natural or near-natural stands (Kuuluvainen and Laiho 2004). Although the microsite distribution was statistically significantly more varied in the paludified biotopes than in the upland ones, the differences may not have been of much ecological importance for tree regeneration and biodiversity.

4.2 Effects of Restoration Treatments

The relative abundances of microsites on or next to CWD or a stump, under a fallen crown and on logging waste increased due to the cutting treatment, which brought the diversity of microsites closer to that of near-natural and natural forests (Kuuluvainen and Laiho 2004). Dead wood was fresh shortly after the restoration treatments such that microsites on or next to CWD or a stump were in the early stage of their succession. Most of the CWD and stumps in our study area were decay stage 1 (according to Renvall 1995), which is not a suitable substrate for tree regeneration (Kuuluvainen and Kalmari 2003). Nevertheless, fresh dead wood serves as a substrate for lichens, polypores, insects, and animals (Berg et al. 1994, Jonsell et al. 1998, Toivanen and Kotiaho 2007). Fresh dead wood in the form of logs may also act as shelters, which are important for tree seedling emergence and establishment as they offer protection against extremes in microclimate (Harper et al. 1965, Vanha-Majamaa et al. 1996, Kuuluvainen and Kalmari 2003, Lampainen et al. 2004, de Chantal et al. 2005) and ungulate browsing (Ripple and Larsen 2001, de Chantal and Granström 2007). Later in the succession, decayed wood serves as a substrate for tree seedlings (McCullough 1948, Harmon and Franklin 1989, Zielonka 2006) and vascular plants (Lee and Sturgess 2001). Colonisation of CWD by P. abies seedlings generally takes place when wood is so decayed that a knife can penetrate at least 4 cm, i.e., 30-60 years after treefall, but colonisation can happen as early as 20 years after treefall too (Zielonka 2006). In a ca. 50-year-old windthrow site in a spruce forest in southern Finland, Kuuluvainen and Kalmari (2003) found seedlings significantly aggregated among microsites, especially on dead wood. Thus it is evident that some microsite effects are not apparent immediately after restoration.

Standing retention trees were still standing immediately after the cutting and burning treatments, thus there was a lack of uprootings. Although decomposition of snags is slower than that of down wood (Yatskov et al. 2003), these fire-killed standing retention trees will eventually fall to provide a continuum of dead wood, either through uprooting or stem breakage, depending upon the interaction of factors influencing decomposition and treefall, such as the presence of pathogens or insects, substrate moisture, and wind storms (Laiho and Prescott 2003). Treefalls generally increase microsite diversity by creating pits and mounds (Beatty and Stone 1986, Peterson and Pickett 1995). In spite of the lack of uprootings, the fire-killed standing retention trees increased the variety of dead wood types (Lilja et al. 2005), which is important for biodiversity (Berg et al. 1994, Jonsell et al. 1998, Siitonen 2001, Wikars 2002, Jonsell et al. 2007).

Microsites were less diverse after cutting and burning than after the cutting treatment alone because the fire consumed small diameter dead wood, such as branches from fallen crowns and logging waste, and flattened mounds. Accordingly, the relative abundances of microsites under fallen crowns, on logging waste and on mounds was lower in burned than in unburned stands. On the other hand, fire exposed stones, thereby increasing the relative abundance of that microsite. Fire also reduced the humus thickness in the studied stands (Kujala and Toivonen 2004), which will facilitate seedling establishment (Sarvas 1937, Viro 1969, Greene et al. 2004). However, tree seedlings in burned stands may be less protected against browsing due to the reduced relative abundance of sheltered microsites under fallen crowns (Ripple and Larsen 2001, de Chantal and Granström 2007); this may be of concern only in areas with high densities of browsing animals. Because the light intensity after the cutting treatment increases and resource availability may change, species diversity and cover may also increase after the restoration treatments, similarly as after windthrow (Carlton and Bazzaz 1998, Wohlgemuth et al 2002). On the other hand, a reduced relative abundance of microsites under fallen crowns in burned stands may be detrimental to species that require shade. Because stands in the paludified biotopes burned unevenly, their microsite distributions were more varied than those of stands in the burned upland biotopes. This indicates that the effect of withinsite biotope variation should be given attention in forest restoration.

