University of Alberta

Impacts of post-fire salvage logging on tree regeneration and understory plant communities in burned stands of the mixedwood boreal forest

by

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ABSTRACT

This study investigated the impacts of post-fire salvage logging on the forest structure, tree regeneration and understory plant community composition of burned, aspen-dominated (*Populus tremuloides* Michx.) mixedwood forest stands of North-eastern Alberta, Canada. Representative wildfire and salvage logged forest stands were compared at both early (2 years post-disturbance) and mid-successional (34 years post-disturbance) forest development stages. Deciduous regeneration in the immediate post-disturbance time period was significantly better in wildfire stands with greater sapling heights and nearly double the stem densities of salvage logged stands. Regeneration of disturbance origin deciduous trees was not significantly different between wildfire and salvaged stands 34 years after disturbance, however, conifer regeneration (arising from post-salvage silvicultural practices) in salvage logged stands was substantial. The understory plant communities of early successional salvage logged stands were characterized by the presence of introduced weedy species, greater species turnover (beta diversity), and marked differences in species composition, notably higher abundances of shrubs and grasses, and lower abundances of post-fire specialist plant species as compared to wildfire stands. The plant communities of mid-successional wildfire and salvage logged stands were fairly similar, but there were some important differences, i.e. high densities of tall shrubs and understory white spruce in the salvaged stands.

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LIST OF ABBREVIATIONS

BIC: Bayesian Information Criterion

DBH: Diameter at Breast Height

Db-RDA: Distance-based Redundancy Analysis

DWM: Downed Woody Materials

GLM: General Linear Model

ISA: Indicator Species Analysis

MRPP: Multi-Response Permutation Procedures

PCoA: Principal Coordinate Analysis

PPFD: Photosynthetic Photon Flux Density

RDA: Redundancy Analysis

TDR: Time Domain Reflectometry

VIF: Variance Inflation Factor

CHAPTER 1

GENERAL INTRODUCTION

The mixedwood boreal forest of western Canada has historically been shaped by various natural disturbances such as insect outbreaks (Bonan & Shugart 1989) and wind events (Barnes et al. 1998), with the primary stand-replacing natural disturbance being wildfire (Johnson 1992). These disturbances result in a heterogeneous landscape characterized by a high degree of both spatial and temporal variability in forest structure and function to which the species of the boreal forest have adapted (Rowe & Scotter 1973, Bonan & Shugart 1989). However, the nature of large-scale, stand-replacing disturbance in the boreal forest has been altered since European settlement, with evidence that the wildfire return interval has increased and the annual area burned has decreased (Murphy 1985). With increased allocation of the productive forested landbase to harvesting in recent decades (Natural Resources Canada 2003), it appears likely that in the future, stand initiation will predominantly result from anthropogenic activities. While there has been a recent trend in forest management to use harvesting strategies that attempt to approximate natural disturbance regimes (for example irregular cutblock edges and variable retention of live trees and snags) (Franklin 1993, Hunter 1993), some evidence suggests that these disturbances are not analogous to fire, at least at the earliest seral stages (Carleton & MacLellan 1994, Lee 1999). To compound this effect, post-fire salvage logging of fire-killed, merchantable sized trees has become a common activity immediately following many wildfires in the boreal forest. Particularly within the last decade, the majority of accessible, merchantable burned forest stands in Alberta have been salvage logged. As a result, unmanaged post-fire ecosystems are becoming less frequent in the boreal forest, suggesting that the ecological function of these early post-fire forests may be compromised and the species dependant upon these stands potentially threatened.

POST-FIRE STAND ATTRIBUTES

Forest development subsequent to wildfire is greatly influenced by the presence of a number of characteristic physical and biological attributes created by wildfire that influence the ecological processes of the stand (Eberhart & Woodard 1987, Lee et al. 1997). The most conspicuous legacy of stand-replacing wildfires is the very high density of standing dead trees (snags). Light levels immediately after wildfire are generally elevated as a result of the death of these canopy trees, which subsequently influences the microclimatic and soil conditions in burned stands. This has significant implications for plant growth as well as for rates of nutrient cycling and mineralization in forest soils (Ahlgren & Ahlgren 1960, Barnes et al. 1998). The high densities of snags in early-post fire stands however, are still capable of casting partial shade, consequently influencing the amount of light reaching the forest floor and potentially acting to moderate environmental extremes such as those occurring during hot and dry periods (Carleton & MacLellan 1994). In some cases, high winds subsequent to wildfire can cause the snags or residual live trees to blow down or wind-snap, creating large amounts of downed wood as well as pits and tip-up mounds where tree roots have been pulled out of the ground. Additionally, by 10-15 years post-fire, most snags have fallen down and started to decay as downed logs on the forest floor (Lee & Crites 1999). These downed logs may provide a significant, stable source of nutrients capable of persisting over decades (Barnes et al. 1998). This becomes particularly important after severe wildfires when surface organic layers are removed and potentially significant levels of soil nutrients (particularly nitrogen) are volatilized (Grier 1975, MacLean et al. 1983, Brais et al. 2000).

Both initial recruitment and subsequent development of plant communities after disturbance are greatly influenced by the availability and characteristics of suitable regeneration substrates (microsites) (Grubb 1977). After wildfire, downed logs and windthrow pits and mounds produce microsites suitable for regenerating plants by acting to ameliorate moisture and nutrient conditions and to reduce competition from plants on the forest floor (Harmon & Franklin 1989). The availability of patches of bare mineral soil, such as those that occur with the removal of surface organic matter after severe wildfires, are important for the recruitment of a number of plant species, in particular white spruce (*Picea glauca*) (Zasada 1971).

Residual patches of unburned vegetation are commonly found embedded within fire boundaries and can play a number of important ecological roles in early post-fire stands (Eberhart & Woodard 1987). They may accelerate the recovery of burned areas by functioning as refugia from which understory plants can recolonize burned habitats (Rowe & Scotter 1973, Turner et al. 1997). Live trees within residual patches, particularly conifers, may provide a significant source of viable seed thereby contributing significantly to the natural regeneration of early post-fire stands (Zasada 1971). Additionally, since some wildfires may consume much of the pre-existing downed woody materials of a stand (Quintillo et al. 1991), residual patches may play a significant role later in forest succession by providing pre-fire downed woody materials that are in advanced states of decay (Lee et al. 1997). This supply of decayed logs may serve as suitable microsites for the establishment and retention of later successional plant species (Lee & Sturgess 2001), thus increasing the heterogeneity and diversity of the young forest stand.

EARLY POST-FIRE COMMUNITIES

Boreal forest stands in the first several years after wildfire are generally characterized by species that are either rare or uncommon at other points in forest succession (Lee 1999), making early post-fire stands of unique importance in the boreal forest (Van Cleve & Viereck 1981, Hutto 1995). A number of insects including pyrophillous beetle species, for example *Melanophila acuminata* (Buprestidae) (Evans 1966), and other early post-fire habitat specialists (Muona & Rutanen 1994) quickly colonize burned trees and are often extremely abundant immediately after wildfire. In apparent response to the increased foraging opportunities afforded by these high densities of larval wood-boring beetles (Murphy and Lehnhausen 1998) and the increased availability of nesting habitat for cavity nesters (Hutto 1995, Hobson & Shieck 1999), a number of bird species, in particular black-backed (*Picoides arcticus*) and three-toed woodpeckers (*Picoides tridactylus)*, have been found to be highly associated with burned forests within the first 2-3 years after wildfire, as compared to other forest stand ages (Hutto 1995, Hoyt & Hannon 2002).

The vascular plant community immediately after wildfire is similarly distinct from plant communities at other stages in forest succession. Unique attributes of early post-fire environments, such as the increased availability of colonization microsites, increased heat absorption through blackened soil and increased light availability, promote the germination of previously dormant seeds and the vegetative resprouting of fire damaged individuals (Turner et al. 1997, Whittle et al. 1997). The typical plant community immediately following wildfire is dominated by shade intolerant, early successional species (Rowe 1983, Crites 1999). Once established, species germinating from wind-blown seeds, for example fireweed (*Epilobium angustifolium*), can quickly come to dominate burned stands through profuse seed production or vegetative reproduction (Rowe 1983). Other species already present in the forest stand prior to disturbance, notably trembling aspen *(Populus tremuloides*), re-establish rapidly after wildfire by resprouting from rhizomes or other underground organs (Barnes 1966, Dix & Swan 1971, Rowe 1983). Conifer species with serotinous or semi-serotinous cones such as jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) may also re-establish quickly after wildfire, provided appropriate mineral soil microsites are available (Greene et al. 1999, Noël 2002).

While the aforementioned suites of species all contribute significantly to the composition of early post-fire plant communities, the distinctiveness of these communities can primarily be attributed to the release of long-lived, buried propagules in the mineral soil seedbank (Johnson 1981, Crites 1999). These species, including corydalis (*Corydalis aurea* and *C. sempervirens)*, American dragonhead (*Dracocephalum parviflorum*), purple-leaved willowherb (*Epilobium ciliatum*) and Bicknell's geranium (*Geranium bicknellii*), require wildfire intense enough to remove surface layers of soil organic matter and break dormancy, but brief enough to avoid killing or destroying the seeds (Ahlgren 1960, Rowe 1983, Fyles 1989). Once established, these species deposit large amounts of seed on the burned, mineral soil surface, which will subsequently be buried under developing soil organic matter and litter, and lie dormant until the next disturbance (Rowe 1983, Qi & Scarratt 1998). These species normally dominate the plant community for only a few years after wildfire (2-5 years) before they are shaded and out-competed by deciduous saplings and other herbaceous vegetation (Johnson 1981, Van Cleve & Viereck 1981).

POST-FIRE SALVAGE LOGGING

Current provincial forest management directives regarding post-fire salvage logging in Alberta (Sustainable Resource Development 2002) acknowledge the importance of maintaining forest ecosystem integrity and non-timber values. However, specific guidelines for sustainable forest management are lacking and the emphasis remains on ensuring timber supply in the face of potentially significant impacts to annual allowable cuts within forest management areas following large scale wildfires. In many cases, the opportunity to salvage log burned stands represents a windfall for forestry companies since timber dues are reduced not only for fire-killed or damaged trees, but also for live trees in patches smaller than four hectares. In addition, existing operating ground rules and reforestation standards for forest tenure holders may be relaxed during salvage logging operations pending approval from the crown. Despite ample evidence of the ecological importance of early post-fire environments and their associated communities, burned areas are still frequently regarded as being destroyed environments, the timber value of which must be somehow recouped. As such, recommendations regarding the retention of forest structure within burned areas are limited and appear to emphasize the maintenance of unburned patches of live trees over that of fire-killed patches and individual snags. In addition, forest tenure holders refusing to salvage fire-killed, merchantable trees may be penalized by having the unsalvaged volume charged against their annual allowable cut or quota.

Post-fire salvage logging generally occurs in the first 2 years following wildfire; since the economic value of burned timber deteriorates rapidly due to insect damage, disease, blow-down, and drying and cracking of the wood (Cerezke 1999). Removal of the majority of standing dead and residual live trees within this critical time period will likely have a number of significant impacts on early post-fire communities.

Species dependent upon the foraging or nesting habitat associated with early post-fire stands have demonstrated negative responses to salvage logging activities in a number of studies. Specifically, changes have been observed in the composition of boreal forest beetle (Cobb 2001) and songbird (Morissette et al. 2002) communities and in the abundance and nesting success of cavity-nesting birds in the Northwestern United States (Hitchcox 1996, Saab & Dudley 1998).

Research to date on the impacts of post-fire salvage logging on plants however, remains quite limited and is primarily restricted to conifer dominated forest ecosystems outside of the boreal forest (Roy 1956, Stuart et al. 1993, Ne'eman et al. 1995, Martinez-Sanchez et al. 1999, McIver & Starr 2001), with the exception of three recent studies in boreal forest stands of Alberta and Quebec (Crites & Hanus 2001, Noël 2002 and Fraser et al. in press). Given the particularly scant nature of research on the impacts of post-fire salvage logging on plants in the boreal forest, the following review, while emphasizing boreal forest research, also refers to research in other pyrogenic forested ecosystems. Therefore, the assumption is that the basic mechanisms underlying how these different forested systems respond to wildfire and salvage logging are somewhat similar.

Evidence suggests that post-fire salvage logging may not only reduce initial tree establishment subsequent to disturbance, but also potentially reduce the subsequent growth and successful development of the regenerating forest stand over time. For example, within the first year following salvage logging, pine (*Pinus halepensis*) seedling mortality in coniferous forest stands of the Mediterranean was 33%; significantly greater than that of in wildfire stands (Martinez-Sanchez et al. 1999). Seedling growth rates also appeared to be negatively effected by salvage logging, at least within the first four years following disturbance. Similar trends in tree regeneration are displayed in aspen-dominated mixedwood boreal stands subject to post-fire salvage logging in northeastern Alberta. In the first year following salvage logging, Fraser et al. (in press) found a 25% reduction in aspen sapling density along with reduced height growth and sapling leaf area in burned-salvage logged forests (hereafter referred to as salvaged stands). These results were attributed both to mechanical damage of established seedlings and suckers by logging equipment (Martinez-Sanchez et al. 1999, Fraser et al. in press) and to the more extreme microclimatic conditions (reduced shade and an associated increase in water stress of seedlings) (Martinez-Sanchez et al. 1999) in salvage logged forests.

However, other literature resulting from research conducted in conifer dominated mixedwood boreal forest stands in Quebec, suggest that of a number of tree species, trembling aspen is the most resilient to salvage logging. Noël (2002) found that black spruce regeneration exhibited a significant reduction in density of seedlings up to two years following salvage logging and jack pine exhibited a negative response to salvage logging only within the first year subsequent to disturbance, while trembling aspen appeared to be resilient to salvage logging with no statistically significant observed impacts on stem density over the study period.

Potential impacts of post-fire salvage logging extend beyond tree regeneration to the richness and composition of the understory plant community. Trends in overall species richness observed in conifer dominated stands outside the boreal forest are unclear, with richness having been found to either increase (Ne'eman et al. 1995) or remain unchanged (Stuart et al. 1993) in burned stands subjected to salvage logging. Scarification and mixing of the mineral soil by logging equipment has the potential to create additional regeneration microsites (in particular patches of disturbed mineral soil) or modify existing ones in a manner that may influence which plant species regenerate successfully in salvaged stands (Crites & Hanus 2001, Noël 2002). In terms of the composition of early post-fire communities, logging equipment used to harvest burned stands could introduce weedy or exotic species resulting in the observed presence of these species in some salvaged stands (Crites & Hanus 2001). Fire-dependent boreal forest species such as Bicknell's geranium and pink corydalis, were present in both wildfire and salvaged forest stands of northeastern Alberta (Crites & Hanus 2001). Since these species would be subject to mechanical damage by logging equipment and the more extreme environment likely created by salvage logging, it is possible that they might experience increased mortality in salvaged stands and subsequently persist at lower abundances. Over multiple rotations of wildfire plus salvage logging, this could potentially compromise the ability of these species to successfully deposit their seeds into the mineral soil seedbank and as a result, the long-term survival of these species could be in question. Evidence from Fennoscandinavian boreal forests suggest that the long-term result of disruption in the natural fire regime and multiple rotations of harvesting is a general reduction in biodiversity and the loss of early post-fire habitat specialists from a number of taxa (Berg et al. 1994, Ostlund et al. 1997).

Compounded disturbances have been argued to be ecologically more serious than single, isolated disturbances since the ecosystem may not have sufficient time or the ability to recover to its original pre-disturbance level of ecological function (Paine et al. 1998). Evidence suggests that salvage logging may act as a secondary disturbance to wildfire in early post-fire plant communities by causing both direct mechanical injury (breakage, flattening) and mortality to regenerating vegetation, as well as indirectly influencing vegetation through changes to light availability and soil properties (such as compaction and nutrient availability) and changes in the availability or characteristics of regeneration microsites. Therefore, given the potentially additive secondary disturbance of salvage logging in burned stands, it seems likely that salvaged stands could be very different from burned stands in terms of tree regeneration and plant community composition and that this difference may persist for a number of years.

THESIS OUTLINE AND OBJECTIVES

The impacts of salvage logging on plant regeneration in post-fire communities of aspen-dominated mixedwoods are largely unknown, as is the extent to which these impacts may continue to influence subsequent stand development. Therefore, in this study I determined how post-fire salvage logging influences tree regeneration and the biodiversity and composition of the understory vascular plant community both immediately following disturbance (2 years post-disturbance) and later in boreal forest succession (34 years post-disturbance). For both stand ages, I examined relationships between changes in environmental attributes (light, microclimate, soil moisture, regeneration microsite availability) associated with salvage logging in wildfire stands to changes in tree regeneration success and the composition and overall richness and diversity of the understory.

In Chapter 2, I examine the influence of structural (amount of residual trees, snags and downed woody materials) and environmental (light, temperature and relative humidity levels) characteristics of wildfire and salvaged stands on tree regeneration (stem density and height). In Chapter 3, I determine the impacts of post-fire salvage logging on the understory vascular plant community. In particular, I determine if vascular plant species richness, beta diversity and composition vary between wildfire and salvaged stands. In Chapter 4, I present general conclusions and management implications resulting from this research and discuss them within the context of current provincial salvage logging policy and sustainable forest management.

LITERATURE CITED

Ahlgren, C.E. 1960. Some effects of fire on forest reproduction in southeastern Minnesota. Journal of Forestry **57**:194-200.

Ahlgren, I.F. & Ahlgren, C.E. 1960. Ecological effects of forest fires. Botanical Review **26**:483-533.

Barnes, B.V. 1966. The clonal growth habit of American aspens. Ecology **47**:439-447.

Barnes, B.V., Zak, D.R., Denton, S.R. & Spurr, S.H. 1998. Forest Ecology, 4th ed. John Wiley & Sons Inc., New York.

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M. & Weslien, J. 1994. Threatened plant, animal and fungus species in Swedish forests: Distribution and habitat associations. Conservation Biology **8**:718-731.

Bonan, G.B. & Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. Annual Review in Ecology and Systematics **20**:1-28.

Brais, S., Paré, D. & Ouimet, R. 2000. Impacts of wild fire severity and salvage harvesting on the nutrient balance of jack pine and black spruce boreal stands. Forest Ecology and Management **137**:231-243.

Carleton, T.J. & MacLellan, P. 1994. Woody vegetation responses to fire versus clear-cutting logging: A comparative survey in the central Canadian boreal forest. Ecoscience **1**:141-152.

Cerezke, H.F. 1999. Management of wood borers in coniferous logs. Publication Number I/739. Forest Health Branch, Forest Protection Division, Lands and Forest Division, Edmonton, Alberta.

Cobb, T. 2001. Disturbance and ecological stability of boreal forest beetle assemblages. MSc. Thesis, University of Regina, Saskatchewan.

Crites, S. 1999. A comparison of early successional understory plant communities following fire and harvesting. In: Lee, P.C. (ed.), Fire and harvest residual (FAHR) project: the impact of wildfire and harvest residuals on forest structure and biodiversity in aspen-dominated boreal forests of Alberta. Publication Number T/495. Alberta Research Council, Vegreville.

Crites, S. & Hanus, S. 2001. Succession of herbaceous, shrub and tree communities following combined treatments of fire and harvesting. Final Report. Alberta Research Council, Vegreville, Alberta.

Dix, R.L. & Swan, J.M. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Canadian Journal of Botany **49**:657-676.

Eberhart, K.E. & Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. Canadian Journal of Forestry **17**:1207-1212.

Evans, W.G. 1966. Perception of infrared radiation from forest fires by *Melanophila acuminata* de Geer (Buprestidae: Coleoptera). Ecology **47**:1061-1065.

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems or landscapes? Ecological Applications **3**:202-205.

Fraser, E., Landhäusser, S. & Lieffers, V. In Press. The effect of fire severity and salvage logging traffic on regeneration and early growth of aspen suckers. Forestry Chronicle.

Fyles, J.W. 1989. Seed bank populations in upland coniferous forests in central Alberta. Canadian Journal of Botany **67**:274-278.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. & Simard, M.J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forest Research **29**:824-839.

Grier, C.C. 1975. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. Canadian Journal of Forest Research **5**:599-607.

Grubb P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews **52**:107-145.

Harmon, M.E. & Franklin, J.F. 1989. Tree seedlings on logs in Picea Tsuga forests of Oregon and Washington. Ecology **70**:48-59.

Hitchcox, S. 1996. Abundance and nesting success of cavity-nesting birds in unlogged and salvage logged burned forest in Northwestern Montana. MSc. Thesis, University of Montana.

Hobson, K. & Shieck, J. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over thirty years. Ecological Applications **9**:849-863.

Hoyt, J.S. & Hannon, S.J. 2002. Habitat associations of black-backed and three-toed woodpeckers in the boreal forest of Alberta. Canadian Journal of Forest Research **32**:1881-1888.

Hunter, M.L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation **65**:115-120.

Hutto, R.L. 1995. Composition of bird communities following stand-replacing fires in northern rocky mountain (USA) conifer forests. Conservation Biology **9**:1041-1058.

Johnson, E.A. 1981. Vegetation organization and dynamics of lichen woodland communities in the Northwest Territories, Canada. Ecology **62**:200-215.

Johnson, E.A. 1992. Fire and vegetation dynamics: Studies from the North American boreal forest. Cambridge University Press, Cambridge.

Lee, P.C. (Ed.). 1999. Fire and harvest residual (FAHR) project: the impact of wildfire and harvest residuals on forest structure and biodiversity in aspen-dominated boreal forests of Alberta. Publication Number T/495. Alberta Research Council, Vegreville.

Lee, P.C. & Crites, S. 1999. Early successional deadwood dynamics in wildfire and harvest stands. In: Lee, P.C. (ed.), Fire and harvest residual (FAHR) project: the impact of wildfire and harvest residuals on forest structure and biodiversity in aspen-dominated boreal forests of Alberta. Publication Number T/495. Alberta Research Council, Vegreville.

Lee, P.C., Crites, S.C., Nietfeld, M., Nguyen, H.V. & Stelfox, J.B. 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecological Applications **7**:691-701.

Lee, P.C. & Sturgess, K. 2001. The effects of logs, stumps and root throws on understory communities within 28-year old aspen-dominated boreal forests. Canadian Journal of Botany **79**:905-916.

MacLean, D.A., Woodley, S.J., Weber, M.G. & Wein, R.W. 1983. Fire and nutrient cycling. In: Wein, R.W. & MacLean, D.A. (eds.), The role of fire in northern circumpolar ecosystems. John Wiley & Sons Inc. New York.

Martinez-Sanchez, J.J., Ferrandis, P., de las Heras, J. & Herranz, J.M. 1999. Effect of burnt wood removal on the natural regeneration of *Pinus halepensis* after fire in a pine forest in Tus valley (SE Spain). Forest Ecology and Management **123**:1-10.

McIver, J.D. & Starr, L. 2001. A literature review on the environmental effects of post-fire logging. Western Journal of Applied Forestry **16**:159-168.

Morissette, J.L., Cobb, T.P., Brigham, R.M. & James, P.C. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Canadian Journal of Forest Research **32**:2169-2183.

Muona, J. & Rutanen, I. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. Annales Zoologici Fennici **31**:109-121.

Murphy, E.C. & Lehnhausen, W.A. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. Journal of Wildlife Management **62**:1359-1372.

Murphy, P.J. 1985. Methods for evaluating the effects of forest fire management in Alberta. PhD. thesis, University of British Columbia, B.C.

Natural Resources Canada, Canadian Forest Service. 2002. National forestry database (web page) http://nfdp.ccfm.org. Accessed May 7, 2003.

Ne'eman, G., Lahav, H. & Izhaki, I. 1995. Recovery of vegetation in a natural east Mediterranean pine forest on Mount Carmel, Israel as affected by management strategies. Forest Ecology and Management **75**:17-26.

Noël, J. 2002. Régénération forestière après feu et coupe de récupération dans le secteur de Val-Paradis, Abitibi. MSc. thesis, Université du Québec à Montréal.

Ostlund, L., Zackrisson, O. & Axelsson, A. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Canadian Journal of Forest Research **27**:1198-1206.

Paine, R.T., Tegner, M.J. & Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. Ecosystems **1**:535-545.

Qi, M. & Scarratt, J.B. 1998. Effects of harvesting method on seed bank dynamics in a boreal mixedwood forest in northwestern Ontario. Canadian Journal of Botany **76**:872-883.

Quintilio, D., Alexander, M.E. & Ponto, R.L. 1991. Spring fires in semi-mature trembling aspen stand in central Alberta. Canadian Forest Service, Northern Forestry Centre, Alberta. Information Report NORX-323.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In: Wein, R.W. & MacLean,D.A. (eds.), The role of fire in northern circumpolar ecosystems. John Wiley & sons Inc. New York.

Rowe, J.S. & Scotter, G.W. 1973. Fire in the boreal forest. Quaternary Research **3**:444-464.

Roy, D.F. 1956. Salvage logging may destroy Douglas-fir reproduction. USDA Forest Service, Research Note 107.

Saab, V.A. & Dudley, J.G. 1998. Responses of cavity-nesting birds to stand-replacement fire and salvage logging in ponderosa pine/Douglas fir forests of Southwestern Idaho. USDA Forest Service, RMRS-RP-11.

Stuart, J.D., Grifantini, M.C. & Fox, L. 1993. Early successional pathways following wildfire and subsequent silvicultural treatment in Douglas-fir/hardwood forests, NW California. Forest Science **39**:561-572.

Sustainable Resource Development. 2002. 2002 Fires: Fire salvage strategy framework. Forest management planning and operations: Directives & guidelines for fire salvage allocation, planning & operations, annual allowable cuts, reforestation and production control. Forest Operations Branch, Lands & Forest Division, Government of Alberta.

Turner, M.G., Romme, W.H., Gardner, R.H. & Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs **64**:411-433

Van Cleve, K. & Viereck, L. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. In: West, D.C. (ed.), Forest succession. Springer-Verlag, New York.

Whittle, C.A., Duchesne, L.C. & Needham, T. 1997. The importance of buried seeds and vegetative propagation in the development of postfire plant communities. Environmental Reviews **5**:78-87.

Zasada, J.C. 1971. Natural regeneration of interior Alaska forests: seed, seedbed and vegetative reproduction considerations. In: Slaughter, C.W., Barney, R.J. & Hansen, G.M. (eds), Fire in the northern environment- A symposium. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, OR.

CHAPTER 2

IMPACTS OF POST-FIRE SALVAGE LOGGING ON TREE REGENERATION IN BURNED STANDS OF THE MIXEDWOOD BOREAL FOREST

INTRODUCTION

The recruitment success of the initial tree cohort immediately following disturbance is a major determinant of the productivity and subsequent successional development of boreal forest plant communities (Zoladeski & Maycock 1990, Barnes et al. 1998, Peters 2002). This initial recruitment is determined by the reproductive characteristics of those species available to recolonize the disturbed site (Rowe 1983, Greene et al. 1999), the characteristics of the establishment environment (Purdy et al. 2002) and the availability of reproductive propagules and suitable regeneration substrates (Dix & Swan 1971, Grubb 1977). It is likely that salvage logging activities will modify seed availability, the characteristics of regeneration microsites, and the environmental conditions of early post-fire stands, thereby influencing both initial tree regeneration and the successional pathway of the regenerating forest.

When present within forest stands prior to disturbance by wildfire, deciduous tree species, in particular trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*), are capable of re-establishing rapidly by resprouting from adventitious buds on surviving roots (Barnes 1966, Dix & Swan 1971, Rowe 1983). The death of canopy trees resulting from moderate intensity wildfires generally stimulates suckering as a result of the release of apical dominance (Farmer 1962, Schier 1972). Additional wildfire effects including increased light absorption by fire-blackened soil, and the removal of shading understory vegetation and insulating layers of litter and organic materials, may also act to stimulate suckering by increasing soil temperatures (Maini & Horton 1966, Peterson & Peterson 1992). Salvage logging may further increase soil heating during the day by removing the partial shade afforded by snags and residual live trees (Carleton &

MacLellan 1994) potentially resulting in increased suckering and growth rates (Steneker 1974). Alternatively, the increased exposure in salvaged stands may prove detrimental to regeneration as a result of increased risk of moisture stress (Martinez-Sanchez et al. 1999) and frost damage (Keenan & Kimmins 1993) to young regenerating trees.

