Assemblages of Vascular Plants on Logs and Stumps within 28-year-old Aspen-dominated Boreal Forests[1]

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Abstract

This study examined the impact of logs and stumps on the understory composition of 28-year-old aspen-dominated boreal forests. Suitable logs covered more than five times the area of stumps in both harvest and wildfire stands. Logs and stumps were colonized by a significantly different assemblage of vascular plants than the forest floor. Initial colonization patterns on dead wood in both wildfire and harvest stands were similar. However, as dead wood decayed, assemblages of vascular plants diverged and became more similar to their respective forest floor assemblages. Regenerating trees and shade tolerant forbs were disproportionately more abundant on logs and stumps, while grasses, shrubs, and shade intolerant forbs were disproportionately more abundant on the forest floor.

Introduction

Treefalls produce a number of different microhabitats (Beatty and Stone 1986). These include root throw pits and mounds, downed boles, stumps, canopy gaps, and leaf and branch piles created from downed canopies. In turn, these microsites create favorable habitats for the establishment of vascular plants by reducing competition with non-vascular and other vascular plants (Harmon and Franklin 1989), facilitating establishment of mycorrhizal relationships (Harvey and others 1987), changing substrate nutrient and moisture conditions (Hale and Pastor 1998), providing suitable physical substrate for establishment of roots (DeLong and others 1997), and increasing light and temperature regimes as with canopy gaps (Canham and others 1990). However, it is unlikely that all plants have an equal ability to utilize these sites. Hence, the differential abilities of plants to colonize sites potentially adds to the spatial and temporal variability within the understory.

In aspen-dominated (*Populus tremuloides* Michx.) boreal forests, treefall microsites may play a significant role in determining the spatial and temporal pattern of understories. Tree falldown rates caused by self-thinning produce elevated densities of logs and stumps. The forest floor coverage of downed logs in

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unharvested stands is relatively high (~10 to 20 percent) compared to other deciduous forests (reviewed in Harmon and others 1986). In turn, the abundance of microsites is potentially an important causal factor in the relatively high diversity of herbaceous and woody-stemmed understory found in boreal forests. Within the boreal forest, the role of stumps and logs as safe sites for tree species has been explored (Cornett and others 1997, DeLong and others 1997, Hornberg and others 1997). Crites and Dale (1998) demonstrated that as logs decay the assemblage of plants shifts from bryophytes to vascular plants.

The overall objective of this study was to examine the contribution to understory heterogeneity created by dead wood on the forest floor. In order to do this we needed to characterize the physical parameters of logs and stumps colonized by vascular plants, measure and project the percent cover of suitable logs and stumps, and compare the composition and relative abundance of species among microsites and forest floor assemblages.

Materials and Methods

Site Description

This study was located in the Marten Hills Forest District, near the town of Slave Lake, Alberta, between 55° and 56° North latitude and 114° and 115° West longitude. We selected four wildfire and four harvest stands from this region. Stands were mesic and dominated (> 80 percent basal area) by trembling aspen, with balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* Moench.), and balsam fir (*Abies balsamea* L.) occurring as secondary tree species.

Selection of the wildfire and harvest stands was based on their close geographical proximity to each other, similar pre-disturbance structure, similar timing of disturbances, and lack of human interference during post-disturbance succession. We used a number of data sources to ensure the wildfire and harvest stands were of similar pre-disturbance composition, age, and post-disturbance succession. All stands were disturbed in 1968. During that year, parts of the Sawridge Hills were subject to a large spring wildfire (> 100,000 ha). Wildfire stands burned as part of that conflagration. Harvest stands were cut during the previous winter as part of regular harvest operations scheduled for that year. These stands did not burn in the subsequent wildfire. Harvest was accomplished by using full tree extraction with conventional feller-buncher and grapple skidder.

