

**EFFECTS OF HARVESTING ON ASPEN DOMINATED
STANDS**

By
Samantha Murray

A thesis presented to the Faculty of Graduate Studies in partial fulfillment of the
requirements for the degree Master of Science

Department of Botany
University of Manitoba
Winnipeg, Manitoba, Canada
R3T 2N2

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BY

SAMANTHA MURRAY

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree
of
MASTER OF SCIENCE**

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ABSTRACT

This study addresses the effects of tree-length harvest, and subsequent regeneration, of trembling aspen (*Populus tremuloides* Michx.) dominated forests of the Duck Mountain Provincial Forest Reserve, Manitoba. Vegetation and environmental factors (including coarse woody debris loadings) were compared between harvested, unharvested edge and interior trembling aspen-dominated forest. Our objectives were to: (1) assess floristic variation of the study area, (2) quantify changes in the structure, composition and diversity of vegetation after harvest, (3) examine the trembling aspen suckering and factors controlling suckering and (4) determine and compare the size distribution and volume of CWD and slash. Three stand types were delineated by cluster analysis of shrub cover: (1) Dry (co-dominated by low shrubs) (2) Fresh (dominated by beaked hazelnut) and (3) Moist (co-dominated by beaked hazel and mountain maple).

Changes associated with post-logged trembling aspen stands were manifested as minor short-term changes in abundance and structure of existing species, rather than major changes in composition and diversity. Post-harvest aspen regeneration was not significantly effected by; (a) slash loadings; (b) stand density prior to harvest; (c) competition e.g. shrub cover; (d) soil variables (pH, conductivity, particle size, LFH depth); (e) harvest season; or (f) stand-type. Variation in aspen sucker density corresponded with age of cutblock (time since harvest), or self-thinning. Coarse woody debris (CWD) is naturally present at relatively high and variable volumes within interior forests. The majority of CWD in trembling aspen stands is in the form of small size

classes in all treatments. A power law relationship between size class (based on a logged scale) and piece frequency was determined for CWD in all treatments.

In general, current harvesting methods (assuming sustainable rotation age) are thought to have little long-term effect on herb and shrub community assemblages and diversity within the Duck Mountain aspen dominated forests. We recommend continuation of the free-to-grow policy currently practiced; artificial thinning of aspen suckers is not required, or recommended. Harvesting is not expected to alter canopy composition with respect to hardwood stocking. Retention of slash over cutblocks (as is the current practice) is also recommended to continue.

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CHAPTER 1

THE BOREAL FOREST ECOSYSTEM

1.1 DISTRIBUTION AND CLIMATE

The boreal biome is a circumpolar belt of conifer-dominated forest that spans northern North America and Eurasia (a total of $12 \times 10^6 \text{ km}^2$). In North America it stretches over 10° of latitude from the coasts of Newfoundland to Alaska (Payette 1992), forming an 800 km wide band across much of the continent. The zone is constricted to 240 km wide between the Hudson Bay and Great Lakes, moderated to the south by the Great Lakes and cooled from the north by Hudson Bay (Carlton and Maycock 1980). Climate is an extremely important factor influencing the distribution of the boreal forest. To the south, the boreal forest corresponds to the January position of the arctic front (the division between cold, Arctic air and warm Pacific air masses) (Bryson 1966). The southern limit also roughly corresponds to the 18°C isotherm (Ochel & Lawrence 1985).

The boreal forest has a continental climate, characterized by long cold winters and short cool to warm summers. Physical geography has a large effect on the conditions observed through the boreal forest. The Western Cordillera follows a north-south alignment, while low-relief plains cover the interior. East of the Cordillera, air masses rarely exchange with warm Pacific air to moderate the continental conditions (Smith 1989). Southern Alberta and Saskatchewan occasionally receive down-slope flows of

pacific air (commonly referred to as "Chinooks"), causing winter temperatures to fluctuate. Polar continental air influences climate of the Canadian Interior Plains, although moist tropical air (from the Gulf of Mexico) occasionally reaches southeastern Manitoba (Klassen 1989). Mixing of Arctic and tropical masses over Manitoba produces frontal activity and generally stormy weather patterns (Klassen 1989).

Climate affects floristic composition and vegetation dynamics of the boreal forest directly (through physiological adaptations) and indirectly (through soil development and disturbance regime). General distribution patterns and dominance of many boreal species may be predicted with environmental parameters related to moisture and air temperature (Lenihan 1993). Temperature and precipitation act upon soils (affecting thermal regime and moisture content) to direct decomposition rates and nutrient cycling, both of which are low in the boreal forest (Prescott et al. 1989).

In general, mean annual temperature decreases toward the center of the boreal forest biome, following north – south and coast – interior gradients (Smith 1989). Precipitation held within pacific air masses is released on the west slopes of the Cordillera, forming a rain shadow over the interior plains (Kendrew & Currie 1955; Smith 1989; Payette 1992). Precipitation is greater than 90 cm in the far-west and eastern portions of the boreal forest, while less than 75 cm falls over the prairie provinces. Close to two-thirds of the precipitation is deposited as rain through the growing season (which ranges between 200+ days in the west and 120 days in the interior)(Smith 1989). Climactic factors, in particular temperature and precipitation, determine frequency and intensity of fire. Dry, warm regions have short fire cycles in general, while moist, cool regions experience

longer fire cycles (Rowe & Scotter 1973; Viereck 1983).

1.2 VEGETATION

The boreal forest has only nine dominant tree species, due in part to the harsh climate of the biome (Payette 1992). One of the furthest ranging species is black spruce (*Picea mariana*), stretching from the Atlantic to Pacific coasts, north into Alaska (Viereck and Johnson 1990). It increases in dominance northward with colder, shallow wet soils and higher frequencies of fire (Viereck and Johnson 1990). Eastern Larch (*Larix laricina*), which is tolerant of wet soils, has a wider range than black spruce, extending into northern Yukon south to north eastern United States (Johnson 1990). White spruce (*Picea glauca*) is also distributed over the continent on drier sites, with higher occurrence in central and western Canada (Nienstaedt & Zasada 1990). In the east, balsam fir (*Abies balsamea*) is a dominant species (Rowe and Scotter 1973). The typical conifer on dry, sandy sites from the east coast to Alberta is jack pine (*Pinus banksiana*) (Rudolf & Laidly 1990). Jack pine is replaced by lodgepole pine (*Pinus contorta* var. *latifolia*) in the Alberta foothills west to the Yukon (Lotan & Critchfield 1990).

Distributed with and within the coniferous forests are three major deciduous (hardwood) species. Hardwoods are most abundant in the southern zones of the boreal forest (the ecotone with prairie). Paper birch (*Betula papyrifera*) reaches from the Atlantic coast to the Pacific, north to the "tree line" and south along the Appalachians to western North Carolina (Safford et al. 1990). Balsam poplar (*Populus balsamifera*)

follows much the same distribution as paper birch, but is more restricted to areas of high soil moisture such as depressions and drainage channels (Zasada & Phipps 1990). The hardwood species with the broadest distribution is trembling aspen (*Populus tremuloides*). Aspen is distributed from the discontinuous permafrost zone south to the United States and along the western Cordillera (Perala 1990). Aspen is dominant over birch and poplar in nutrient rich, well-drained soils (Perala 1990).

1.3 DISTURBANCE IN THE BOREAL FOREST

1.3.1 Fire

Fire is arguably the most important disturbance in the boreal forest (Ritchie 1956; Dix & Swan 1971; Heinselman 1973; Carleton & Maycock 1978; Johnson 1979; Wein & Maclean 198; Payette 1992; Bonan 1992; Johnson 1992). In the absence of human activity, fire cycles in North America range between 50 years in the south and 250+ years in the mesic forests of the east (Larsen 1980). Classical Clementsian succession concepts may not be applicable under the frequent disturbance regime of the boreal forest (Rowe 1961; Johnson 1979). Disturbance frequently occurs within the life span of dominant canopy species, with insufficient time between disturbance for "later-successional" species to establish or become dominant (Johnson 1979). Although infrequent, fire may also play an important role in the vegetation dynamics of boreal wetlands.

Intensity and frequency of fire are highly variable in the boreal forest (Heinselman 1973). Fire characteristics are highly variable across the landscape and affect the

vegetation dynamics and floristic composition differently at any given location, resulting in a mosaic of forest stands with different stand ages and disturbance history. The cumulative fire history has a major influence on current vegetation, influencing seed sources, soil development, canopy closure, stand age, and many other general site characteristics (Heinselman 1973; Cogbill 1975; Bergeron & Dubuc 1989; Zasada et al. 1992).

- **Adaptation to Fire**

Boreal communities are adapted to fire cycles of varied duration. Pioneer species dominate regions with short fire cycles, evading or enduring frequent fire. Fire intolerant species, those regenerating from the seed bank, are favored in areas of infrequent or low intensity fires (Rowe 1983; Zasada et al. 1992). Overall, boreal plants are characterized as “generalist” species, capable of withstanding recurrent changes in their environment (Payette 1992).

A) Clonal Growth

Frequent fires favor shade-intolerant, sprouting species and ephemerals from the seed bank. Boreal hardwoods (such as white birch, balsam poplar and trembling aspen) and most boreal shrubs and forbs reproduce by seed and vegetative shooting (Rowe 1983; Zasada et al. 1992). Suckering by aspen, poplar and many shrub species is a general adaptation to regenerate after removal of dominant stems, a beneficial adaptation in region affected by fire and logging. However, high intensity (i.e. severe) fires may

completely kill plant root systems and burn the dormant seed bank (Rowe and Scotter 1973).

B) Seed bed

All boreal species show optimal germination and establishment on exposed mineral substrates (Van Wagner 1983). Fire promotes seed germination and survival by removing litter accumulations and exposing the mineral seed bed (Johnson 1992). Removal of insulating vegetation and the subsequent "blackening" effect (which raises albedo) increases soil temperatures, promoting germination and root growth (Viereck 1983). Plants establishing immediately after fire are provided with a high light, high nutrient, warm microclimate with direct access to mineral soil. Increased ground temperatures can act to stimulate plant growth, or, if shade tolerant, inhibit regeneration (Smith and James 1978). Successful germination and seedling establishment on organic soils, as well as regeneration by layering, is more common in mesic to hydric boreal species such as white cedar, larch (Johnson 1990), black spruce (Viereck & Johnson 1990), balsam fir (Furyaev 1983) and white spruce (Peterson & Peterson 1992).

1.3.2 Gap Dynamics

Between fires other disturbances such as tree fall, pathogen infection, insect outbreaks, and mammal herbivory contribute to changes in the understory and allow persistence of pioneer species in the absence of frequent large-scale disturbance (Pare et al. 1993; DeGrandpre et al. 1993). Small-scale disturbance, represented by gap dynamics,

adds a dimension of complexity to naturally homogeneous stands. Gaps provide areas for invasion and establishment within an otherwise fixed environment, where resources such as light or mineral seedbed may be limited. Small gaps are also important for regeneration within closed stands, adding to biodiversity within the boreal forest.

1.3.3 Timber Harvest

Ecosystem stability, wildlife habitat, carbon storage, recreation, aesthetic, spiritual, employment, and timber source are all values given to the boreal forest as a natural resource (Bohning et al. 1993). With the current management practice of fire suppression, logging has become an increasingly important source of disturbance in the boreal forest. In the past most logging operations have focused on the harvest of softwoods for timber, plywoods and pulp (91% in Manitoba, MNR 1996). The recent development of composite building materials (oriented strand boards) has increased interest in hardwood harvesting practices (Peterson & Peterson 1992). Aspen, and to a lesser extent balsam poplar, are now economically important tree species in the rapidly regenerating mixed and pure stands of southern Canada (MNR 1996). Work continues to establish post-logging treatments that provide both adequate stand regeneration and reflect natural vegetation dynamics of the boreal forest. The ability of aspen stands to regenerate via suckering (versus re-planting) adds another economic advantage to the shift from softwood to hardwood harvest.

- **Emulating natural disturbance**

Logging has replaced fire as the dominant disturbance type in many areas of the southern boreal forest (Brumelis and Carleton 1989). A recent focus in forest research is the goal of developing harvesting methods that emulate natural disturbance. Ideally, forest managers would mimic natural ecosystem dynamics when harvesting in disturbance driven ecosystems, and thereby maintain the organisms and the biotic and abiotic processes within the system (Bergeron and Harvey 1997).

Clear cutting is often characterized as successional retrogression, or reverting a site to an early successional stage (Yarie 1993). Cuts are used to mimic natural disturbance with a natural regeneration of common fire-adapted species (Yarie 1993). However, species such as black spruce often fail to regenerate successfully after logging, giving way to hardwoods or balsam fir (Brumelis and Carlton 1988). Even hardwoods may not regenerate suitably on some sites (Bartos and Mueggler 1982). A combination of ecological variables (e.g. soil conditions, seed source, stand age, light availability and moisture) and harvest variables (e.g. harvest method and season) combine to determine the extent and composition of regeneration after logging.

1.3.3.1 The physical effects of harvest

Forest structure and dynamics of post-logged forest largely depend on the harvest system employed (McInnis and Roberts 1994). Factors such as the machinery used, skidding patterns, soil moisture at time of harvest, harvest season, and harvest intensity all influence impacts of harvesting (Harvey et al. 1995). Ecological variables such as shading, moisture, soil texture, depth, drainage, stoniness and organic matter thickness determine the ability to which a site's vegetation can re-establish after disturbance. Soil sensitivity to compaction and erosion have a major impact on regeneration success and the plausibility of different silvicultural techniques and management plans (Harvey and Bergeron 1989). Site disturbances from harvest equipment such as compaction, reduced soil aeration and root injury may all adversely affect aspen regeneration in some areas (Bates et al. 1993).

A) Season

Many impacts of harvesting, particularly those associated with soil condition, are influenced by the season of harvest. Harvesting during winter while soils are frozen reduces or prevents compaction of fine textured and saturated soils. Winter logging is recommended on soils with imperfect to very poor drainage, or with B horizons with a finer texture than loamy sand (Bates et al. 1993). Snow cover also protects the organic layer and understory from disturbance. Understory vegetation remains intact to sequester the nutrient flush after logging, reducing losses from leaching. However, heavy shading

from shrubs and ruderals may inhibit germination and development of shade intolerant herbs and tree species on winter cuts (Olsson & Staaf 1995).

In contrast, summer harvest results in relatively high site disturbance. Surface soils are exposed, leaving patches of mineral soil for shade intolerant seedlings to develop. Understory vegetation is equally effected, with greater disruption to the shrub layer than in winter cuts. The difference in disturbance intensity associated with harvest season may be an important tool used to manage the subsequent development of a harvested stand. For example, where shrubs potentially out-compete tree regeneration, summer harvest may be used to disrupt the understory. On sites prone to compaction or saturation (peatlands and clay sites), winter harvest may be preferred to protect soil quality after harvest (Peterson and Peterson 1992).

B) Scarification and rutting

Scarification is a treatment used after clearing to expose mineral soil and encourage natural regeneration of softwoods from the seed bank (McInnis and Roberts 1994). However, shallow root systems of advanced softwood regeneration may be damaged by scarification (McInnis and Roberts 1994). Scarification and rutting also cause reduced sucker regeneration in aspen, reducing both height growth and crown closure (Bates et al. 1993). Harvesting equipment can cause direct damage to the parent root system, and provide entry wounds for pathogen infection (Bates et al. 1993). Injuries, or resulting scars, are also a sink for carbohydrates that would otherwise be immobilized for developing suckers (Bates et al. 1993). Rock raking is a similar process used to provide a

mineral substrate, although much of the nutrient-rich surface soils are removed and piled at the edge of the cut, away from areas of future forest development (Nobel et al. 1977). Rock raking not only damages existing roots, but also creates long-term nutrient depletion of the cut site. Removal of the insulating organic matter that lines the forest floor, may stress young roots and suckers by creating fluctuating soil temperatures and moisture levels (Bates et al 1993).

Changes resulting from mechanical site preparation have a major influence on the degree and manner in which surficial organic matter decomposes, including associated effects on soil fertility and nutrient availability (Lundmark-thelin and Johansson 1997). The relatively moist microclimate within trenches promotes dominant decomposer organisms and favors rapid decomposition (Lundmark-Thelin and Johansson 1997). Scarification and disc trenching increases nitrification by incorporating organic matter with surface mineral soil and stimulating decomposition (Yarie 1993; Bekunda et al. 1990). Mineral pools on clearcuts with scarification can be comparable to those of a mature white spruce stand, or have as high turn over as a *Populus* and alder forest. However, high rates of decomposition and concurrent mineralization result in increased nutrient loss through leaching on scarified sites (Lundmark-Thelin and Johansson 1997). Further losses in leaching result from the delayed re-vegetation process associated with scarification, since mechanically disturbed sites must regenerate from the seed bank rather than through rapid clonal development (McInnis and Roberts 1994).

C) Compaction

Skid trails are areas of repeated travel for logging machinery. Horse skidding and manhandling methods of the past were less destructive to the soil surface than mechanical methods, but are no longer cost-effective (Brumelis and Carleton 1987). Trafficking over skid trails and landings by modern harvesting machinery often results in soil disturbances such as compaction, or an increase in bulk density and soil strength, kneading, churning, rutting and displacement of soil surface, exposing sub-soil and puddling water (Miller et al. 1996). It is difficult to separate the effects of soil disturbance from other contributors to vegetation growth and survival (Miller et al. 1996). Skid trails are also used by big game, and may lead to "above-normal" herbivory and trampling in adjacent vegetation (Miller et al. 1996).

In general, infiltration and aeration are reduced on the compacted sites, decreasing survival and growth of seedlings (Harvey and Bergeron 1989). Differences in soil texture are subject to varying degrees of compaction, with finer textured soils at higher risk of compaction than sands and gravels. Lacustrine clays are most effected by compaction, as evidenced by water pooling in ruts along machinery paths (Harvey and Bergeron 1989). Yarding on loams and clay-loams (Brunisols) can increase bulk density by over 40% immediately after harvest, and remain higher 8 years after cutting (Miller et al. 1996). Fine textured, poorly drained soils in hardwood stands are prone to mechanical and harvest-related aspen regeneration problems (Bates et al. 1993). Soils are most vulnerable to compaction during spring harvests, when soil moisture is elevated by snowmelt and runoff (Bates et al. 1993).

D) Saturation

Removal of surface vegetation after logging reduces evapotranspiration, increases runoff and raises the ground water table, thereby resulting in higher saturation of the mineral soil (Lundmark-thelin and Johansson 1997). At the same time, upper humus layers become increasingly vulnerable to periodic desiccation from above-normal soil temperatures throughout the growing season (Lundmark-Thelin and Johansson 1997). Water demand may also be reduced immediately after logging, until sufficient vegetation regenerates and gains access to the water table. Soil saturation for long periods can inhibit both vegetative regeneration and seed development by reducing aeration and delaying or reducing soil warm-up in spring and early summer (Bates et al. 1993).

