Boreal Plant Community Diversity 10 Years After Glyphosate Treatment

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ABSTRACT: *This study examined 10 and 12 yr posttreatment effects of broadcast and spot application of glyphosate for site preparation on structural diversity, species richness and diversity, and crop tree growth in two boreal forest plant communities in northeastern British Columbia. At the broadcast-sprayed site, reduced dominance of the tall shrub layer was associated with increased structural diversity and increased richness of the herb layer 10 yr after treatment. At the spot-sprayed site, no significant differences in plant community structure or diversity could be detected after 12 yr. At both sites, glyphosate application increased the growth of planted white spruce* (Picea glauca) *seedlings without eliminating deciduous trees and shrubs. The results indicate that a single application of glyphosate to prepare sites for reforestation can improve crop tree performance without adversely affecting vascular plant community diversity. West. J. Appl. For. 15(1):15–26.*

The herbicide treatment option is one of the important methods for managing forest vegetation at the preharvest, site preparation, and forest establishment stages of the forest development cycle. While the herbicide glyphosate (Roundup®, registered in Canada for forestry use now as Vision®) has been successfully and cost-effectively used to achieve reforestation objectives in British Columbia and other parts of Canada, concerns of its impact on the environment and on nontimber resources have been raised (Campbell 1990, Freedman 1991, Wagner 1993). One of these concerns is that glyphosate use may have a negative impact on the complexity and structural diversity of plant communities (Enns et al. 1993, Clements and Keeping 1996). However, most of the studies upon which this concern is based are short term (generally not exceeding 7 yr) or poorly replicated (Balfour 1989, Santillo et al. 1989, Neary et al. 1990, Freedman et al. 1993, Lautenschlager 1993).

In the 1980s, a set of trials was established in northern interior British Columbia to evaluate the effectiveness of various site preparation methods for establishing conifer plantations across a range of forest ecosystems (Bedford and McMinn 1990). These trials are among the oldest and best-replicated site preparation studies in northern Canada. Treatment methods evaluated included prescribed burn, herbicide, and several mechanical site preparation techniques. This paper presents the results of vegetation responses to site preparation with glyphosate, 10 and 12 yr after treatment at two sites located within the boreal forest zone. In one of the study areas, glyphosate was broadcast-applied at 2.5 kg ae/ha, while in another study area glyphosate was spot-sprayed in a 1 m radius around each newly planted tree seedling at an experimental rate of 5 kg ae/ha. Our objectives were to determine whether glyphosate treatments would have long-term undesirable effects on plant species richness, diversity, or vegetation structure. We expected treatment effects on vegetation to be more apparent at the broadcast-sprayed site than the spot-sprayed site.

Methods

Study Areas

The two study areas, Iron Creek and Wonowon, are located near Fort St. John, northeastern British Columbia, in the Peace variant, Moist Warm subzone of the Boreal White and Black Spruce biogeoclimatic zone (BWBSmw1) (Pojar

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et al. 1987, Delong et al. 1990). On the whole, the study areas are similar ecologically, with equivalent plant communities, soil moisture and nutrient regimes, and stand productivity (estimated SI_{50} = 15–18 m). Iron Creek has a slightly cooler, moister, and more variable climate than Wonowon. While the two areas share most of the same plant species, Iron Creek has higher deciduous tree and shrub cover and more herb species because of its disturbance history and slightly wetter soils.

Description and History of Iron Creek Study Area

This study area is located 150 km NW of Fort St. John (lat. 56°38′N; long. 122°19′W) at 820 m elevation on a gentle (5–10%) easterly toe slope. Soils are slightly nutrient-rich, generally stone free, moderately well to imperfectly drained Luvisols derived from clay loam-textured morainal parent material. The organic layer ranges from 10 to 35 cm in depth. The dominant plant association is the subhygric white spruce–currant–bluebells (BWBSmw1/06) grading upslope to the mesic white spruce–trembling aspen–moss association (BWBSmw1/01) (Delong et al. 1990). The mature forest harvested from the area consisted of white spruce *(Picea glauca)*, lodgepole pine *(Pinus contorta)*, trembling aspen *(Populus tremuloides)*, and balsam poplar *(P. balsamifera)*. It was selectively logged in 1966 to remove large spruce, followed by clearcut harvesting in 1977. The area subsequently regenerated with dense aspen, other deciduous trees, shrubs, bluejoint *(Calamagrostis canadensis)* and fireweed *(Epilobium angustifolium)*. In the winter of 1985/1986, the entire cut-block was prepared for conifer planting by mechanically shearing the vegetation. The debris was piled in long windrows with little mineral soil exposure (Figure 1A). Mechanical shearing was followed by rapid regeneration of noncrop vegetation, requiring further treatment to ensure crop tree regeneration.

Description and History of Wonowon Study Area

Wonowon (lat. 56°37′; long. 121°49′) is located at Mile 101 on the Alaska Highway, approximately 53 km east of