Ground measurements, aerial photographs, pre-disturbance timber inventories, and interviews with government and industry personnel confirmed that stands were 110-120 years, aspen-dominated, and had basal areas of ~35 m^2/ha prior to disturbance. Wildfire stands were > 75 ha while harvest stands ranged in size from 35 to 75 ha. To control for disparities in size and shape, all measurements were taken inside of a 50-m buffer from the stand edge. Within each of the stands ten 1-ha plots were randomly established. Within each of these plots, four 50 x 50-m blocks were established.

Field Methods

To sample the suitability of logs for vascular plants, we surveyed 200 to 300 m of line intersects within each stand. On each line a minimum of 200 logs ($\geq$ 5 cm diameter at the point of intersection) were sampled. The vascular plants were identified to species and recorded on each side ($\leq$ 50 cm) of the intersecting line. The diameter and length of log sampled were also recorded.

To estimate the projected area of logs, three randomly placed 25-m transects per plot were surveyed using a line intersect method. We only recorded the most common classes and sizes of logs supporting vascular plants. Only logs from decay classes 5 to 7 and ≥ 20 cm diameter were used in estimations of percent microsite cover. Decay classes 5 to 7 represent progressively more decayed logs (Lee and others 1997). Decay class 5 represents logs with < 50 percent of large wood fragments lost, presence of small decayed blocks, and a deformed trunk outline. Decay class 7 logs have nearly 100 percent humification and no evidence of hard wood.

The suitability and percent cover of stumps was based on walking searches in all plots. The area searched was 100 x 50 m (5,000 m^2). Within each search area, stumps with a top diameter of $\geq$ 4 cm were recorded. Each stump was measured along the longest axis and the bisecting perpendicular axis. An elliptical formula was used to calculate the approximate area covered by each. From these surveys, we developed a "hard" and "soft" classification system for stumps. Hard stumps were visually characterized by a distinct outline with some evidence of hard wood, while soft stumps exhibited a deformed outline and little evidence of hard wood. Soft stumps had characteristics similar to those of decay class 7 logs.

To quantify the percent cover of vascular plants on logs and stumps, we focused on the common decay and diameter classes supporting vascular plants. From a random point within each block, the nearest ($\geq$ 20 cm diameter) logs of decay classes 5, 6, and 7 were selected. A 20 x 20-cm quadrat was randomly placed on the logs and visual percent cover estimates were made for each species of vascular plants. Non-vascular plants were also recorded in broad groups: lichens, mosses, and liverworts. In a similar fashion, the nearest hard and soft stumps were selected from the same point within each block. Stumps had to have a top diameter of $\geq$ 30 cm. A 20 x 20-cm quadrat was placed on the top of the stump, and on the side in each cardinal direction. Percent cover was visually estimated for each species. Estimations on stump sides were based on placement of the quadrat parallel to the stump surface. Forest floor coverages were estimated from quadrats randomly placed at least 2 m from logs or stumps.

Analysis

Comparisons of species per sample and percent forest floor cover were made using an ANOVA with a Standard-Neuman-Kuels post hoc. In all cases, significance differences were set at $P<0.05$. Detrended correspondence analysis (DCA) was the primary ordination technique used to evaluate the relationships between microsites and species assemblages (Hill 1979). The statistical package PCord was used to perform all DCAs (McCune and Mefford 1995). Detrending was accomplished by dividing the first axis into 26 segments. Ninety-five percent confidence ellipses were assigned based on algorithms from the JMP statistical package (Anonymous 1995).

Results

Physical Characteristics

Both the diameter and decay stage of logs and stumps were important factors in determining the degree of colonization by vascular plants. We found that logs and stumps $\geq$ 20 cm diameter captured 95 percent of the colonizing species. In general, smaller diameter logs and stumps were only colonized by small forbs such as *Mitella nuda* L., *Linnaea borealis* L., and *Cornus canadensis* L., whereas larger diameter logs and stumps were colonized not only by forbs but also by shrubs and saplings such as *Salix spp.* L., *P. glauca*, and *B. papyrifera*. Decay class 4 logs and stumps were the earliest stage colonized by vascular plants. However, only two species, *L. borealis* and *Mertensia paniculata* were found on these stumps and logs.

