

Plant species diversity on logged versus burned sites in central Alaska

Daniel C. Rees¹, Glenn Patrick Juday^{*}

Forest Sciences Department, University of Alaska Fairbanks, P.O. Box 757200, Fairbanks, AK 99775, USA

Abstract

Natural fires and logging are two of the main disturbances affecting upland boreal forest in Alaska. The objectives of this study were to determine whether logged sites differ from burned sites in (1) overall plant species richness, (2) successional trajectories, and (3) species diversity at particular stand structural development stages. We compared plant species diversity on sites burned in natural fires to sites that were logged and not subsequently burned in central Alaska. We sampled 12 logged and 12 burned former upland white spruce (*Picea glauca* (Moench) Voss) forests in four stand development stages representing stand initiation (stage A), early stem exclusion (stage B), understory reinitiation (stage C), and mature hardwood (stage D) stages. In this study the dates of disturbance varied from 1990 to 1994 in stage A, 1978 to 1983 in stage B, 1957 to 1965 in stage C, and 1900 to 1920 in stage D plots. All sites were similar in slope, aspect, and soil type. Vascular plants were identified to the species level (except for certain willows) and bryophytes and lichens were identified to the level of presumptive (usually unknown) species within family groups. Organic layer thickness was significantly greater on logged sites compared to burned sites overall and at each stage. Burned sites (all stages combined) supported more species (146) than logged sites (111), and more species at each stand development stage. Burned plots in stages A and B supported abundant cover of a few apparent fire specialist species (*Ceratodon purpureus* (Hedw.) Brid., *Marchantia polymorpha* L. and *Leptobryum pyriforme* (Hedw.) Wils.) that were present in only minor amounts on logged sites. Burned plots exhibited higher species turnover from stage to stage and among all stages than logged plots. Species dominant in burned stage A plots were nearly absent in burned stage C and D plots, while logged stage A dominants, which were common mature forest species, increased in each subsequent stage. We compared floristic similarity between our disturbance plots and mature upland white spruce stands in Bonanza Creek Long-Term Ecological Research (LTER) site. Only five species found in the LTER dataset were not also present in this study, which suggests that nearly all species compositional change in our study area occurs during the first century after disturbance. Logged sites appear to begin and continue succession with a greater share of the original mature forest understory plants, while burned sites initiate succession with more distinctive and specialized plant species. © 2002 Published by Elsevier Science B.V.

Keywords: Alaska; Fire; Logging; Soil organic matter; Plant species diversity; Bryophytes; Lichens

^{*} Corresponding author. Tel.: +1-907-474-6717;
fax: +1-907-474-7439.

E-mail addresses: dan.rees@wainwright.army.mil (D.C. Rees),
gjuday@lter.uaf.edu (G.P. Juday).

¹ Present address: Directorate of Public Works,
ATTN: APVR-WPW-EV, 1060 Gaffney Road #6500,
Fort Wainwright, AK 99703-6500, USA.
Tel.: +1-907-353-9318; fax: +1-907-353-9867.

1. Introduction

Fire and logging are two major disturbances in upland boreal forests of North America (Johnson, 1992), including Alaska (Vioreck and Schandelmeier, 1980). Fire has long played a crucial role in the ecology of the North American boreal ecosystem, and

many species of plants have evolved to depend upon this disturbance for their survival (Shafi and Yarranton, 1973). Localized logging started in interior Alaska about 1900, occurred at low levels during the middle of the 20th century, and has increased since the 1970s (Wurtz and Gasbarro, 1996).

The goal of forest policies in many boreal regions is to simultaneously develop sustainable productivity and maintain biodiversity within the framework of tested and reliable resource management techniques (Lamas and Fries, 1995; Riley, 1995). This new emphasis reflects concerns for biodiversity as logging has become widespread and natural fire has been greatly diminished or eliminated in parts of the boreal world.

In Sweden, 286 species, including vertebrates, invertebrates, vascular plants, bryophytes, lichens, and fungi, are threatened due to land use changes in forestry, especially increased logging and fire suppression (Nilsson and Ericson, 1992). Logging on short rotations has reduced many of the structural components, spatial patterns, and processes affecting plant species diversity in the post-fire disturbed Fennoscandian boreal forest (Esseen et al., 1992). The near elimination of fire in the Scandinavian landscape has made post-fire succession stands, burnt substrates, and coarse woody debris rare.

The objectives of this study were to determine whether logged versus burned sites across a range of times since disturbance in central Alaska differ in (1) overall plant species richness, (2) successional trajectories, and (3) species diversity at particular stand development stages.

2. Methods

2.1. Study area and sample site selection

All plots were located between 65°50' and 63°20'N latitude and 142°30' and 150°00'W longitude in the Tanana and Yukon River drainages of central Alaska. Sampling was restricted to typical commercial forest sites, which are generally south-facing slopes with inceptisols formed in deep permafrost-free loess deposits, generally overlying Precambrian schist. In this region moderately sloping southerly aspects primarily support mixed stands of aspen (*Populus*

tremuloides Michx.), paper birch (*Betula papyrifera* Marsh.), and white spruce (*Picea glauca* (Moench) Voss), with only infrequent pure stands of the latter (Zasada and Packee, 1995).

We chose sample sites that met the following criteria: (1) the site was originally an upland white spruce-dominated forest type before disturbance as determined through forest inventory data (Crimp et al., 1997), aerial photos, fire scars, burned or cut stumps and boles, and white spruce charcoal bark fragments in the soil; (2) stand development stage (Oliver, 1981) could be determined; (3) soils were within the subgroup cryochrepts, a type generally formed in loess according to Rieger et al. (1979); (4) slopes were <25°; (5) aspect was south (between 90 and 270° true azimuth); and (6) elevation was 150–700 m. In our study area stand development stages occurred within the following age ranges: stand initiation stage A (2–5 years since disturbance), stem exclusion stage B (13–18 years since disturbance), understory reinitiation stage C (30–38 years since disturbance), and mature hardwood stage D (75–95 years since disturbance).