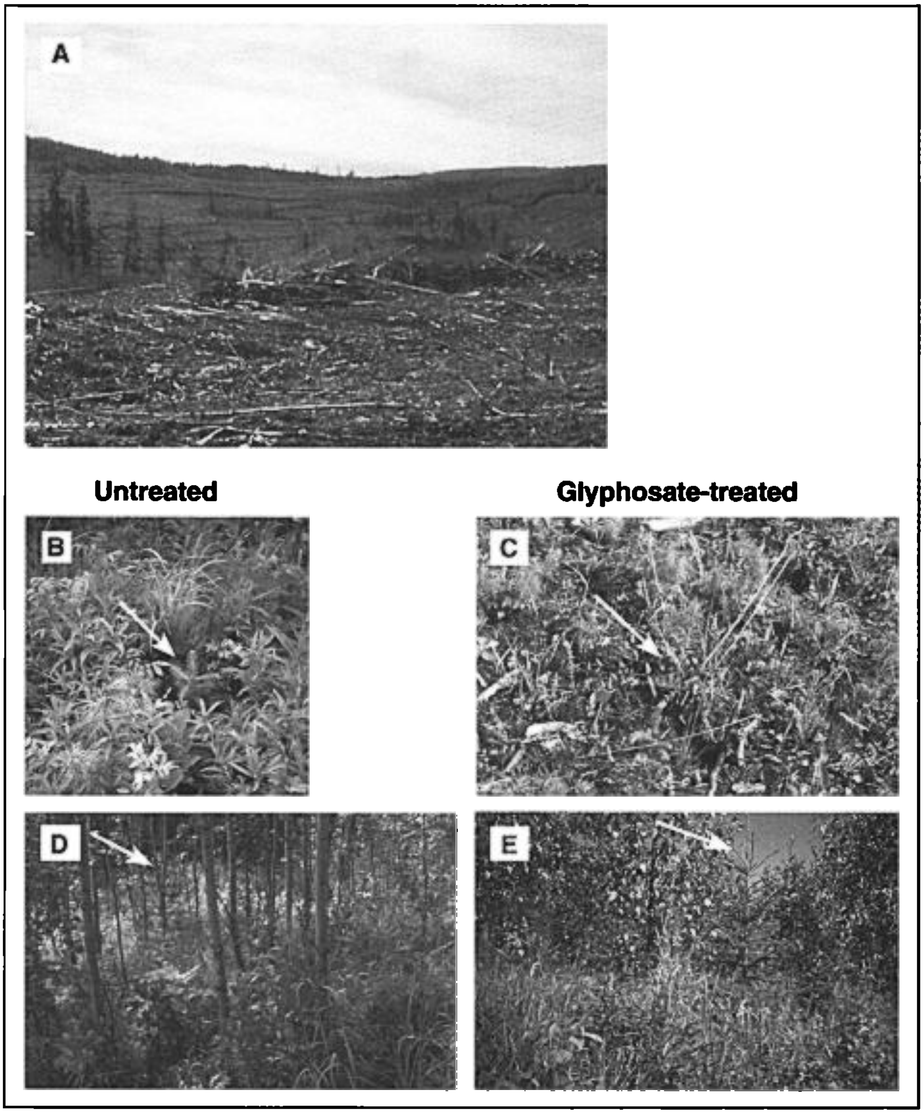

Figure 1. Ten-year vegetation development at Iron Creek. (A) overview of the windrowed study area immediately prior to treatment (1986). Untreated (B) and glyphosate-treated (C) vegetation in July 1987. Untreated (D) and glyphosate-treated (E) plots in July 1996. (Arrows indicate planted white spruce.)

Iron Creek. The study area is at 900 m elevation on a gentle (5%) north and northeast-facing slope. Soils are moderately nutrient-rich, imperfectly to moderately well drained Brunisolic, Orthic, and Dark Gray Luvisols developed from clayey till and lacustro-till parent materials with few coarse fragments. The subhygric white spruce–currant–bluebells and the mesic white spruce–trembling aspen–feathermoss plant associations (BWBSmw1/06 and BWBSmw1/01) (Delong et al. 1990) are distributed across the study area. The previous stand at Wonowon was 120 yr old and consisted of a mixture of lodgepole pine, white spruce, trembling aspen, and paper birch (*Betula papyrifera*). Mean stand height was 23 m, with conifer stocking averaging 140 m^3/ha. The stand was clearcut between June and October 1977, leaving some aspen trees, which were later girdled. The site was left to regenerate naturally. A 1982 survey showed that the area was not satisfactorily restocked with conifers (144 stems/ha spruce and pine) and that dense vegetation dominated by bluejoint impeded conifer regeneration (Figure 2A).

Plot Layout and Treatment

Iron Creek

In 1986, five treatment blocks with similar vegetation and physical characteristics were located within the mechanically sheared brush-regenerated study area. Untreated (con-

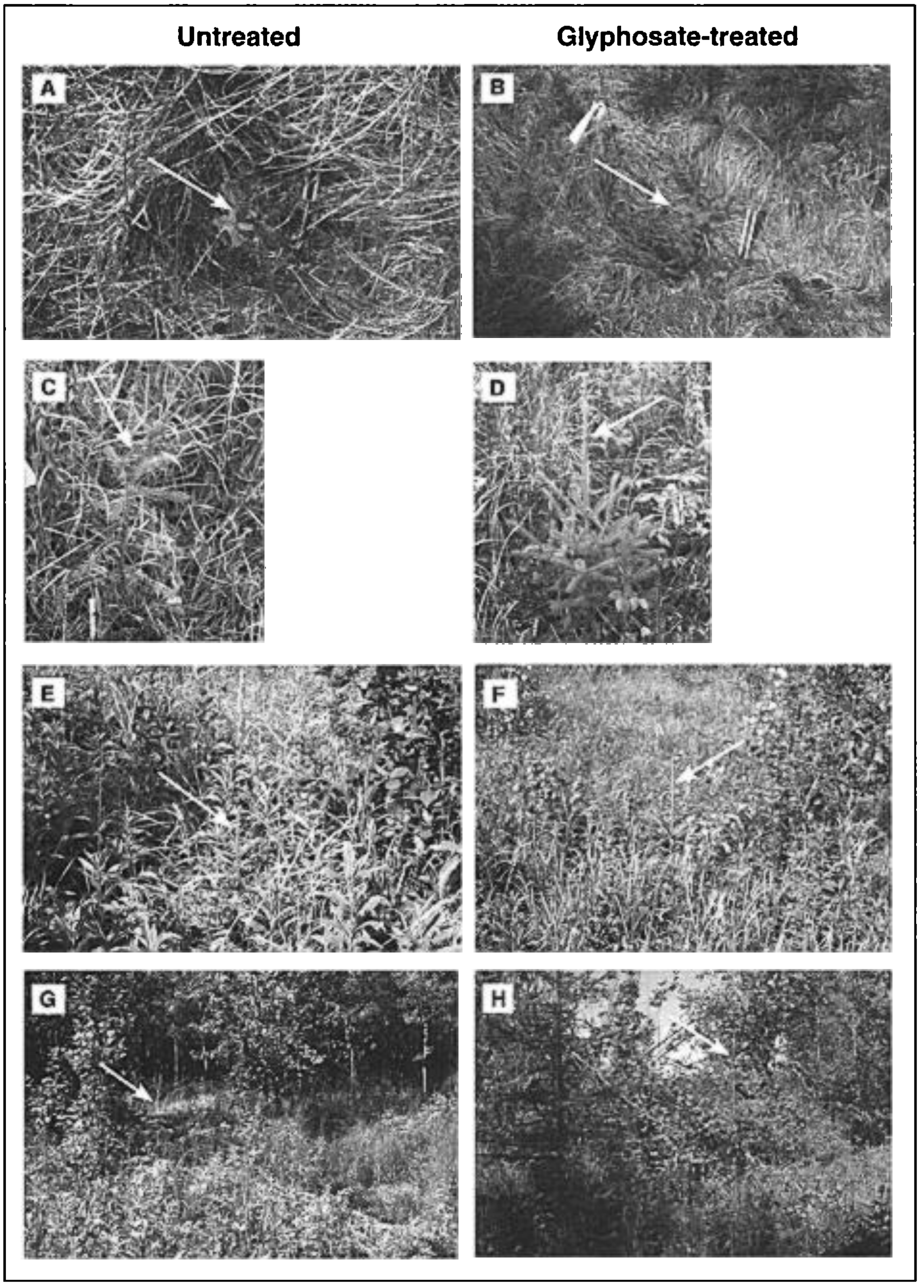

Figure 2. Twelve-year vegetation development at Wonowon. Untreated seedling within hand scalped planting spot (A) and spot-sprayed seedling with dead vegetation (B) in their first growing season (1985). Untreated (C) and spot-sprayed (D) seedlings in their third growing season (1987). Well-developed vegetation on untreated and spot-sprayed treatment plots in 1989 (E and F) and 1996 (G and H). (Arrows indicate planted white spruce.)

trol) and glyphosate-treatment plots, each measuring approximately 40 × 30 m, were established randomly between the windrows on each of the five blocks. On August 21, 1986, the herbicide-treatment plots were broadcast sprayed with Roundup® at 2.5 kg ae/ha using a CO_2 pressurized backpack sprayer. In the spring of 1987, plantable spots on both the untreated and glyphosate-treated plots were prepared by hand scalping small patches of vegetation and litter and planted with 80 one-year-old containerized white spruce seedlings (PSB 313). The inner 30 × 25 m of each treatment plot (containing 48 sample trees) was used as sampling area for crop trees and other vegetation. The perimeter of the plot served as a buffer.

