

Silvicultural Disturbance Severity and Plant Communities of the Southern Canadian Boreal Forest

Sybille Haeussler, Lorne Bedford, Alain Leduc,
Yves Bergeron and J. Marty Kranabetter

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Boreal forest ecosystems are adapted to periodic disturbance, but there is widespread concern that conventional forest practises degrade plant communities. We examined vegetation diversity and composition after clearcut logging, mechanical and chemical site preparation in eight 5- to 12-yr old studies located in southern boreal forests of British Columbia and Quebec, Canada to find useful indicators for monitoring ecosystem integrity and to provide recommendations for the development and testing of new silvicultural approaches. Community-wide and species-specific responses were measured across gradients of disturbance severity and the results were explained in terms of the intermediate disturbance hypothesis and a simple regeneration model based on plant life history strategies. Species richness was 30 to 35% higher 5 to 8 years after clearcut logging than in old forest. Total and vascular species diversity generally peaked on moderately severe site treatments, while non-vascular diversity declined with increasing disturbance severity. On more-or-less mesic sites, there was little evidence of diversity loss within the range of conventional silvicultural disturbances; however, there were important changes in plant community composition. Removing soil organic layers caused a shift from residual and resprouting understory species to ruderal species regenerating from seeds and spores. Severe treatments dramatically increased non-native species invasion. Two important challenges for the proposed natural dynamics-based silviculture will be 1) to find ways of maintaining populations of sensitive non-vascular species and forest mycoheterotrophs, and 2) to create regeneration niches for disturbance-dependent indigenous plants without accelerating non-native species invasion.

Keywords ecosystem integrity, degradation, species diversity, species composition, site preparation, biodiversity indicators, life history strategies

Authors' addresses *Haeussler*, C2 Site 81 RR#2 Monckton Rd., Smithers, B.C., Canada V0J 2N0; *Bedford*, B.C. Ministry of Forests, P.O. Box 9513 Stn. Prov. Govt., Victoria, B.C., Canada, V8W 9C2; *Leduc & Bergeron*, Groupe de recherche en écologie forestière interuniversitaire, Université du Québec à Montréal, CP 8888, Succursale A, Montréal, Québec, Canada, H3C 3P8; *Kranabetter*, B.C. Ministry of Forests, Bag 5000, Smithers, B.C., Canada, V0J 2N0 **Fax** (*Haeussler*) +1 250 847 6082 **E-mail** skeena@bulkley.net

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1 Introduction

Ecologists and forest managers recognize that periodic disturbances are an essential feature of boreal forests, but there is widespread concern that conventional clearcutting and stand establishment practises degrade forest ecosystems, particularly with respect to their structural and species diversity. The challenge for boreal silviculture and for ecosystem management more generally, is to negotiate the tricky balance between disturbances that are necessary to maintain the productivity and integrity of ecosystems, and those that are excessive or degrading.

We define *ecosystem degradation* as an event or process that reduces the productivity or value of an ecosystem, or that delays or prevents an ecosystem from recovering from disturbance through normal successional processes. *Ecosystem integrity* is defined here simply as an absence of degradation. Comprehensive discussions of this multifaceted concept can be found in Angermeier and Karr (1994), DeLeo and Levin (1997) and Perry and Amaranthus (1997). It is evident both from our definition and these reviews that there is no purely technical solution (Hardin 1968) to the problem of deciding whether the integrity of an ecosystem has been maintained; some human value judgements are always involved. However, careful scientific structuring and analysis of the problem and improved knowledge of ecosystem response to disturbance can contribute substantially to the rational selection of management solutions (Soulé 1994, Wilson 1998).

A simple way to depict the disturbance: degradation paradox is by means of the familiar *intermediate disturbance hypothesis* (Connell 1978) (Fig. 1a). An intermediate disturbance relationship can be hypothesized, not just for species diversity, but for a variety of other measures or indicators of ecosystem integrity, such as the soil productivity required to maintain tree growth or the structural diversity of wildlife habitat. However, our ability to define acceptable levels of forest disturbance – or conversely, unacceptable levels of ecosystem degradation – is complicated by the fact that disturbance curves for any two measures of ecosystem integrity are unlikely to coincide (Fig. 1b).

In Canada today, definition and assessment

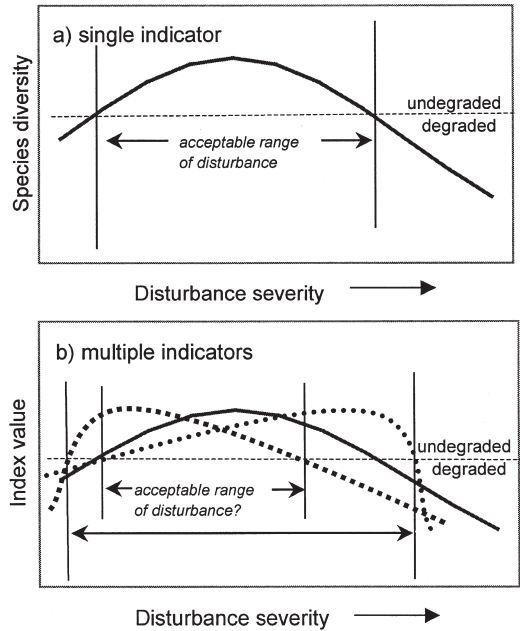


Fig. 1. Application of the intermediate disturbance model to the concept of ecosystem degradation. a) With species diversity as the sole measure of ecosystem integrity, it is relatively easy to define acceptable limits of disturbance. b) With multiple indicators it becomes more difficult. In both diagrams, the horizontal line separating degraded from undegraded ecosystems is arbitrarily set at 60% of the maximum value of the indices.

of ecosystem integrity remain contentious, but there is broad agreement among scientists and the public that boreal forest management practises must change if they are to maintain biological diversity and ecosystem integrity over the long term (Veeman et al. 1999). In response, Canadian boreal forest research has entered a new phase in which knowledge of natural disturbance dynamics is actively incorporated into stand and landscape level forest management (Bergeron et al. 1999, Spence et al. 1999, Bergeron et al. 2002). Across the country, ecological approaches are being used to plan and execute major silvicultural systems experiments and adaptive management projects in which long term conservation of biological diversity and maintenance of ecosystem integrity are primary management objectives. This follows an earlier period of mainly stand-

level silvicultural research where the emphasis was on solving tree regeneration problems and the establishment and growth of young plantations. As the new round of natural dynamics-based studies gets underway, we consider it important to summarize and profit from what was learned from the earlier generation of regeneration studies about the ecological impacts of conventional clearcutting and site preparation practises.

Our objective in this paper is to synthesize the results of eight stand-level studies carried out in northern British Columbia and western Quebec over the past 20 years that provide information on the impacts of conventional silvicultural practises on the diversity and composition of southern boreal plant communities. We look for trends across the studies, compare them to other published work from boreal and northern temperate regions, and tie our findings to the intermediate disturbance hypothesis and to a simple conceptual model of community response based on plant life history characteristics (Grime 1979). Finally, we make some recommendations to assist the current round of research projects in more effectively assessing the impacts of the proposed natural dynamics-based forestry on plant community diversity and integrity.

2 Study Areas and Design

2.1 British Columbia

Five large, well-replicated experimental projects from central and northeastern British Columbia are included (Table 1). The Wonowon, Iron Creek and Inga Lake study areas are located in mixedwood boreal forests of northeastern British Columbia, east of the Rocky Mountains (56°N, 121–122°W). The Bednesti study and Long-Term Soil Productivity Study (LTSPS) are located in sub-boreal coniferous forests of central British Columbia (52–54°N, 121–126°W). All study sites were either clearcut-logged or completely cleared with brush-blades on frozen snowpacks prior to the experiments, and all have a randomized block design with three to five replications of each experimental treatment. Except for Bednesti, the sites have deep, medium- to fine-textured glacial

till soils with fresh to moist soil moisture regimes and average soil nutrient availability.