Patterns of Species Richness

The overall species richness of the wildfire and harvest stands was identical: 70 species for each. This indicated that the background number of species available for colonization on dead wood was similar between the stands. Species richness on logs ranged from 21 to 26 species, while stumps varied from 22 to 38 species depending on disturbance type and decay class.

To facilitate comparisons among different microsites, we analyzed the richness data on a per sample basis. Forest floor samples from wildfire and harvest stands exhibited a similar mean species richness of 12.9 and 11.7 per sample, respectively (*table 1*; $P > 0.05$). Species per sample on logs or stumps were lower than those found on the forest floor (*table 1*; $P < 0.05$). In comparisons between wildfires and harvest, four of eight microsite types exhibited more species per sample in the wildfire stand while other microsites exhibited no differences between wildfire and harvest stands.

In both stand types, the number of species per sample increased on greater decay classes of logs and stumps (*table 1*; $P < 0.05$). In wildfire stands, decay of logs from class 5 to 7 increased 4.2 species while decay over the same stages in harvest stands increased only 1.4 species. In wildfire stands, decay from hard to soft stumps increased richness by 1.3 species on the sides and increased richness by 3.2 species on stump tops. In harvest stands, decay from hard to soft stumps increased richness by 3.3 and 3.2 species per sample on stump sides and tops, respectively.

Percent Microsite Cover

In both stand types, percent microsite cover was ordered logs > stumps (ANOVA; df=1, F range 29.9 to 38.9, $P<0.001$; *fig. 1)*. In general, the wildfire stand had a greater percentage of the forest floor covered by suitable dead wood *(fig. 1)*.

Decay and Assemblages

Both logs and stumps exhibited different assemblages of vascular plants than the forest floor of either wildfire or harvest stands. In both stands, decay stages of logs and stumps were spread along the first DCA axis *(fig. 2)*. In general, species assemblages on logs and stumps converged with that of the forest floor as logs and stumps decayed. Decay class 5 logs were the least similar to forest floor samples, while decay class 7 logs were the most similar. Hard stump sides were the least similar to the forest floor while soft tops, hard tops, and soft sides were the most similar.

Table 1—*Mean species per sample quadrat (±1 S.E.) for each type of microsite within 28-year-old wildfire- and harvest-origin aspen-dominated boreal forests.*[1]

Microsite	Wildfire	Harvest
Forest floor*	12.9±0.46	11.7±0.48
Log decay class 5	6.2±0.51^{a}	6.1±0.62^{a}
Log decay class 6	7.7±0.57^{b}	7.0±0.35^{a,b}
Log decay class 7*	10.4±0.64^{c}	7.5±0.37^{b}
Hard stump side*	6.9±0.34^{b}	4.6±0.30^{a}
Hard stump top*	7.2±0.41^{b}	6.7±0.30^{b}
Soft stump side	8.2±0.32^{c}	7.9±0.34^{b,c}
Soft stump top	10.4±0.42^{d}	9.9±0.57^{d}

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[1] Superscript letters denote significant differences within log or stump decay classes ($P < 0.05$). All microsites were significantly less than forest floor sample. Asterisks denote significant differences between wildfire and harvest samples ($P < 0.05$).