We located older disturbed sites from historical records and archives of the Rasmuson Library of the University of Alaska, personal communication with loggers, and through field investigations. None of the logged sites was subsequently burned, scarified, or planted. Before 1970 logged stands were typically high graded, although we selected sites on which stem removal was nearly complete. Recent (post-1970) timber harvesting followed silvicultural standards for clearcutting, and primarily took place in winter. Broadcast burning is rarely practiced following logging in central Alaska. We did not sample the partially burned perimeter of fires, but partially burned inclusions within fire perimeters were incorporated by the randomization effect of the sampling protocol. We could not select sites completely at random because of the limited number of recent burned sites and old logged sites. This factor also limited the power of comparisons of burned with logged sites by reducing sample size to three replicates per stand development stage.

2.2. Sampling methods

We conducted systematic-random sampling at three replicate disturbance sites in each of the four

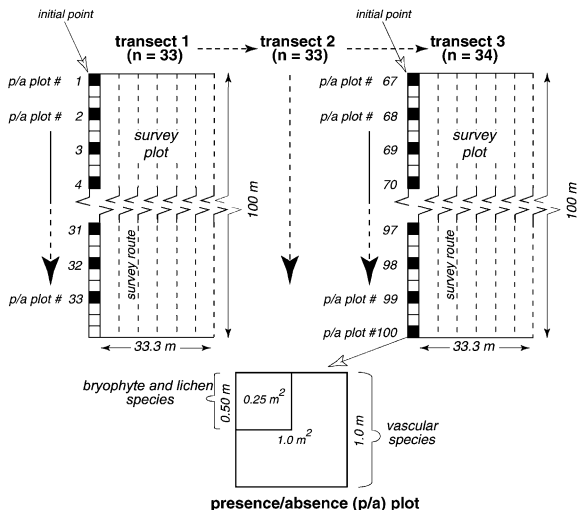


Fig. 1. Plot layout for one site, representing one replicate sample of a stand development stage within one disturbance type. Presence/absence plots ($n = 100$) are every third square meter in three $1 \text{ m} \times 100 \text{ m}$ belt transects. Note the location of the nested bryophyte and lichen subplot within each vascular species presence/absence plot. Survey plots were systematically examined for species visible from six parallel lines 5.5 m apart.

stand development stages for both logged and burned disturbance types (12 sites per disturbance type, 24 overall) from June through August 1995. We established a grid for each replicate site we sampled by laying out three equidistant lines on which random numbers determined initial points for three belt transects of $1 \text{ m} \times 100 \text{ m}$ parallel to contour (Fig. 1).

We recorded all vascular plant species in 1 m^2 presence/absence plots situated every third meter along each belt transect (Fig. 1). We recorded bryophytes and lichens in a nested subplot occupying the southeast $1/4 \text{ m}^2$ of each vascular species presence/absence plot (Fig. 1). We sampled a total of 100 presence/absence plots at each disturbance site by adding an extra plot in the last of the three transects (33, 33 and 34 plots, respectively). We used presence/absence as a measure of abundance to avoid biases associated with percent cover estimations (Magurran, 1988). Taxa encountered by this effort are referred to subsequently as presence/absence species. Vascular species were recorded only if rooted within the plot.

We conducted a systematic search for additional vascular and bryophyte and lichen species outside the presence/absence plots at each replicate site. The

search was performed by walking along six equidistant lines of 100 m length located 5.5 m apart starting at 5.5 m and parallel to each 100 m belt transect and recording the visible species (Fig. 1). Plant taxa encountered in that effort are subsequently referred to as survey species.

We measured forest floor organic layer depth in every 10th vascular presence/absence plot in the center of the square meter. We measured slope and aspect at each initial point. For the entire dataset the mean aspect ($P > 0.148$, 1 d.f., $F = 2.314$) and the mean slope ($P > 0.139$, 1 d.f., $F = 2.426$) of burned and logged sites were not significantly different. We measured canopy cover in each cardinal direction at the initial point using a concave spherical crown densiometer held at breast height (1.37 m).

We collected voucher specimens for all species and deposited them at the University of Alaska Museum in Fairbanks, Alaska. Unknown taxa were sorted into those with similar morphology, probably representing species or closely related groups of species. Unless stated otherwise we apply the term species to taxa that were either positively identified to species or to morphologically distinct unknown taxa that represented presumptive species or related species groups. Any bias in species richness figures in this study would thus represent underestimation. Nomenclature follows Hultén (1968) for vascular plants, Vitt et al. (1988) for bryophytes, and Thomson (1984) for macro lichens.

2.3. Analyses

All site and species variables were compared within the same developmental stage (stages A–D) between logged and burned plots and between development stages within the same disturbance type. Two-way analysis of variance (ANOVA) was used to compare organic matter depth, canopy cover, and slope. We applied circular statistical analyses (Fisher, 1993) to aspect measurements in addition to two-way ANOVA tests.

Plant species diversity was measured using richness and abundance. Our measure of abundance is the sum of plots in which a species was present, compared to the overall total number of plots for a given stand development stage. Our abundance figure is equivalent to relative frequency as used by Curtis and McIntosh

(1950). Because the great majority of the species we encountered display little variation in size within a given stratum, frequency of occurrence is the essential variable in measuring abundance on a plot or stand basis. We expressed this measure of abundance as a proportion and not in percentage terms in order to avoid confusion with the literature based on abundance measures derived from percent cover estimations. Statistical tests were not used on diversity indices because they are presented as pooled numeric descriptors of disturbance and stand development stages.

Species turnover (TO) index (Schoonmaker and McKee, 1988) was calculated as a direct measure of floristic change within developmental stages of similar disturbance type:

$$TO = \frac{L + G}{a + b} \quad (1)$$

where L is the number of species lost, G the number of species gained between developmental stages, and a and b are the species in each stage, respectively. The entire dataset was also examined for possible early successional dependent species by identifying species restricted to stages A and B.