The Wonowon, Iron Creek, Inga Lake and Bednesti studies are silvicultural trials established in the mid-1980s to test the effectiveness of a variety of chemical and mechanical site preparation treatments on the regeneration and growth of planted white spruce (*Picea glauca* (Moench) Voss) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) (Bedford and McMinn 1990). Each treatment was replicated 5 times on 30 m × 25 m plots planted with 48 coniferous sample trees. Vegetation development was variously monitored over the first ten years of each study. Detailed assessment of plant community composition and diversity was carried out 12 (Wonowon) and 10 (Iron Creek, Inga Lake and Bednesti) years after treatment on randomly located 1 m² to 25 m² nested quadrats within each treatment plot (Haeussler et al. 1999, Boateng et al. 2000).

The LTSPS was established in the early 1990s to study the effect of site disturbance from clearcut logging on long-term soil productivity (Kranabetter and Chapman 1999). Unlike the other studies it includes three geographically separated installations (Topley, Log Lake, Skulow Lake), and has 9 experimental treatments (3 levels of soil compaction, 3 levels of organic matter removal on 70 m × 40 m plots) designed to impair, rather than enhance, soil productivity and tree growth. Plots were planted with 100 hybrid white spruce (*P. glauca* × *P. engelmannii* Parry) and 100 lodgepole pine seedlings. Plant communities were variously assessed in undisturbed old forest prior to logging and were monitored on systematically-located 2.5 m radius circular sub-plots one, two and 5 years after treatment.

2.2 Quebec

Three vegetation studies conducted in boreal mixedwood forests west of Lac Duparquet in the Abitibi region of western Quebec (48°30'N, 79°25'W) provide comparative data on the effect of clearcutting and mechanical site preparation on the composition and diversity of southern boreal plant communities in eastern Canada (Table 2). The studies were carried out before and after

Table 1. Description of British Columbia study sites.

| Site | Wonowon | Iron Creek | Inga Lake | Bednesti | Log Lake | Topley | Skulow Lake |
|---|---|---|--|---|---|--|--|
| Location | North-eastern BC 150 km N of Ft. St. John | North-eastern BC 150 km NW of Ft. St. John | North-eastern BC 60 km NW of Ft. St. John | Central BC 50 km E of Prince George | Central BC 65 km N of Prince George | West-central BC 50 km NE of Houston | Central BC 30 km NE of Williams Lake |
| Latitude | 56°37'N | 56°38'N | 56°37'N | 53°50'N | 54°20'N | 54°37'N | 52°20'N |
| Longitude | 121°49'W | 122°19'W | 121°38'N | 123°23'W | 122°37'W | 126°18'W | 121°55'W |
| Elevation | 900 m | 820 m | 890 m | 850 m | 785 m | 1100 m | 1050 m |
| Biogeoclimatic classification ^{a)} | BWBSmw1/06 and BWBSmw1/01 | BWBSmw1/06 and BWBSmw1/01 | BWBSmw1/01 and BWBSmw1/07 | SBSdw3/05 (minor SBSdw3/01) | SBSwk1/01 | SBSmc2/01 | SBSdw1/01 and SBSdw1/08 |
| Soil moisture regime | Moist (fresh) | Moist (fresh) | Fresh to moist | Dry to fresh | Fresh to moist | Fresh to moist | Fresh (wet patches) |
| Soil nutrient regime | Medium (+) | Medium (+) | Medium | Poor | Medium | Medium | Medium (-) |
| Soil texture | Clay loam | Silt loam to clay loam | Silt loam to clay loam | Sandy to silt loam | Silt loam over loam | Loam | Loam to clay loam |
| Preharvest stand | Lodgepole pine, white spruce, trembling aspen, paper birch | White spruce, lodgepole pine, trembling aspen, balsam poplar | Willows, alder, trembling aspen, balsam poplar, paper birch | Lodgepole pine with black and hybrid white spruce understory | Subalpine fir, Douglas-fir, hybrid white spruce | Lodgepole pine, subalpine fir, hybrid white spruce | Lodgepole pine, hybrid white spruce |
| Experimental treatments (in order of severity) | 1) Untreated clearcut 2) Glyphosate spot treatment (1 m radius spots at 5 kg ae/ha) | 1) Untreated clearcut 2) Glyphosate broadcast ground application (30 m × 40 m plots at 2.5 kg ae/ha) | 1) Cleared only 2) Disk-trenched 3) Plowed & bedded 4) Plowed & inverted 5) Roto-cleared & mixed & burned 6) Windrowed & burned | 1) Cleared only 2) Disk-trenched 3) Plowed & bedded 4) Roto-cleared & mixed 5) Windrowed & burned | 1991/92 (l) 1992/93 (l) 1994,'95,'98 1992,'94,'95,'98 1993/94 (l) | Long Term Soil Productivity Study (LTSPS): 3 × 3 factorial combination of: Organic Matter Removal: 1) Tree boles only removed; 2) Boles + crowns removed 3) Boles + crowns + forest floor removed and Soil Compaction: 1) No compaction; 2) Lightly compacted; 3) Heavily compacted | 1993/94 (l) 1994 1995,'96,'99 1999 |
| Year logged (l) or cleared (c) | 1977 (l) | 1977 (l) | 1986/87 (c) | 1986/87 (c) | 1991/92 (l) | 1992/93 (l) | 1993/94 (l) |
| Treatment year | 1984 | 1986 | 1987 | 1987 | 1992/93 | 1993 | 1994 |
| Assessment year | 1996 | 1996 | 1997 | 1997 | 1994,'95,'98 | 1992,'94,'95,'98 | 1995,'96,'99 |
| References | Boateng et al. 2000 | | Haeussler et al. 1999 | | Kranabetter 1999, Kranabetter and Chapman 1999 | | |

^{a)} DeLong et al. (1990, 1993), Banner et al. (1993); BWBS = Boreal Black and White-Spruce biogeoclimatic zone; SBS = Sub-Boreal Spruce biogeoclimatic zone

Table 2. Description of Quebec studies.

| Data set | Old growth forest | Clearcut | Clearcut + site preparation |
|---------------------------------|-------------------------------|-----------------------|---|
| Stand age | 230 yrs | 6–8 yrs | 6–8 yrs |
| Silvicultural treatments | none | clearcut only | 1) disc-trenched 2) winter shearblading 3) plowing & mixing |
| Quadrat size | 1 m ² | 4 m ² | 4 m ² |
| Number of quadrats by site type | | | |
| – fresh to moist clay | 192 | 30 | 156 |
| – humid clay | 96 | 24 | 52 |
| – fresh to moist till | 192 | 39 | 32 |
| Total | 480 | 93 | 240 |
| References | Bergeron and Bouchard 1984 | Harvey et al. 1995 | Durand et al. 1988 |

logging and site preparation within a balsam-fir-dominated forest mosaic originating after a large wildfire dated to 1760 (Dansereau and Bergeron 1993). The first data set (Bergeron and Bouchard 1984), which constitutes the state of undisturbed old forest plant communities, comprised 480 quadrats (1 m²) located within 20 m × 50 m sample plots distributed throughout the fire area. The second data set (Harvey et al. 1995) included 93 quadrats located within 6- to 8-year-old clearcut logged areas in the same fire area. The final data set (Durand et al. 1988) included 240 quadrats (4 m²) from 6- to 8-year-old cutovers that underwent mechanical site preparation prior to planting.