E) Temperature

Clear cutting generally increases the diurnal amplitude of soil surface temperatures (Lundmark-Thelin and Johansson 1997). Typical harvest practices remove or disrupt the organic layer while removing vegetation, both of which moderate fluctuations in soil temperature. Clear cutting in winter (under snow cover), with branch debris left on site, maintains soil temperatures and moisture conditions similar to those of an intermediate successional forest (Yarie 1993). Winter logging also retains the organic layer at the soil surface, which is equally important in maintaining soil moisture and controlling evaporation (Yarie 1993). Relatively high wind velocities on cut sites also influence temperature by further increasing evaporative losses, and lead to extremes in temperature relative to uncut stands.

1.3.3.2 Harvest Intensity

Although clear cuts are characterized by the removal of all stems in a cut area, the actual biomass removed varies with the clear cut method employed. Two types of clearcuts are commonly used for fire-adapted species: 1. Full-tree harvest and 2. Tree-length harvest. Under full-tree harvest, individual trees are cut and skidded from the harvest site to be de-limbed and cut to length. Full tree harvesting permanently removes most above ground biomass from the original growing locations. Tree length harvesting cuts stems to length at, or close to, the original growing location, retaining branches, leaves or needles over the harvest area (known as slash or residual). The amount of nutrient removed in above ground biomass after logging is assumed to have effects on soil quality and site productivity (Aber et al. 1978, Olsson et al. 1996).

A major concern in forest soil research is the possibility of long term reduction in site productivity with prolonged removal of residual (full tree harvest vs. tree length harvest)(Olsson et al. 1996). Greatest nutrient concentrations are generally found in the foliage, followed in concentration by fine roots, twigs, coarse roots, stem bark and stem wood (Kimmins 1977). It follows that younger trees, and trees with relatively large crowns, have higher amounts of nutrient on a per volume basis than old trees or small crowned trees. Therefore, differential harvesting by tree age and species, along with harvest intensity (tree-length or full-tree) will influence the retention of nutrients on the harvested area (Kimmins 1977). Rotation length also affects nutrient demands on a site. For example, changing from one 30 year aspen harvest to three 10 year harvests (full-

tree) can decrease Ca, K, P and N by 173%, 234%, 239% and 345% respectively (Boyle 1975 in Kimmins 1977). In general, risks of soil impoverishment increase as rotations shorten (Kimmins 1977).

Different harvest techniques result in various levels of organic matter recovery to the forest system. Whole tree harvesting removes 2-4 times the nutrients of conventional harvest, where slash and debris are left on-site (Olsson and Staff 1995). Removal of organic matter during whole-tree harvest results in exposed conditions for regenerating vegetation (Olsson and Staaf 1995). The quantity of material removed has a major effect on the forest floor. After 15 years it is predicted that tree length harvest site would have up to 60% more forest floor biomass than whole tree harvested hardwood stands (Aber et al. 1978). Reductions in the amount of organic matter in soils may lead to a corresponding decrease in water retention and nutrient load (Olsson et al. 1996). Decreased levels of organic matter in soil, and the effect on cation exchange capacity and moisture retention, may be most important on dry or previously low productivity sites (Olson et al 1995).

Dead wood (including slash) acts as a buffer, immobilizing nitrogen in a carbon rich substrate via microbial action, to be released slowly through decomposition (Aber et al. 1978). In coniferous forests, higher concentrations of both organic and inorganic nitrogen are found under slash piles than adjacent slash-free sites (Rosen and Lundmark-Thelin 1987). In general, forests are held in an early state of succession for a longer period of time following full tree harvest, taking longer for soil organic matter to build and develop

mature forest characteristics (Aber et al. 1978). Potential for fiber loss, and corresponding effects on soil, increases with multiple rotations (Aber et al. 1978).

A) Temperature and moisture under slash

Slash provides a moderating influence on soil temperature after harvest, reducing the amplitude of surface soil temperatures (Rosen and Lundmark-Thelin 1987). Temperature fluctuations are reduced by approximately 50% under slash depths of 30 cm in coniferous harvest areas. Soil exposed during the harvest process experiences moisture fluctuations throughout the growing season. However, slash cover results in less variable moisture conditions by reducing evapotranspiration. Temperature and moisture levels under slash favour and enhance decomposition, resulting in rapid mineralization of plant nutrients.

B) Decomposition

Conditions after harvest, including increased moisture, temperatures, available nutrients, and organic matter, favour rapid decomposition. Woody debris added to the forest floor is also relatively small (in the form of bark and twigs) and decomposes quickly (Aber et al. 1978). Differences in rate of decomposition with size classes can influence the degree to which slash becomes a physical barrier to regenerating vegetation. Dense slash layers can impede development of some sensitive species (Olsson and Staaf 1995). Overall, decomposition on clearcuts results in faster mineralization of phosphorus and other nutrients compared to unharvested forest (Bekunda et al. 1990).

C) Leaching after harvest

Harvest intensity influences the magnitude of nutrient leaching after clear cutting (Staaf and Olsson 1994). Soil water chemistry is most stable in plots harvested by conventional methods (slash left evenly on site) that maintain less variable moisture under slash (Staaf and Olsson 1994). In general, removal of trees increases leaching for the first 4 to 10 years after cutting (Staff and Olsson 1994). Vegetation cover following harvest may not be sufficient to retain released nutrients, resulting in a loss of N leachate and eutrophication of ground water. Electrical conductivity of tree length harvested plots can be twice as high as whole tree harvested plots, inferring that the nutrients after whole tree harvesting are flushed through the topsoil and leach from the root zone. This effect may no longer be detectable within 4 years of harvest, when nitrogen mineralization rates return to those of unharvested stands (Staaf and Olsson 1994).

Piling slash (rather than evenly distributing it) may lead to increased nutrient loss from the harvested system (Staaf and Olsson 1994). Moisture retained under slash, and soluble organic compounds, may stimulate nitrifier activity when slash is retained at high density. High leaching under slash may also result from suppression of new vegetation, until vegetation is able to take up available nutrients and become stimulated by nutrient addition (Kimmins 1977; Nykvist and Rosen 1985; Rosen and Lundmark-Thelin 1987; Staaf and Olsson 1991; Staaf and Olsson 1994).

In some locations, whole tree harvest may lead to lower leaching of nutrients than conventional (tree length) harvest. Sites with rapid vegetation development, primarily grasses, show stabilized nutrient concentrations after harvest (Staff and Olsson 1994). Site preparation that retards development of vegetation on new cut blocks results in nutrient loss after forest cutting. Within ruts of mechanically prepared sites, rates of decomposition and concurrent mineralization are higher than on unprepared land, further increasing losses through leaching (Lundmark-Thelin and Johansson 1997). Mechanical preparation also delays re-vegetation by disrupting or preventing clonal development (Lundmark-Thelin and Johansson 1997).

D) Shading from slash

Slash acts as an important source of shade in clearcut areas. The physical presence of slash influences species composition and abundance on cut over areas (McInnis and Roberts 1994). Slash loadings alter the intensity of direct solar radiation reaching the forest floor, impacting the recruitment of species within the seed bank. 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). Shade-intolerant species such as white birch, red maple, pincherry and raspberry attain higher stocking densities on exposed sites after full-tree harvest, where light intensity and surface soil temperatures are highest, compared to tree length sites with retained slash (McInnis and Roberts 1994). The effect of solar radiation on the forest floor has a greater influence on the regeneration of species such as white birch than scarification and a mineral seed bed (McInnis and Roberts 1994).

CHAPTER 2

TREMBLING ASPEN AND BALSAM POPLAR

2.1 ASPEN DOMINATED COMMUNITIES

Balsam poplar and trembling aspen are both considered early successional species. It has been noted that aspen stands may be succeeded by shade tolerant trees such as black and white spruce over time (Carleton & Maycock 1978; Bergeron & Dubuc 1989). The two *Populus* spp. share similarities in climatic range, growth rate, modes of regeneration and shade tolerance (Rowe 1956). However, balsam poplar is better adapted to establishment on silty alluvial deposits and out-competes aspen on poorly drained sites (Zasada & Phipps 1990; Perala 1990). By comparison, trembling aspen performs better on higher nutrient, well-drained substrates. Aspen is found in association with most other boreal tree species (Peterson and Peterson 1992). It occurs as early successional remnants in mixed forests with white or black spruce and balsam fir. On recently burned sites it may also be found with jack pine. Mixed hardwood assemblages with poplar and birch are common, although aspen may occasionally occur with oak.

2.1.1 Aspen Parkland

At the southern fringe of the boreal forest, aspen forms an ecotone with prairie grasslands. In contact with grassland, aspen may be considered the climax tree species of

the successional sequence (Bird 1961). Given sufficient moisture and infrequent fire, aspen may gradually replace prairie grasses and form a closed forest. Further expansion into prairie from existing groves occurs via root suckering.

Aspen seedlings are out-competed by grasses in open prairie, but new groves may establish on disturbed patches (Bird 1961). In the past, frequent prairie fire limited the invasion of aspen into bordering grasslands. Conversion of prairie to farmland, and subsequent reduction in fire frequency, has resulted in extension of aspen into southern Canada's prairie remnants.

2.1.2 Boreal Forest

Trembling aspen is in greatest abundance in central and northern portions of its range (Rowe 1961). At the ecotone with northern coniferous forest, aspen forests form the sub-climax canopy prior to white spruce dominance (Rowe 1961). Succession from aspen forest to white spruce may follow two separate patterns on upland sites (Peterson and Peterson 1992). Rapid regeneration and growth of aspen (and birch) after fire results in a hardwood canopy, often with later spruce recruitment. As aspen is crowded or degenerates, spruce remains (Rowe 1961). Another pattern, if site conditions are optimal and a seed source is available, is for spruce and aspen seedlings to develop concurrently. In the latter case, even-aged white spruce may dominate the canopy without a preceding hardwood stage. A commonly encountered intermediate stage of this forest community may show aspen and spruce co-existing in a comparable height class, with both species initiating growth at the same time after disturbance.

One approach to describing the shift from an aspen and poplar-dominated canopy to softwoods is to characterize it as a textbook example of unidirectional successional change (Peterson and Peterson 1992). However, others find that fire-dominated boreal systems do not necessarily follow the traditional view of aspen succession as described by Rowe (1961). Repeated disturbance, if it occurs more frequently than the minimum age for seed production in the local softwood species, may remove the seed source for softwoods and result in pure aspen or aspen/poplar forest. Self-replacing aspen stands are also recorded on some locations (Lavertu et al 1994; Hamel and Kenkel 2001).

Three types of aspen succession have been outlined by past (Peterson and Peterson 1992) and recent work (Hamel and Kenkel 2001): 1. "Decadent" aspen forests are described as stands with low levels of regeneration, high mortality of mature aspen and no replacement by conifers; eventually replaced by shrubs and grasses; 2. "Stable" aspen, with high aspen stocking after disturbance and evidence of multiple generations of aspen, low mortality and few conifers; 3. "Seral" aspen forests, described by high aspen stocking after disturbance, but with conifers increasing in dominance as aspen regeneration decreases. The seral type is said to dominate mixedwood stands across the prairies (Peterson and Peterson 1992).

Vegetation dynamics of aspen forests may also be largely dependent on influences other than fire. In Saskatchewan, successional trends are influenced by landform rather than fire history (Rowe 1955). Aspen stands on low till ridges between depressions dominated by black spruce were replaced by black spruce. Aspen on dry sand landforms

in the same region were later replaced by jack pine stands, or black spruce-birch on north facing slopes and jack pine-white spruce on south facing slopes. Such variability makes it virtually impossible to describe succession in aspen dominated communities as a unidirectional process.

2.2 *POPULUS TREMULOIDES*

2.2.1 Distribution

P. tremuloides and *P. balsamifera* are sympatric throughout most of the boreal biome. *P. tremuloides* has the widest distribution of all North American native tree species, extending from Newfoundland west to north west Alaska bordering the northern tree limit, south through the Yukon and British Columbia (Perala 1990). Trembling aspen is found in the southeast to New Jersey. To the west it reaches further south through the mountains of western United States to California, Arizona, Texas and Nebraska (Perala 1990). Remnant populations are also found in Mexico (to Guanajuato).

2.2.2 Climate

Trembling aspen is distributed between the 24°C mean July isotherm to the south, and 13°C mean July isotherm in the North, indicating a tolerance to a wide range of climatic conditions (Maini 1968). In Montana, the species has endured extremes of -57°C in January and 41°C in July (Perala 1990). Although its northern limits fall within the permafrost zone, it is generally restricted to warmer (permafrost-free) sites (Perala 1990).

Water surplus is the primary limitation on distribution of the species, followed by temperature extremes during the growing season (Perala 1990). Trembling aspen is restricted to sites where precipitation exceeds evapotranspiration. Water requirements influence the southern extent of aspen distribution in the western mountains, and the southern limit in the prairies.

2.2.3 Edaphic Requirements

Trembling aspen is found on soils ranging from Solonchic, Podzolic and Brunisolic orders with shallow rocky to heavy clay and loamy textures (Perala 1990). Best growth is observed on basic parent materials such as calcareous shales and limestones (Perala 1990) (as found in southern Manitoba). The rapid growth potential of aspen and poplar is optimized on well-drained, nutrient rich (high magnesium, potassium, nitrogen and calcium) substrates with high organic content.

Sand soils are usually low in nutrients and available water. These detrimental growth conditions are reflected by slow growth in the Great Lakes where 50 year old trees reach only 17 m in height. On loams, 50 year growth increases to 21 m and silty loams up to 25 m (Perala 1990). Best growth is observed on high percent silt/clay soils (not heavy clays), producing high-density timber. Aspen growth is largely limited to sites with a water table between 0.6 m and 2.5 m. Water regime also affects aspen distribution on a topographic scale. For example, aspen shows preferential abundance on warm, high precipitation southwest slopes, but may be excluded by birch on cold northern aspects of the same topographic feature (Perala 1990).

Aspen requires high light for healthy, rapid growth. Shade intolerance results in natural self-thinning of aspen stands, which results in a tree form characterized by long, clean stems topped by shallow open crowns (Perala 1990; Peterson & Peterson 1992).

2.2.4 Reproduction

Both *P. tremuloides* and *P. balsamifera* are able to reproduce sexually (via seed production) and asexually (suckering via roots and in poplar, roots and shoots from a trunk or branch), giving a regenerative advantage over coniferous species. The combination of sexual and vegetative reproduction ("suckers") also allows for rapid invasion (or re-emergence) of *Populus* stands after disturbance (whether at a local or landscape scale).

2.2.4.1 Sexual Reproduction

Optimal conditions for germination and establishment of aspen from seed are rare, thus limiting the contribution that seedlings make to forest canopies when competing with healthy suckers (asexually produced shoots) (Perala 1990). Desiccation, fungi and temperature fluctuations result in high mortality of seedlings. However, seedling-origin stands are documented on primarily burnt and exposed mineral substrates. Seed regeneration may be most significant at the northern limits of aspen distribution, where soil conditions are not conducive to suckering (Zasada et al. 1992).

Seedling densities range from 1000 to 16000 individuals per hectare, depending on the sucker / seedling ratio (Peterson & Peterson 1992). Growth is rapid for approximately 20 years, slowing beyond sexual maturity (Perala 1990). Height growth of seedlings is lower than suckers on the same site (Perala 1990; Peterson & Peterson 1992). Regardless of stand origin, natural thinning occurs rapidly. As individual suckers or seed-origin trees are overtopped, they become stunted and eventually die (Zasada et al. 1992).

Populus species are predominantly dioecious. Groups of suckers originating from a single seed tree are considered a "clone". In aspen, female clones are larger than male clones when they reach sexual maturity (Peterson & Peterson 1992). Aspen matures sexually between 10 to 20 years of age (Maini and Horton 1966). Upon maturity, good seed crops are produced every 4-5 years. However, open grown individuals may mature in 1-2 years and produce seeds annually (Perala 1990). Optimal seed production is reached between 50 and 70 years. Flowers are produced in early to late spring and wind pollinated soon after development. The effective fertilization period is extended by variation in pollen development and release among clones. The fruiting catkins develop 4-6 weeks after fertilization (Perala 1990). Aspen seeds are light (5000-8000 seeds per gram) with silky hairs to aid in dispersal via wind and water. Dispersal occurs 3-5 weeks after ripening.

Strict seed bed conditions are required for successful germination, since seeds lack endosperm and a dormancy period (Perala 1990; Peterson & Peterson 1992). Under favorable germination conditions, seed viability is only 2-4 weeks (Perala 1990). The substrate must be nutrient rich, with appropriate moisture levels for successful

germination and establishment. Mineral beds meet nutrient requirements but are subject to rapid desiccation. Maini and Horton (1966) found most successful germination in moist or wet microhabitats. Moderate temperatures and minimal competition are also required for seedlings to establish (Steneker 1974). Seedlings grow up to 30 cm in height in their first year, while tap roots grow down approximately 25 cm (Perala 1990). Roots grow to 2 m by the second year, forming mycorrhizae where appropriate inocula exist (Peterson & Peterson 1992).

2.2.4.2 Asexual Reproduction (Suckering)

The majority of aspen regeneration occurs via vegetative shoots from lateral root meristems. Stump and stem suckering is also exhibited in aspen, but this ability is limited to young trees (Peterson & Peterson 1992). Aspen as young as one year old can produce suckers from lateral roots (Perala 1990). Aspen root systems measure over 30 m laterally, and are concentrated in the upper 50 cm to 75 cm of the soil (Gifford 1966). Aspen roots show the same vertical distribution throughout succession. Root densities remain highest in the top 30 cm of mineral soil for stands aged between 48 and 232 years (Finer et al 1997). Suckers emerging from parent roots have diameters ranging between 1 and 94 cm (Lavertu et al. 1994). Root suckers originate from elongation and differentiation of meristems on surface roots within the top 10 cm of soil (Horton and Maini 1964). Meristem maturation (and root growth itself) is highly sensitive to soil temperatures (Maini and Horton 1966; Steneker 1974). Maini and Horton (1966) found highest and most rapid suckering occurred in aspen held between 17.8°C and 30.6°C. Lowest suckering was observed under the temperature extremes of 14.4°C and 35.0°C.

Optimal conditions for shoot development are release of apical dominance, allowing a relative increase in cytokins for tip development, and an increase in soil temperature to 23.3°C. Removal by fire of the parent tree, associated vegetative cover, litter mat and subsequent competitors achieves both requirements (Maini and Horton 1966; Perala 1990). Removal of apical dominance by harvesting also stimulates sucker development. Highest suckering is achieved on well to imperfectly drained fine textured soils (Harvey and Bergeron 1989). Optimal conditions result in typical sucker densities of over 25,000 trees per ha., with canopy closure occurring as soon as 2-3 years after a disturbance.