A large proportion of aspen roots are concentrated near the soil surface and as a result, aspen are often susceptible to damage by repeated traffic of logging equipment, particularly when harvesting occurs on unfrozen and wet soils (Stone & Elioff 1998). Salvage logging generally begins in the fall and winter following wildfire and may extend up to two years following the initial disturbance (Barker 1989, Cerezke 1999, pers. obs.). Therefore, it is likely that logging equipment will cause mechanical damage (breakage or scraping) to young aspen saplings, particularly the advanced regeneration that suckered the previous spring or fall. The likely combination of root and stem damage in regenerating aspen stands subjected to salvage logging may result in less successful regeneration than that observed in wildfire stands. Fraser et al. (in press) found that salvage logging in burned aspen dominated mixedwoods caused mechanical damage to previously established aspen suckers and consequently resulted in a decline in both the number and height of aspen saplings in the first year following salvage logging as compared with wildfire stands. More significantly, they also found a large reduction in aspen leaf area/sucker in salvaged stands which suggests that salvage logging may negatively impact rates of photosynthesis, thereby influencing sapling growth. In addition, this reduced photosynthetic biomass could result in diminished carbohydrate reserves for the maintenance of root respiration in the parental root system, potentially resulting in root die-back (Barnes et al. 1998, Landhäusser & Lieffers 2003). These will influence the growth of the regenerating stand and will likely substantially influence the primary productivity and future growth of these forests.

In contrast to the reproductive strategy of aspen, boreal forest conifer species recruit predominantly from seed. Several species including jack pine, lodgepole pine and black spruce, are well adapted to frequent disturbance by wildfire and can exhibit a high degree of cone serotiny (Rowe 1983, Greene et al. 1999). White spruce however, relies on the dispersal of seeds into burned areas from mature trees either in residual patches or from outside the wildfire perimeter (Bergeron & Dansereau 1993, Galipeau et al. 1997, Greene et al. 1999). Eberhart & Woodard (1987) concluded that the majority of the area burned by very large wildfires could be greater than 100 m from residual patches or the burned forest edge, a distance which may prove prohibitive for conifer seed dispersal (Zasada 1985). In some cases however, mature white spruce burned in the summer may still produce viable seed in the year following disturbance by wildfire (Zasada 1985, E. Macdonald unpubl. data). The majority of viable seed is normally produced by tall, large diameter conifers, however, these trees are also the most economically valuable and will be the most likely to be salvage logged. Therefore, it is likely that natural recruitment of white spruce into burned areas may potentially occur quite slowly and may be even more limited following salvage logging as a result of the removal of remaining seed trees.

Evidence suggests that the majority of successful regeneration for white spruce occurs on patches of exposed bare mineral soil or thin layers of organic matter in the first 3-5 years following disturbance by wildfire (Zasada 1985, Peters 2002, Purdy et al. 2002). Mixing and scraping of forest soils by logging equipment may result in increased availability of mineral soil regeneration microsites, potentially promoting increased seedling recruitment. Noël (2002) attributed the observed increase in mineral soil substrates in burned boreal stands to salvage logging activities. Delimbing and on-site processing during salvage logging operations may disperse cones throughout the salvage block and result in more even dispersal and germination of conifer seedlings. However, the removal of canopy trees after salvage logging may result in more extreme microclimatic conditions for regenerating seedlings. The partial shade cast by snags and downed woody material in early post-fire stands may play a role in ameliorating extreme environmental conditions (Carleton & MacLellan 1994), thereby acting to ensure that mineral microsites retain adequate levels of soil moisture (McRae et al. 2001). Martinez-Sanchez et al. (1999) observed that in the first year following salvage logging, *Pinus halepensis* seedling mortality in salvaged Mediterranean pine forest stands was twice that of wildfire stands. They attributed the higher mortality rate of salvaged stands to both direct mortality resulting from mechanical damage by logging equipment and increased seedling mortality (resulting from increased moisture stress) in the first summer following salvage logging. Seedling growth rates and heights were also significantly lower in salvaged stands for at least four years subsequent to disturbance (Martinez-Sanchez et al. 1999) suggesting that post-fire salvage logging may have a longer-term influence on the productivity and development of these forests.

The objective of this study was to determine if salvage logging alters post-fire tree regeneration immediately following disturbance, and whether differences persist at a later stage in forest succession (34 years following initial disturbance). I hypothesized that the density and height of regenerating trees in salvage logged stands would be different from that observed in stands disturbed by wildfire alone. To test this hypothesis, I determined whether the stem density and height of regenerating trees varied at a treatment level between wildfire and salvaged stands. I was subsequently interested in determining if the observed differences in tree regeneration detected immediately following disturbance could be partially attributed to specific modifications of the post-fire physical environment arising from salvage logging activities. Therefore, I characterized a number of environmental and stand characteristics of post-disturbance treatment stands and developed models to determine which of these variables were important in influencing the initial tree regeneration of wildfire and salvaged stands respectively.

METHODS

Study Area

The study area is located within the mid-boreal mixedwood ecoregion (Strong & Leggat 1992) of Alberta, between 55° and 56°N latitude and 110° and 114°W longitude. Upland forests of this area are dominated by trembling aspen (*Populus tremuloides*) or less commonly by balsam poplar (*P. balsamifera*), with white spruce (*Picea glauca*) occurring as the dominant conifer species in most mixed stands. Other species present in varying proportions in forest stands across this region include paper birch (*Betula papyrifera*), jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*).

The well-drained, upland forested areas of this ecoregion are characterized by gray luvisolic soils overlying morainal deposits of glacial till (Wynnyk et al. 1963, Strong & Leggat 1992). Topography is undulating to gently rolling with low to intermediate slopes. The continental, sub-humid climate is typified by warm summers averaging 13.5°C (May through August) and cold winters with average temperatures of –13.2°C (November through February) (Strong & Leggat 1992). Most precipitation falls as rain over the summer months, with the mean annual precipitation being 397mm (Strong & Leggat 1992).

Site Selection & Study Design

The impacts of post-fire salvage logging on tree regeneration were examined in several wildfires of two different ages post-disturbance (2 and 34 years), representing early and mid-successional stages in mixedwood boreal forest development. The older age category chosen for this study was primarily a function of the availability of older salvaged stands in Alberta. The practice of salvaging burned, merchantable trees from wildfires has become a commonplace activity only within the past two decades, therefore, the 34 year old salvage logged stands represent the oldest examples I could find of post-fire salvage logging in Alberta. However, it is important to recognize that this study does not represent a chronosequence approach, since the salvaging regime between the two successional stages differ significantly both in methods and in goals. The recent wildfires were harvested for deciduous trees, primarily aspen, with salvage blocks retaining up to 12% of the original residual live trees and snags, and were subsequently left to regenerate naturally (G. Dribnenki, Alberta-Pacific Forest Industries Inc., pers. com.). In contrast, the older wildfires were harvested for coniferous trees with most of the residual deciduous trees cleared and burned on slash piles and the resulting salvaged blocks silviculturally treated with straight blade scarification and aerial seeding of white spruce (D. Ellison, Alberta Environment, pers. com.). For both successional stages, salvaged stands were logged within one year post-fire. Early salvaged stands were logged in the winter of 1999/2000 and the older salvaged stands were logged in the fall and winter of 1968/1969 and likely bladed and aerial seeded in 1969. Wildfire stands of both successional stages were free of silvicultural or other post-fire management activities.

Stand selection was based on information compiled from provincial forest inventories (Phase III maps and digital Alberta Vegetation Inventory data), the provincial fire database (Alberta Forest Management Division), interpretation of historical aerial photographs, and interviews with industry and government personnel. Fire boundaries, Alberta Vegetation Inventory data (where available) and access data (township grid, roads, seismic lines and pipelines) for recent wildfires were digitally overlain using the geographic information system (GIS) software ArcView v.3.0a. Selected study stands were mature (between 90 and 110 years old), aspen dominated mixedwoods (>60% canopy cover) of fire origin prior to disturbance by wildfire. All selected stands burned in large wildfires (>1900 ha), most of which burned in the spring and early summer (Table 2.1). Since crown fires rarely occur in aspen stands primarily due to the higher moisture content of its foliage and lush understory, wildfires must generally occur in the spring before full leaf flush in order to result in sufficient tree mortality to be considered a stand-replacing disturbance (Johnson 1992). Based on these criteria, three representative stands each of early wildfire and salvaged treatments were selected from 1999 wildfires and two representative stands each of older wildfires and salvaged treatments were selected from 1968 wildfires (Tables 2.1 & 2.2). Early wildfire and salvaged stands (2 years post-disturbance) were sampled over the summer months (mid-May through August) of 2001 and the older wildfire and salvaged stands (34 years post-disturbance) were sampled over the summer of 2002.

In a nested design, fifteen 100m^2 sampling sites (subsamples) were established in all three early salvaged stands and two of the three early wildfire stands (see Table 2.2 for treatment sample sizes). The third early wildfire stand was of limited size and therefore only thirteen sites could be established within its stand boundaries. This resulted in a total of 43 and 45 sites in early wildfire and salvaged stands respectively. It should be noted that all early wildfire stands were small in size (~10ha maximum) due to the low availability of unsalvaged wildfires in general. Twenty 100m^2 sites were established in all four older wildfire and salvaged stands for a total of 40 sites for each treatment (Table 2.2). Sites within stands were a minimum of 50m apart and were located using a random draw of map co-ordinates based on a ruled map of each stand. Sites falling within 50m of salvage block or burn edges, pipelines, haul roads and log decks were discarded and new sites selected.

Data Collection

Early Successional Stands

Stand & Environmental Characteristics

One 50m^2 circular plot (3.99m radius) centered in the middle of each 100m^2 sampling site (see Figure 2.1 for site sampling layout) was used to evaluate the density of all live trees and snags of greater than 5cm diameter at breast height (DBH=1.3m). Trees and snags were identified to species and evidence of burning or charring on the bole recorded (where 1= unburnt; 2= lightly (<25%) charred; 3= 26-75% charred; 4= burnt to charcoal). Tree and snag DBH were also recorded. Elevated or partially blown-down snags were included in the density count only if the snag had originally been rooted within the plot and the bole at DBH was greater than 1.5m above the ground.

Amount and characteristics of downed woody materials (DWM) were quantified using a 25m line intercept transect (Marshall et al. 2000) bisecting the 50m^2 circular tree plot on a randomly determined compass bearing (see Figure 2.1). In order to be recorded, logs could not be rooted, had to be greater than 5cm at their widest end, and greater than 50cm in length. The diameter, length and species of each log, and the length of the line intercept were recorded for each piece of DWM crossing the transect. Each log was visually classified into one of seven decay classes (Table 2.3) and one of four burn classes (where 1= unburnt; 2= lightly (<25%) charred; 3= 26-75% charred; 4= burnt to charcoal). Two measurements of log surface hardness were obtained using a handheld soil penetrometer. This method provides a more quantitative evaluation of log decay, particularly for logs of more advanced decay stages (Lee & Sturgess 2001).

Availability of different forest floor regeneration substrates was assessed using the 25m transect. The length of the intercept for patches of mineral soil, organic soil/litter, moss and other substrates (i.e. substrates occurring at low frequencies such as pits and tip-up mounds) intersecting the transect were recorded and expressed as a percent cover based on the length of the cumulative intersect distance for each forest floor type divided by the total length of the transect.

Slope and aspect were determined respectively using a clinometer and compass at plot center of the 50m^2 circular plot. For a random subset of sites in each stand, measurements of ambient air temperature and relative humidity levels of the surrounding site were recorded using dataloggers (HOBO PRO H8 series, Onset Computer Corp. Bourne, MA) programmed to record readings at one hour intervals for two to four days. These values were then subsequently averaged to create one measurement of temperature and relative humidity for each site. Measurements were standardized using a control datalogger located in an adjacent fully open area (~180° skyview) and programmed to take readings synchronous with those of dataloggers deployed in treatment stands. Measurements for both temperature and relative humidity are therefore expressed as the mean difference (in °C and % respectively) from the open benchmark level. Dataloggers were fixed to wooden stakes approximately 50cm above ground level and covered with protective plastic housings.

Levels of light transmittance (below canopy Photosynthetic Photon Flux Density, PPFD) were measured on uniformly overcast days between 10:00am and 3:00pm. Evidence suggests that measurements of light transmission on overcast days are less variable and therefore provide a more accurate approximation of average daily PPFD levels than do measurements estimated from sunny days (Parent & Messier 1996, Lieffers et al. 1999). Below canopy levels of PPFD (between wavelengths of 400 to 700nm) were measured using a handheld ceptometer (AccuPAR, Decagon Devices Inc. Pullman, WA) composed of 80 sensors. Fifteen measurements of below canopy PPFD were taken at plot center for each site. These measurements were standardized against measurements of above canopy PPFD (full light transmission) using a quantum point sensor (LICOR Inc.) located in an adjacent fully open area (~180° skyview) and programmed to take light transmission readings synchronous with those in treatment sites. The quantum point sensor and the handheld ceptometer were calibrated with each other in the adjacent fully open area (full light). The below canopy measurements of PPFD obtained from the treatment sites were calibrated and then standardized against the above canopy PPFD measurements; therefore light transmission measurements are expressed as percent of full light. These fifteen values were then averaged to create one measurement of light transmission for each site.

Tree Regeneration

All tree regeneration data and associated plot level environmental data were collected between July 6th and August 19th, 2001. Tree regeneration was evaluated within two 1m x 1m plots located at right angles to and 10m distant from the 25m DWM transect (at distances of 5m and 20m along the transect) (see Figure 2.1). Density of all live tree saplings was determined by stem counts within each 1m x 1m plot. Species and height of all saplings were recorded. These values were then averaged (from the two 1m x 1m plots) to create one measurement of sapling stem density and height for each site. Distance to the nearest conifer seed source (where 1=not applicable i.e. conifer seedlings present were a result of anthropogenic seeding or planting, 2= cones present i.e. fallen tree, 3=<100m, 4=100-500m and 5=>500m), the species of conifer and the relative strength of the seed source (where 1= single live tree of canopy or sub-canopy height; 2= single live reproductive tree above canopy height; 3= live patch of reproductive trees) were determined for each plot.

Visual estimates of percent cover were made for lichens and bryophytes, total vegetation (all vascular, non-sapling vegetation), litter, wood and mineral soil in each plot. Average depth of representative patches of litter, moss and organic soil layers (where applicable) were also recorded for each plot. Percent canopy cover at plot center was determined by averaging four measurements at sapling height using a convex spherical densiometer. Soil compaction was assessed using a handheld soil penetrometer. Measurements of soil compaction were taken in each of the four corners of the plot and subsequently averaged to create one value per plot. Soil moisture (percent volumetric water content) was determined by taking the average of two measurements recorded using a time domain reflectometry system (Moisture Point TDR Model MP-917, Environmental Sensors Inc.). Measurements were taken a minimum of 48 hours after significant rain events. However, numerous malfunctions of the TDR system resulted in a highly unbalanced soil moisture dataset, consequently these data were not used in subsequent analyses.

Mid-Successional Stands

Stand & Environmental Characteristics

In order to account for the increased variability arising from the silvicultural techniques applied in the mid-successional stands, slightly larger circular plots (5m radius, ~78.5m^2) (see Figure 2.1 for site sampling layout) were used to evaluate the density of pre-fire (pre 1968) residual trees and snags. Based on tree core data collected by Lee & Crites (1999) in the same wildfire stands, trees with a DBH of 20.4cm or greater were assumed to be of pre-fire origin. Trees (DBH>20.4cm) and snags (DBH>12cm) were identified to species and DBH recorded. Evidence of burning or charring on the boles of snags was recorded (where 1= unburnt; 2= lightly (<25%) charred; 3= 26-75% charred; 4= burnt to charcoal).

Sampling protocols for collection of data on DWM and environmental characteristics (slope, aspect, light transmittance and ambient air temperature and relative humidity levels) in mid-successional stands are identical to those presented above for early successional stands with the exception of soil moisture measurements. Soil moisture (percent volumetric soil water content) was determined by taking the average of two measurements recorded using a dielectric soil moisture sensor (ThetaProbe ML2x, DeltaT Devices Inc.). Measurements were taken a minimum of 48 hours after significant rain events.

Tree Regeneration

All tree regeneration data was recorded between June 3rd and August 29th, 2002. To adequately sample the density of post-fire origin trees, regeneration was evaluated within the 78.5m^2 circular plots (5m radius) centered within the 100m^2 site (Figure 2.1). DBH, condition (alive or dead), height, and species of all trees were recorded. Tree heights were measured using a Suunto clinometer [where height (m)= distance x (tree top% – tree base%)] except for trees less than 2m tall, in which case a tape measure was used. Tree height measurements were then averaged to create one value for tree heights for each site. As with the early successional stands, distance to the nearest conifer seed source, the species of conifer and the relative strength of the seed source was evaluated for each plot.

Data Analysis

Due to the differences in salvage logging regimes, early and mid-successional stands were analyzed separately.

Estimates of total volume of DWM per hectare were calculated for each site for both time periods using Van Wagner's method (1968) [equation 2.1] where v= m^3 DWM/ha; l= transect length; and d= log intersect diameter:

$$v = \left(\frac{\pi^2}{8l}\right)\sum_{i=1}\left(d_i^{\,2}\right) \qquad [2.1]$$

The volumes of DWM in both early (decay classes 1-4; Table 2.3) and late (decay classes 5-7) stages of decay were also calculated for each site.

Descriptive statistics were calculated by treatment for stand, environmental and regeneration data for both time periods. All variables were tested for normality and homoscedasticity using Shapiro-Wilks's and Levene's tests respectively (Zar 1999). A significance level of α=0.05 was used for all statistical analyses.

The template for statistical analysis for both time periods was as follows. Tree regeneration was tested for significant differences between treatments. In cases of significant results, this was followed by multiple regression analysis and significance testing to evaluate the influence of environmental and stand attributes of post-disturbance stands on tree regeneration.

Early Successional Stands

The density of regenerating stems per hectare for each site was calculated separately for deciduous and coniferous tree species. Variation in mean height and stem density between treatments were evaluated using nested general linear models (GLMs) [equation 2.2] (PROC GLM in SAS v.8.02 1999-2000) where Y_{ijk}=dependant variable;

a_i=treatment; $b_{j(i)}$=stand within treatment and e_{ijk}=residual error (sampling sites within stand within treatment).

$$Y_{ijk} = \mu + a_i + b_{j(i)} + e_{ijk} \qquad [2.2]$$

Stand within treatment was used as the error term in the calculation of the F-ratio for treatment effects, and the residual error was used as the error term in the calculation of the F-ratio for the nested term (stand within treatment) (Zar 1999). F-ratios and p-values for these analyses were based on Type III sums of squares. Although stands were considered a random factor in these analyses, post hoc comparisons between stands were made using Tukey's HSD test to determine if statistically significant differences in regeneration were apparent between replicate stands.

The influence of stand and environmental characteristics as explanatory variables for tree regeneration (stem density and height) were examined using multiple linear regression models (PROC REG). Models were fitted for the wildfire and salvage treatments separately. Variables tested as explanatory variables of tree regeneration in these models are listed in Table 2.4. Ambient air temperature and relative humidity were not tested in these models because measurements were available for only a subset of sites within each treatment.

Explanatory and response variables in these models were measured in numerous different units, therefore the explanatory variables were standardized [equation 2.3] resulting in all variables being expressed on a similar scale with a mean of zero and a standard deviation of one.

$$y_i = \frac{y_i - \bar{y}}{s} \qquad [2.3]$$

Standardization allows for the partial regression slopes of the standardized explanatory variables to be compared between variables and interpreted independently of their respective original units (Chatterjee & Price 1991, Quinn & Keough 2002). Both a correlation matrix between explanatory variables and high variance inflation factor (VIF) values suggested that percent cover of DWM and organic soil depth were strongly collinear with a number of other variables (including total volume of DWM, plot level percent cover of wood and litter layer depth), as a result both variables were excluded from further analysis. A preliminary check of the suitability of the dataset for linear regression analysis was conducted by fitting an additive model of all the remaining explanatory variables to stem density and height data. Diagnostic checks for outliers, influential values and non-linear patterns to residuals were evaluated by examining plots of studentized residuals and Cook's D_i against predicted values. In cases of influential outlying observations (high Cook's D_i value with studentized residuals outside of the range of ± 2), the influence of removal of these values on the fit of the model was examined. Model selection was based on Schwarz's (1978) Bayesian Information Criterion (BIC) [equation 2.4] where p=number of explanatory variables included in a specific model and n=number of observations.

$$BIC = n[\ln(SS_{Residual})] + (p+1)\ln(n) - n\ln(n) \qquad [2.4]$$

BIC identifies all possible subsets of explanatory variables from the full regression model, compares the best subsets within each subset size and indicates the best-fitting parsimonious model based on sample size and total number of predictors (Furnival & Wilson 1974, Quinn & Keough 2002). Acceptance of the "best" final model involved examination of the model residuals and comparison with other highly ranked subset models.

These regression analyses suggested a number of common underlying mechanisms associated with deciduous regeneration in wildfire and salvaged stands. Therefore, explanatory variables likely associated with these mechanisms were evaluated for variability between treatments. Variation in light level (percent of full PPFD), ambient air temperature (^{o}C mean difference from open benchmark) and relative humidity (percent mean difference from open benchmark) were each evaluated using nested general linear models (GLMs) [equation 2.2].

Mid-Successional Stands

Preliminary graphical exploration of live deciduous tree data suggested the presence of a second regeneration cohort following the original post-disturbance regeneration in stands of both treatments. As a result, stem density was calculated separately for each site for both the initial post-disturbance regeneration cohort (approximated by all trees of DBH $\geq$ 5 cm) and the apparent second cohort of all saplings and trees of up to 5 cm DBH. In addition, the density of dead deciduous post-disturbance origin trees (all trees of $\geq$ 1.3 m in height and of < 12 cm DBH) and the average height of the initial post-disturbance cohort were calculated for each site. Density of dead deciduous trees was square-root transformed to meet the requirements of normality.

Variation in mean tree densities and height between treatments were evaluated using nested general linear models (GLMs) [equation 2.2]. Stand within treatment was used as the error term in the calculation of the F-ratio for treatment effects, and the residual error was used as the error term in the calculation of the F-ratio for the nested term (stand within treatment) (Zar 1999). F-ratios and p-values for these analyses were based on Type III sums of squares. Although stands were considered a random factor in these analyses, post hoc comparisons between stands were made using Tukey's HSD test to determine if statistically significant differences in regeneration were apparent between replicate stands.

Results of GLM analyses indicated that there were no significant effects of salvage logging on mean tree density or height, as a result, no further statistical analyses were conducted on these data.

RESULTS

Early Successional Stands

Stand & Environmental Characteristics

Unsurprisingly, salvage logging of burned forest stands resulted in a drastic decline in the density of snags and residual live trees when compared to that of wildfire stands (Table 2.5). Residuals sampled in wildfire stands were almost exclusively fire-killed snags and while the majority of residuals retained in salvage logged stands were also snags at the time of sampling (Table 2.5), many showed no visible evidence of scorching or other fire damage. The diameter (DBH) and species (deciduous or coniferous) of residuals between wildfire and salvaged stands were roughly equivalent and there appeared to be no appreciable soil compaction as a result of traffic from salvage logging equipment (Table 2.5).

The total volume of DWM was much higher in salvaged stands likely as a result of the creation of slash from salvaging operations, however this was not reflected to the same degree in the percent cover of DWM between treatment stands. For both wildfire and salvaged stands, the majority of DWM was in early decay stages (decay classes 1-4; Table 2.3), although salvaged stands had a slightly lower proportion of DWM in later decay stages than that of wildfire stands (Table 2.5).

The removal of post-fire residuals and the associated reduction in canopy closure resulting from salvage logging resulted in significantly higher light levels ($P<0.01$; Table 2.6) in salvaged stands than those of wildfire stands (Table 2.5, Figure 2.2). Accordingly, ambient air temperatures were significantly higher ($P=0.04$; Table 2.6) and relative humidity was on average lower ($P=0.06$; Table 2.6) in salvaged stands compared with levels in wildfire stands (Table 2.5). Air temperature and relative humidity were not significantly different between stands of the same treatment (Table 2.6) and thus did not appear to reflect the observed between stand variability in light ($P<0.01$; Table 2.6, Figure 2.2).

Availability of forest floor regeneration substrates did not appear to vary between treatments for the two predominant microsite types of mineral soil and litter/organic soil (Table 2.5). However, availability of bryophyte covered non-woody microsites and other substrates was higher in wildfire stands compared with that of salvaged stands (Table 2.5).

Tree Regeneration

The majority of tree regeneration in both treatments was composed of deciduous saplings (primarily trembling aspen) with only roughly 4% of the total regeneration composed of coniferous seedlings (primarily jack pine with some white spruce) (Table 2.5). Moreover, conifer regeneration was also highly variable across study stands. Available coniferous seed trees were generally of canopy or sub-canopy height in stands of both treatments. However, seed sources in salvaged stands generally occurred within 100 m of sampling sites but were between 100 m to 500 m away from sites in wildfire stands (Table 2.5). The sample size for coniferous regeneration was insufficient to allow for quantitative evaluation of treatment effects, therefore all further results refer to deciduous regeneration only.

Salvage logging had a significant negative effect on both stem density (P=0.05; Figure 2.3 a) and average height (P=0.01; Figure 2.3 b) of deciduous saplings (Table 2.7). Regeneration averaged 157 239 ± 6573 (± 1 S.E.) stems per hectare (sph) in wildfire stands, almost double that of the 85 111 ± 6411 sph average of salvaged stands. Sapling height was taller in wildfire stands with an average height of 1.01 ± 0.03 m compared with 0.59 ± 0.03 m in salvaged stands. Stem density (P<0.01; Figure 2.3 a) and average sapling height (P=0.01; Figure 2.3 b) were highly variable within treatments (Table 2.7), particularly among wildfire stands. Regeneration in the wildfire stand Benson appeared in general, to be less successful with significantly lower sapling densities than Chard and lower sapling heights than Mena. Salvaged stands were homogeneous in terms of sapling height but Cowper had significantly lower sapling densities than the other two salvaged stands (Figure 2.3).

In wildfire stands, the final explanatory model for deciduous stem density ($P<0.01$) selected using BIC explained 40.9% of the total variation in the sampled density data (Table 2.8). Light level (% full PPFD), residual density and litter depth all positively influenced stem density in wildfire stands whereas percent cover of herbaceous vegetation had a significant negative influence (equation: $\text{sapling density}_{\text{wildfire}} = 155\,930 + 22\,626 \times \text{light level} + 16\,534 \times \text{residual density} + 12\,045 \times \text{litter depth} - 24\,806 \times \%$ herb cover; adjusted $r^2=0.35$). Based on the standardized coefficients of the variables selected for this model, light level had the largest explanatory influence on stem density, followed by residual density, herbaceous vegetation cover and litter depth. In contrast, the fit of the final explanatory model selected for deciduous sapling height ($P=0.02$) was poorer (adjusted $r^2=0.13$), explaining only 17.7% of the total variation in the observed sapling height data (Table 2.8). The relative influence of the two selected explanatory variables on sapling height were roughly equivalent, with total volume of DWM having a negative relationship with sapling height and canopy closure having a positive relationship (equation: $\text{sapling height}_{\text{wildfire}} = 1.02 + 0.05 \times \text{canopy closure} - 0.05 \times \text{total volume DWM}$).

The only explanatory variable identified by BIC as influential in explaining variability in the stem density of deciduous saplings in salvaged stands was total volume of DWM ($P=0.01$; Table 2.9). Stem density in salvaged stands fell as total volume of DWM increased, although volume of DWM explained only 14.9% of the variation in the stem density data (equation: $\text{sapling density}_{\text{salvaged}} = 84\,773 - 18\,998$ total volume DWM; adjusted $r^2=0.13$). In salvaged stands, the final explanatory model for sapling height ($P<0.01$) selected using BIC explained 46.3% of the total variation in the observed height data (Table 2.9). Observed sapling height increased with both litter depth and shrub cover, with the relative influence of these explanatory variables on sapling height being almost equal (equation: sapling $height_{salvaged} = 0.60 + 0.11 \times$ litter depth $+ 0.11 \times$ shrub cover; adjusted $r^2=0.44$).