Wonowon

The experimental layout was similar to Iron Creek. Five treatment blocks were established within the bluejoint-dominated study area. An untreated (control) plot and glyphosate-treatment plot, each measuring approximately 40 × 30 m, were randomly located within each treatment block. Plantable spots on each treatment plot were hand-scalped and planted with 80 bareroot white spruce seedlings (2+1 transplant stock) in June 1984. In September 1984, a 1 m radius spot surrounding each planted seedling within the inner 30 × 25 m area of the glyphosate-treatment plot was sprayed with Roundup® at an experimental rate of 5 kg ae/ha (Figure 2C). Herbicide spray coverage within each glyphosate-treated plot averaged about 35% of the surface ground area. One complete block at Wonowon was later omitted from the study after the untreated plot was found to be located in a different type of plant community than all other plots in the study area. As at Iron Creek, monitoring and sampling of crop trees and other vegetation was conducted within the inner 48 sample tree portion of the treatment plot (30 × 25 m).

Vegetation Sampling

Tenth and twelfth yr post-herbicide-treatment vegetation sampling was carried out at Iron Creek and Wonowon, respectively, from July 24 to 27, 1996. A modification of the sampling procedures of Stickney (1980) and Luttmerding et al. (1990) was used. All vegetation sampling was conducted by the same individual. Within each of the untreated and glyphosate-treated plots, three plant community assessment plots were established at a random bearing and distance from plot center. Each plant community assessment plot consisted of a nested series of square subplots to sample four vegetation layers: (1) tall shrubs and trees > 2m height (5 × 5 m subplot); (2) low shrubs and trees < 2 m height (3 × 3 m subplot); (3) herbs and dwarf shrubs (1 × 1 m subplot); and (4) forest-floor mosses and foliose and fruticose lichens (1 × 1 m subplot). An ocular estimate of percent crown cover was made for each plant species within the subplot. A representative top height ("modal height") was measured for each plant species and for each layer within the subplot. On glyphosate-treated plots at Wonowon, we estimated the percentage of each 1 × 1 m subplot that had been sprayed by tracing a 1 m radius circle around each nearby white spruce sample tree. Larger subplots were assumed to contain an unbiased mix of sprayed and unsprayed surface area.

Total height and basal diameter of the surviving white spruce sample trees, ranging from 27 to 47 per plot, were measured in late August (Wonowon) and early September (Iron Creek) of 1996.

Data Analysis

We examined both data sets for differences in vegetation structure, structural diversity, species composition, species richness, species diversity, and white spruce performance (height, diameter, and stem volume) between untreated and glyphosate-treated plots. Analysis of variance (ANOVA) was based on a randomized block design with five blocks and two treatments at Iron Creek and four blocks and two treatments at Wonowon. Vegetation data from the three plant community assessment subplots per treatment plot were pooled to produce a single value for each treatment plot. Square root transformation was used to normalize the species richness data before analysis.

Crown cover (summed by species), height (modal height for each layer), and a volume index (summed by species and estimated as VI = Σ[percent cover × height]/100) for each layer separately and for all layers combined served as measures of vegetation structure. We compared both absolute and relative amounts of vegetation in each of the layers.

To quantify structural diversity, we regrouped the vegetation data into eight structural or physiognomic classes: (a) coniferous trees; (b) deciduous trees and tall shrubs > 2 m; (c) low shrubs, 25 cm to 2 m; (d) dwarf shrubs and evergreen forbs < 25 cm; (e) tall forbs ≥ 25 cm; (f) low deciduous forbs < 25 cm height; (g) grasses, sedges, and rushes, and (h) mosses and lichens. We summed the total crown cover within each of these structural classes to produce abundance values for Shannon's and Simpson's diversity indices (Magurran 1988), where Shannon's index:

$$H' = -\sum_{i=a}^{h} p_i \ln(p_i) \quad (1)$$

and Simpson's index:

$$D = 1 - \sum_{i=a}^{h} p_i^2 \quad (2)$$

where p_i = proportion of total crown cover included in structural class i ($i = a, b...h$, defined above).

To quantify species diversity we used species richness (s = number of species/plot [total of three subplots]), Shannon's index (which is sensitive to rare species), and Simpson's index (which is influenced mainly by the dominant species). Formulas used for the two diversity indices were as in (1) and (2) above, with:

$$p_i = y_i \,/ \sum_{i=1}^{s} y_i \quad (3)$$

where y_i = mean (over subplots) crown cover of species $i(1,2...s)$.

We also developed right-tail sum (T_j) and Δ_β diversity profiles for the glyphosate-treated and untreated plant communities at both sites using procedures detailed by Gove et al. (1992). Right-tail sum profiles allow the intrinsic diversity ordering (Patil and Taillie 1979) of two plant communities to be compared. They are prepared by ranking each species i in descending order of p_i and plotting the coordinate pairs (j, Tj) where:

$$T_j \sum_{i=j+1}^{s} p_i \tag{4}$$

where $j = 1, \ldots s{-}1$

If C1 and C2 are two communities, and $T_{j(\mathrm{C1})}$ lies everywhere above $T_{j(\mathrm{C2})}$, then C1 is considered intrinsically more diverse than C2. T_j profiles are sensitive to abundant species at small values of j and sensitive to rare species when j is close to s. The Δ_β profile is a family of diversity indices such that each value of β yields a different diversity index: species richness (s) is measured at $\beta = -1$, Shannon's index at $\beta = 0$, and Simpson's index at $\beta = 1$. It is produced by plotting coordinate pairs (β , Δ_β) where:

$$\Delta_\beta = \frac{\left(1 - \sum_{i=1}^{s} p_i^{\beta+1}\right)}{\beta} \tag{5}$$

where $-1 \le \beta \le 1$, and i is unranked.

Mean crown cover by species of all four to five plots/treatment was used for the diversity profiles.

In a silvicultural trial of this type there is a risk of incorrectly concluding that the herbicide treatment had no significant effect on the variable of interest (i.e., a Type II error). To determine the reliability of the experiment to detect treatment mean differences, we carried out *post hoc* power analyses (Nemec 1991) for response variables where the mean difference between glyphosate-treated and untreated plots was < 0 and $P > 0.05$.

Results

Vegetation Structure and Structural Diversity: Iron Creek

Ten years after site preparation, both the untreated and glyphosate-treated plots at the Iron Creek study area had a well developed, but discontinuous cover of deciduous trees and tall shrubs 3 to 7 m tall, a lush 50–120 cm tall shrub-herb understory, and a sparse (5–10%) cover of mosses and lichens (Figure 1D, E). Total crown cover, summed across all species and averaged over blocks, was 113% on untreated plots and 116% on glyphosate-treated plots (not significantly different, $P = 0.79$). VI averaged 212 on untreated and 104 on glyphosate-treated plots ($P = 0.08$) (Figure 3). The major structural difference between glyphosate-treated and untreated plots was in the tall shrub layer. During field inspections, most of the glyphosate-treated plots could be readily distinguished from the surrounding untreated matrix by the reduced amount of deciduous trees and tall shrubs, which averaged 10.6% cover and 353 cm in height, compared to 29.6% and 482 cm on untreated plots (P-values: cover = 0.02, height = 0.05). Low shrub, herb, and moss-lichen layers had no significant treatment differences in cover, height, or VI (P-values all > 0.12).