The presence/absence scores of each stage A vascular and bryophyte and lichen species was summed for each stand development stage by disturbance type. Dominant species in stage A were defined as those with presence/absence scores in the upper quartile. The abundance scores of stage A dominant species were then calculated in the remaining three stand development stages, providing a measure of the abundance of stage A dominant species in later stand development stages. The procedure was repeated for stage D dominant species and their abundance scores through all earlier stages.

A comparison was made between species identified in this study and those encountered in three mature (ca. 200 years old) upland white spruce monitoring plots that matched our site criteria in Bonanza Creek Long-Term Ecological Research (LTER) site. Floristic similarity was compared between stand development stages and LTER data using Sørensen's index (SI):

$$SI = \frac{2c}{a + b} \quad (2)$$

where c is the number of species in common between comparisons having a and b species, respectively (Mueller-Dombois and Ellenberg, 1974). An index value of 1 represents complete identity of communities and a value of 0 is obtained when no species are found in common.

3. Results

3.1. Organic layer and canopy cover

Organic layer depth was consistently greater at each stage on logged plots compared to burned plots and overall (Fig. 2). Organic depth was significantly different between disturbances ($P > 0.000$, 1 d.f., $F = 47.6$) and within each disturbance ($P > 0.001$, 3 d.f., $F = 11.0$). The interaction of within-disturbance versus between-disturbance effects on organic layer depth was not significant ($P > 0.48$, 3 d.f., $F = 0.86$). Overall canopy cover across all stages was not significantly different between disturbance types ($P > 0.832$, 1 d.f., $F = 0.047$). On logged plots stage A average canopy cover (11%) was attributed to residual trees and on burned plots to standing dead

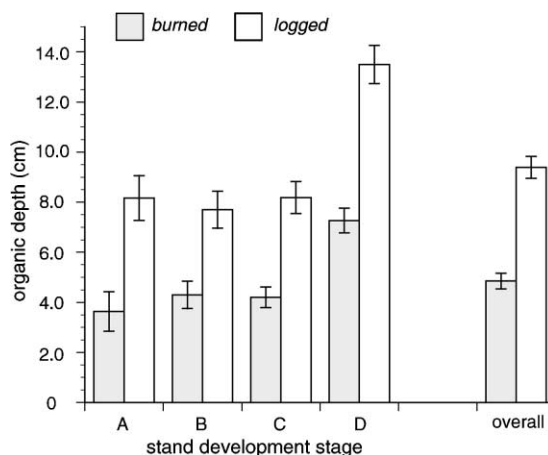


Fig. 2. Mean soil organic layer depth by stand development stage and overall by disturbance type. Stand development stages are defined as stage A—stand initiation (2–5 years since disturbance), stage B—stem exclusion (13–18 years since disturbance), stage C—understory reinitiation (30–38 years since disturbance), and stage D—mature hardwood (75–95 years since disturbance). Columns depict means of three replicate sites composed of 10 point estimates per site (± 1 S.E.).

trees (37%). Canopy closure (canopy cover > 75%) occurred in stage B on logged plots (76%) while burned plots maintained an open canopy (32%). Canopy cover values on stage C and D burned plots (91 and 94%) and logged plots (79 and 87%) were similar.

3.2. Species richness

We identified a total of 160 taxa (includes species groups as explained in Section 2) in this study. We found 126 vascular taxa (117 identified to species), 27 mosses (13 to species), 3 liverworts (2 to species), and 13 macro lichens (6 to species). More species occupied burned plots (146) than logged plots (111) overall, and in each stand development stage (Fig. 3A). The highest species total on burned plots (93) occurred in stage C, and on logged plots (77) in stage A.

Vascular species numbers were highest in stage A (51) on logged plots and in stage B (67) on burned plots (Fig. 3B) and lowest in stage C (logged) or stage D (burned). By contrast, for both disturbance types bryophyte and lichen species richness was lowest in

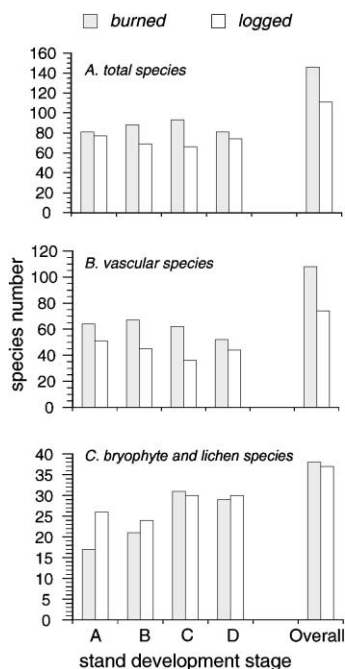


Fig. 3. Total (A), vascular (B), and bryophyte and lichen (C) species count by stand development stage and overall. Note differences in scale of species counts.

stages A and B and reached a maximum in the post-canopy closure stages (Fig. 3C). Bryophyte and lichen species numbers on logged plots were greater in stages A and B than on burned plots (Fig. 3C). Bryophyte and lichen species numbers were similar in stand development stages C and D both within and between disturbance types (Fig. 3C). The total number of all species on presence/absence plots across all stages was greater on burned sites (105 spp.) than on logged sites (80 spp.), but the number of bryophyte and lichen species (32) encountered in presence/absence plots across all stages was identical for both disturbance types. We found more bryophyte and lichen survey species at each stand development stage on logged plots compared to burned. On burned plots, the species turnover index from stage to stage was consistently greater than on logged plots (Fig. 4). Turnover index for stages A–D comparison on burned plots was greater than the stages A–D turnover index for logged plots (Fig. 4).