5 Conclusions and Implications for Forest Restoration

Our experimental study demonstrated that many essential microsite characteristics of early successional natural forests can rapidly be restored to structurally impoverished mature managed *Picea* stands despite a significant portion of wood volume being harvested. The resulting microsite distribution differed whether or not fire was used in combination with partial cutting with dead wood creation. We also showed that microsite distribution between paludified and upland biotopes differed considerably after restoration of mature managed *Picea* stands, especially when using a combination of cutting and fire.

These results indicate that to achieve the predefined goal(s) of restoration, the treatment(s) should be chosen according to the site characteristics. For example, a cutting treatment can be combined with fire when restoration is aimed at creating habitat for fire-dependent species. On the other hand, fire should be left out if the goal is to create sheltered microsites to protect seedlings against browsing in problematic areas. Small paludified biotopes can be tentatively left unburned so that they can serve as colonization centres and seed sources and thereby increase biodiversity. On the other hand, if paludified biotopes must be burned, a large amount of down wood retention should be used to ensure an even burning result and creation of habitat for fire-dependent species. These examples show that knowledge of local site characteristics and their interaction with different restoration treatments is needed to achieve the goals set for restoration at the stand and landscape levels.

Acknowledgements

The Häme Polytechnic, the Finnish Forest and Park Service, UPM-Kymmene Ltd., the City of Hämeenlinna and the Finnish Forest Research Institute provided the stands for the study and implemented the treatments. A lot of people participated in the burning activities and field inventories; we want to thank them all. We are also grateful for financial support from the Foundation for Research of Natural Resources in Finland and the Graduate School in Forest Sciences. This research is part of the FIRE-project in the SUNARE (Sustainable use of Natural Resources 2001–2004) program financed by the Academy of Finland and part of the EU-project SPREAD (Forest Fire Spread Prevention and Mitigation). Peterson's involvement in this research was made possible by a Fulbright Teaching and Research Fellowship to the University of Helsinki, and the hospitality of the Department of Forest Ecology.

References

- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici 5(3): 169–211.
- Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology 65(5): 1406–1419.
- & Stone, E.L. 1986. The variety of soil microsite created by tree falls. Canadian Journal of Forest Research 16(3): 539–548.
- Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M. & Weslien, J. 1994. Threatened plant, animal, and fungus species in Swedish forests – distribution and habitat associations. Conservation Biology 8(3): 718–731.
- Bergeron, Y., Leduc, A., Harvey, B. & Gauthier, S. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fennica 36(1): 81–96.
- Bradshaw A.D. 1997. What do we mean by restoration? In: Urbanska, K.M., Webb, N.R. & Edwards, P.J. (eds.). Restoration ecology and sustainable development. Cambridge University Press, Cambridge, U.K. p. 8–14. ISBN 0-521-59989-X.

- Cajander, A.K. 1926. The theory of forest types. Acta Forestalia Fennica 29(3). 108 p.
- Carey, A.B. 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. Forestry 76(2): 127–136.
- Carlton, G.C. & Bazzaz, F.A. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. Ecology 79(4): 1305–1319.
- de Chantal, M. & Granström, A. 2007. Aggregations of dead wood after wildfire act as browsing refugia for seedlings of Populus tremula and Salix caprea. Forest Ecology and Management 250(1–2): 3–8.
- , Kuuluvainen, T., Lindberg, H. & Vanha-Majamaa, I. 2005. Early regeneration of Populus tremula from seed after forest restoration with fire. Scandinavian Journal of Forest Research 20(6): 33–42.
- Everham, E.M. & Brokaw, N.V.L. 1996. Forest damage and recovery from catastrophic wind. Botanical Review 62(2): 113–185.
- Granström, A. 2001. Fire management for biodiversity in the European boreal forest. Scandinavian Journal of Forest Research 16(3): 62–69.
- Greene D.F., Noel J., Bergeron Y., Rousseau, M. & Gauthier, S. 2004. Recruitment of Picea mariana, Pinus banksiana, and Populus tremuloides across a burn severity gradient following wildfire in the southern boreal forest of Quebec. Canadian Journal of Forest Research 34(9): 1845–1857.
- Harmon, M.E. & Franklin, J.F. 1989. Tree seedlings on logs in Picea–Tsuga forests of Oregon and Washington. Ecology 70(1): 48–59.
- Harper, J.L., Williams, J.T. & Sagar, G.R. 1965. The behaviour of seeds in the soil I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seeds. Journal of Ecology 53(2): 273–286.
- Hautala, H. & Vanha-Majamaa, I. 2007. Immediate tree uprooting after retention-felling in a coniferous boreal forest in Fennoscandia. Canadian Journal of Forest Research 36(12): 3167–3172.
- , Jalonen, J., Laaka-Lindberg, S. & Vanha-Majamaa, I. 2004. Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. Biological Conservation 13(8): 1541–1554.
- Hörnberg, G., Ohlson, M. & Zackrisson, O. 1995. Stand dynamics, regeneration patterns and longterm continuity in boreal old-growth Picea abies