When the volume of vegetation was expressed in relative rather than absolute terms (Figure 4), a substantial structural shift from tall shrubs to low shrubs and herbs on glyphosate-treated plots was evident ($P = 0.019$). On untreated plots, 67% of the total volume of vegetation was in tall shrubs, 10% in low shrubs, 23% in herbs, and 0.07% in mosses and lichens. In contrast, glyphosate-treated plots had 43% tall shrubs, 27% low shrubs, 31% herbs, and 0.1% mosses and lichens.

The structural shift caused by herbicide application was also evident when vegetation layers were subdivided into eight structural classes (Table 1). Glyphosate-treated plots had a more even distribution of vegetation among the eight classes. Shannon's index indicated that the glyphosate-treated plots were structurally more diverse than untreated plots (1.36 vs. 0.98; $P = 0.030$). Simpson's index was also somewhat higher on glyphosate-treated plots (0.66 vs. 0.48) but in this case $P = 0.056$.

Species Composition: Iron Creek

Trembling aspen, green alder *(Alnus crispa* ssp. *crispa)*, and balsam poplar dominated the tall shrub layer at Iron Creek. Other deciduous trees included the willows *Salix scouleriana*, *S. planifolia*, and *S. bebbiana*, and a few paper birch. Planted and some naturally regenerated white spruce averaged just 2% cover on untreated plots and 3% cover on glyphosate-treated plots. The major low shrubs on both treatments were prickly rose *(Rosa acicularis)*, red raspberry *(Rubus idaeus)*, highbush-cranberry (*Viburnum edule)*, and several *Ribes* species. On untreated plots, the herb layer was dominated by bluejoint (VI = 23) and fireweed (VI = 9.4) with significant amounts of creamy peavine *(Lathyrus ochreleucus)* (VI = 3), wood horsetail *(Equisetum sylvaticum)* (VI=1) and coltsfoot *(Petasites frigidus* ssp. *palmatus*) (VI = 0.8) as well as minor amounts of 32 other species. Glyphosate-treated plots were dominated by two grasses, bluejoint (VI = 13) and hairy wild rye *(Leymus innovatus)* (VI = 6), and fireweed (VI = 4), together with cow parsnip *(Heracleum lanatum)* (VI = 1.6), coltsfoot (VI = 1.1), creamy peavine (VI = 0.8), wood horsetail (VI = 0.8) and 36 other minor species. Two shrub, eight herb and three lichen species were found on untreated plots but not on glyphosate-treated plots; one shrub, 15 herb, and three moss species were found on glyphosate-treated but not the untreated plots. Two nonnative species (*Taraxacum officinale* [VI = 0.03] and *Trifolium pratense* [VI = 0.002]) were found on untreated plots, compared to three nonnatives (*T. officinale* [VI = 0.4], *Trifolium hybridum* [VI = 0.2], and *Festuca rubra* [VI = 0.007]) on glyphosate-treated plots.

Table 2 summarizes treatment differences in the cover and VI of the 12 major plant competitors with white spruce. The dominant species in each layer—aspen, green alder, prickly rose, bluejoint, and fireweed—had lower

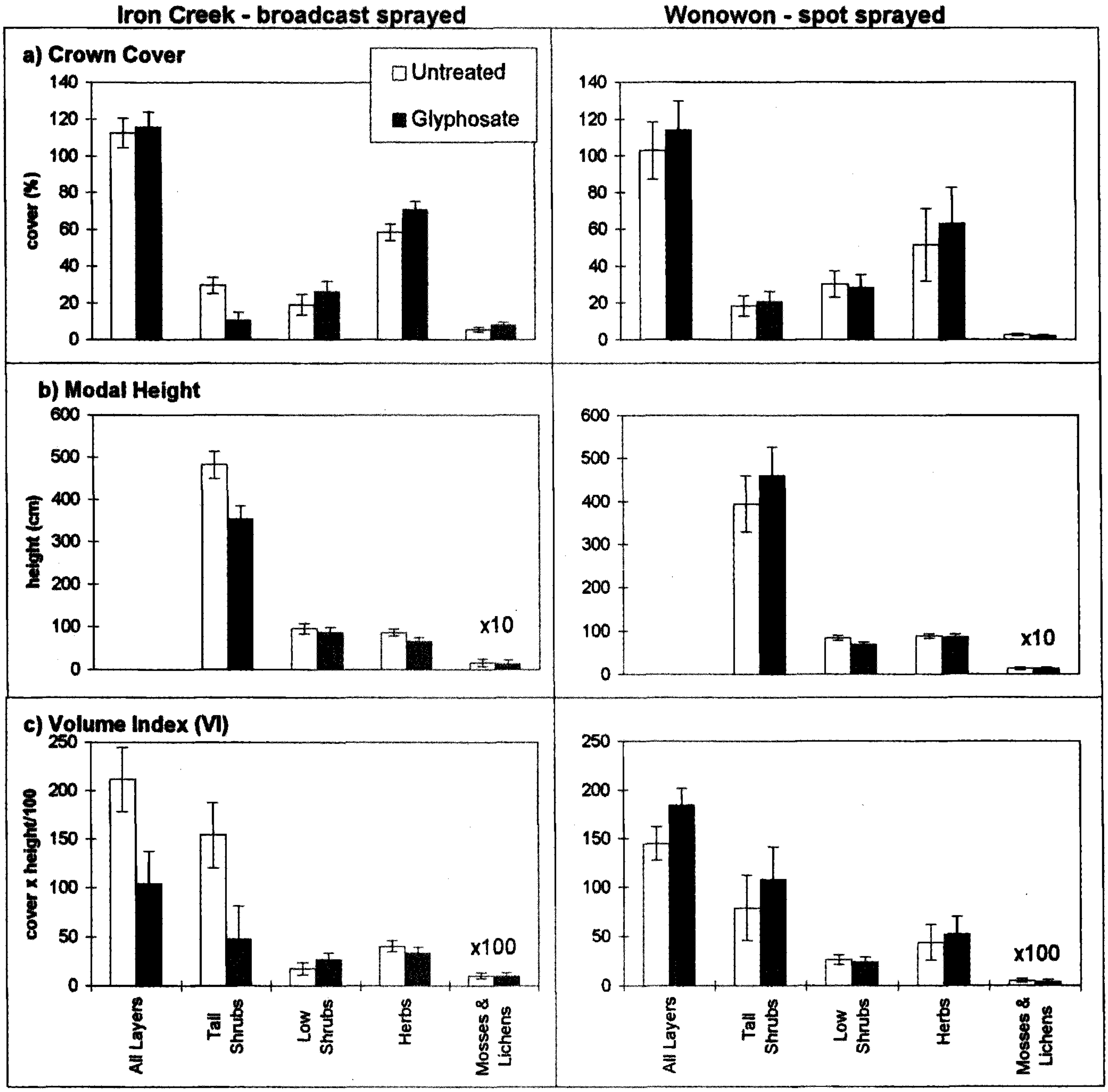

Figure 3. Amount of vegetation by layer on untreated (open bars) and glyphosate-treated (shaded bars) plots at Iron Creek and Wonowon: (a) Crown cover (%) summed for all species in the layer; (b) Modal height (cm) for each layer; and (c) Volume Index (VI) the sum of (crown cover x modal height)/100 for each species in the layer. Error bars are ± 1 standard error estimate of the mean difference between treatments. Height and VI values and errors for the moss-lichen layer are magnified by 10 and 100, respectively, to improve visibility.

