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Effects of Harvesting on Aspen Dominated Stands

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Effects of Harvesting on Aspen Dominated Stands

Forest succession and post-logging regeneration dynamics in the Duck Mountain ecoregion, west-central Manitoba

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EXECUTIVE SUMMARY

Recent research in boreal forest ecosystems has focussed on developing harvesting methods that emulate natural disturbance, maintain biodiversity, and result in long-term ecosystem sustainability and productivity. This study addresses the effects of tree-length harvesting on subsequent stand regeneration in trembling aspen (*Populus tremuloides* Michx.) dominated forests of the Duck Mountain Provincial Forest Reserve, Manitoba. Vegetation and environmental factors, including coarse woody debris (CWD) loadings, were compared among harvested, unharvested edge and interior forest stands. Our objectives were to: **(1)** assess the floristic variation of aspen stands within the study area, **(2)** quantify changes in vegetation structure, composition and diversity after harvest, **(3)** determine and compare the size distribution and volume of CWD of pre- and post-harvested stands, and **(4)** examine trembling aspen suckering and factors controlling suckering.

Three ecological sub-types for aspen-dominated stands in the Duck Mountains were recognized, based on soil moisture availability and relative shrub dominance. The “dry sub-type” is characterized by the presence of aspen parkland shrubs such as prickly rose, saskatoon, common snowberry, and raspberry, with lesser amounts of beaked hazelnut. The “fresh sub-type” is characterized by high abundance of beaked hazelnut. The “moist sub-type” is characterized by the presence of mountain maple, often in association with beaked hazelnut.

Vegetation changes associated with logging of trembling aspen stands were manifested as short-term alterations in the structure-abundance of the pre-existing species pool. Minor changes in species composition between cut and uncut areas were attributable to temporary invasion of ruderal (weedy) species. Grassland, open forest and ruderal species functional groups increased in abundance after harvesting in all aspen sub-types, while the abundance of bryophytes, ferns, closed-forest herbaceous species, and tall shrub declined. These changes in abundance are temporary and are attributable to the short-term environmental effects of logging operations, which include increased light reaching the forest floor following canopy removal, exposure of mineral soil, and removal of tall shrub stems. Rapid aspen regeneration and canopy closure following logging, in combination with shading from coarse woody debris (logging slash), serve to minimize the effect of post-harvest exposure on understory vegetation.

The current practice of retaining slash on cutblocks has much to recommended it. Slash retention minimizes the losses of organic matter and nutrients resulting from harvesting, is a source of decayed logs for seedling establishment, and provides cover and refugia for various species in what would otherwise be an exposed environment. CWD is naturally present at relatively high and variable volumes in mature, unharvested aspen stands. Pre-harvest differences in CWD volumes were equalized to intermediate loadings on cutblocks. The majority of CWD in both unharvested aspen stands and cutblocks occurs in the smallest size classes. A power-law relationship between size class and frequency was found, with cutblocks having a significantly greater proportion of small pieces of CWD than unharvested stands.

Post-harvest aspen regeneration density was unaffected by slash loadings, stand density prior to harvest, shrub competition, edaphic factors, harvest season (winter vs. summer), and aspen sub-type. Post-harvest regeneration of trembling aspen and balsam poplar generally

reflected pre-harvest hardwood proportions on all cutblocks. Harvesting is therefore not expected to alter stand composition. Trembling aspen regeneration from suckers was prolific in most stands. Aspen sucker densities ranged from 40,000 to 180,000 per ha (mean density 80,000 per ha), which meets or exceeds densities recommended for full stand stocking. Aspen suckers undergo rapid natural self-thinning, with density declining by over 65% in the first four years following harvesting. The "free-to-grow" policy as currently practiced (i.e. allowing stands to naturally regenerate following clearcutting) results in effective stand restocking – artificial planting or thinning are not required, nor recommended.

In conclusion, current aspen harvesting practices appear to have no long-term deleterious impact on plant community composition, structure and diversity. It is recommended that a "natural mosaic" of various stand ages be maintained through sustainable harvest rotations that emulate the historical natural wildfire disturbance regime of the region. Such a management policy will ensure the long-term ecological sustainability of aspen-dominated stands in the Duck Mountain Provincial Forest Reserve.

ACKNOWLEDGEMENTS

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INTRODUCTION

The boreal forests of North America are disturbance-driven systems characterized by relatively few species, most exhibiting life histories adapted to frequent and catastrophic disturbance (Rowe 1961). Fire is generally regarded as the dominant disturbance in the boreal forest, creating major changes in local conditions and promoting landscape-scale spatial and temporal heterogeneity.

Frequent disturbance favours shade-intolerant, resprouting species and ephemerals from the seed bank. The boreal hardwoods trembling aspen (*Populus tremuloides* Michx), balsam poplar (*P. balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.), and most boreal shrub and forb species, reproduce by a combination of seed and vegetative shoots (Rowe 1961; Zasada et al. 1992). Root suckering by trembling aspen, balsam poplar and many shrub species is a highly adaptive regeneration strategy in regions affected by fire, clearcut harvesting and other disturbance events (Bond and Midgley 2001). A combination of ecological variables (e.g. soil factors, seed source, stand age, light availability and moisture) and harvest variables (e.g. harvest method and season) combine to determine the extent of root suckering and stand composition following clearcut harvesting.

Logging has replaced fire as the predominant disturbance in many regions of the southern boreal forest (Brumelis and Carleton 1989). In the past, boreal forest logging operations generally focussed on harvesting of softwoods for timber, plywood and pulp production (91% of the total in Manitoba, Manitoba Natural Resources 1996). The standard silvicultural practice in softwood stands is to clearcut and reseed or replant. Recent developments in composite building materials, particularly oriented strand board, have resulted in a shift toward harvesting of boreal hardwoods (Peterson and Peterson 1992; Manitoba Natural Resources 1996). As a result, trembling aspen (and to a lesser extent balsam poplar) have become economically important tree species in rapidly regenerating mixed and pure forest stands of southern Canada (Manitoba Natural Resources 1996) and the north-eastern Unites States (Bartos and Mueggler 1982).

In recent years forestry research has focussed on developing harvesting methods that emulate natural disturbance, so as to maintain biodiversity and long-term ecosystem productivity. Ideally, forest managers should endeavor to mimic natural ecosystem dynamics when harvesting timber in disturbance-driven ecosystems, in order to sustain the biotic and abiotic processes driving such systems (Bergeron and Harvey 1997). The ability of trembling aspen stands to naturally regenerate vegetatively following clear-cut harvesting offers the potential for resource extraction with minimal long-term impacts on community composition, structure and dynamics.

A number of authors have described the effects of clear-cut harvesting on forest stand composition and regeneration in the boreal forest (Steneker 1974; Nobel et al. 1977; Strong and La Roi 1983; Brumelis and Carleton 1988; Harvey and Bergeron 1989; Lavertu et al. 1994), and in southern aspen forest (Bartos and Mueggler 1982; Bella 1986; Bates et al. 1993). In boreal regions, most studies comparing pre- and post-logged forest stands have focussed on the ‘invasion’ of aspen into logged softwood stands (e.g. Nobel et al. 1977; Brumelis and Carleton 1988; Harvey and Bergeron 1989; Lavertu et al. 1994). The effects of clear-cut harvesting on the structure and composition of mature aspen-dominated forests are less understood (Bartos and Mueggler 1982; Lavertu et al. 1994). Logging practices such as tree-length harvesting and on-site slash (coarse woody debris) retention were originally developed by the softwood harvest industry to retain conifer seed sources and promote nutrient recycling. The impact of tree-length harvesting and slash retention on aspen suckering and understory regeneration have not been well studied in northern boreal hardwood forests.

OBJECTIVES

In 1996, the province of Manitoba awarded Louisiana-Pacific Canada Ltd. an Environmental License to sustainably manage the boreal mixedwood forests of the Duck Mountains. In addition to the hardwood volume harvested by Louisiana-Pacific, a number of smaller operators harvest softwoods in the region.

This study examines the impacts of tree-length harvesting and slash retention on trembling aspen-dominated forest stands in the Duck Mountain ecoregion of Manitoba. The study objectives are: (1) to describe and summarize floristic variation of trembling aspen-dominated stands in the region; (2) to quantify changes in the structure, composition and diversity of vegetation following clear-cut harvesting of these stands; (3) to determine and compare the size distribution and volume of coarse woody debris (CWD) in cutblocks, unharvested forest edges and adjacent unharvested interior forest; (4) to examine variation in aspen suckering following clear-cut logging, and determine the factors controlling vegetative suckering. Vegetation and environmental factors (including CWD loadings) were sampled throughout the Duck Mountain Provincial Forest Reserve in harvested, unharvested edge and interior aspen-dominated forest.

STUDY METHODS

Study Area

The study was conducted within the Duck Mountain Provincial Forest Reserve, which is located in west-central Manitoba ($57^{o}02$’–$57^{o}48$’ north and 350^{o}–385^{o} east). The Forest Reserve surrounds Duck Mountain Provincial Park. The Duck Mountains are part of the Manitoba Escarpment, which rises approximately 500m above the Manitoba Lowlands to the east (Cockery 1996). The Escarpment is overlain by deep ground moraine material deposited as the Wisconsin ice sheet receded 12,500 years ago (Lang 1974). Remnant beach ridges from glacial lake Agassiz occur along the eastern slopes of the Escarpment (Ritchie and Yarranton 1978).

The elevation contrast between the Escarpment and the Manitoba lowlands to the east is sufficient to modify local mesoclimate. Air masses passing over the Saskatchewan Plain to the west face little resistance until reaching the Escarpment, which acts as a “wind break” that shelters the eastern slopes (Kendrew and Currie 1955). As airmasses move upward over the Manitoba Escarpment, they cool and release moisture. As a result, the Escarpment receives 2-3 more inches of precipitation than the adjacent lowlands (Kendrew and Currie 1955). Climate stations in the surrounding areas record annual precipitation between 25 cm and 66 cm (Canadian Department of Mines 1957). Although no weather stations are located in the Duck Mountains, it is suspected that annual precipitation at the top of the Manitoba Escarpment is somewhat higher.

The Forest Reserve buffering the Provincial Park boundary consists of a ‘ring’ of aspen-dominated forest surrounding the conifer-dominated stands found at higher elevations in the central region of the Park. Hardwood stands (trembling aspen, balsam poplar and paper birch) are common throughout the Forest Reserve. Clear-cut harvesting of hardwood cutblocks has been carried out in the Forest Reserve since the winter of 1996. Trees are de-limbed on-site (tree-length harvesting) and the slash (coarse woody debris) is retained and distributed over the cutblock. Winter cutting is generally carried out in areas where soil quality and drainage would be compromised by summer harvest. Summer harvesting is thus largely restricted to relatively dry or well-drained regions with coarse-textured soils. When encountered, residual softwoods are buffered by uncut hardwoods, resulting in ‘fingers’ and islands of uncut remnant forest in many cutblocks.

Sampling Design

Sampling was restricted to hardwood stands dominated by trembling aspen (greater than 60% cover) harvested between the summer of 1996 and winter of 1998-1999. A total of 34 cutblocks were enumerated during the 1999 and 2000 summer field seasons (**Figure 1, Table 1**). Access limitations prevented equal sampling of winter and summer harvested cutblocks.

A stratified random sampling design was used in sampling each cutblock. Three strata were used in the 1999 field season, and two strata in the 2000 field season. A single transect oriented perpendicularly to the cutblock edge was randomly located in each stratum. Three 10m x 10m plots were located along each transect: (1) harvested (‘cut’) plot, located within the cutblock a minimum of 40 m from the cutblock edge and any remnant forest patches within the cutblock; (2) forest edge (‘edge’) plot, located in intact forest at the edge of the cutblock; (3) unharvested (‘interior’) plot, located in adjacent uncut forest at least 50 m from the cutblock (**Figure 2**). Logging roads and equipment staging areas (which generally make up < 5% of the cutblock) were avoided when locating ‘harvested’ plots.

Table 1 : Stand summary characteristics of aspen dominated forest enumerated within Duck Mountain Provincial Forest Reserve (Manitoba)

stand number	stand type	cutblock age	harvest region	harvest season	canopy species (% cover)				CWD volume (m3)			slope (site x10^3)	aspect (site)	soil order
					Pt	**Pb**	**Bp**	**Pm**	**cut**	**edge**	**interior**			
1	dry	3	wine lake	summer	52	1	0	0	197	54	165	4.1	200	luvisol
2	dry	2	wine lake	summer	57	0	0	0	240	63	55	8.6	220	luv/brun
3	dry	1	wine lake	summer	60	2	0	0	150	72	46	4.1	200	luv/brun/chern
4	dry	1	route west	summer	65	2	0	0	241	163	213	24.0	330	brun/gley
5	dry	2	route west	summer	33	20	0	1	276	139	83	15.0	180	luv/brun
6	dry	4	route west	summer	53	3	0	0	120	66	132	24.0	330	luv/brun
7	dry	3	route west	summer	64	4	0	0	175	115	89	24.0	330	luv/gley
8	dry	1	route west	summer	43	1	10	3	219	53	40	40.0	330	luv/brun
9	dry	2	route west	summer	63	0	0	0	52	39	39	10.9	180	luv/brun/chern
10	dry	1	wine lake	summer	45	13	0	0	168	142	104	4.1	200	luvisol
11	dry	3	wine lake	summer	65	0	0	0	54	22	40	4.3	290	luv/brun/chern
12	dry	1	arm lake	winter	68	0	0	0	293	194	81	10.9	220	gley/brun/luv
13	dry	3	arm lake	winter	60	0	0	0	70	129	72	3.1	220	luv/brun
mean					**56**	**3**	**1**	**0**	**173**	**96**	**89**			
14	fresh	2	Jackfish	winter	48	3	0	0	180	80	115	17.1	130	brunisol
15	fresh	3	cryderman	summer	50	1	0	0	72	70	105	30.0	330	brun/gley
16	fresh	4	route west	summer	58	0	0	0	91	61	92	20.0	330	luv/brun/gley
17	fresh	1	madge	winter	70	0	0	0	227	15	74	30.0	170	luvisol
18	fresh	2	madge	summer	63	0	0	0	178	56	30	17.1	190	luv/brun
19	fresh	2	wine lake	summer	60	0	0	0	84	69	69	7.5	200	luvisol
20	fresh	1	upper dam	summer	48	0	0	3	225	102	81	6.3	230	luv/brun
21	fresh	2	upper dam	summer	53	3	0	0	247	165	56	10.0	230	luvisol
22	fresh	2	arm lake	winter	49	0	0	16	92	168	105	38.7	220	luv/bru
23	fresh	3	upper dam	summer	60	0	0	0	87	81	76	9.2	230	luvisol
mean					**56**	**1**	**0**	**2**	**148**	**87**	**80**			
24	moist	1	cryderman	summer	52	0	2	0	224	315	257	10.9	230	gley/luv
25	moist	2	cryderman	summer	63	0	0	0	263	145	148	40.0	330	gley/luv
26	moist	2	minitonas	winter	47	5	23	0	191	202	159	30.0	30	gley/luv
27	moist	1	minitonas	winter	54	0	26	0	289	82	143	17.1	330	gley/luv
28	moist	2	cryderman	summer	50	1	25	0	139	177	404	10.9	330	gleysol
29	moist	1	cryderman	summer	53	15	2	0	191	197	178	60.0	330	gleysol
30	moist	4	cryderman	summer	48	20	0	0	299	145	494	24.0	290	gleysol
31	moist	4	cryderman	summer	25	0	45	0	520	433	309	15.0	270	gley/luv
32	moist	3	minitonas	winter	55	0	33	0	283	326	186	60.0	50	luv/gley/brun
33	moist	3	route west	summer	73	0	0	0	85	53	72	40.0	170	luv/brun
34	moist	3	madge	winter	55	0	0	0	91	150	68	10.9	190	luvisol
mean					**52**	**4**	**14**	**0**	**234**	**202**	**220**			