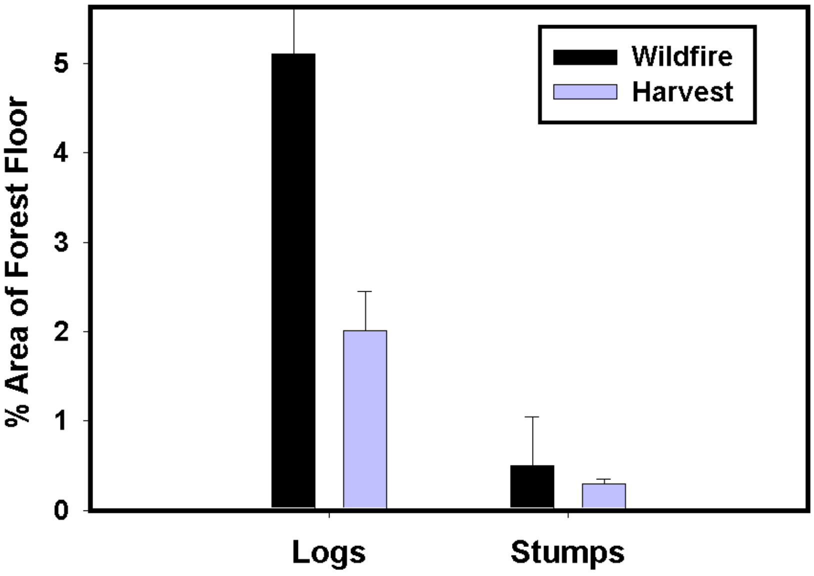
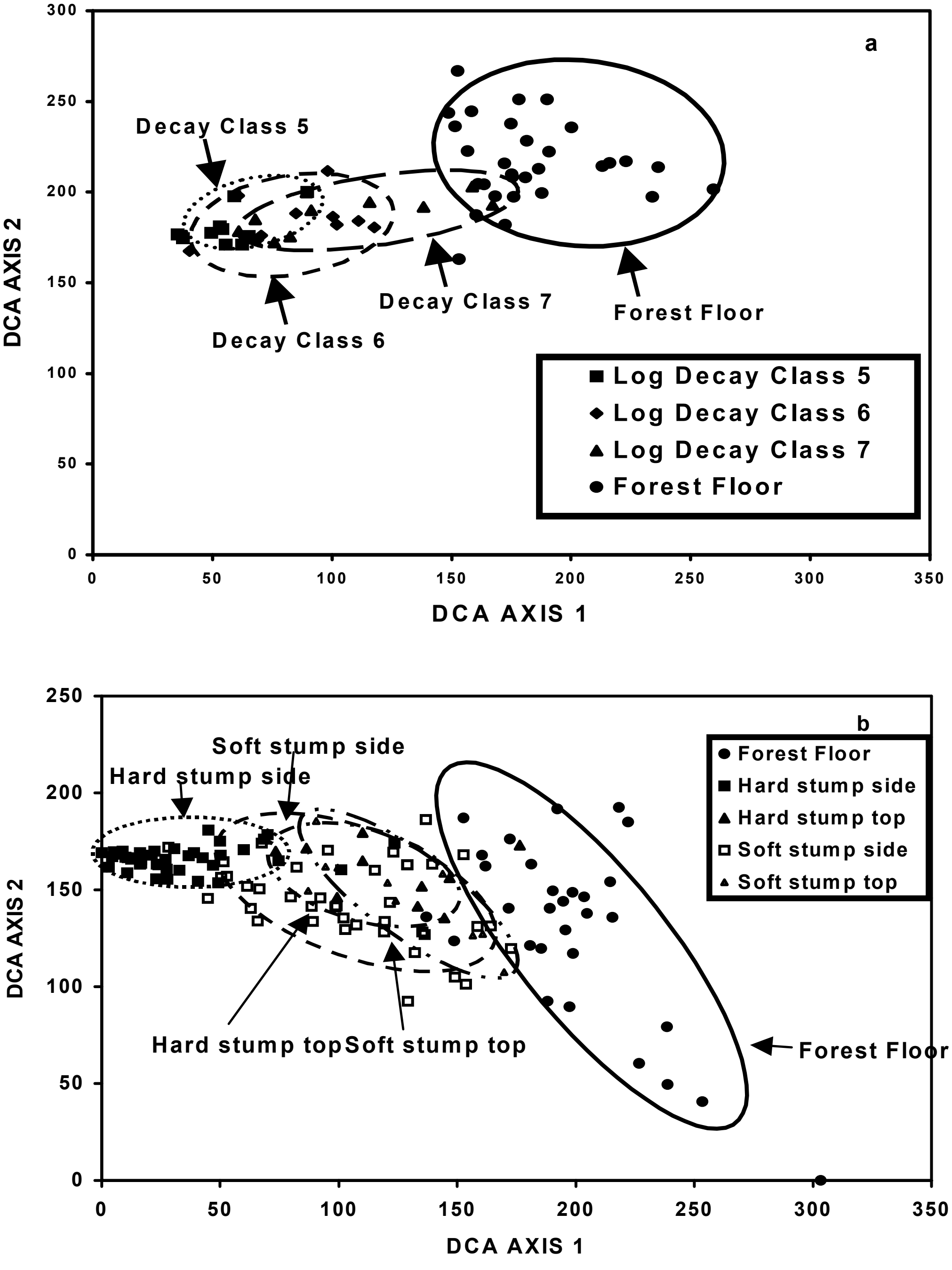