mean values on glyphosate-treated plots than untreated plots; while secondary species like red raspberry and fuzzy wild rye were higher. None of the differences was significantly greater or less than 0 at $\alpha = 0.05$. The power of the experiment to reliably detect differences in the cover of individual species was low, however, because of high within-treatment variability and relatively low sample size. For example, prickly rose averaged 7.6% cover on untreated plots, and 3.8% on glyphosate-treated plots, a difference of 3.8% (Table 2). The *P*-value (0.368) indicated no significant difference. However, the difference would have to be as large as ± 21% to be 90% certain of achieving a significant result and ±15% if the probability were reduced to 70%.

Species Richness and Diversity: Iron Creek

In total, 64 plant species were recorded on glyphosate treated plots at Iron Creek, compared to 59 on untreated plots. On average, 39 species were found on each glyphosate-treated plot, not significantly different from the 34 species per untreated plot ($P = 0.17$) (Table 3). Neither Shannon's diversity index, which is sensitive to rare species, nor Simpson's diversity index, influenced mainly by the dominant species, detected any loss of

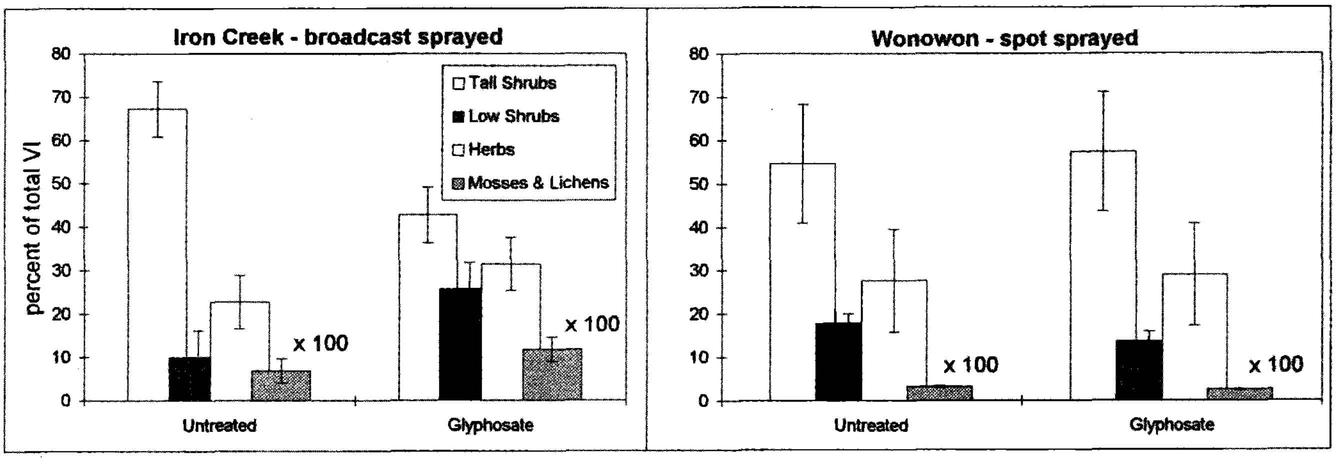

Figure 4. Vegetation structure on untreated and glyphosate-treated plots at Iron Creek and Wonowon. The volume of vegetation (VI) for each layer is expressed as a percentage of the total VI for all layers combined. Error bars (± 1 standard error of the mean difference) are for within-layer comparisons of the two treatments. Values and errors for the moss-lichen layer are magnified by 100 to improve visibility.

species diversity on glyphosate-treated plots. Shannon's index for all layers was 2.97 on glyphosate-treated plots and 2.45 on untreated plots ($P = 0.067$). Simpson's index was 0.92 on glyphosate-treated plots and 0.83 on untreated plots ($P = 0.14$). On both the right-tail sum and Δ_β diversity profiles (Figure 5), glyphosate-treated plots were higher than untreated plots for the entire length of the profile, with no intersections, indicating that they were intrinsically more diverse than untreated plots. The profiles were developed from pooled data from five blocks and contain a more complete sample of the plant community than the block means used for ANOVA (Table 3); however, they can not be subjected to tests of significance.

There was no difference in species richness, Shannon's diversity, or Simpson's diversity for tall or low shrub layers ($P \geq 0.22$), but herb layers on glyphosate-treated plots had significantly more species than those on untreated plots (25.6 vs. 19.0; $P = 0.047$), and both diversity indices were higher, although not significantly so. Species richness and diversity indices for the moss-lichen layer

Table 1. Structural diversity of vegetation on untreated (U) and glyphosate-treated (G) plots at Iron Creek.

	Iron Creek—broadcast sprayed					Wonowon—spot sprayed				
	Untreated mean	Glyphosate mean	Diff. G–U	SE diff.	*P*-value	Untreated mean	Glyphosate mean	Diff. G–U	SE diff.	*P*-value
Structural class	Percent total crown cover					Percent total crown cover				
Conifers	2	3	1			5	7	2		
Deciduous trees and shrubs >2 m	26	8	–18			15	13	–3		
Deciduous trees and shrubs 25 cm–2m	15	21	6			29	23	–6		
Dwarf shrubs and woody herbs <25 cm	4	11	7			3	7	4		
Tall forbs >25 cm	17	14	–3			21	20	–1		
Low forbs <25 cm	9	14	4			6	7	1		
Grasses and grass-like plants	22	23	0			17	21	3		
Mosses and lichens	4	6	2			3	2	–1		
Structural diversity	Index value					Index value				
Shannon's diversity index	0.98	1.36	0.39	0.12	0.030	1.63	1.75	0.12	0.14	0.44
Simpson's diversity index	0.48	0.66	0.18	0.07	0.056	0.77	0.80	0.02	0.03	0.52

Table 2. Iron Creek ANOVA results comparing crown cover and volume index of the major plant competitors.