The Quebec studies are retrospective surveys with differing sample and quadrat sizes rather than controlled, replicated experiments. They therefore provide only a general indication of the impact of clearcutting and site preparation on plant community diversity and composition. However, comparison with the British Columbia research broadens both the geographic interpretation of our results and the range of soil conditions tested. Each Quebec study included three combinations of surficial deposit and soil moisture regime: 1) fresh to moist glaciolacustrine clays; 2) humid glaciolacustrine clays; 3) fresh to moist glacial till.

All studies monitored vascular plants and macroscopic forest floor bryophytes and lichens. Non-vascular epiphytic and decaying wood species were not included.

3 Analytical Methods

In each study, we ranked the silvicultural treatments in order of increasing disturbance severity, and tested the response of simple plant community-based indices of ecosystem integrity across the gradient of forest disturbance. The indices included measures of a) alpha and gamma species diversity (richness and Shannon's H') (Whittaker 1972); b) overall species composition; and c) performance or productivity of indicator species and species groups. For the diversity and performance/productivity descriptors, we looked for hump-shaped intermediate disturbance response curves (Fig. 1) and used ANOVA to compare treatments. ANOVAs for the British Columbia studies were based on standard randomized-block designs as previously described (Haeussler et al. 1999, Boateng et al. 2000, Sanborn et al. 2000) except where LTSPS sites were tested individually and soil compaction served as the blocking factor. For species composition, we used a Sørensen or Bray-Curtis index (Legendre and Legendre 1998; McCune and Mefford 1999) based on species % cover to determine the mean similarity among all untreated plots on the same site and for treated vs. untreated plots at each level of silvicultural disturbance. We then used ANOVA to test the hypothesis that % similarity to untreated plots decreased with increasing silvicultural treatment severity.

At Lac Duparquet we restricted our analysis to species presence data to avoid incompatibilities

in abundance estimates among the three studies. ANOVAs were constructed as recommended by Powers (1989) for retrospective data by calculating means for each of the three site types and using site type as the blocking factor. We used a jackknife estimate of gamma species richness (Heltshel and Forrester 1983) to correct for differences in quadrat size and sampling intensity, and compared alpha richness only on the two clearcut datasets with equal quadrat sizes.

4 Results and Discussion

4.1 Changes in Species Diversity

4.1.1 Clearcutting Effect

In Canada, public concern about the ecological effects of forest practises has centred on contrasts between recently clearcut and old-growth forest conditions (Kimmins 1992). This focus resulted from the recent, rapid expansion of clearcutting into virgin landscapes dominated by mature forest, and because there are few managed forests in intermediate and older age classes. Until recently, however, nearly all silvicultural trials were established post-harvest; thus only one of our British Columbia study installations, the Topley LTSPS site, included an inventory of pre-logging plant communities. The Topley results are consistent with an adjacent unlogged-logged

comparison at Skulow Lake, with the Quebec retrospective survey results, and with unpublished field data from forest sites in our study regions, and they agree generally with published results from other North American coniferous forest regions (Halpern 1989, Roberts and Gillam 1995, Halpern and Spies 1995).

In our studies, total species richness of vascular plants and forest floor bryophytes was 30 to 35 percent higher 5 to 8 years after clearcut logging (with or without site preparation) than in mature or old, previously unmanaged boreal forest (Fig. 2). For example, at Topley, species numbers on 70 m × 40 m plots in 140-year-old conifer forest averaged 46, compared to 60 species 6 years after clearcutting ($p=0.04$). At Lac Duparquet, gamma species richness averaged 82 species in 220-year-old forest and 111 species in 6-year-old clearcuts ($p=0.01$). These increases are similar in size to those reported by Halpern and Spies (1995) for conifer forest in the U.S. Pacific Northwest.

Most boreal forest understory plants are adapted to a wide range of pre- and post-disturbance light and moisture conditions and possess various regenerative mechanisms that enable them to survive logging or quickly regenerate from rhizomes, rootstocks, dormant seeds or spores (Rowe 1983, Haeussler et al. 1990). At Topley, for example, 74% of the species found in old forest were present 1 year after treatment, 80% within 5 years. At Skulow Lake, the comparable values were 79% and 86%. Clearcuts had higher

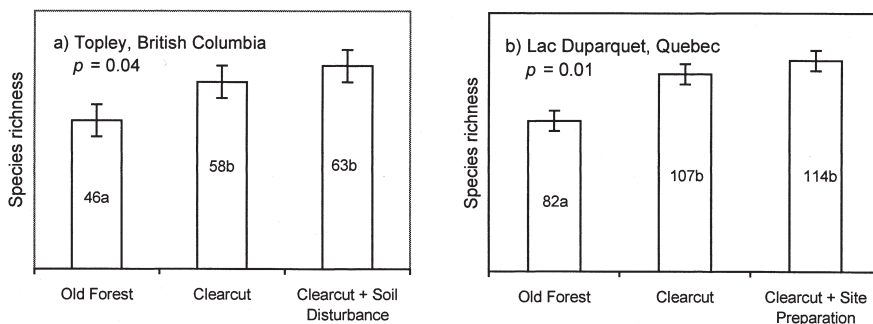


Fig. 2. Species richness of vascular plants and forest floor bryophytes and lichens in old forest and 6 to 8 years after clearcutting at a) Topley and b) Lac Duparquet. Error bars are ± 1 SE and columns with the same letter are not significantly different at $p=0.05$.

species richness than old forests (Fig. 2) because the 10–20% of forest floor species lost after clearcutting were consistently replaced by many more pioneering or ruderal herbs, shrubs, broadleaved trees and bryophytes that do not persist in forest understories, but were able to germinate from dormant seeds or diaspores, or disperse onto vacant seedbeds after disturbance.

Pre- and post-logging comparisons of old forests and clearcut conditions provide useful insights into the potential impacts of clearcutting on plant diversity, but there are two important limitations to this approach. For one, it is not possible to isolate effects resulting from human intervention from effects that simply reflect differences between early and late successional forest communities. A better approach (though limited in Canada by a shortage of mature, managed forests) is to contrast managed and unmanaged forests of similar age. Comparisons of clearcut- and wildfire-origin plant communities in North American boreal forests have shown important short- and long-term differences between post-burn and post-logged plant communities exist that could not be predicted by comparing undisturbed old forests with recent clearcuts (Noble et al. 1977, Abrams and Dickmann 1982, Carleton and MacLellan 1994, Johnston and Elliot 1996, Crites 1999, Nguyen-Xuan et al. 2000, Reich et al. 2001). These include a reduced abundance of pyrophilous (fire-loving) species such as reindeer lichens, *Geranium bicknellii* Britt. and black spruce, and increased abundance of trembling aspen.

The second important limitation is that clearcutting itself (i.e., removal of the overstory tree canopy) is just one in a chain of silvicultural activities that ultimately determine the character of the plant community. The effects of logging-related soil disturbance and the site preparation activities that follow clearcutting are addressed in the sections that follow.

4.1.2 Site Treatment Effect

Five of the six post-logging datasets we analysed showed no decrease in the species diversity (Shannon's H') of plant communities 5 to 12 years after site preparation or logging disturbance

compared with cleared but untreated sites (Fig. 3). Although treatment differences were not statistically significant in 4 of 5 cases, the overall trend was increased species diversity within the range of disturbance created by conventionally prescribed logging and site preparation treatments. On some sites, there was a slight decrease in diversity after extreme disturbances that completely consumed or removed soil organic layers. These results support the intermediate disturbance hypothesis. The single exception was the Bednesti site (Fig. 3f), where species diversity declined monotonically as the severity of mechanical site preparation increased ($p=0.008$).