swamp-forests. Journal of Vegetation Science 6(2): 291–298.

- , Ohlson, M. & Zackrisson, O. 1997. Influence of bryophytes and microrelief conditions on Picea abies seed regeneration patterns in boreal oldgrowth swamp forest. Canadian Journal of Forest Research 27(7): 1015–1023.
- , Zackrisson, O., Segerström, U., Svensson, B.W., Ohlson, M. & Bradshaw, R.H.W. 1998. Boreal swamp forests: Biodiversity "hotspots" in an impoverished forest landscape. BioScience 48(10): 795–802.
- Hytteborn, H., Packham, J.R. & Verwijst, T. 1987. Tree population dynamics, stand structure and species composition in the montane virgin forest of Vallibacken, northern Sweden. Vegetatio 72(1): 3–19.
- Jonsell, M., Weslien, J. & Ehnstrom, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7(6): 749–764.
- , Hansson J. & Wedmo, L. 2007. Diversity of saproxylic beetle species in logging residues in Sweden – comparisons between tree species and diameters. Biological Conservation 138(1–2): 89–99.
- Jonsson, B.G. & Esseen, P.-A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. Journal of Ecology 78(4): 924–936.
- Juvakka, M., Viinikainen, J., Puputti, I. & Kuupakko, S. 1995. Vesijaon tutkimusalue, hoito- ja käyttösuunnitelma 1994–2003. [Plan for the management and use of forests in Vesijako research area 1994–2003]. Metlan tutkimusmetsien julkaisusarja 5. Vantaa. 228 p. ISSN 1238-0830. (In Finnish).
- Konôpka, B. 2001. Analysis of interspecific differences in tree root system cardinality. Journal of Forest Science 47(8): 366–372.
- Kouki, J., Löfman, S., Martikainen, P., Rouvinen S. & Uotila, A. 2001: Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research 16(3): 27–37.
- Kujala, A. & Toivonen, T. 2004. Biodiversity oriented prescribed burning at Evo and Vesijako in 2002 effects on humus and tree stands. University of Applied Sciences, Bachelor's thesis, Forestry program. 61 p. (In Finnish, with English abstract).

Kuuluvainen, T. 2002. Disturbance dynamics in boreal

forests: defining the ecological basis of restoration and management of biodiversity. Silva Fennica 36(1): 5–12.

- & Kalmari, R. 2003. Regeneration microsites of Picea abies seedlings in a windthow area of a boreal old-growth forest in southern Finland. Annales Botanici Fennici 40(6): 401–413.
- & Laiho, R. 2004. Long-term forest utilization can decrease forest floor microhabitat diversity: evidence from boreal Fennoscandia. Canadian Journal of Forest Research 34(2): 303–309.
- Laiho, R. & Prescott, C.E. 2003. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Canadian Journal of Forest research 34(4): 763–777.
- Laine, J. & Vasander, H. 1990. Suotyypit. [The mire types]. Karisto Oy, Hämeenlinna. 80 p. ISBN 951-26-3396-5 (In Finnish)
- Lampainen, J., Kuuluvainen, T., Wallenius, T.H., Karjalainen, L. & Vanha-Majamaa, I. 2004. Long-term forest structure and regeneration after wildfire in Russian Karelia. Journal of Vegetation Science 15(2): 245–256.
- Lee, P. & Sturgess, K. 2001. The effects of logs, stumps, and root throws on understory communities within 28-year-old aspen-dominated boreal forests. Canadian Journal of Botany 79(8): 905–916.
- Lemberg, T. & Puttonen, P. 2003. Kulottajan käsikirja. [Guide for prescribed burning]. Metsälehtikustannus. 113 p. ISBN 952-5118-41-X (In Finnish).
- Lilja, S., de Chantal, M., Kuuluvainen, T., Vanha-Majamaa, I. & Puttonen, P. 2005. Restoring natural characteristics in managed Norway spruce [Picea abies (L.) Karst.] stands with partial cutting, dead wood creation and fire: immediate treatment effects. Scandinavian Journal of Forest Research 20(6): 68–78.
- Long, Z.T., Carson, W.P. & Peterson, C.J. 1998. Can disturbance create refugia from herbivores: an example with hemlock regeneration on treefall mounds. Journal of the Torrey Botanical Society 125(2): 165–168.
- Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94(1): 199–209.
- McCullough, H.A. 1948. Plant succession on fallen logs in a virgin spruce-fir forest. Ecology 29(4): 508–513.