We encountered species restricted to both early successional logged plots only and burned plots only, and species common to both logged and burned early successional plots. Seventeen species were encountered in burned stage A or B plots only, including four weedy species (Hultén, 1968) and one lichen (Table 1). Eight species were encountered in logged stage A or B plots only, including four weedy species (Hultén, 1968) and two bryophytes (Table 1). Twelve species were encountered in stage A or B plots on both logged

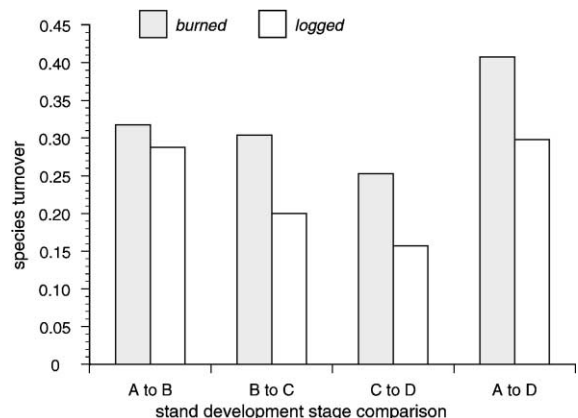


Fig. 4. Species turnover between stages within disturbance types. Calculations based on combined total of vascular and bryophyte and lichen taxa.

Table 1
Species encountered in only early successional stand development stages A and B^a

Burned only	Burned and logged	Logged only
<i>Achillea borealis</i> Bong.	<i>Achillea sibirica</i> Ledeb.	<i>Abietinella</i> (b)
<i>Antennaria rosea</i> Grene	<i>Carex canescens</i> L.	<i>Barbula</i> (b)
<i>Carex media</i> R. Br.	<i>Corydalis sempervirens</i> (L.) Pers. (f)	<i>Chenopodium glaucum</i> L. (w)
<i>Chenopodium capitatum</i> (L.) Aschers. (w)	<i>Dracocephalum parviflorum</i> Nutt. (w)	<i>Corydalis aurea</i> Willd. (f)
<i>Crepis tectorum</i> L. (w)	<i>Epilobium adenocaulon</i> Haussk. (w)	<i>Dryopteris dilatata</i> (Hoffm.) Gray
<i>Erigeron glabellus</i> Nutt.	<i>Epilobium palustre</i> L.	<i>Phleum pratense</i> L. (w)
<i>Hedysarum alpinum</i> L.	<i>Geranium bicknellii</i> Britt. (f)	<i>Polygonum achoreum</i> Blake (w)
<i>Hordeum jubatum</i> L. (w)	<i>Lycopodium clavatum</i> L.	<i>Potentilla norvegica</i> L. (w)
<i>Hypogymnia</i> (l)	<i>Poa lanata</i> Scribn. and Merr.	
<i>Ledum palustre</i> subsp. <i>decumbens</i> (Ait.) Hult.	<i>Salix arbusculoides</i> Anderss.	
<i>Lupinus arcticus</i> S. Wats.	<i>Senecio conterminus</i> Greenm.	
<i>Lycopodium obscurum</i> L.	<i>Spiraea beauverdiana</i> Schneid.	
<i>Oxyccoccus microcarpus</i> Turcz.		
<i>Parnassia palustris</i> L.		
<i>Rorippa hispida</i> (Desv.) Britt. (w)		
<i>Rubus arcticus</i> L.		
<i>Senecio yukonensis</i> Pors.		

^a Life form or habitat specialization as follows—l: lichen; w: weedy species (Hultén, 1968); b: bryophyte; f: fire-specialist (Argus et al., 1992). Nomenclature follows Hultén (1968) for vascular plants, Vitt et al. (1988) for bryophytes, and Thomson (1984) for macro lichens.

and burned sites. Three vascular species identified as fire-specialists (Argus et al., 1992) occurred in stage A and B plots, two on both logged and burned plots and one on logged plots only (Table 1).

3.3. Species composition and dominance

On burned plots only two out of ten early successional (stage A) dominant vascular species (*Calamagrostis canadensis* (Michx.) Beauv. and *Epilobium angustifolium* L.) were dominant also in late succession (stage D) (Table 2). By contrast, on logged plots five out of eight early successional dominant vascular species were also dominants in stage D. On logged plots early successional vascular dominants were most abundant in terms of presence/absence in stage B and least abundant in stage A (Fig. 5A). On burned plots the dominant early successional vascular species were most abundant in stage B and least abundant in stage D (Fig. 5A).

The most abundant bryophyte and lichen species on burned stage A and B presence/absence plots were early successional disturbance specialist species (*Ceratodon purpureus*, *Marchantia polymorpha*, and *Leptobryum pyriforme*) (Table 2). Some of the most abundant bryophyte and lichen species on logged plots in stages A and B (*Hylocomium splendens* and

Pleurozium schreberi) are understory species of mature forest. Dominant bryophyte and lichen species of burned and logged stage A plots were distinct, sharing only one out of six species in common.

On logged plots the sum of presence/absence scores of bryophyte and lichen early successional dominants increased linearly through succeeding stages (Fig. 5B). By contrast, on burned plots the species that dominated in terms of presence/absence scores were scarce in stages C and D (Fig. 5B). The sum of presence/absence scores of bryophyte and lichen early successional dominants on burned plots was almost an order of magnitude greater than the equivalent figure for early succession dominants on logged plots (Fig. 5B).

Late successional (stage D) dominant vascular plants on logged plots were nearly identical to dominants of burned plots (Table 2). On both logged and burned plots presence/absence scores for late successional vascular dominants increased from stage A through succeeding stages, except for lower abundance on stage C logged plots. The abundance of late successional dominants in stages A and B was greater on logged plots than on burned plots for both vascular species (Fig. 6A) and bryophytes and lichens (Fig. 6B). In contrast to the pattern of early successional dominants, dominant bryophyte and lichen species of stage D plots were almost identical