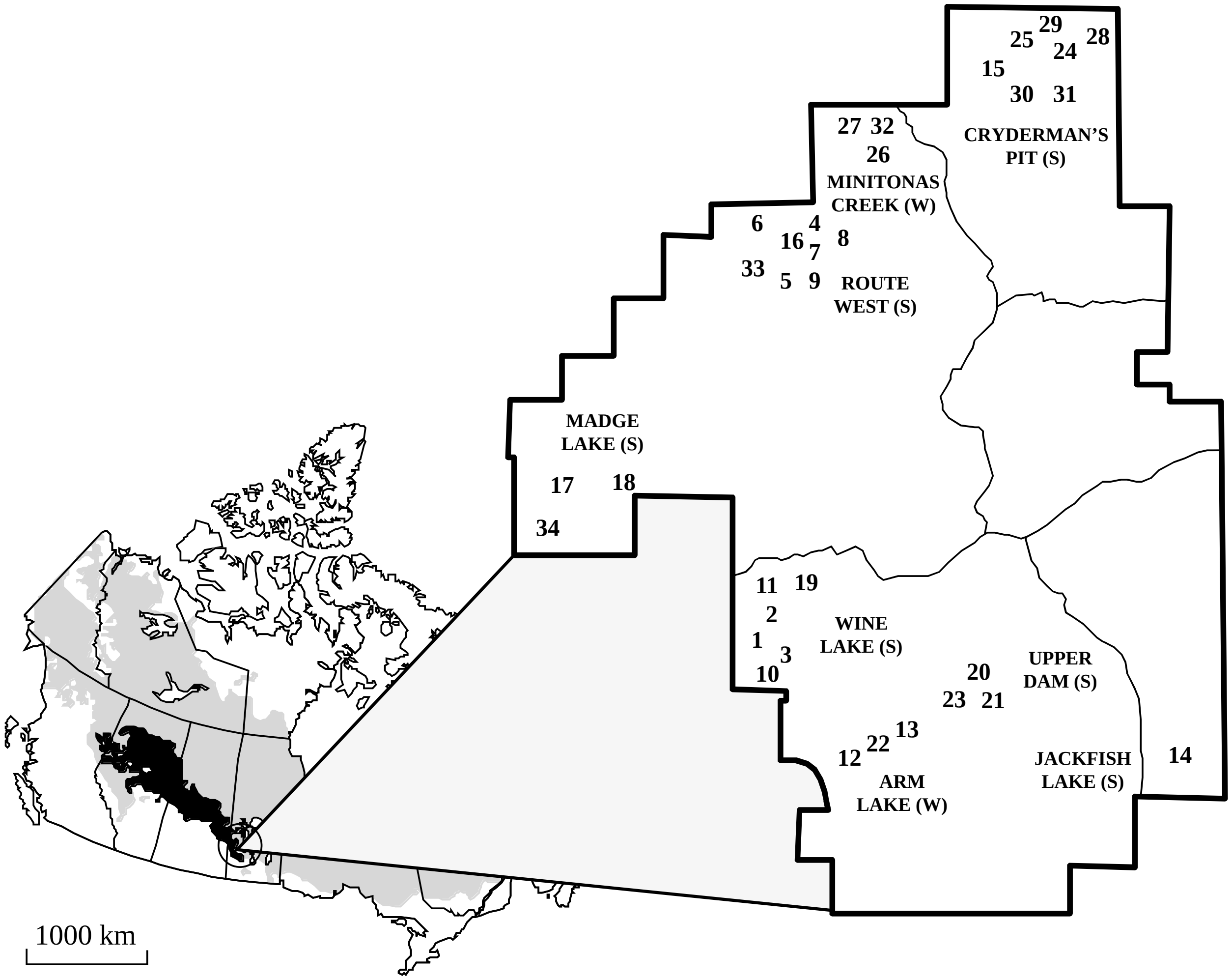


Figure 1. Map of logging regions within Duck Mountain Provincial Forest indicating enumerated stand locations. For stand information refer to Table 1.

Data Collection

Tree species

Density, cover and bole size of all overstory trees (> 3m in height) were recorded within each 10m x 10m plot. Regenerating tree (suckers and seedlings < 3m in height) densities and percent cover values were recorded in each of four 2 x 2 m quadrats located within each plot (**Figure 3**). A random subset of up to 20 aspen and balsam poplar suckers plot (up to five from each 2m x 2m quadrat) were measured (height and basal diameter) and collected for later age determination in the laboratory.

Understory species

Density, cover and height of shrub species were estimated within each 2 x 2 m quadrat. Percent cover of herbaceous species (including ferns, bryophytes and lichens) were estimated within each of four 1 x 1 m subplots randomly located within each 2 x 2 m quadrat (**Figure 3**).

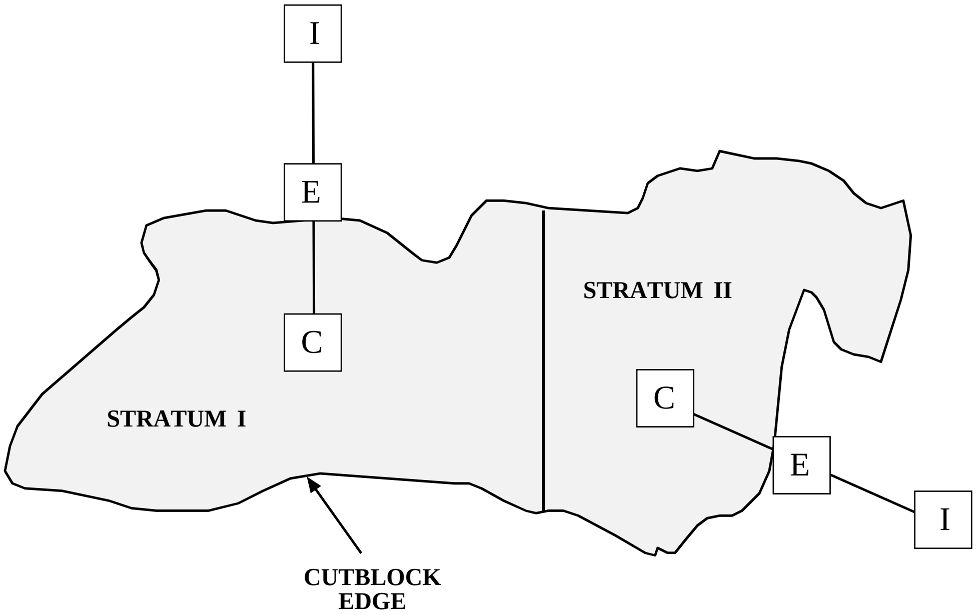


Figure 2. The stratified random sampling design used to enumerate vegetation and CWD across harvested aspen stands in cutblock (C), edge (E) and interior forest (I) treatments.

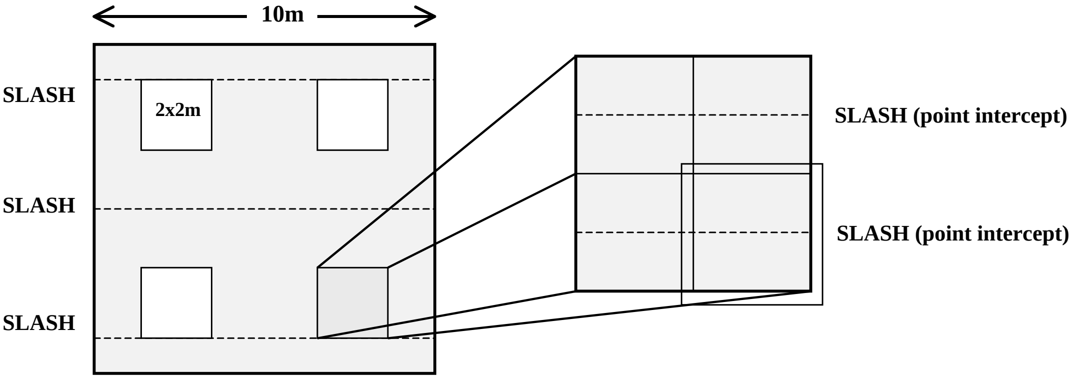


Figure 3. Sampling design for enumerating vegetation and CWD within 10m x 10m plots. Canopy cover and density were recorded within the entire 10m x 10m plot. Sucker and shrub density and cover were recorded within each 2m x 2m sub-unit (4 blocks per plot). Herb cover was estimated within one 1m x 1m quadrat of each 2m x 2m sub-unit (4 blocks per plot). Slash intercepts (all CWD) were recorded along three transects at the 10m x 10m plot level. Slash point intercepts were recorded along two transects within the 2m x 2m subunits.

Soils and landscape

The soil profile was described at each plot, and a soil sample (top 30 cm of mineral soil) collected. Soil analysis included determination of pH, conductivity, and soil particle size (percent sand, silt and clay). Slope and aspect were recorded at each plot (on site), and for the regional landscape as a whole (determined from topographic maps).

Coarse woody debris

Coarse woody debris was recorded using Van Wagner's line-intercept technique (Van Wagner 1968). In each 10m x 10m plot, the diameter of each intercepted piece of woody debris was recorded along three systematically-located transects 10 m in length (**Figure 3**). Each piece of CWD was also assigned to one of four decay classes: (1) Newly fallen, with no visible signs of decay, (2) More than 25% of the bark removed, but otherwise intact; (3) Most or all bark removed, and some degree of structural decay; (4) Considerable structural decay ("punky"). A second technique was employed to estimate relative abundance of CWD on a finer scale, by recording diameter and decay class at point intercepts every 20 cm along two 2 m transects within each 2m x 2m subplot.

RESULTS

Delineation and Description of Trembling Aspen Sub-Types

Analysis and results

<u>Vegetation</u>

All stands in this study were dominated by aspen (> 60 % cover), although regional associations with balsam poplar, paper birch and white spruce were relatively common. Despite similar canopy composition, the understory communities varied between sites and logging regions. Analysis of the herbaceous vegetation indicated little variation among stands; herbaceous species appear to be more sensitive to micro-site variation within stands. By contrast, the shrub species showed strong inter-stand variation. A cluster analysis based on the percent cover (log-transformed) of understory shrubs in the 'unharvested' plots was used to delineate trembling aspen sub-types within the study area. Shrub associations are diagnostic at the stand level, and correspond well with stand-scale edaphic and landscape conditions. Three aspen sub-types were delineated (**Table 2**):

1. **Dry (*n* = 13):** co-dominated by low shurbs (prickly rose (*Rosa acicularis* Lindl.), saskatoon (*Amelanchier alnifolia* Nutt.), common snowberry (*Symphoricarpos albus* (L.) Blake) and raspberry (*Rubus idaeus* L.)), and beaked hazelnut (*Corylus cornuta* Marsh).

2. **Fresh (*n* = 10):** dominated by beaked hazelnut, with < 10 % low shrub cover.

3. **Moist (*n* = 11):** co-dominated by mountain maple (*Acer spicatum* Lam.) and beaked hazel.

Characteristic herbs of each aspen sub-type are presented in **Table 3**. Although most herb species were found at similar abundance throughout the study area, some have been designated as indicator species for the aspen sub-types.

Table 2. Mean species percent cover of dominant understory shrubs within aspen dominated forest. The highlighted combinations are indicative of the stand types shown (dry, fresh, moist)

	all sites (n = 34)	**dry** (n = 13)	**fresh** (n = 10)	**moist** (n = 11)
Corylus cornuta	25.95	**15.53**	**40.96**	24.62
Acer spicatum	4.01	0.05	0.01	**12.34**
Rosa acicularis	5.20	**7.98**	2.90	4.01
Symphoricarpos albus	2.09	**3.07**	2.09	0.93
Amelanchier alnifolia	1.96	**3.23**	1.55	0.82
Rubus ideaus	1.29	**2.43**	0.40	0.75
Prunus virginiana	1.43	1.73	1.47	1.04

Table 3. Mean species percent cover of dominant understory herbs within aspen dominated forest. The highlighted combinations are indicative of the stand type shown (dry, fresh or moist)

	all sites (*n* = 34)	**dry** (*n* = 13)	**fresh** (*n* = 10)	**moist** (*n* = 11)
Aralia nudicaulis	10.73	13.25	13.36	5.35
Rubus pubescense	3.90	4.08	4.01	3.57
Fragaria virginiana	2.47	4.46	1.24	1.23
Mertensia paniculata	2.38	3.56	2.26	1.09
Oryzopsis asperifolia	2.20	3.15	2.19	1.10
Cornus canadensis	1.82	2.17	1.76	1.45
Viola canadensis	1.29	1.18	1.75	1.01
Maianthemum canadense	1.04	1.25	0.98	0.85
Aster ciliolatus	0.86	1.03	0.81	0.71
Pyrola asperifolia	0.80	1.00	0.84	0.55
Mitella nuda	0.75	0.19	0.35	**1.78**
Thalictrum venulosum	0.75	**1.78**	0.21	0.02
Petasites palmatus	0.65	0.99	0.43	0.45
Lathyrus venosus	0.52	0.59	0.33	0.60
Galium boreale	0.50	0.70	0.44	0.33
Disporum trachycarpum	0.46	0.37	0.64	0.39
Lathyrus ochrolucus	0.44	**0.76**	0.31	0.19
Solidago canadensis	0.39	**0.95**	0.03	0.05
Epilobium angustifolium	0.35	**0.85**	0.03	0.04
Galium triflorum	0.33	0.24	0.22	0.54
Elymus sp.	0.31	0.49	0.24	0.15
Sanicula marilandica	0.30	0.46	0.10	0.00
Vicia americana	0.29	**0.63**	0.09	0.07
Heracleum lanatum	0.29	**0.67**	0.10	0.00
Apocynum andrsaemifolium	0.28	0.33	0.41	0.10
Smilacina stellata	0.28	**0.60**	0.00	0.15
Calamagrostis canadensis	0.26	0.55	0.07	0.10
Carex sp.	0.25	0.12	0.09	0.57
Ozmorhiza depauperata	0.25	0.28	0.30	0.17
Matteuccia struthiopteris	0.24	0.00	0.00	**0.75**
Equisetum pretensis	0.20	0.14	0.06	0.39

Environment

The relationship between the three aspen sub-types and measured environmental variables were investigated using canonical correspondence analysis, CCA (**Figure 4**). The first CCA ordination axis reflects a general gradient of increasing moisture availability from left to right. Stands of the moist sub-type are positively associated with greater landscape slope, sandy-loam soils, a deeper LFH layer, and higher nutrient status (conductivity). These stands are typically found on north and east-facing slopes in the northern portion of the Forest Reserve, where groundwater flow results in a reliable supply of soil water and nutrients throughout the growing season. The fresh and dry sub-types show a greater degree of overlap in the CCA ordination space. The dry sub-type is positively associated with clay-loam soils and lower nutrient status (conductivity). These stands often occur in flat areas and on gentle south-facing slopes in the southern portion of the Forest Reserve.

Differences in vegetation and environment among the three aspen sub-types may result different recovery patterns following clear-cut harvesting. In recognition of this, subsequent analyses are undertaken for each sub-type.

Response of the Plant Community to Clearcut Harvesting

Methods

In order to effectively summarize responses of understory shrubs and herbaceous vegetation to clear-cut harvesting, plant species were classified into functional types. Shrub species were classified according to growth form (**Table 4)**: *tall shrubs* reach over 2m in height at maturity, while *low shrubs* are < 2m in height at maturity.

Herbaceous species were assigned to functional types based on autecological traits and lifeform characteristics (**Table 5**). *Bryophytes* (with a fern sub-group) includes all mosses, liverworts, ferns and fern allies. Herbaceous species included in the *ruderal* group are ‘weedy’ and shade-intolerant, and generally require a mineral seedbed for establishment. Most are annuals or biennials, and some are not native to North America. The *grassland* group includes perennial grasses and composites that typically occur in mixed-grass prairie and aspen parkland habitats. These species tend to be somewhat drought-tolerant and are moderately shade-intolerant. The *open forest* group includes species that are intolerant of deep shade. These species typically inhabit open-canopied forests that have relatively stable soil moisture conditions. Species within the *closed forest* group are very shade-tolerant and are able to persist beneath a closed forest canopy.