Mid-Successional Stands

Stand & Environmental Characteristics

The average density of total (both trees and snags) pre-disturbance origin residuals was quite similar between treatment stands, however, wildfire stands were characterized by nearly double the density of snags than that retained in salvaged stands (Table 2.10). Live and identifiable standing deadwood residuals in both treatments were of similar size (DBH) and were almost exclusively hardwoods (Table 2.10). Salvage logged stands had very high densities of tall shrubs (greater than 1.3 m in height) composed predominately of willows (*Salix* spp.), alders (*Alnus* spp.) and cherries (*Prunus* spp.), with salvaged stands having shrub densities of more than double that of wildfire stands. Soil compaction was slightly higher in salvaged stands compared to that of wildfire stands (Table 2.10).

Both the total volume of DWM and percent cover of DWM were slightly higher in wildfire stands as compared to salvaged stands (Table 2.10). For both wildfire and salvaged stands, the majority of DWM was in late decay stages (decay classes 5-7; Table 2.3), although salvaged stands had a slightly lower proportion of DWM in earlier decay stages than that of wildfire stands (Table 2.10).

Canopy closure was lower on average in wildfire stands, however this openness was not reflected in significantly higher light levels than those of salvage logged stands, perhaps as a result of the higher densities of tall shrubs in salvaged stands (Table 2.10). There appeared to be no appreciable differences in ambient air temperature, relative humidity or soil moisture between treatment stands (Table 2.10).

Tree Regeneration

Conifer regeneration in salvaged stands appeared to be very successful with white spruce densities averaging 3034 ± 429 sph (Table 2.10). By comparison, natural spruce regeneration in wildfire stands averaged 968 ± 410 sph and was much more variable across study stands. Coniferous seed trees in wildfire stands would generally have been single live reproductive trees above canopy height at the time of disturbance but were generally greater than 500 m from sampling sites. Treatment effects were not quantitatively evaluated for coniferous regeneration because of the confounding influence of the silvicultural techniques applied (straight blade scarification and aerial seeding of white spruce) in the salvaged stands.

There were no significant effects of salvage logging on the density or average height of the initial deciduous tree cohort (live trees of DBH ≥ 5 cm), the density of dead deciduous trees (all dead trees of ≥ 1.3 m in height) or on the density of the second tree cohort (live trees of DBH < 5 cm) (Tables 2.10 & 2.11). Deciduous regeneration was homogeneous between study stands with the exception of the density of the second tree cohort which varied significantly between stands ($P<0.01$; Table 2.11, Figure 2.4).

DISCUSSION

Post-fire salvage logging activities in burned mixedwood boreal forest stands had a pronounced effect on the regeneration of deciduous saplings within two years of their initial disturbance by wildfire. Deciduous saplings in these salvaged stands had both significantly lower stem densities and reduced average heights compared with those in wildfire stands. Our results however, did not provide evidence of a similar regeneration response persisting in aspen dominated mixedwood stands 34 years following the combined disturbance of post-fire salvage logging and site preparation.

Post-Disturbance Conifer Regeneration

Natural conifer regeneration in wildfire and salvaged stands was highly variable at both stand ages. Residual seed trees were generally fairly young, small diameter trees which likely did not produce large amounts of viable seed at the time of disturbance. Mineral seedbeds generally remain receptive for only 3-5 years following wildfire because rapid vegetation recolonization and accumulation of litter and organic material reduces seedbed receptivity (Purdy et al. 2002). Mineral soil microsites were still present two years following disturbance when these stands were sampled. Therefore, assuming suitable mineral microsites were also present in the early successional stands immediately following disturbance, conifer recruitment was likely limited primarily by seed rather than microsite availability. Unfortunately, the low sample size and high degree of variability in conifer seedling density in early successional stands prevents any discussion of the impacts of post-fire salvage logging activities on conifer regeneration. Since the substantial conifer recruitment in the mid-successional salvaged stands was likely a direct result of the silvicultural techniques (blade scarification and aerial spruce seeding) applied in these stands post-salvage; the effects of salvage logging on conifer regeneration were not evaluated statistically.

Environmental Influences on Early Post-Disturbance Deciduous Regeneration

Regression models suggested a number of common underlying mechanisms, namely microclimatic and fire severity effects, that were influential in determining deciduous tree regeneration in both wildfire and salvaged stands immediately following disturbance. Of the explanatory variables included in the regression models, light level, herbaceous cover, and total volume of DWM were likely associated with soil temperature effects on tree regeneration; residual density and canopy closure were likely related to microclimatic conditions of post-disturbance stands; and litter depth was likely related to the influence of wildfire severity on tree regeneration or alternatively, to the increased leaf litterfall associated with higher densities of deciduous saplings.

Soil temperature has been demonstrated to be one of the most important environmental factors influencing deciduous suckering subsequent to disturbance and the removal of apical dominance (Barnes 1966, Maini & Horton 1966, Zasada & Schier 1973, Peterson & Peterson 1992, Barnes et al. 1998). Results from greenhouse studies using root segments of aspen suggest that higher soil temperatures stimulate both earlier bud initiation (and thus greater apparent height growth relative to aspen at lower soil temperatures) and greater total number of suckers (Maini & Horton 1966, Zasada & Schier 1973). This is congruent with my finding that light level was the strongest environmental influence on deciduous stem density in wildfire stands. While light level itself does not have a direct effect on bud initiation, the increased soil temperatures associated with increased light levels and increased radiation absorption by blackened soils in post-fire environments, would increase aspen bud initiation and therefore influence the subsequent height growth and stem density of the regenerating stand.

The significance of the negative relationship of herbaceous cover to aspen sucker density is likely a result of a combination of both reduced soil temperatures arising from soil shading, and increased competition effects associated with higher amounts of herbaceous vegetation. Soil temperatures are likely to be lower under dense herbaceous cover as a result of increased soil shading, subsequently resulting in reduced aspen regeneration. Competition, notably from *Calamagrostis canadensis*, has also been observed to significantly reduce aspen sucker initiation and growth in harvested stands (Hogg & Lieffers 1991, Landhäusser & Lieffers 1998). It is likely that a similar regeneration response to competition could be expected in areas of lower wildfire severity within the burned stands.

Higher volumes of DWM appeared to inhibit deciduous regeneration in both wildfire (sapling height) and salvaged (sapling density) stands. DWM created as a result of logging activities may act to insulate the soil and has been linked to reductions in aspen regeneration in the first several years after harvesting (Bella 1986, Bates et al. 1989). A similar mechanism is likely in place in early post-disturbance wildfire and salvaged stands. The physical impediment of DWM may also restrict or delay both the initial establishment and growth of aspen in some areas of high DWM volumes.

Interestingly, both canopy closure, and density of residual trees and snags appeared to have a positive effect on both the density and height of deciduous regeneration in early wildfire stands. The shading effect of residual trees and snags and their canopies would normally be expected to significantly reduce the amount of light reaching the soil and thereby reduce soil temperatures and sucker initiation (Maini & Horton 1966). Apical control of any living residuals would also be expected to reduce overall sucker densities (Farmer 1962, Schier 1972). However, wildfire stands were characterized by a more moderated microclimatic environment than salvaged stands, being in general cooler and more humid. Saplings in areas with high residuals could be less exposed, resulting in reduced risk of frost damage (Keenan & Kimmins 1993), and lower air temperatures and higher relative humidities could reduce moisture stress in saplings. Thus, deciduous regeneration in wildfire stands could be subject to lower mortality (higher sapling density) and increased growth (taller saplings) as compared with salvage logged stands. A similar mechanism was suggested in *Pinus halepensis* stands of the Mediterranean where reduced mortality rates and higher growth rates of seedlings in wildfire stands were attributed to the increased shade of post-fire environments and the subsequently reduced water stress experienced by seedlings in these stands when compared to that of salvaged stands (Martinez-Sanchez et al. 1999).

Residuals in wildfire stands were identified as being almost exclusively snags, however, up to 20% of residuals in some salvaged stands were still alive at the time of sampling. Therefore, some apical dominance may still be in effect in salvaged stands, potentially contributing to the reduced sapling densities observed in these stands. The failure of the explanatory models to identify residual density as being influential in salvage logged stands is likely a result of lumping both live and dead trees together in the calculation of residual density. Unfortunately, an analysis of the influence of live residuals on deciduous regeneration is precluded by the low sample size of this study, high between stand heterogeneity, and low densities of residuals in salvaged stands in general.

Litter depth had a strong positive relationship with deciduous regeneration in both wildfire and salvaged stands that could be associated with wildfire severity. Severe wildfires have the potential to remove all or most of the litter layer and can simultaneously result in high or prolonged heating of the underlying mineral soil (Johnson 1992). With the majority of aspen suckers initiating from roots near the top of the soil profile, severe wildfires have the potential to kill these near-surface roots (Brown & DeByle 1987, Wang 2003). Aspen roots deeper in the soil profile also have the potential to sucker, however, lower numbers of roots and reduced soil temperatures at these depths would result in reduced levels of suckering (Brown & DeByle 1987). Therefore, aspen regeneration in areas subjected to lower severity wildfire where surface roots are more likely to have survived, are likely to exhibit better regeneration than that of areas subjected to high fire severities. However, the positive relationship of litter depth to deciduous regeneration may also simply be a reflection of the higher leaf litterfall associated with higher densities of deciduous saplings, since the higher the density of saplings, the higher the amount of leaf litter created beneath them.

Other Influences on Early Post-Disturbance Deciduous Regeneration

Model fit for height of deciduous regeneration in wildfire stands and density of stems in salvaged stands was relatively poor with a great deal of the variation in the observed data remaining unexplained. Sampling for this study occurred up to two years following the initial disturbance of treatment stands, measurements even this relatively short time post-disturbance may not have adequately reflected stand and environmental conditions immediately following disturbance that directly influence regeneration processes. In addition, some major attributes of the post-disturbance environment that could potentially affect deciduous regeneration were not sampled directly; these include soil moisture, fire severity, mechanical damage by salvaging equipment and carbohydrate level of the parent root system.

The greater densities and heights of deciduous saplings observed in early wildfire stands in my study may be partially attributed to the longer interval of undisturbed regeneration time in these stands compared with stands that are subsequently redisturbed by salvage logging activities. Salvage logging in Alberta generally occurs soon after wildfire suppression and continues for up to two years after the initial disturbance. Therefore, some salvage logging may occur on unfrozen soils up to two years after the stand was originally disturbed by wildfire. Sucker initiation could be expected to be well underway by this point and subsequent re-disturbance by salvage logging equipment could cause significant root and stem damage to young saplings. Aspen roots are generally concentrated near the surface of the soil (Peterson & Peterson 1992), and as a result, roots surviving the initial wildfire would be exposed to abrasion damage or breakage in areas of high logging traffic (i.e. skid trails). Basham (1988) found significant reductions in aspen sapling height and diameter growth as a result of mechanical scarification treatments applied 3 years following harvesting. Physical damage to young regenerating aspen stems as a result of salvage logging could be of a similar, albeit less severe nature. While this study did not directly quantify mechanical damage to regeneration, evidence of broken stems was observed in a number of instances in salvaged cutblocks. Fraser et al. (in press) similarly found that salvage logging in aspen dominated mixedwood stands resulted in physical damage to previously established suckers, which consequently resulted in reductions in the first year height growth and density of aspen saplings.

In addition to reduced undisturbed regeneration time in salvaged stands, saplings damaged during salvage logging would be required to put energy into the growth of new leaders or entirely new suckers. Sucker density and growth immediately following disturbance is greatly influenced by the level of root carbohydrates remaining in the parental root system; suckers arising from root systems with depleted carbohydrate reserves generally exhibit suppressed growth (DesRochers & Lieffers 2001, Landhäusser & Lieffers 2002). Thus, having supported the initial suckering and growth of numerous ramets immediately following wildfire, it is likely that carbohydrate reserves in the parental root system would be reduced and as observed in this study, subsequent suckering and sapling growth would be less vigorous. The lower photosynthetic biomass observed in other salvage logged stands (Fraser et al. in press) coupled with root carbohydrate reserves that are more than likely reduced, may potentially be insufficient to maintain respiration of the parental root system (DesRochers & Lieffers 2001, Landhäusser & Lieffers 2002). This will influence the growth of the regenerating stand and will likely substantially influence the primary productivity and future growth of salvage logged stands relative to unsalvaged wildfire forests.

Longer-Term Perspectives on Tree Regeneration

Despite statistically significant effects of salvage logging on deciduous regeneration in early post-disturbance stands, it should be noted that stem densities and heights of aspen regeneration observed in this study were well within the range of what has been reported for natural post-fire regeneration (Peterson & Peterson 1992). After disturbance, initial deciduous regeneration can exhibit extensive variation between areas, stands and even between individual clones (Peterson & Peterson 1992). However, it is likely that effects of salvage logging that consistently and significantly reduce initial recruitment, would modify the development and productivity of the regenerating stand and place these stands on a different successional pathway than that of unsalvaged wildfire stands. Recent evidence suggests that aspen stands with higher initial stem densities are better able to maintain the original clonal root system which subsequently allows for a more evenly distributed, faster growing and healthier aspen stands (DesRochers & Lieffers 2001, Landhäusser & Lieffers 2002).

In stands regenerating with lower density of aspen, such as those occurring following salvage logging, there would be greater amounts of light reaching the understory, which could subsequently promote increased growth of grasses and shrubs. Marsh reed grass (*Calamagrostis canadensis*) often successfully competes with regenerating saplings and has been suggested to have a significant, negative influence on aspen height growth, density and productivity in harvested mixedwood boreal stands

(Landhäusser & Lieffers 1998, MacIsaac & Crites 1999). The significantly higher densities of tall shrubs evident in 34 year old salvaged stands would tend to support this argument, however, no significant effects of salvage logging were detected in the deciduous regeneration of these older stands.

Although not statistically significant, the mid-successional wildfire stands had higher densities of dead deciduous trees originating from the initial regeneration cohort following disturbance. This would suggest that similar to the early successional stands, the mid-successional wildfire stands had higher initial deciduous recruitment than that of the salvage logged stands following disturbance. However, it is likely that through the process of self-thinning, the wildfire stands were reduced to a stem density similar to that of the salvaged stands. It could be suggested then, that aspen dominated mixedwood forests are fairly resilient to the secondary disturbances of salvage logging and silvicultural treatments. However, the high amount of inherent variability of the mid-successional stands, combined with the relatively low power of this study, could have made it difficult to detect any residual, lingering effects of salvage logging on stands of this age. The influence of salvage logging in these stands might have been apparent in other regeneration characteristics of the stand such as diameter growth that were not evaluated.

The most noticeable differences in mid-successional stands appeared to be related primarily to the silvicultural techniques applied in the salvage logged stands, with the older salvaged stands having much higher densities of white spruce and tall shrubs than wildfire stands. This likely has already had (see chapter 3), and will continue to have, significant effects on the successional development, vegetative composition, and productivity of these stands relative to those disturbed by wildfire alone.

It is important to note that the salvage logging regime in the mid-successional stands is different than that of the recent stands and therefore, the lack of significant regeneration effects in stands of this age does not necessarily mean that the impacts we observed of salvage logging activities as currently practiced, will not be apparent later in forest succession. The salvage logging treatment in the 34 year old post-disturbance treatment stands appears to have been less severe with respect to the removal of dead wood materials than that of more recently salvage logged stands. Salvage logging in these mid-successional stands targeted conifer trees and merely cleared and burned the remaining deciduous trees on slash piles rather than removing the tree boles entirely. As a result, salvaged stands had only approximately 20% lower volume of DWM than unsalvaged wildfire stands. The continued presence of relatively high levels of DWM in these mid-successional salvaged stands relative to unsalvaged wildfire stands, may have served to mitigate some of the impacts of salvage logging by modifying microclimatic conditions of the understory (Carleton & MacLellan 1994) and continuing to provide a long term source of nutrients and organic matter (Brais et al. 2000) in these sites.

LITERATURE CITED

Barker, P.F. 1989. Timber salvage operations and watershed resource values. In: Proceedings of the symposium on fire and watershed management. USDA General Technical Report PSW-109.

Barnes, B.V., Zak, D.R., Denton, S.R. & Spurr, S.H. 1998. Forest Ecology, 4th edition. John Wiley & sons Inc., New York.

Barnes, B.V. 1966. The clonal growth habit of American aspens. Ecology **47**:439-447.

Basham, J.T. 1988. Decay and stain 10 years later in aspen suckers subjected to scarification at age 3. Canadian Journal of Forest Research **18**: 1507-1521.

Bates, P.C., Blinn, C.R. & Alm, A.A. 1989. Aspen stand development following harvest in the lake states region. Northern Journal of Applied Forestry **6**:178-183.

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

Bergeron, Y. & Dansereau, P.R. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. Journal of Vegetation Science **4**:827-832.

Brais, S., Paré, D. & Ouimet, R. 2000. Impacts of wild fire severity and salvage harvesting on the nutrient balance of jack pine and black spruce boreal stands. Forest Ecology and Management **137**:231-243.

Brown, J.K. & DeByle, N.V. 1987. Fire damage, mortality and suckering in aspen. Canadian Journal of Forest Research **17**:1100-1109.

Carleton, T.J. & MacLellan, P. 1994. Woody vegetation responses to fire versus clear-cutting logging: A comparative study in the central Canadian boreal forest. Ecoscience **1**:141-152.

Cerezke, H.F. 1999. Management of wood borers in coniferous logs. Publication Number I/739. Forest Health Branch, Forest Protection Division, Land and Forest Service, Edmonton, Alberta.

Chatterjee, S. & Price, B. 1991. Regression analysis by example, 2nd edition. John Wiley & Sons, Inc., New York.

DesRochers, A. & Lieffers, V.J. 2001. Root biomass of regenerating aspen (Populus tremuloides) stands of different densities in Alberta. Canadian Journal of Forest Research **31**:1012-1018.

Dix, R.L. & Swan, J.M. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Canadian Journal of Botany **49**:657-676.

Eberhart, K.E. & Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. Canadian Journal of Forest Research **17**:1207-1212.

Farmer, R.E. 1962. Aspen root sucker formation and apical dominance. Forest Science **8**:403-410.

Fraser, E., Landhäusser, S. & Lieffers, V. In Press. The effect of fire severity and salvage logging traffic on regeneration and early growth of aspen suckers. Forestry Chronicle.

Furnival, G.M & Wilson, R.B. 1974. Regressions by leaps and bounds. Technometrics **16**:499-511.

Galipeau, C., Kneeshaw, D. & Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Canadian Journal of Forest Research **27**:139-147.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. & Simard, M.J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forest Research **29**:824-839.

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews **52**:107-145.

Hogg, E.H. & Lieffers, V.J. 1991. The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. Canadian Journal of Forest Research **21**:387-394.

Johnson, E.A. 1992. Fire and vegetation dynamics: Studies from the North American boreal forest. Cambridge University Press, Cambridge.

Keenan, R.J. & Kimmins, J.P. 1993. The ecological effects of clear-cutting. Environmental Reviews **1**:121-144.

Landhäusser, S.M. & Lieffers, V.J. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis canadensis*. Canadian Journal of Forest Research **28**:396-401.

Landhäusser, S.M. & Lieffers, V.J. 2003. Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. Journal of Ecology **90**:658-665.

Lee, P.C. & Crites, S. 1999. Early successional deadwood dynamics in wildfire and harvest stands. In: Fire and harvest residual (FAHR) project: the impact of wildfire and harvest residuals on forest structure and biodiversity in aspen-dominated boreal forests of Alberta. Edited by P.C. Lee. Publication Number T/495. Alberta Research Council, Vegreville.

Lee, P.C. & Sturgess, K. 2001. The effects of logs, stumps and root throws on understory communities within 28-year old aspen dominated boreal forests. Canadian Journal of Botany **79**:905-916.

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, G. & Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal of Forest Research **29**:796-811.

MacIsaac, D.A. & Crites, S. 1999. Deciduous regeneration one year following wildfire and harvest in aspen dominated mixedwoods of north-central Alberta. In: Fire and harvest residual (FAHR) project: the impact of wildfire and harvest residuals on forest structure and biodiversity in aspen-dominated boreal forests of Alberta. Edited by P.C. Lee. Publication Number T/495. Alberta Research Council, Vegreville.

Maini, J.S. & Horton, K.W. 1966. Vegetative propagation of *Populus* spp. I. Influence of temperature on formation and initial growth of aspen suckers. Canadian Journal of Botany **44**:1183-1189.

Marshall, P.L., Davis, G. & LeMay, V.M. 2000. Using line intersect sampling for coarse woody debris. General Technical Report TR-003. B.C. Ministry of Forests, Vancouver Forest Region, Nanaimo, B.C.

Martinez-Sanchez, J.J., Ferrandis, P., de las Heras, J. & Herranz, J.M. 1999. Effect of burnt wood removal on the natural regeneration of *Pinus halepensis* after fire in a pine forest in Tus valley (SE Spain). Forest Ecology and Management **123**:1-10.

McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J. & Woodley, S. 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. Environmental Reviews **9**:223-260.

Noël, J. 2002. Régénération forestière après feu et coupe de récupération dans le secteur de Val-Paradis, Abitibi. MSc. thesis, Université du Québec à Montréal.

Parent, S. & Messier, C. 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. Canadian Journal of Forest Research **26**:151-154.

Peters, V.S. 2002. Keystone processes affect succession in boreal mixedwoods – the relationship between masting in white spruce and fire history. PhD. thesis, University of Alberta.

Peterson, E.B. & Peterson, N.M. 1992. Ecology, management and use of aspen and balsam poplar in the prairie provinces. Canadian Forest Service, Northern Forest Centre, Alberta, Special Report 1.

Purdy, B.G., Macdonald, S.E. & Dale, M.R.T. 2002. The regeneration niche of white spruce following fire the mixedwood boreal forest. Silva Fennica. **36**:289-306.

Quinn, G.P. & Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In: Wein, R.W. & MacLean, D.A. (eds.), The role of fire in northern circumpolar ecosystems. John Wiley & sons Inc. New York.

Schier, G.A. 1972. Apical dominance in multishoot cultures from aspen roots. Forest Science **18**:147-149.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics **6**:461-464.

Stone, D.M. & Elioff, J.D. 1998. Soil properties and aspen development five years after compaction and forest floor removal. Canadian Journal of Soil Science **78**:51-58.

Strong, W.L. & Leggat, K.R. 1992. Ecoregions of Alberta. Resource Information Branch Publication Number T/245. Land Information Services Division, Alberta Forestry, Lands and Wildlife, Edmonton, Alberta.

Van Wagner, C.E. 1968. The line intersect method for forest fuel sampling. Forest Science **14**:20-26.

Wang, G.G. 2003. Early regeneration and growth dynamics of Populus tremuloides suckers in relation to fire severity. Canadian Journal of Forest Research **33**:1998-2006.

Wynnyk, A., Lindsay, J.D., Heringa, P.K. & Odynsky, W. 1963. Exploratory soil survey of Alberta map sheets 83-O, 83-P and 73-M. Preliminary soil survey report 64-1, Research Council of Alberta, Edmonton, Alberta.

Zasada, J.C. 1985. Production, dispersal and germination of white spruce and birch and first year seedling establishment after the Rosie Creek fire. In: Juday, G.P. & Dyrness, C.T. (Eds.). Early results of the Rosie Creek fire research project. Agriculture and forestry experiment station, Misc. Public. 85-2. University of Alaska.

Zasada, J.C. & Schier, G.A. 1973. Aspen root suckering in Alaska: effect of clone, collection date and temperature. Northwest Science **47**: 100-104.

Zar, J.H. 1999. Biostatistical analysis. 4th edition. Prentice-Hall Inc., New Jersey.

Zoladeski, C.A. & Maycock, P.F. 1990. Dynamics of the boreal forest in northwestern Ontario. American Midland Naturalist **124**:289-300

Table 2.1. Attributes of wildfires encompassing selected treatment stands. Fire ID represents a provincial fire identifier used in the Alberta fire incidence database. Stand location is identified using legal land locations (meridian, township, range and section) of the Canadian cartographic grid system. Reference names assigned to study stands are identified as superscripts under the appropriate disturbance type heading where 1= Benson, 2= Cowper, 3= Chard, 4= Mena, 5= Philomena, 6= Fawcett, 7= Calling Lake, 8= Flattop, 9= Slave, 10= Kinuso.

Fire ID	Year	Fire Start Date	Size (ha)	Fire Start Location		Disturbance Type		Stand Location
				Latitude	Longitude	Wildfire	Salvage	Mer-Twn-Rng-Sec(s)
E02-038-99	1999	May-25	7 207	55.8 N	110.7 W	√^{1}		04-78-05-27, 26 & 35
							√^{2}	04-78-05-22, 27, 34 & 35
E02-043-99	1999	May-25	3 801	55.9 N	111.0 W	√^{3}		04-79-07-13 & 18
E02-091-99	1999	July-12	4 333	55.3 N	111.9 W	√^{4}		04-73-12-10, 16 & 17
							√^{5}	04-73-12-09 & 17
E04-026-99	1999	May-24	1 952	55.4 N	114.2 W		√^{6}	05-74-01-09 & 04
DL3-005-68	1968	May-19	15 030	55.1 N	113.3 W	√^{7}		04-71-22-21 & 28
DS2-020-68	1968	June-19	401 327	54.4 N	114.3 W	√^{8}		05-71-06-25, 26, 35 & 36
							√^{9}	05-71-05-31 & 05-71-06-36
DS3-021-68	1968	July-19	77 839	55.1 N	115.3 W		√^{10}	05-72-11-34 & 35

Table 2.2. Study design and sample size (number of replicate stands and nested subsamples for each disturbance type).

Disturbance Type	Forest Successional Stage	
	Early (2 years post-disturbance)	Mid (34 years post-disturbance)
Wildfire	3 stands (43 sites)	2 stands (40 sites)
Salvage	3 stands (45 sites)	2 stands (40 sites)

Table 2.3. Characteristics and associated decay classifications for downed woody materials (modified from McCullough 1948 and Lee et al. 1997).

Decay Class	Decay Characteristics of Downed Woody Materials
1	Log whole and undecayed; branches and twigs present and intact; wood hard
2	Log sound, wood hard; twigs mostly lacking
3	Some branches remaining; wood soft in places
4	No branches; wood fungi present; wood soft with small crevices and small pieces lost
5	Large wood fragments lost; outline of trunk deformed; vascular plants beginning to colonize
6	Wood mostly well decayed; log completely moss covered and colonized by various vascular plants
7	Humification nearly 100%; hard to define as log, outline indeterminable; no evidence of hard wood

Table 2.4. Summary of explanatory variables tested in multiple linear regression models of deciduous tree regeneration (sapling density and height) in early successional stands (2 years post-disturbance).

Variable	Description of Variable Measurements
Light	% Full PPFD; based on plot center/site
Canopy	% Canopy closure; based on plot center/site
Residuals	Density (sph) of residual trees & snags; based on $50m^2$ circular plot
DWM cover	% Cover DWM based on 25m DWM transect
Total DWM	Volume DWM (m^3/ha); based on 25m DWM transect
Early DWM	Volume DWM (m^3/ha) in decay stages 1-4; based on 25m DWM transect
Compaction	Soil compaction (kg/cm^2); based on 1x1m plots
Litter depth	Litter layer depth (cm); based on 1x1m plots
Moss depth	Bryophyte layer depth (cm); based on 1x1m plots
Organic depth	Organic soil depth (cm); based on 1x1m plots
Moss cover	% Bryophyte cover; based on 1x1m plots
Litter cover	% Litter cover; based on 1x1m plots
Herb cover	% Herb cover; based on 1x1m plots
Shrub cover	% Shrub cover; based on 1x1m plots
Wood cover	% wood c over; based on 1x1m plots

Table 2.5. Descriptive statistics for stand, environmental and regeneration variables in early (2 years) post-disturbance treatments. Values provided are means ±1 *S.E.* with the exception of distance and strength of conifer seed sources which are median values. Wildfire *n*=3 stands (with 43 sites total) and salvage *n*=3 stands (with 45 sites total).