	Crown cover (%)					Volume index (% cover × ht/100)				
Major competing species	Untreated mean	Glyphosate mean	Diff. G–U	SE diff.	*P*-value	Untreated mean	Glyphosate mean	Diff. G–U	SE diff.	*P*-value
Trees and shrubs										
Trembling aspen (*Populus tremuloides*)	15.5	6.1	–9.4	6.4	0.22	88	20	–68	51	0.25
Green alder (*Alnus crispa* ssp. *crispa*)	8.6	3.4	–5.2	0.8	0.07	35	8.9	–26.1	15.3	0.16
Balsam poplar (*Populus balsamifera*)	5.1	5.4	0.3	3.4	0.95	24	20	–4	15	0.77
Willow (*Salix* spp.)	4.3	6.6	2.3	3.6	0.57	9.2	8.8	–0.4	4.0	0.93
Paper birch (*Betula papyrifera*)	0.3	1.0	0.7	0.6	0.29	0.27	0.91	0.64	0.53	0.30
Prickly rose (*Rosa acicularis*)	7.6	3.8	–3.8	3.7	0.37	6.1	2.8	–3.3	3.6	0.41
Red raspberry (*Rubus idaeus*)	2.0	4.7	2.7	1.1	0.08	1.0	1.7	0.7	0.8	0.46
Highbush-cranberry (*Viburnum edule*)	1.4	1.3	–0.1	0.3	0.65	0.8	0.6	–0.2	0.2	0.28
Herbs										
Bluejoint (*Calamagrostis canadensis*)	22.5	13.6	–8.8	9.7	0.41	22.8	12.5	–10.3	11.1	0.41
Fireweed (*Epilobium angustifolium*)	10.4	5.9	–4.5	3.5	0.27	9.4	4.2	–5.2	3.6	0.22
Fuzzy wild rye (*Leymus innovatus*)	0.8	10.7	9.9	6.9	0.23	0.3	5.2	4.9	2.4	0.27

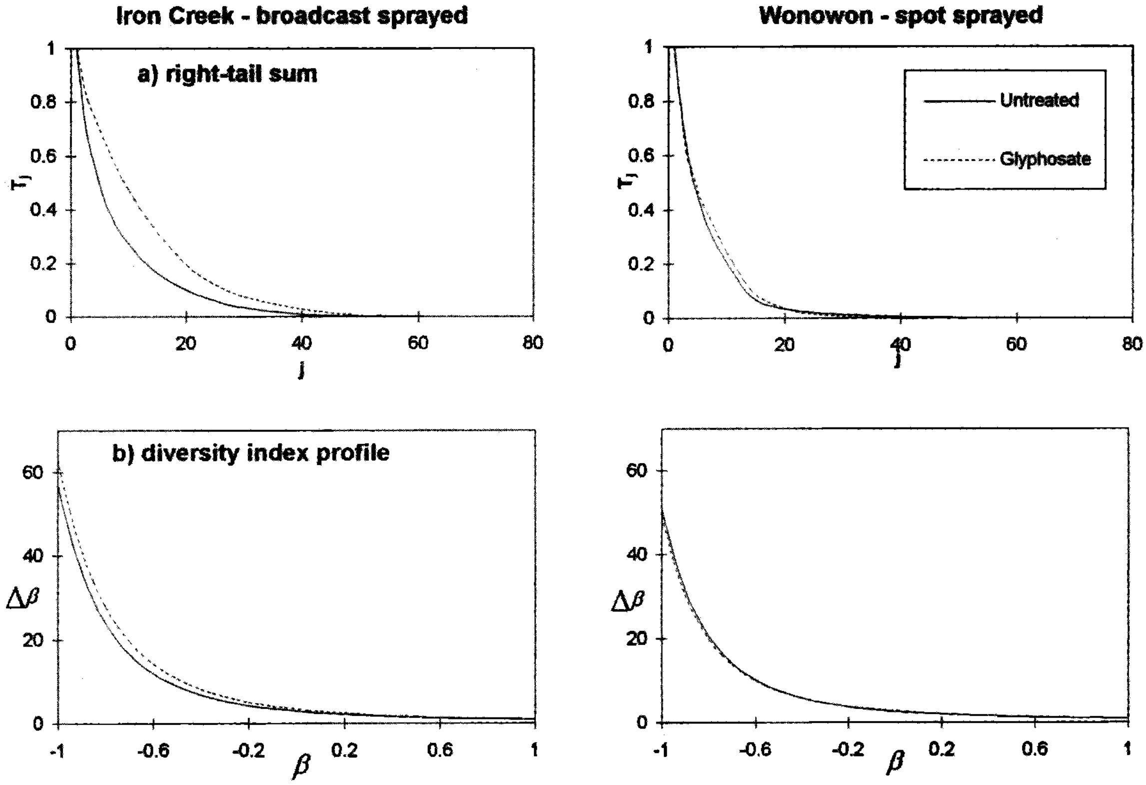

Figure 5. Diversity profile plots for Iron Creek and Wonowon showing (a) right-tail sum (T_j); and (b) diversity index (Δ_β) profiles for untreated (solid line) and glyphosate-treated (dashed line) plots. All plant species are included. Crown cover % is used as the measure of species abundance.

were consistently lower for the glyphosate-treated plots, but with P-values ≥ 0.30.

White Spruce Performance: Iron Creek

At 10 yr, white spruce seedlings were 35% taller (P = 0.037), 48% larger in diameter (P = 0.009), and had 172% greater stem volume (P = 0.036) on glyphosate-treated plots than untreated plots (Table 4).

Vegetation Structure and Structural Diversity: Wonowon

Twelve years after site preparation, it was not possible to visually identify the glyphosate-treated plots at Wonowon, except that planted white spruce looked larger and healthier (Figure 2E–H). Both treatments had a well distributed 4 to 5 m tall shrub overstory averaging 20% cover, a dense layer of herbs and low shrubs 70 to 100 cm tall, and few mosses or

Table 3. Effects of glyphosate application on (a) species richness, (b) Shannon's species diversity index, and (c) Simpson's species diversity index.

	Iron Creek—broadcast sprayed					Wonowon—spot sprayed				
Response variable and vegetation layer	Untreated mean	Glyphosate mean	Diff. G–U	SE diff.	P-value	Untreated mean	Glyphosate mean	Diff. G–U	SE diff.	P-value
Species richness										
All layers	33.8	39.2	5.4	3.26	0.1741	27.0	27.3	0.3	3.15	0.9778
Tall shrubs	4.2	3.8	–0.4	0.51	0.4465	4.0	3.8	–0.2	0.75	0.7895
Low shrubs	10.4	9.8	–0.6	0.40	0.2190	8.0	8.5	0.5	1.32	0.7251
Herbs	19.0	25.6	6.6	2.38	0.0474	9.8	12	2.2	1.65	0.2678
Mosses and lichens	3.6	3.2	–0.4	0.60	0.5746	7.8	5	–2.8	1.49	0.1873
Shannon's index										
All layers	2.45	2.97	0.52	0.20	0.0661	2.42	2.48	0.06	0.22	0.7970
Tall shrubs	0.83	1.08	0.25	0.22	0.3265	1.10	1.05	–0.05	0.21	0.8025
Low shrubs	1.86	1.84	–0.02	0.11	0.9017	1.46	1.65	0.19	1.32	0.5381
Herbs	1.88	2.39	0.51	0.24	0.1033	1.47	1.66	0.19	0.18	0.3553
Mosses and lichens	0.73	0.50	–0.23	0.20	0.3189	1.62	0.96	–0.66	0.26	0.0871
Simpson's index										
All layers	0.83	0.92	0.09	0.05	0.1371	0.88	0.88	0	0.04	0.9593
Tall shrubs	0.44	0.58	0.14	0.12	0.3179	0.59	0.59	0	0.08	0.9970
Low shrubs	0.78	0.80	0.02	0.04	0.6875	0.72	0.75	0.03	0.07	0.6259
Herbs	0.72	0.84	0.12	0.08	0.2079	0.71	0.74	0.03	0.05	0.5053
Mosses and lichens	0.43	0.27	–0.16	0.13	0.3000	0.73	0.49	–0.24	0.09	0.0680

Table 4. White spruce seedling performance on untreated (U) and glyphosate-treated (G) plots at Iron Creek.