Floristic Composition

Analysis

The percent cover of each functional type was compared across treatments (cut, edge and interior plots) using two-way ANOVA (log-transformed data) to assess changes in floristic

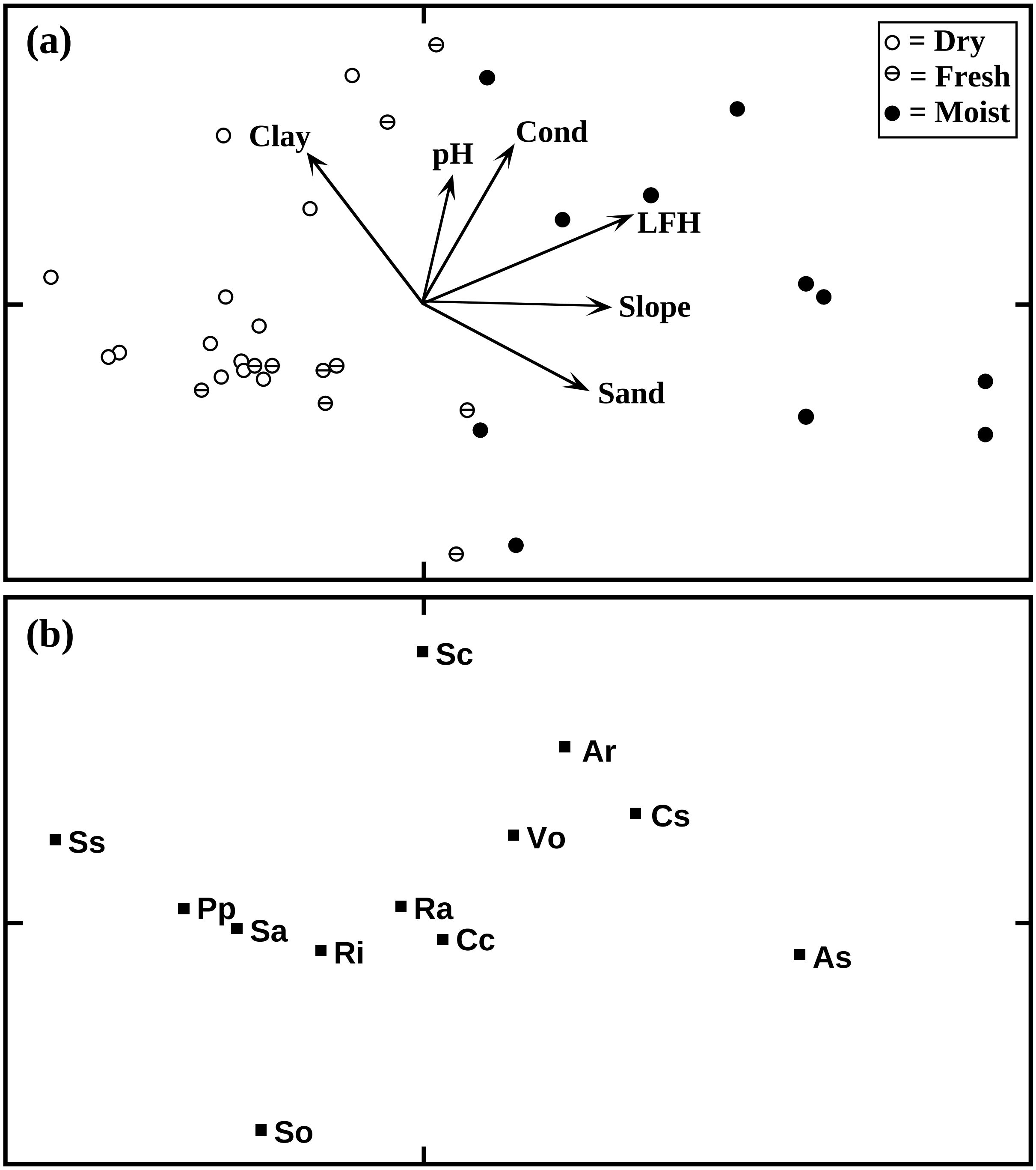


Figure 4. Canonical correspondence analysis (CCA) ordination of the 34 stands, based on shrub species composition constrained by six environmental variables. (a) CCA results, stands (coded by aspen sub-type) and environmental variables (vectors); (b) CCA results, biplot scores of selected shrub species. Codes: Ar = *Alnus rugosa* (speckled alder); As = *Acer spicatum* (mountain maple); Cc = *Corylus cornuta* (beaked hazelnut); Cs = *Cornus stolonifera* (red-osier dogwood); Pp = *Prunus penyslvanica* (pincherry); Ra = *Rosa acicularis* (wild rose); Ri = *Rubus idaeus* (raspberry); Sa = Symphoricarpos albus (snowberry) ; Sc = Sheperdia canadensis (buffalo berry); So = *Symphoricarpos occidentalis* (buckbrush); Ss = *Salix* spp. (willows); Vo = *Viburnum opulus* (cranberry).

composition. The three aspen sub-types were analyzed separately. Plots were blocked by site to account for stand-to-stand differences in floristics and environmental conditions. Responses are summarized as mean +/- standard error, and ANOVA statistics.

Table 4. Species composition of shrub functional groups (based upon structural morphology at maturity)

LOW SHRUBS	TALL SHRUBS
Rosa acicularis	*Corylus cornuta*
Rubus ideaus	*Acer spicatum*
Diervilla lonicera	*Prunus virginiana*
Viburnum edule	*Cornus stolonifera*
Ribes triste	*Prunus pensylv.*
Lonicera dioica	*Viburnum opulus*
Rosa woodsii	*Alnus rugosa*
Ribes oxycanthoides	*Salix spp.*
Ribes americanum	*Rhamnus alifolia*
Ribes hudsonianum	*Alnus crispa*
Symphoricarpos albus	*Amelanchier alnifolia*
Sheppherdia	
Symph.occ.	

Results

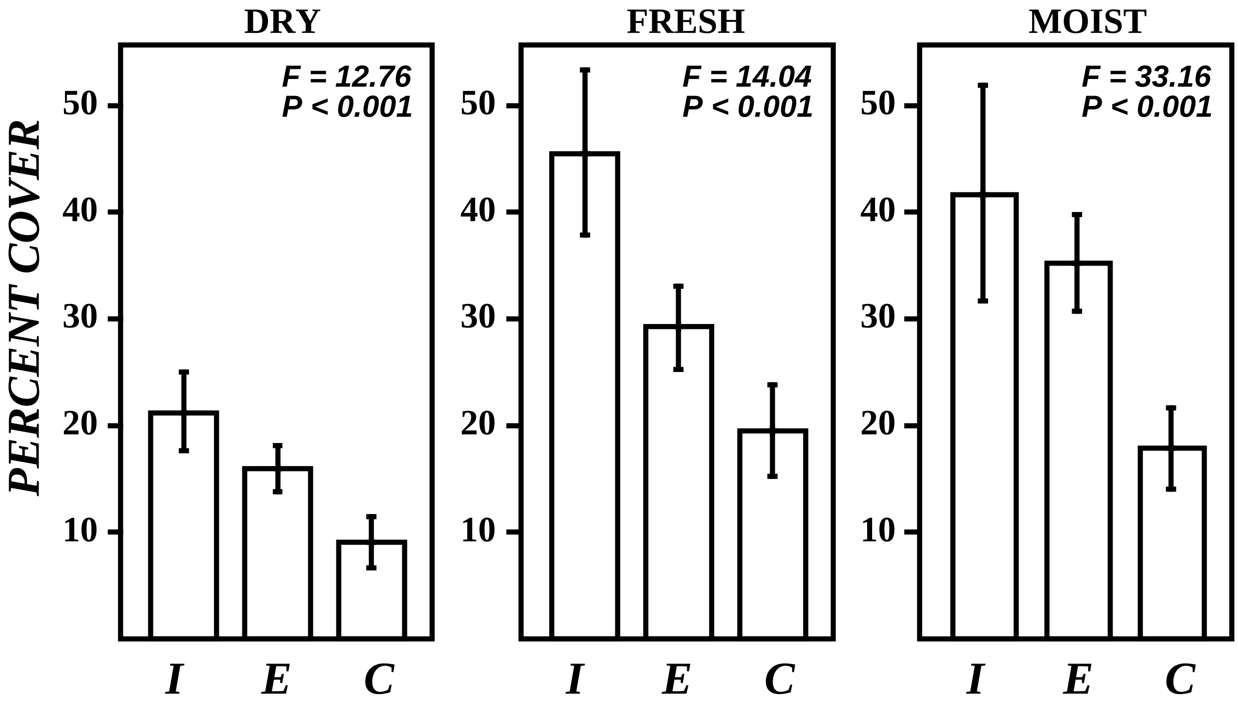
Trends in floristic composition across treatments are summarized in **Figure 5**. Overall responses are similar for the three sub-types. In all three sub-types, species in the tall shrub, bryophyte and closed forest groups decline in abundance following clearcut harvesting. Low shrub abundance decreases after harvest in dry sites, but increases after harvest on moist sites. Species of the open forest, grassland and ruderals groups increase in abundance following clear-cut harvesting.

Proportional cover values of plant functional types in the cut, edge and interior plots for each of the three sub-types are summarized in **Figure 6**. Similar trends are seen for each of the three sub-types. Tall shrub cover declines following harvesting, particularly in the moist sub-type. Low shrub cover is unchanged in the dry sub-type, but increases in the fresh and moist sub-types. The relative cover of closed forest herbs and bryophytes declines following clear-cut harvesting, whereas the relative cover of open forest herbs, grassland herbs and ruderals increases. Despite these changes in relative cover, the overall floristic composition of cutblocks is very similar to that of the interior forest.

Table 5. Species composition of herbaceous functional groups (based upon autecological traits and lifeform characteristics)

FERNS AND BRYOPHYTES	GRASSLAND HERBS	OPEN FOREST HERBS	CLOSED FOREST HERBS	RUDERALS
ferns/horsetails/clubmosses	*Achillea millefolium*	*Anemone canadensis*	*Actea rubra*	*Aquilegia canadensis*
Botrycium virginianum	*Achillea sibericum*	*Anemone cinquifolia*	*Aralia nudicaulis*	*Aster umbellatus*
Dryopteris austriaca	*Agastache foeniculum*	*Apocynum andrsaemifolium*	*Carex sp.*	*Astragalus sp.*
Gynocarpium dryopteris	*Agropyron sp.*	*Arctostephalus ursaursi*	*Corallorhiza maculata*	*Chenopodium album*
Matteuccia struthiopteris	*Agrostis sp.*	*Arenaria lateriflora*	*Cornus canadensis*	*Chenopodium capitatum*
Equisetum arvense	*Aster ciliolatus*	*Corydalis semipervirens*	*Disporum trachycarpum*	*Cirsium arvense*
Equisetum pretensis	*Aster laevis*	*Epilobium angustifolium*	*Habenaria viridis*	*Crepis tectorum*
Equisetum scirpoides	*Aster spatulata*	*Fragaria virginiana*	*Linnaea borealis*	*Epilobium glandulosum*
Equisetum sylvaticum	*Bromus sp.*	*Galium boreale*	*Mitella nuda*	*Galeopsis tetrahit*
Lycopodium annotinum	*Calamagrostis canadensis*	*Galium triflorum*	*Monensis uniflora*	*Geranium bicknellii*
Lycopodium dendrodeom	*Carex spp.*	*Heracleum lanatum*	*Monotropa uniflora*	*Lactuca tatarica*
bryophytes/lichens/liverworts	*Cinna latifolia*	*Hieracium umbellatum*	*Oryzopsis asperifolia*	*Lathyrus ochrolucus*
Brachythecium sp.	*Cirsium flodmanii*	*Lathyrus venosus*	*Pyrola asperifolia*	*Melilotus sp.*
Campylium sp.	*Dracocephalum parviflorum*	*Lilium philadelphicum*	*Pyrola eliptica*	*Plantago major*
Cladina sp.	*Elymus sp.*	*Maianthemum canadense*	*Pyrola secunda*	*Polygonum convolvulus*
Cladonia sp.	*Geum appelicum*	*Mertensia paniculata*	*Pyrola virens*	*Senecio eremophilus*
Dicranum sp.	*Halenia deflexa*	*Ozmorhiza depauperata*	*Smilacina stellata*	*Sonchus arvensis*
Euranchyum sp.	*Linaria vulgaris*	*Petasites palmatus*	*Trientalis borealis*	*Stellaria media*
Haplocladium sp.	*Luzula pilosa*	*Petasites sagittatus*	*Trillium cernum*	*Taraxacum officinale*
Marchantia sp.	*Poa sp.*	*Petasites vitifolius*		*Trifolium sp.*
Mnium sp.	*Schizachne sp.*	*Rubus pubescense*		*Urtica dioica*
Oncophorus wahllenbergii	*Solidago bicolor*	*Sanicula marilandica*		*Vicia americana*
Peltigera sp.	*Solidago canadensis*	*Stellaria longifolia*		
Pleurosium shreberi	*Solidago spathulata*	*Thalictrum dasycarpum*		
Polytricum sp.		*Thalictrum venulosum*		
Pyasiella sp.		*Viola canadensis*		

(a) Tall Shrubs



(b) Low Shrubs

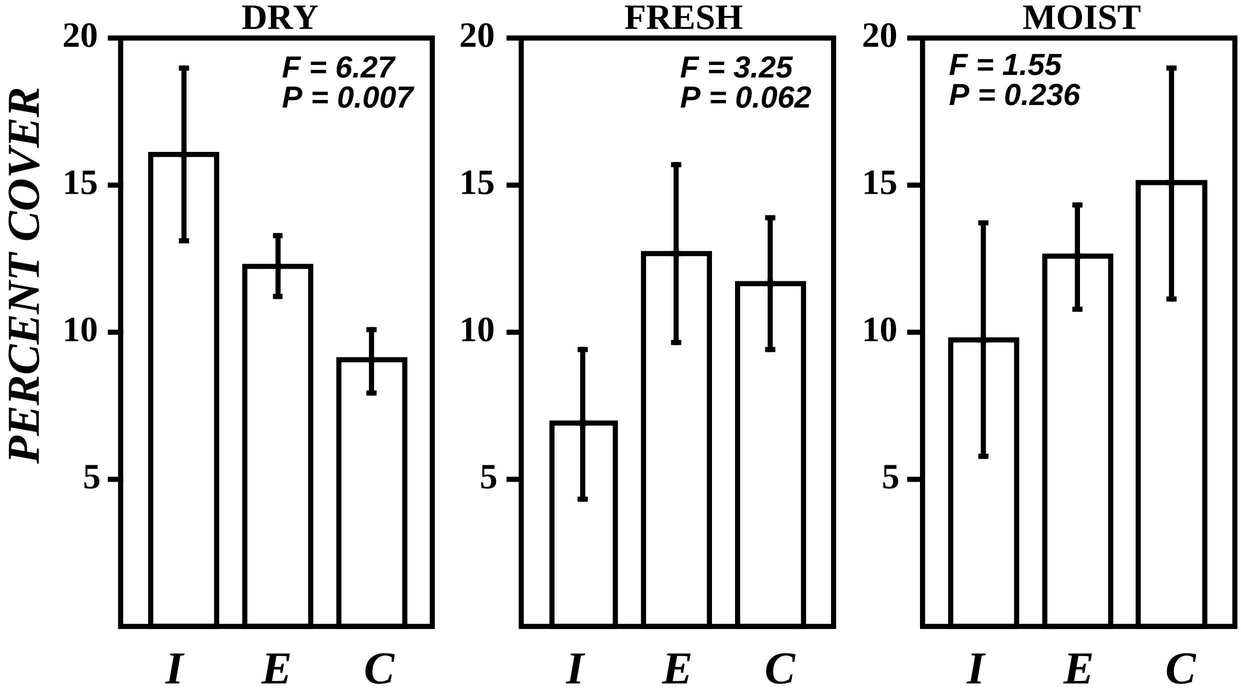
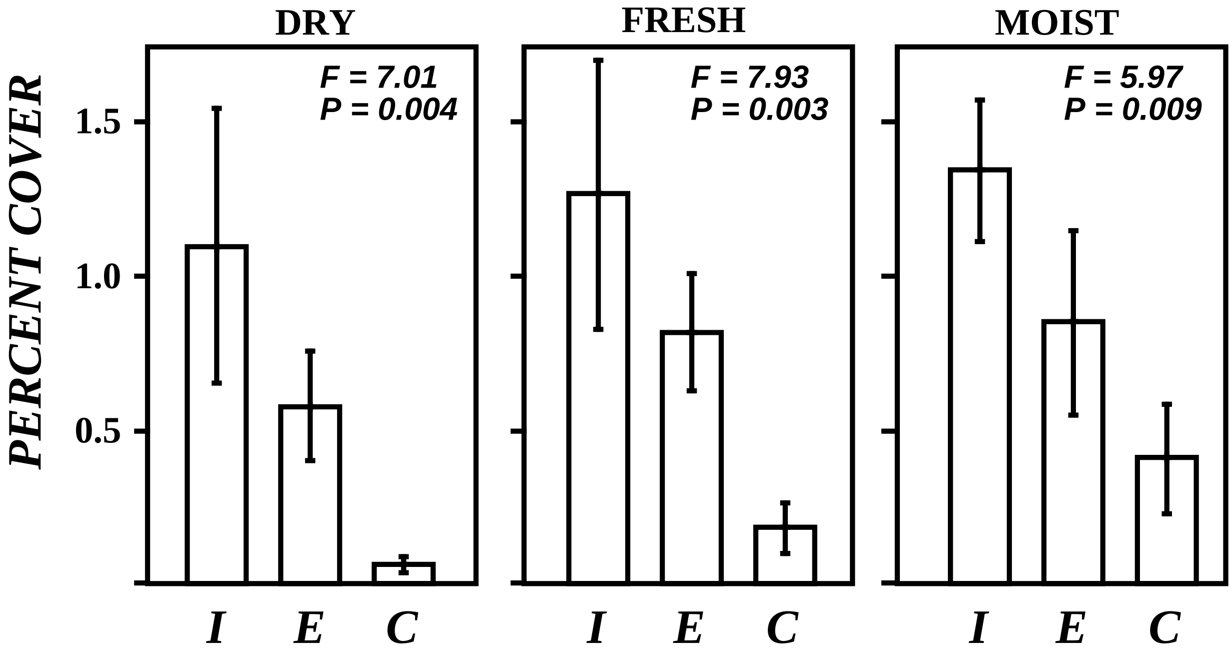