Soil moisture and decreased soil aeration associated with saturation (Maini and Horton 1966), seasonal changes in root carbohydrate storage (Scheir and Zasada 1973), and clonal variation also influence suckering ability and density. Ability to sucker does not decrease with age until breakup (or decay of over mature stands)(Steneker 1974; Schier 1982). However, some stands show continued ability to replace stems throughout the "typical" age of stand breakup (Lavertu et al 1994).

Clones can vary in size, shape and/or growth pattern. Clone size is a function of age, density of initial cohort, proximity to neighboring clones and disturbance regime since establishment. Clones can often be identified by slight morphological similarities in adjacent trees (bark, leaf, disease resistance, shape etc.) and timing of leaf flush or leaf fall (Peterson and Peterson 1992).

A) Suckering after fire

Fire was an important component in the perpetuation of aspen in the past. More recently, lack of fire through suppression (Bartos and Mueggler 1981), habitat fragmentation (Brown and Debyle 1987; Kay 1997) and ungulate browsing (Bartos and Mueggler 1981) may threaten the long-term persistence of aspen in some areas. Fire promotes suckering by removing stems, thereby removing hormonal inhibitors and releasing root buds from apical dominance (Bartos and Mueggler 1981; Brown and Debyle 1987). Litter and woody debris are also consumed by fire, resulting in high soil surface temperatures and minimal shading of the forest floor.

Initial sucker densities range from 8000 to over 55000 per ha within the first two years after fire (Brown and Debyle 1987). Maximum densities are reached in the first year after burning, followed by a period of self-thinning. Suckering densities are not influenced by fire severity (Brown and Debyle 1987; Bartos and Mueggler 1981). Brown and Debyle (1987) found no relationships between number of new suckers after fire and burn depth, mortality of pre-fire trees, basal area of pre-fire stand or dead tree basal area. Variation in sucker densities after fire are thought to include vigor of adults, age and size of stems, density of shallow roots and depth, soil, competition and clonal variation.

A) Suckering after logging

Logging also removes mature trees, releasing roots from apical dominance and opening the canopy to increase light reaching the forest floor (Steneker 1974; Bartos and Mueggler 1981). Suckers emerge in high densities after logging on most sites throughout the southern boreal forest and aspen parkland biomes. Sucker densities can reach 77000 stems per hectare following a clear cut followed by a rapid self-thinning (up to 65% mortality)(Shier and Campbell 1978; Lavertu et al 1994). Sucker densities after logging are often sufficient to delay the reestablishment of a formerly dominant species, even with only a few aspen present prior to harvest (Lavertu et al. 1994). Cutting and subsequent aspen regeneration usually retards the establishment of a later successional species.

A) Persistence of clones

Aspen maintains an extensive root system for many years after conifers dominate a stand. Aspen present in a conifer-dominated forest, at least 230 years old, produced sucker densities of 21875 stems per ha after clear cutting (Lavertu et al. 1994). The first suckers to emerge after clearing were over 15 m from the nearest aspen stump, and had covered the clearcut within a few weeks (Lavertu et al.1994). Within some aspen dominated stands, a portion of mature trees were shown to originate well after the initial stand-level disturbance (or overall stand age), representing second and third generation of aspen regenerating from the root system (Lavertu et al. 1994; Hamel and Kenkel 2001).

2.2.4.3 “Natural” Limitations to Regeneration

A) Small mammals

Aspen, and to a lesser extent balsam poplar, are important food sources for mammals in the boreal forest. Many small mammals girdle trees and remove buds, damaging trees by direct feeding and increasing susceptibility to disease. Porcupines (*Erethizon dosatum*) may feed heavily on branches and trunks in the winter, preferring young shoots and leaves in the summer. Snowshoe hare (*Lepus americanus*) and cottontails (*Sylvilagus* spp.) feed on young trees and seedlings in the summer, eating shoots and stems. During winter they feed on young bark, often girdling young trees. Rabbits are able to forage on increasingly higher plant parts as snow depths increase, providing access to 1-2 m of the lower branches and stem. Other small mammals, such as mice (*Peromyscus* spp.) may also girdle trees beneath the snow (at ground level) in times of food stress.

Beaver (*Castor canadensis*) cut down large numbers of trees as a food source and construction material along water courses (Perala, 1990). The 5 cm size class of aspen is preferred, although almost any size may be taken. The best forage for beaver is aspen bark and young growth. A mature beaver eats between 1 and 2 kg of aspen bark per day, requiring approximately 200 trees in a year (Peterson & Peterson 1992). Beaver also cause indirect mortality of aspen through flooding. Successful regeneration of aspen along stream beds is important to bank stability and water quality (Peterson & Peterson 1992).

B) Ungulates

Moose (*Alces alces*), elk (*Cervus canadensis*) and deer (*Odocoileus* spp.) can all have a significant effect on aspen forests by breaking, browsing, rubbing and debarking trees (Heinselman 1973). Aspen is a major browse species for many ungulates, second only to willow. Moose, elk and white tailed deer feed heavily on aspen in the winter (Cairns & Telfer 1980; Bartos and Mueggler 1981; Peterson & Peterson 1992; Telfer 1970), when snow cover limits the availability of graminoid and shrub forage. Ideal aspen forage is found in relatively young stands under 2.4 m, for example those which have been recently burned or logged (Peterson & Peterson 1992). Some studies show that moose prefer the crown twigs of mature felled trees over young growth (Telfer & Cairns 1978). Moose are known to break and bend over trees up to 10cm in diameter to reach foliage. However, moose in Alberta tend to favor aspen stands less than 10m for feeding grounds (Rolley 1980). In general, ungulates feed on leaves and young shoots, although bark and lignified stems will be eaten in the absence of other food sources, during late winter for example. Removal of dominant shoots results in "bushy", stunted growth. Bark damage may directly kill trees through girdling, or more frequently results in scarring and entrance wounds for secondary infection by pathogens and insects.

Ungulates can have a severe effect on the regeneration abilities of aspen. In Kootany and Yoho National Parks ungulate populations prevented aspen growth (in height) and successful regeneration (Kay 1997). Browsing can be sufficient to hold stands at only 1-2m in height. Aspen stands freed from intense browsing, in exclosure studies, resumed natural growth after 2-3 years. Ungulate herbivory has also shown to affect vegetation

dynamics and successional trajectories in the absence of other disturbances. "Normal" or historical aspen stands (those without heavy browsing) were multi-aged. However, heavy browsing maintained aspen forests in a seral state, while maturing conifers remained to dominate the canopy (Kay 1997). In the absence of fire (which removes encroaching conifers), ungulate herbivory may be sufficient to gradually exclude aspen stands from some portions of its present distribution (Kay 1997).

Vegetation dynamics and succession in aspen forest and mixed stands may have an equal impact on the population dynamics of ungulate populations. The patchy habitat produced by fire, and concurrent increase in deciduous browse, often result in an ungulate population increase. However, these populations normally diminish as the forest ages, and browse becomes less accessible (Peterson & Peterson 1992).

C) Insects

The largest group of insects affecting aspen (and balsam poplar) are the defoliators, primarily Lepidoptera (butterflies and moths) and Coleoptera (beetles) (Peterson and Peterson 1992). Important Lepidoptera include forest tent caterpillar (*Malacosoma disstria*), bruce spanworm (*Operophtera bruceata*) (not seen in Saskatchewan or Manitoba), large aspen tortrix (*Choristoneura conflictana*) and aspen leaf miners (*Phyllonorycter* spp.). Beetle herbivores include aspen leaf beetle (*Chrysomela crotchii*) and the poplar and willow borer (*Cryptorhynchus lapathi*).

Defoliators such as the forest tent caterpillar consume a large amount of leaf volume,

but damage is short lived. Outbreaks appear every 10 years (approximately) and last 3-6 years (Cerezke 1991). Aspen is the preferred species, although other hardwoods are attacked during severe infestations. Larval feeding occurs as buds develop in early spring (April or early May). Initially, larvae feed on opening buds, but later feed on whole leaves from the outer crown inward. Early feeding kills many aspen buds. Two or more years of severe defoliation may result in reduced growth, smaller leaf size or branch mortality. Tree mortality (up to 80%) may occur after 3 or more years of defoliation (Peterson and Peterson 1992), although other stress factors (such as drought or early spring frosts) are often involved. Trees weakened by defoliation are more susceptible to decay, stem canker disease and boring insects. Infestations are characterized by a profusion of silken threads that are used for transport between feeding sites and resting platforms. Mature larvae produce cocoons after a season of feeding. Adult moths appear in July, and deposit a brown band of eggs around small twigs.

The large aspen tortrix primarily attacks poplar and willow, although it may feed on aspen as a precursor to tent caterpillar outbreaks (Peterson and Peterson 1992). Larvae hatch approximately 10 days prior to leaf flush to feed on leaf buds and later leaves. At maturity, females lay eggs in clusters on upper surfaces of leaves, or anywhere if no leaves are available.

Three species of aspen and poplar leaf miners are common throughout the prairies (Peterson and Peterson 1992). *Phyllocnistis populiella*, the aspen serpentine leaf miner, forms snake-like mines in upper and lower leaf surfaces. *Phyllonorycter salicifoliella* mines the underside of aspen leaves in a blotchy pattern. With severe infestations, leaf

miners may cause premature leaf drop. Leaf miners are only locally abundant, and normally result in little economic damage.

Aspen is a host to many boreal wood-boring insects. The most common is the aspen carpenter worm (*Acosus centerensis*) and the poplar-and-willow borer (Brandt 1994). Other bark beetles (Scolytidae), longhorned or roundheaded beetles (Cerambycidae) and flat head wood borers (Buprestidae) attack dead, dying or unhealthy trees (Brandt 1994). Wood bores not only weaken trees structurally, but also provide entry for pathogen infection and other insect attack. Attacked trees may be susceptible to wind and snow damage. Aspen carpenter worms are found throughout Alberta, Saskatchewan and Manitoba. Adults emerge in June and July to deposit eggs near wounds and in bark crevices. Eggs hatch approximately 2 weeks later and burrow into the stem. Larvae feed and develop into adults over a 3-4 year period. The poplar-and-willow borer was introduced from Europe, and is now found throughout Alberta and Manitoba wherever willow grows (Brandt 1994). Although no official accounts of poplar-and-willow borer are known for Saskatchewan, it is probable that the species also occurs there. It takes only 2 years for the poplar-and-willow borer to reach maturity. Adults feed on new shoots prior to mating. Egg deposition occurs in the summer. Females puncture the bark of new shoots and deposit 1-3 eggs in each puncture. Larvae initially feed by mining the bark, but later move into the wood.

B) Pathogens

Over 250 species of fungi are known to infect North American aspen, although most are responsible for the decay of dead timber and fallen trees (Peterson and Peterson 1992). 17 fungal species are identified as causing decay in standing live trees in Alberta (Thomas et al. 1960). Decay can be divided into three major categories: Root and butt rot; trunk rot and stain; and sapwood decay and stain.

Armillaria spp. are the primary cause of butt and root rot in many stands. Nine species have been identified, the most prevalent being *Armillaria ostoyae* (Peterson and Peterson 1992). Yellow stringy rot occurs within the bottom 1 m of the trunk. Mortality rates due to infection are not known, but infection may affect rotation times and the ability of aspen to regenerate vegetatively. Mushrooms are produced in the late summer to early spring surrounding decayed wood at the base of the tree and on infected rhizomes. Internal evidence of *Armillaria* resembles black "shoestrings" through infected wood. The "shoestrings" generally extend into the neighboring soil.

Phellinus tremulae is the most common decay-causing fungus of mature trees, characterized by moon-shaped "conks" around the trunk (responsible for trunk rot) (Peterson & Peterson, 1992). In Ontario, over 60% of aspen are infected by *Phellinus tremulae*, with 75% of volume lost to disease attributable to this species. Decay occurs throughout the main stem, producing a decay column that extends above and below the conk approximately 370 cm. *P. tremulae* is not transmitted to new suckers after the parent trees are removed, although scarification after suckers have emerged increases

early infection of the stand (Peterson and Peterson 1992).

Two species are responsible for stain in aspen, *Peniophora polygonia* and *Radulum casearium* (Peterson and Peterson 1992). Stain is a discolouration of wood, with small pockets of decay along the trunk. Infected wood usually remains firm, although it may be more brittle than uninfected wood and result in splitting. Both species are difficult to identify in the field, since they lack conspicuous external indicators. Stain species may sufficiently alter the host tissues to allow for infection by more destructive pathogens such as *Phellinus tremulae*. However *P. tremulae* and *P. polygonia* appear to antagonize each other, forming distinct demarcations between the two types of infection.

E) Frost

Frost damage affects both aspen and poplar trees of any age and stand type (Zalasky & Hiratsuka 1992). Alternation of freezing and thawing temperatures kills some tissues, causing surrounding tissue to grow abnormally. Cambium and bud tissues are highly sensitive to the damage caused as ice crystals expand within them. Symptoms of frost damage include dieback (from a few branches to whole crowns), frost heaving of tree roots, cankers, burls and ribs. Dead branches and leaves tend to remain on the tree. Bud sports, which are frozen and deformed buds, may also develop into abnormal leaves and shoots, resulting in stunted bushy branching. Frost heaving uproots and exposes roots, inhibiting growth and weakening the tree. Frost cankers are formed as bark freezes, splitting and exposing inner wood. The split bark can heal to form a scar, or repeatedly freeze and crack along the trunk. In response to damage, the tree produces thick bark

around the canker or split, re-enforcing the damaged region. Frost damaged tissues are often sites for infection by fungal pathogens. Most damage occurs in the spring and fall, although "Chinooks" along the east slopes of the Rocky Mountains produce freeze-thaw conditions throughout the winter months in Alberta and Saskatchewan.

F) Fire

Stem survival after fire in aspen is influenced by bark thickness (Brown and Debyle 1987). Consequently, young trees and seedlings, which have very thin and delicate bark, incur severe damage and mortality if burned (Peterson & Peterson 1992). Thick bark at the base of mature trees may be protective against light ground fire. Even with thick basal bark, low intensity ground fires scar aspen at the base of the tree, and act as an infection point for canker diseases.

Fires that char over 75% of stem circumference, and brown bark over 90%, directly and immediately kill aspen. Trees surviving fire show less than 50% charring and 60% browning of their circumference (Brown and DeByle 1987). Fires in aspen tend to be light to moderate intensity. However, in mixed forests, highly flammable fir trees "torch" aspen resulting in trunk charring 5-10 times higher than in pure aspen stands (Brown and Debyle 1987). Intensities required to kill aspen are equivalent to those required to maintain spread of fire in a typical pure aspen burn. Flame heights of 45 to 60cm will kill most trees less than 25 cm dbh. Lower flame heights are not self sustained, and do not cause high mortality (Brown and Debyle 1987).

G) Flooding

Flood tolerance in aspen is very low, limiting its distribution in areas subject to frequent inundation (Peterson & Peterson 1992). In contrast, aspen is relatively successful on dry sites, including those prone to periodic drought. Once established, aspen clones develop extensive root systems concentrated below the systems of understory herbs and grasses, in effect reducing competition for water between the strata (Peterson & Peterson 1992). Leaf area is also relatively low in pure aspen stands, resulting in relatively low water demand. Drought rarely kills aspen stands, but stressed trees may be more vulnerable to insect damage and pathogen infection, than those on sites with ample soil water (Peterson & Peterson 1992). The direct effect of drought is usually a period of natural thinning, followed by regeneration.

2.3 *POPULUS BALSAMIFERA*

2.3.1 Distribution

Balsam poplar is less widely distributed than aspen. It is notably absent west of the Rocky Mountains, where it is replaced by *Populus trichocarpa*. Unlike trembling aspen, its distribution does not extend far south of Lake Michigan (restricted to the "typical" band of boreal forest).

2.3.2 Climate

Most of balsam poplar's range has a continental climate, although it does occupy regions in the maritime zone (Zasada & Phipps 1990). Temperatures range between the extremes of -62°C in the winter and 44°C in the summer. Precipitation levels over balsam poplar habitat are equally variable (between 300 mm in Alaska and 1400 mm in the maritimes), although the species seldom occurs on sites affected by prolonged periods of drought.

2.3.3 Edaphic Requirements

Balsam poplar can be found on soils developed from till, outwash, loess and lacustrine deposits. Growth of poplar is best on drained, nutrient rich (high magnesium, potassium, nitrogen and calcium) soils with a high organic content and a neutral pH, but it is often out-competed by aspen on optimal sites. Maximum development is seen on floodplains from Alaska to Alberta. Substrates are commonly flooded through spring break-up, resulting in annual layering of sediment and organic matter. Prior to poplar establishment, hydrology has the dominant influence on soil formation, as the stand matures the vegetation itself controls soil development (Zasada & Phipps 1990). Poplar actually enriches local soil conditions through the addition of calcium as leaf litter decomposes (Rowe 1956).

In young stands, balsam poplar roots obtain moisture from the water table and capillary zone above. Precipitation sources become increasingly important as the stand

ages. Balsam poplar is one of the few boreal tree species associated with poorly drained clay soils. It is frequently found in association with aspen on well-drained sites, although balsam poplar is restricted to drainage channels and local depressions. Excess water in early spring may result in stands with a higher proportion of balsam poplar to aspen.

Balsam poplar is shade intolerant, requiring high light for rapid growth. As in aspen, mature poplar have long self-pruned stems (produced by heavy natural thinning) topped by a light canopy (Perala 1990; Peterson & Peterson 1992).

2.3.4 Reproduction

2.3.4.1 Sexual Reproduction

Balsam poplar produces seed from 8-10 years of age (Zasada & Phipps 1990), with large crops being produced almost every year (Viereck et al. 1983). Unlike aspen, the sex ratio of clones is 1:1, although males occupy drier, less fertile sites than females. Flowering begins in early May (delayed in northern populations), followed by dispersal in June. Dispersal is initiated by dry, warm weather and lasts two weeks, although some seed may remain on trees for up to six weeks. Seeds are dispersed long distances (as in aspen) via wind and water. Water dispersal may be more important in balsam poplar than aspen since balsam poplar is often associated with open water.

Most seed dies within 4-5 weeks, but dry or cold conditions can prolong viability. Aspen seed does not have endosperm and cannot exhibit dormancy. Germination occurs

between 5°C and 35°C given sufficient moisture. Optimal germination is achieved on moist mineral seed beds, although germination may occur on moist, organic substrates with low seedling survival (Zasada & Phipps 1990).

Balsam poplar establishes quickly on sand bars and exposed flood plains. Growth is rapid on exposed sites in the absence of shading by competitors, showing similar shade tolerance to aspen. Poplar is also characterized as an early successional species, although it tends to outlive aspen. Within 15-25 years it can assume dominance, and retain it for 50 to 75 years. After 100-200 years this species generally disappears from the canopy, replaced by more shade tolerant species such as white spruce (Zasada & Phipps 1990).