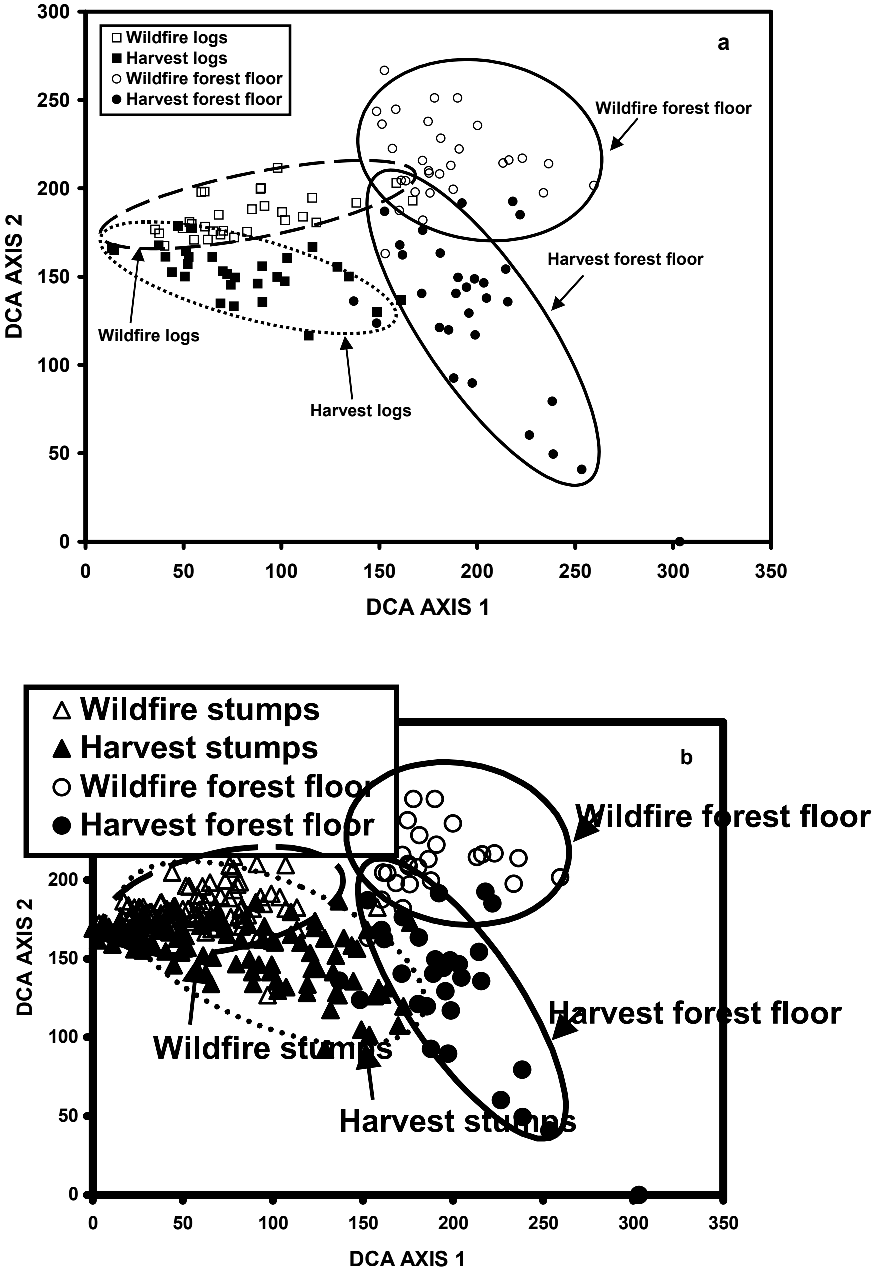
Figure 1—Percentage of the forest floor covered by suitable logs and stumps within aspen-dominated boreal forest.