Figure 5. Comparisons of understory vegetation cover for (a) tall shrubs; (b) low shrubs; (c) bryophytes; (d) closed forest species; (e) open forest species; (f) grassland species; (g) ruderal species across harvest treatment (I = interior, E = edge and C = cut forest), for each of the three aspen sub-types (dry, fresh and moist). Analysis of variance results (F and associated P-values) are also given. Refer to Tables 4 and 5 for the species composition of functional groups.

(c) Bryophytes



(d) Closed Forest Species

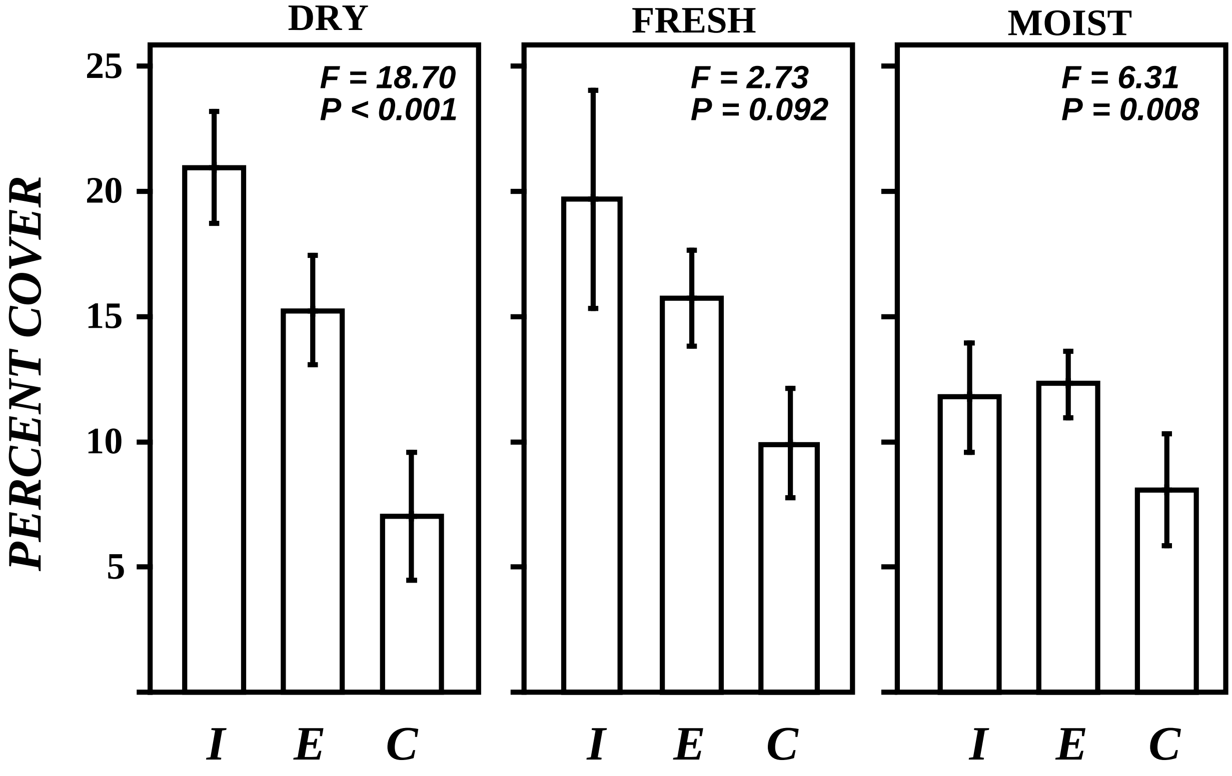
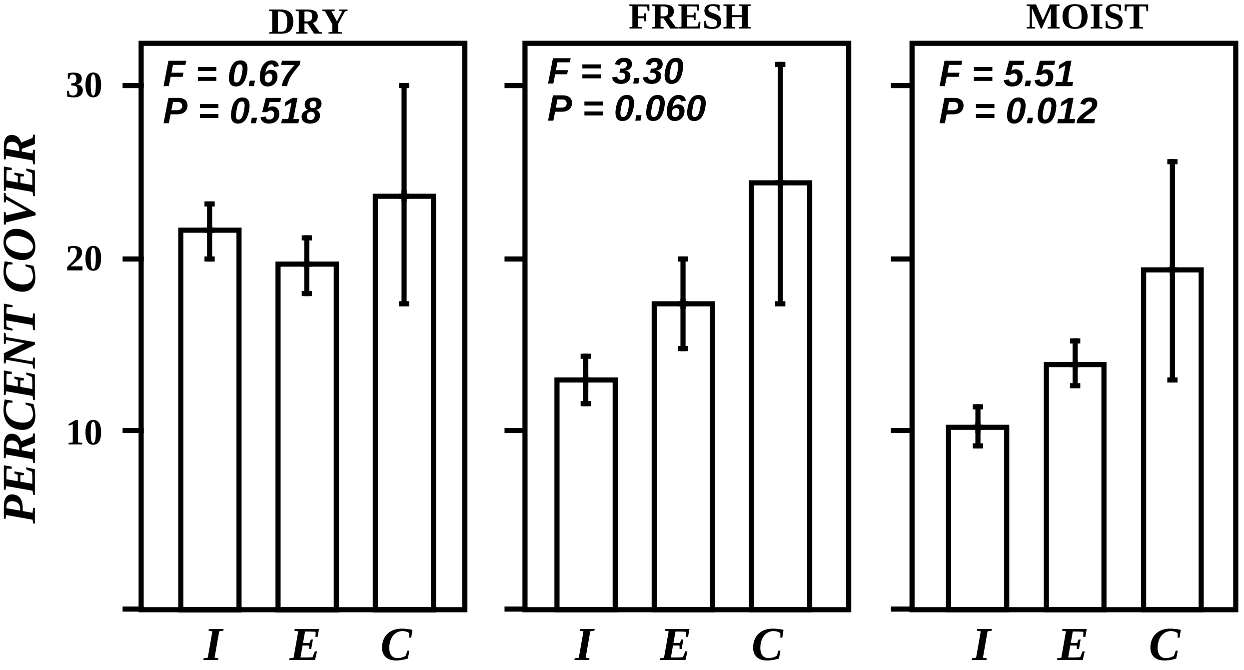
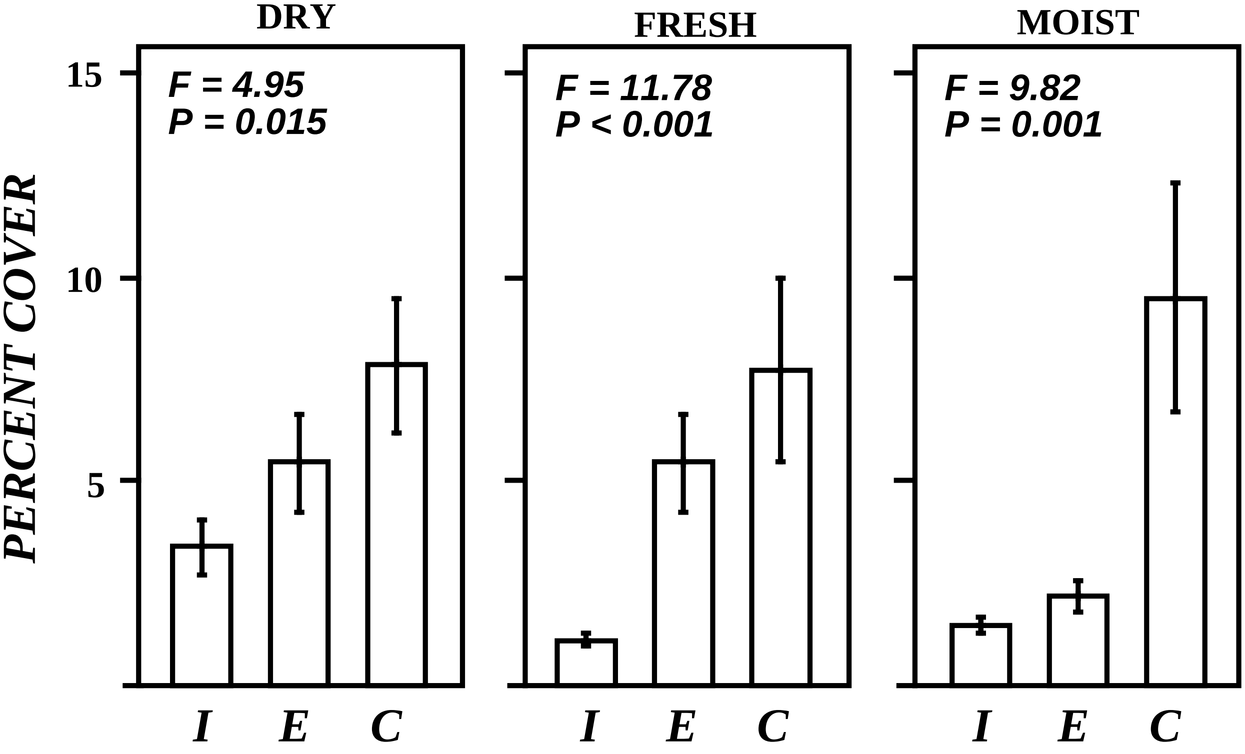


Figure 5 (continued).

(e) Open Forest Species



(f) Grassland Species



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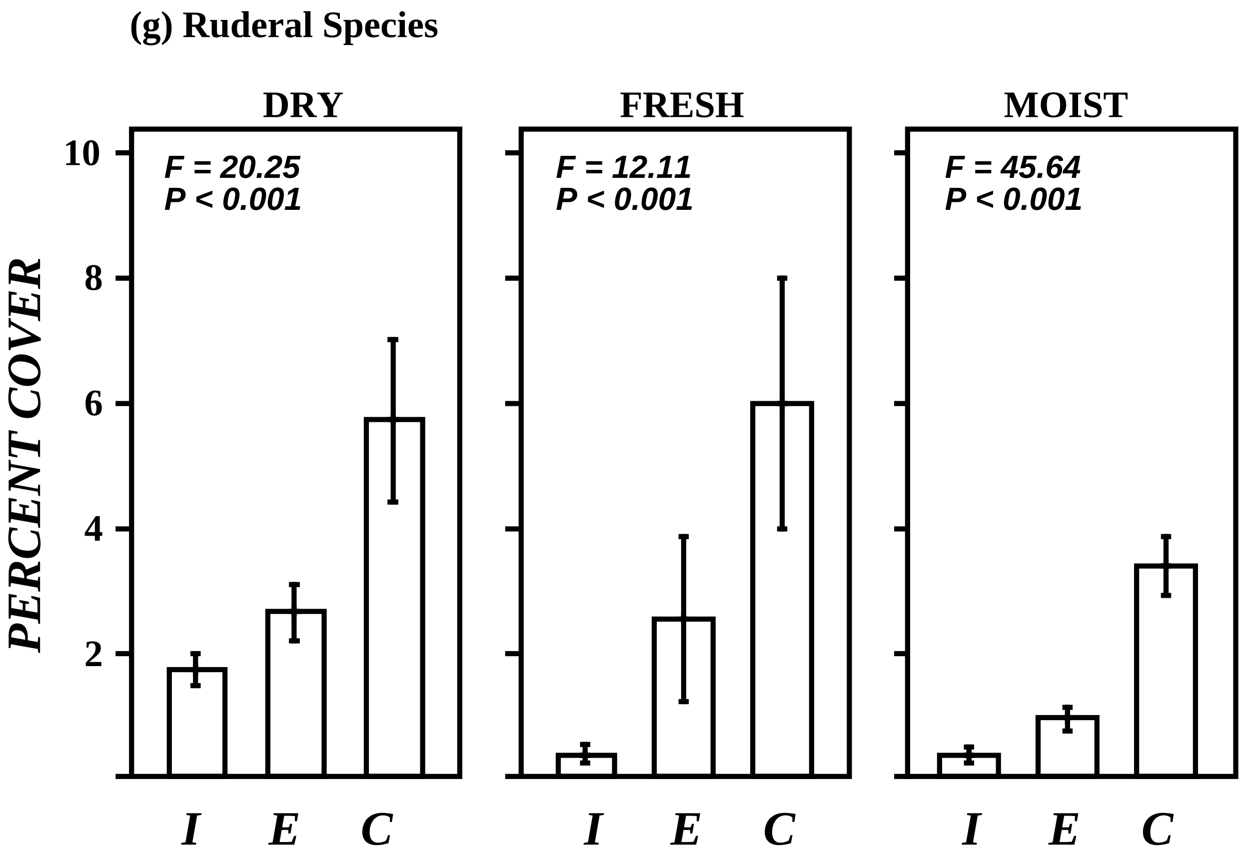

(g) Ruderal Species

Figure 5 (continued).

Floristic Diversity

Analysis

Effective species richness (based on the Gini-Simpson coefficient) was calculated using log transformed cover values. Separate analyses were performed for the shrub and herbaceous species in each of the three aspen sub-types. Changes in floristic diversity in response to harvest treatment were assessed using two-way ANOVA. Responses are summarized as mean +/- standard error, and ANOVA statistics.

Results

Effective species richness of shrub and herb communities were not significantly different among the harvest treatments in the dry and moist aspen sub-types (**Figure 7)**. For the fresh sub-type, effective species richness of both the herbs and shrubs increased significantly following clear-cut harvesting.