2.3.4.2 Asexual reproduction (suckering)

A significant amount of poplar regeneration occurs via suckering from both stump and stem. This ability is retained in *P. balsamifera* through maturity (Zasada and Phipps 1990). Regeneration from stem injury and buried limbs is a beneficial trait in sites logged and scoured by heavy machinery (Zasada and Phipps 1990). When similar stem and root damage is inflicted to aspen, suckering ability is reduced (Peterson & Peterson 1992). New stems can develop from broken and intact roots, adventitious and pre-formed buds on stumps and tree bases, and buried stems and branches. Stem densities after disturbance are less than those exhibited by aspen, but balsam poplar sprouts grow faster and coarser on moist sites (Rowe 1956). Greatest densities are achieved when the organic layer is disturbed, removing competitors and increasing soil temperatures (Zasada & Phipps 1990).

2.3.4.2 “Natural” Limitations to Regeneration

A) Small mammals

Herbivore damage to balsam poplar is less severe than aspen because buds and leaves of balsam poplar are high in terpene and phenolic resins. Snowshoe hare and small rodents avoid the unpalatable parts by feeding on internodes of twigs and stems. Girdling may result from heavy feeding. Beavers also prefer aspen over poplar, affecting the relative abundance of these two species in the catchment area. Flood tolerance in poplar reduces indirect mortality by beaver flooding (Peterson and Peterson 1992).

B) Ungulates

Damage from moose, elk and deer is similar to that incurred by aspen stands. They often break, browse, rub and debark trees, avoiding distasteful buds and leaves to feed on stems (Heinselman 1973). However, the relative in-palatability of poplar in comparison with aspen, and the associated difference in browsing pressure incurred by the two species, may determine how the species associate together (Rowe 1956).

C) Insects

The forest tent caterpillar defoliates both poplar and aspen, but damage is short lived.

Effects and patterns of attack are essentially the same in both species (Cerezke 1991). Two or more years of severe defoliation may result in reduction of growth or branch mortality. *Choristoneura conflictana* also defoliates balsam poplar, often preceding an outbreak of the forest tent caterpillar. As in aspen, defoliation is not usually fatal. The leaf miner, *Phyllonorycter nipigon*, mines the underside of poplar leaves, although damage is local and of little economic importance (Peterson and Peterson 1992).

There are many hardwood borers that attack balsam poplar, most of which also attack aspen (Brandt 1994). In general, these wood boring insects attack a variety of hardwoods, although the species preferred (or host) may change over the insect's distribution. The following species attack poplar throughout the prairies: the carpenter worm (*Prionoxystus robiniae*), the poplar carpenter worm (*Acosus centerensis*) and the cottonwood crown borer (*Sesia tilialis*). Other wood boring beetles, flatheaded wood borers and longheaded or roundheaded beetles may also be important. Life cycles and mode of attack are common to both aspen and poplar. The species unique to poplar, the poplar carpenter worm, is only found in Manitoba and Saskatchewan. Damaged poplar is subject to windthrow and secondary infection to the same extent as aspen.

D) Pathogens

Balsam poplar is more resistant to fungal decay than aspen (Rowe 1956). However, poplar and aspen share a number of common foliage and stem pathogens. These include mildew, leaf rust, leaf spot, leaf blight, cancers and gall. Pathogens of balsam poplar include the fungi *Phellinus tremulae* (see aspen section) and *Pholiola destruens* which cause trunk rot (Peterson and Peterson 1992). *Armillaria ostoyae* is the common cause of butt and root rot in balsam poplar.

E) Fire

Effects of fire on balsam poplar are similar to those seen in aspen. Fire damage is linked to bark thickness, and is most severe on young trees and seedlings that have thin succulent bark (Peterson & Peterson 1992). Mature poplar have relatively thick bark, and would presumably providing greater protection from low intensity fires than aspen bark. However, low intensity ground fires often result in scarring as in aspen, and act as an infection point for pathogens (e.g. canker disease). Charring also effects poplar when hot air sears and splits bark along one side of the tree. Although poplar is relatively resistant to decay, lesions resulting from fire provide entry for fungi.

F) Frost

Snow and hail occasionally damages aspen and poplar in Colorado, Saskatchewan,

Manitoba and Alberta, where wet snow or ice load and break branches (Peterson & Peterson 1992). Poplar suckers are less susceptible to frost damage than aspen, although damage may occur in trees of any age or stand type (Zalasky & Hiratsuka 1992). As in aspen, damage results in direct physical abnormalities, and increases susceptibility to pathogen infection.

G) Flooding

Balsam poplar is relatively tolerant to flooding, commonly occurring on sites that are inundated by spring meltwater or heavy runoff (alluvial beds and flood plains). Poplar produces new roots in order to withstand saturated soil and low oxygen conditions. Poplar possess pre-formed root primordia along the stem, which are an adaptation to flooding conditions and the subsequent heavy deposition of sediment around the tree as water levels subside (Peterson & Peterson 1992).

CHAPTER 3

EFFECTS OF HARVESTING ON THE FLORISTIC COMPOSITION, DIVERSITY AND STRUCTURE OF ASPEN-DOMINATED STANDS

ABSTRACT

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 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.

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 (*Rosa ascicularis*), saskatoon (*Amelanchier alnifolia*), common snowberry (*Symphoricarpus alba*), and raspberry (*Rubus idaeus*), with minor amounts of beaked hazelnut (*Corylus cornuta*). The "fresh sub-type" is characterized by high abundance of

beaked hazelnut. The "moist sub-type" is characterized by the presence of mountain maple (*Acer spicatum*), often co-dominant with beaked hazelnut.

In order to assess effects of harvest treatment on the floristic community, herb and shrub species were assigned to functional groups. 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 shrubs declined. These changes in abundance are thought to be temporary, and are attributable to the short-term environmental effects of logging operations, including 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.

3.1 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. Logging also creates a large-scale disturbance that reverts stands to an early successional stage (Yarie 1993).

Frequent disturbance favours shade-intolerant, resprouting species and ephemerals from the seed bank. The boreal hardwoods trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*) and paper birch (*Betula papyrifera*), 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 regeneration following clearcut harvesting.

In recent years, forestry research has focussed on developing harvesting methods that emulate natural disturbance, so as to sustain the biotic and abiotic processes within these disturbance-driven ecosystems (Bergeron and Harvey 1997). There has been a recent shift in boreal forest logging operations from softwood to hardwood harvest, with associated increased utilization of hardwoods in the manufacture of composite building materials (Peterson and Peterson 1992; Manitoba Natural Resources 1996). 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.

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. To achieve these objectives, vegetation and environmental factors were sampled

throughout the Duck Mountain Provincial Forest Reserve in harvested, unharvested edge and interior aspen-dominated forest.

3.2 STUDY AREA

The study was conducted within the Duck Mountain Provincial Forest Reserve, which is located in west-central Manitoba ($57^{\circ}02'$ – $57^{\circ}48'$ north and 350° – 385° east). The Forest Reserve surrounds Duck Mountain Provincial Park. The Duck Mountains are part of the Manitoba Escarpment, which rises approximately 500 m 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).

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 5-8 more centimeters 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.

3.3 MATERIALS AND METHODS

3.3.1 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 3.1, Table 3.1). 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. Mean values were calculated for each cutblock for subsequent analysis (i.e. 34 sites are the replicates).

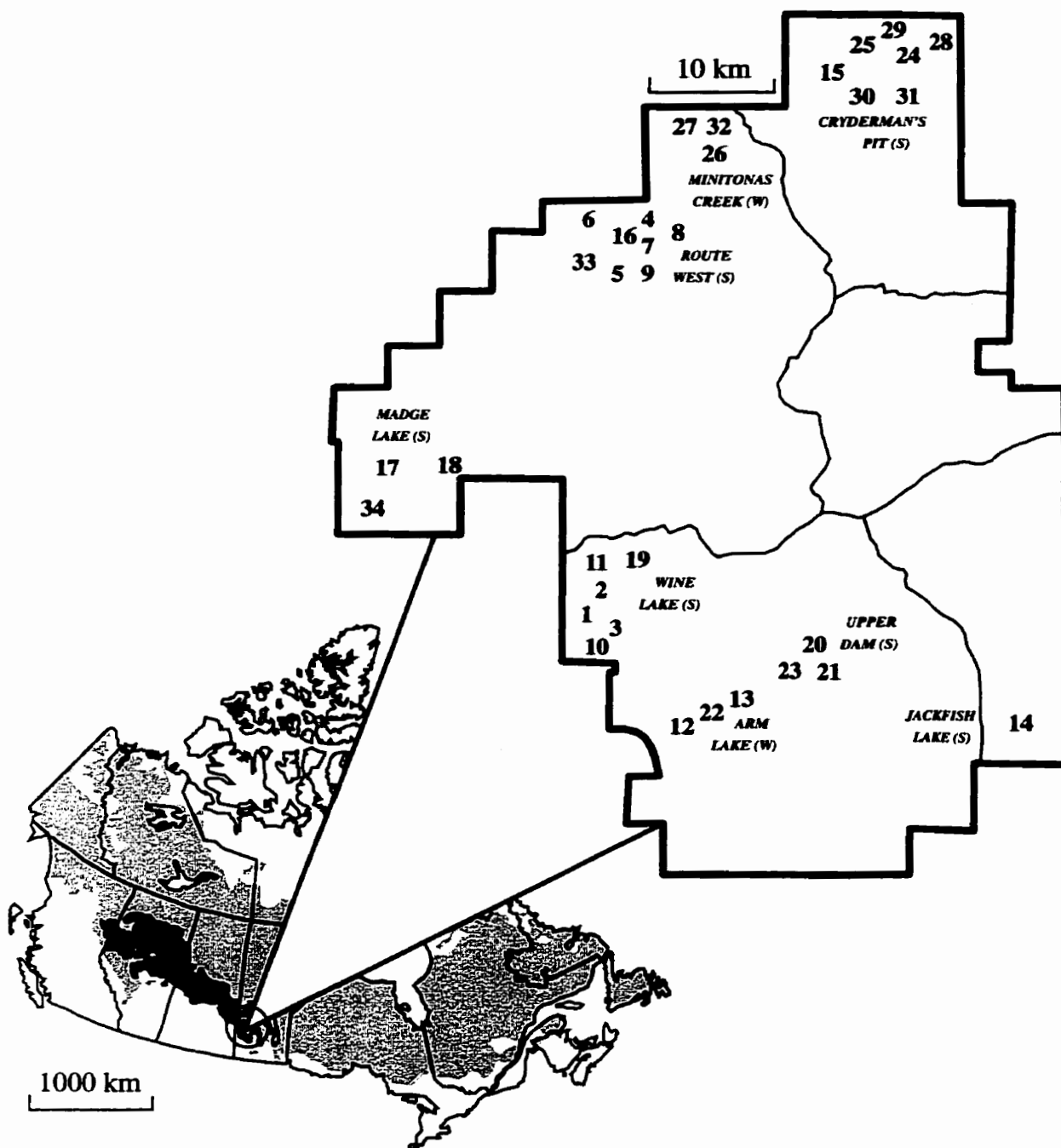


Figure 3.1. Map of logging regions within Duck Mountain Provincial Forest indicating enumerated stand locations. For stand information refer to Table 1.

Table 3.1. 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/ha)			slope (site x10 ³)	site aspect (°)	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/chem
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/chem
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/chem
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/brun
23	fresh	3	Upper dam	summer	60	0	0	0	87	81	76	9.2	230	luvisol
mean					56	1	0	2	148	87	88			
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	282	220			

A single transect oriented perpendicularly to the cutblock edge was randomly located in each stratum. Three 10 m x 10 m 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 3.2**). Logging roads and equipment staging areas (which generally make up < 5% of the cutblock) were avoided when locating 'harvested' plots.

3.3.2 Data Collection

Density, cover and bole size (diameter at 30 cm) of all overstory trees (> 3 m in height) were recorded within each 10 m x 10 m plot. Regenerating tree (suckers and seedlings < 3 m in height) densities and percent cover values were recorded in each of four 2 x 2 m quadrats located within each plot (**Figure 3.3**). 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 3.3**).

Soil profiles were described at each plot, and a soil sample (top 30 cm of mineral soil) was 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).

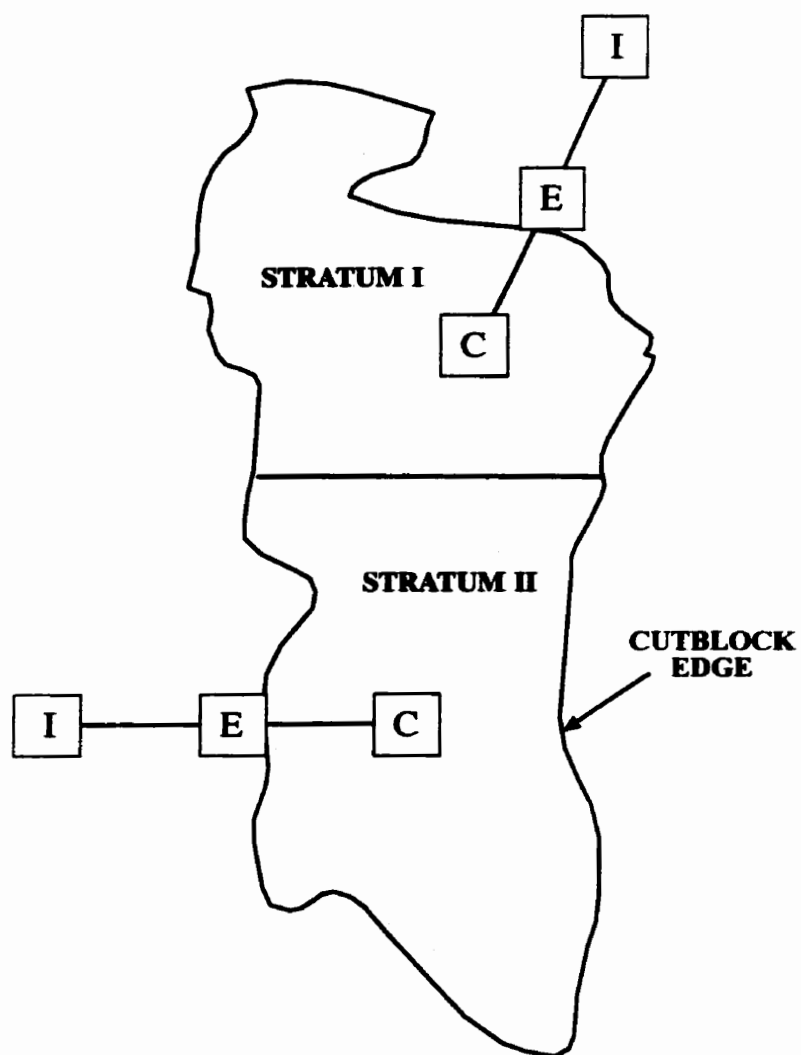


Figure 3.2. The stratified random sampling design used to enumerate vegetation and CWD across harvested aspen stands in cutblock (C), edge (E) and interior forest (I) treatments.

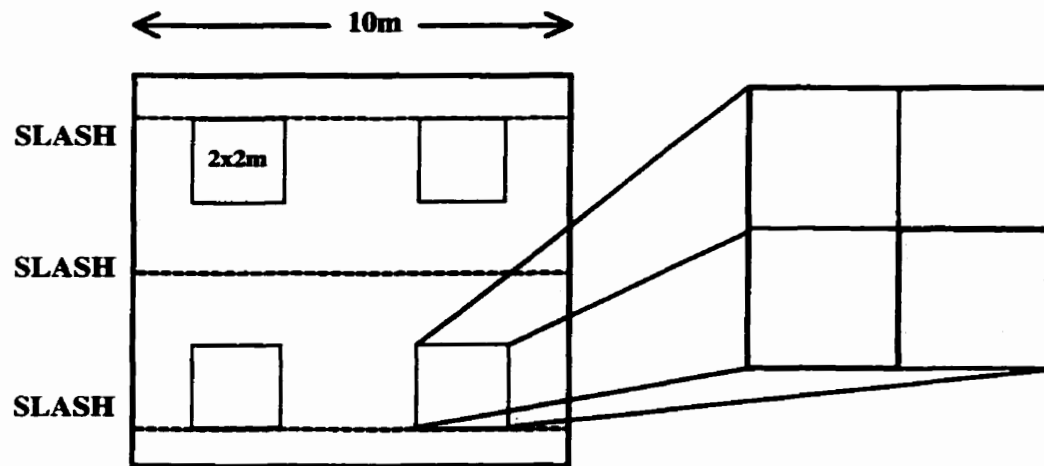


Figure 3.3. Sampling design for enumerating vegetation and CWD within 10m x 10m plots. Canopy cover and density were recorded within the entire 10m x 10m plot. Sucker and shrub density and cover were recorded within each 2m x 2m sub-unit (4 blocks per plot). Herb cover was estimated within one 1m x 1m 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.

3.3.3 Analytical Methods

3.3.3.1 Delineation and Description of Trembling Aspen Sub-Types

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. Exploratory analyses of the herbaceous vegetation indicated little variation at the stand level; 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 (ter Braak 1986) 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 (Tables 3.2 and 3.3):

1. **Dry ($n = 13$):** co-dominated by low shrubs prickly rose, saskatoon, common snowberry and raspberry, and beaked hazelnut.
2. **Fresh ($n = 10$):** dominated by beaked hazelnut, with < 10 % low shrub cover.
3. **Moist ($n = 11$):** co-dominated by mountain maple and beaked hazel.