Figures 2—DCA ordination of plot of decay class 5, 6, and 7 logs and forest floor plots from wildfire (a) and plot of hard and soft stumps and forest floor plots from harvest (b) stands. Ordination plots of decayed logs from harvest stands and stumps from wildfire stands exhibit similar patterns but are not shown.

Wildfire and Harvest Assemblages

Assemblages of vascular plants on wildfire and harvest forest floors were different. Most of the variance between disturbance types was partitioned along the second DCA axis *(fig. 3).* Regardless of whether logs or stumps were associated with wildfires or harvests, initial assemblages of plants were similar. As both logs and stumps decayed the assemblages diverged and became more similar to their respective forest floor types.



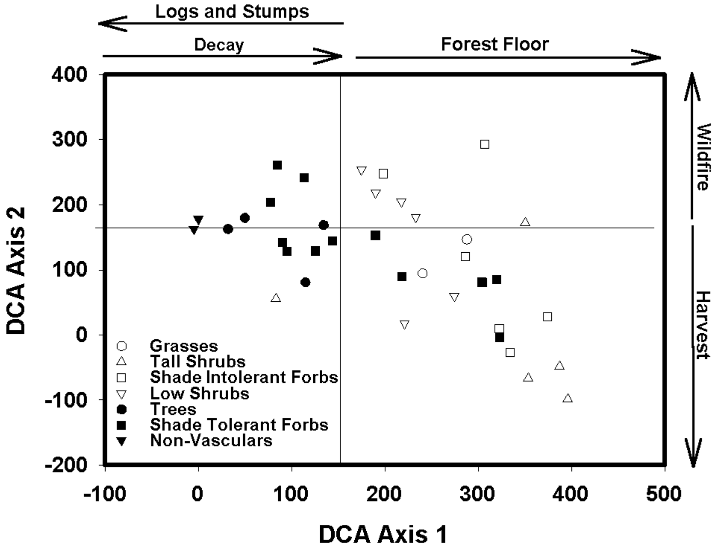
Figures 3—DCA ordination of log and stump plots and forest floor plots from wildfire (a) and harvest (b) stands.

Species Associations

In general, life history and physiognomy of species determined associations with microsites and forest floor sites. To reduce the complexity of plotting and interpreting all species, we classified species with ≥ 1 percent mean cover into the following categories: non-vasculars, grasses, shade tolerant forbs, shade intolerant forbs, low shrubs, tall shrubs, and regenerating trees *(fig. 4)*. Non-vascular plants were classified by broad taxonomic categories, in this case, lichens and mosses.