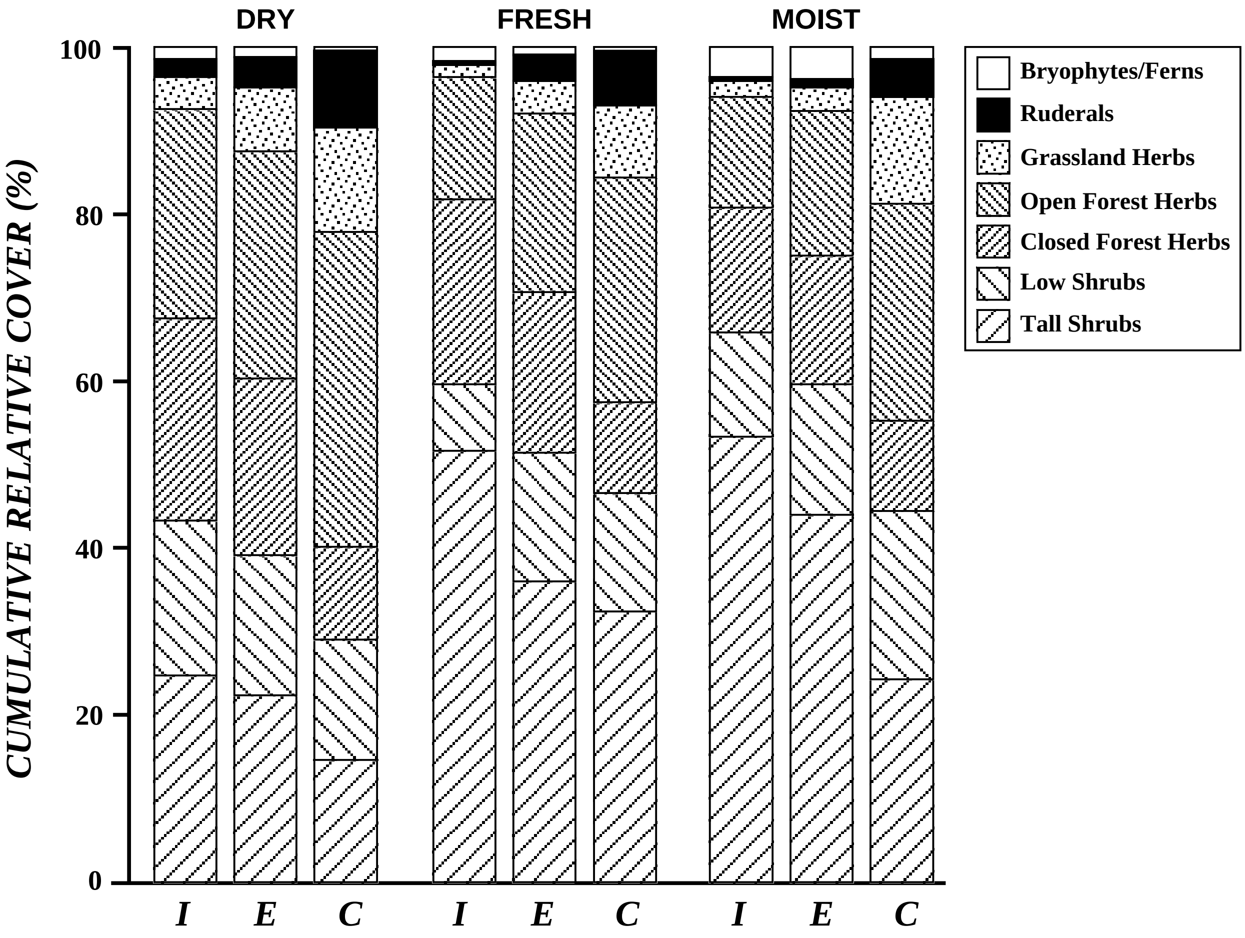


Figure 6. Cumulative relative cover of species functional groups across harvest treatments (I = interior, E = edge, C = cut forest) for each of the three aspen sub-types (dry, fresh and moist). Refer to Tables 4 and 5 for species composition functional groups.

Volume and Size (Diameter) Distribution of Coarse Woody Debris

Methods

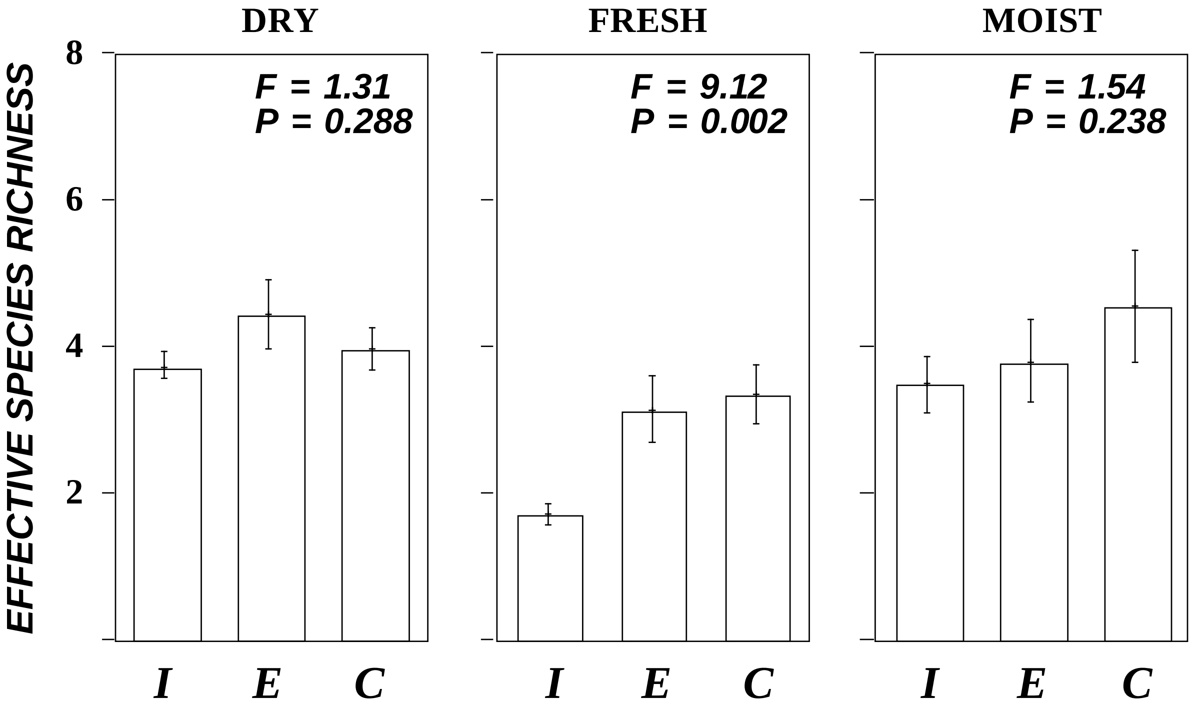
Three 10 m slash transects were combined for each plot, for a total of 30 m of sampled transect per plot. For each plot, the diameter values of all intercepted pieces of coarse woody debris were converted to CWD volume estimates using the formula derived by Van Wagner (1968).

CWD Volume

Analysis and Results

CWD volumes (log-transformed data) were compared among the three harvest years, and between harvest seasons (winter vs. summer), for each of the cut, edge and interior plots using ANOVA. No significant differences were found among harvest years (cut: F = 1.81, P = 0.166; edge: F = 0.05, P = 0.986; interior, F = 2.16, P = 0.113) or between harvest seasons (cut: F = 0.075, P = 0.785; edge: F = 0.507, P = 0.482; interior, F = 0.022, P = 0.884). Data from all 34

(a) Shrubs



(b) Herbs

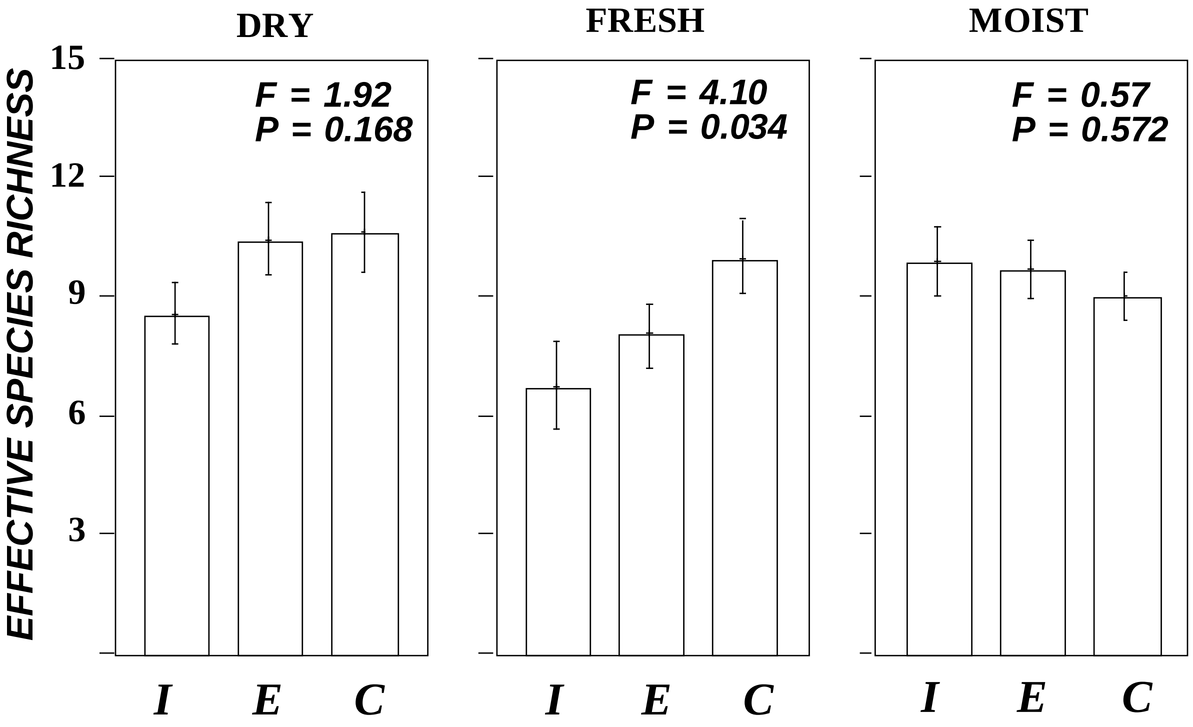


Figure 7. Comparison of effective species richness (based on the Gini-Simpson coefficient) for (a) shrubs and (b) herbs across harvest treatment (I = interior, E = edge and C = cut forest), for each of the three aspen sub-types (dry, fresh and moist). Analysis of variance results (F and associated P-values) are also given.

stands were therefore pooled in order to compare CWD volumes among the cut, edge and interior treatments using two-way ANOVA (blocked by site).

CWD volumes were significantly different among the cut, edge and interior treatments (F = 11.59, P < 0.001). This was attributable to significantly higher slash loadings in the cut plots (mean = 185.66 m^3/ha), compared to edge (mean = 127.81 m3/ha) and interior plots (mean = 128.86 m^3/ha). Slash loadings in the cut plots were not significantly different among the three aspen sub-types (F = 1.812, P = 0.180), but significant differences were seen for the edge (F = 5.931, P = 0.007) and interior plots (F = 9.918, P < 0.001). CWD volumes of edge and interior plots were highest in the moist sub-type.

CWD Size Class Distribution

Analysis and results

Frequency distributions of CWD diameter classes (log scale) for the cut, edge and interior plots across all 34 sites are shown in **Figure 8**. In all cases, there is a monotonic decline in frequency with increasing CWD diameter. Log-log plots of the frequency - size class distribution relationships are linear (**Figure 9**), indicating a power-law (or hyperbolic law) relationship. The log-log slope for the cut treatment is significantly steeper than the interior treatment slope (t = 4.29, P < 0.001), indicating that the size distributions of CWD differ between cut and interior treatments. A steeper slope for the cut treatment indicates a higher relative proportion of CWD in the smaller diameter classes.

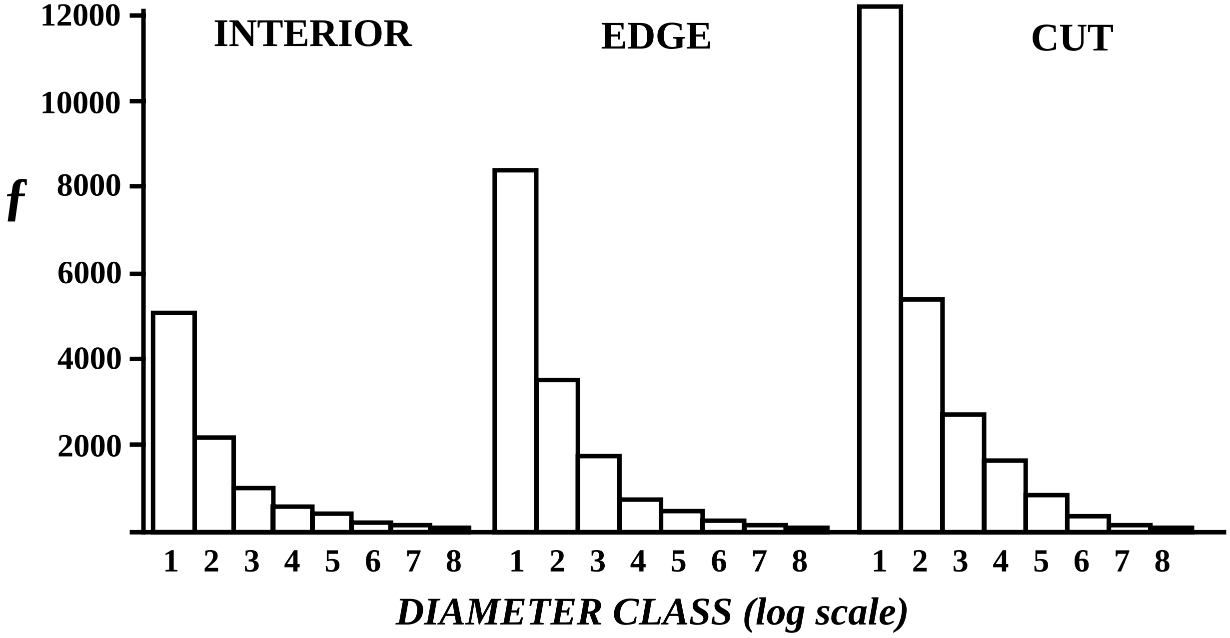


Figure 8. Frequency distributions (semi-log plots) of coarse woody debris (CWD) size classes in interior, edge and tree-length harvested aspen stands.

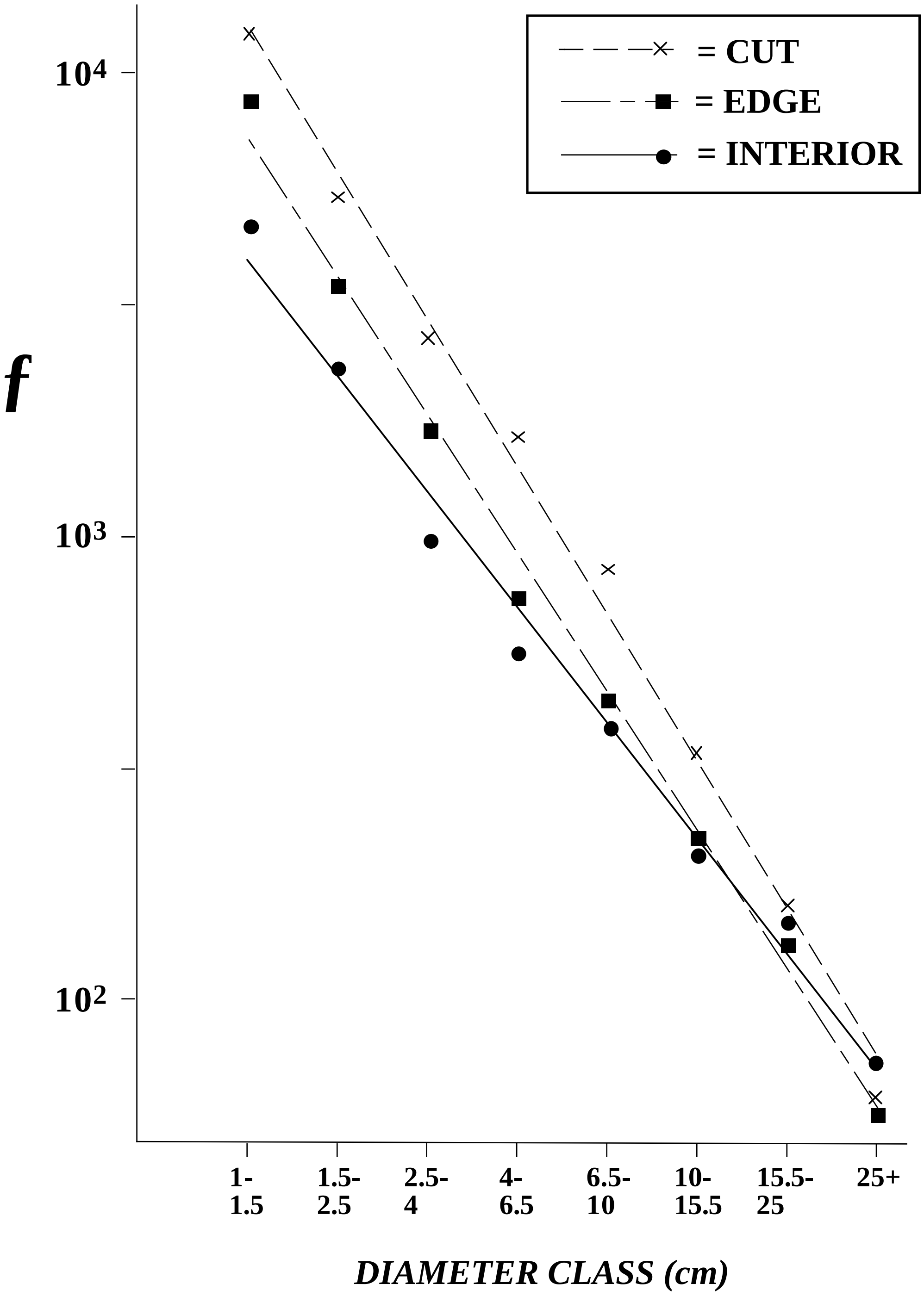


Figure 9. Hyperbolic (power-law) relationship between frequency and diameter class of coarse woody bebris (CWD) in interior, edge and tree-length harvested aspen stands.