	Wildfire	Salvage
Residual tree & snag density (stems/ha)	1966.7 ± 181.4	146.9 ± 30.7
% Deciduous trees of total residuals	88.0 ± 3.7	87.7 ± 6.6
Residual DBH (cm)	14.3 ± 0.4	14.2 ± 0.9
% Snags of total residuals	100.0 ± 0.01	87.2 ± 6.95
% DWM cover	3.8 ± 0.4	5.5 ± 0.4
DWM volume (m^3/ha)	63.7 ± 7.6	110.0 ± 12.9
% Early decay DWM	75.0 ± 4.3	80.9 ± 3.8
% Late decay DWM	24.9 ± 4.3	19.1 ± 3.8
Light (% full PPFD)	15.2 ± 1.98	60.9 ± 4.05
% Canopy cover	17.7 ± 1.1	3.1 ± 0.7
Temperature (°C mean difference from open)	-1.2 ± 0.1	-0.56 ± 0.14
RH (% mean difference from open)	10.1 ± 0.9	7.1 ± 0.7
Soil compaction (kg/cm^2)	1.6 ± 0.06	1.8 ± 0.05
Distance to conifer seed source	4 (100-500m)	3 (<100m)
Strength of conifer seed source	1*	1 *
% Cover of mineral soil	6.1 ± 2.5	11.0 ± 3.5
% Cover of litter/organic material	80.7 ± 3.4	86.7 ± 3.5
% Cover of bryophytes	10.7 ± 2.0	1.8 ± 0.9
% Cover of other substrates	2.6 ± 0.8	0.6 ± 0.2
% Conifer seedlings of total regeneration	4.3 ± 6.4	4.0 ± 7.7
% Deciduous saplings of total regeneration	95.7 ± 9.4	96.0 ± 9.2

*single live tree of canopy or sub-canopy height (see Chapter 2 methods text)

Table 2.6. Results of nested GLM models for light and microclimatic variables in early post-disturbance treatments. Degrees of freedom (*d.f.*), F-values (*F*) and probability of type I error rate (*P*) of each variable in the GLM model are presented. Data are pooled to the site level for all variables with both wildfire and salvage *n*=3 stands (with 21 sites total).

	Light (% full PPFD)			**Temperature** (°C mean difference from open)			**Relative Humidity** (% mean difference from open)		
	Model R^2=0.62			Model R^2=0.37			Model R^2=0.22		
Source	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
Treatment	1	25.75	**<0.01**	1	8.95	**0.04**	1	6.57	0.06
Stand(Treatment)	4	4.50	**<0.01**	4	1.63	0.19	4	0.95	0.45
Error	82			36			36		

Table 2.7. Results of nested GLM models for regeneration variables in early post-disturbance treatments. Degrees of freedom (*d.f.*), F-values (*F*) and probability of type I error rate (*P*) of each variable in the GLM model are presented. Data are pooled to the site level for both variables. Wildfire *n*=3 stands (with 43 sites total) and salvage *n*=3 stands (with 45 sites total).

	Deciduous Stem Density (stems/ha)			**Deciduous Stem Heights** (m)		
	Model R^2=0.52			Model R^2=0.58		
Source	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
Treatment	1	8.09	**0.047**	1	24.60	**0.01**
Stand(Treatment)	4	7.63	**<0.01**	4	3.92	**0.01**
Error	82			82		

Table 2.8. Final explanatory models for deciduous stem density and sapling height based on BIC selection for early post-disturbance wildfire stands. Explanatory variables are listed in order of most to least influential based on standardized estimates. Coefficient estimates and standard errors (*S.E.*), t-values (*t*) and probability of type I error rate (*P*) for each explanatory variable included in the final model are presented.

Deciduous Stem Density (stems/ha)

Model: $F_{4,38}=6.58$ $P<0.01$ $R^2=0.41$ $R^2_{adj}=0.35$

Variable	Estimate	*S.E.*	*t*	*P*
Intercept	155 930	6121	25.47	<0.01
Light	22 626	6319	3.58	<0.01
Residual Density	16 534	6533	2.53	0.02
Herbaceous Cover	-14 806	6475	-2.29	0.03
Litter Depth	12 045	6381	1.89	0.06

Deciduous Sapling Height (m)

Model: $F_{2,39}=4.18$ $P=0.02$ $R^2=0.18$ $R^2_{adj}=0.13$

Variable	Estimate	*S.E.*	*t*	*P*
Intercept	1.02	0.03	40.64	<0.01
Canopy Closure	0.05	0.03	2.14	0.04
Total Volume DWM	-0.05	0.03	-1.82	0.06

Table 2.9. Final explanatory models for deciduous stem density and sapling height based on BIC selection for early post-disturbance salvaged stands. Explanatory variables are listed in order of most to least influential based on standardized estimates. Coefficient estimates and standard errors (*S.E.*), t-values (*t*) and probability of type I error rate (*P*) for each explanatory variable included in the final model are presented.

Deciduous Stem Density (stems/ha)

Model: $F_{1,42}=7.34$ $P=0.01$ $R^2=0.15$ $R^2_{adj}=0.13$

Variable	Estimate	*S.E.*	*T*	*P*
Intercept	84 773	6931	12.23	<0.01
Total Volume DWM	-18 998	7011	-2.71	0.01

Deciduous Sapling Height (m)

Model: $F_{2,41}=17.68$ $P<0.01$ $R^2=0.46$ $R^2_{adj}=0.44$

Variable	Estimate	*S.E.*	*T*	*P*
Intercept	0.6	0.03	22.29	<0.01
Shrub Cover	0.11	0.03	4.16	<0.01
Litter Depth	0.11	0.03	4.04	<0.01

Table 2.10. Descriptive statistics for stand, environmental and regeneration variables in mid-successional (34 years post-disturbance) treatments. Values provided are means ±1 *S.E.* with the exception of distance and strength of conifer seed sources which are median values. Both wildfire and salvage *n*=2 stands (with 40 sites total).

	Wildfire	Salvage
Total residual density (stems/ha)	36.2 ± 11.4	27.0 ± 13.7
Snag density	31.8 ± 10.9	15.9 ± 6.7
Residual DBH (cm)	34.0 ± 2.4	31.0 ± 2.5
Tall shrub density	1987.8 ± 460.3	4981.5 ± 655.9
% DWM cover	7.2 ± 0.7	5.1 ± 0.5
DWM volume (m^3/ha)	222.9 ± 24.6	172.1 ± 20.2
% Early decay DWM	27.0 ± 3.4	20.3 ± 4.6
% Late decay DWM	73.0 ± 3.4	79.7 ± 4.6
Light (% full PPFD)	9.7 ± 0.57	10.9 ± 1.01
% Canopy cover	75.8 ± 2.9	86.9 ± 0.5
Temperature (°C mean difference from open)	-1.2 ± 0.15	-1.4 ± 0.08
RH (% mean difference from open)	11.2 ± 1.3	12.3 ± 1.0
Soil compaction (kg/cm^2)	1.14 ± 0.06	1.40 ± 0.09
Soil moisture (% volumetric water capacity)	17.1 ± 1.2	15.1 ± 0.5
Live deciduous density	4000.31 ± 212.24	3217.08 ± 271.32
Live deciduous height (m)	11.94 ± 0.27	12.04 ± 0.14
Dead deciduous density	4292.05 ± 394.19	2914.30 ± 317.34
2nd cohort live deciduous density	748.03 ± 152.11	1012.58 ± 163.47
Conifer seedling density	967.7 ± 409.7	3033.8 ± 428.7
Distance to conifer seed source	5 (>500m)	N/A; Anthropogenic source
Strength of conifer seed source	2*	N/A; Anthropogenic source

* Single live reproductive tree above canopy height (see Chapter 2 methods text)

Table 2.11. Results of nested GLM models for regeneration variables in 34-year old post-disturbance treatment stands. Degrees of freedom (*d.f.*), F-values (*F*) and probability of type I error rate (*P*) of each variable in the GLM model are presented. Data are pooled to the site level for all variables. Both wildfire and salvage *n*=2 stands (with 40 sites total).

	Live Deciduous Stem Density (stems/ha)			**Live Deciduous Stem Height** (m)			**Dead Deciduous Stem Density** (stems/ha)			**2nd Cohort Live Deciduous Stem Density** (stems/ha)		
	Model R^2=0.10			Model R^2=0.07			Model R^2=0.10			Model R^2=0.22		
Source	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
Treatment	1	3.24	0.21	1	0.19	0.71	1	11.10	0.08	1	0.17	0.72
Stand(Treatment)	2	1.62	0.20	2	2.62	0.08	2	0.66	0.52	2	10.08	**<0.01**
Error	76			76			76			76		

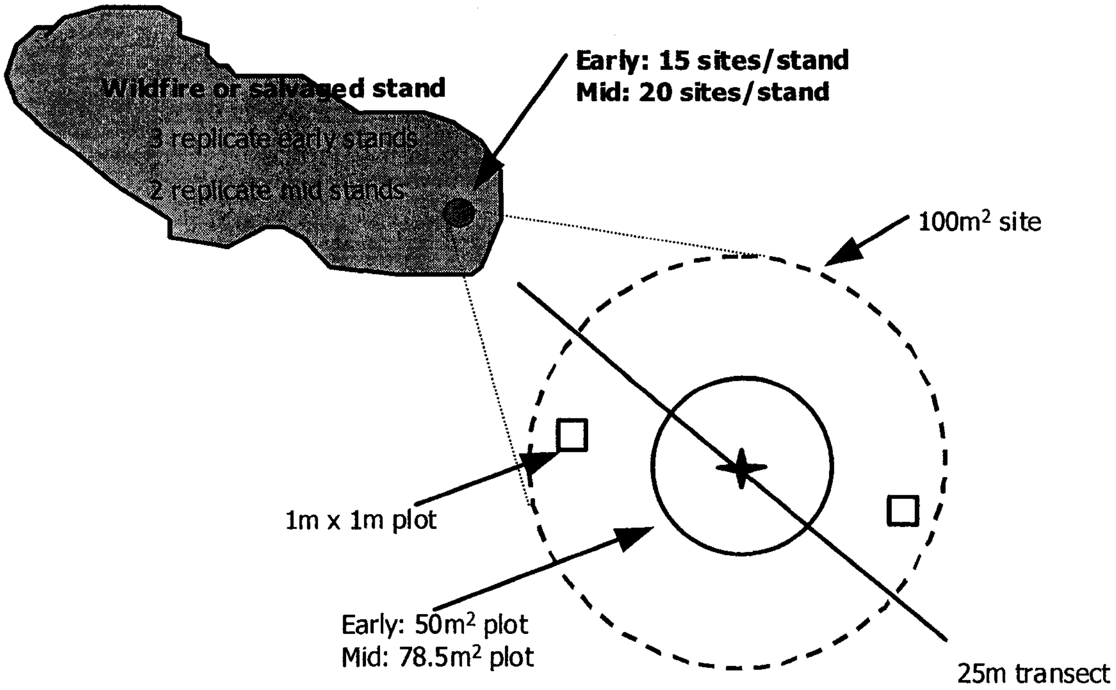

Figure 2.1. Schematic of sampling design for treatment stands. Each of the three replicate stands for the early succssional treatment encompassed fifteen randomly placed 100m2 sites (excepting one wildfire stand which had only thirteen). Each site included one 25m DWM transect, one 50m2 tree plot and two 1x1m regeneration/ understory plots. Both replicate stands for 34-years post-disturbance treatments encompassed twenty randomly placed 100m2 sites. Each site included one 25m DWM transect, one 78.5m2 tree plot and two 1x1m understory plots.

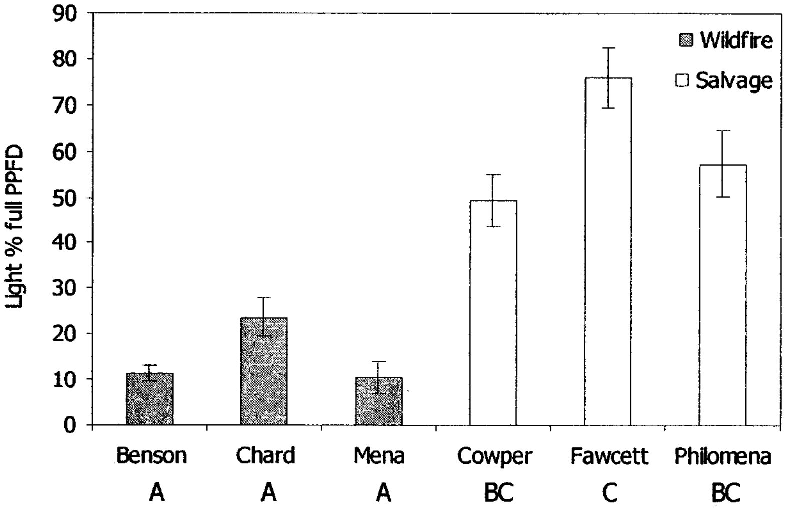

Figure 2.2. Mean (±1*S.E.*) light levels (% full PPFD) in early successional stands. Treatment effects were significant at $P<0.01$ with significant differences (resulting from Tukey's HSD tests) between stands (adjusted for treatment and stand level effects) indicated by different letters. All stands $n=15$ sites, except Chard $n=13$ sites.

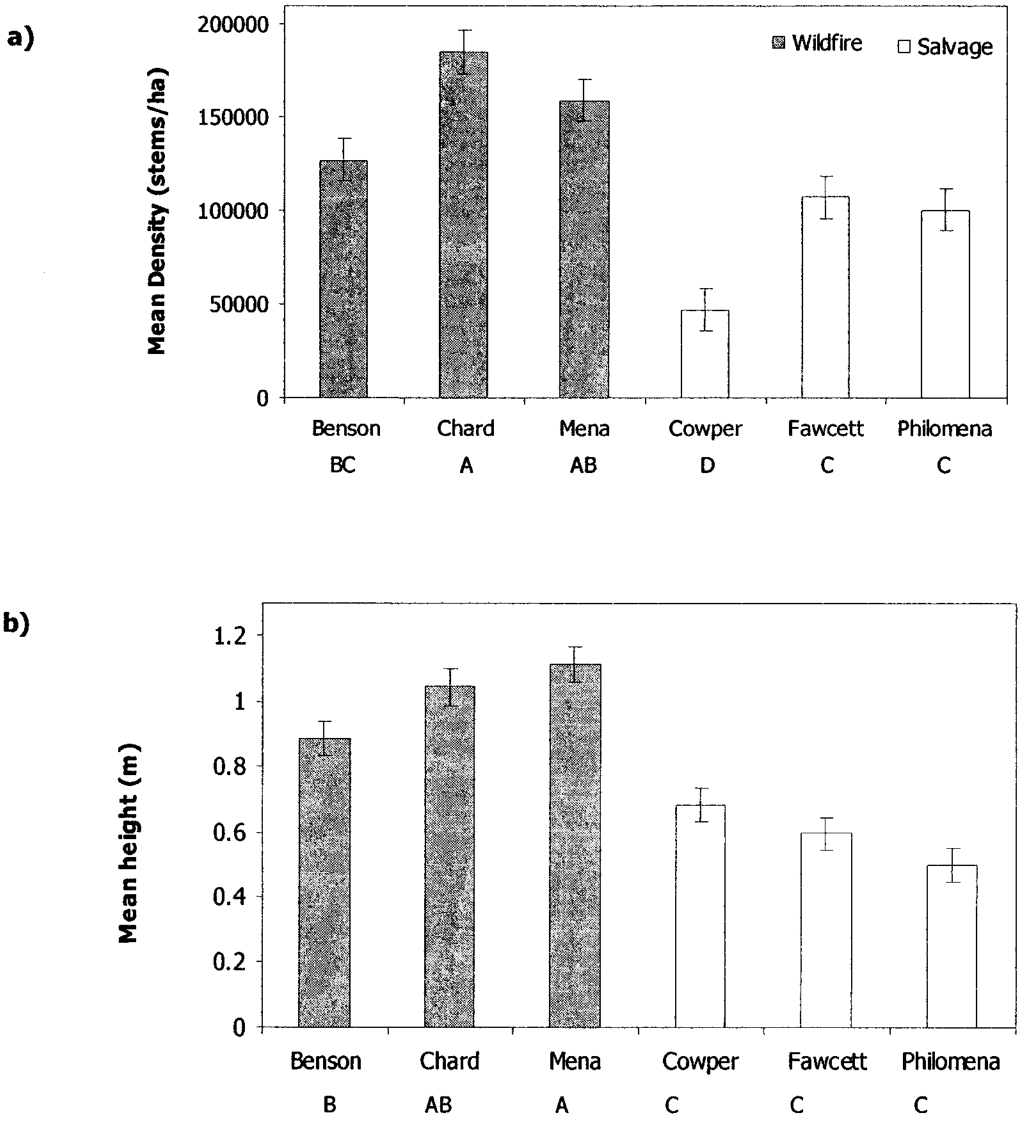

Figure 2.3. Mean (±1*S.E.*) deciduous stem densities (a) and heights (b) in early successional treatment stands. Treatment effects for stem densities and heights were significant at *P*=0.05 and *P*=0.01 respectively with significant differences (resulting from Tukey's HSD tests) between stands (adjusted for treatment and stand level effects) indicated by different letters. All stands *n*=15 sites, except Chard *n*=13 sites.

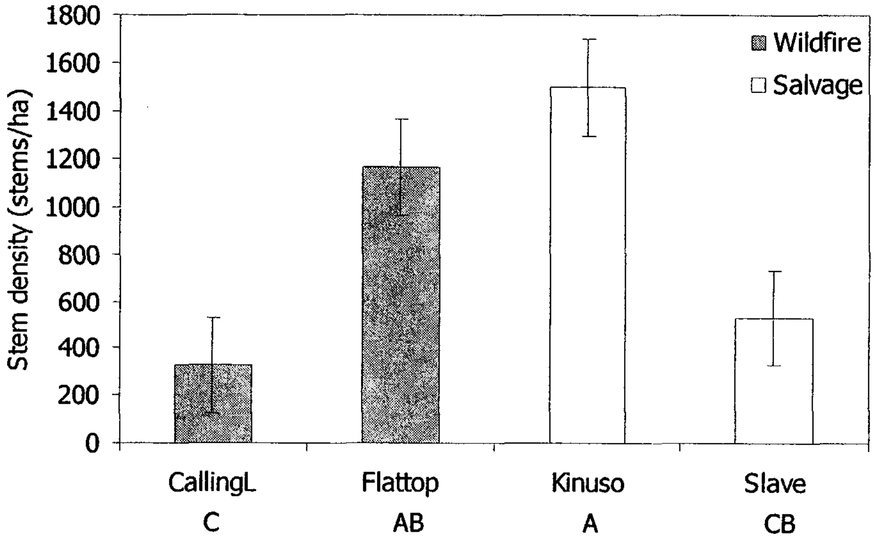

Figure 2.4. Mean (±1*S.E.*) density (stems/ha) of second cohort deciduous saplings (DBH ≤ 5cm) in mid successional (34 years post-disturbance) treatment stands. Significant differences (resulting from Tukey's HSD tests) between stands (adjusted for treatment and stand level effects) indicated by different letters. All stands *n*=20 sites.

CHAPTER 3

IMPACTS OF POST-FIRE SALVAGE LOGGING ON THE UNDERSTORY VASCULAR PLANT COMMUNITY IN BURNED STANDS OF THE MIXEDWOOD BOREAL FOREST

INTRODUCTION

Early post-fire boreal forest stands are characterized by a distinctive combination of environmental and stand attributes that influence both the initial recruitment and the subsequent development of boreal forest plant communities (Rowe 1983, Eberhart & Woodard 1987, Turner et al. 1997, Whittle et al. 1997). These attributes include the increased availability of colonization microsites (Zasada 1971, Harmon & Franklin 1989, Noël 2002), high densities of standing dead trees, increased light and nutrient availability, increased soil temperatures resulting from radiant heating of blackened soil, and the removal of shading and insulating layers of vegetation and surface litter (Ahlgren & Ahlgren 1960, Barnes et al. 1998, Turner et al. 1997, Whittle et al. 1997). Salvage logging activities can modify some characteristics of this initial post-disturbance forest environment and influence the regeneration of the initial tree cohort (see Chapter 2; Martinez-Sanchez et al. 1999, Noël 2002, Fraser et al. in press). This will likely influence both the understory establishment environment and the initial recruitment and subsequent successional development of the understory plant communities of these stands.

Early post-fire forest stands support a characteristic plant community that is distinct from those of forest stands at other stages in boreal forest succession (Crites 1999). These communities tend to be dominated by shade intolerant, early successional species that typically re-establish vegetatively from surviving underground organs or germinate from wind-dispersed or buried, previously dormant seed (Rowe 1983, Turner et al. 1997, Whittle et al. 1997, Crites 1999). Depending on fire severity, many plant species that are commonly found at later stages in forest development are also found in these early post-disturbance plant communities, albeit with different abundances (Barnes et al. 1998, Fortin et al. 1999). However, the primary source of the distinctiveness of these early post-fire communities is the dominance of species originating from the soil seedbank such as corydalis species (*Corydalis sempervirens*[1] and *C. aurea*), Bicknell's geranium (*Geranium bicknellii*), and American dragonhead (*Dracocephalum parviflorum*), which are dependent upon wildfire to break dormancy and remove surface layers of soil organic matter (Johnson 1981, Fyles 1989, Crites 1999). The dominance of these species is short-lived, however, as they are generally out-competed by the vigorous growth of other herbaceous vegetation and deciduous tree saplings within a few years and thereafter persist in the soil seedbank awaiting the next severe stand replacing fire (Johnson 1981, Fortin et al. 1999).

Salvage logging of snags and residual live trees from recently burned forest stands likely has a number of important implications for the richness and composition of early post-fire plant communities. The removal of standing post-fire residuals in salvaged stands results in light levels that are elevated over those naturally occurring in wildfire stands and this consequently modifies the microclimatic conditions of these stands (see Chapter 2) likely indirectly influencing plant growth (Martinez-Sanchez et al. 1999). On unfrozen soils or those with little snow cover, logging equipment may modify the availability or characteristics of regeneration microsites as a result of soil compaction, and the scarification and mixing of the organic and mineral soil (Noël 2002). This modification in the availability or characteristics of regeneration microsites may influence which species are able to successfully regenerate in salvaged stands[2] (Ne'eman et al. 1995, Crites & Hanus 2001). Mechanical damage (breakage, flattening) of regenerating vegetation caused by salvage logging equipment may result in direct mortality or reduced plant vigor and abundance (Martinez-Sanchez et al. 1999, Fraser et al. in press). This

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[1] Authorities for all vascular plant species are included in Appendix 3.1.

[2] Characteristics of select regeneration microsites and the vascular plant communities associated with them were collected as part of this research but have not been formally written up as part of this thesis. However, a brief description of sampling methods, along with summary statistics are presented in Appendix 3.2.

may be of particular concern for those ephemeral plant species dependent upon adequate input of viable, reproductive propagules into the soil seedbank to ensure long term persistence. Salvage logging may also result in the introduction of invasive or exotic species to previously uncolonized forest stands, due to either the increased road access associated with logging development or to direct dispersal of seed via logging equipment (Crites & Hanus 2001).

The environmental attributes of post-fire forest stands and the resulting composition of plant communities in the initial establishment phase immediately following disturbance are likely to have a significant influence on subsequent development of the plant community through forest succession (Barnes et al. 1998). Initial alterations to the forest environment or the plant community as a result of salvage logging may persist and create an alternate successional trajectory from that normally observed in the understory plant communities of wildfire origin stands in the boreal forest. In addition, direct effects of salvage logging may persist for several decades with the loss of the snags which would have eventually fallen and become downed logs. This high volume of downed woody material would have served a number of ecological functions including contributing to soil nutrients and organic matter (Brais et al. 2000), and acting to shade and modify the microclimatic conditions of the understory environment (Carleton & MacLellan 1994). The absence of this high volume of downed wood in the following decades may result in additional modification to the natural post-fire successional trajectory of the understory community that are currently unforeseen.

The objective of this study was to evaluate the impact of salvage logging on the species richness, turnover, and community composition of post-fire vascular plant communities. In chapter 2, it was established that salvage logging significantly altered a number of structural (amount of downed wood and residual live trees and snags, availability of certain regeneration microsites, density and height of regenerating deciduous tree saplings) and environmental (light, microclimatic conditions) attributes associated with early post-fire environments. Since these factors also influence the growth and establishment of plants, it is likely that they could alter the understory plant community and that any differences arising from salvage logging may potentially continue to persist over time. Therefore, I hypothesized that the species richness, turnover, and community composition of post-fire plant communities would be different from that of post-fire plant communities that have been salvage logged and that these differences could be partially attributed to the modified structural and environmental conditions of salvage logged stands. To test this hypothesis I determined whether the species richness and community composition of post-fire plant communities varied as a result of treatment effects (wildfire vs. salvage logged) and correlated environmental and structural characteristics of wildfire and salvage logged stands with their plant communities.

METHODS

Study area, design and site selection were identical to those presented in Chapter 2.

Data Collection

Stand & Environmental Characteristics

See Chapter 2 for detailed description of protocols for sampling of post-fire residuals, downed woody material and environmental attributes (slope, aspect, light, soil moisture and compaction, ambient air temperature and relative humidity) in both early and mid-successional stands.

Understory Vascular Plant Community

All understory plant community data and associated plot level environmental data were collected between July 6th and August 19th, 2001 for early successional stands and between June 3rd and August 29th, 2002 for mid-successional stands. Understory plants were evaluated within two 1 m x 1 m plots located at right angles to and 10 m distant from the 25 m DWM transect (at distances of 5 m and 20 m along the transect) (see Chapter 2; Figure 2.1). All vascular plants were identified to the species level and visual estimates of percent cover (to the nearest percent) were made for each species. Cover values were then averaged to create one measurement of abundance for each species for each site (early successional: wildfire *n*=43 sites, salvage *n*=45 sites and mid-successional: wildfire and salvage *n*=40 sites). In addition, a complete vascular plant species list (total species richness) for each sampling site (100 m^2) was determined as a combination of all species encountered in the two 1 m^2 understory plots plus any new species encountered during an intensive 30 minute search of each sampling site by two people. All unknown species were collected and subsequently identified at the University of Alberta vascular plant herbarium. Nomenclature follows Moss (1983). Percent cover was also estimated for litter, wood (of diameter >5cm), mineral soil, mosses, liverworts, fungi, and lichens within each 1 m^2 plot. Depth of litter, moss and organic soil layers were measured within each 1 m^2 plot.

Data Analysis

All analyses of early and mid-successional stands were conducted separately as a result of the differences in salvage logging regimes between these two age classes. Descriptive statistics were calculated by treatment for stand, environmental and understory data for each of the two age classes.

Species Richness & Diversity

A number of species diversity measures were calculated for the understory plant community. Only those plants identified to the species level were included in calculations of species diversity, whereas plants identified to the genus level (i.e. *Salix* spp. or *Carex* spp.) were excluded to provide a more conservative estimate of species diversity.

Following Whittaker (1972), three levels of diversity (alpha, beta and gamma) were calculated at two scales (the stand and treatment levels) for each of the two age classes. Alpha diversity represents species richness per sampling unit and gamma diversity represents the overall diversity of a collection of sampling units. At the stand level scale, alpha diversity was considered to be species richness per site (100 m^2) (based on the complete species list generated from the intensive site searches) and gamma diversity was calculated as the total number of species in each stand. At the treatment level scale, alpha diversity was considered to be the average species richness per stand (based on the complete species lists created for each of the 13-15 100 m^2 sites in early successional stands and the 20 100 m^2 sites in mid-successional stands) and gamma diversity was calculated as the total number of species in each treatment. For the purposes of this study, beta diversity represents the amount of spatial turnover or change in species composition between local assemblages of species and was calculated using Whittaker's method (1972) [equation 3.1] where β_w=beta diversity, S_c=gamma diversity and S=species richness in the sampling units (alpha diversity).

$$\beta_w = \frac{S_c}{S} \qquad [3.1]$$

Hence, at the stand level, beta diversity represents species turnover between sampling sites within stands, and at the treatment level, beta diversity represents turnover between stands within treatments. As beta diversity increases, sampling units differ more markedly from one another in terms of their species assemblages.

Diversity indices for herbs, shrubs and total vascular plant species were also calculated at the stand level using two datasets. Diversity indices were calculated with both the species presence data (compiled using the species lists for each sampling site) and abundance data (relative percent cover data collected using the understory plots and pooled to the site level) using the Shannon-Wiener index (H') [equation 3.2] where s= number of species and p_i=proportion of sampling sites in which species i was observed (presence data) or the abundance of the i^{th} species expressed as a proportion of total cover (abundance data).