The ordination plot of species can be crudely divided into four quadrats. Each quadrat represented species associations with particular types of microsites *(fig. 4)*. The right portion of the first DCA axis represents species whose greatest abundance was associated with the forest floor, while the left portion represents species whose greatest abundance was associated with logs or stumps *(fig. 4)*. In a similar manner, the upper portion of the second DCA axis represents species whose greatest abundance was associated with the wildfire stands, while the lower portion suggests an association with harvest stands.

By using this classification, the relationship between species groups and microsites becomes clearer. Lichens and mosses were found on the extreme left of DCA axis 1, indicating dominance in the early stages of log and stump decay. Species groups of vascular plants primarily associated with stumps and logs included some of the shade tolerant forbs and seedlings of the common trees *(fig. 4)*. Seven of the eleven common shade tolerant forbs were associated with logs and stumps. These included *Arailia nudicaulis* L., *C. canadensis*, *Galium triflorum* Michx., *L. borealis*, *M. nuda*, *Rubus pubescens* Raf., and *Trientallis borealis* Raf. Common tree species included *A. balsamifera, B. papyrifera, P. glauca,* and *P. balsamifera.* In contrast, a number of groups were primarily associated with forest floor assemblages. These included the common grasses, shade intolerant herb species, low shrubs, and tall shrubs. One notable exception was *Salix* spp. whose seedlings, like those of regenerating trees, tended to be found on decaying logs and stumps.



Figures 4—DCA ordination of common (≥ 1 percent cover) species categorized by groups: regenerating trees, tall shrubs, low shrubs, shade intolerant forbs, shade tolerant forbs, grasses, and non-vascular plants. See *appendix A* for species within each group.

Discussion

This study demonstrated the importance of logs and stumps in aspen-dominated boreal forests. Our results indicated that logs in advanced stages of decay and stumps were colonized by a significantly different subset of species than the forest floor. Though this study did not track the decay and subsequent colonization of individual microsites, the sequence of decay stages strongly suggested a patterned succession of vascular plants on decaying logs and stumps. As found by McCullough (1948) in spruce forest, we also observed that the domination of lichens and mosses on logs and stumps began to succeed to vascular plants about midway through the decay process. As logs or stumps continued to decay, the assemblage of plants on logs or stumps also changed, eventually becoming more similar to forest floor assemblages. With our two stand types, microsite communities diverged and became more similar to their respective wildfire or harvest forest floor communities.

Changes in the assemblages of plants with decay stage were presumably related to the ability of plants to disperse and establish on logs and stumps through vegetative means, and the ability of both seeds and clones to establish roots. Our first indication of colonization was on decay class 4 logs. This decay class was characterized by the initial breakdown and softening of the log or stump surface. The opening of cracks on the surface allowed for the accumulation of organic matter in cracks and perhaps access to softer heartwood and sapwood in the interior of the log.

In contrast, even hard stumps maintained assemblages of vascular plants. The cracks on the surface and sides of even hard stumps were sufficient to allow the establishment of roots. In part, the relative permanency of stumps, first as part of a living tree, allowed for an accumulation of organic matter within cracks prior to tree death. Aside from being a suitable medium for the germination of seeds and penetration by stolons or rhizomes, both water holding capacity and available nutrients increased with decay (reviewed in Harmon and others 1986). Though the availability of nutrients is less on logs and stumps than on the forest floor, seedlings and clonal plants require less than larger, established plants. In the case of vegetative plants, nutrients may be shunted from ramets on the forest floor to those on the log. In turn, ramets on logs may provide photosynthates and moisture to forest floor ramets.