Variation in Aspen Suckering and Contributing Factors

Analysis and Results

Factors Determining Aspen Density

Multiple regression models were used to investigate the effects of (a) age of clearcut; (b) stand density prior to harvest; (c) slash loadings; (d) shrub cover; (e) soil variables (pH, conductivity, particle size, LFH depth) of aspen suckering. Of all the variables tested, only the clearcut age (time since harvest) contributed significantly to explaining variation in suckering density (F = 5.942, P = 0.003).

Differences in suckering density between harvest seasons (summer vs. winter) and among the three aspen sub-types were assessed using analysis of covariance (ANCOVA). In both analyses, cutblock age was used as the covariate to remove the effects of differences in timing of harvest. There were no significant differences in sucker density between summer and winter harvests (F = 0.554, P = 0.44), or among the three sub-types (F = 1.401, P = 0.29).

Aspen Density and Growth Over Time

The density of aspen suckers declines significantly over time (F = 5.94, P = 0.003). This indicates that self-thinning is occurring, reducing mean density from 8.1 stems/m^2 in the first year following clear-cut harvesting to 3.4 stems/m^2 by the fourth year (Figure 10). Variation in sucker density is greater in the first year, suggesting that self-thinning is greatest in stands with initially high densities.

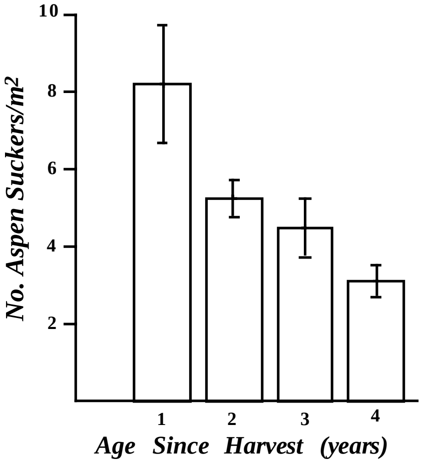


Figure 10. Temporal changes in the density of trembling aspen suckers in recently tree-length harvested aspen stands. Changes are attributable to natural self-thinning.

Mean aspen sucker height as a function of cutblock age is shown in **Figure 11**. Mean sucker height is approximately 70 cm in the first year following clear-cut harvesting. In the next three years, suckers increase in height by approximately 25-30 cm per year.

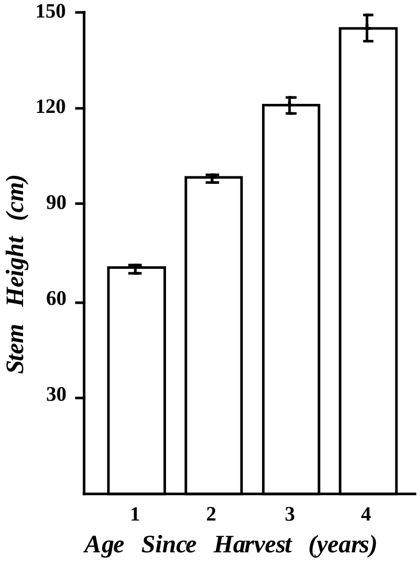


Figure 11. Height growth of aspen suckers in recently tree-length harvested aspen stands.

Density of Aspen and Poplar in Cut, Edge and Interior

Aspen and balsam poplar suckering densities are highest in the cut plots, much lower at in the edge plots, and very uncommon in the interior forest (**Figure 12**). Mean aspen suckering density in cut plots is 6.29 stems/m^2, compared to only 0.51 stems/m^2 for balsam poplar.

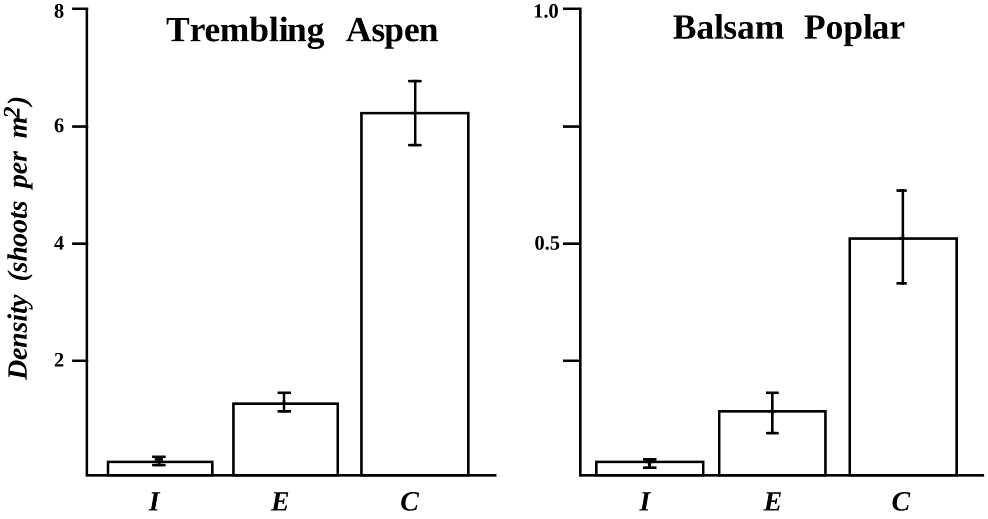


Figure 12. Mean (± S.E.) suckering density of trembling aspen and balsam poplar in interior (I), edge (E) and cut (C) stands. Note different scales on the two graphs.

DISCUSSION

Floristic Variation of Stand types

The recovery rate and species composition of forest stands following natural or human disturbance are largely dependent upon the flora present prior to the disturbance (Archibold 1978). Pre-fire shrub cover and micro-topography have the greatest influence on species richness in regenerating burn sites (Smith and James 1977). Establishing ecological variation prior to disturbance is therefore necessary for predicting and interpreting vegetation development following a disturbance. The three aspen sub-types defined in this study represent a continuum of soil moisture conditions from dry to moist. Within aspen stands, differences in soil moisture conditions are most strongly reflected in the dominant shrubs present within a stand.

Dry aspen sub-type

The trembling aspen “ring” that surrounds Duck Mountain Provincial Park borders trembling aspen ‘parkland’ to the northwest and south. The ‘dry’ aspen sub-type occurs within this grassland - aspen forest ecotone, particularly on gentle south-facing exposed slopes adjacent to agricultural land. Repeated settlement fires from adjacent farmland to the south swept into the Provincial Forest between 1910 and 1930 (Hamel and Kenkel 2001). As a result, most stands belonging to the ‘dry’ sub-type are relatively young (approximately 80 years old). The characteristic vegetation consists of relatively shade-intolerant generalist species. The shrub community is a parkland-like understory of “scrubby” species, with no individual species dominating. Typical herbs associated with dry sites, include fireweed (*Epilobium angustifolium* L.), golden rod (*Solidago canadensis* L.), wild vetch (*Vicia americana* Muhl.), veiny meadow rue (*Thalictrum venulosum* Trel.), strawberry (*Fragaria virginiana* Duchesne), tall bluebells (*Mertensia paniculata* (Ait.) Gray). The absence of a tall shrub subcanopy results in relatively high cover and diversity of herbaceous and low shrub species. Ruderal and generalist species (such as wild vetch, and creamy peavine, *Lathyrus ochroleucus* Hook.) are also characteristic of the ‘dry’ aspen sub-type.

Species composition of the dry sub-type is indicative of seasonal water limitation. Rose, saskatoon, northern gooseberry (*Ribes oxyacanthoides* L.), golden rod, asters (*Aster* spp.) are typical aspen parkland species associated with drier grassland habitats. Most stands in the dry sub-type have a southern exposure and occur on lands grading from the Manitoba Escarpment into the Valley River and Shell River valleys. Southern exposures result in increased evapotranspiration in late spring and early summer, resulting in reduced moisture availability later in the growing season.

Stands of the dry sub-type are characterized by soils of high clay content, resulting in the accumulation of spring meltwater in localized depressions. These local areas of impeded drainage favour flood-tolerant species such as balsam poplar (Zasada and Phipps 1990). Stands of trembling aspen with localized higher density regions of balsam poplar are relatively common in the dry aspen sub-type in the Duck Mountains. Seasonally saturated clay soils also restrict the ability of beaked hazelnut to form a dominant sub-canopy in these stands (Johnson et al. 1995).

Fresh aspen sub-type

The major distinction between dry and fresh aspen sub-types is the abundance of beaked hazelnut in the latter. Average hazelnut cover exceeds 40% in fresh stands, and many stands are characterized by a dense tall shrub sub-canopy dominated by hazelnut. Beaked hazelnut is the most common upland boreal forest shrub in central North America, often forming impenetrable thickets that reduce understory plant diversity and inhibit advance regeneration (Buckman 1964; Kurmis and Sucoff 1989). The combination of better soil drainage (increased sand content) and greater slope results in improved drainage and increased nutrient availability, favouring the establishment and persistence of tall beaked hazel thickets (Meuller-Dumbois 1964; Walshe 1980; Johnson et al 1995). Fresh sites are generally located at greater distances from agricultural land, and so were not subjected to the settlement fires that burned into the Forest Reserve between 1910 and 1930. Most stands are therefore greater than 100 years old, and have a well-developed aspen canopy and dense tall shrub canopy that together reduce or eliminate shade-intolerant species in the understory. Low shrubs are restricted to < 10% cover under the dense hazel sub-canopy.

Moist aspen sub-type

The moist aspen sub-type is the most distinctive vegetation assemblage of the three sub-types. It is characterized by a combination of ‘true’ boreal and sub-boreal plant species. Mountain maple is a conspicuous component of the tall shrub canopy, and is often codominant with beaked hazel. Very little light reaches the forest floor of these stands, resulting in a shade-tolerant understory community. Typical understory species include bishop’s cap (*Mitella nuda* L), and clubmosses (*Lycopodium* spp.). The ostrich fern (*Matteuccia struthiopteris* (L) Todaro var. *pensylvanica* (Wild.) Morton.), a species indicative of high soil moisture and nutrient status (Meuller-Dumbois 1964), is characteristic of the moist aspen sub-type.

Mountain maple is common on well-drained soils along streams and on moist hillsides (Johnson et al. 1995). Such conditions are most commonly encountered in the northeast region of the Duck Mountain Forest Reserve. Rich, moist soils are required for the establishment and persistence of a thick mountain maple sub-canopy (Meuller-Dumbois 1964). Sandy soil on a sloping gradient results in good soil aeration and drainage, resulting in co-dominance of beaked hazel and mountain maple (Walsh 1980; Johnson et al. 1995).

The northern aspect of stands of the moist aspen sub-type protects them from excessive evapotranspiration in late spring and early summer. Furthermore, groundwater drainage through the sandy soils from the Manitoba Escarpment results in a reliable supply of water and nutrients throughout the growing season. This is reflected in the higher soil conductivity and organic matter accumulation characteristic of these stands. Paper birch often co-occurs with trembling aspen on well-drained moist slopes. Balsam poplar is restricted to local depressions and surrounding wetlands. This sub-type is similar to the ‘very moist’ ecological association described by Meuller-Dumbois (1964), which is characterized by trembling aspen, birch and balsam poplar with isolated white spruce (*Picea glauca* (Moench) Voss) and green ash (*Fraxinus pennsylvanica* Marsh. Var. austini Fern.) in the canopy, with mountain maple and beaked hazelnut as the dominant shrubs.

Changes in Plant Communities After Harvest

Post-disturbance vegetation is strongly tied to that present prior to disturbance, and is not necessarily associated with type of disturbance (Nobel et al. 1977). Clear-cutting is often characterized as a successional ‘retrogression’, reverting sites to an early successional stage (Yarie 1993). Research in sustainable forestry has in recent years focussed on developing harvesting methods that emulate natural disturbance, so as to maintain the biodiversity and long-term productivity normally associated with post-fire stands (Bergeron and Harvey 1997). If properly implemented, clearcutting effectively mimics natural disturbance processes and results in the natural regeneration of fire-adapted species (Yarie 1993).

Adaptations to fire enable many boreal shrub and herb species to “endure” and recover quickly after disturbance (Nguyen-Xuan et al. 2000). Clonal shrubs and trees regenerate from rhizomes, basal sprouts, layering and root suckering soon after disturbance (Rowe 1983; Zasada et al. 1992). Perennials generally resprout from root systems, and respond readily to changes in site conditions (Bartos and Mueggler 1982). Damage incurred by harvesting is not generally sufficient to kill or prevent regeneration of pre-disturbance vegetation, with the result that dominant shrub assemblages and site affinities persist after harvest (Harvey et al 1995). Rapid regeneration of existing species from buried propagules also limits the invasion of weedy ruderal species.

Floristic composition

The initial period of establishment after disturbance determines the species composition and successional pathways of fire-origin stands (DeGrandpre et al. 1993), and similar influences are expected in post-logged forest stands. In post-logged trembling aspen stands, vegetation changes generally reflect alterations in species abundance and dominance rather than composition change (Bartos and Mueggler 1982). As in post-fire regeneration, differences in competitive ability and resource acquisition are manifested as rapid, short-term changes in the abundance and growth characteristics of dominant species, not major changes in composition (Shafi and Yarranton 1973a, b; Smith and James 1978).

Environmental differences in the understory of trembling aspen forests in Duck Mountain following harvesting are a result of: (a) changes in light conditions following canopy removal; (b) soil disturbance and mineral soil exposure; (c) mechanical removal of upright woody shrubs. Removal of the tree canopy and woody shrubs increases the amount of light reaching the forest floor, resulting in decreased abundance of bryophytes, ferns, and shade-tolerant herbaceous species following harvest. Physiological stress in response to environmental modification, together with increased competition from shade intolerant ruderal species, results in a decline of closed forest species after harvest (Harvey et al. 1995).

Rapid post-logging suckering of tall shrubs and trembling aspen partially ameliorates the exposure-related effects of harvesting on fresh and moist sites in the Duck Mountains. Water availability in moist sites may also mitigate the effects of exposure after harvest. For example, ostrich fern was observed growing on one, two and three year old cutblocks by late August. Even shade-loving species such as nodding trillium (*Trillium cernuum* L.), bishop's cap, bunchberry (*Cornus canadensis* L.), western Canada violet (*Viola canadensis* Greene) and wintergreens (*Pyrola* spp.) persist following harvest. Harvey et al (1995) found similar persistence of deep shade species following harvesting of mixed-wood stands, with a few shade-adapted species actually increasing in cover (e.g. wild sarsaparilla, *Aralia nudicaulis* L.). Slash deposition and rapid regeneration of other species provide local 'refugia' for shade-tolerant species on cutblocks within the first year following harvesting. Persistence of interior 'evader' species after harvest in black spruce (*Picea mariana* (Mill.) BSP) stands was attributed to maintenance of forest duff after harvest (Nguyen-Xuan et al. 2000).