White spruce response variable	Iron Creek—broadcast sprayed: Untreated mean	Glyphosate mean	Diff. G–U	SE diff.	P-value	Wonowon—spot sprayed: Untreated mean	Glyphosate mean	Diff. G–U	SE diff.	P-value
Total height (cm)	149	201	52	16	0.037	171	261	90	35	0.077
Basal diameter (cm)	2.3	3.4	1.1	0.2	0.009	2.6	4.2	1.6	0.5	0.046
Stem volume (cm^3)	307	836	529	168	0.036	460	1757	1297	408	0.048

lichens (≤ 5 cover). There were no significant differences in cover, height, or VI for any of the vegetation layers or for all layers combined (Figure 3; P-values ≥ 0.09 for all within-layer comparisons). Total crown cover for all species averaged 103% on untreated vs. 114% on glyphosate-treated plots ($P = 0.65$); modal height averaged 394 and 460 cm, respectively ($P = 0.39$); and VI was 145 vs. 184 ($P = 0.20$).

In relative terms there were no major differences in vegetation structure between the untreated and glyphosate-treated plots at Wonowon (P -values ≥ 0.16 for all within-layer comparisons) (Figure 4). On untreated plots, 55% of the volume of vegetation was tall shrubs, 18% low shrubs, 28% herbs, and 0.03% mosses and lichens. On glyphosate-treated plots, the profile distribution was similar: 57% tall shrubs, 14% low shrubs, 29% herbs, and 0.03% mosses and lichens.

Analysis of the eight structural classes (Table 1) also showed relatively little difference in vegetation structure of spot-sprayed and untreated plots. There was no evidence that structural diversity was reduced by spot spraying as both Shannon's and Simpson's indices were slightly, but not significantly, higher on the glyphosate-treated plots ($P \geq 0.44$).

Species Composition: Wonowon

Paper birch, trembling aspen, and green alder dominated the tall shrub layer at Wonowon with crown cover between 4% and 6%, and VI between 13 and 32 for each species (Table 5). White spruce and naturally regenerated lodgepole pine averaged 5% cover on untreated plots and 9% cover on glyphosate-treated plots. The major low shrubs on both treatments were prickly rose, highbush-cranberry, red raspberry, and various *Ribes* and willow species. There was significantly less prickly rose on glyphosate-treated plots than on untreated plots (VI = 10.6 vs. 3.7, $P = 0.05$), but no differences were found for the other major shrub species ($P \geq 0.31$ for all VI values) (Table 5). On both untreated and glyphosate-treated plots, the herb layer was dominated by bluejoint (mean VI = 23, $P = 0.65$ for treatment difference) and fireweed (mean VI = 17, $P = 0.76$) (Table 5). Other herbs with either crown cover % > 1 or VI > 1 were wood horsetail, tall bluebells (*Mertensia paniculata*), trailing raspberry (*Rubus pubescens*), bunchberry (*Cornus canadensis*), coltsfoot, and twinflower (*Linnaea borealis*). One shrub, five herb, eight moss, and eight lichen species were found on untreated plots but absent from glyphosate-treated plots; three shrub, 10 herb, two moss and one lichen species were found on glyphosate-treated plots but absent on untreated plots. None of the nonvascular plants averaged more than 0.5% cover because of the well developed herb and low shrub cover. No nonnative species were found on either treatment type.

Species Richness and Diversity: Wonowon

A total of 46 plant species were recorded on glyphosate-treated plots at Wonowon compared to 51 on untreated plots. The right-tail sum and Δ_β diversity profiles for glyphosate-treated and untreated plots closely tracked each over their entire length, with several intersections, suggesting no difference in the intrinsic diversity of the two plant communities (Figure 5). The ANOVA results for all layers combined were also virtually identical (Table 3): average species richness per plot was 27.3 species for glyphosate-treated plots and 27.0 for untreated plots ($P = 0.98$), Shannon's index was 2.48 on glyphosate-treated plots and 2.42 on untreated plots ($P = 0.80$), and Simpson's index was 0.88 for both treatments ($P = 0.96$). No differences could be detected in the richness or diversity of tall shrub, low shrub, or herb layers ($0.27 \leq P < 1.0$), and the magnitude of reductions in tall shrub richness and diversity was trivial (Table 3). In all cases, the mean value of diversity indices for the moss-lichen layer was lower on glyphosate-treated plots. Mean species richness was lower by 2.8 species ($P = 0.19$), Shannon's index was lower by 0.66 ($P = 0.09$) and Simpson's index was lower by 0.24 ($P = 0.19$) (Table 3). None of these differences was significant at $\alpha = 0.05$. However, an analysis of the power of these three tests indicates that, even if the differences were

Table 5. Wonowon ANOVA results comparing crown cover and volume index of the major plant competitors.

Major competing species	Crown cover (%): Untreated mean	Glyphosate mean	Diff. G–U	S.E. diff.	p–value	Volume index (% cover × ht/100): Untreated mean	Glyphosate mean	Diff. G–U	SE diff.	p–value
Trees and shrubs										
Paper birch (*Betula papyrifera*)	6.0	6.8	0.8	6.7	0.91	26	30	4	28	0.90
Trembling aspen (*Populus tremuloides*)	4.6	6.0	1.4	5.2	0.81	19	34	14	27	0.63
Green alder (*Alnus crispa* ssp. crispa)	3.8	4.5	0.7	4.5	0.88	14	13	–1	15	0.96
Willow (*Salix* spp.)	1.9	2.2	0.3	2.3	0.37	4.3	8.3	4.0	3.8	0.37
Prickly rose (*Rosa acicularis*)	11.8	5.8	–6.0	2.5	0.10	10.6	3.7	–6.9	2.2	0.05
Highbush–cranberry (*Viburnum edule*)	7.3	10.4	3.1	1.5	0.14	5.8	7.2	1.4	1.3	0.35
Red raspberry (*Rubus idaeus*)	7.5	7.1	–0.4	2.1	0.86	5.3	3.4	–1.9	1.5	0.31
Herbs										
Bluejoint (*Calamagrostis canadensis*)	20.0	25.6	5.6	8.6	0.56	24	30	6	11	0.65
Fireweed (*Epilobium angustifolium*)	17.1	20.0	2.9	6.3	0.67	16	18	2	7	0.76

6.5 for species richness, 1.1 for Shannon's index, or 0.37 for Simpson's index, there is only a 70% chance that they would have been detected.

White Spruce Performance: Wonowon

Twelve-year-old white spruce seedlings were 53% taller ($P = 0.077$), 62% wider in diameter ($P = 0.046$), and 282% larger in stem volume ($P = 0.048$) on glyphosate-treated plots than on untreated plots (Table 4).