Table 2
Dominant species of early (A) and late (D) stand development stages^a

Burned only	Burned and logged	Logged only
Vascular early successional dominants		
<i>Betula papyrifera</i>	<i>Epilobium angustifolium</i>	<i>Equisetum pratense</i> L.
<i>Salix</i>	<i>Calamagrostis canadensis</i>	<i>Rosa acicularis</i> Lindl.
<i>Populus tremuloides</i>	<i>Mertensia paniculata</i> (Ait.) G. Don	<i>Cornus canadensis</i> L.
<i>Vaccinium vitis-idaea</i> L.	<i>Rubus idaeus</i> L.	<i>Viburnum edule</i> (Michx.) Raf.
<i>Equisetum scirpoides</i> Michx.		
<i>Picea glauca</i>		
Bryophyte and lichen early successional dominants		
<i>Marchantia polymorpha</i> L.	<i>Ceratodon purpureus</i> (Hedw.) Brid.	<i>Hylocomium splendens</i> (Hedw.) B.S.G.
<i>Leptobryum pyriforme</i> (Hedw.) Wils.		<i>Polytrichum juniperinum</i> Hewd.
		<i>Pleurozium schreberi</i> (Brid.) Mitt.
Vascular late successional dominants		
<i>Cornus canadensis</i>	<i>Equisetum pratense</i>	
	<i>Viburnum edule</i>	
	<i>Rosa acicularis</i>	
	<i>Epilobium angustifolium</i>	
	<i>Linnaea borealis</i> L.	
	<i>Moehringia lateriflora</i> (L.) Fenzl	
	<i>Calamagrostis canadensis</i>	
	<i>Geocaulon lividum</i> (Richards.) Fern	
	<i>Galium boreale</i> L.	
Bryophyte and lichen late successional dominants		
<i>Pleurozium schreberi</i>	<i>Hylocomium splendens</i>	<i>Plagiommium</i>
	<i>Hypnobryales</i>	
	<i>Drepanocladus</i>	
	<i>Dicranum</i>	
	<i>Cladonia</i>	

^a Dominant species were defined as those with sums of presence/absence scores in the upper quartile within a stand development stage for burned and logged disturbances.

on burned and logged sites. Only two out of seven stage D dominant species were not shared between logged and burned plots (Table 2).

The oldest stage (D) of forest development sampled in this study was approximately half the age of the LTER stands. Nearly four times as many species were encountered in all stages of both disturbances in this study as were encountered in the LTER mature white spruce plots. However, all but five species (lichens *Cetraria islandica* (L.) Ach., *Lobaria linita* (Ach.) Rabenh., the tree *Picea mariana* (Mill.) Brit., Sterns and Pogg., and understory flowering plants *Pyrola chlorantha* Sw. and *Pyrola minor* L.) were shared between the LTER plots and this study. These exceptions were found at the LTER plots only. All logged stages were more similar in composition to

mature white spruce stands than were any of the burned stages (Fig. 7).

4. Discussion

One of the most significant findings of this study is the clear and consistent difference in organic layer depths at all stages between the two disturbance types. In central Alaska deep organic layers are poor seedbeds (large number of seeds required to produce each germinant) for a variety of species including the dominant forest trees (Zasada et al., 1992). Complete removal of the organic layer through fire eliminates vegetative reproductive structures and creates a site requiring plant reproduction by colonization from

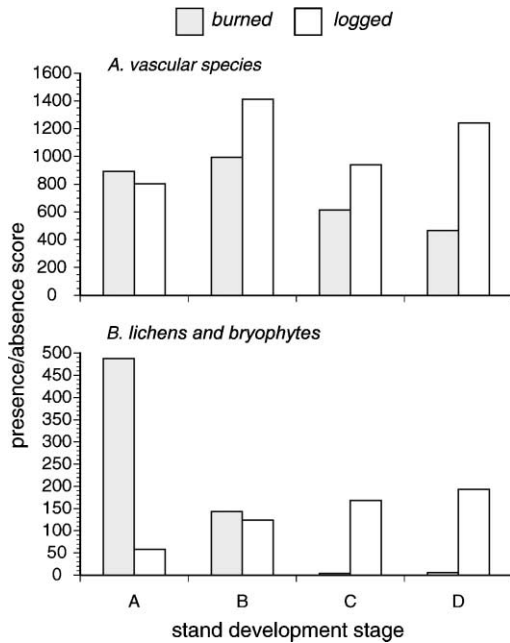


Fig. 5. Abundance of dominant stage A vascular species (A) and bryophyte and lichen species (B) across all stages. Abundance is the proportion of plots in which a species was present in a given stand development stage. Dominant species were defined as those with sums of presence/absence scores in the upper quartile within stage A for burned and logged disturbances.

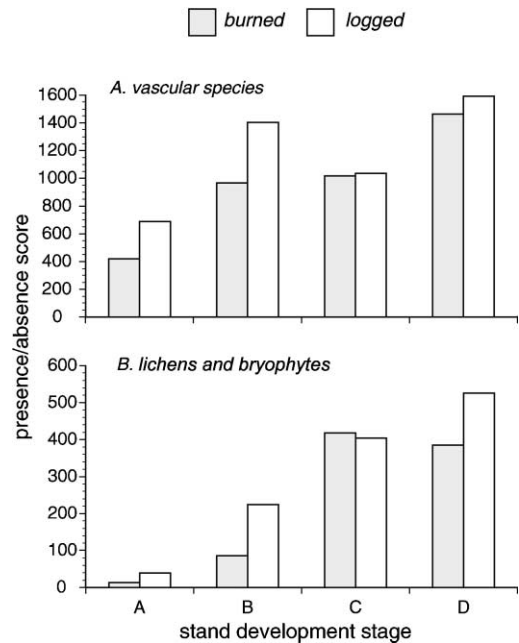


Fig. 6. Abundance of dominant stage D vascular species (A) and bryophyte and lichen species (B) across all stages. Abundance is the proportion of plots in which a species was present in a given stand development stage. Dominant species were defined as those with sums of presence/absence scores in the upper quartile within stage D for burned and logged disturbances.

newly arrived seeds, spores, or plant fragments (Viereck, 1983; Schimmel and Granström, 1995). Less severe fires that consume only part of the organic layer can stimulate existing reproductive structures of resident vegetation (Viereck, 1983).

The greater thickness of the organic layer on our logged plots is associated with lower abundance and/or exclusion of species requiring site colonization. Compared to burned plots, we found that logged plots supported: (1) fewer species (Fig. 3), (2) a greater proportion of late successional dominants in early stand development stages (Fig. 6), and (3) lower species turnover from early to late stages (Fig. 4). Logged plots also supported only minor amounts of early successional specialist bryophyte and lichen species. These results suggest that reduced organic layer thickness on burned sites may be one of the principal factors causing their greater species richness. Burning appears to eliminate more of the pre-existing community and return the site to an earlier successional condition than logging.