When species diversities of shrub, herb and moss-lichen layers were examined separately, we found that trends for vascular species (not shown here) paralleled trends for overall species diversity, but non-vascular diversity declined as treatment severity increased (Fig. 4). Treatment differences were statistically significant in only 2 of 5 studies.

Post-hoc power analyses to examine the non-significant negative responses showed that even with five replications, the randomized block design of our trials provided low statistical power and created a high risk of a Type II error – that is, of concluding that there was no significant decrease (or increase) in species diversity when, in fact, there was (Nemec 1991, Boateng et al. 2000). In other words, these silvicultural trials were quite insensitive to either increases or decreases in species diversity.

The species diversity patterns observed in Figs. 3 and 4 illustrate how competitive exclusion processes interact with plant life history characteristics (Huston 1994) at different disturbance severities and on different ecosystems to affect the intermediate disturbance relationship. Relatively productive ecosystems such as our mixedwood boreal sites (Fig. 3 a, b, d & e) support a wide array of plant life forms (grasses, herbs, shrubs, broadleaved trees, conifers) and life history strategies (Grime 1979). As disturbance severity increases, the variety of life forms increases as new regeneration niches are created and competitive exclusion is delayed. Diversity begins to decline only when disturbance is so severe that most or all forest understory species are eradicated. By contrast, on less fertile sites such as

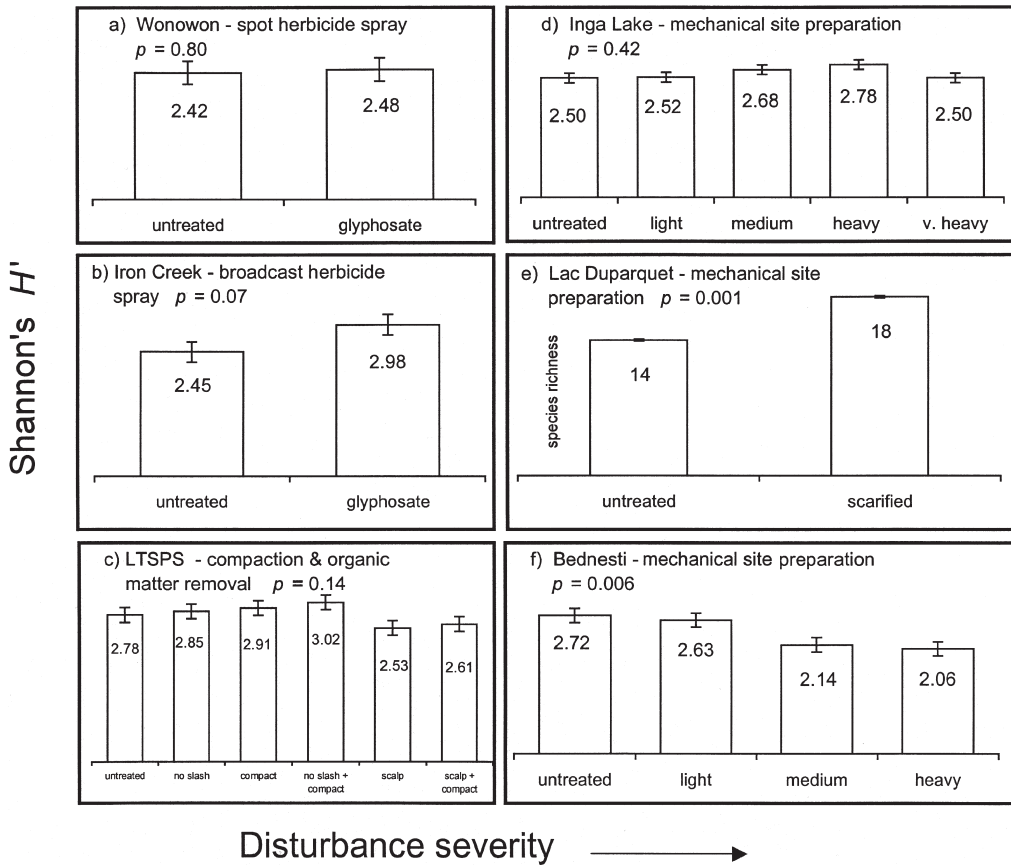


Fig. 3. Within-community (alpha) species diversity on untreated and treated clearcut sites (vascular plants plus forest floor bryophytes and lichens). Species diversity is measured as Shannon's H' for the British Columbia studies and as species richness at Lac Duparquet, Québec. Error bars are ± 1 SE. (Graphs a, b, d, e modified from Haeussler et al. 1999 and Boateng et al. 2000).

Bednesti (Figs. 3f & 4e) the planted pine trees quickly cause loss of diversity through competitive exclusion because these ecosystems support primarily stress-tolerant plants or small stature (mosses, lichens, dwarf woody ericoids) that recover more slowly from disturbance. Maximum diversity is thus observed at higher disturbance severities on the mixedwood sites than on the less fertile pine-dominated ecosystem. Moreover, since the majority of non-vascular species are late successional stress-tolerants (Grime 1979), diversity in Fig. 4 declines at lower severities than when vascular and non-vascular species are considered together (Fig. 3).

In summary, our results suggest that on mesic to moist ecosystems of average or better soil nutrient availability, early successional vascular species diversity is not diminished by conventional mechanical and chemical site preparation treatments, nor by moderate levels of mineral soil disturbance and soil compaction associated with ground-based logging systems that do not unduly scalp the upper soil horizons. As Fig. 5 illustrates, these disturbances probably lie on the left hand side of the disturbance-diversity curve of Fig. 1a. For non-vascular species, on the other hand, peak diversity appears to lie at lower disturbance severities than occurs in conventional

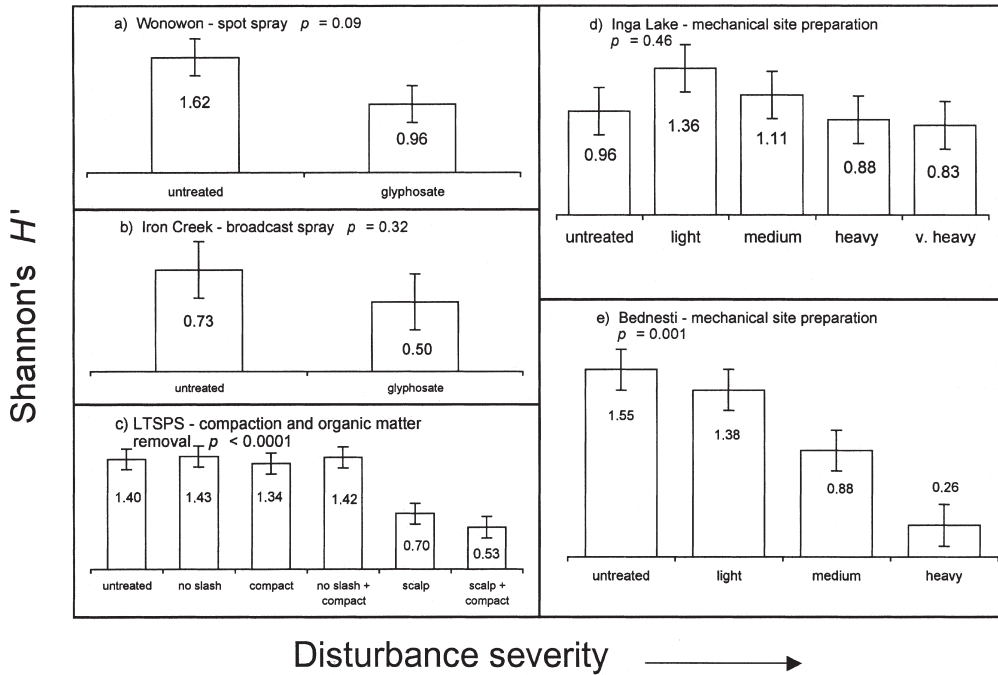


Fig. 4. Non-vascular species diversity (macroscopic forest floor mosses, liverworts and lichens) on untreated and clearcut sites in British Columbia. Species diversity is measured as Shannon’s H' and error bars represent ± 1 SE. (Graphs a, b, d, e modified from Haeussler et al. 1999 and Boateng et al. 2000).