Table 3.2. 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)
<i>Corylus cornuta</i>	25.95	15.53	40.96	24.62
<i>Acer spicatum</i>	4.01	0.05	0.01	12.34
<i>Rosa acicularis</i>	5.20	7.98	2.90	4.01
<i>Symphoricarpos albus</i>	2.09	3.07	2.09	0.93
<i>Amelanchier alnifolia</i>	1.96	3.23	1.55	0.82
<i>Rubus idaeus</i>	1.29	2.43	0.40	0.75
<i>Prunus virginiana</i>	1.43	1.73	1.47	1.04

Table 3.3. 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	dry	fresh	moist
	(n = 34)	(n = 13)	(n = 10)	(n = 11)
<i>Aralia nudicaulis</i>	10.73	13.25	13.36	5.35
<i>Rubus pubescense</i>	3.90	4.08	4.01	3.57
<i>Fragaria virginiana</i>	2.47	4.46	1.24	1.23
<i>Mertensia paniculata</i>	2.38	3.56	2.26	1.09
<i>Oryzopsis asperifolia</i>	2.20	3.15	2.19	1.10
<i>Cornus canadensis</i>	1.82	2.17	1.76	1.45
<i>Viola canadensis</i>	1.29	1.18	1.75	1.01
<i>Maianthemum canadense</i>	1.04	1.25	0.98	0.85
<i>Aster ciliolatus</i>	0.86	1.03	0.81	0.71
<i>Pyrola asarifolia</i>	0.80	1.00	0.84	0.55
<i>Mitella nuda</i>	0.75	0.19	0.35	1.78
<i>Thalictrum venulosum</i>	0.75	1.78	0.21	0.02
<i>Petasites palmatus</i>	0.65	0.99	0.43	0.45
<i>Lathyrus venosus</i>	0.52	0.59	0.33	0.60
<i>Galium boreale</i>	0.50	0.70	0.44	0.33
<i>Disporum trachycarpum</i>	0.46	0.37	0.64	0.39
<i>Lathyrus ochroleucus</i>	0.44	0.76	0.31	0.19
<i>Solidago canadensis</i>	0.39	0.95	0.03	0.05
<i>Epilobium angustifolium</i>	0.35	0.85	0.03	0.04
<i>Galium triflorum</i>	0.33	0.24	0.22	0.54
<i>Elymus spp.</i>	0.31	0.49	0.24	0.15
<i>Sanicula marilandica</i>	0.30	0.46	0.10	0.00
<i>Vicia americana</i>	0.29	0.63	0.09	0.07
<i>Heracleum lanatum</i>	0.29	0.67	0.10	0.00
<i>Apocynum androsaemifolium</i>	0.28	0.33	0.41	0.10
<i>Smilacina stellata</i>	0.28	0.60	0.00	0.15
<i>Calamagrostis canadensis</i>	0.26	0.55	0.07	0.10
<i>Carex sp.</i>	0.25	0.12	0.09	0.57
<i>Osmorhiza depauperata</i>	0.25	0.28	0.30	0.17
<i>Matteuccia struthiopteris</i>	0.24	0.00	0.00	0.75
<i>Equisetum pratense</i>	0.20	0.14	0.06	0.39

Relationships between shrub communities and environmental variables were assessed by canonical correspondence analysis ordination of the 34 stands (ter Braak 1986). Chord distance was used as the distance metric in order to “standardize” growth differences between sample years and cutblock ages (for both exploratory herb community analyses and the presented results). Differences in vegetation and environment among the three aspen sub-types may result in different recovery patterns following clear-cut harvesting. In recognition of this, subsequent analyses are undertaken for each sub-type.

3.3.3.2 Assessing Vegetation Response

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 3.4**): *tall shrubs* reach over 2 m in height at maturity, while *low shrubs* are < 2 m in height at maturity. Herbaceous species were assigned to functional types based on autecological traits and lifeform characteristics (**Table 3.5**). *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

Table 3.4. Species composition of shrub functional groups (based upon structural morphology at maturity).

LOW SHRUBS	TALL SHRUBS
<i>Rosa acicularis</i>	<i>Corylus cornuta</i>
<i>Rubus idaeus</i>	<i>Acer spicatum</i>
<i>Diervilla lonicera</i>	<i>Prunus virginiana</i>
<i>Viburnum edule</i>	<i>Cornus stolonifera</i>
<i>Ribes triste</i>	<i>Prunus pensylvanica</i>
<i>Lonicera dioica</i>	<i>Viburnum opulus</i>
<i>Rosa woodsii</i>	<i>Alnus rugosa</i>
<i>Ribes oxycanthoides</i>	<i>Salix spp.</i>
<i>Ribes americanum</i>	<i>Rhamnus alnifolia</i>
<i>Ribes hudsonianum</i>	<i>Alnus crispa</i>
<i>Symphoricarpos albus</i>	<i>Amelanchier alnifolia</i>
<i>Shepherdia canadensis</i>	
<i>Symphoricarpos occidentalis</i>	

Table 3.5. 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
<u>ferns/horsetails/clubmosses</u>	<i>Achillea millefolium</i>	<i>Anemone canadensis</i>	<i>Actaea rubra</i>	<i>Aquilegia canadensis</i>
<i>Botrychium virginianum</i>	<i>Achillea sibirica</i>	<i>Anemone quinquefolia</i>	<i>Aralia nudicaulis</i>	<i>Aster umbellatus</i>
<i>Dryopteris austriaca</i>	<i>Agastache foeniculum</i>	<i>Apocynum androsaemifolium</i>	<i>Carex</i> sp.	<i>Astragalus</i> sp.
<i>Gynocarpium dryopteris</i>	<i>Agropyron</i> spp.	<i>Arctostaphylos uva-ursi</i>	<i>Corallorhiza maculata</i>	<i>Chenopodium album</i>
<i>Matteuccia struthiopteris</i>	<i>Agrostis</i> sp.	<i>Arenaria lateriflora</i>	<i>Cornus canadensis</i>	<i>Chenopodium capitatum</i>
<i>Equisetum arvense</i>	<i>Aster ciliolatus</i>	<i>Corydalis semipervirens</i>	<i>Disporum trachycarpum</i>	<i>Cirsium arvense</i>
<i>Equisetum pratense</i>	<i>Aster laevis</i>	<i>Epilobium angustifolium</i>	<i>Habenaria viridis</i>	<i>Crepis tectorum</i>
<i>Equisetum scirpoides</i>	<i>Bromus</i> sp.	<i>Fragaria virginiana</i>	<i>Linnaea borealis</i>	<i>Epilobium glandulosum</i>
<i>Equisetum sylvaticum</i>	<i>Calamagrostis canadensis</i>	<i>Galium boreale</i>	<i>Mitella nuda</i>	<i>Galeopsis tetrahit</i>
<i>Lycopodium annotinum</i>	<i>Carex</i> spp.	<i>Galium triflorum</i>	<i>Monensia uniflora</i>	<i>Geranium bicknellii</i>
<i>Lycopodium dendroideum</i>	<i>Cinna latifolia</i>	<i>Heracleum lanatum</i>	<i>Monotropa uniflora</i>	<i>Lactuca pulchella</i>
<u>bryophytes/lichens/liverworts</u>	<i>Cirsium flodmanii</i>	<i>Hieracium umbellatum</i>	<i>Oryzopsis asperifolia</i>	<i>Lathyrus ochroleucus</i>
<i>Brachythecium</i> spp.	<i>Dracocephalum parviflorum</i>	<i>Lathyrus venosus</i>	<i>Pyrola asarifolia</i>	<i>Melilotus</i> sp.
<i>Campylium</i> sp.	<i>Elymus</i> spp.	<i>Lilium philadelphicum</i>	<i>Pyrola elliptica</i>	<i>Plantago major</i>
<i>Cladina</i> sp.	<i>Geum aleppicum</i>	<i>Maianthemum canadense</i>	<i>Pyrola secunda</i>	<i>Polygonum convolvulus</i>
<i>Cladonia</i> sp.	<i>Halenia deflexa</i>	<i>Mertensia paniculata</i>	<i>Pyrola virens</i>	<i>Senecio eremophilus</i>
<i>Dicranum</i> sp.	<i>Linaria vulgaris</i>	<i>Osmorhiza depauperata</i>	<i>Smilacina stellata</i>	<i>Sonchus arvensis</i>
<i>Eurhynchium</i> sp.	<i>Luzula pilosa</i>	<i>Petasites palmatus</i>	<i>Trientalis borealis</i>	<i>Stellaria media</i>
<i>Haplocladium</i> sp.	<i>Poa</i> spp.	<i>Petasites sagittatus</i>	<i>Trillium cernuum</i>	<i>Taraxacum officinale</i>
<i>Marchantia</i> sp.	<i>Schizachne</i> sp.	<i>Petasites vitifolius</i>		<i>Trifolium</i> sp.
<i>Mnium</i> sp.	<i>Solidago bicolor</i>	<i>Rubus pubescens</i>		<i>Urtica dioica</i>
<i>Oncophorus wahlenbergii</i>	<i>Solidago canadensis</i>	<i>Sanicula marilandica</i>		<i>Vicia americana</i>
<i>Peltigera</i> sp.	<i>Solidago spathulata</i>	<i>Stellaria longifolia</i>		
<i>Pleurozium shreberi</i>		<i>Thalictrum dasycarpum</i>		
<i>Polytrichum</i> sp.		<i>Thalictrum venulosum</i>		
<i>Pylaisiella</i> sp.		<i>Viola canadensis</i>		

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.

The percent cover of each functional type was compared across treatments (cut, edge and interior plots) using a randomized block design ANOVA (log-transformed data) to assess changes in floristic 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 \pm standard error, and ANOVA statistics. Mean shrub height and densities (log transformed data) were compared across harvest treatments for each of the short shrub and tall shrub functional groups using ANOVA.

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 also assessed using randomized block ANOVA. Responses are summarized as mean \pm standard error, and ANOVA statistics.

3.4 RESULTS

3.4.1 Description of Trembling Aspen Sub-Types

A) Vegetation

Despite similar canopy composition, shrub species showed strong variation between stands. Shrub associations are diagnostic of three aspen sub-types at the stand level (Dry, Fresh and Moist. **Table 3.1**), corresponding with environmental conditions. Characteristic herbs of each aspen sub-type are presented in **Table 3.3**. 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.

B) Environment

The relationship between the three aspen sub-types and measured environmental variables were investigated using canonical correspondence analysis, CCA (**Figure 3.4**). 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

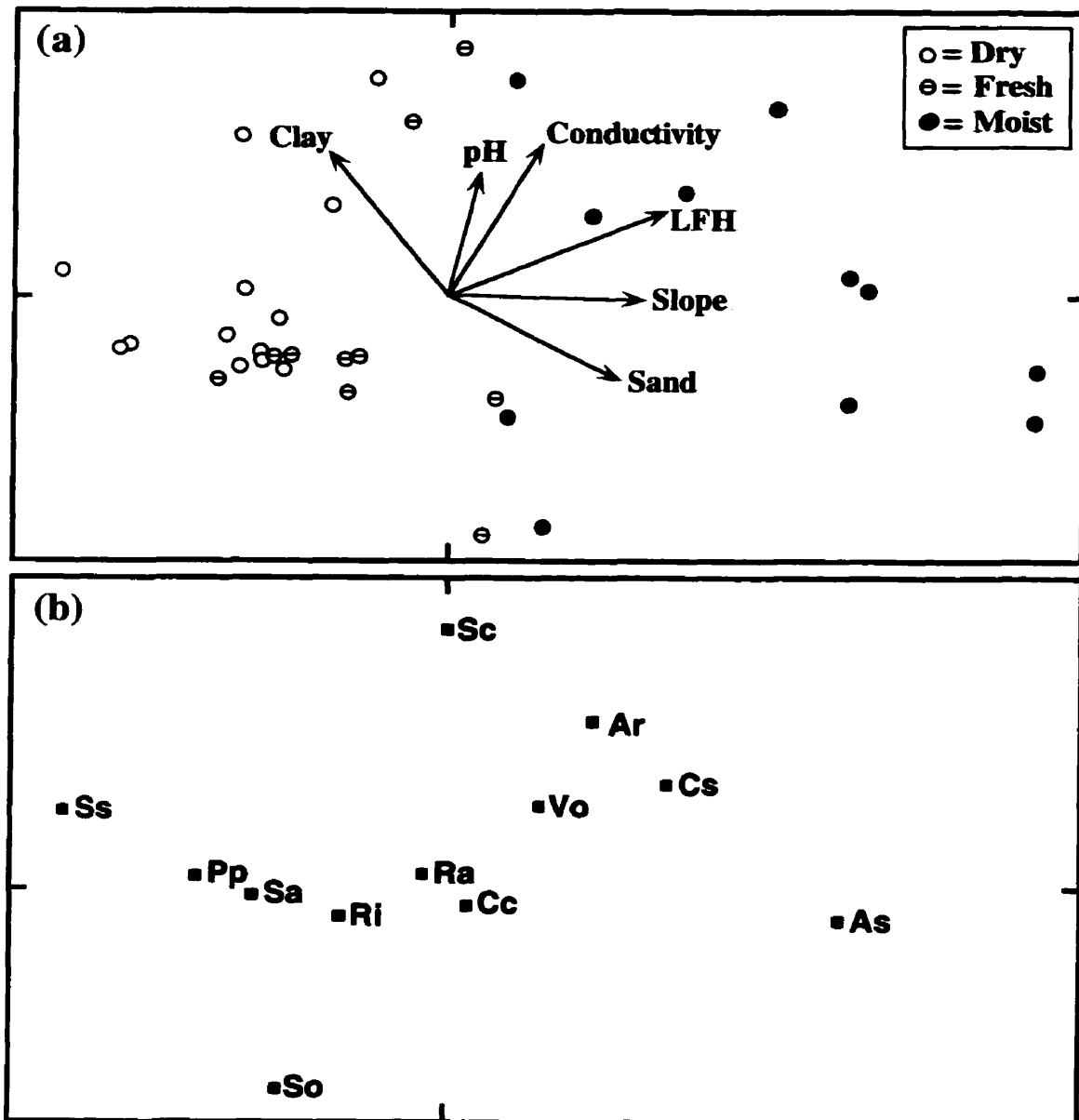


Figure 3.4. Canonical correspondence analysis (CCA) ordination of the 34 stands, based on shrub species composition constrained by six environmental variables. (a) CCA results, stands (coded by aspen sub-type) and environmental variables (vectors); (b) CCA results, biplot scores of selected shrub species. Eigenvalues and canonical correlations: $\lambda_1 = .096$, $R^2 = .653$, $\lambda_2 = .067$, $R^2 = .820$. Explained variation along the first (horizontal) axis is 23.45%. Codes: Ar = *Alnus rugosa* (speckled alder); As = *Acer spicatum* (mountain maple); Cc = *Corylus cornuta* (beaked hazelnut); Cs = *Cornus stolonifera* (red-osier dogwood); Pp = *Prunus pensylvanica* (pincherry); Ra = *Rosa acicularis* (wild rose); Ri = *Rubus idaeus* (raspberry); Sa = *Symphoricarpos albus* (snowberry); Sc = *Shepherdia canadensis* (buffaloberry); So = *Symphoricarpos occidentalis* (buckbrush); Ss = *Salix* spp. (willows); Vo = *Viburnum opulus* (cranberry).

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.

3.4.2 Floristic Composition

Trends in floristic composition across treatments are summarized in **Figure 3.5**. 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 3.6**. Similar trends are seen for each of the three sub-types. Despite small changes in relative cover, the overall floristic composition of cutblocks is very similar to that of the interior forest.

3.4.3 Floristic Structure

Mean shrub densities did not differ between harvest treatments for either the low shrub or tall shrub functional groups ($F = 2.01$, $P = 0.14$ and $F = 0.67$, $P = 0.51$

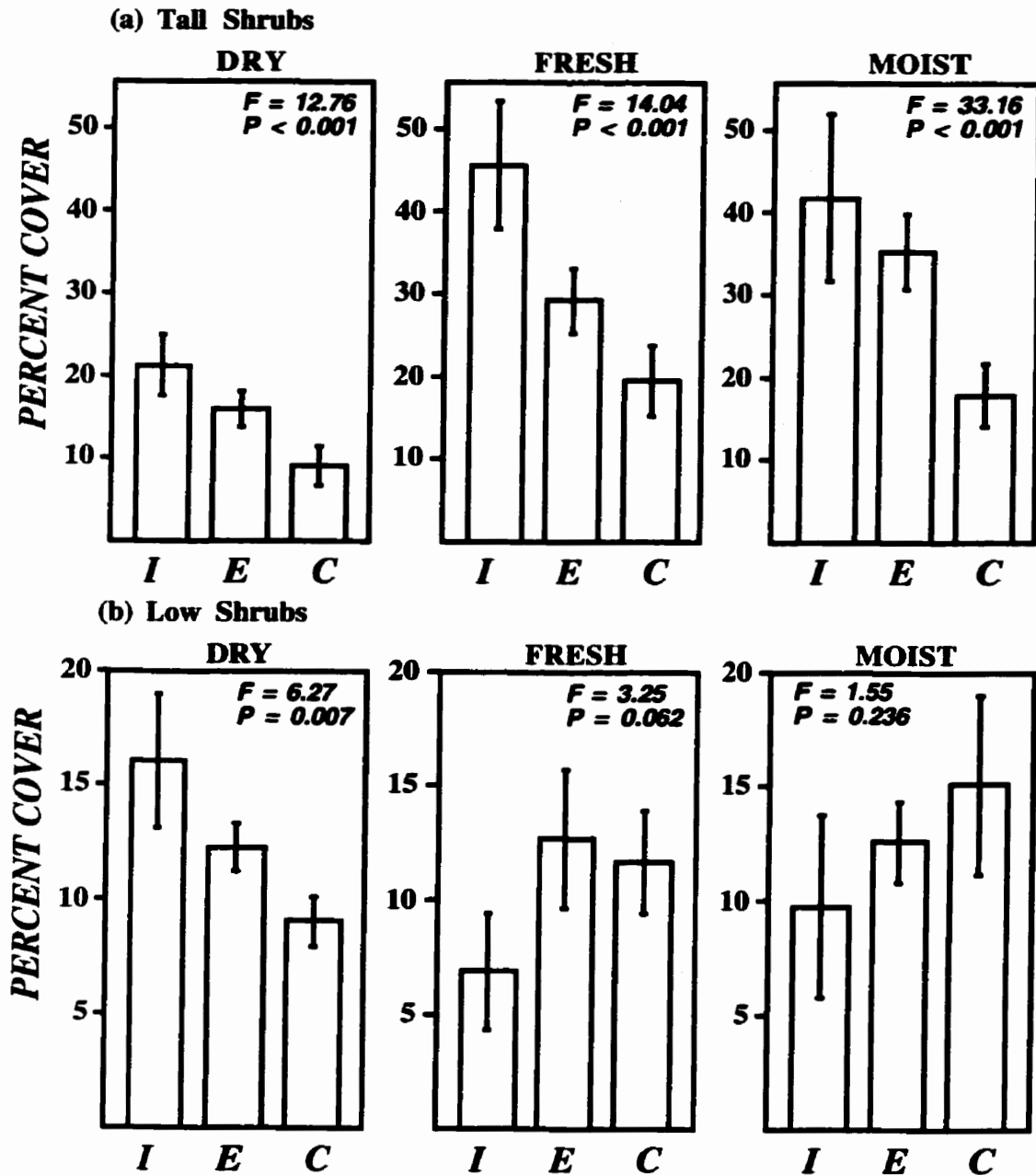


Figure 3.5. Comparisons of understory vegetation cover for (a) tall shrubs; (b) low shrubs; (c) bryophytes; (d) closed forest species; (e) open forest species; (f) grassland species; (g) ruderal species across harvest treatment (I = interior, E = edge and C = cut forest), for each of the three aspen sub-types (dry, fresh and moist). Analysis of variance results (F and associated P-values) are also given. Degrees of freedom for dry, fresh and moist stand types are 38, 29 and 32 respectively. Refer to Tables 4 and 5 for the species composition of functional groups.