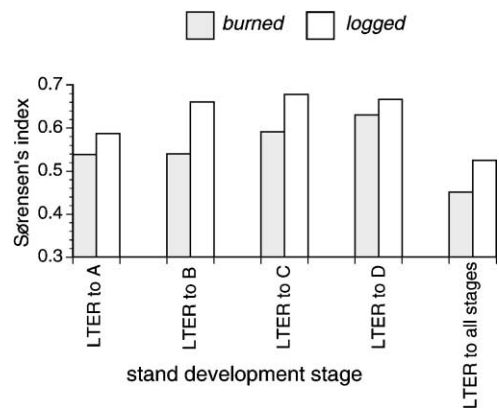


Fig. 7. Comparison of Sørensen's index in current study vs. Bonanza Creek LTER data. Floristic similarity is compared between four stand development stages and between disturbance types overall.

In forests, plant species richness is also strongly influenced by overstory canopy closure following disturbance (Bazzaz, 1975). After a forest canopy develops, light becomes limiting at the ground layer, especially for vascular species that were dominant in full sun conditions. Because overall canopy cover was not significantly different between burned and logged plots in this study, differences in light levels cannot explain the difference in overall species richness between the two disturbance types. We found that canopy closure occurred at a later stand development stage on burned plots (stage C) than on logged plots (stage B). This suggests that succession proceeds more rapidly on logged than burned sites. Timoney et al. (1997) found that after logging, species composition and dominance changed more rapidly on logged plots than during natural succession in northcentral Alberta. The more open conditions of stage B burned plots compared to logged plots in our study may contribute to the greater vascular species richness in our burned stage B plots (Fig. 3B). However, the difference in species number between stage B burned and logged plots is not markedly greater than at other stand development stages. In future studies it would be valuable to determine whether there is a systematic difference in length of time before canopy closure between disturbance types, and if so, to what degree such a difference might explain differences in species richness.

In the boreal forest overall vascular plant species richness is low compared to other biomes (Waide et al., 1999). The overall plant species richness of 147 vascular, moss, and hepatic taxa (excluding lichens) for all plots in this study compares closely with 162 similar taxa from the clay belt of Ontario (Shafi and Yarranton, 1973). We identified 117 vascular species, compared to 440 vascular species identified in a wider array of habitats in a more species-rich southern portion of the boreal forest of Ontario and Quebec south of James Bay (Carleton and Maycock, 1980). Our finding that vascular species richness was greatest early in succession (stages A and B) and bryophyte and lichen richness and abundance was greatest late in succession (stages C and D) is consistent with the pattern reported by Waide et al. (1999). We identified 30 moss and hepatic taxa which we presume represent distinct species. Because we attempted to categorize only the commonly encountered species from these

groups, our count is a considerable underestimate of the total species from these groups actually present. An analysis of the bryophyte flora of the North American boreal forest produced a count of 100 mosses and 33 hepatics in white spruce–fir and black spruce stands (La Roi and Stringer, 1976) a figure considerably closer to a maximum that could be expected from plot-based studies similar to ours. Given the different responses of vascular and bryophyte and lichen species to disturbances observed in this study, measuring species richness-based primarily or exclusively on vascular species would particularly under represent actual species richness in later successional stages.

The trajectories of total species richness were different on burned versus logged plots. Total species richness increased on burned plots and decreased on logged plots through stage C (Fig. 3A). The main exception to the general pattern of greater species richness on burned versus logged plots is for bryophytes and lichens in stages A and B (Fig. 3C), indicating that bryophyte and lichen species tend to be eliminated by fire and/or persist following logging. We also infer that burned sites had high rates of species recruitment, because species richness increased through stage C despite high turnover rates (Fig. 4).

Although species composition was broadly similar on logged and burned plots some species were unique to a specific disturbance type. More commonly, the abundance of certain species differed between disturbance types. We found that several bryophyte and lichen species that are known to be fire-related in Fennoscandia (Esseen et al., 1992) (*C. purpureus*, *Polytrichum juniperinum*, *Polytrichum piliferum* Hewd., *M. polymorpha*) were abundant following fire in our data and in Alaska generally, but are only patchily distributed on logged sites. We found *Calypso bulbosa* (L.) Rchb. f. a vascular species made rare as a result of logging in Fennoscandia (Esseen et al., 1992), only on stage C and D logged plots. Nearly all species unique to early successional (stages A and B) logged plots were either mosses left over from the older forest that was cut or vascular species that are identified in our study area as weeds (Table 1). On both types of disturbance we encountered species that are reported to increase following logging in Fennoscandia (Esseen et al., 1992), including *E. angustifolium*, *Rubus idaeus*, and Eurasian species with close relationships

to Alaskan species within the genera *Geranium*, *Solidago*, and *Calamagrostis*.

The dominant species of early (stage A) succession were different between logged and burned plots, while in late succession (stage D) the dominant species (Table 2) and total species richness (Fig. 3A) were similar, a pattern consistent with convergence through time. Shafi and Yarranton (1973) also found convergence of boreal forest species in mid- or late-stages of succession across the range of sites they sampled. On burned plots a fire-related set of species dominated in stage A. Logged plots supported markedly smaller populations of fire specialist early successional bryophytes and lichens than burned plots. Because the tree species aspen, paper birch, and white spruce were among the dominants in stage A burned plots but not logged plots, we infer that fire disturbance may be more effective at recruiting new tree seedlings than logging.

On burned plots we found that early successional dominant vascular species were more abundant in stage A than in stage D, while the opposite was true on logged plots (Fig. 5A). This divergence in trajectory of abundance by disturbance type suggests that burned sites are dominated early in succession by a set of vascular species favored by fire specifically, rather than by disturbance in general. It is also striking to note the difference between the great abundance and then virtual disappearance of bryophyte and lichen stage A dominants on burned plots compared to the linear increase of bryophyte and lichen stage A dominants across stand development stages on logged plots (Fig. 5B). This is one of the clearest indications in this study of a highly fire-adapted set of species following different successional pathways than those found on logged sites.