Most understory plants adapted to fire disturbance are termed "facultative stress tolerators", defined as species that resume growth immediately following favorable changes in microhabitat conditions (Brumelis and Carleton 1989). Many of the herbaceous species encountered in a post-logged boreal understory can persist in deep shade, but expand rapidly and flower profusely when the canopy is removed (Brumelis and Carleton 1989). In our study, grassland, open forest and ruderal species were found to increase immediately after harvest in all stand types. Marsh reed grass (*Calamagrostis canadensis* (Michx.) Nutt.), fringed aster (*Aster ciliolatus* Lindl.), goldenrod, *Elymus* spp., *Bromus* spp., wild vetch and perennial sow thistle (*Sonchus arvensis* L.), are examples of post-logging increasers. The relatively high proportion of shade-intolerant species in harvested stands of the dry aspen sub-type reflects the greater proportion of shade intolerant species (including ruderals) that were present prior to harvesting.

Disturbance of the mineral soil during harvest favours the invasion or expansion of ruderal species (Harvey et al.1995; Nguyen-Xuan et al. 2000). The increased abundance and diversity of annuals and short-lived perennials reflects an initial "adjustment period" after disturbance (Bartos and Mueggler 1982). However, in our study only six (of 22) ruderal species were unique to harvested sites in the Duck Mountains, and ruderals were always a very minor floristic component. Furthermore, we found no evidence of a delay period of increased ruderal invasion after the first year following harvest. Restricted ruderal invasion has been attributed to rapid canopy closure within two years following harvest and rapid stabilization of species composition after clear-cut logging (Bartos and Mueggler 1982). Retention of coarse woody debris and winter harvesting also minimize mineral soil exposure, limiting the invasion of ruderal species.

Floristic structure

Other changes in post-harvest vegetation are attributable to structural removal of the shrub layer by mechanical harvesting equipment. Most of the shrubs characteristic of aspen stands in the Duck Mountains undergo rapid vegetative regeneration from underground parts or layers following disturbance (Buckman 1964; Vincent 1965; Archibold 1979). In our study, tall shrub cover was reduced by 20-30% following harvest. The damage incurred by tall shrubs (primarily beaked hazelnut and mountain maple) during harvesting results in a shift from a tall laterally branched growth form, to single vertical stems. This change in structure reduces the shading effect of the shrub layer and reduces shrub dominance. Physical damage to tall shrubs in fresh and moist aspen sub-types results in increased cover of low shrubs, suggesting that low shrubs are “released” from competition with beaked hazel and mountain maple.

Research pertaining to understory response following the removal of a shrub sub-canopy in harvested trembling aspen stands is scarce. Past studies assessing the effects of harvesting on understory vegetation were undertaken in areas with a mixed hardwood-softwood canopy (Brumelis and Carleton 1988; Harvey and Bergeron 1989; Lavertu et al. 1994; Harvey et al. 1995). In most of these stands, insufficient light reaches the forest floor for the development of a dense shrub sub-canopy (Lieffers et al. 1999). In Minnesota, dense beaked hazel thickets may reduce understory diversity and inhibit advance regeneration (Buckman 1964).

Floristic diversity

We found that effective species richness of understory vegetation was not affected by harvesting in stands belonging to the dry and moist aspen sub-types. Slight changes in species composition between cut and uncut sites are expected in the year following cutting, as invading species combine with pre-existing understory (Bartos and Mueggler 1982; Harvey et al.1995). In our study, only stands of the fresh sub-type increased in effective richness following harvesting. In these stands, removal of the dense beaked hazelnut shrub canopy results in release of grassland, open forest herbs and low shrub vegetation, increasing equitability. Other studies have found that changes in effective richness often reflect increased equitability after harvest rather than a change in species richness (Bartos and Mueggler 1982). Increases in post-harvest species diversity has also been attributed to soil disturbance and increased cover-abundance of ruderal species (Bartos and Mueggler 1982; Harvey et al.1995).

Coarse Woody Debris (CWD)

CWD volume

CWD occurs naturally at relatively high volumes in mature trembling aspen forest stands in the Duck Mountains. Aspen mortality from self-thinning results in continuous incorporation of CWD to the forest floor in developing and mature stands (Lee 1998). In stands over 90 years in age, standing and fallen snag density increase considerably as tree senescence occurs (Lee 1998). In our study, stands belong to the moist aspen sub-type had the highest background levels of CWD. This likely reflects the greater mean age of these stands (approximately 110 years, compared to 70 and 90 years for dry and fresh sub-types respectively).

We found considerable spatial variation in background CWD volumes in the mature forest stands sampled. Variation in the abundance of coarse woody affects nutrient cycling and availability in stands. Spatial variation in CWD volume was much less in harvested sites, suggesting that harvesting equalizes CWD loadings within and among stands.

Most studies dealing with the effects of logging slash have been undertaken in softwood stands (e.g. Kimmins 1977; Rosen and Lundmark-Thelin 1987; Bekunda et al. 1990; McInnis and Roberts 1994; Olsson and Staaf 1995; Olsson et al.1996). In boreal trembling aspen stands, the environmental implications and benefits of slash retention appear to be similar to those of softwood stands (Aber et al. 1978; Bella 1986). Slash is retained on cutblocks to minimize the amount of woody material (and associated nutrient and carbon loads) removed during harvesting. Decay of coarse woody debris increases soil organic matter content, thereby increasing water retention and nutrient loadings (Kimmins 1977; Olsson et al. 1996). In hardwood stands, it has been estimated that tree-length harvested sites will have up to 60% greater forest floor biomass than whole-tree harvested sites after 15 years following harvesting (Aber et al. 1978).

CWD from tree-length harvest reduces the typical “nutrient flush” that follows harvesting (Aber et al. 1978). The ability of regenerating vegetation to utilize all available nitrogen after harvesting is limited in both hardwood and softwood stands, resulting in some losses from the system through leaching and run-off (Aber et al. 1978; Rosen and Lundmark-Thelin 1987). Slash has a mulching effect on soils by lowering the C/N ratio of the humus layer, which affects the quality of organic matter in the soil (Olsson et al. 1996). Slash also reduces or prevents exposure-related mortality of shade tolerant seedlings and residual understory, by providing shade and moderating water and temperature extremes (McInnis and Roberts 1994).

CWD size-class distribution

Logging slash is composed of many size classes of woody debris, including branches and bark, needles or leaves, and branches and boles. Conditions after harvest (including increased moisture, temperature, available nutrients, and organic matter) favour rapid decomposition. Differences in decomposition rate influence the degree to which slash becomes a physical barrier to regenerating vegetation (Olsson and Staaf 1995). Smaller size classes of slash provide a fertilizer effect, since they decompose rapidly and do not form an impenetrable physical barrier (Olsson and Staaf 1995). Our results reveal that the vast majority of CWD in harvested stands of trembling aspen is in the form of small size classes, particularly bark and twigs (cf. Aber et al. 1978). These smaller sizes classes decay much more rapidly than do large boles (Miller 1983). In addition, small size classes have a higher bark-to-wood ratio, resulting in greater concentrations of nutrients compared to large pieces (Miller 1983; Hendrickson 1987). We found that unharvested stands had greater relative amounts of CWD in the larger size classes compared to harvested sites, indicating slower incorporation of organic matter into the soil. This effect is magnified by the lower overall volume of CWD in unharvested stands.

The physical presence of slash may influence species composition and abundance in regenerating cutblocks (McInnis and Roberts 1994). Slash loadings reduce the intensity of solar radiation reaching the forest floor and reduce exposure of mineral soil, which together impact recruitment of species from the seed bank. Slash also reduces exposure-related mortality of shade-tolerant species, by providing shade and by moderating water and temperature extremes (McInnis and Roberts 1994). In our study, the persistence of species such as bishop's cap, bunchberry and bryophytes in recent clearcuts was attributable to shading by coarse woody debris loadings.

Trembling Aspen Suckering

The majority of trembling aspen regeneration is from vegetative shoots (suckers) derived from lateral root meristems. Vegetative suckering in aspen is thought to be an adaptation to recurrent catastrophic fire disturbance (Maini and Horton 1966; Steneker 1974). Optimal conditions for sucker development include release of apical dominance and increased soil temperatures (Maini and Horton 1966; Steneker 1974). These two requirements are achieved by wildfires, which remove mature trees and associated canopy cover, reduce the thickness of the litter mat, and remove potential competitors such as tall shrubs (Maini and Horton 1966; Perala 1990). Logging also removes mature trees, releasing aspen clones from apical dominance and opening the canopy to increase the amount of light reaching the forest floor (Steneker 1974; Bartos and Mueggler 1981).

Factors determining trembling aspen density

Sucker density as a function of time

Suckers emerge at high densities after logging on most sites in southern boreal forest and trembling aspen parkland ecosystems (Nobel et al. 1977; Schier and Campbell 1978; Bartos and Mueggler 1982; Brumelis and Carleton 1988; Harvey and Bergeron 1989; Bates et al. 1993; Lavertu et al. 1994). In our study, sucker densities ranged from 40,000 to 180,000 suckers per ha (mean density of 80,000 suckers per ha) in the year following harvesting. Such densities are typical for "good" sites, and easily meet or exceed those required for full stocking of aspen stands (Peterson and Peterson 1992).

Most suckers originate and achieve highest growth rates within the first full growing season, although some sites show new sucker emergence in both the first and second years after harvest (Shier and Campbell 1978; Lavertu et al. 1994). Deposition of multiple growth rings in some Duck Mountain suckers prevented accurate age determination. However, individuals with one and two growth rings were sampled in two and three year old cuts, suggesting secondary recruitment after the initial sucker emergence. Past work indicates that high initial densities prohibit new sucker production beyond two years following clearing (Lavertu el al. 1994).

Young trembling aspen stands undergo strong self-thinning, particularly if initial densities are high (Shier and Campbell 1978; Lavertu et al.1994; Mallik et al.1997). The self-thinning rate reflects an equilibrium state between competition and density. In northwestern Québec, sucker mortality was high in the first year (ranging from 35% and 65%) and somewhat reduced in the second year (ranging from 16% and 22%) following clearcutting (Lavertu et al.1994). In Ontario, trembling aspen stem densities decreased by 20% to 30% between the 6th and 7th year following harvesting (Mallik et al. 1997). Suckers frequently develop in clumps, which thin to two or three stems after five years of development and to single stems within 10 years (Shier and Campbell 1978). Clumped distributions of suckers were observed in the Duck Mountain stands. We found that approximately two-thirds of aspen suckers are removed through natural self-thinning by the fourth year following harvesting.

Slash

Trembling aspen root suckers originate from elongation and differentiation of meristematic tissue on ‘surface’ roots, i.e. those within 10 cm of the soil surface (Maini and Horton 1966). Meristem maturation and root growth are highly sensitive to soil temperature (Maini and Horton 1966; Steneker 1974). As a result, practices which result in higher light and heat levels at the forest floor will maximize sucker density (Steneker 1974; Schier and Campbell 1978; Peterson and Peterson 1992; Lavertu et al. 1994). Slash shades the forest floor and thus has the potential to decrease soil temperature and thereby inhibit root suckering. In addition, dense piles of slash can act as physical barriers to regenerating suckers (Bella 1986; Peterson and Peterson 1992; Bates et al. 1993). The effects of slash shading (and shortening of the growing season) may be more detrimental in cooler regions (Bella 1986, Bates et al. 1993).

In southern Saskatchewan, differential self-thinning of aspen suckers eliminated initial differences in density between slash treated and slash-free plots after five years of growth (Bella 1986). Our results indicate that the typical slash loadings of harvested stands in the Duck Mountains have no detrimental effect on aspen regeneration densities. This in turn suggests that typical slash loadings do not lower soil temperatures to any appreciable extent. We did note, however, that poor regeneration may occur in areas with abnormally dense slash piles. Such areas are generally restricted to equipment loading areas and road obstructions, both of which are very minor components of a typical cutblock.

Harvest season

Harvest season (summer vs. winter cutting) can potentially influence the regenerative ability of trembling aspen. In Saskatchewan, the removal of shading competitors during a summer harvest can yield up to double the initial sucker densities of winter cuts (Bella 1986). However, higher mortality of trembling aspen suckers in summer cutblocks results in equal stocking densities in summer and winter cuts by five years post-harvest (Bella 1986). In Minnesota, by contrast, winter harvesting resulted in higher regeneration and growth compared to summer cuts (Bates et al. 1993). Relatively high suckering in winter harvested stands was attributed to reduced mechanical damage by equipment traffic and higher root carbohydrate levels (Schier and Zasada 1973; Bates et al. 1993). In northern regions, soil temperature may be more limiting to sucker development than carbohydrate levels. Consequently, soil scarification and competitor removal by summer harvesting may be more beneficial in northern regions (Bella 1986; Bates et al. 1993).

Our results indicate that aspen regeneration in the Duck Mountains is unaffected by harvest season. Presumably, the seasonal timing of harvesting in the Duck mountains is well suited to stand-level conditions. The combination of winter and summer harvesting practices suited to local (stand level) conditions balances the benefits and costs associated with each harvest method, and yields sufficient stocking after disturbance to ensure sustainable stand replacement.

Clonal variation

Our research in the Duck Mountains indicates that aspen suckering density is unrelated to edaphic conditions, stand type, harvest season, slash volume, pre-harvest stand density, or shrub competition. Previous research has demonstrated no relationship between sucker density and pre-harvest stand age and tree density (Lavertu et al. 1994), pre-harvest root density (Shier and Campbell 1978), and fire severity (Bartos and Mueggler 1981; Brown and Debyle 1987). Based on these results, many researchers have proposed that genetic variation among aspen clones is the primary determinant of sucker density following disturbance (Bartos and Mueggler 1981; Brown and Debyle 1987; Lavertu et al.1994).

Density of trembling aspen and balsam poplar in cut, edge and interior

Trembling aspen and balsam poplar suckering, albeit at low density, was observed in some of the mature (unharvested) stands enumerated in our study. This suggests that aspen suckering occurs even in the absence of large-scale disturbances (see also Hamel and Kenkel 2001). The suckering ability of trembling aspen is thought to decrease after stand “breakup”, when stands become “decadent” (Maini and Horton 1966; Steneker 1974; Schier 1982). The age at which stand break-up occurs is site specific, ranging from 60 to 90 years or more (Peterson and Peterson 1992). However, stands up to 230 year in age can produce stand-replacing sucker densities after a large-scale disturbance (Lavertu et al. 1994; Bergeron 2000).

In the Duck Mountains, suckering may result in the self-replacement of trembling aspen as gaps are formed in the canopy during stand break-up (Hamel and Kenkel 2001). Recent research indicates that some aspen stands form multi-aged and self-replacing canopies (Peterson and Peterson 1992; Lavertu et al. 1994; Comming et al. 1999; Hamel and Kenkel 2001). Selectively harvested aspen stands in Saskatchewan also undergo secondary canopy replacement, resulting in uneven-aged stands (Peterson and Peterson 1992).

Multi-aged aspen stands may become more common in the Duck Mountains in the absence of large-scale human or natural disturbance. Many aspen stands within the Duck Mountains originated after the huge catastrophic fire of 1885 (Harrison 1934) and are approaching or have reached the stand “break-up” stage (Peterson and Peterson 1992).

Trembling aspen growth

The trees and large shrubs regenerating in post-harvested stands exhibit different growth strategies. Trembling aspen has a vertical growth strategy that allows shoots to over-top shorter plants and thus successfully compete for light (Mallik et al. 1997). In the Duck Mountains, trembling aspen suckers average over 75 cm in height at the end of the first growing season. This compares to 90 cm in Québec (Lavertu et al 1994), and about 100 cm in northern Minnesota (Bates et al. 1993). The slightly lower values obtained in the Duck Mountains may reflect differences in the time of sampling: heights were measured from the end of June to the end of August, as stands were sampled.