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \qquad [3.2]$$

Herb, shrub and total species richness data (number of species per sampling site based on the species presence list) met the conditions of normality and homoscedasticity using Shapiro-Wilks's and Levene's tests, respectively (Zar 1999). Variation in richness of herbs, shrubs and total vascular plants between treatments were evaluated using nested general linear models (GLMs) [equation 3.3] (PROC GLM in SAS v.8.02 1999-2000) where Y_{ijk}=dependant variable; a_i=treatment; $b_{j(i)}$=stand within treatment and e_{ijk}=residual error (sampling sites within stand within treatment).

$$Y_{ijk} = \mu + a_i + b_{j(i)} + e_{ijk} \qquad [3.3]$$

Stand within treatment was used as the error term in the calculation of the F-ratio for treatment effects, and the residual error was used as the error term in the calculation of the F-ratio for the nested term (stand within treatment) (Zar 1999). F-ratios and p-values for these analyses were based on Type III sums of squares. Although stands were considered a random factor in these analyses, post hoc comparisons between stands were made using Tukey's HSD test to determine if statistically significant differences in species richness were apparent between replicate stands. A significance level of α=0.05 was used for all statistical analyses.

Plant Community Composition

Multivariate analyses were used to examine differences in the composition of the understory plant communities of wildfire and salvage logged stands. Sørensen (Bray-Curtis) distance was used to express community resemblances for all multivariate analyses. This distance measure is generally acknowledged to provide a better approximation of ecological distance for multivariate species data than other common distance measures such as the Euclidean or Chi-squared metrics (Faith et al. 1987, Legendre & Legendre 1998, McCune & Grace 2002).

Potential multivariate outliers were detected by examining a frequency distribution of average Sørensen distances between each plot and every other plot in species space. Plots with an average distance greater than 2.3 standard deviations from the overall mean were considered to be moderately strong outliers (McCune & Grace 2002). The influence of the removal of any outlier plots on the results of multivariate analyses were examined. A similar procedure was followed to reveal potential outlier species in sample space. The removal of plots or species identified as outliers did not appear to substantially influence the results of the multivariate analyses, therefore, all plots and species were retained in subsequent analyses.

Multi-response permutation procedures (MRPP) were used to test for differences in the species composition of understory plant communities between wildfire and salvaged stands. MRPP provides a nonparametric multivariate test of differences in species assemblages between pre-defined treatment groups by calculating p-values using permutation tests (Mielke & Berry 2001, McCune & Grace 2002). The 'chance-corrected within-group agreement' statistic (*A*) calculated by MRPP describes the homogeneity of the species assemblages within the pre-defined groups compared to that expected by random. When species assemblages within groups are no different than those expected by chance then $A=0$, and the samples of the treatment groups overlap and occupy the same multivariate species space. When species assemblages of sampling units within treatment groups are more similar than expected by chance then $A>0$ (to a maximum of $A=1$), and the samples of treatment groups occupy different regions of multivariate species space. It should be noted that even when compositional differences between groups are readily apparent, values of *A* less than 0.10 are commonly observed in community data and values of *A* greater than 0.30 may be considered to be quite high (McCune & Grace 2002).

Indicator Species Analysis (ISA) (Dufrêne & Legendre 1997) was used to determine the ability of individual plant species to differentiate species assemblages between treatments. Perfect indicators of treatment groups would have an indicator value of 100 where individuals of that species are observed within all sites of one treatment group alone. Statistical significance of indicator values was determined with 10 000 Monte Carlo permutations.

Outlier analysis, MRPP and ISA were performed using PC-Ord v.3.2 (McCune & Mefford 1997). For both early and mid-successional time periods, MRPP and ISA were based on species cover data (pooled to the stand level for MRPP and to the site level for ISA) with all rare plant species (defined as species which occur in less than 5% of all sampling units) retained.

Distance-based Redundancy Analysis (db-RDA) (Legendre & Anderson 1999, McArdle & Anderson 2001) using Sørensen distances was the ordination method selected to visually examine the influence of environmental and treatment factors on understory species composition. One of the primary advantages of db-RDA over other direct ordination methods, is that it can be used with any ecologically suitable distance measure including Sørensen distance. db-RDA uses Principal Coordinate Analysis (PCoA) to extract the principal coordinates of the calculated matrix of Sørensen distances used to represent species composition in sample space. These principal coordinates are Euclidean (metric) representations of the original semi-metric Sørensen distances and as such may be appropriately analyzed using the linear model of species responses inherent in Redundancy Analysis (RDA). The matrix of principal coordinates created by PCoA now becomes the 'species' matrix analyzed using RDA.

PCoAs were based on Sørensen distances of species presence data compiled using the species lists for each site. Removal of rare species frequently enhances the ability of ordination analyses to extract patterns in multivariate datasets as a result of the removal of the additional variability created by these species (McCune & Grace 2002). For both early and mid-successional time periods, however, the dominant principal coordinates extracted remained the same between those datasets which retained rare species and those that did not. Therefore, all rare species were retained for db-RDA.

Environmental variables used to constrain ordination analyses for both early and mid-successional time periods are listed in Table 3.1. Quantitative environmental variables were measured in numerous units and were therefore standardized [equation 3.4] to a similar scale with a mean of zero and a standard deviation of one. Where $y_i = i^{th}$ observation of environmental variable y; $\bar{y}$ =mean of y and s=standard deviation.

$$y_i = \frac{y_i - \bar{y}}{s} \qquad [3.4]$$

Based on both correlation matrices and high variance inflation (VIF) values, site level percent cover of litter and plot level percent cover of wood and litter layer depth were determined to be strongly collinear with a number of other environmental variables and as a result were excluded from further analysis. Environmental variables were added using forward stepwise selection with the significance of each variable tested using 1000 Monte Carlo permutation tests. Final ordinations were constrained using only those environmental variables that accounted for a significant ($P \leq 0.05$) amount of variation in the principal coordinates of the plant community species data. Correlation coefficients between environmental variables and the dominant principal coordinate axes were calculated for each environmental variable in the final ordination.

To facilitate the interpretation of relationships of individual plant species to the ordination axes and environmental and treatment factors, the original species presence data were included in the final ordinations as supplemental variables, thereby allowing for the projection of these species into the db-RDA ordination space. Supplemental (original species presence) data were superimposed on triplot ordination diagrams of 'species' (principal coordinate axes), samples and environmental variables. Sites in the ordination diagrams were coded by treatment.

The calculation of Sørensen distance matrices from the original plant community data and the subsequent PCoA of these matrices were performed using PrCoord v.1.0 and RDA was performed using CANOCO v.4.5 (ter Braak & Smilauer 2002).

RESULTS

A complete species list of all vascular plant species identified in both early and mid-successional treatment stands of this study are listed in Appendix 3.1.

Early Successional Stands

Species Richness & Diversity

A total of 114 vascular plant species were recorded, with 93 species identified in wildfire stands and 111 species identified in salvaged stands (Tables 3.2 & 3.3). Of all plant species identified, 35% occurred infrequently (were present in less than 5% of all sampling units) (Table 3.3). In general, most measures of species richness (alpha, gamma, total herb and shrub) and diversity were consistently greater in salvage stands than those in wildfire stands (Table 3.2).

The number of shrub species per sampling site was significantly higher in salvage stands ($P=0.04$) with an average of 11 ± 0.3 (± 1 *S.E.*) species per site compared with 9 ± 0.3 species in wildfire stands (Table 3.4, Figure 3.1). There was a significant amount of heterogeneity in herb ($P<0.01$) and total species richness ($P<0.01$) that was attributable to variability between stands (Table 3.4, Figure 3.1 a & c). In particular, stands within the salvage treatment were highly variable with the Fawcett stand having significantly higher species richness than other salvaged stands and the Cowper stand having species richness which was indistinguishable from that of the wildfire stands (Table 3.4, Figure 3.1 a & c).

Species turnover, as measured by beta diversity between sampling sites within stands, tended to be higher in salvaged stands in comparison to that of wildfire stands (Table 3.2). The high number of plant species recorded as occurring only within salvaged stands (21 unique species in salvaged stands compared with only 3 in wildfire stands) and the high proportion of rare species (92% of rare species occurred in salvaged stands versus only 47% in wildfire stands) (Table 3.3) likely contributed to the higher observed beta diversities within salvage stands (Table 3.2). At the coarser treatment scale, however, species turnover between stands was, in general low with wildfires being only slightly more heterogeneous than salvaged forests (Table 3.2).

Plant Community Composition

Salvage logging had a strong impact on post-fire vascular plant communities and resulted in significant differences in species composition between wildfire and salvage logged stands (P=0.03; Table 3.5). This pattern is paralleled in the results of the ordination analyses, with wildfire and salvage sites showing strong separation along the first ordination axis (x-axis) (Figure 3.2). The combination of lower beta diversity between sites within stands for wildfires, as mentioned previously (Table 3.2), and the more pronounced within treatment aggregation of wildfire sites compared with that of salvaged sites (Figure 3.2), suggests that the composition of plant communities in salvaged sites was more spatially heterogeneous than that of wildfire sites.

Final explanatory environmental variables selected using stepwise selection to constrain the ordinations explained 30% of the total variation in Sørensen community distances (P<0.01; Table 3.6). The first db-RDA axis explained 13% of the variation in Sørensen community distances (P<0.01; Table 3.6) and was strongly correlated with the first PCoA axis (Figure 3.3). This strong correlation demonstrates that the Sørensen community distances of the original species data have been well preserved in the final ordination space, with the solutions between the constrained db-RDA ordinations and the unconstrained PCoA ordinations remaining consistent (ter Braak & Smilauer 2002). Of the environmental variables selected to constrain the db-RDA ordination, percent canopy cover and light level were the most strongly correlated with this first PCoA axis (Table 3.7, Figure 3.3). The separation of wildfire sites from salvaged sites was most pronounced along this first PCoA axis with the majority of wildfire sites lying at the low light/high canopy cover end of the gradient (Figure 3.2). The second db-RDA axis represented 8% of the community variation (Table 3.6) and was also strongly correlated with the second PCoA axis (Figure 3.3). This second PCoA was less strongly correlated with any individual descriptor than those of the first PCoA axis (Table 3.7). Nonetheless, of those descriptors selected to constrain the db-RDA ordination, deciduous sapling density and litter cover were the most strongly correlated with the second PCoA axis (Table 3.7, Figure 3.3). The separation of treatment sites along this second PCoA axis suggests that wildfire sites are characterized by higher sapling densities and reduced cover of litter and volume of downed woody materials than salvage sites (Figure 3.2).

Based on the *a posteriori* projection of the original species occurrence data into the db-RDA ordination space, plant species associated with the wildfire treatment (based on species with $\geq$30% correlation in occurrence data with ordination axes) included fireweed (*Epilobium angustifolium*), Bicknell's geranium, bunchberry (*Cornus canadensis*), pink corydalis and bryophytes (Figure 3.2). Indicator species analysis confirmed that the aforementioned species were significant indicators of early post-fire plant communities (Table 3.8). In addition, wild sarsaparilla (*Aralia nudicaulis*), prickly rose (*Rosa acicularis*), common horsetail (*Equisetum arvense*) and coarse groupings of non-vascular species, and lichens and fungi were identified as being strong indicators of wildfire stands (Table 3.8).

Plant species associated with the salvage treatment in db-RDA ordination space included marsh reed grass (*Calamagrostis canadensis*), hairy wild rye (*Elymus innovatus*), bishop's-cap (*Mitella nuda*) and wild vetch (*Vicia americana*) (Table 3.2). Based on indicator species analysis, indicator values of species differentiating the plant communities of salvaged stands were generally lower than that of wildfire communities, with only marsh reed grass, hairy wild rye, purple-stemmed aster (*Aster puniceus*) and purple peavine (*Lathyrus ochroleucus*) demonstrating strong affinities for the salvage logged treatment (Table 3.8). However, salvaged stands were still characterized by a number of significant indicator plants including weedy (Canada thistle (*Cirsium arvense*), common dandelion (*Taraxicum officinale*) and perennial sow thistle (*Sonchus arvensis*)), shrubby (bracted honeysuckle (*Lonicera involucrata*) and common bearberry (*Arctostaphylos uva-ursi*)) and interior forest species (bishop's-cap) (Table 3.8).

Mid-Successional Stands

Species Richness & Diversity

A total of 127 vascular plant species were recorded within treatment stands, of which, 111 species and 115 species were identified from wildfire and salvage stands respectively (Table 3.9, Table 3.10). Slightly over a quarter of all plant species identified were encountered only infrequently (Table 3.10). Most measures of species richness (alpha, gamma, total herb and shrub) and diversity were generally very similar for all stands, with the exception of the Calling Lake wildfire stand which remained consistently lower in terms of almost all measures of richness as compared to the other stands (Table 3.9).

Variability in plant species richness per site did not reflect treatment level effects but instead appeared to be a reflection of between stand heterogeneity, with average richness of herbs ($P<0.01$), shrubs ($P<0.01$) and total vascular plants ($P<0.01$) all differing significantly among stands of the same treatment (Table 3.11, Figure 3.4). The majority of this variability can be attributed to the relatively species poor Calling Lake wildfire stand which consistently had lower average species richness than every other stand (Figure 3.4).

Species turnover as measured by beta diversity at the stand level (between sites within treatment stands), was slightly lower in salvage logged stands in comparison to that in wildfire stands (Table 3.9). Species turnover among stands within treatments was much lower by comparison and very similar between both the wildfire and salvage treatments (Table 3.9). Both the low values for beta diversity and its consistency across the treatments in general, may be due in part to the fact that both wildfire and salvage stands had similar numbers of uniquely occurring species (12 and 16 species respectively) and similar proportions of infrequently occurring plant species with 64%

and 67% of all rare species occurring in wildfire and salvaged stands respectively (Table 3.10).

Plant Community Composition

Based on MRPP analysis, the composition of the vascular plant communities of wildfire and salvage logged stands were broadly overlapping with no significant differences evident between treatments (*P*=0.16; Table 3.5). Within treatment group homogeneity (*A*) was no different than that expected by chance, however the higher average within group distances of wildfire stands reflected a greater degree of variability in the composition of wildfire stands in comparison to that of the salvage logged stands (Table 3.5). These results were reflected in the ordination diagram that showed two distinct, disparate clusters of wildfire sites but which, when taken as a whole, broadly overlapped the distribution of the salvaged sites (Figure 3.5). A cluster of six sites from the Calling Lake wildfire stand (at the far right of the diagram) were entirely disjunct from all other wildfire sites in terms of their species composition and likely skewed the results of MRPP analysis contributing both to the lack of significant separation between plant communities and the greater degree of compositional heterogeneity in wildfire stands revealed by that analysis (Table 3.5, Figure 3.5).

Final explanatory environmental variables selected to constrain the ordinations accounted for 24% of the total variation in Sørensen community distances (*P*<0.01; Table 3.12). The first db-RDA axis explained 12% of the variation in Sørensen community distances (*P*<0.01; Table 3.12) and was strongly correlated with the first PCoA axis (Figure 3.6), therefore, the Sørensen community distances of the original species data were well preserved in these ordinations. Of the environmental variables constraining the db-RDA ordination, litter cover and conifer density were the most strongly associated with this first PCoA axis (Table 3.13, Figure 3.6). The second db-RDA axis accounted for an additional 5% of community variation (Table 3.12) and was strongly correlated with the second PCoA axis (Figure 3.6). Correlations of the second

PCoA axis with individual environmental variables were weak (Table 3.13). The most strongly correlated environmental variables with the second PCoA axis were soil moisture, tall shrub density and litter cover, the last of which was also strongly correlated with the first PCoA axis (Tables 3.13, Figure 3.6). Consequently, aggregation of sample sites along gradients of measured environmental variables did not split neatly along PCoA axes (in particular for the second PCoA axis), suggesting that species composition was responding to interactions of environmental variables or that some other environmental factors significantly influencing community composition were not measured (Figure 3.6). However based on the interpretation of the environmental vectors constraining these ordinations, species composition of salvaged sites appeared to be influenced primarily by conifer and tall shrub density, with the majority of salvaged sites being found at the high end of these environmental gradients (Figure 3.5). The six outlying plots from the Calling Lake fire had very high densities of post-fire origin white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*) (conifer stem density data not shown), which likely modified the understory plant community to be more similar to that of the salvage stands. However, the pattern of aggregation of the majority of the wildfire stands suggests that the dominant environmental influence on understory composition in these sites was litter cover and soil moisture (Figure 3.5).

Half of the species identified as significant indicators of plant communities in mid-successional wildfire stands had been previously identified as characteristic of early successional wildfire environments (prickly rose, fireweed, lichen species and bunchberry), the exception of which was marsh reed grass which had been identified as a significant component of salvage logged communities (Table 3.14). The remaining species identified as indicators of plant communities in mid-successional wildfire stands included wild gooseberry (*Ribes oxycanthoides*), sweet-scented bedstraw (*Galium triflorum*), wild vetch (*Vicia americana*), fairy-bells (*Disporum trachycarpum*) and tall lungwort (*Mertensia paniculata*) (Table 3.14).

Wild strawberry (*Fragaria virginiana*), wild lily-of-the-valley (*Maianthemum canadense*) and shrub species including saskatoon (*Amelanchier alnifolia*), common wild rose (*Rosa woodsii*) and bracted honeysuckle all demonstrated a strong affinity for mid-successional salvaged stands (Table 3.14).

DISCUSSION

Early post-fire plant communities of the boreal mixedwood forest are significantly modified by salvage logging activities that occur within the first two years of their initial disturbance by wildfire. Salvage logging appears to promote more compositionally heterogeneous plant communities than those of undisturbed wildfires, with salvaged stands being characterized by higher shrub species richness. Salvage logged stands also showed evidence of pronounced changes to the composition of the plant community with lower relative abundances of species considered to be fire dependent and higher abundances of introduced, weedy species and grasses.

The understory communities of the mid-successional, post-fire salvaged forest stands appear to be responding more to the silvicultural techniques employed in these stands and to site specific edaphic characteristics, than to any residual, lingering effects of salvage logging *per se*. Mid-successional wildfire stands were characterized by some of the same species that differentiated wildfire stands at the early post-disturbance time period, whereas the salvaged stands were characterized primarily by shrub species. The composition of the understory plant communities of mid-successional stands were fairly similar between wildfire and salvage logged stands. However, there were several important differences arising from the combined influence of salvage logging and post-salvage silvicultural prescriptions (i.e. the high densities of tall shrubs and understory white spruce) that appeared to be the driving the plant communities of these stands towards an alternate successional trajectory beyond the range observed in aspen dominated fire origin stands of this age.

Understory Plant Community Species Richness & Composition

The variability in species richness in early post-disturbance forests observed between replicate stands suggests that the understory plant communities of these stands likely reflect stand level variability within treatments in the environmental influences (i.e. soil moisture, nutrient availability, disturbance severity) and ecological processes (i.e. dispersal, competition) that typically govern plant growth and interactions (Dix & Swan 1971, Bonan & Shugart 1989, Barnes et al. 1998). However, results from this study suggest that in the first several years following disturbance, species richness and diversity were greater in plant communities subjected to salvage logging than in those disturbed by wildfire alone. However, this increased species richness is not necessarily an ecologically positive outcome, since in many cases, including in this study, it is attributable to the presence of introduced species. Salvage logged stands in this study generally appeared to maintain the same complement of species as wildfire stands (including those species considered to be fire-dependent, such as Bicknell's geranium and corydalis species) with the further addition of a number of introduced, weedy species. Many of the introduced, weedy species (common dandelion, Canada thistle, perennial sow thistle) were distinctive enough to act as indicator species characterizing the understory plant communities of early salvage logged stands. In mixedwood forest stands, Crites and Hanus (2001) found that the understory plant communities of salvaged stands included introduced, weedy species whereas comparable wildfire stands generally did not. Research in conifer dominated stands outside of the boreal forest also conclude that salvage logging introduces weedy species to post-fire stands, thereby increasing understory species richness (Ne'eman et al. 1995).

Introduced species are generally shade intolerant and are reliant upon the availability of mineral soil microsites for successful colonization (Rowe 1983, Brothers & Springarn 1992). The high light environment created by the removal of snags and residual live trees in salvaged stands, coupled with the abundance of exposed mineral soil substrates created by the original wildfire, likely creates a highly favorable colonization environment. These species may have been initially introduced to salvaged stands as a result of direct dispersal via logging equipment, indirectly as a result of increased access associated with logging road development or from windborne seed produced from plants in nearby wellsites, seismic lines or cutblocks (Brothers & Springarn 1992, Crites & Hanus 2001, MacFarlane 2003). It should be noted however, that while salvaged stands did have introduced species present and these species did function to differentiate the salvaged plant community from that of wildfire communities, they were still at relatively low abundances and could not be considered to be invasive since they did not appear to cause changes in the abundance and frequency of native species at the sites where they were present.

The understory communities of early successional salvage logged stands had significantly higher shrub species richness than that found in wildfire stands. These results were somewhat unexpected. It is possible that shrub species richness was higher in salvaged stands prior to disturbance, and that this higher richness subsequently manifested itself again following disturbance with many of the shrub species re-establishing vegetatively. It is also possible, that despite rigorous site selection criteria, that salvaged stands were intrinsically different from wildfire stands in terms of their fire severity, since for economic reasons, very intense fires are less likely to be salvaged. Many boreal forest shrub species are well adapted to periodic disturbance by wildfire, with the majority resprouting from dormant buds on underground roots or rhizomes (Rowe 1983, Whittle et al. 1997). As such, successful vegetative regeneration is highly reliant upon fire severity with more severe fires lethally heating reproductive tissues and resulting in the selective regeneration of individuals and species with greater tolerance (Rowe 1983). If indeed salvaged stands were burned by less intense wildfires prior to logging, it is possible that the higher shrub species richness in these stands is attributable not to treatment effects of salvage logging *per se* but to increased species survivorship owing to the lower severity fires in these stands.

Species richness in the mid-successional forests did not appear to vary as a result of any residual effects from salvage logging activities, and appeared to be highly variable between stands. The two major factors contributing to differences in species richness in early post-disturbance stands, namely high numbers of introduced species and shrubs in salvaged stands, were not apparent in these mid-successional stands. While introduced plant species were very occasionally present in mid-successional stands of both treatments, normally along animal trails or adjacent to stand edges (pers. obs.), their presence could most likely be attributed to accidental dispersal rather than the continued persistence of populations arising from the salvage logging activities of three decades earlier. These results are not unexpected, given that introduced, weedy species are generally shade intolerant and do not compete well under the low light conditions of closed canopy, interior forests (Brothers & Springarn 1992). It is also likely that any colonization of mid-successional stands by introduced, weedy species following the initial stand disturbances may have been of an order of magnitude lower than that occurring within present day disturbed stands, given the less fragmented landscape and potentially reduced presence of reproductive propagules for these species at that time.

While shrub species richness itself did not vary between mid-successional salvage logged and wildfire stands, the prominence of shrubby species in the vascular plant community could be seen in the form of the very high abundances and densities of shrubs in these mid-successional salvaged stands as compared with those in wildfire stands. Indeed, the primary indicator species of the mid-successional salvage logged treatment were shrub species, including saskatoon, common wild rose and bracted honeysuckle. Similar results were found in 20 year old salvaged (and silviculturally treated) aspen dominated mixedwood stands, where these sites were characterized by higher than average abundances of shrub species (Crites & Hanus 2001). Higher richness of shrub species at early successional stages of salvage logged forests may translate into the prominence (in terms of density or cover) of some of these same species later on in the stand's development which could subsequently influence the development of the rest of the understory community. Since light availability to the understory can be influenced not only by canopy composition and cover but also by dense layers of tall shrubs (Constabel & Lieffers 1996), it is likely that the high densities of tall shrubs in mid-succssional salvaged stands would have a significant influence on the composition of the herbaceous understory in these stands.

Understory plant communities associated with the early successional salvage logged stands displayed greater turnover in terms of their species composition (beta diversity within stands) than understory plant communities associated with wildfire stands. Salvage logging activities in conifer forest ecosystems have been credited with increasing the variety and number of microsites for plant establishment, in particular, that of mineral soil microsites (Noël 2002), which could subsequently encourage a wider variety of species to colonize these stands. It is likely that this increased variety in available regeneration microsites would create a more heterogeneous colonization environment at the stand level which would be reflected in increased beta diversity of these stands. While availability of mineral soil microsites was not significantly influenced by salvage logging activities in this study (see chapter 2), sites were surveyed more than two years following disturbance and as a result it is entirely possible that many of these microsites had already been colonized by the time they were sampled and were therefore not detected as mineral microsites. The continued presence of fire-dependent, seedbanking species, albeit at lower relative abundances, the additional presence of introduced, weedy species and a high proportion of infrequently occurring species (occurring in less than 5% of all sampling units) in salvaged stands also contributed to the greater degree of compositional heterogeneity of these stands relative to wildfire stands.

Environmental Influences on Plant Community Composition

Differences in community composition between treatments at early successional stages appeared to be correlated most strongly with light availability. Higher deciduous sapling densities in wildfire stands coupled with the lower light levels (see chapter 2) associated with the retention of snags and residual live trees suggest that competition for light (but also presumably for nutrients, moisture and space) in the understory of wildfire stands was high. The significance of litter cover in influencing the understory plant communities of this successional stage is likely a reflection of fire severity effects. Intense wildfires tend to kill species reliant on vegetative reproduction and expose the buried soil seedbank (Rowe 1983). The depth to which wildfire burns the soil will determine the subsequent composition of the understory since the composition of the soil seedbank changes with soil depth (Fyles 1989). Therefore, severe initial disturbance by wildfire involving the removal of all surface litter and organic material, may enhance the chances of successful germination for deeply buried seeds originating from the last intense disturbance. The relative abundances of fire dependent, seedbanking species (Bicknell's geranium and pink corydalis) were significantly higher in wildfire stands as compared with salvaged stands and, as such, were among some of the plant species identified as being diagnostic of these early wildfire stands. The mechanism by which the relative abundances of these species was so dramatically reduced in salvaged stands was not directly quantified by this study, but the more extreme microclimatic conditions (see chapter 2) combined with the low moisture retention capacity of mineral soil seedbeds (McRae et al. 2001) or actual mechanical damage from logging equipment are reasonable conjectures. Regardless of the mechanism, the significantly lower relative abundances of these species and their subsequently reduced contribution to the soil seedbank begs the question of their long term persistence on a managed forest landscape.

The composition of plant communities associated with mid-successional salvaged stands appeared to be primarily driven by the dense subcanopy of understory white spruce arising from the silvicultural techniques employed in these stands (blade scarification and aerial seeding). The six disjunct sites from the Calling Lake wildfire stand were very similar in understory composition to the mid-successional salvaged stands and similarly appeared to be driven by the high density of naturally regenerating conifers in these stands. Tree species composition and its acknowledged influence on stand characteristics such as light availability and litter quality, have a significant influence on the development of the understory plant community (Barnes et al. 1998, McKenzie et al. 2000). While light availability under forest canopies composed primarily of trembling aspen may be relatively high, the majority of available light is generally intercepted by taller shrubs and tree saplings before it even reaches the understory (Constabel & Lieffers 1996, Messier et al. 1998). Consequently, the high densities of tall shrubs and/or dense spruce understories, such as were found in mid-successional salvaged stands and the six Calling Lake wildfire sites, could substantially reduce the amount of light reaching the herbaceous layers of the understory. This is concurrent with the observed dominance of more shade tolerant, herbaceous species in the understory communities of these stands compared with unsalvaged wildfire communities. With the absence of a dense spruce subcanopy in the majority of mid-successional wildfire sites, the understory communities of these stands appeared to be primarily influenced by other environmental characteristics of the stand such as soil moisture or nutrient availability. This provides strong evidence that the initial tree regeneration of a disturbed forest, whether naturally occurring or modified by management activities, will have a significant influence on the successional development of that forest in the future. With the combination of the salvage logging regime in the mid-successional stands being in some ways less severe (i.e. less dead wood removed) than in current practice, and the confounding influence of post-salvage silvicultural practices in these stands, it is difficult to speculate on what the effects of salvage logging as currently practiced might be on plant communities in the long term. However, based on these results, it is suggested that salvage logging may alter the successional pathways of the understory community from the range normally observed in undisturbed wildfire stands.

LITERATURE CITED

Ahlgren, I.F. & Ahlgren, C.E. 1960. Ecological effects of forest fires. Botanical Review **26**:483-533.