Discussion

We cannot make statistical inferences about differences between the broadcast spray at Iron Creek and the spot spray at Wonowon because the herbicide application techniques used were unreplicated; any difference could be due to ecological site factors or stand age. The results support, but do not confirm, our expectation that glyphosate effects on the structure and diversity of the plant community would be more pronounced after a broadcast spray.

In general, there were no major differences in plant species composition or overall reductions in the richness and diversity of plant communities detected in either of the two boreal forest sites a decade or more after glyphosate application. At Iron Creek, the dominance of the tall shrub layer was reduced while the richness of the herb layer was increased. Spot glyphosate application at Wonowon had little or no effect on stand structure and diversity or species richness and diversity. At both sites there was a slight, but not significant trend towards reduced moss and lichen diversity on glyphosate treated areas.

Although the glyphosate application greatly enhanced the growth of planted white spruce, the deciduous tree and shrub component dominated the stand 10 and 12 yr after treatment. At this point, our results indicate that structural diversity was either unchanged (Wonowon) or increased because vegetation was more equitably distributed among various physiognomic classes (Iron Creek). The enhanced structural diversity following glyphosate application at Iron Creek is very similar to the response we observed following medium and high severity mechanical site preparation at another deciduous-dominated boreal ecosystem in the same region (Haeussler et al. 1998).

Few herbicide studies have documented significantly decreased species diversity for more than a few years after herbicide application, except where multiple applications have been used as in agriculture or right-of-way management (e.g., Neary et al. 1990). On the other hand, several studies have documented short-term increases in the diversity or abundance of herbs on forest sites following single applications of glyphosate or other site preparation techniques (Swindel et al. 1984, Jobidon 1990, Freedman et al. 1993, Horsley 1994, Simard and Heinemann 1996). Swindel et al. (1984) argue that such increases can be expected whenever site preparation reduces, but does not eliminate, the residual pretreatment vegetation and provides openings for the establishment of early successional forbs and grasses. Since herbs make the major contribution to plant species diversity of most temperate or northern mixed forest plant communities (Whittaker 1965), an increase in herb diversity increases overall plant community diversity. At Iron Creek, herbicide damage to the two dominant herbs, bluejoint grass and fireweed, and to shrub species may have allowed less aggressive herbs such as fuzzy wild rye to become established. No increase in herb diversity occurred on the glyphosate-treated plots at Wonowon, perhaps because bluejoint and fireweed in the untreated perimeter were readily able to reoccupy the small treated patches (Lieffers et al. 1993).

In the diversity analyses presented here, all species or structural classes are valued equally. However, maintaining or increasing α (within-community) diversity or richness does not translate directly into protecting biodiversity at the stand level. Certain "keystone" species can play a role in maintaining ecosystem function and integrity that may be out of proportion to their measured abundance in the community (Hunter 1990). Also, sensitive and uncommon plant species, notably cryptogams or small forbs requiring specialized microhabitats such as shaded logs, may be lost from a community following herbicide application. These may be replaced in the diversity analyses by early successional herbs that flourish in highly disturbed environments and thus are at no risk of habitat loss (e.g. Freedman et al. 1993). We have addressed these concerns by testing for differences in the diversity of individual vegetation layers and in the abundance of key species, but our experiment lacks the power to explore this issue fully.

In the boreal forest, large deciduous trees contribute greatly to biological diversity by providing critical habitat for many vertebrates, particularly cavity-nesters (Enns et al. 1993, Lance et al. 1996), as well as for invertebrates and epiphytic plants with specialized micro-habitat requirements (Niemala 1997, Crites and Dale 1998). At Wonowon, deciduous trees were clearly retained in the stand by the spot-spraying treatment (Table 5). At Iron Creek, the tall shrub layer was substantially reduced, but no broadleaved species were eliminated, and at 10 yr, differences in deciduous tree cover and volume were not great when both low and tall shrub layers were combined (Table 2). The small area of treated plots (40 × 30 m) probably allowed deciduous trees to reoccupy the treated area more quickly than if a larger area had been treated (Harper et al. 1997b).

Many studies in boreal or northern temperate forests have shown that glyphosate rarely eliminates the dominant or target plant species (Lautenschlager 1993, Sullivan et al. 1998), since most of the shrub and herb species that compete aggressively with conifers possess a variety of regenerative mechanisms enabling them to recover quickly following disturbance (Haeussler et al. 1990). For small or sparsely distributed taxa, such as understory herbs and bryophytes, the effect of glyphosate is poorly documented. Like the others, our study was not able to reliably detect differences in the abundance of minor species because of inadequate sample size and lack of pretreatment stratification to reduce variability and locate rarer species. Unfortunately, modification of the study design to obtain the statistical power needed to detect differences in minor species abundance may not be practical for an operational trial of this kind.

At the time of sampling, there was little evidence of a trend towards fewer late successional forest understory species and more weedy pioneers on glyphosate-treated plots, possibly because of the length of time since disturbance. At Iron Creek, the 13 species present on untreated plots but not on glyphosate-treated plots included a mixture of successional generalists and early seral forbs as well as two species restricted to infrequent wet microhabitats. The 19 species present only on the glyphosate-treated plots represented a cross-section of life-history strategies from invasive pioneers like *Agrostis scabra* to tiny, shade-tolerant understory specialists like *Moneses uniflora*. At Wonowon, there were few pioneering species on either treatment type, which may reflect less site disturbance, more years since disturbance, or greater dominance by bluejoint and fireweed.

Species richness and diversity indices for the moss-lichen layer were consistently lower on glyphosate-treated plots. Although none of the differences were statistically significant and all of the nonvascular species recorded are common and widespread, we believe further investigation is warranted to determine whether or not this trend is real. The effects of silvicultural herbicides on bryophytes and lichens are poorly understood, but certain species, particularly forest mesophytes, are known to be sensitive to herbicides (Newmaster et al. 1998). Possible explanations for loss of nonvascular species include direct herbicide-induced damage; increased competition from bluejoint, fireweed, and other herbs; and increased exposure to sun and drought in the first few years after spraying.

Conclusions

From a silvicultural perspective, the glyphosate applications at Iron Creek and Wonowon were judged successful. Our early assessments (unpublished) showed that both herbicide treatments were able to reduce the influence of competing vegetation, resulting in improved growth of newly planted white spruce seedlings. Enhancement of spruce performance was still evident 10 and 12 yr after treatment, similar to results obtained by Harper et al. (1997a). It is more difficult to assess the success or failure of treatments from a biodiversity perspective because objectives are unquantified and there are more variables to consider. In addition, evaluation of the effects of changes to community composition and diversity within a single stand must be done within a larger landscape level context (Lautenschlager 1993, Sullivan et al. 1998). Within the scope and spatial scale of the study, our results suggest that the diversity of vascular plant species and community structure was not adversely affected by glyphosate application 10 and 12 yr after treatment.

We also stress that the effectiveness or impact of the glyphosate treatment cannot be fully assessed in isolation from other stand management activities that either preceded it or will follow. For example, in these two study areas, future decisions on whether or not to apply stand management treatments such as thinning will have a greater impact on the recruitment of large deciduous trees and on long-term spruce performance than a single application of glyphosate at the site preparation stage.

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