Many of the vascular and bryophyte and lichen species that dominated stage A presence/absence plots on logged sites (Table 2) are typical of mature forest conditions, especially the bryophytes. These bryophytes are favored by moderate light levels and the higher relative humidity of an intact forest canopy. We infer that fewer mature forest bryophyte and lichen species present are physically destroyed during logging compared to burning, and as a result fewer of these bryophytes and lichens are likely to disappear from logged sites. However, following logging mature understory feathermosses such as *H. splendens* persist

but then have elevated mortality from desiccation (Busby et al., 1978), becoming restricted to infrequent patches of shade and cover. These findings suggest that succession on logged sites was initiated with a large component of survivors from the previous stand while fire caused the widespread recruitment of new species, a response also reported by Dyrness (1973) in the Douglas-fir region of the Pacific Northwest US. Our finding that more bryophyte and lichen species were found in our logged survey plots than burned plots is consistent with this interpretation. Following logging these bryophytes and lichens are not required to recolonize, but simply grow and expand in place from dispersed patches of survivors unlike the smaller number of more uniformly dominant bryophyte and lichen species that colonize burned sites.

Species composition of logged plots was more similar to that of LTER mature white spruce at each stage than was composition of burned plots (Fig. 7). This supports our interpretation that logged sites begin and continue succession with a greater share of the mature forest understory survivors, while burned sites initiate succession with more distinctive and specialized plant species. By comparing species richness from our study with richness data from LTER mature white spruce plots, we obtained a surrogate measure of the similarity in species richness between post-disturbance plots and those stands in pre-disturbance condition. Only five species found in the LTER mature white spruce dataset were not also present in this study, which suggests that nearly all species compositional change in our study area occurs during the first century after disturbance, with few additional plant species recruited in the second century. Of the five species found only in the LTER mature white spruce dataset *P. chlorantha* is used as an indicator of undisturbed forest with high conservation value in Norway (Haugset et al., 1996) and in northern Alberta (Timoney et al., 1997). *P. minor* is found in similar types and associations as *P. chlorantha* (Robertson and Robertson, 1985), and we suggest that both species may be useful indicators of mature upland white spruce forest conditions in central Alaska.

To date, most logging of white spruce in central Alaska has taken place as small disturbances in a vast and largely intact natural forest system. The influence of natural forest on the regeneration of the logged sites is greater than if logging had taken place in a matrix of

logged land. Additional effects of logging on species diversity beyond those identified in this study could be expected if future logging occurs in landscapes where the matrix is managed forest land (Franklin and Forman, 1987). In Scandinavia at least 95% of the boreal forest has been harvested (Esseen et al., 1992) and bryophytes and lichens make up 13.4% of threatened species that have been made rare primarily by the elimination of older forest. By contrast, vascular plant species, many of which are associated with early succession burned habitats, are only 4.0% of the total threatened species in Scandinavia (Nilsson and Ericson, 1992). Berg et al. (1994) also found that in the Swedish boreal forest the impact of logging has been greater on bryophytes and lichens than vascular species.

5. Implications for management

We have established that organic layer depth is consistently greater on logged sites in central Alaska than on burned sites. Because greater organic depth is associated with cooler soil temperatures, reduced nutrient availability, and lowered site productivity (Van Cleve and Viereck, 1981; Van Cleve and Yarie, 1986; Curran and Ballard, 1990), we recommend that managers consider broadcast burning of at least some logged sites. The benefits we expect from this treatment would include greater species richness, and greater abundance of fire-specialist species including *C. purpureus*, *M. polymorpha*, and *L. pyriforme*. Timoney et al. (1997) found these species also increased following fire (and flooding) in northcentral Alberta. The greatly reduced abundance of these species on logged plots compared to burned plots suggests that they are at risk of being made rare if logging (without fire) were to become the predominant disturbance in the central Alaska landscape. We also recommend post-logging burning where forest management goals include increased levels of aspen, paper birch, and white spruce that regenerate naturally.

Based on our finding of a considerable degree of species overlap and similarity of richness and dominance patterns in mid- and late-succession logged and burned plots, we have identified few mid- or late-successional species that are likely to decline from

logging. Two species, *P. chlorantha* and *P. minor*, did not appear in our logged or burned plots and apparently are associated with older upland white spruce forest. Most of the species at risk of decline in abundance from logging compared to burning by wildland fire in central Alaska are associated with early successional conditions.

Acknowledgements

Funding for this project was provided by the Natural Resource Fund of the University of Alaska, National Science Foundation Grant DEB #9211769 in support of the Bonanza Creek Long-Term Ecological Research site, and the McIntire-Stennis Cooperative Forestry Research Program. Access and location assistance were provided by the Alaska Department of Natural Resources, Division of Forestry. The USDI BLM Alaska Fire Service provided fire records. Joy Jenkins and Robert Solomon assisted in the collection of field data. We acknowledge the assistance of anonymous reviewers and particularly special editor Allison Dibble for her many helpful comments.

References

- Argus, G., Boas, F., Coupe, R., DeLong, C., Douglas, G., Goward, T., MacKinnon, A., Pojar, J., Pojar, R., Roberts, A., 1992. In: MacKinnon, A., Pojar, J., Coupe, R. (Eds.), *Plants of Northern British Columbia*. Lone Pine Publishing, Vancouver, BC, Canada, 352 pp.
- Bazzaz, F.A., 1975. Plant species diversity in old-growth successional ecosystems in southern Illinois. *Ecology* 56, 485–488.
- Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conserv. Biol.* 8 (3), 718–731.
- Busby, J.R.T., Bliss, L.C., Hamilton, C.D., 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. *Ecol. Monogr.* 48, 95–110.
- Carleton, T.J., Maycock, P.F., 1980. Vegetation of the boreal forests south of James Bay: non-centered component analysis of the vascular flora. *Ecology* 61 (5), 1199–1212.
- Crimp, P.M., Phillips, S.J., Worum, G.T., 1997. Timber resources on state forestry lands in the Tanana Valley. Division of Forestry, Department of Natural Resources, State of Alaska, Anchorage, AK, 80 pp.
- Curran, M.P., Ballard, T.M., 1990. Some slash burning effects on soil and trees in British Columbia. In: Gessel, S.P., Lacate,