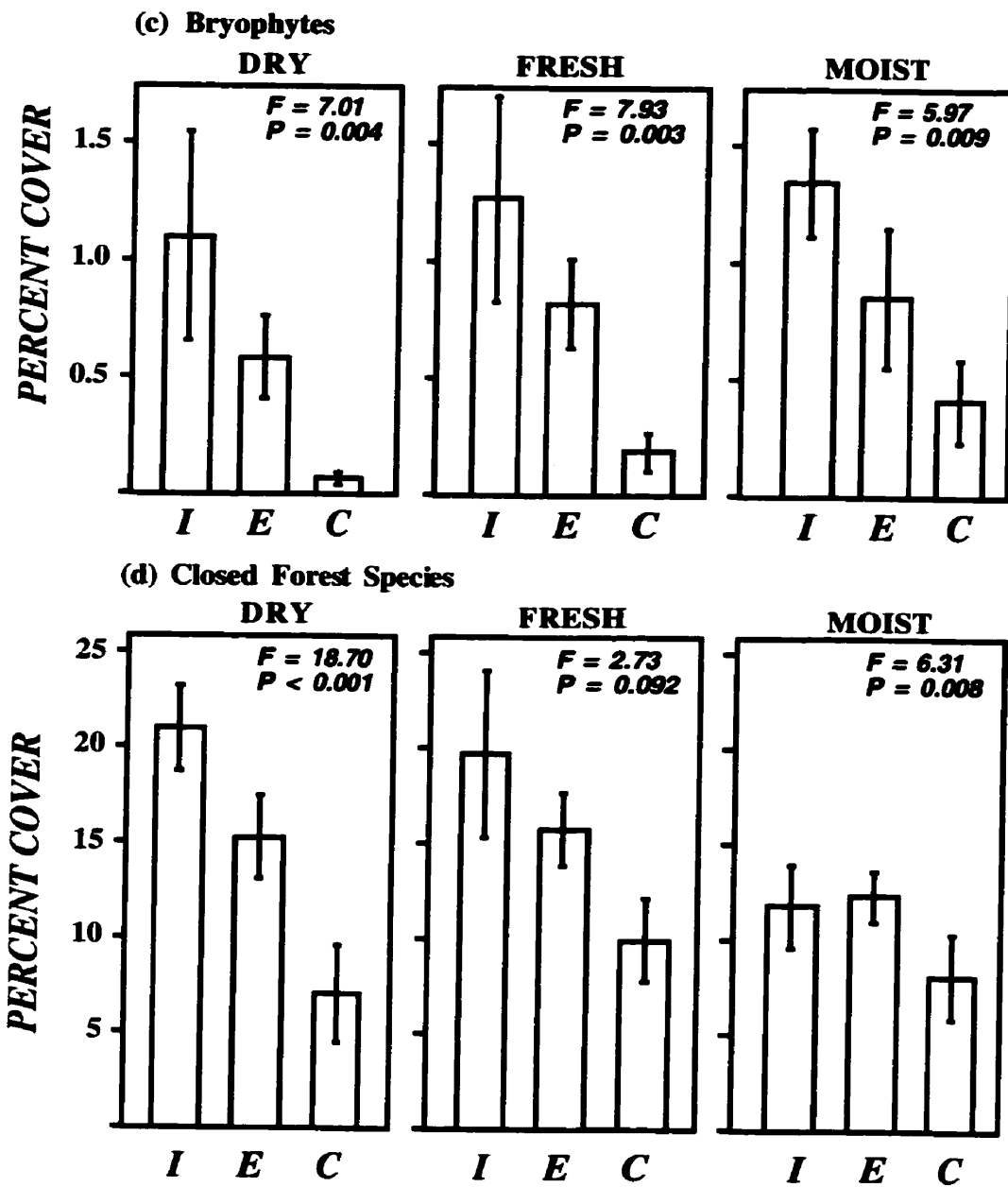


Figure 3.5 (continued).

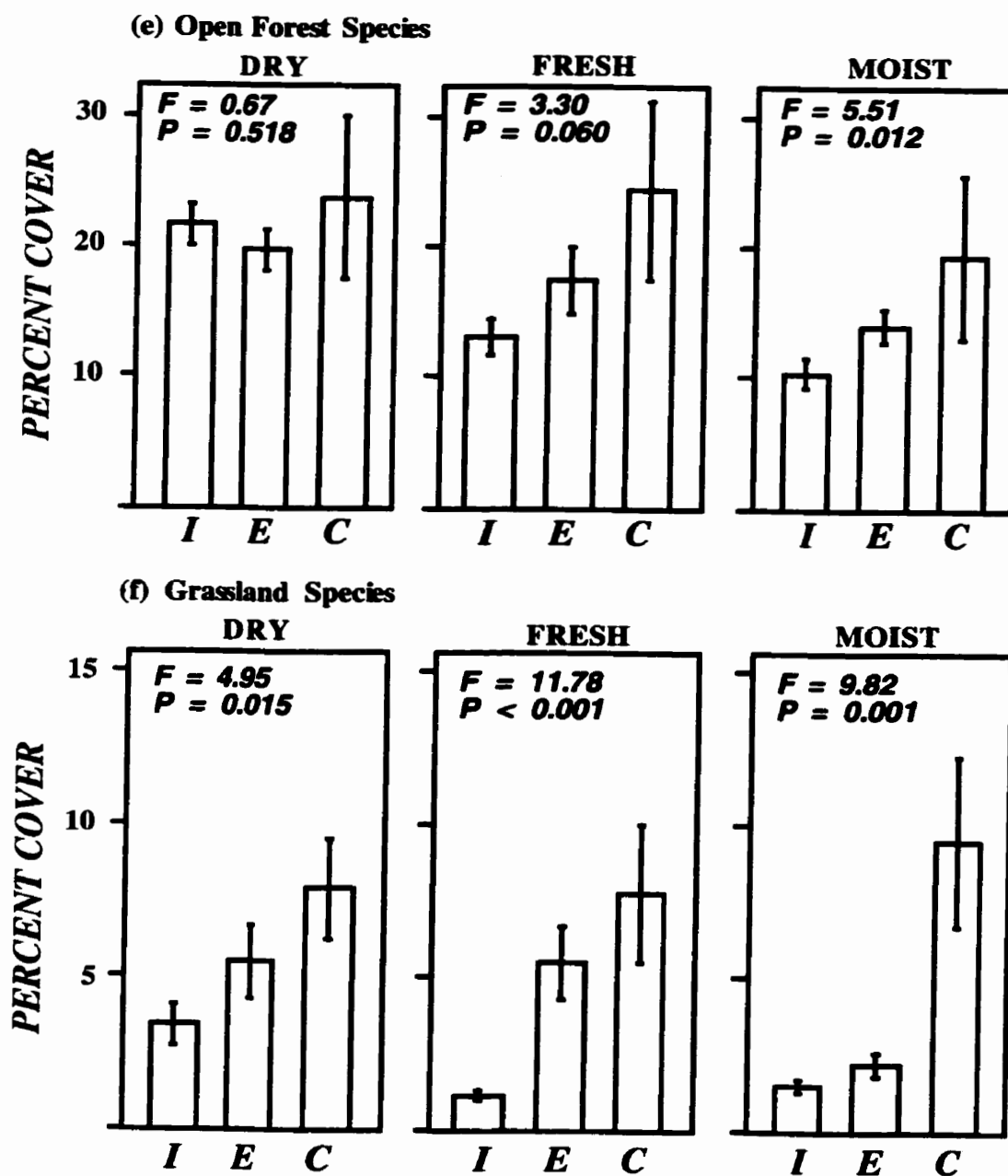


Figure 3.5 (continued).

(g) Ruderal Species

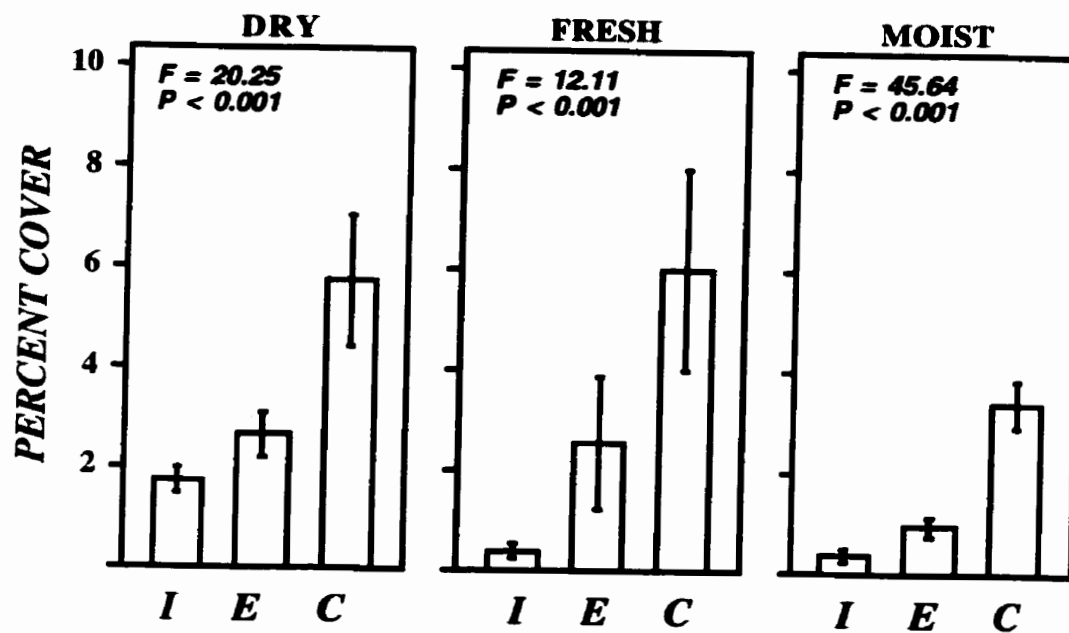


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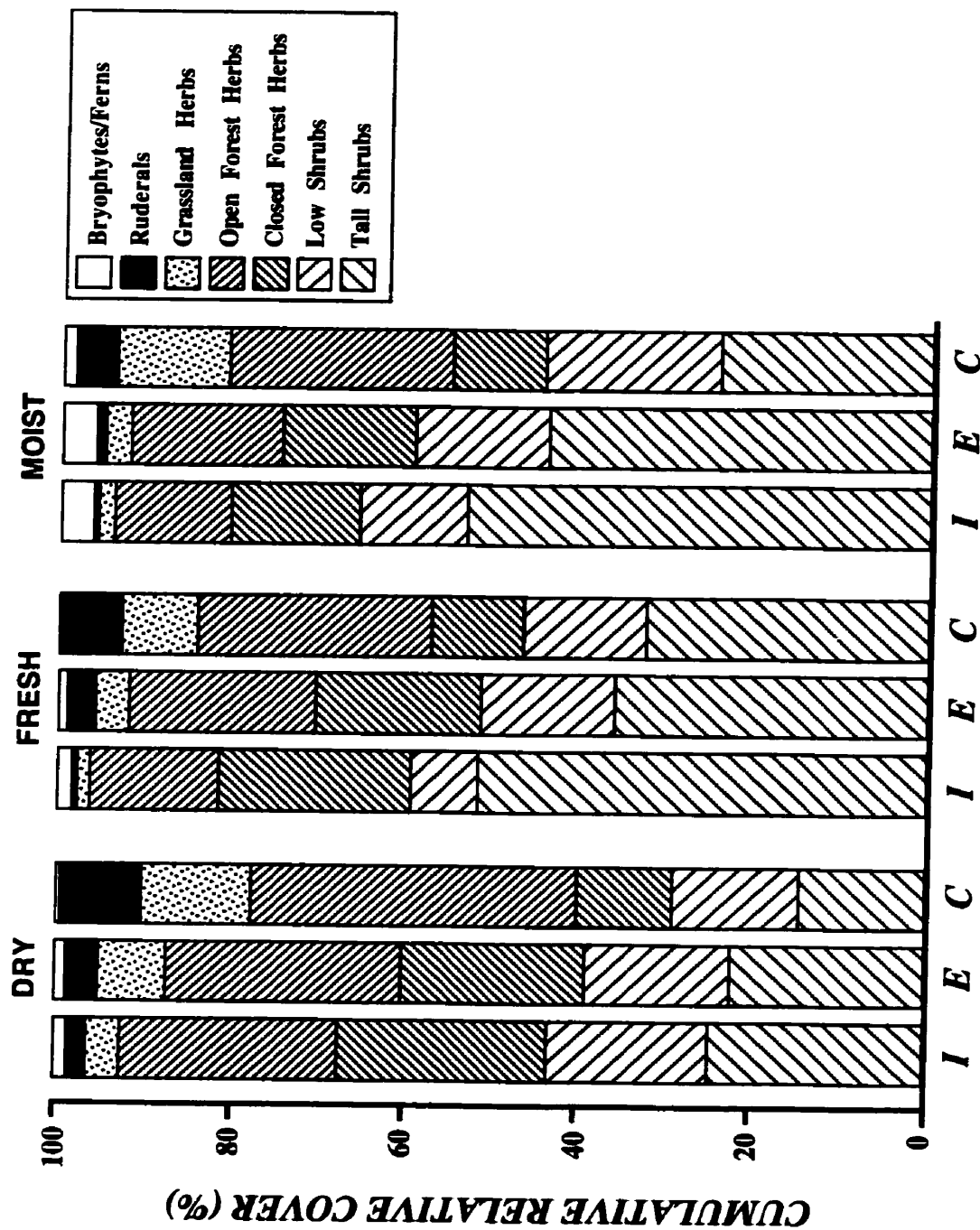


Figure 3.6. Cumulative relative cover of species functional groups across harvest treatments (I = interior, E = edge, C = cut forest) for each of the three aspen sub-types (dry, fresh and moist). Refer to Tables 4 and 5 for species composition functional groups.

respectively). Tall shrub heights were significantly reduced after harvest ($F = 24.4$, $P < 0.001$). The dominant shrub in most stands, beaked hazelnut, decreased from a mean height (in all stands) of 107 cm in the interior to 72 cm in edge treatments and 39 cm after harvest. Mountain maple height was reduced from a mean of 59 cm in interior to 17 cm on cut blocks. Mean height of both dominant shrub species were less than the mean height of one year old aspen after harvesting (i.e. less than 70 cm). The mean height of low shrubs were also slightly lower after harvest than interior treatments ($F = 4.22$, $P = 0.02$).

3.4.4 Floristic Diversity

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 3.7**). For the fresh sub-type, effective species richness of both the herbs and shrubs increased significantly following clear-cut harvesting.

3.5 DISCUSSION

3.5.1 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). Establishing ecological variation prior to disturbance is therefore

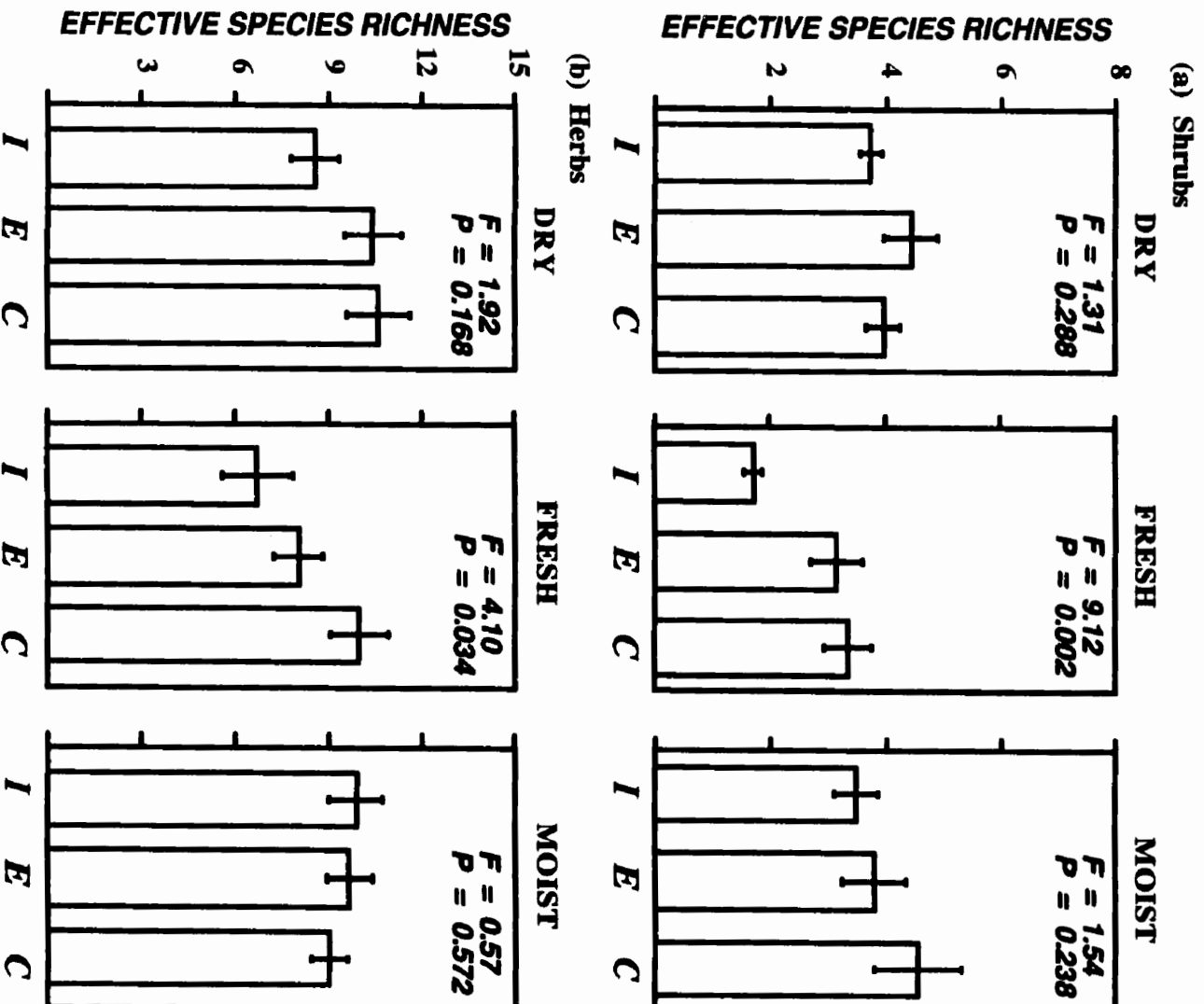


Figure 3.7. Comparison of effective species richness (based on the Gini-Simpson coefficient) for (a) shrubs and (b) herbs across harvest treatment (I = interior, E = edge and C = cut forest), for each of the three aspen sub-types (dry, fresh and moist). Analysis of variance results (F and associated P-values) are also given. Degrees of freedom for dry, fresh and moist stand types are 38, 29 and 32 respectively.

necessary for predicting and interpreting post-disturbance vegetation development. 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.

A) Dry aspen sub-type

Species composition of the dry sub-type is indicative of seasonal water limitation. Rose, saskatoon, northern gooseberry (*Ribes oxycanthoides*), golden rod, and 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 Swan 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.