Barnes, B.V., Zak, D.R., Denton, S.R. & Spurr, S.H. 1998. Forest Ecology, 4th ed. John Wiley and Sons Inc., New York.

Bonan, G.B. & Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. Annual Review in Ecology and Systematics **20**:1-28.

Brais, S., Paré, D. & Ouimet, R. 2000. Impacts of wild fire severity and salvage harvesting on the nutrient balance of jack pine and black spruce boreal stands. Forest Ecology and Management **137**:231-243.

Brothers, T.S. & Springarm, A. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology **6**:91-100.

Carleton, T.J. & MacLellan, P. 1994. Woody vegetation responses to fire versus clear-cutting logging: A comparative survey in the central Canadian boreal forest. Ecoscience **1**:141-152.

Constabel, A.J. & Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Canadian Journal of Forest Research **26**:1008-1014.

Crites, S. 1999. A comparison of early successional understory plant communities following fire and harvesting. In: Lee, P.C. (ed.), Fire and harvest residual (FAHR) project: the impact of wildfire and harvest residuals on forest structure and biodiversity in aspen-dominated boreal forests of Alberta. Publication Number T/495. Alberta Research Council, Vegreville.

Crites, S. & Hanus, S. 2001. Succession of herbaceous, shrub and tree communities following combined treatments of fire and harvesting. Final report, Alberta Research Council, Vegreville.

Dix, R.L. & Swan, J.M. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Canadian Journal of Botany **49**:657-676.

Dufrêne, M. & Legendre, P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Eberhart, K.E. & Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. Canadian Journal of Forestry **17**:1207-1212.

Faith, D.P., Minchin, P.R. & Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio **69**:57-68.

Fortin, M.J., Payette, S. and Marineau, K. 1999. Spatial vegetation diversity index along a postfire successional gradient in the northern boreal forest. Ecoscience **6**:204-213.

Fraser, E., Landhäusser, S. & Lieffers, V. In Press. The effect of fire severity and salvage logging traffic on regeneration and early growth of aspen suckers. Forestry Chronicle.

Fyles, J.W. 1989. Seed bank populations in upland coniferous forests in central Alberta. Canadian Journal of Botany **67**:274-278.

Harmon, M.E. & Franklin, J.F. 1989. Tree seedlings on logs in *Picea Tsuga* forests of Oregon and Washington. Ecology **70**:48-59.

Johnson, E.A. 1981. Vegetation organization and dynamics of lichen woodland communities in the Northwest Territories, Canada. Ecology **62**:200-215.

Legendre, P. & Anderson, M.J. 1999. Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. Ecological Monographs **69**:1-24.

Legendre, P. & Legendre, P. 1998. Numerical ecology. 1st edition, Elsevier, Amsterdam.

MacFarlane, A. 2003. Vegetation response to seismic lines: edge effects and on-line succession. MSc. Thesis, University of Alberta.

Martinez-Sanchez, J.J., Ferrandis, P., de las Heras, J. & Herranz, J.M. 1999. Effect of burnt wood removal on the natural regeneration of *Pinus halepensis* after fire in a pine forest in Tus valley (SE Spain). Forest Ecology and Management **123**:1-10.

McArdle, B.H. & Anderson, M.J. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology **82**:290-297.

McCune, B. & Grace, J.B. 2002. Analysis of ecological communities. MjM Software Design, Oregon.

McCune, B. & Mefford, M.S. 1997. Multivariate analysis of ecological data. Version 3.20, MjM Software, Oregon.

McKenzie, D., Halpern, C.B. & Nelson, C.R. 2000. Overstory influences on herb and shrub communities in mature forests of western Washington, U.S.A. Canadian Journal of Forest Research **30**:1655-1666.

McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J. & Woodley, S. 2001. Comparisions between wildfire and forest harvesting and their implications in forest management. Environmental Reviews **9**:223-260.

Messier, C., Parent, S. & Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forest. Journal of Vegetation Science **9**:511-520.

Mielke, P.W., Jr. & Berry, K.J. 2001. Permutation methods: A distance function approach. Springer Series in Statistics.

Moss, E.H. 1983. Flora of Alberta. A manual of flowering plants, conifers, ferns and fern allies found growing without cultivation in the province of Alberta, Canada. 2nd edition, revised by J.G. Packer. University of Toronto Press, Toronto.

Ne'eman, G., Lahav, H. & Izhaki, I. 1995. Recovery of vegetation in a natural east Mediterranean pine forest on Mount Carmel, Israel as affected by management strategies. Forest Ecology and Management **75**:17-26.

Noël, J. 2002. Régénération forestière après feu et coupe de récupération dans le secteur de Val-Paradis, Abitibi. MSc. thesis, Université du Québec à Montréal.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In: Wein, R.W. & MacLean, D.A. (eds.), The role of fire in northern circumpolar ecosystems. John Wiley & Sons Inc., New York.

ter Braak, C.J.F. & Smilauer, P. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5). Microcomputer Power, New York.

Turner, M.G., Romme, W.H., Gardner, R.H. & Hargrove, W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs **64**:411-433.

Whitaker, R.H. 1972. Evolution and measurement of species diversity. Taxon **21**:213-251.

Whittle, C.A., Duchesne, L.C. & Needham, T. 1997. The importance of buried seeds and vegetative propagation in the development of postfire plant communities. Environmental Reviews **5**:78-87.

Zar, J.H. 1999. Biostatistical analysis. 4th edition. Prentice-Hall Inc., New Jersey.

Zasada, J.C. 1971. Natural regeneration of interior Alaska forests: seed, seedbed and vegetative reproduction considerations. In: Slaugher, C.W., Barney, R.J. & Hansen, G.M. (eds.), Fire in the northern environment- A symposium. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, OR.

Table 3.1. Summary of environmental variables tested using multiple linear regression to constrain db-RDAs of understory plant community data in early and mid-successional treatment stands.

Variable	Description of Variable Measurements	Forest Successional Stage	
		Early	Mid
light	Light availability (% Full PPFD); based on plot center/site	√	√
can	% Canopy closure; based on plot center/site	√	√
resid	Density (sph) of residual trees & snags; based on 50m^2 circular plot	√	
shrub	Density of live tall shrubs (>1.3m in height); based on 78.5m^2 circular plot		√
conifer	Density of live conifers; based on 78.5m^2 circular plot		√
saplings	Density of live deciduous saplings; based on 1x1m plots (early stands) and 78.5m^2 plots (mid stands)	√	√
dstems	Density of dead deciduous trees; based on 78.5m^2 plots		√
stems	Density of live deciduous trees; based on 78.5m^2 plots		√
cov	% Cover DWM based on 25m DWM transect	√	√
vol	Volume DWM (m^3/ha); based on 25m DWM transect	√	√
evol	Volume DWM (m^3/ha) in decay stages 1-4* (early decay stages); based on 25m DWM transect	√	√
comp	Soil compaction (kg/cm^2); based on 1x1m plots	√	√
moist	Soil moisture (percent volumetric soil water content); based on 1x1m plots		√
dlit	Litter layer depth (cm); based on 1x1m plots	√	√
dmoss	Bryophyte layer depth (cm); based on 1x1m plots	√	√
dorg	Organic soil depth (cm); based on 1x1m plots	√	√
lit	% Litter cover; based on 1x1m plots	√	√
wood	% Wood cover; based on 1x1m plots	√	√
ft1	Availability of bare mineral soil microsites; based on % cover on 25m transect	√	√
ft2	Availability of organic soil microsites; based on % cover on 25m transect	√	√
ft3	Availability of bryophyte covered, non-woody microsites; based on % cover on 25m transect	√	√
ft4	Availability of other regeneration microsites; based on pooled % cover on 25m transect	√	√
ft5	Availability of early decay stage (stages 1-4*) log microsites; based on % cover on 25m transect	√	√
ft6	Availability of late decay stage (stages 5-7*) log microsites; based on % cover on 25m transect	√	√
trough	Extent of site prepared forest floor; based on % cover of identifiable 'troughs' on 25m transect		√

* See Table 2.3 for definitions of log decay classifications

Table 3.2. Diversity (mean alpha, beta and gamma, total richness of herbs and shrubs) and diversity (Shannon-Wiener (SW) indices) of vascular plant species in early post-disturbance treatment stands.

			Diversity					SW-- Complete Species List			SW-- Abundance		
		n	mean alpha	beta	gamma	total herb	total shrub	herb	shrub	total	herb	shrub	total
Between Stands													
Wildfire	Benson	15	27.9	2.58	72	51	21	3.64	2.81	4.00	2.13	1.73	2.64
	Chard	13	28.3	2.12	60	42	18	3.43	2.66	3.81	2.23	1.65	2.50
	Mena	15	27.3	2.53	69	49	20	3.53	2.77	3.92	2.19	1.33	2.52
Salvage	Cowper	15	29.3	2.80	82	59	23	3.69	2.89	4.05	2.24	2.35	2.96
	Fawcett	15	37.2	2.50	93	68	25	3.86	2.92	4.19	2.48	1.36	2.62
	Philomena	15	33.7	2.61	88	61	27	3.81	3.06	4.20	2.44	2.16	3.00
Between Treatments													
Wildfire		43	67.0	1.37	93	67	24						
Salvage		45	87.7	1.27	111	80	31						

Table 3.3. Vascular plant species occurence in early post-disturbance treatment stands expressed as the proportion of sites within which each species was present. Species unique to a given treatment are indicated by √. Plant species considered to be shrubs in the calculations of species richness and diversity are indicated by *. Plant species codes consisting of the first two letters of the genus and species name are presented. Wildfire *n*=43 sites and salvage *n*=45 sites.

Frequency of Occurence				Species	Species Code
Wildfire		Salvage			
0.24		0.40		*Achillea millefolium*	Acmi
0.03	√	0.00		*Achillea sibirica*	Acsi
0.16		0.40		*Actaea rubra*	Acru
0.00		0.07	√	*Agropyron repens*	Agre
0.11		0.07		*Agropyron spp.*	Agrospp
0.03		0.04		*Agropyron trachycaulum*	Agtr
0.00		0.04	√	*Agrostis scabra*	Agsc
0.58		0.51		*Alnus crispa**	Alcr
0.29		0.40		*Amelanchier alnifolia**	Amal
0.00		0.02	√	*Androsace septentrionalis*	Anse
0.79		0.69		*Aralia nudicaulis*	Arnu
0.21		0.40		*Arctostaphylos uva-ursi**	Aruv
0.03		0.13		*Arnica cordifolia*	Arco
0.03		0.09		*Aster ciliolatus*	Asci
0.11		0.36		*Aster conspicuus*	Asco
0.50		0.62		*Aster puniceus*	Aspu
0.03		0.09		*Astragalus americanus*	Asam
0.00		0.04	√	*Betula glandulosa**	Begl
0.39		0.51		*Betula papyrifera*	Bepa
0.03	√	0.00		*Botrychium lunaria*	Bolu
0.00		0.09	√	*Bromus ciliatus*	Brci
0.11		0.20		*Bromus inermis*	Brin
0.97		1.00		*Calamagrostis canadensis*	Caca
0.03		0.07		*Campanula rotundifolia*	Caro
0.24		0.29		*Carex aurea*	Caau
0.26		0.27		*Carex siccata*	Casi
0.63		0.64		*Carex spp.*	Carexsp
0.00		0.04	√	*Chenopodium capitatum*	Chca
0.05		0.20		*Cirsium arvense*	Ciar
0.03		0.04		*Coptis trifolia*	Cotr
1.00		0.93		*Cornus canadensis*	Coca
0.00		0.02	√	*Cornus stolonifera**	Cost
0.16		0.07		*Corydalis aurea*	Coau
0.42		0.24		*Corydalis sempervirens*	Cose

Table 3.3. Continued

0.00		0.07	√	*Corylus cornuta*	Coco
0.00		0.02	√	*Delphinium glaucum*	Degl
0.00		0.07	√	*Disporum trachycarpum*	Ditr
0.13		0.16		*Dracocephalum parviflorum*	Drpa
0.76		0.82		*Elymus innovatus*	Elin
1.00		1.00		*Epilobium angustifolium*	Epan
0.16		0.09		*Epilobium ciliatum*	Epci
0.39		0.22		*Equisetum arvense*	Eqar
0.18		0.16		*Equisetum pratense*	Eqpr
0.68		0.60		*Equisetum sylvaticum*	Eqsy
0.03		0.04		*Erigeron philadelphicus*	Erph
0.55		0.60		*Fragaria virginiana*	Frvi
0.71		0.76		*Galium boreale*	Gabo
0.05		0.07		*Galium triflorum*	Gatr
0.03	√	0.00		*Gentianella amerella*	Geam
0.95		0.62		*Geranium bicknelli*	Gebi
0.16		0.56		*Halenia deflexa*	Hade
0.03		0.09		*Hieracium umbellatum*	Hium
0.11		0.18		*Hordeum jubatum*	Hoju
0.63		0.71		*Lathyrus ochroleucus*	Laoc
0.16		0.09		*Lathyrus venosus*	Lave
0.37		0.20		*Ledum groenlandicum**	Legr
0.03		0.44		*Lilium philadelphicum*	Liph
0.82		0.58		*Linnaea borealis**	Libo
0.13		0.53		*Lonicera involucrata**	Loin
0.39		0.29		*Lycopodium annotinum*	Lyan
0.03		0.04		*Lycopodium complanatum*	Lyco
0.95		0.96		*Maianthemum canadense*	Maca
0.05		0.02		*Melampyrum lineare*	Meli
0.74		0.69		*Mertensia paniculata*	Mepa
0.29		0.47		*Mitella nuda*	Minu
0.00		0.07	√	*Moehringia lateriflora*	Mola
0.24		0.24		*Orthilia secunda*	Orse
0.00		0.02	√	*Parnassia palustris*	Papa
0.03		0.11		*Pedicularis labradorica*	Pela
0.84		0.73		*Petasites palmatus*	Pepa
0.03		0.04		*Petasites sagittatus*	Pesa
0.08		0.18		*Picea glauca*	Pigl
0.42		0.29		*Pinus banksiana*	Piba
0.03		0.13		*Plantago major*	Plma
0.08		0.13		*Poa pratensis*	Popr
0.13		0.29		*Populus balsamifera*	Poba

Table 3.3. Continued

1.00	1.00		*Populus tremuloides*	Potr
0.08	0.09		*Potentilla gracilis*	Pogr
0.03	0.11		*Potentilla tridentata*	Potri
0.13	0.20		*Prunus pensylvanica**	Prpe
0.11	0.13		*Pyrola asarifolia*	Pyas
0.00	0.09	√	*Ranunculus acris*	Raac
0.00	0.02	√	*Rhinanthus minor*	Rhmi
0.00	0.02	√	*Ribes americanum**	Riam
0.03	0.09		*Ribes hudsonianum**	Rihu
0.00	0.09	√	*Ribes lacustre**	Rila
0.00	0.09	√	*Ribes oxycanthoides**	Riox
0.45	0.51		*Ribes triste**	Ritr
0.92	0.91		*Rosa acicularis**	Roac
0.26	0.38		*Rubus idaeus**	Ruid
0.68	0.87		*Rubus pubescens**	Rupu
0.47	0.47		*Salix spp*	Salix
0.08	0.11		*Schizachne purpurascens*	Scpu
0.00	0.11	√	*Senecio vulgaris*	Sevu
0.03	0.13		*Shepherdia canadensis**	Shca
0.03	0.58		*Sonchus arvensis*	Soar
0.00	0.04	√	*Stellaria longipes*	Stlong
0.13	0.27		*Symphoricarpos albus**	Syal
0.00	0.27	√	*Symphoricarpos occidentalis**	Syoc
0.00	0.04	√	*Tanacetum vulgare*	Tavu
0.11	0.29		*Taraxicum officinale*	Taof
0.03	0.18		*Thalictrum venulosum*	Thve
0.66	0.51		*Trientalis borealis*	Trbo
0.03	0.29		*Trifolium spp.*	Trispp
0.08	0.11		*Vaccinium caespitosum**	Vaca
0.79	0.71		*Vaccinium myrtilloides**	Vamy
0.03	0.04		*Vaccinium vitis-idaea**	Vavi
0.74	0.78		*Viburnum edule**	Vied
0.53	0.56		*Vicia americana*	Viam
0.03	0.09		*Viola adunca*	Viad
0.24	0.33		*Viola canadensis*	Vica
0.11	0.02		*Viola nephrophylla*	Vine
0.24	0.42		*Viola renifolia*	Vire

Table 3.4. Results of nested GLM models for herbaceous, shrub and total vascular plant species richness in early post-disturbance treatments. Degrees of freedom (*d.f.*), F-values (*F*) and probability of type I error rate (*P*) of each variable in the GLM model are presented. Data are pooled to the site level with wildfire *n*=3 stands (with 43 sites total) and salvage *n*=3 stands (with 45 sites total).

	Herb Species Richness			Shrub Species Richness			Total Species Richness		
	Model R^2=0.44			Model R^2=0.28			Model R^2=0.43		
Source	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
Treatment	1	2.45	0.19	1	9.28	**0.04**	1	6.27	0.06
Stand(Treatment)	4	9.97	**<0.01**	4	2.29	0.07	4	5.91	**<0.01**
Error	82			82			82		

Table 3.5. Results of MRPP analysis of between group species composition of post-disturbance treatments. Average within-group distances, chance-corrected within-group agreement (*A*) and probability of type I error rate (*P*) are presented. Data are pooled to the stand level for both time periods.

Forest Successional Stage	Average within-group distance		*A*	*P*
	Wildfire	Salvage		
Early (2 years post-disturbance)	0.29	0.30	0.13	**0.03**
Mid (34 years post-disturbance)	0.31	0.23	0.04	0.16

Table 3.6. Summary of axes statistics for distance based Redundancy Analysis (db-RDA) of early successional understory plant communities. Eigenvalues representing % variance of Sørensen species matrix explained by each axes, trace (sum of all canonical eigenvalues) and correlations between PCoA axes and db-RDA axes are presented.

	db-RDA Axis 1*	db-RDA Axis 2	db-RDA Axis 3	db-RDA Axis 4	Trace**
Eigenvalue	0.13	0.08	0.04	0.02	0.30
PCoA axes-environment correlation	0.82	0.77	0.68	0.64	

*significant at $P<0.01$ with $F=10.6$ based on Monte Carlo permutation tests

**significant at $P<0.01$ with $F=4.42$

Table 3.7. Correlation coefficients of significant environmental variables with the first two principal coordinate (PCoA) axes in db-RDA of understory plant communities in early successional stands.

Environmental Variable	PCoA Axis 1	PCoA Axis 2
Canopy cover	0.70	0.04
Light level	-0.65	-0.13
Litter cover	-0.27	0.48
Sapling density	0.41	-0.47
Bryophyte depth	0.46	0.05
Organic soil depth	-0.37	-0.03
Total volume DWM	-0.31	0.37

Table 3.8. Results of Indicator Species Analysis for early successional (2 years post-disturbance) wildfire and salvage treatments. Average percent cover of indicator species, indicator values (*IV*) and probability of type I error rate (*P*) based on 10000 Monte Carlo permutations.

Treatment	Species	Mean Cover		*IV*	*P*
		Wildfire	Salvage		
Wildfire	Mosses & Liverworts	14.99	1.81	91.1	<0.01
	Epilobium angustifolium	22.59	7.78	72.3	<0.01
	Geranium bicknelli	0.53	0.06	64.8	<0.01
	Cornus canadensis	6.67	3.59	60.1	<0.01
	Corydalis sempervirens	0.52	0.03	15.1	<0.01
	Equisetum arvense	0.51	0.03	16.5	<0.01
	Lichen species	2.31	0.89	12.8	0.01
	Aralia nudicaulis	6.43	3.03	39.7	0.03
	Fungi	0.19	0.12	20.3	0.04
	Rosa acicularis	9.97	5.87	47.2	0.05
Salvage	*Calamagrostis canadensis*	5.73	18.19	75.8	<0.01
	Elymus innovatus	1.63	5.32	55.2	<0.01
	Lonicera involucrata	0.00	0.02	15.8	<0.01
	Aster puniceus	0.47	1.52	26.7	<0.01
	Arctostaphylos uva-ursi	0.02	0.31	15.1	0.01
	Cirsium arvense	0.00	0.08	8.0	0.02
	Mitella nuda	0.11	0.27	16.6	0.02
	Taraxacum officinale	0.02	0.08	8.9	0.04
	Lathyrus ochroleucus	0.48	0.78	30.4	0.05
	Sonchus arvensis	0.01	0.10	8.1	0.05

Table 3.9. Diversity (mean alpha, beta and gamma, total richness of herbs and shrubs) and diversity (Shannon-Wiener (SW) indices) of vascular plant species in mid-successional (34 years post-disturbance) treatment stands.

			Diversity					SW-- Complete Species List			SW-- Abundance		
		n	mean alpha	beta	gamma	total herb	total shrub	herb	shrub	total	herb	shrub	total
Between Stands													
Wildfire	Calling Lake	20	35.8	2.21	79	53	26	3.55	3.07	4.02	2.56	2.37	3.11
	Flattop	20	45.3	2.14	97	67	30	3.74	3.21	4.20	2.66	2.24	3.09
Salvage	Kinuso	20	45.05	2.04	92	63	29	3.64	3.23	4.05	2.51	2.38	3.03
	Slave	20	46.4	2.03	94	66	28	3.82	3.18	4.23	2.24	2.40	3.00
Between Treatments													
Wildfire		40	88.0	1.26	111	78	33						
Salvage		40	93.0	1.24	115	83	32						

Table 3.10. Vascular plant species occurence in mid-successional (34 years post-disturbance) treatment stands expressed as the proportion of sites within which each species was present. Species unique to a given treatment are indicated by √. Plant species considered to be shrubs in the calculations of species richness and diversity are indicated by *. Plant species codes consisting of the first two letters of the genus and species name are presented. Wildfire and salvage n=40 sites.

Frequency of Occurence				Species	Species Code
Wildfire		Salvage			
0.30		0.15		*Abies balsamea*	Abba
0.33		0.65		*Achillea millefolium*	Acmi
0.08		0.30		*Achillea sibirica*	Acsi
0.93		0.98		*Actaea rubra*	Acru
0.13		0.15		*Agropyron spp.*	Agrospp
0.08		0.10		*Agrostis scabra*	Agsc
0.30		0.50		*Alnus crispa**	Alcr
0.58		0.83		*Amelanchier alnifolia**	Amal
0.05		0.08		*Anemone canadensis*	Arnu
0.93		1.00		*Aralia nudicaulis*	Anca
0.05		0.20		*Arnica chamissonis*	Arch
0.03	√	0.00		*Arnica cordifolia*	Arco
0.43		0.65		*Aster conspicuus*	Asco
0.85		0.98		*Aster puniceus*	Aspu
0.08	√	0.00		*Betula glandulosa**	Begl
0.73		0.88		*Betula papyrifera*	Bepa
0.00		0.03	√	*Botrychium lunaria*	Bolu
0.00		0.23	√	*Botrychium virginianum*	Bovi
0.20		0.05		*Bromus ciliatus*	Brci
0.78		0.80		*Calamagrostis canadensis*	Caca
0.03		0.15		*Calamagrostis inexpansa*	Cain
0.03	√	0.00		*Caltha palustris*	Capa
0.08		0.00		*Campanula rotundifolia*	Caro
0.08		0.13		*Carex aurea*	Caau
0.15		0.38		*Carex spp.*	Carex
0.03	√	0.00		*Chrysosplenium tetrandrum*	Chte
0.13		0.03		*Circaea alpina*	Cial
0.08		0.03		*Clematis occidentalis*	Cloc
0.05		0.05		*Corallarhiza maculata*	Coma
0.00		0.15	√	*Corallarhiza trifida*	Cotr
1.00		0.85		*Cornus canadensis**	Coca
0.78		0.90		*Cornus stolonifera**	Cost
0.03		0.05		*Corylus cornuta**	Coco
0.28		0.20		*Delphinium glaucum*	Degl
0.30		0.15		*Disporum trachycarpum*	Ditr

Table 3.10. Continued

0.35		0.10		*Dryopteris carthusiana*	Drca
0.13		0.03		*Elymus innovatus*	Elin
0.95		0.93		*Epilobium angustifolium*	Epan
0.05	√	0.00		*Epilobium ciliatum*	Epci
0.73		0.70		*Equisetum arvense*	Eqar
0.13		0.23		*Equisetum pratense*	Eqpr
0.88		0.90		*Equisetum sylvaticum*	Eqsy
0.03		0.25		*Fragaria vesca*	Frve
0.30		0.60		*Fragaria virginiana*	Frvi
0.00		0.05	√	*Galeopsis tetrahit*	Gate
0.95		1.00		*Galium boreale*	Gabo
1.00		0.98		*Galium triflorum*	Gatr
0.05		0.03		*Geum aleppicum*	Geal
0.05		0.23		*Geum macrophyllum*	Gema
0.60		0.65		*Gymnocarpium dryopteris*	Gydr
0.00		0.03	√	*Habenaria orbiculata*	Haor
0.03		0.03		*Halenia deflexa*	Hade
0.48		0.40		*Heracleum lanatum*	Hela
0.85		1.00		*Lathyrus ochroleucus*	Laoc
0.10		0.05		*Lathyrus venosus*	Lave
0.10		0.30		*Ledum groenlandicum**	Legr
0.70		0.65		*Linnaea borealis**	Libo
0.00		0.03	√	*Listera borealis*	Lisbor
0.70		0.88		*Lonicera dioica**	Lodi
0.95		1.00		*Lonicera involucrata**	Loin
0.18		0.15		*Lycopodium annotinum*	Lyan
0.03		0.03		*Lycopodium complanatum*	Lyco
0.03	√	0.00		*Lycopodium obscurum*	Lyob
0.70		0.98		*Maianthemum canadense*	Maca
0.05		0.45		*Matteuccia struthiopteris*	Mast
0.00		0.08	√	*Mentha arvensis*	Mear
0.98		1.00		*Mertensia paniculata*	Mepa
0.95		0.98		*Mitella nuda*	Minu
0.15		0.08		*Moehringia lateriflora*	Mola
0.03		0.03		*Moneses uniflora*	Moun
0.03	√	0.00		*Oplopanax horridum*	Opho
0.05		0.08		*Orthilia secunda*	Orse
0.28		0.20		*Osmorhiza depauperata*	Osde
0.88		0.98		*Petasites palmatus*	Pepa
0.73		0.98		*Picea glauca*	Pigl
0.00		0.03	√	*Poa palustris*	Popa
0.18		0.10		*Poa pratensis*	Popr

Table 3.10. Continued

0.00		0.03	√	*Poa spp.*	Poa
0.75		0.83		*Populus balsamifera*	Poba
1.00		0.98		*Populus tremuloides*	Potr
0.00		0.05	√	*Potentilla norvegica*	Pono
0.18		0.10		*Prunus pensylvanica**	Prpe
0.05		0.05		*Prunus virginiana**	Prvi
0.80		0.93		*Pyrola asarifolia*	Pyas
0.05	√	0.00		*Pyrola chlorantha*	Pych
0.03	√	0.00		*Ribes americanum**	Riam
0.20		0.20		*Ribes glandulosum**	Rigl
0.20		0.40		*Ribes hudsonianum**	Rihu
0.73		0.73		*Ribes lacustre**	Rila
0.95		0.95		*Ribes oxycanthoides**	Riox
0.98		0.98		*Ribes triste**	Ritr
1.00		0.83		*Rosa acicularis**	Roas
0.60		0.73		*Rosa woodsii**	Rowo
0.83		0.90		*Rubus idaeus**	Ruid
1.00		1.00		*Rubus pubescens**	Rupu
0.08		0.18		*Salix discolor*	Sadi
0.65		0.95		*Salix spp.*	Salix
0.10		0.05		*Sanicula marilandica*	Sama
0.03		0.05		*Schizachne purpurascens*	Scpu
0.03		0.05		*Scutellaria galericulata*	Scga
0.03	√	0.00		*Senecio vulgaris*	Sevu
0.03		0.25		*Shepherdia canadensis**	Shca
0.13		0.10		*Smilacina racemosa*	Smra
0.20		0.20		*Smilacina stellata*	Smst
0.10		0.53		*Solidago canadensis*	Soca
0.00		0.03	√	*Sonchus arvensis*	Soar
0.28		0.08		*Sorbus scopulina**	Sosc
0.00		0.03	√	*Spiranthes romanzoffiana*	Spro
0.08		0.10		*Stellaria longifolia*	Stlo
0.00		0.05	√	*Stellaria longipes*	Stlong
0.00		0.03	√	*Stellaria media*	Stme
0.25		0.23		*Streptopus amplexifolius*	Stam
0.30		0.53		*Symphoricarpos albus**	Syal
0.05		0.00		*Tanacetum vulgare*	Tavu
0.13		0.33		*Taraxicum officinale*	Taof
0.00		0.05	√	*Thalictrum dasycarpum*	Thda
0.05		0.03		*Thalictrum venulosum*	Thve
0.03	√	0.00		*Tiarella trifoliata*	Titr
0.48		0.48		*Trientalis borealis*	Trbo

Table 3.10. Continued

0.03	0.05		*Trifolium spp.*	Trispp
0.13	0.13		*Urtica dioica*	Urdi
0.00	0.08	√	*Vaccinium myrtilloides**	Vamy
1.00	0.98		*Viburnum edule**	Vied
0.65	0.58		*Vicia americana*	Viam
0.28	0.25		*Viola canadensis*	Vica
0.13	0.15		*Viola nephrophylla*	Vine
0.98	0.93		*Viola renifolia*	Vire

Table 3.11. Results of nested GLM models for herbaceous, shrub and total vascular plant species richness in mid-successional (34 years post-disturbance) treatments. Degrees of freedom (*d.f.*), F-values (*F*) and probability of type I error rate (*P*) of each variable in the GLM model are presented. Data are pooled to the site level with both wildfire and salvage *n*=2 stands (with 40 sites total).