Aside from decay stage, our results strongly indicated that larger diameter logs accumulated more species than smaller logs. This is not surprising since a wider and taller log provides a greater isolating effect from the influence of the forest floor. Huenneke and Sharitz (1986) demonstrated that logs ($\geq$ 30 cm diameter) were more readily colonized by trees, shrubs and vines in natural and second growth bald cypress-tupelo swamps *(Taxodium distichum-Nyssa aquatica)* than smaller diameter branches (5 cm to 30 cm) or twigs (< 5 cm diameter). In this and other swamp forest systems, larger diameter logs provided a measure of protection against the frequent flooding (Hornberg and others 1997, Titus 1990). Harmon and Franklin (1989) concluded that competition with moss and herbaceous understories on the forest floor was the driving mechanism for the dominance of regeneration of *P. sitchensis* and *T. heterophylla* on logs in Oregon and Washington. Although we have no direct measures for the underlying release mechanisms on logs or stumps, the prevalence of tree seedlings and smaller, shade tolerant forbs suggests that it may be competitive release. Grasses such as *Calamagrotis canadensis* and shrubs were found primarily on the forest floor. Both these groups are highly effective competitors of tree seedlings (Lieffers and Stadt 1994, Place 1965) and possibly of low, shade tolerant forbs.

The percent microsite cover value for the wildfire stand (> 5 percent) in this study is more comparable to conifer rather than other deciduous systems. Harmon (1989) projected a suitable cover of 5.4 percent in *Picea-Tsuga* forests of coastal Oregon and Washington. Takahashi (1994) found projections of 2.6 to 6.0 percent within *Abies-Picea* forests of northern Japan depending upon soil type. In contrast, Thompson (1980) found suitable logs covering only 1.9 percent of an oak-hickory *(Qurecus-Carya)* forest floor in Illinois. The cover for all logs (suitable and unsuitable) in deciduous forests were generally lower (1.6 to 4.0 percent) than in aspens stands (reviewed in Harmon and others 1986).

Our analysis suggested that log, stump, and forest floor assemblages between wildfire and harvest were different. Species associations within harvest stands were comprised of more tall shrubs and shade intolerant forbs. Furthermore, harvest stands exhibited lower coverage of logs and stumps than the wildfire stand. This is largely caused by the absence of a falldown of fire-killed snags as in wildfire stands. Harvest stands exhibited an increased shrub richness and cover, and lower richness and cover of low, shade tolerant herb species. Our results suggest that the lack of logs may, in part, explain this difference in understory communities. A fuller comparison of the role of microsites in producing differences between wildfire and harvest stands would require a larger sample size of stands while controlling or accounting for within-stand variance.

This study has shown the importance of logs and stumps to the understory heterogeneity of aspen-dominated boreal stands. Although this study did not directly measure a temporal sequence, we hypothesize that selective colonization of logs and stumps plays a significant role. The succession of upland boreal forests often features a conversion from early aspen domination to later mixed wood or conifer domination, while understory communities shift from shrub and shade intolerant species to low, shade tolerant forbs (Rowe 1956). Our results suggest that logs and stumps facilitate these successional shifts in the understory and canopy. Further research is needed to fully determine whether the input and decay of logs and stumps, in part, mediates vegetation succession in boreal forests.

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Appendix A—*Species names of the 25 most common species (≥ 1 percent cover) categorized by functional groups.*

Regenerating trees
Populus tremuloides
Betula papyrifera
Populus balsamifera
Picea glauca

Tall shrubs
Salix spp,
Amelanchier alnifolia
Alnus tenuifolia
Alnus crispa
Prunus virginiana

Low shrubs
Viburnum edule
Rosa acicularis
Lonicera involucrata
Rubus idaea
Lonicera dioica
Ribes triste

Shade intolerant forbs
Epilobium angustifolia
Aster ciliolatus
Solidago gigantea
Smilacina stellata
Aster conspicuus
Solidago canadensis

Shade tolerant forbs
Rubus pubescens
Cornus Canadensis
Mitella nuda
Linnaea borealis
Galium trifolium
Maianthemum canadense
Galium boreale
Galeopsis tetrahit
Aralia nudicalis
Mertensia paniculata
Viola Canadensis
Trientalis borealis

Grasses
Elymus innovatus
Calamagrostis canadensis

Non-vasculars
Lichens
Mosses