- D.S., Wetman, G.F., Powers, R.F. (Eds.), Proceedings of the 7th North American Forest Soils Conference, University of British Columbia, Vancouver, BC, Canada, July 1988. Faculty of Forestry, University of British Columbia, Vancouver, BC, Canada, pp. 355–361.
- Curtis, J.T., McIntosh, R.P., 1950. The inter-relations of certain analytic and synthetic phytosociological characters. *Ecology* 31, 434–455.
- Dyrness, C.T., 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. *Ecology* 54 (1), 57–69.
- Esseen, P.A., Ehnstrom, B., Ericson, L., Sjoberg, K., 1992. Boreal forests—the focal habitats of Fennoscandia. In: Hansson, L. (Ed.), *Ecological Principles of Nature Conservation*. Elsevier, London, UK, pp. 252–325.
- Fisher, N.I., 1993. *Statistical Analysis of Circular Data*. Cambridge University Press, Cambridge, UK, 277 pp.
- Franklin, J.F., Forman, R.T.T., 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecol.* 1, 5–18.
- Haugset, T., Alfredsen, G., Lie, M.H., 1996. Nøkkelbiotoper og arts mangfold i skog. Naturvernforbundet i Oslo og Akershus, Oslo, Norway, 110 p.
- Hultén, E., 1968. *Flora of Alaska and Neighboring Territories*. Stanford University Press, Stanford, CA, 1008 pp.
- Johnson, E.A., 1992. *Fire and Vegetation Dynamics: Studies from the North American Boreal Forest*. Cambridge University Press, Cambridge, MA, 129 pp.
- La Roi, G.H., Stringer, M.H.L., 1976. Ecological studies in the boreal spruce–fir forests of the North American taiga. II. Analysis of the bryophyte flora. *Can. J. Bot.* 54, 619–643.
- Lamas, T., Fries, C., 1995. Emergence of a biodiversity concept in Swedish forest policy. *Water Air Soil Pollut.* 82, 57–66.
- Magurran, A.E., 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ, 179 pp.
- Mueller-Dombois, D., Ellenberg, H., 1974. *Aims and Methods of Vegetation Ecology*. Wiley, New York, NY, 547 pp.
- Nilsson, S.G., Ericson, L., 1992. Conservation of plant and animal populations in theory and practice. In: Hansson, L. (Ed.), *Ecological Principles of Nature Conservation*. Elsevier, London, UK, pp. 71–112.
- Oliver, C.D., 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.* 3, 153–168.
- Rieger, S., Schoephorster, D.B., Furbush, C.E., 1979. *Exploratory Soil Survey of Alaska*. USDA Soil Conservation Service, 213 pp.
- Riley, L.F., 1995. Criteria and indicators of sustainable forest management in Canada. *Water Air Soil Pollut.* 82, 67–70.
- Robertson, D.C., Robertson, J.A., 1985. Ultrastructural aspects of *Pyrola mycorrhizae*. *Can. J. Bot.* 63 (6), 1089–1098.
- Schimmel, J., Granström, A., 1995. Fire severity and vegetation response in the boreal Swedish forest. *Ecology* 77 (5), 1436–1450.
- Schoonmaker, P., McKee, A., 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *For. Sci.* 34 (4), 960–979.
- Shafi, M.I., Yarranton, G.A., 1973. Vegetational heterogeneity during a secondary (postfire) succession. *Can. J. Bot.* 51, 73–90.
- Thomson, J.W., 1984. *American Arctic Lichens (The Macrolichens)*. Columbia University Press, New York, NY, 504 pp.
- Timoney, K.P., Peterson, G., Wein, R., 1997. Vegetation development of boreal riparian plant communities after flooding, fire, and logging, Peace River, Canada. *For. Ecol. Manage.* 93, 101–120.
- Van Cleve, K., Viereck, L.A., 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), *Forest Succession, Concepts, and Application*. Springer, New York, NY, pp. 185–210.
- Van Cleve, K., Yarie, J., 1986. Interaction of temperature, moisture, and soil chemistry in controlling nutrient cycling and ecosystem development in the taiga of Alaska. In: Van Cleve, K., Chapin III, F.S., Flanagan, P.W., Viereck, L.A., Dyrness, C.T. (Eds.), *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function*. Springer, New York, NY, pp. 160–189.
- Viereck, L.A., 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. In: Wein, R.W., MacLean, D.A. (Eds.), *The Role of Fire in Northern Circumpolar Ecosystems*. Wiley, New York, NY, pp. 201–220.
- Viereck, L.A., Schandelmeier, L., 1980. Effects of fire in Alaska and adjacent Canada—a literature review. BLM-Alaska Technical Report 6, USDI Bureau of Land Management, Anchorage, AK, 124 pp.
- Vitt, D.E., Marsh, J.E., Bovey, R.B., 1988. Mosses, lichens, and ferns of northwest North America. Lone Pine Publishing, Edmonton, Alta., Canada, 296 pp.
- Waide, R.B., Willig, M.R., Mittelbach, G., Steiner, C., Gough, L., Dodson, S.I., Juday, G.P., Parmenter, R., 1999. The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.* 30, 257–300.
- Wurtz, T.L., Gasbarro, A.F., 1996. A brief history of wood use and forest management in Alaska. *For. Chron.* 72 (1), 47–50.
- Zasada, J.C., Packee, E.C., 1995. The Alaska region. In: Barrett, J.W. (Ed.), *Regional Silviculture of the United States*, 3rd Edition. Wiley, New York, NY, pp. 559–605.
- Zasada, J.C., Sharik, T.L., Nygren, M., 1992. The reproductive process in boreal forest trees. In: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), *A Systems Analysis of the Global Boreal Forest*. Cambridge University Press, New York, NY, pp. 85–125.