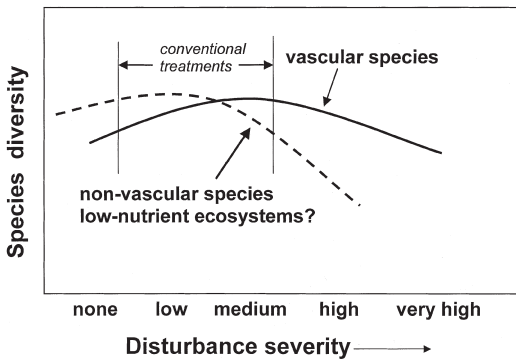


Fig. 5. Generalized response of vascular and non-vascular species diversity to increasing disturbance severity. Most conventional silvicultural site preparation treatments fall on the left-hand side of the curve for vascular species, but appear to reduce non-vascular species diversity. Diversity curves for less productive pine-dominated ecosystems such as Bednesti may be shifted to the left of those for more productive mixedwood boreal ecosystems.

clearcut and site preparation operations. We also hypothesize that the curve is shifted further to the left for nutrient-poor ecosystems such as Bednesti than for mixedwood boreal ecosystems with finer textured soils (Wonowon, Iron Creek, Inga Lake, Lac Duparquet glacio-lacustrine), and that mesic conifer-dominated ecosystems such as our LTSPS sites lie somewhere in between. We intend to test this hypothesis in a properly replicated study.

4.2 Changes in Species Composition

4.2.1 Community-wide Responses

A feature of standard diversity indices is that they value all species equally (Magurran 1988). Thus, two experimental treatments such as the untreated and very heavily disturbed plots at Inga Lake can have identical Shannon’s H' values (Fig. 3d), and yet support highly dissimilar plant communities (Fig. 6d). Forest conservation efforts have

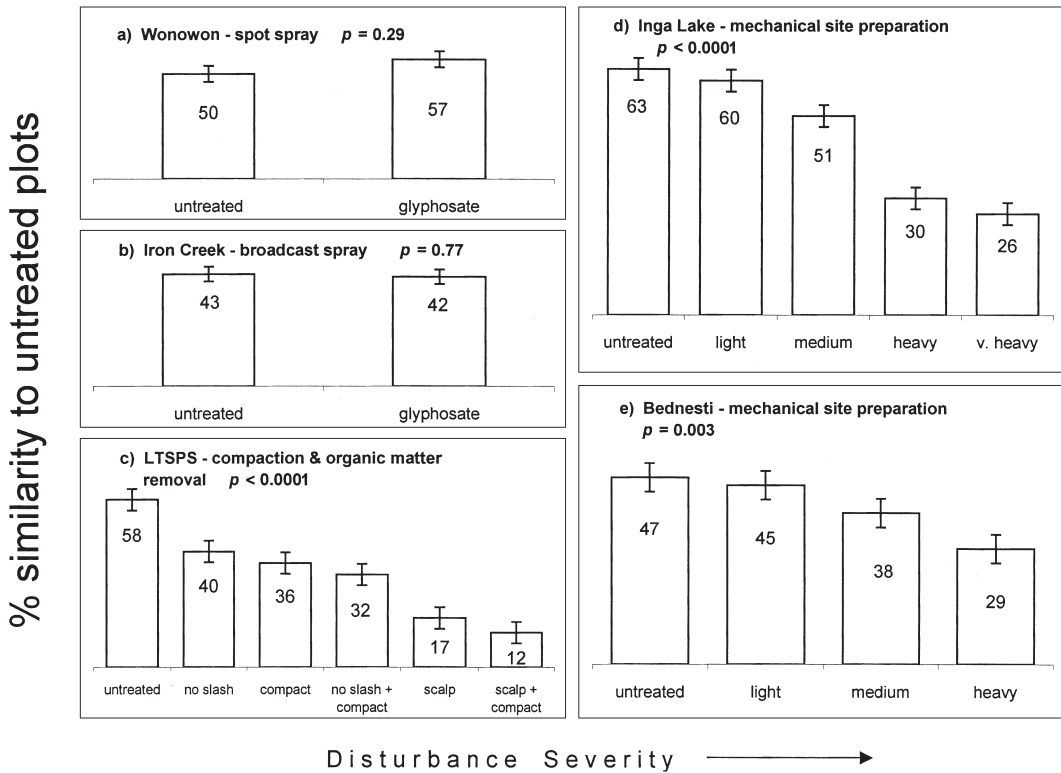


Fig. 6. Effect of disturbance severity on plant community composition. % Similarity = $[1 - \text{Sørensen's index}] \cdot 100\%$. Untreated bars represent the similarity in species composition among replicate untreated plots at the same site. Light disturbances such as glyphosate herbicide and disk trenching did not significantly alter plant community composition in comparison to untreated plots, whereas heavier disturbances such as scalping of organic matter, high-speed soil mixing and windrow burning caused highly significant changes.

tended to focus on the issue of species diversity above all, but as Chapin and others (2000) have emphasized, in the conservation of biological diversity and ecological integrity, *species composition does matter!*

Our studies suggest that, in general, species composition is more sensitive to silvicultural disturbances than species diversity, at least for treatments of medium and higher severity. DCA ordinations of trials with little environmental variation among blocks (Haeussler et al. 1999, not shown here) demonstrated that disturbance severity was the most important factor affecting species composition, accounting for 45–52 percent of the total variation in the datasets. Up to 12 years after treatment, there were statistically

significant differences in species composition between untreated plots and plots subjected to organic matter scalping, deep plowing, high speed mixing, and windrow burning (Fig. 6). However, less severe treatments such as glyphosate herbicide and disk trenching did not have lasting effects on species composition.

Disturbance alters the composition of plant communities by a) damaging or destroying living vegetation and propagules, b) creating space and seedbeds for regeneration and c) changing resource availability in ways that affect competitive relationships among plant species. To illustrate, at Lac Duparquet mechanical site preparation decreased the proportion of forest residents (species found in the old growth dataset)

Table 3. Effect of site preparation on species composition at Lac Duparquet. Values are percent of total species richness.

| Site type | Forest residents | | Invaders | | | | Total | |
|---------------------|------------------|----------------------|----------|----------------------|--------------|----------------------|----------|----------------------|
| | Clearcut | Clearcut + Site prep | Ruderals | | Non-ruderals | | Clearcut | Clearcut + Site prep |
| | | | Clearcut | Clearcut + Site prep | Clearcut | Clearcut + Site prep | | |
| Fresh to moist clay | 76 | 62 | 17 | 25 | 7 | 13 | 24 | 38 |
| Humid clay | 76 | 64 | 14 | 22 | 10 | 13 | 24 | 35 |
| Fresh to moist till | 85 | 74 | 8 | 15 | 7 | 11 | 15 | 26 |
| All site types | 79 | 67 | 13 | 21 | 8 | 12 | 21 | 33 |
| Std error of mean | 2 | | 0.2 | | 0.6 | | 0.7 | |
| Treatment p-value | 0.005 | | 0.001 | | a) | | a) | |

a) No statistical tests done because not statistically independent of the other two tests.

and increased the proportion of invasive ruderals on all three soil types (Table 3, $p < 0.005$). A conceptual model of the process of species replacement, based primarily on 1- to 2-year post-disturbance data from the LTSPS sites (Kranabetter 1999), is presented in Fig. 7. As disturbance severity increases, consuming living and dead organic matter, the residual plant community that survived logging is replaced progressively by species regenerating from the budbank, the seedbank, and finally, from newly dispersed, exogenous seed (Fig. 7a). And because species with different competitive strategies differ in their regenerative and dispersal capabilities, the community shifts from dominance by stress-tolerant late successional species and successional generalists in undisturbed and lightly disturbed communities, to invasive competitors and ruderals after extreme disturbances that remove or consume most or all organic material (Fig. 7b). Example species from our British Columbia and Quebec sites are listed in Table 4. We plan to properly parameterize this model for sites with differing pre-logging proportions of each competitive strategy across a gradient of soil conditions.