	Herb Species Richness			Shrub Species Richness			Total Species Richness		
	Model R^2=0.46			Model R^2=0.52			Model R^2=0.55		
Source	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*
Treatment	1	0.98	0.43	1	0.69	0.49	1	1.16	0.39
Stand(Treatment)	2	21.35	**<0.01**	2	30.07	**<0.01**	2	29.57	**<0.01**
Error	76			76			76		

Table 3.12. Summary of axes statistics for distance based Redundancy Analysis (db-RDA) of mid-successional understory plant communities. Eigenvalues representing % variance of Sørensen species matrix explained by each axes, trace (sum of all canonical eigenvalues) and correlations between PCoA axes and db-RDA axes are presented.

	db-RDA Axis 1*	db-RDA Axis 2	db-RDA Axis 3	db-RDA Axis 4	Trace**
Eigenvalue	0.12	0.05	0.04	0.02	0.24
PCoA axes-environment correlation	0.8	0.74	0.76	0.6	

*significant at *P*<0.01 with *F*=9.37 based on Monte Carlo permutation tests

**significant at *P*<0.01 with *F*=2.82

Table 3.13. Correlation coefficients of significant environmental variables with the first two principal coordinate (PCoA) axes in db-RDA of understory plant communities in mid-successional stands.

Environmental Variable	PCoA Axis 1	PCoA Axis 2
Litter cover	-0.51	-0.32
Conifer density	0.50	-0.21
Bryophyte covered non-woody substrate availability	0.40	-0.20
Soil moisture	-0.27	-0.36
Tall shrub density	0.35	-0.31
Organic soil depth	-0.21	-0.14
Density dead deciduous trees	0.18	-0.19
Site prepared forest floor	0.06	-0.10

Table 3.14. Results of Indicator Species Analysis for mid-successional (34 years post-disturbance) wildfire and salvage treatments. Average percent cover of indicator species, indicator values (*IV*) and probability of type I error rate (*P*) based on 10000 Monte Carlo permutations.

Treatment	Species	Mean Cover		IV	P
		Wildfire	Salvage		
Wildfire	*Rosa acicularis*	6.38	2.93	49.7	<0.01
	Epilobium angustifolium	1.73	0.31	49.4	<0.01
	Calamagrostis canadensis	1.08	0.50	48.4	<0.01
	Ribes oxycanthoides	2.28	0.49	33.0	<0.01
	Lichen species	0.68	0.08	14.3	<0.01
	Galium triflorum	0.78	0.42	37.7	0.01
	Vicia americana	0.26	0.02	12.5	0.02
	Disporum trachycarpum	0.16	0.00	6.7	0.02
	Cornus canadensis	5.69	3.50	46.5	0.03
	Mertensia paniculata	3.49	2.31	33.7	0.04
Salvage	*Amelanchier alnifolia*	0.00	1.59	29.2	<0.01
	Fragaria virginiana	0.29	0.77	24.8	<0.01
	Rosa woodsii	1.28	4.48	22.4	<0.01
	Maianthemum canadense	0.67	1.37	36.6	0.01
	Lonicera involucrata	5.61	9.14	37.8	0.03

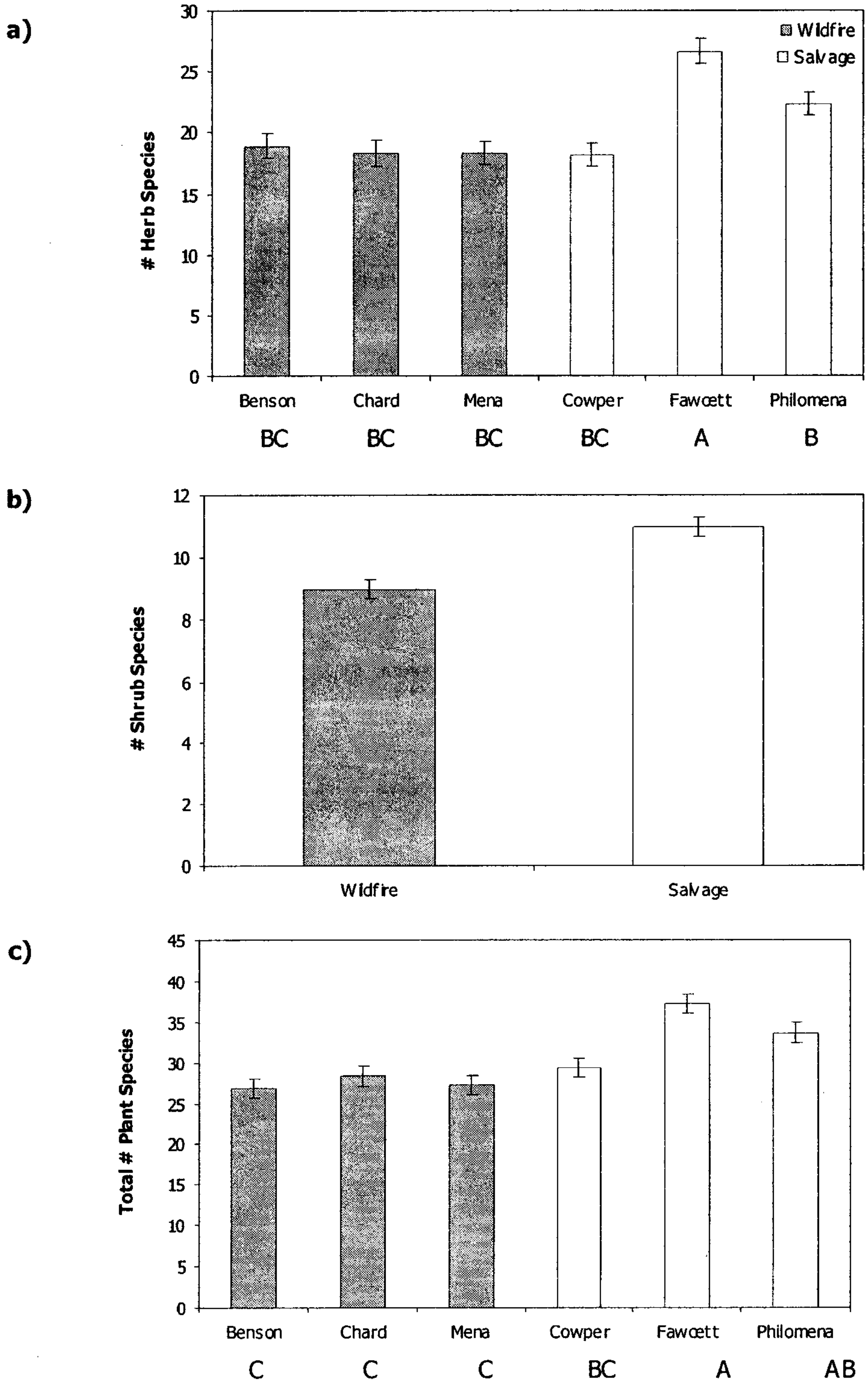

Figure 3.1. Mean (± 1 *S.E.*) herbaceous (a), shrub (b) and total (c) plant species richness per site in early post-disturbance treatment stands. Treatment effects for shrub species richness were significant at *P*=0.04. Significant differences (resulting from Tukey's HSD tests) between stands for herb and total species richness (adjusted for treatment and stand level effects) are indicated by different letters. All stands *n*=15 sites, except Chard *n*=13 sites.

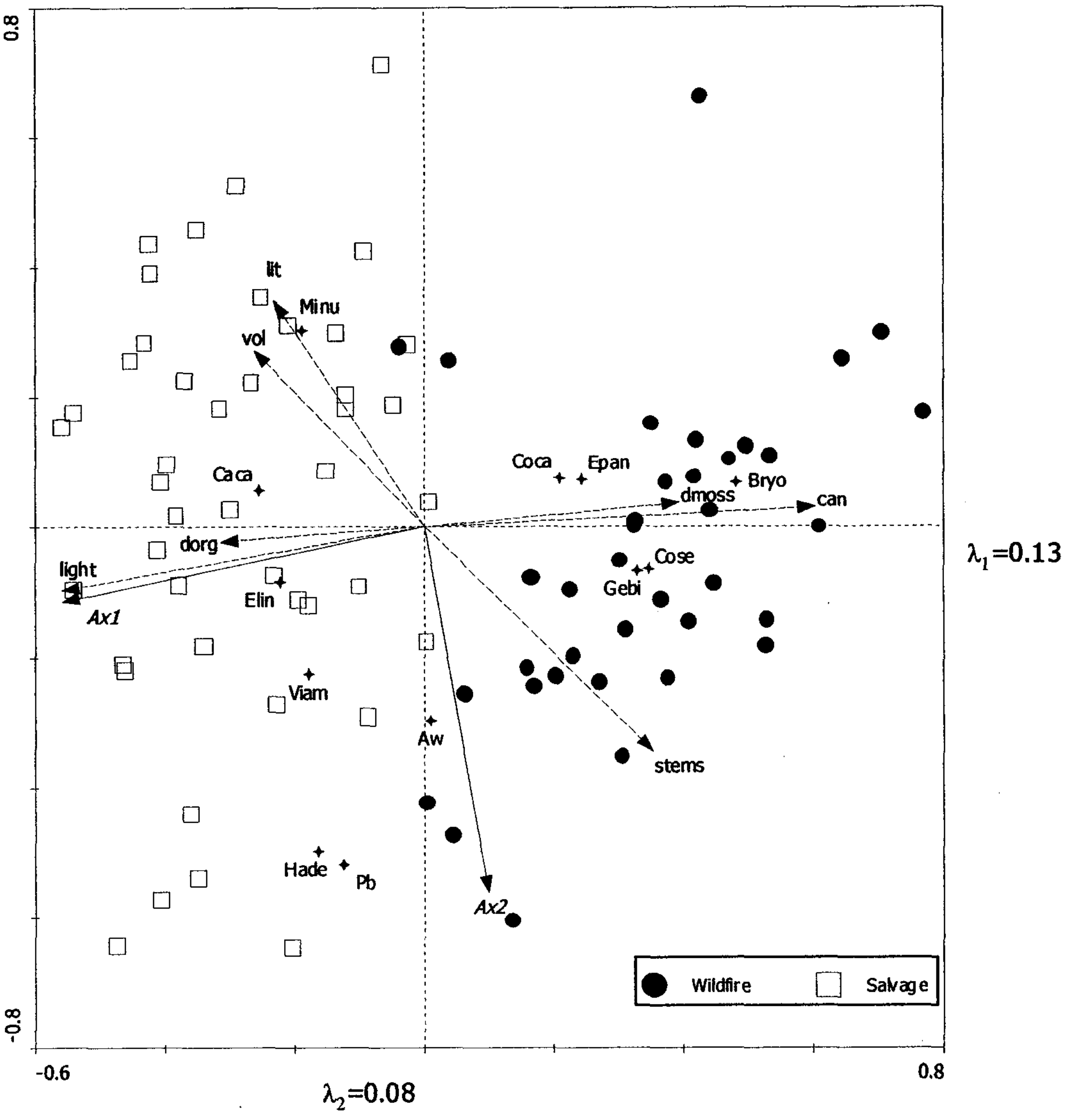

Figure 3.2 db-RDA ordination of early successional wildfire and salvage sites in sample space constrained by environmental variables explaining significant variation in Sørensen distances of understory species data. Sites are represented by symbols coded by treatment. Centroids of plant species with greater than 30% correlation with the ordination axes are represented by red star symbols and identified by the first two letters of the plant's genus and species names (refer to Table 3.3 for full names). Blue dashed radiating arrows indicate the relative strength and direction of correlation of environmental variables (refer to Table 3.1 for full names and variable descriptions, and Table 3.7 for correlation coefficients) with the ordination. Solid radiating arrows show axes derived from PCoA analysis of the species data which had greater than 55% of their variability explained by the first two db-RDA ordination axes. For interpretation purposes, the "species" and environmental scores are scaled respectively to 0.1 and 2x that of the sample scores.

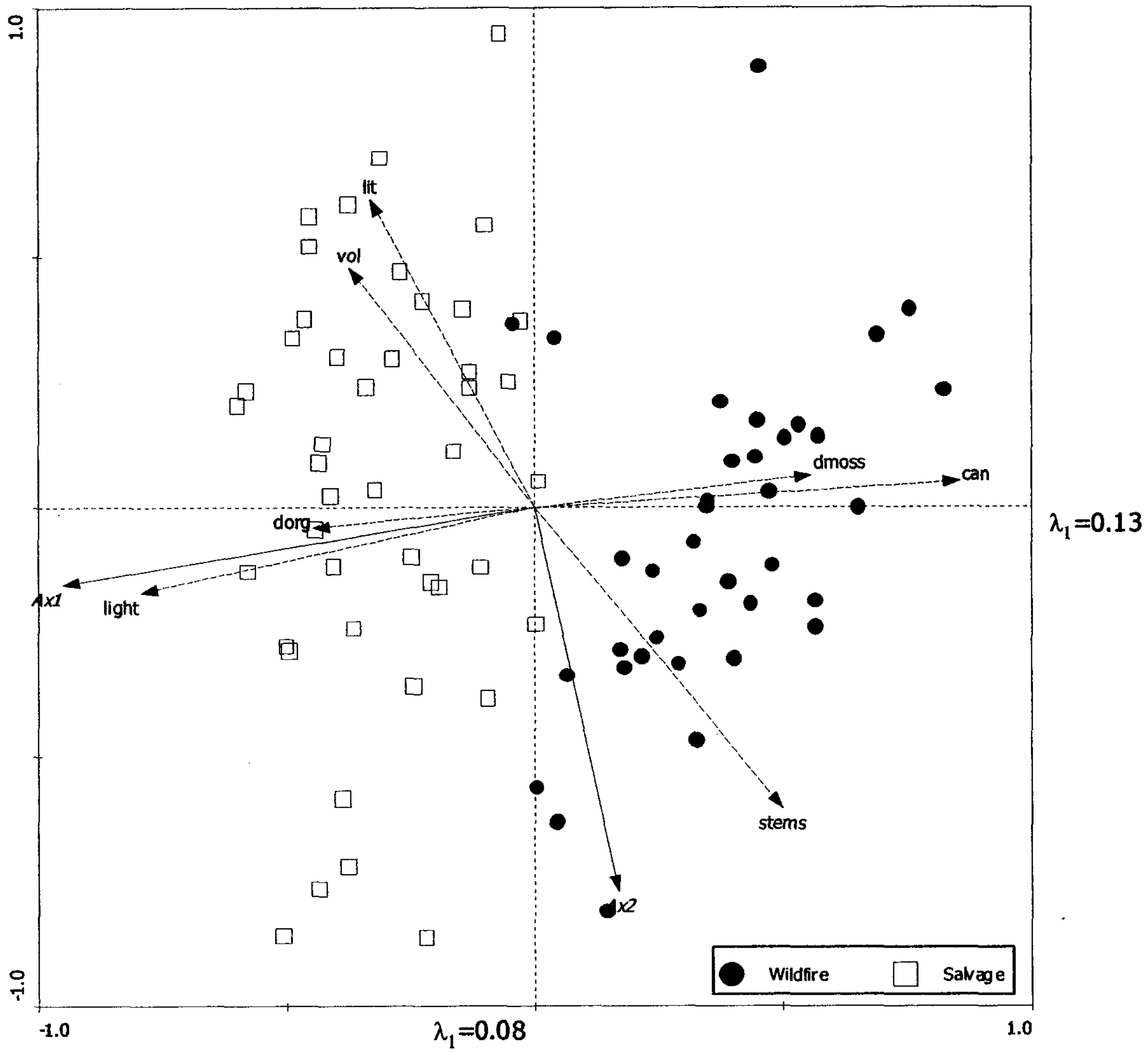

Figure 3.3. db-RDA ordination of early successional wildfire and salvage sites in species space constrained by environmental variables explaining significant variation in Sørensen distances of understory species data. Sites are represented by symbols coded by treatment. Blue dashed radiating arrows indicate the relative strength and direction of correlation of environmental variables (refer to Table 3.1 for full names and variable descriptions, and Table 3.7 for correlation coefficients) with the ordination. Solid radiating arrows show axes derived from PCoA analysis of the species data which had greater than 55% of their variability explained by the first two db-RDA ordination axes. For interpretation purposes, the "species" and sample scores are both scaled to 0.4x that of the environmental scores.

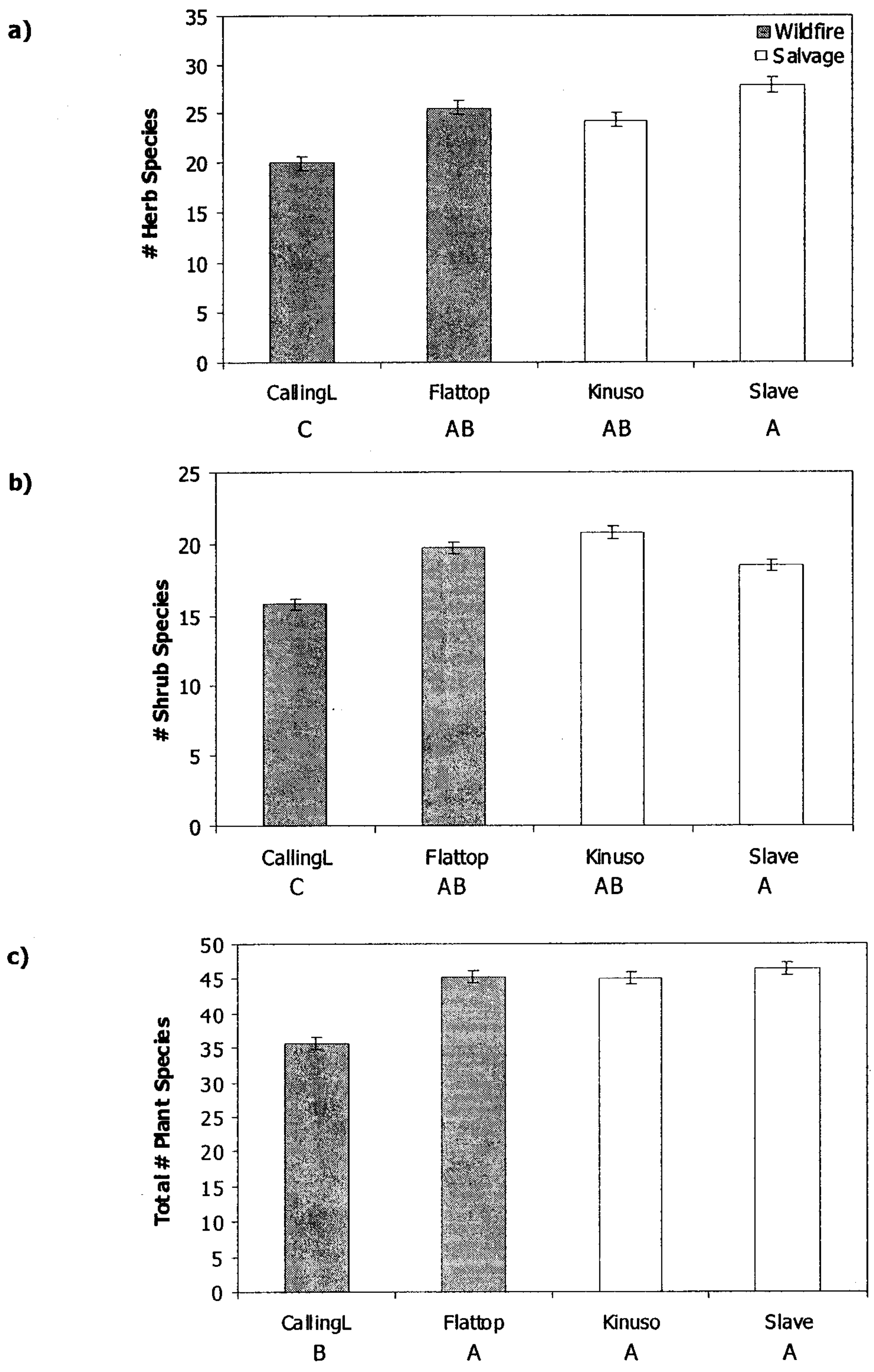

Figure 3.4. Mean (± 1 *S.E.*) herbaceous (a), shrub (b) and total (c) plant species richness per site in mid-successional (34 years post-disturbance) treatment stands. Stand level differences were significant at $P<0.01$ with differences (resulting from Tukey's HSD tests) (adjusted for treatment and stand level effects) indicated by different letters. All stands $n=20$ sites.

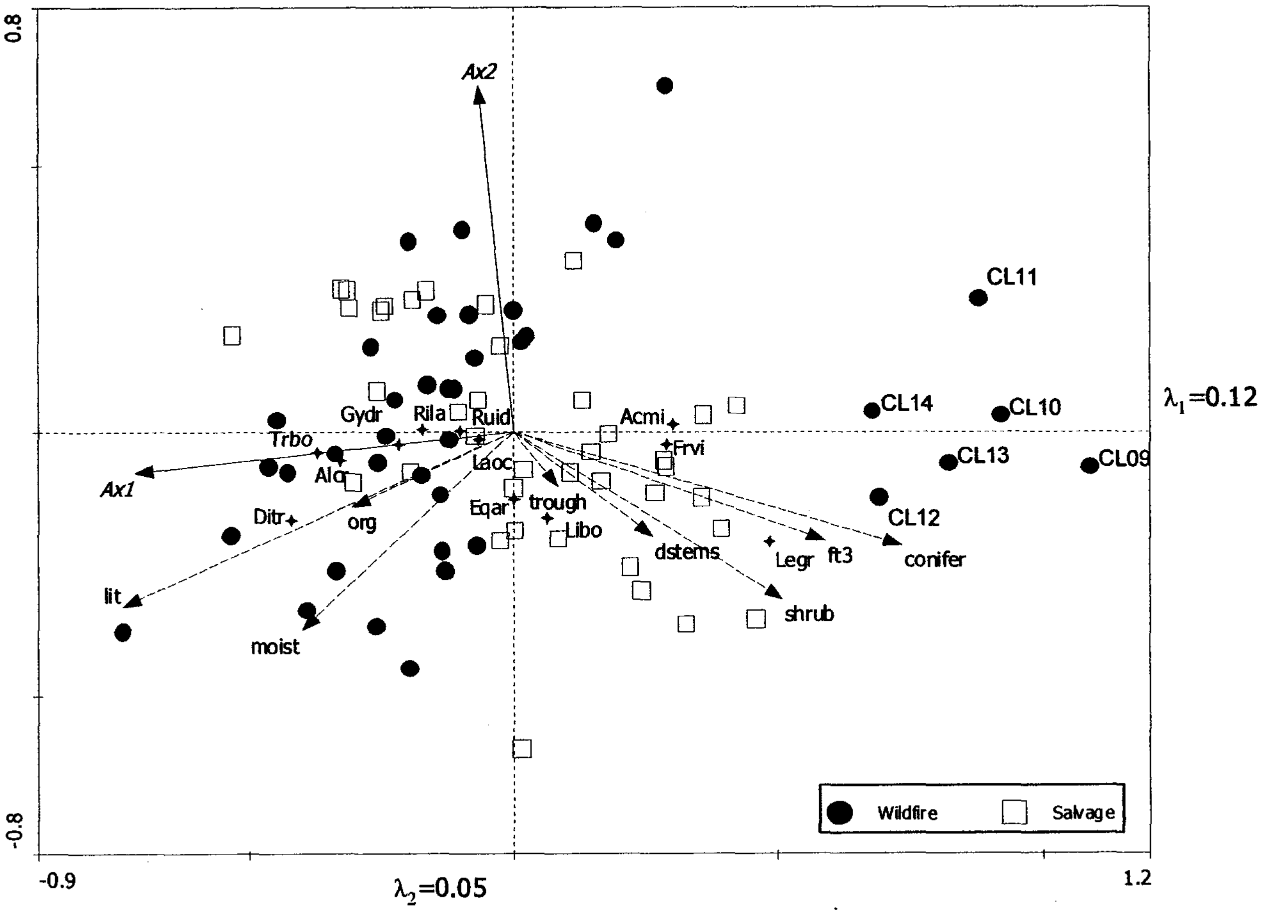

Figure 3.5 db-RDA ordination of mid-successional wildfire and salvage sites in sample space constrained by environmental variables explaining significant variation in Sørensen distances of understory species data. Sites are represented by symbols coded by treatment. Centroids of plant species with greater than 50% correlation with the ordination axes are represented by red star symbols and identified by the first two letters of the plant's genus and species names (refer to Table 3.10 for full names). Blue dashed radiating arrows indicate the relative strength and direction of correlation of environmental variables (refer to Table 3.1 for full names and variable descriptions and Table 3.13 for correlation coefficients) with the ordination. Solid radiating arrows show axes derived from PCoA analysis of the species data which had greater than 35% of their variability explained by the first two db-RDA ordination axes. For interpretation purposes, the "species" and environmental scores are scaled respectively to 0.1 and 3.4x that of the sample scores. Disjunct Calling Lake wildfire sites indicated by the CL9-14 identifier labels.