The dominant shrub in Duck Mountain, beaked hazel, has a horizontal growth strategy. The species develops relatively short stems and a dense rhizome system, and so effectively competes with other species for space and light (Buckman 1964; Mallik et al. 1997). These growth strategies influence the long-term structure of regenerating stands soon after harvest. The ability of trembling aspen to overtop tall shrubs (mountain maple and beaked hazel) minimizes competition and ensures that post-harvested aspen stands do not revert to permanent shrublands.

MANAGEMENT APPLICATIONS

Historically, catastrophic fires were critical to maintaining dense stands of aspen on the landscape. Since the early 1900's, reductions in the frequency and severity of fire through active fire suppression (Bartos and Mueggler 1981) and habitat fragmentation (Brown and Debyle 1987; Kay 1997) have occurred. Reduced fire frequency may threaten the long-term persistence of trembling aspen in some regions. Indeed, trembling aspen communities may require a disturbance such as clearcutting or burning to replace old stands with young ones. Without such disturbances, most aspen stands in the Duck Mountains will likely revert to "decadent" open forests or shrublands, or will be succeeded by softwoods (Hamel and Kenkel 2001). Maintenance of a "natural landscape mosaic" of various stand ages, through sustainable harvest rotations that emulate the natural disturbance regime, is recommended for long-term ecosystem health.

Our results indicate that current aspen harvesting practices in the Duck Mountains have little if any long-term detrimental impact on plant community structure, composition or diversity. Changes in local conditions following harvesting are temporary and not of sufficient magnitude to permanently alter or compromise stand floristics. Recent (1998-present) cutblocks in the Duck Mountains have highly convoluted edges, with large patches and peninsulas of residual forest left unharvested. This fire-like spatial disturbance pattern provides structural complexity and a ready seed source for plant colonization into cutblocks. Remnant forest patches also provide habitat and protection of large "wildlife" trees, snags and advance regeneration.

Logging Coarse Woody Debris (or Slash)

The current practice of retaining and distributing slash over cutblocks has much to recommend it. Slash retention minimizes the loss of organic matter and nutrients from harvested aspen ecosystems. As post-logged forests develop and mature, residual slash is an important source of decayed logs for advance regeneration of tree species such as white spruce, balsam fir and white birch. Debris piles in cutblocks are an important source of cover and refuge for plant and animal species that would otherwise be eliminated in exposed post-harvesting environments. Small areas of atypically high slash loadings add to the habitat heterogeneity of cutblocks without detrimentally affecting stand-level restocking densities. Indeed, practices that create local heterogeneity will ultimately increase stand-level biological diversity.

Aspen Regeneration

Regeneration of trembling aspen is moderate to prolific in post-harvested stands in the Duck Mountains. High suckering densities were observed in the year following disturbance, with considerable self-thinning occurring over the next few years. We recommend continuation of the "free-to-grow" policy as currently practiced – artificial thinning of regenerating stands is not required, nor recommended (cf. Bella 1986). Moreover, artificial thinning may result in secondary sucker recruitment, rather than increases in the growth of existing suckers. Competition among suckers results in natural self-thinning and selection of the most ecologically fit individuals.

A management concern of industry partners is the potentially detrimental effect of shading from residual forest patches on aspen suckering. Although this problem was not directly studied, we did note that suckers development along the periphery of cutblocks occurs at "typical" densities. We also noted that such suckers are often taller than those growing in more exposed areas of a cutblock. Possible causes for accelerated height growth along the periphery of cutblocks include augmentation of carbohydrates from unharvested ramets, and increased vertical growth in response to shading. Further research is needed to examine this phenomenon and to address its potential implications on cutblock design.

A second issue of concern to industry partners is balsam poplar regeneration. Balsam poplar is not a preferred species in the production of fiberboard and other commercial products. Our results indicate that balsam poplar sucker growth rates are similar to those of trembling aspen in upland sites. When present in moist stands, balsam poplar appeared to outgrow aspen in local depressions and other moist sites (cf. Peterson and Peterson 1992). We found that post-harvest regeneration of trembling aspen and balsam poplar generally reflected pre-harvest proportions. In most stands, balsam poplar suckering was low compared to that of trembling aspen. We conclude that harvesting is not expected to alter canopy composition or hardwood restocking.

Competition with marsh reedgrass (Calamagrostis canadensis)

Overall aspen regeneration met or exceeded levels required for full stocking in all cutblocks, but in two cutblocks in the moist aspen sub-type locally low regeneration densities were observed. In these areas, the post-harvest vegetation was characterized by a proliferation of marsh reedgrass. In Alberta, marsh reedgrass is a major competitor on clearcuts, particularly in stands occurring on moist to wet, nutrient-rich soils (Lieffers et al. 1993). This invasive grass forms dense swards that depress soil temperatures and act as a physical barrier to aspen sucker regeneration (Hog and Lieffers 1991).

Marsh reed grass was found at low densities throughout the Duck Mountains, and occasionally formed small meadows in wet depressions following harvest. These depressions generally corresponded to similar wet meadows in adjacent unharvested stands and were a minor component of the landscape. Harvesting in these moist stands resulted in saturated soil conditions over portions of the cutblock. In wet depressions, low densities of aspen suckers over-topped the grass, and these are expected to develop into a low-density aspen canopy. More elevated areas had more typical aspen regeneration densities. The elevated water table observed in post-harvested stands may be attributable to reduced evapotranspiration losses associated with canopy removal, possibly in conjunction with water impoundment and/or altered site drainage resulting from logging roads and mechanical harvesting activities. The latter effects are easily mitigated by trenching or removing roads to maintain pre-harvest drainage patterns. Our results indicate that stands belonging to the moist aspen sub-types (mountain maple present in the shrub layer) are most susceptible to slight alterations of the water table.

REFERENCES

Aber, J.D., Botkin, D.B., and Melillo, J.M. 1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwoods. Can. J. For. Res. 8: 306-315.

Archibold, O.W. 1979. Buried viable propagules as a factor in postfire regeneration in northern Saskatchewan. Can. J. Bot. 57: 54-58.

Bartos, D.L. and Mueggler, W.F. 1981. Early succession in aspen communities following fire in western Wyoming. J. Range Manage. 34: 315-318.

Bartos, D.L. and Mueggler, W.F. 1982. Early succession following clearcutting on aspen communities in northern Utah. J. Range Manag. 35: 764-768.

Bates, P.C., Blinn, C.R. and Alm, A.A. 1993. Harvesting impacts on quaking aspen regeneration in northern Minnesota. Can. J. For. Res. 23: 2403-2412.

Bekunda, M.A., Smethurst, P.I., Khanna, P.K., and Whillet, I.R. 1990. Effects of post-harvest residue management on labile soil phosphorus in a *Pinus radiata* plantation. For. Ecol. Manage. 38: 13-26.

Bella, I.E. 1986. Logging practices and subsequent development of aspen stands in east-central Saskatchewan. For. Chron. 62: 81-83.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Québec’s southern boreal forest. Ecology 81: 1500-1516.

Bergeron, Y. and Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Québec. For. Ecol. Manage. 92: 235-242.

Bond, W. J. and Midgley, J.J. 2001. Ecology and sprouting in woody plants: The persistence niche. Trends Ecol. Evol. 16:45-51.

Brown, J.K. and DeByle, N.V. 1987. Fire damage and suckering in aspen. Can. J. For. Res. 17: 1100-1109.

Brumelis, G. and Carelton, T.J. 1988. The vegetation of postlogged black spruce lowlands in central Canada. I. Trees and tall shrubs. Can. J. For. Res. 18: 1470-1478.

Brumelis, G. and Carlton, T.J. 1989. The vegetation of post-logged black spruce lowlands in central Canada: II: Understory vegetation. J. Appl. Ecol. 26: 321-339.

Buckman, R.E. 1964. Effects of prescribed burning on hazel in Minnesota. Ecology 45: 626-629.

Cockery, T.M. 1996. Geology and landforms of Manitoba. Pp. 11-30. In The Geography of Manitoba: its land and its people. Edited by J. Welsted, J. Everitt and C. Stadel. The University of Manitoba Press. 328pp.

Comming, S.G., Schmeigelow, F.K.A., and Burton, P.J. 1999. “in prep.” Gap Dynamics in boreal aspen stands: is the forest older than we think? Sustainable Forest Management Network. University of Alberta. 31pp.

DeGrandpre, L., Gagnon, D and Bergeron, Y. 1993. Changes in understory of Canadian southern boreal forest after fire. J. Veg. Sci. 4: 803-810.

Harrison, J.D.P. 1934. The Forests of Manitoba. Department of the Interior, Forest Service, Ottawa. Forest Service Bulletin No. 85.

Harvey, B.D. and Bergeron, Y. 1989. Site patterns of natural regeneration following clear-cutting in northwestern Québec. Can. J. For. Res. 19: 1458-1469.

Harvey, B.D., Leduc, A., and Bergeron, Y. 1995. Early post-harvest succession in relation to site type in the southern boreal forest of Québec. Can. J. For. Res. 25: 1658-1672.

Hamel, C., and Kenkel, N. 2001. Structure and Dynamics of boreal forest stands in the Duck Mountains, Manitoba. Final Project Report. Sustainable Forest Management Network. University of Alberta. pp. 50.

Hendrickson, O. 1987. Winter nutrients in northern conifers and hardwoods. For. Sci. 33: 1068-1074.

Hog, E.H., and Lieffers, V.J. 1991. The impacts of *Calamagrostis canadensis* on soil thermal regimes after logging in Northern Alberta. Can. J. For. Res. 21: 382-394.

Johnson, D., Kershaw, L., MacKinnon, A., and Pojar, J. 1995. Plants of the Western Boreal Forest and Aspen Parkland. Lone Pine, Edmonton. 392pp.

Kay, C.E. 1997. The condition and trend of aspen, *Populus tremuloides*, in Kootenay and Yoho National Parks: Implications for ecological integrity. Can. Field Natural. 111: 607-616.

Kendrew, W.G. and Currie, B.W. 1955. The Climate of Central Canada. The Queen’s Printer and Controller of Stationary, Ottawa. 194 pp.

Kimmins, J.P. 1977. Evaluation of the consequences for future tree productivity of the losses of nutrients in whole-tree harvesting. For. Ecol. Manage. 1: 169-183.

Kurmis, V. and Sucoff, E. 1989. Population density and height distribution of *Corylus cornuta* in undisturbed forests of Minnesota: 1965-1984. Can. J. Bot. 67: 2409-2413.

Lang, A.H. 1974. Guide to the geology of Riding Mountain National Park and its vicinity—history of its upland and other scenery. Miscellaneous report 20. Geological Survey of Canada, Department of Energy, Mines, and Resources, Ottawa. 68 pp.

Lavertu, D., Mauffette, Y. and Bergeron, Y. 1994. Effects of stand age and litter removal on the regeneration of *Populus tremuloides*. J. Veg. Sci. 5: 561-568.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. For. Ecol. Manage. 105: 263-272.

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29: 796-811.

Liefffers, V.J., MacDonald, S.E., and Hogg, E.H. 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. Can. J. For. Res. 23: 2070-2077.

Maini, J.S. and Horton, K.W.1966. Vegetation propagation of *Populus* spp. I. Influence of temperature on formation and initial growth of aspen suckers. Can. J. Bot. 44: 1183-1189.

Mallik, A.U., Bell, F.W., and Gong, Y. 1997. Regeneration behavior of competing plants after clear cutting: implications for vegetation management. For. Ecol. Manage. 95: 1-10.

Manitoba Natural Resources. 1996. Five year report on the status of forestry. MG-14283. Manitoba Natural Resources, Forestry branch.

McInnis, B.G. and Roberts, R. 1994. The effects of full-tree harvests on natural regeneration. North. J. Appl. For. 11: 131-137.

Miller, W.E. 1983. Decomposition rates of aspen bole and branch litter. For. Sci. 29: 351-356.

Meuller-Dumbois, D. 1964. The forest habitat types in southeastern Manitoba and their application to forest management. Can. J. Bot. 42: 1417-1444.

Nobel, M.G., DeBoer, L.K., Johnson, K.L., Coffin, B.A., Fellows, L.G., and Christensen, N.A. 1977. Quantitative relationships among some *Pinus banksiana-Picea mariana* forests subjected to wildfire and postlogging treatments. Can. J. For. Res. 7: 368-377.

Nguyen-Xuan, T., Bergeron, Y., Simard, D., Fyles, J.W., and Pare, D. 2000. The importance of forest floor disturbance in early regeneration patterns of the boreal forest of western and central Québec: a wildfire versus logging comparison. Can. J. For. Res. 30: 1353-1364.

Olsson, B.A. and Staaf, H. 1995. Influence of harvesting intensity of logging residues on ground vegetation in coniferous forests. J. Appl. Ecol. 32: 640-654.

Olsson, B.A., Staaf, H., Lundkvist, H., Bengtsson, J., and Rossen, K. 1996. Carbon and Nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. For. Ecol. Manage. 82: 19-32.

Perala, D.A. 1990. *Populus tremuloides*. In Silvics of North America: 2. Hardwoods. Edited by R.M. Burnes and B.H. Honkala. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1. pp. 555-569.

Peterson, E.B. and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. Spec. Rep. 1. For. Can., Northwest reg., North. For. Cent., Edmonton, Alberta. pp. 252.

Ritchie J.C. and Yarranton, G.A. 1978. Patterns of change in the late-Quaternary vegetation of the Western Interior of Canada. Can. J. Bot. 56: 2177-2183.

Rosen, K. and Lundmark-Thelin, A. 1987. Increased nitrogen leaching under piles of slash—a consequence of modern forest harvesting techniques. Scand. J. For. Res. 2: 21-29.

Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests in northwestern Alberta. Can. J. Bot. 39: 1007-1017.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In The role of fire in circumpolar ecosystems. Edited by Wein, R.W. and Maclaen, D.A. John Wiley and sons, New York. pp. 135-154.

Schier, G.A. 1982. Sucker regeneration in some deteriorating Utah aspen stands: development of independent root systems. Can. J. For. Res. 12: 1032-1035.

Schier, G.A. and Campbell, R.B. 1978. Aspen sucker regeneration following burning and clearcutting on two sites in the Rocky Mountains. For. Sci. 24: 303-308.

Schier, G.A., and Zasada, J.C. 1973. Role of carbohydrate reserves in the development of root suckers in *Populus tremuloides*. Can. J. For. Res. 3: 243-250.

Shafi, M.I. and Yarranton, G.A. 1973a. Diversity, floristic richness, and species evenness during a secondary postfire succession. Ecology 54: 897-902.

Shafi, M.I. and Yarranton, G.A. 1973b. Vegetational heterogeneity during a secondary (postfire) succession. Can. J. Bot. 51: 73-90.

Smith, D.W., and James, T.D.W. 1978. Changes in the shrub and herb layers of vegetation after prescribed burning in *Populus tremuloides* woodland in southern Ontario. Can. J. Bot. 56: 1792-1797.

Steneker, G.A. 1974. Factors affecting the suckering of trembling aspen. For. Chron. 50: 32-34.

Strong, W.L and La Roi, G.H. 1983. Rooting depths and successional development of selected boreal forest communities. Can. J. For. Res. 13: 577-588.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. For. Sci. 14: 20-26.

Vincent, A.B. 1965. Growth habits of mountain maple in the Ontario Claybelt. For. Chron. 41:330-344.

Walshe, S. 1980. Plants of Quetico and the Ontario Shield. University of Toronto Press, Toronto. 152pp.

Yarie, J. 1993. Effects of selected forest management practices on environmental parameters related to successional development on the Tanana River floodplain, interior Alaska. Can. J. For. Res. 23: 1001-1014.

Zasada, J.C. and Phipps, H.M. 1990. *Populus balsamifera*. In Silvics of North America: 2. Hardwoods. Edited by R.M. Burnes and B.H. Honkala. Agricultural Handbook 654. USDA, Forest Service, Washington D.C. Vol. 1. pp. 518-529.

Zasada, J.C., Sharik, T.L., and Nygren, M. 1992. The reproductive process in boreal forest trees. In A systems analysis of the global boreal forest. Edited by H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge University Press, New York. pp. 85-125.