- Ott, L. 2000. An introduction to statistical methods and data analysis. 5th edition. Duxbury Press, Boston, MA. ISBN 978-0534251222.
- Peterson, C.J. & Campbell, J.T. 1993. Microsite differences and temporal change in plant communities of treefall pits and mounds in an old-growth forest.
 Bulletin of the Torrey Botanical Club 120(4): 451–460.
- & Pickett, S.T.A. 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology 76(3): 763–774.
- , Carson, P.W., McCarthy, B.C. & Pickett, S.T.A. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos 58(1): 39–46.
- Renvall, P. 1995. Community structure and dynamics of woodrotting Bacidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35(1): 1–51.
- Ripple, W.J. & Larsen, E.J. 2001. The role of postfire coarse woody debris in aspen regeneration. Western Journal of Applied Forestry 16(2): 61–64.
- Sarvas, R. 1937. Über die natürliche Bewaldung der Waldbrandflächen. Eine waldbiologische Untersuchung auf der trockenen Heideböden Nord-Finlands. Communicationes Instituti Forestales Fenniae 33(1). 255 p. (In Finnish with German summary).
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11–41.
- Simard, M.J., Bergeron, Y. & Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: The importance of substrate. Journal of Vegetation Science 9(4): 575–582.
- Similä, M., Kouki, J., Martikainen, P. & Uotila, A. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation 106(1): 19–27.
- Toivanen, T. & Kotiaho, J.S. 2007. Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity. Biodiversity and Conservation 16(11): 3193–3211.
- Uotila, A., Maltamo, M., Uuttera, J. & Isomäki, A. 2001. Stand structure in semi-natural and managed forests in eastern Finland and Russian Karelia. Ecological Bulletins 49: 149–158.

- Vanha-Majamaa, I. & Jalonen, J. 2001. Green tree retention in Fennoscandian forestry. Scandinavian Journal of Forest Research 3(3): 79–90.
- , Tuittila, E.-S., Tonteri, T. & Suominen, R. 1996. Seedling establishment after prescribed burning of a clear-cut and partially cut mesic boreal forest in southern Finland. Silva Fennica 30(1): 31–45.
- , Lilja, S., Ryömä, R., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Tamminen, P., Toivanen, T. & Kuuluvainen, T. 2007. Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: The EVO experiment. Forest Ecology and Management 250(1–2): 77–88.
- Viro, P. 1969. Prescribed burning in forestry. Communicationes Instituti Forestales Fenniae 67(7). 49 p.
- 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. Canadian Journal of Forest Research 34(7): 1400–1409.
- Wikars, L.-O. 2002. Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation 6(1): 1–12.
- Wohlgemuth, T., Kull, P. & Wüthrich, H. 2002. Disturbance of microsites and early tree regeneration after windthrow in Swiss mountain forests due to the winter storm Vivian 1990. Forest, Snow and Landscape Research 77(1–2): 17–47.
- Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J.A. & Langor, D. 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Canadian Journal of Forest Research 34(2): 417–430.
- Yatskov, M., Harmon, M.E. & Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Canadian Journal of Forest Research 33(7): 1211–1226.
- Zielonka, T. 2006. When does dead wood turn into a substrate for spruce development? Journal of Vegetation Science 17(6): 739–746.

Total of 63 references