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*), golden rod (*Solidago canadensis*), wild vetch (*Vicia americana*), veiny meadow rue (*Thalictrum venulosum*), strawberry (*Fragaria virginiana*), and tall bluebells (*Mertensia paniculata*). 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*) are also characteristic of the 'dry' aspen sub-type.

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).

B) 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.

C) 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 co-dominant 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*) and clubmosses (*Lycopodium* spp.). The ostrich fern (*Matteuccia struthiopteris* var. *pensylvanica*), 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*) and green ash (*Fraxinus pennsylvanica* var. *austini*) in the canopy, with mountain maple and beaked hazelnut as the dominant shrubs.

3.5.2 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). 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.

3.5.2.1 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 compositional 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 favourable

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 this 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.

3.5.2.2 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).

3.5.2.3 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 the 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).

CHAPTER 4

ASPEN REGENERATION FOLLOWING CLEAR-CUT HARVESTING IN ASPEN DOMINATED STANDS, DUCK MOUNTAIN, MANITOBA

ABSTRACT

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 examines the effects of tree-length harvesting and slash retention on trembling aspen-dominated forest stands in the Duck Mountain ecoregion of Manitoba. The study objective is 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. 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. 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 neither required, nor recommended.

4.1 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 United States (Bartos and Mueggler 1982).

Current Forest research is focussed upon developing harvesting methods that emulate natural disturbance, thereby maintaining biodiversity and long-term ecosystem productivity (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.

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 objective is 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.

4.2 STUDY AREA

The study was conducted within the Duck Mountain Provincial Forest Reserve, which is located in west-central Manitoba ($57^{\circ}02'$ – $57^{\circ}48'$ north and 350° – 385° east). The Forest Reserve surrounds Duck Mountain Provincial Park. The Duck Mountains are part of the Manitoba Escarpment, which rises approximately 500 m 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 (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 and leeward side of the of the Manitoba Escarpment is higher than recorded.

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 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.

4.3 MATERIALS AND METHODS

4.3.1 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 3.1, Table 3.1). 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 3.2). Logging roads and equipment

staging areas (which generally make up < 5% of the cutblock) were avoided when locating 'harvested' plots.

4.3.2 Data Collection

Regenerating tree (suckers and seedlings < 3 m in height) densities and percent cover values were recorded in each of four 2 x 2 m quadrats located within each plot (**Figure 3.3**). A random subset of up to 20 aspen and balsam poplar suckers plot (up to five from each 2 x 2 m quadrat) were measured (height and basal diameter) and collected for later age determination in the laboratory. Density, cover and height of shrub species were estimated within each 2 x 2 m quadrat (**Figure 3.3**).

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 was recorded using Van Wagner's line-intercept technique (Van Wagner 1968). In each 10 m x 10 m plot, the diameter of each intercepted piece of woody debris was recorded along three systematically-located transects 10 m in length (**Figure 3.3**).

4.3.3 Analytical Methods

Step-wise 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) on aspen suckering. Differences in suckering density between harvest seasons (summer vs. winter) and among the three aspen sub-types were assessed using analysis of covariance (ANCOVA) using cutblock age as the covariate to remove the effects of differences in timing of harvest.

4.4 RESULTS

4.4.1 Delineation of Trembling Aspen Stand Types

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. Differences in vegetation and environment among the three aspen sub-types could potentially result in different recovery patterns following clear-cut harvesting. In recognition of this, three trembling aspen sub-types (*Dry, Fresh and Moist*) were delineated by a cluster analysis of log-transformed percent cover of understory shrubs in the 'unharvested' plots, and compared in subsequent analysis (refer to chapter 3).

4.4.2 Factors Determining Aspen Density

Of all the variables tested (age of clearcut, stand density prior to harvest, slash loadings, shrub cover, soil variables: pH, conductivity, particle size, LFH depth) only the clearcut age (time since harvest) contributed significantly to explaining variation in suckering density ($F = 5.942$, $P = 0.003$, $df = 32$). There were no significant differences in sucker density between summer and winter harvests ($F = 0.554$, $P = 0.44$, $df = 31$), or among the three sub-types (*dry, fresh and moist*) ($F = 1.401$, $P = 0.29$, $df = 31$).

4.4.3 Aspen Density and Growth Over Time

The density of aspen suckers declines significantly over time ($F = 5.94$, $P = 0.003$, $df = 32$). This indicates that self-thinning is occurring, reducing mean density from 8.1 stems/m² in the first year following clear-cut harvesting to 3.4 stems/m² by the fourth year (**Figure 4.1**). Variation in sucker density is greater in the first year, suggesting that self-thinning is greatest in stands with initially high densities.

Mean aspen sucker height as a function of cutblock age is shown in **Figure 4.2**. 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. The dominant shrubs in most stands, beaked hazelnut and mountain maple, had mean post-harvest heights (in all stands) of 39 cm and 17 cm respectively. Mean height of both

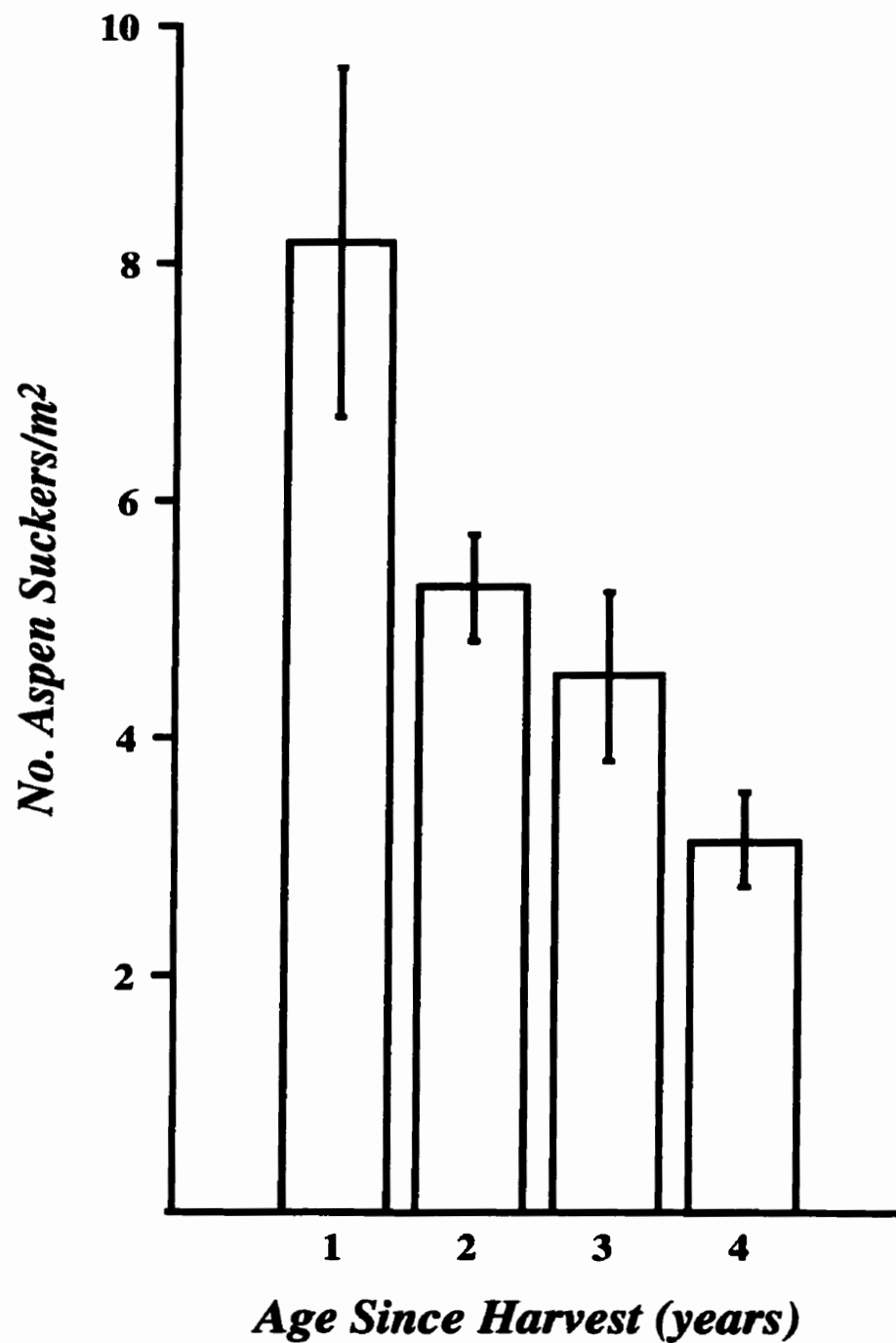


Figure 4.1. Temporal changes in the density of trembling aspen suckers in recently tree-length harvested aspen stands. Changes are attributable to natural self-thinning.

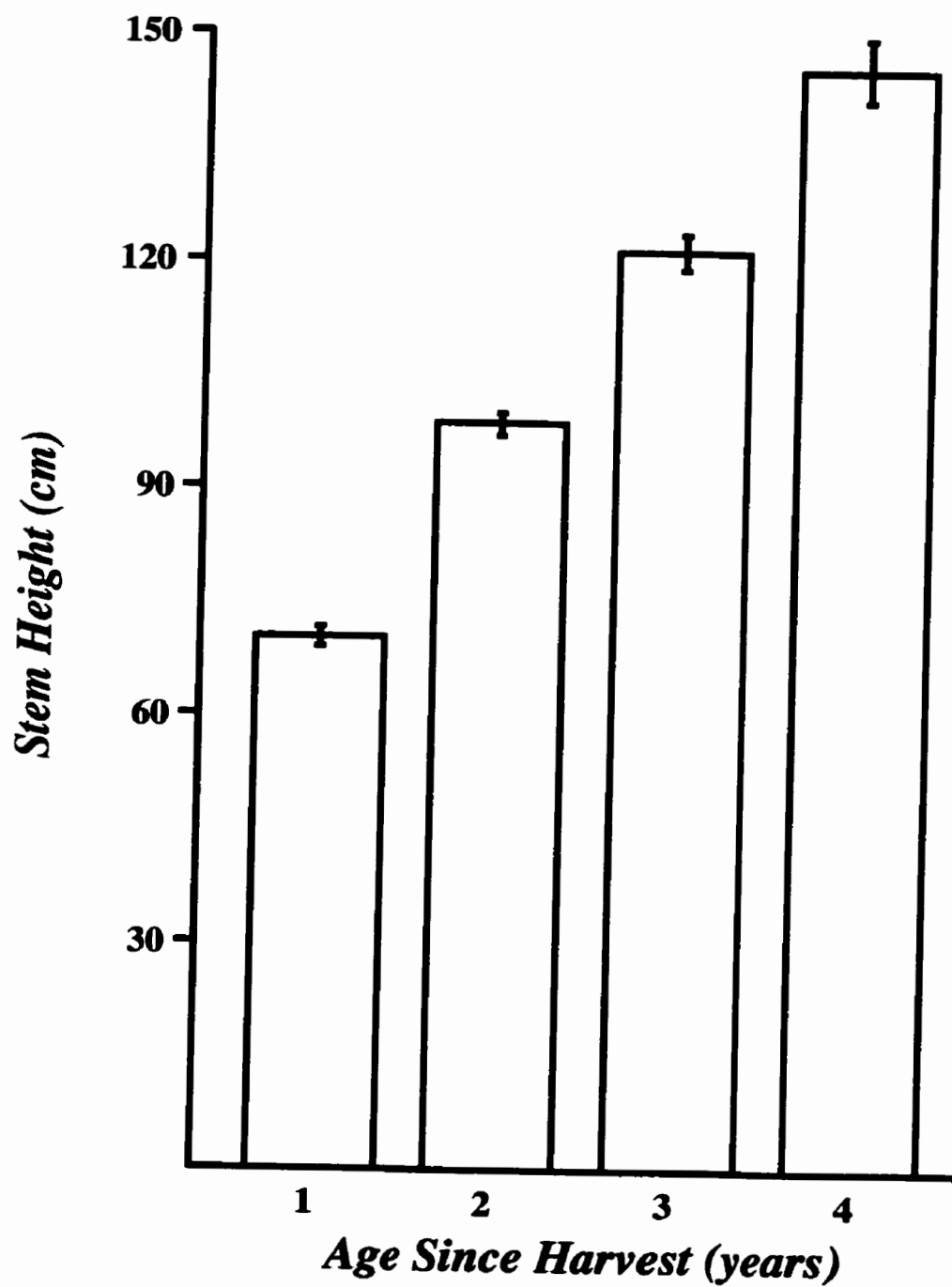


Figure 4.2. Height growth of aspen suckers in recently tree-length harvested aspen stands.

dominant shrub species were less than the mean height of one year old aspen after harvesting (i.e. less than 70 cm).

4.4.4 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 4.3**). Mean aspen suckering density in cut plots ranging from 1 to 4 years after harvest is 6.29 stems/m², compared to only 0.51 stems/m² for balsam poplar.

4.5 DISCUSSION

The majority of trembling aspen regeneration is from vegetative shoots (suckers) derived from lateral root meristematic tissue on 'surface' roots, i.e. those within 10 cm of the soil surface (Maini and Horton 1966). 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 fires, 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).

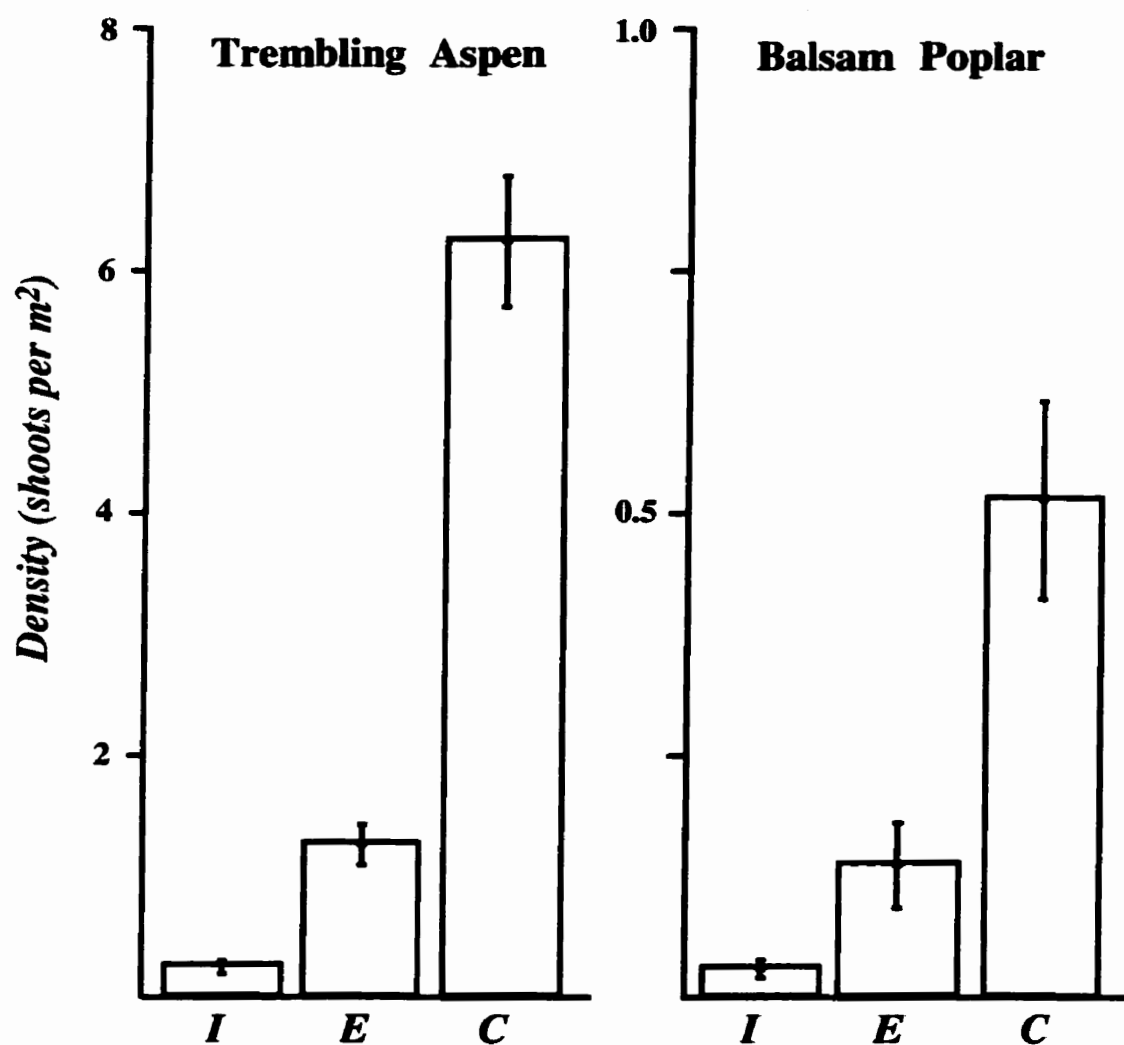


Figure 4.3. Mean (\pm S.E.) suckering density of trembling aspen and balsam poplar in interior (I), edge (E) and cut (C) stands. Note different scales on the two graphs.

4.5.1 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 this 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 et 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. Approximately two-thirds of aspen suckers are removed through natural self-thinning by the fourth year following harvesting in the Duck Mountains.

4.5.2 Slash

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). The typical slash loadings of harvested stands in the Duck Mountains have little detrimental effect on aspen regeneration with respect to stocking

density and height. This in turn suggests that typical slash loadings do not decrease soil temperatures sufficiently to prohibit sucker development. However, poor regeneration may occur in areas with abnormally dense slash piles (pers. obs.). Such areas are generally restricted to equipment loading areas and road obstructions, both of which are relatively minor components of a typical cutblock.

4.5.3 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).

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 within four years of disturbance to enable stand replacement.

4.5.4 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).

4.5.5 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 the Duck Mountain forests. 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).

4.5.6 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) rather than low growth rates.

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.

CHAPTER 5

VOLUME AND SIZE-FREQUENCY DISTRIBUTION OF COARSE WOODY DEBRIS IN MATURE AND RECENTLY HARVESTED TREMBLING ASPEN STANDS

ABSTRACT

This study compares the volumes and size-frequency distributions of coarse woody debris (CWD) in recently harvested cutblocks, cutblock edges, and adjacent undisturbed forest in 34 trembling aspen stands in the Duck Mountains, Manitoba. Coarse woody debris is naturally present at relatively high volumes in mature, unharvested aspen stands. In cutblocks, "slash" loading (coarse woody debris purposely retained on-site during stand harvesting) increases the volume of CWD (186 m³/ha, vs. 129 m³/ha in adjacent unharvested stands). Large differences in CWD volumes among mature unharvested stands are equalized following harvesting, which is attributable to the "spreading" of CWD onto the forest floor as trees are harvested. The majority of CWD in both unharvested aspen stands and cutblocks occurs in the smallest size classes. The frequency distributions of CWD size-classes are described using a power-law relationship. Cutblocks have a significantly greater proportion of small pieces of CWD compared to unharvested stands. In recognition of the previously reported ecological benefits associated with post-harvest CWD retention, it is recommended that the current practice of retaining slash on cutblocks is continued.