4.2.2 Indicator Species or Species Group Responses

A variety of different ecological indicators have been proposed to monitor biodiversity and the sustainability of forest operations (McKenney et al. 1994, Kneeshaw et al. 2000, Lindenmayer et

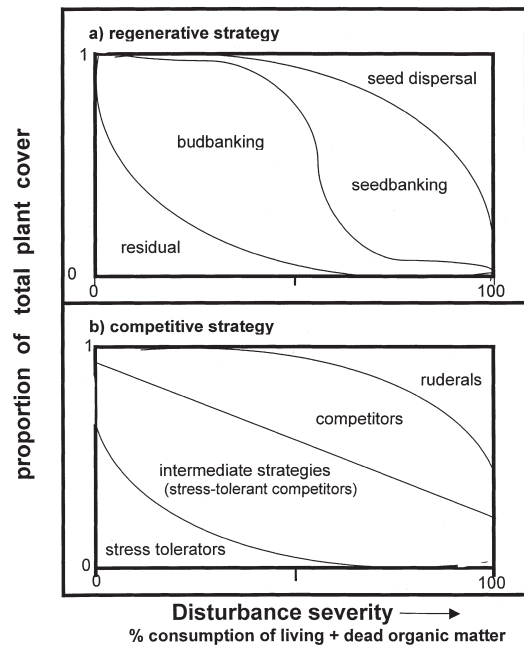


Fig. 7. Changes in a) regenerative and b) competitive traits of plants with increasing disturbance severity (after Grime 1979). The proportion of total plant cover occupied by each strategy is represented by the distance between the upper and lower curves or lines bounding that strategy. Models are based on 1 and 2 yr plant regeneration data from the LTSPS sites (Kranabetter 1999) and inferred from known life-history characteristics of dominant species at the other study sites.

Table 4. Examples of plant species representing each of the four major regeneration strategies after clearcutting and site preparation.

| Residual | Budbank | | Increasing tolerance of disturbance | | Seedbank | Post-disturbance seed dispersal |
|---|---|---|--|---|----------|---------------------------------|
| | Limited lateral spread | Rapid lateral spread | Budbank + seedbank | | | |
| Decreasers | | | | Invaders | | |
| Trees <i>Abies lasiocarpa</i> <i>Abies balsamea</i> | Trees <i>Populus tremuloides</i> | <i>Betula papyrifera</i> | Trees <i>Pinus contorta</i> <i>Pinus banksiana</i> | Trees <i>Populus balsamifera</i> | | |
| Shrubs <i>Lonicera</i> spp. <i>Viburnum edule</i> <i>Sorbus</i> spp. | Shrubs <i>Vaccinium</i> spp. <i>Amelanchier</i> spp. <i>Alnus crispa</i> <i>Cornus stolonifera</i> <i>Shepherdia canadensis</i> | <i>Rubus parviflorus</i> <i>Ribes lacustre</i> | Shrubs <i>Sambucus</i> spp. <i>Ribes laxiflorum</i> <i>Ribes glandulosum</i> <i>Rubus idaeus</i> <i>Prunus</i> spp. | Shrubs <i>Salix</i> spp. <i>Alnus</i> spp. (delayed) | | |
| Forbs <i>Linnaea borealis</i> <i>Rubus pedatus</i> <i>Orthilia secunda</i> <i>Lycopodium</i> spp. <i>Anemone lyallii</i> | Forbs <i>Cornus canadensis</i> <i>Arnica cordifolia</i> <i>Clintonia</i> spp. <i>Pyrola asarifolia</i> <i>Rubus pubescens</i> | <i>Viola orbiculata</i> | Forbs <i>Epilobium angustifolium</i> <i>Aster macrophyllum</i> <i>Petasites palmatus</i> <i>Equisetum arvense</i> <i>Gymnocarpium dryopteris</i> | Forbs <i>Taraxacum officinale</i> <i>Hieracium</i> spp. <i>Cirsium</i> spp. <i>Epilobium</i> spp. <i>Anaphalis margaritacea</i> | | |
| Graminoids <i>Oryzopsis</i> spp. | Graminoids <i>Calamagrostis canadensis</i> <i>Festuca occidentalis</i> | <i>Cinna latifolia</i> | Graminoids <i>Carex aenea</i> several other <i>Agrostis scabra</i> <i>Luzula</i> spp. | Graminoids <i>Poa</i> spp. <i>Phleum pratense</i> <i>Festuca occidentalis</i> | | |
| Cryptogams <i>Hylocomium splendens</i> <i>Ptilium crista-castrensis</i> <i>Dicranum fuscescens</i> <i>Barbilophozia</i> spp. | Cryptogams <i>Pleurozium schreberi</i> <i>Dicranum polysetum</i> <i>Peltigera</i> spp. <i>Ptilidium</i> spp. | <i>Autacomium palustre</i> <i>Brachythecium</i> spp. | Diaspore bank – Cryptogams <i>Ceratodon purpureus</i> <i>Polytrichum juniperinum</i> <i>Marchantia polymorpha</i> | | | |

al. 2000). It is important that potential indicators be locally tested for their operational usefulness, rather than being adopted uncritically from other forest regions where ecosystems, forest history and management regimes may be very different. Plant indicators that may be potentially useful for monitoring the integrity of boreal plant communities include: 1) rare or endangered plants, 2) sensitive species, 3) keystone or surrogate species, 4) species of management importance, and 5) non-native species:

- 1) No endangered or threatened species were found at, or are known from, any of our study areas. In Canada, there are no boreal forest plants on the national list of species at risk (Canadian Wildlife Service 2000) and fewer than 10 of the vascular and non-vascular plants on provincial red lists for British Columbia and Quebec can be found in upland boreal forest habitats (British Columbia Conservation Data Centre 2000, Société de la faune et des parcs du Québec 2000). This situation contrasts sharply with FennoScandia where many hundreds of boreal plants, especially cryptogams, are listed as threatened or endangered because of forest management activities (Lampolahti and Syrjänen 1992, Berg et al. 1994). It is probably a moot point whether the large disparity between the two continents results from biogeographical factors and differences in the history and extent of habitat destruction, or is an artefact of the size of political jurisdictions and the degree of botanical awareness. Whatever the reason, it is clear that in Canada today, it is more appropriate to monitor and conserve the biodiversity and integrity of southern boreal forests at lower and higher levels of biological organization (i.e., locally significant plant populations, communities, ecosystems and landscapes) than to focus on protection of rare and endangered plant species.
 - 2) Sensitive species include plants that are not currently at risk, but whose populations may become locally threatened if forest management practises do not explicitly consider their habitat needs. In our studies, we identified three groups of plant species that were eliminated or greatly diminished by clearcutting and did not recover appreciably within the 5 to 12 year time period covered in our studies. These were: i) mycoheterotrophic vascular species, ii) late successional non-vascular species, and iii) ecologically marginal species.
- i) Mycoheterotrophic plants are a small group of vascular plants in the Orchidaceae, Monotropaceae and Pyrolaceae (sub)families, including *Chimaphila* spp., *Corallorhiza* spp., *Goodyera* spp., *Listera* spp., *Monotropa uniflora* L., *Moneses uniflora* L., and some *Pyrola* spp. These understory forbs derive some or all of their nutrition from the ectomycorrhizal network linked to overstory trees (Henderson 1919, Smith and Read 1997). They typically root in moist, decaying wood and rarely tolerate full sunlight. Although these are common, very widespread, mostly circumpolar species, they are seldom abundant at any site. Their specialized microhabitat requirements and often limited dispersal or regenerative capabilities may make them sensitive to forest disturbance (Thyssel and Carey 2000).
It is self-evident that mycoheterotrophic species are able to persist in boreal landscapes subject to recurring wildfire and other catastrophic disturbances, but there are no boreal North American studies that specifically address how mycoheterotrophs react to either natural disturbance or silvicultural practices. In the U.S. Pacific Northwest, it is thought that mycoheterotrophic species can be extirpated for 40 or more years following clearcutting or fire (Thyssel and Carey 2000). These species are difficult to monitor in conventional silviculture experiments because of their low frequency and cover.
 - ii) Many lichens, liverworts and mosses, particularly epiphytic and decaying wood species, require specialized substrates and humid microenvironmental conditions that are lacking in clearcuts (Söderström 1989, Lesica et al. 1991, Esseen and Renhorn 1998). Like the mycoheterotrophs, these species are nearly eliminated when the forest is cut and may be slow to re-establish in maturing forests as habitat conditions improve (Dettki et al. 2000). At Topley and our other LTSPS sites, common late successional bryophytes and lichens such as *Ptilium crista-castrensis* (Hedw.) DeNot., *Barbilophozia lycopodiodes* (Wallr.) Loeske and *Peltigera* spp. had begun to recolonize the forest floor 6 years after clearcutting, but minor species such as *Plagiomnium medium* (B.S.G.) Kop. and *Nephroma arcticum* (L.) Torsell had not yet reappeared. None of our studies monitored epiphytes, nor the minute bryophytes and lichens that colonize the undersurfaces of decaying logs and other forest

crevices. Such species are unlikely to reappear until the substrate conditions and sheltered micro-environments they require are present (Söderström 1988). Fennoscandian research (Gustafsson and Hallingbäck 1988, Söderström et al. 1992, Berg et al. 1994, Kuusinen 1994, Uliczka and Angelstam 1999) shows that non-vascular plants are at particular long-term risk from forest management practises that do not allow for recruitment of large old trees, large snags, coarse woody debris and deciduous trees and tall shrubs. In the North American boreal forest, the effects of forest practises on bryophyte and lichen communities are comparatively little studied (but see Selva 1994, Webb 1996, Crites and Dale 1997, Newmaster et al. 1999, Pharo and Vitt 2000).

- iii) Ecologically marginal species are plants growing beyond the expected range of soil, climate, or successional conditions for the species (Schumaker and Babble 1980). Such plants can be found on every tract of forest land and often are vulnerable to disturbance. At Topley, outlier individuals of *Gaultheria hispidula* (L.) Bigel., *Empetrum nigrum* L. and *Sphagnum girgensohnii* Russow – typically found on oligotrophic ecosystems – and *Menziesia ferruginea* Smith and *Amelanchier alnifolia* (Nutt.) Nutt. – common in colder and warmer climatic regimes, respectively – were extirpated by clearcutting either because they were directly uprooted and lacked the means to recolonize, or because environmental conditions in the open were too physiologically stressful. Small populations of ecologically marginal plants contribute to the richness of a site and potentially to the genetic diversity of the species (Soulé 1973, Schumaker and Babble 1980). However, disturbance also creates opportunities for new colonization by marginal species (Swindel et al. 1984). To illustrate, at Topley we mapped a solitary frond of *Athyrium filix-femina* (L.) Roth growing in a wet micro-pocket in the unlogged forest. Although this fern did not reappear after logging, several new lady ferns germinated in logging ruts created at some distance from the original plant.

Late successional mycoheterotrophs, certain epiphytic lichens and decaying wood specialists are potential groups of sensitive indicator species in areas where intensive short-rotation forest management is expected to dominate. Newmaster et al. (1999) have identified a group of mesophytic

mosses that are highly sensitive to glyphosate herbicide, and in regions with active fire suppression, species that depend on periodic wildfire such as pioneering lichens (Nguyen-Xuan et al. 2000) may be another sensitive group. Rose (1992) describes an Index of Ecological Continuity, calculated from lists of epiphytic lichens that are exceptionally ‘faithful’ to ancient woodland conditions, used to rank or monitor the quality of British forest habitats. Similar indices could be developed with fire-adapted or old growth specialists in Canadian boreal forests. Ecologically marginal plants, though they pose interesting questions for future research (e.g., do anthropogenic changes cause functional and biogeographic shifts in species considered marginal?), are not sufficiently understood to usefully serve as bio-indicators for forest management.

- 3) Keystone species play a pivotal role in ecosystem processes or provide habitat for a disproportionate number of dependent species (Perry and Amaranthus 1997). Surrogate species, which may also be keystones, are species that are closely associated with species thought to be at risk, but too difficult to monitor. On our mixedwood and conifer-dominated boreal sites, large old trembling aspen, balsam poplar (*Populus balsamifera* L.) or Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), both standing and fallen, could function both as keystones and surrogates because of their essential role in nutrient cycling and the critical habitat they provide for cavity nesters, invertebrates and epiphytes potentially at risk from short-rotation conifer management (Lance et al. 1996, Niemelä 1997, Boudreault et al. 2000, Légaré et al. 2001). At Lac Duparquet, mature white cedar (*Thuja occidentalis* L.) is a potential surrogate because of its strong association with old growth forest and sensitive late successional species (Bergeron 2000, Mosseler and Thompson 2000).
- 4) Crop trees or other species of management value such as important berry or wildlife browse species may serve as useful indicators of either the productivity of an ecosystem or its capability to support services of value to humans. Conversely, dominance by problem competitors such as *Calamagrostis canadensis* (Michx.) Beauv. (Liefers et al. 1994), *Rubus idaeus* L. (Lautenschlager 1999), or *Kalmia angustifolia* L. (Mallik 1995) may point out where management practises have gone awry.

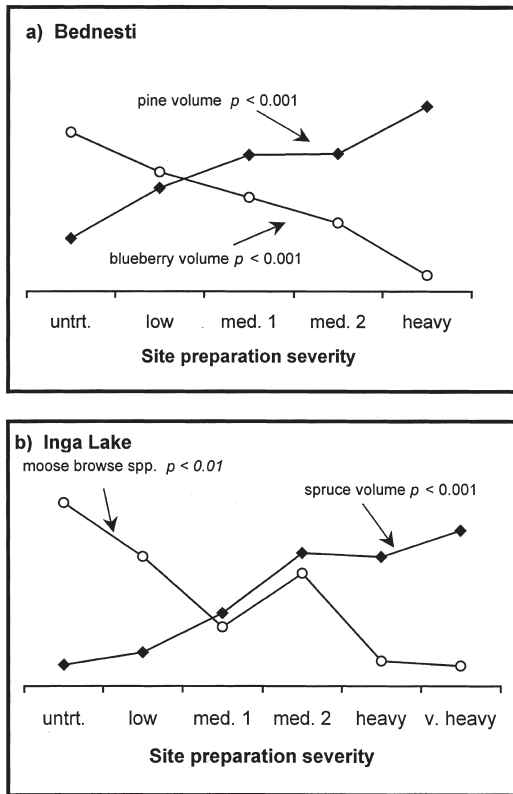


Fig. 8. Tradeoffs between important management indicator species ten years after site preparation. a) Stem volume of planted lodgepole pine vs. cover×height of blueberry (*Vaccinium myrtilloides* Michx.) at Bednesti. b) Stem volume of planted white spruce vs. cover×height of 5 major moose (*Alces alces* Linn.) browse species. Quantities of blueberries and moose browse produced were not measured in these studies and may not be directly proportional to the cover×height of these species. (modified from Haeussler et al. 1999).

Fig. 8. presents management indicator species curves for the Bednesti and Inga Lake sites. None of the curves are hump-shaped, suggesting that ecological optima for these species could lie outside of the range of silvicultural treatments tested. However, the curves do illustrate three points: i) that value tradeoffs are inevitable when two indicators have different ecological optima with respect to disturbance; ii) that acceptable disturbance levels depend on value perspectives (e.g., a silvicultur-

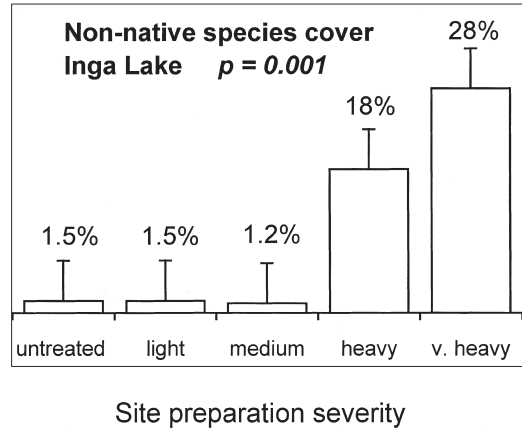


Fig. 9. Effect of increasing disturbance severity on abundance of invasive non-native species 10 years after treatment at Inga Lake. Error bars are +1 SE.

ist may consider untreated sites to be degraded because of poor performance by pine and spruce crop trees, whereas a hunter or berry picker would find heavy disturbance levels unacceptable); and iii) that where management goals are well-defined, a silvicultural treatment can often be selected that provides reasonable outcomes for both objectives. At Bednesti, low severity disk trenching improved pine growth with little loss of blueberry; at Inga Lake, a breaking plow (med. 2) greatly enhanced white spruce growth while maintaining respectable levels of moose browse. Interestingly, both of these treatment options maintained indigenous species diversity at or near peak levels during early successional stages (Fig. 3 d, f).

5) Among the many indicators of ecosystem integrity we tested in our studies, the one showing the clearest threshold effect in response to disturbance was the abundance of non-native species. Fig. 9, from the Inga Lake site, illustrates a trend that appears to be widespread in our study regions – on previously unmanaged forest ecosystems with no history of agricultural use, non-native species currently occur at low abundance, but increase dramatically where severe disturbances strip or consume soil organic layers. Less severe site preparation treatments such as glyphosate, disk trenching and plowing did not cause appreciable non-native species invasion in our studies. We think an ocular % cover estimate

of non-native vascular plant abundance is one of the simplest plant indicators of a loss of ecosystem integrity for the southern Canadian boreal forest. Not only does this index monitor how well indigenous plant communities are being maintained, it also provides evidence that essential soil-plant linkages underlying ecosystem function have been disrupted (Perry and Amaranthus 1997).

5 Conclusions and Recommendations for Future Studies

Plant communities on fresh to moist, more-or-less medium-textured soils with no previous logging history appeared to recover well from conventional logging and site preparation disturbances with little loss of species diversity. Very few of the plant community indicators we tested were significantly reduced compared to untreated conditions except after disturbances that completely stripped soil organic layers or severely depleted indigenous budbanks and seedbanks. However, species composition did change substantially from communities dominated by residual and resprouting understory species at low disturbance severity to communities dominated by pioneering and ruderal species of seed origin after heavy disturbance. Non-vascular plants were generally more sensitive to disturbance than vascular plants, and we found some evidence that non-mesic ecosystems were more sensitive to changes in species composition or losses of species diversity than mesic or average ecosystems. Severe disturbances greatly increased the risk of non-native species invasion.

Management to maintain the biological diversity and integrity of southern Canadian boreal plant communities should avoid becoming focused on rare and endangered plant species and on maintaining or monitoring within-community diversity. Neither of these approaches is likely to protect the unique characteristics of the vast southern boreal forest landscape, which has low rates of endemism and rarity, nor the communities at highest risk, which are often low in species diversity. A more effective approach is develop and locally test a comprehensive set of value-

based indicators based on identified risk factors that will help to maintain the full existing range of plant community composition, structure and function and local populations of all indigenous species, regardless of rarity.

Because plant communities are inherently more variable than tree growth parameters, standard forestry trials with 3–5 replications of each experimental treatment plot rarely have the statistical power needed to detect real changes in the species composition and diversity of plant communities. Future studies should either reduce variability through careful pre-selection of measurement plots that are appropriate to the hypotheses being tested, or increase replication or sample size through creative alternatives to the traditional randomized block ANOVA design.

Value-neutral diversity indices such as species richness, Shannon's and Simpson's indices can mask important changes in community composition and structure that affect the conservation of plant biodiversity. Future studies should ask focused questions about those elements of biodiversity believed to be at risk from particular forest management regimes and select indices to effectively monitor their response, rather than simply testing whether a given silvicultural practise increases, decreases or maintains plant diversity. For example, the new natural dynamics-based forestry approaches now being tested in the Canadian boreal forest might profitably ask the following questions: 1) For late successional mycoheterotrophs and non-vascular plants that are intolerant of clearcutting and require old growth structural elements for survival, can we design new silvicultural systems that either retain populations of these species or enable them to effectively disperse into stands as they mature? or 2) How can we design silvicultural systems that are resistant to invasions of non-native species yet still provide habitat for indigenous pioneer species that require moderate to severe disturbance?

Our studies were confined to a single set of experimental treatments and to a single, early successional stage, but as the Fennoscandian experience clearly shows, impacts of forest management on plant communities result from multiple silvicultural treatments over longer time frames. We are now finding that our site prepara-

tion trials are too small to incorporate later treatments such as brushing or spacing. New studies should consider how to accommodate multiple treatments over entire forest rotations. To more quickly obtain information about the long term effects of forest management practises, experimental projects should be coupled with retrospective or comparative studies that contrast managed and unmanaged (naturally disturbed) plant communities, particularly if older, managed stands are available for study.

Most major silvicultural research trials, notably in British Columbia, are located on more-or-less average, or *zonal*, ecosystems in order to limit environmental variability while maintaining the broadest possible applicability of the results. Where significant environmental variation exists, it is usually included as a non-replicated blocking factor. Our studies suggest, as predicted by plant life-history theory, that moisture/nutrient gradients may cause plant communities to respond in fundamentally different ways to disturbance. It is therefore important to test the sensitivity or resilience of azonal ecosystems to proposed silvicultural regimes rather than merely extrapolating from trends observed on zonal sites.

And finally, although stand- or community-level studies such as those discussed here provide essential information about the local effects of silvicultural practises on the integrity of boreal plant communities, such studies can not be divorced from the larger landscape- and regional-level context in which profound changes to boreal land use patterns, biotic distributions and climate are currently taking place.

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