5.1 INTRODUCTION

Coarse woody debris (CWD) is an important component of forested ecosystems. It provides habitat for a wide diversity of organisms, and plays a critical role in ecosystem energy flow and nutrient cycling (Harmon et al. 1986). In undisturbed forests, CWD inputs involve the transfer of living to dead woody material, through individual tree death, branch fall, root mortality, and so forth (Lee 1998). In forest stands harvested for timber, CWD is often increased as the result of "slash" loadings (Bella 1986). Slash is defined as coarse woody debris that is purposely retained on-site during the harvesting of tree boles. Slash retention minimizes the losses of organic matter and nutrients resulting from harvesting, provides a source of decayed logs for seedling establishment, and provides cover and refugia for various species in what would otherwise be an exposed environment. Logging practices such as tree-length harvesting and on-site slash 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. The objective of this study is to determine and compare the size distribution and volume of coarse woody debris (CWD) in cutblocks, unharvested forest edges and adjacent unharvested interior forest.

5.2 STUDY AREA

The study was conducted within the Duck Mountain Provincial Forest Reserve, which is located in west-central Manitoba (57°02'–57°48' north and 350–385° east). The Forest Reserve surrounds Duck Mountain Provincial Park. The Duck Mountains are part of the Manitoba Escarpment, which rises approximately 500 m above the Manitoba Lowlands to the east (Cockery 1996). The Escarpment is overlain by deep ground moraine deposited by the Wisconsin ice sheet approximately 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).

Contrast in elevation between the Escarpment and the Manitoba lowlands to the east is sufficient to modify the local mesoclimate. The escarpment produces a rain shadow effect, yielding 5-8 more centimeters of precipitation on the ridge 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 thereby 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.

5.3 MATERIALS AND METHODS

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 3.1, Table 3.1). 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 10 m x 10 m 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 3.2). Logging roads and equipment

staging areas (which generally make up < 5% of the cutblock) were avoided when locating 'harvested' plots.

Coarse woody debris was recorded using Van Wagner's line-intercept technique (Van Wagner 1968). In each 10 m x 10 m plot, the diameter of each intercepted piece of woody debris was recorded along three systematically-located transects 10 m in length (Figure 3.3). 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).

5.4 RESULTS

5.4.1 CWD Volumes

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 stands were therefore pooled in order to compare CWD volumes among the cut, edge and interior treatments using randomized block design 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 = $185.66 \text{ m}^3/\text{ha}$), compared to edge (mean = $127.81 \text{ m}^3/\text{ha}$) and interior plots (mean = $128.86 \text{ m}^3/\text{ha}$). Slash loadings in the cut plots were not significantly different among Dry, Fresh and Moist 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 ($F = 9.918$, $P < 0.001$). The moist sub-type had the highest CWD volumes in edge and interior plots.

5.4.2 CWD Size Class Distributions

Frequency distributions of CWD diameter classes (log scale) for the cut, edge and interior plots (across all 34 sites) are shown in **Figure 5.1**. Each frequency distribution summarizes all CWD intercepted along a total of 2,280 m (2.28 km) of line transect. 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 5.2; Table 5.1**), indicating a power-law (or hyperbolic law) relationship:

$$f_{\sigma} = a \sigma^b$$

where f_{σ} = frequency of the σ^{th} size (diameter) class, a = constant, and b = power-law or fractal exponent (Schroeder 1991).

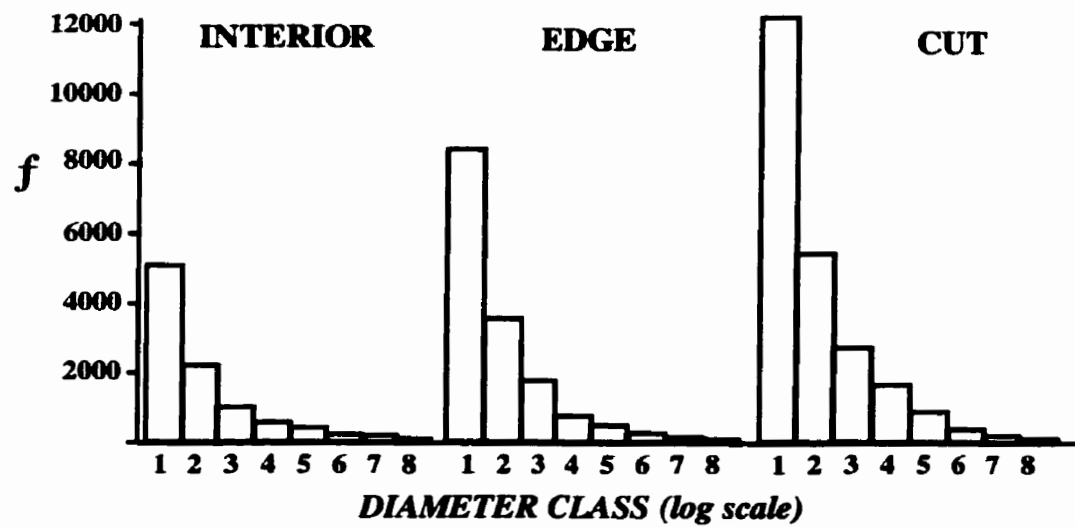


Figure 5.1. Frequency distributions (semi-log plots) of coarse woody debris (CWD) size classes in interior, edge and tree-length harvested aspen stands.

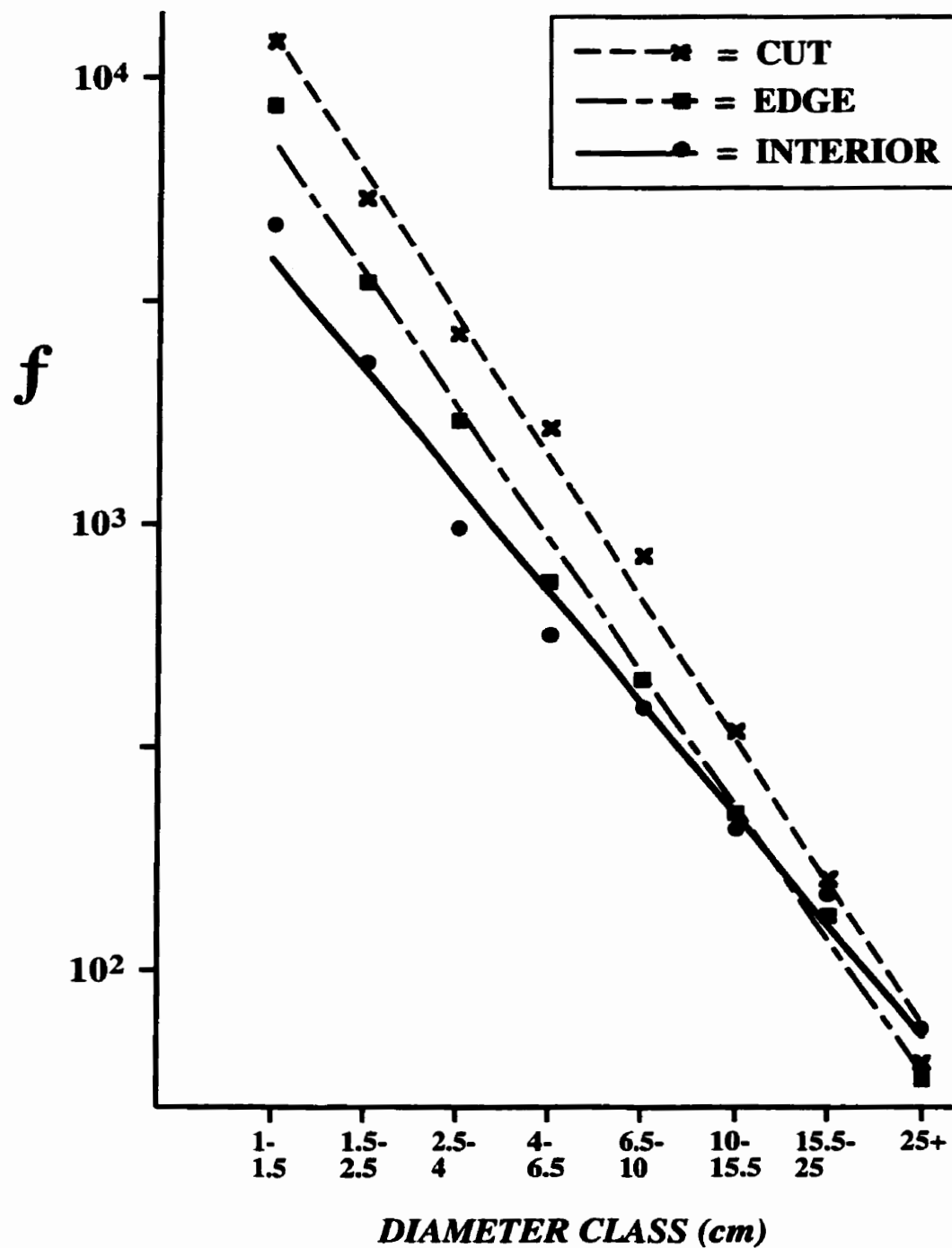


Figure 5.2. Hyperbolic (power-law) relationship between frequency and diameter class of coarse woody debris (CWD) in interior, edge and tree-length harvested aspen stands.

Table 5.1. Regression analysis results, log-log plots of the frequency-size class distribution relationships for cut, edge and interior treatments (n = 8 size classes for each treatment). Regression plots are shown in Figure 5.5.

Treatment	Intercept	Slope	R2
INTERIOR	3.8378	-0.2484	0.986
EDGE	4.1628	-0.2997	0.995
CUT	4.4240	-0.3186	0.993

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.

5.5 DISCUSSION

5.5.1 CWD Volumes

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). Stands belonging 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).

There was 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).

5.5.2 CWD Size-Class Distributions

Size-class distributions of coarse woody debris within the Duck Mountain, in both intact and logged aspen stands, follow a power-law or fractal relationship. Many biological patterns and processes are fractal in nature, i.e. broadly self-similar and scale-invariant (reviewed in Kenkel and Walker 1996). Since branch-order relationships in trees are fractal (Crawford and Young 1990; Zeide 1991; Long 1994), it is not surprising that the size-class distributions of CWD are fractal as well. Coarse woody debris present on the forest floor provides “habitat” occupied by various ground-dwelling organisms, including small mammals, insects, mosses, lichens, and innumerable species making up the detritus community. Habitats with a fractal structure support a proportionally greater number of smaller organisms than larger ones (Morse et al. 1985), and promote long-term species coexistence (Palmer 1992; Kruys and Jonsson 1999). In fractal habitats, ecosystem processes such as microbial decomposition and nutrient cycling are also expected to display scale-invariant properties (Miller 1983; Bolton and Boddy 1993).

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) favor 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). The vast majority of CWD in the Duck Mountain 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 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. 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 this 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.

The current practice of retaining slash on cutblocks is recommended to continue. Normal slash loads within the Duck Mountains did not prevent stand restocking (chapter 4). In addition, slash provides cover and refugia for various species in what would otherwise be an exposed environment, and is provides a source of decayed logs for seedling establishment in the absence of mature tree-fall (McInnis and Roberts 1994). Slash retention also minimizes the losses of organic matter and nutrients resulting from harvesting.

CHAPTER 6

CONCLUSION

6.1 EMULATING NATURAL DISTURBANCE

Like fire, clearcutting reverts a site to an early successional stage (Yarie 1993). Cuts are used to emulate natural disturbance by removing canopy shading thereby promoting natural regeneration of common fire-adapted species (Yarie 1993). However, species such as black spruce often fail to regenerate successfully after logging, resulting in post harvest stands dominated by hardwoods or balsam fir (Brumelis and Carlton 1988). Even hardwoods may not regenerate suitably on some sites (Bartos and Mueggler 1982). A combination of ecological variables (e.g. soil conditions, seed source, stand age, light availability and moisture) and harvest variables (e.g. harvest method and season) combine to determine the extent and composition of regeneration after logging.

6.1.1 Comparison of Post-logged and Post-fire Conditions

Most differences in regeneration between logging and fire are associated with soil quality, namely organic matter removal, seed bed, and nutrient release. Both burning and scarifying harvest methods expose mineral soil. However, burning of the forest floor releases nitrogen, potassium and sulphur as potash, while returning carbon in its inorganic form to the soil (Kimmins 1977). Direct observation of differences between harvest methods and fire is difficult. However, the recent focus of forest managers to mimic natural disturbance is providing ongoing research in this field of boreal forestry.

Vegetation types found after disturbance are strongly tied to those present prior to disturbance, and not necessarily associated with the type of disturbance (Nobel et al. 1977). The majority of research comparing post-fire and post-logging vegetation has been conducted within mixedwood and conifer dominated stands (Nobel et al. 1977, Outcalt and White 1981, Brumelis and Carleton 1988, Brumelis and Carleton 1989). Virgin jack pine and black spruce forests share more vegetation similarities with logged and lightly slash-burned sites than those affected by wild fire or soil raking (Nobel et al. 1977). Greatest vegetational change occurs on natural fire sites, with species invading after fire that are not seen on logged sites of any harvest treatment (Nobel et al. 1977). The microhabitats produced after fire provide niches that are absent from logged communities. Differences in species composition are lost as post-fire communities age and initial invaders are excluded by changing canopy and soil conditions. Herb cover appears to be similar five years after harvest on a burned clearcut and an unburned clearcut (Outcalt and White 1981). Fire tends to discourage development of shrubs, yielding higher cover values on unburned clearcuts (Outcalt and White 1981).

In hardwood systems, vegetation assemblages quickly regenerate after logging resulting in proportions comparable to those present prior to harvest, despite lacking the soil conditions present immediately after fire. Tree-length clearcutting of trembling aspen stands may sufficiently emulate natural disturbance to maintain many of the abiotic and biotic vegetational processes present within relatively young post-fire stands.

6.2 MANAGEMENT APPLICATIONS

Fire was an important component in the perpetuation of trembling aspen in the past. More recently, fire suppression (Bartos and Mueggler 1981), habitat fragmentation (Brown and Debye 1987, Kay 1997) and ungulate browsing (Bartos and Mueggler 1981) may threaten the long-term persistence of trembling aspen in some areas. Depending upon management objectives, trembling aspen communities may "require" a disturbance such as clearcutting or burning to replace old stands with young stands and provide the desired community types for forest and park managers. Maintenance of a "natural mosaic" of various stand ages, through sustainable harvest rotations in the proportions and patch sizes historically created by fire, is recommended for long-term ecosystem health in the absence of natural fires.

Current harvesting practices within the trembling aspen dominated forests of Duck Mountain Provincial Forest Reserve are thought to have little long-term effect on the herb and shrub community assemblages and diversity. Changes in local conditions after harvest are considered temporary, and not sufficient to permanently eliminate species from the cutblocks. The "typical" pattern of more recent cutblocks (1998-present) in the Duck Mountains is highly convoluted (or patchy) leaving residual forest throughout harvested stands. This fire-like distribution provides a seed source for cutblocks. Re-establishment of locally effected shade tolerant species should occur after canopy recovery and the return of pre-harvest conditions. Remnant patches also provide some protection for large "wildlife" trees and advanced regeneration.

6.2.1 Logging Coarse Woody Debris (or Slash)

The retention of slash over cutblocks (as is the current practice) is recommended to continue. Slash retention minimizes losses of organic matter and nutrients from the system resulting from harvesting. As post-logged forests mature with an absence of standing dead trees, slash will be the primary source of decayed logs for seedling establishment of species such as white spruce and white birch. Debris piles are also important sources of cover and refuge in an otherwise exposed environment (for both flora and fauna). Micro-sites with abnormally high slash loadings add to the heterogeneity of cutblocks, without detrimentally effecting stocking densities at the stand level. In general, practices that create local heterogeneity will ultimately increase biological diversity.

6.2.2 Aspen Regeneration

Regeneration of trembling aspen is prolific in most Duck Mountain stands. High densities were observed within a year of disturbance, followed by rapid self-thinning. We recommend continuation of the free-to-grow policy currently practiced; artificial thinning is not required, nor recommended. Artificial thinning may result in secondary sucker development rather than increases in growth of existing suckers. Competition between suckers results in the natural selection of the most ecologically fit individuals into the canopy.

A management concern from industry partners is the potentially detrimental effect of shading from residual vegetation patches on aspen stocking. Although this problem was not directly studied, suckers developing in the cutblock periphery were of "typical" densities, but were often larger than those in more exposed portions of the cutblock. Possible causes for accelerated growth may be augmentation of carbohydrates from unharvested rametes (on the same root system), or increased vertical growth in response to shading. Further research is suggested to test and/or explain this phenomenon and its potential ramifications on cutblock design.

A second issue is that of balsam poplar regeneration. Balsam poplar suckers showed similar development (height and growth) to trembling aspen in the co-dominant assemblages of dry stands. When present in moist stands, balsam poplar appeared to out-compete aspen (growing larger and taller) in locally restricted areas. These patterns of dominance in sympatric populations were also reported by Peterson and Peterson (1992). However, post-harvest regeneration of trembling aspen and balsam poplar generally reflected pre-harvest proportions on all cutblocks. Harvesting is not expected to alter canopy composition with respect to hardwood stocking.

6.2.3 Competition with Marsh Reed Grass (*Calamagrostis canadensis*)

Although overall aspen regeneration exceeded levels required for full stocking in most cutblocks, two moist cutblocks (sites 26 and 32) showed abnormally low regeneration in portions of the cutblocks (one of two strata—see fig. 3.2). Harvesting resulted in the proliferation of marsh reed grass over large portions of these sites. In

Alberta, marsh reed grass is a problem competitor on clearcuts with moist to wet, nutrient-rich soils (Lieffers et al. 1993). It forms dense beds sufficient to depress soil temperatures (with insulating litter) and exclude rooting space (Hogg and Lieffers 1991).

Marsh reed grass was found at low densities throughout the study area (in all three stand types), occasionally forming small meadows in wet depressions after harvest. These ordinarily corresponded with similar wet meadows in the interior forest and were a minor component of the landscape. Harvesting in the atypical stands resulted in saturated soil conditions (standing-surface water) over much of the cutblock. Low densities of suckers over-topped the grass, and were expected to develop into a trembling aspen canopy. Slightly elevated portions (approximately 15 cm) had typical regeneration. The elevated water table observed in these previously-forested areas may be a result of reduced transpiration losses (associated with canopy removal), or impoundment / altered drainage with equipment trafficking. The latter may be mitigated by trenching logging roads that are perpendicular to the direction of overland water flow. Both cutblocks appeared to have blocked or disrupted drainage. Moist stand types (mountain maple-hazelnut sub-canopy) are susceptible to slight changes in water table. It is recommended that overland flow be channeled away from large-scale (previously forested) depressions after harvest to minimize marsh reed grass competition.

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