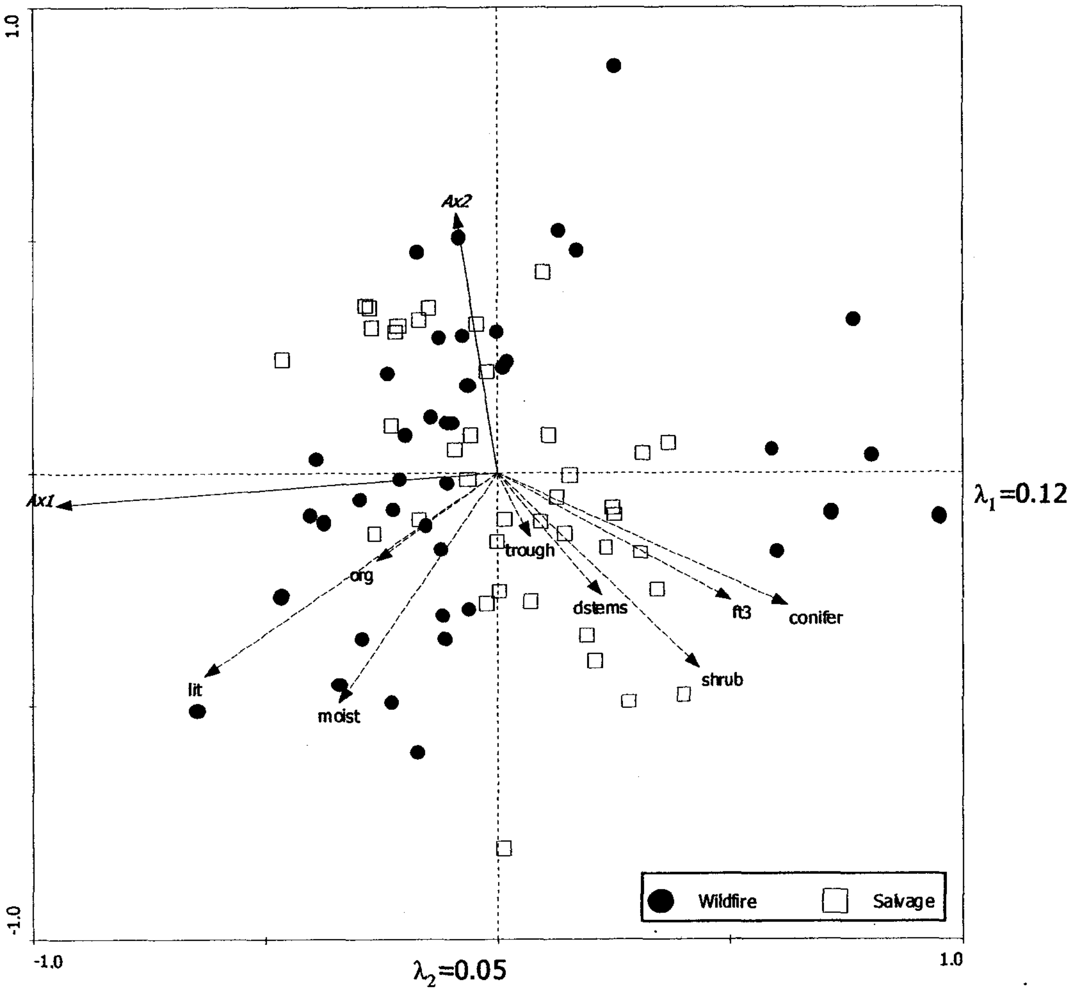

Figure 3.6. db-RDA ordination of mid-successional wildfire and salvage sites in species space constrained by environmental variables explaining significant variation in Sørensen distances of understory species data. Sites are represented by symbols coded by treatment. Blue dashed radiating arrows indicate the relative strength and direction of correlation of environmental variables (refer to Table 3.1 for full names and variable descriptions and Table 3.13 for correlation coefficients) with the ordination. Solid radiating arrows show axes derived from PCoA analysis of the species data which had greater than 35% of their variability explained by the first two db-RDA ordination axes. For interpretation purposes, the "species" and sample scores are scaled respectively to 0.4 and 0.3x that of the environmental scores.

CHAPTER 4

GENERAL CONCLUSIONS AND MANAGEMENT IMPLICATIONS OF RESEARCH

SUMMARY AND CONCLUSIONS

Results of this research demonstrated that post-fire salvage logging significantly impacts tree regeneration and plant community composition in burned, aspen dominated mixedwood forest stands, and suggests that modifications occurring at the time of disturbance may continue to manifest themselves over time as altered successional forest development. Results from early post-disturbance stands indicate that salvage logging can result in poorer initial regeneration of deciduous trees (in terms of both density and height) in burned mixedwood forest stands. It is likely that changes to the initial post-disturbance forest environment arising from salvage logging operations, in combination with this reduced initial tree recruitment, will influence the future successional development of these stands through modified rates of tree growth and mortality, and associated changes to the understory environment and plant community. Future impacts of post-fire salvage logging, as currently practiced, on burned mixedwood stands may not be analogous to those observed in the older mid-successional stands studied here because of differences in harvesting techniques and the confounding effect of silvicultural treatments in these stands. Nonetheless, results from these mid-successional stands provide evidence that management activities occurring immediately post-fire will continue to influence the development of those stands into later stages of forest succession. Thus, in spite of the high degree of variability in sampled mid-successional stands, some aspects of salvaged stands remained divergent from those of undisturbed wildfire stands up to 34 years following the initial disturbance event(s). Specific results from this research are summarized below.

Unsurprisingly, salvage logging resulted in a number of changes to the structure of recently burned mixedwood forest stands which were contributing factors to the differences in tree regeneration and plant communities of these stands. The most notable change in forest structure was that of a drastic decline in the density of residual live and dead trees in salvaged stands compared with that of unmanaged wildfire stands. This removal of the remaining forest canopy and standing dead trees resulted in significantly higher light levels than that in recently burned stands and likely contributed to the higher air temperature and lower relative humidity of salvage logged environments. Logging slash created as a result of salvaging operations resulted in higher volumes of DWM in early successional salvaged stands that were not apparent in wildfire stands where the majority of the dead wood remained standing at the time of sampling. Mid-successional salvaged stands were characterized by nearly half the snag density and lower amounts of DWM than that of wildfire stands. By this point in time, more than 34 years following the initial disturbance(s) in these stands, the majority of snags in the mid-successional wildfire stands had fallen down, and the deficit in DWM in salvaged stands arising from salvage logging activities had become apparent.

Regeneration of deciduous trees within the immediate post-disturbance time period was significantly better in wildfire stands than in those that had been salvage logged. Regeneration density in recently burned wildfire stands was nearly double that of salvaged stands, and saplings regenerating in wildfire stands were substantially taller than their counterparts in salvaged stands. Evidence of a similar regeneration response persisting in the density or height of post-disturbance origin deciduous trees 34 years following the combined disturbance of post-fire salvage logging and site preparation was not evident in this study. However, mid-successional salvaged stands had substantial conifer regeneration that was most likely attributable to the silvicultural techniques (straight blade scarification and aerial seeding of white spruce) applied post-salvage to these stands. Mid-successional salvaged stands were also characterized by double the density of tall shrubs than that of wildfire stands.

Early post-disturbance plant communities in salvaged stands were characterized by the presence of introduced weedy species, greater species turnover (beta diversity between sites within stands) and higher shrub species richness than the plant communities of unsalvaged wildfire stands. The most pronounced differences between the plant communities of salvage logged and wildfire stands however, were related to the species composition of the understory plant community. In particular, salvage logged stands had higher abundances of grasses and shrubs, and lower abundances of post-fire specialist species compared to wildfire stands. The understory plant communities of mid-successional wildfire and salvage logged stands were fairly similar. However, there were several important differences between post-disturbance plant communities that suggest that salvage logged and undisturbed wildfire stands may not follow the same successional trajectory. The composition of plant communities associated with mid-successional salvaged stands appeared to be influnced by the high density of tall shrubs and understory white spruce arising from the silvicultural techniques employed in these stands. These stands were characterized by a higher number of shrub species and more shade tolerant, interior forest herbaceous species than unsalvaged wildfire stands.

MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

In spite of the recent focus of forest managers on modeling harvest practices on natural disturbance regimes (Franklin 1993, Hunter 1993, DeLong & Tanner 1996), harvesting does not produce stands analogous to those created immediately following wildfire (Carleton & MacLellan 1994, Hobson & Shieck 1999, Lee 1999). Thus far, the presence of early successional post-fire stands on the boreal landscape has been maintained largely due to the periodic occurrence of very large scale wildfires. While salvage logging of merchantable, burned stands has become very common over the past decade, salvaging operations have been primarily restricted to those stands that are readily accessible. It is likely however, that with increased industrial development, the boreal forest will become increasingly accessible, resulting in widespread salvage logging of burned, commercially valuable forests wherever they occur on the landscape.

My results have demonstrated that salvage logging significantly alters early post-fire plant communities and negatively impacts the ability of deciduous tree species to regenerate. It is likely that these modifications arising from salvage logging in the immediate post-disturbance time period will influence future forest development and therefore, the timber and habitat value, biodiversity, and overall ecological function of these stands relative to unsalvaged, wildfire origin forests. A growing body of other research in the boreal forest also suggests that post-fire salvage logging significantly reduces the ecological function of recently burned forests for communities of various taxa (Cobb 2001, Morissette et al. 2002, Stambaugh 2003, Stepnisky 2003). In other boreal forest ecosystems where multiple harvest rotations and fire suppression have eliminated wildfire origin stands from the landscape, the end result has been an impairment of ecological function (Turner et al. 1998) in these forests along with a loss of biodiversity in general and the loss of fire dependent species in particular (Berg et al. 1994, Ostlund et al. 1997). Post-fire salvage logging is therefore a forest management practice of significant ecological concern, requiring well defined, comprehensive management directives.

Salvage logging is a relatively new forest management practice in Alberta, and the associated provincial policy framework (Sustainable Resource Development 2002) governing it is correspondingly vague with regard to the operational implementation of objectives related to identified non-timber values (for example tree retention, maintenance of biodiversity, watershed and soil protection, access management etc.). As such, there is still a great potential for improvement in the manner in which recently burned forests are managed in this province. Accordingly, I have identified what I consider to be the most significant management recommendation arising from the results of this research.

- Recently burned, merchantable forest stands have substantial ecological value (in particular with regard to post-fire specialist plant species) and this needs to be recognized by forest managers in salvage harvesting plans. Therefore, within recent wildfires, some merchantable burned stands should be protected from salvage logging entirely. The question of what proportion of burned forest to leave on the landscape was not addressed by this study and should be the subject of future research (see future research suggestions below).

I have a further suggestion regarding post-fire salvage logging practices, that while not directly derived or supported from the results from this thesis, I nonetheless believe to follow logically from my results regarding the impacts of salvage logging on deciduous tree regeneration.

- Currently, salvage logging of very large fires may commence immediately following wildfire suppression and extend for up to two years in order that the maximum volume of fire-damaged timber is salvaged before it degrades beyond the point of commercial usefulness. As a result, salvage logging may frequently occur on unfrozen soils and in burned stands supporting well established deciduous suckers. Therefore, in salvaged blocks where the composition of the desired future stand is deciduous dominated, I would suggest that salvage logging should occur only on frozen soils with adequate snow to protect advanced regeneration as much as possible.

FUTURE RESEARCH

This study represents one of the first attempts to document the impact of post-fire salvage logging on the plant communities of mixedwood boreal forest stands (also see Crites & Hanus 2001). Like most preliminary studies, it raises a number of further questions that need to be addressed in future research relating to the sustainable management of post-fire stands and their associated communities.

The most significant question raised by this study is that of the amount of burned forest required to maintain viable populations of post-fire specialist plant species at a landscape level on a landbase actively managed for timber production. There are numerous inadequacies in our current knowledge of boreal forest ecosystems relating to this question, not the least of which is the lack of baseline information on the natural range of variability in the relative abundance of recently burned, merchantable forest stands in the boreal forest. It is difficult to make scientifically justifiable management recommendations regarding the retention of burned forests without having first identified the level at which these stands naturally occur in the boreal forest and the rate at which they are being salvage logged. Therefore, I suggest that greater effort be made to monitor the amount of unsalvaged, merchantable forests retained at a landscape level to determine if these unmanaged, early post-fire forests and their associated communities are indeed potentially at risk. Another unknown factor relating to this question involves the lack of reliable knowledge on the population dynamics (including such characteristics as seed production, long term seed viability, dispersal ability etc.) of identified fire dependent species. Long term seed viability for example, in conjunction with the reduced relative abundances (and presumably seed set) resulting from the secondary disturbance of these communities by salvage logging operations, would certainly have a bearing on the persistence of these species through multiple rotations of forest harvesting. The maintenance of variable amounts of burned trees at the stand level may allow for the maintenance of these distinctive early post-fire plant communities. However, the identification of thresholds for the persistence of these communities in response to variable intensities of salvage logging at a landscape scale has yet to be addressed by future research.

Salvage logging as currently practiced, typically focuses on merchantable forest stands, leaving behind the young, burned stands of low commercial value. It is likely that the soil seedbanks of these younger forest stands are comparable to those of merchantable stands in terms of their species composition. Therefore, the retention of these unmerchantable, burned stands in the place of merchantable burned forest stands, may act to off-set the negative ecological ramifications of salvage logging on the long-term persistence of early post-fire plant communities. Again however, this conjecture has not been tested and needs to be addressed with further study.

As a result of stand selection criteria, this study was not able to evaluate the influence of post-fire salvage logging on the recruitment of conifer species, most notably white spruce. With the majority of viable seed produced by the most economically valuable trees, it is likely that the removal of these seed trees over the course of salvage logging operations could potentially have a significantly negative impact on the natural recruitment of white spruce in salvage logged, burned areas. Alternately, the likely availability of suitable mineral regeneration microsites in burned, salvaged stands may mean that salvage logged stands may be good candidates for mixedwood management strategies.

Current management guidelines regarding residual retention in salvaged stands appear to preferentially emphasize the retention of live tree patches over that of fire-killed patches or snags. It is likely that live deciduous residuals retained preferentially over snags in salvaged cutblocks may reduce tree regeneration through the maintenance of apical dominance. It is also likely that patch retention of fire-killed residuals related to partial salvage logging of burned stands may influence deciduous regeneration through modifications to the microclimatic environment of these stands. These influences could potentially be of significant management concern and are therefore worthy of future research.

LITERATURE CITED

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M. & Weslien, J. 1994. Threatened plant, animal and fungus species in Swedish forests: Distribution and habitat associations. Conservation Biology **8**:718-731.

Carleton, T.J. & MacLellan, P. 1994. Woody vegetation responses to fire versus clear-cutting logging: A comparative survey in the central Canadian boreal forest. Ecoscience **1**:141-152.

Cobb, T. 2001. Disturbance and ecological stability of boreal forest beetle assemblages. MSc. thesis, University of Regina, Saskatchewan.

Crites, S. & Hanus, S. 2001. Succession of herbaceous, shrub and tree communities following combined treatments of fire and harvesting. Final report, Alberta Research Council, Vegreville.

DeLong, S.C. & Tanner, D. 1996. Managing the pattern of forest harvest: lessons from wildfire. Biodiversity and Conservation **5**:1191-1205.

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems or landscapes? Ecological Applications **3**:202-205.

Fraser, E., Landhäusser, S. & Lieffers, V. In Press. The effect of fire severity and salvage logging traffic on regeneration and early growth of aspen suckers. Forestry Chronicle.

Hobson, K. & Shieck, J. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over thirty years. Ecological Applications **9**:849-863.

Hunter, M.L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation **65**:115-120.

Lee, P.C. (Ed.). 1999. Fire and harvest residual (FAHR) project: the impact of wildfire and harvest residuals on forest structure and biodiversity in aspen-dominated boreal forests of Alberta. Publication Number T/495. Alberta Research Council, Vegreville.

Morissette, J.L., Cobb, T.P., Brigham, R.M. & James, P.C. 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Canadian Journal of Forest Research **32**:2169-2183.

Ostlund, L., Zackrisson, O. & Axelsson, A. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Canadian Journal of Forest Research **27**:1198-1206.

Stambaugh, C.A. 2003. Community-level response of birds to burned and salvage-logged forests. MSc. thesis, University of Alberta.

Stepnisky, D.P. 2003. Response of *Picoides* woodpeckers to salvage harvesting of burned, mixedwood boreal forest: exploration of pattern and process. MSc. thesis, University of Alberta.

Sustainable Resource Development. 2002. 2002 Fires: Fire salvage strategy framework. Forest management planning and operations: Directives & guidelines for fire salvage allocation, planning & operations, annual allowable cuts, reforestation and production control. Forest Operations Branch, Lands & Forest Division, Government of Alberta.

Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems **1**:511-523.

Appendix 3.1. List of all vascular plant species recorded in both early (2 years post-disturbance) and mid (34 years post-disturbance) successional wildfire and salvage logged mixedwood stands. Nomenclature follows Moss (1983).

LYCOPODIACEAE /Club-moss Family

Lycopodium annotinum (L.)	Stiff Club-moss
Lycopodium complanatum (L.)	Ground Cedar
Lycopodium obscurum (L.)	Ground Pine

EQUISETACEAE /Horsetail Family

Equisetum arvense (L.)	Common Horsetail
Equisetum pratense (Ehrh.)	Meadow Horsetail
Equisetum sylvaticum (L.)	Woodland Horsetail

OPHIOGLOSSACEAE /Adder's-tongue Family

Botrychium lunaria (L.) Sw.	Moonwort
Botrychium virginianum (L.) Sw.	Grape Fern

POLYPODIACEAE /Fern Family

Dryopteris carthusiana (Vill.) H.P. Fuchs	Narrow Spinulose Shield Fern
Gymnocarpium dryopteris (L.) Newm.	Oak Fern
Matteuccia struthiopteris (L.) Todaro	Ostrich Fern

PINACEAE /Pine Family

Abies balsamea (L.) Mill.	Balsam Fir
Picea glauca (Moench) Voss	White Spruce
Pinus banksiana Lamb.	Jack Pine

GRAMINEAE /Grass Family

Agropyron repens (L.) Beauv.	Quack Grass
Agropyron trachycaulum (Link.) Malte	Slender Wheatgrass
Agropyron spp.	
Agrostis scabra Willd.	Tickle Grass
Bromus ciliatus L.	Fringed Brome
Bromus inermis Leyss.	Smooth Brome
Calamagrostis canadensis (Michx.) Beauv.	Marsh Reed Grass
Calamagrostis inexpansa A. Gray	Northern Reed Grass
Elymus innovatus Beal	Hairy Wild Rye
Hordeum jubatum L.	Foxtail Barley
Poa palustris L.	Fowl Bluegrass
Poa pratensis L.	Kentucky Bluegrass
Poa spp.	
Schizachne purpurascens (Torr.) Swallen	False Melic

CYPERACEAE /Sedge Family

Carex aurea Nutt.	
Carex siccata Dewey	
Carex spp.	

LILIACEAE /Lily Family

Disporum trachycarpum (S. Wats.) B. & H.	Fairy-bells
Lilium philadelphicum L.	Western Wood Lily

Maianthemum canadense Desf.	Wild Lily-of-the-valley
Smilacina racemosa (L.) Desf.	False Solomon's-seal
Smilacina stellata (L.) Desf.	Star-flowered Solomon's-seal
Streptopus amplexifolius (L.) DC.	Twisted-stalk
ORCHIDACEAE /Orchid Family	
Corallarhiza maculata Raf.	Spotted Coral-root
Corallarhiza trifida Chatelain	Pale Coral-root
Habenaria orbiculata (Pursh) Torr.	Round-leaved Orchid
Listera borealis Morong	Northern Twayblade
Spiranthes romanzoffiana Cham. & Schlecht.	Ladies'-tresses
SALICACEAE /Willow Family	
Populus balsamifera L.	Balsam Poplar
Populus tremuloides Michx.	Trembling Aspen
Salix discolor Muhl.	
Salix spp.	
BETULACEAE /Birch Family	
Alnus crispa (Ait.) Pursh	Green Alder
Betula glandulosa Michx.	Bog Birch
Betula papyrifera Marsh.	Paper Birch
Corylus cornuta Marsh.	Beaked Hazelnut
URTICACEAE	
Urtica dioica L.	Common Nettle
CHENOPODIACEAE /Goosefoot Family	
Chenopodium capitatum (L.) Aschers.	Strawberry Blite
CARYOPHYLLACEAE /Pink Family	
Moehringia lateriflora (L.) Fenzl.	Blunt-leaved Sandwort
Stellaria longifolia Muhl.	Long-leaved Chickweed
Stellaria longipes Goldie	Long-stalked Chickweed
Stellaria media (L.) Cyrill.	Common Chickweed
RANUNCULACEAE /Crowfoot Family	
Actaea rubra (Ait.) Willd.	Red and White Baneberry
Anemone canadensis L.	Canada Anemone
Caltha palustris L.	Marsh Marigold
Clematis occidentalis (Hornem.) DC.	Purple Clematis
Coptis trifolia (L.) Salisb.	Goldthread
Delphinium glaucum S. Wats.	Tall Larkspur
Ranunculus acris L.	Tall Buttercup
Thalictrum venulosum Trel.	Veiny Meadow Rue
Thalictrum dasycarpum Fisch. & Ave-Lall	Tall Meadow Rue
FUMARIACEAE /Fumitory Family	
Corydalis aurea Willd.	Golden Corydalis
Corydalis sempervirens (L.) Pers.	Pink Corydalis

SAXIFRAGACEAE /Saxifrage Family

Chrysosplenium tetrandrum (Lund) T. Fries	Green Saxifrage
Mitella nuda L.	Bishop's-cap
Tiarella trifoliata L.	False Mitrewort

PARNASSIACEAE /Grass-of-Parnassus Family

Parnassia palustris L.	Northern Grass-of-Parnassus

GROSSULARIACEAE /Current or Gooseberry Family

Ribes americanum Mill.	Wild Black Current
Ribes glandulosum Grauer	Skunk Current
Ribes hudsonianum Richards.	Wild Black Current
Ribes lacustre (Pers.) Poir.	Bristly Black Current
Ribes oxycanthoides L.	Wild Gooseberry
Ribes triste Pall.	Wild Red Current

ROSACEAE /Rose Family

Amelanchier alnifolia Nutt.	Saskatoon
Fragaria vesca L.	Woodland Strawberry
Fragaria virginiana Duchesne	Wild Strawberry
Geum aleppicum Jacq.	Yellow Avens
Geum macrophyllum Willd.	Yellow Avens
Potentilla gracilis Dougl. *ex* Hook.	Graceful Cinquefoil
Potentilla norvegica L.	Rough Cinquefoil
Potentilla tridentata Ait.	Three-toothed Cinquefoil
Prunus pensylvanica L.f.	Pin Cherry
Prunus virginiana L.	Choke Cherry
Rosa acicularis Lindl.	Prickly Rose
Rosa woodsii Lindl.	Common Wild Rose
Rubus idaeus L.	Wild Red Raspberry
Rubus pubescens Raf.	Running Raspberry
Sorbus scopulina Greene	Western Mountain-Ash

LEGUMINOSAE /Pea Family

Astragalus americanus (Hook.) M.E. Jones	
Lathyrus ochroleucus Hook.	Cream-coloured Pea Vine
Lathyrus venosus Muhl.	Purple Pea Vine
Trifolium spp.	
Vicia americana Muhl.	Wild Vetch

GERANIACEAE /Geranium Family

Geranium bicknelli Britt.	Bicknell's Geranium

VIOLACEAE /Violet Family

Viola adunca J.E. Smith	Early-blue Violet
Viola canadensis L.	Western Canada Violet
Viola nephrophylla Greene	Bog Violet
Viola renifolia A. Gray	Kidney-leaved Violet

ELAEAGNACEAE /Oleaster Family

Shepherdia canadensis (L.) Nutt.	Canadian Buffalo-berry

ONAGRACEAE /Evening Primrose Family

Circaea alpina L.	Enchanter's Nightshade
Epilobium angustifolium L.	Fireweed
Epilobium ciliatum Raf.	Purple-leaved Willowherb

ARALIACEAE /Ginseng Family

Aralia nudicaulis L.	Wild Sarsasparilla
Oplopanax horridum (Sm.) Miq.	Devil's-club

UMBELLIFERAE /Carrot Family

Heracleum lanatum Michx.	Cow Parsnip
Osmorhiza depauperata Philippi	Spreading Sweet Cicely
Sanicula marilandica L.	Snake-root

CORNACEAE /Dogwood Family

Cornus canadensis L.	Bunchberry
Cornus stolonifera Michx.	Red-osier Dogwood

PYROLACEAE /Wintergreen Family

Moneses uniflora (L.) A. Gray	One-flowered Wintergreen
Orthilia secunda (L.) House	One-sided Wintergreen
Pyrola asarifolia Michx.	Common Pink Wintergreen
Pyrola chlorantha Sw.	Greenish-flowered wintergreen

ERICACEAE /Heath Family

Arctostaphylos uva-ursi (L.) Spreng.	Common Bearberry
Ledum groenlandicum Oeder	Common Labrador Tea
Vaccinium caespitosum Michx.	Dwarf Bilberry
Vaccinium myrtilloides Michx.	Blueberry
Vaccinium vitis-idaea L.	Bog Cranberry

PRIMULACEAE /Primrose Family

Androsace septentrionalis L.	Fairy Candelabra
Trientalis borealis Raf.	Northern Star-flower

GENTIANACEAE /Gentian Family

Gentianella amarella (L.) Borner	Felwort
Halenia deflexa (Sm.) Griseb.	Spurred Gentian

BORAGINACEAE /Borage Family

Mertensia paniculata (Ait.) G. Don.	Tall Mertensia

LAMIACEAE /Mint Family

Dracocephalum parviflorum Nutt.	American Dragonhead
Galeopsis tetrahit L.	Hemp Nettle
Mentha arvensis L.	Wild Mint
Scutellaria galericulata L.	Skullcap

SCROPHULARIACEAE /Figwort Family

Castilleja miniata Dougl. *ex* Hook.	Common Red Paint-brush
Melampyrum lineare Desr.	Cow-wheat
Pedicularis labradorica Wirsing	
Rhinanthus minor L.	Yellow Rattle

PLANTAGINACEAE /Plantain Family

Plantago major L.	Common Plantain

RUBIACEAE /Madder Family

Galium boreale L.	Northern Bedstraw
Galium triflorum Michx.	Sweet-scented Bedstraw

CAPRIFOLIACEAE /Honeysuckle Family

Linnaea borealis L.	Twin-flower
Lonicera caerulea L.	Fly Honeysuckle
Lonicera dioica L.	Twinning Honeysuckle
Lonicera involucrata (Richards.) Banks	Bracted Honeysuckle
Symphoricarpos albus (L.) Blake	Snowberry
Symphoricarpos occidentalis Hook.	Buckbrush
Viburnum edule (Michx.) Raf.	Low-bush Cranberry

CAMPANULACEAE /Bluebell Family

Campanula rotundifolia L.	Harebell

COMPOSITAE /Composite Family

Achillea millefolium L.	Common Yarrow
Achillea sibirica Ledeb.	Many-flowered Yarrow
Arnica chamissonis Less.	Leafy Arnica
Arnica cordifolia Hook.	Heart-leaved Arnica
Aster ciliolatus Lindl.	Lindley's Aster
Aster conspicuus Lindl.	Showy Aster
Aster puniceus L.	Purple-stemmed Aster
Aster spp.	
Cirsium arvense (L.) Scop.	Canada Thistle
Erigeron philadelphicus L.	
Hieracium umbellatum L.	Narrow-leaved Hawkweed
Petasites palmatus (Ait.) A. Gray.	Palmate-leaved Coltsfoot
Petasites sagittatus (Pursh) A. Gray	Arrow-leaved Coltsfoot
Senecio vulgaris L.	Common Groundsel
Solidago canadensis L.	Canada Goldenrod
Sonchus arvensis L.	Perennial Sow Thistle
Tanacetum vulgare L.	Common Tansy
Taraxacum officinale Weber	Common Dandelion

Appendix 3.2. Summary of physical characteristics and vascular plant communities of select regeneration microsites in early (2 years post-disturbance) and mid-successional (34 years post-disturbance) wildfire and salvage logged mixedwood forest stands.

OVERVIEW OF METHODS

Regeneration microsites sampled in this study included decayed logs ($\geq$ decay class 5), and patches of mineral and organic (litter plus LFH of $\geq$ 8 cm deep) soil substrates in early successional stands, and decayed logs ($\geq$ decay class 5), and soil substrates (includes silviculturally created microsites, i.e. areas showing evidence of scarification "troughs" or "piles", in salvaged stands) in mid-successional stands. A random stratified subsample of microsites identified within each 100 m^2 site were sampled using 20 x 20 cm plots. Sample size for each microsite type varied by site since availability of microsites were spatially variable, however, roughly 10 microsites per microsite type were sampled per stand.

Understory plant community data and associated microsite level environmental data were collected using 20 x 20 cm plots centered on each microsite. All vascular plants were identified to the species level and visual estimates of percent cover made for each species rooted in the microsite. Height and species of any regenerating tree saplings rooted in microsites were recorded. Average canopy closure, and depth and cover of moss and litter layers were evaluated for all microsites. Log hardness, decay class, size and burn condition, and total nitrogen, carbon and phosphorous were evaluated for all decayed log microsites. Measurements of soil compaction, moisture, and nutrient availability (NH_4, NO_3, PO_4, and total nitrogen and carbon) were taken for all soil microsites.

SUMMARY STATISTICS

Summary statistics are displayed below for decayed log and soil regeneration microsites for early (2 years post-disturbance) and mid (34 years post-disturbance) successional wildfire and salvaged stands. Values provided are means per 20 x 20 cm microsite plot $\pm$ 1 S.E. with the exception total species richness which is the total number of species per microsite type per stand. Dashes indicate missing data. For this summary, log microsites of different decay classes, and mineral and organic soil substrates were each pooled into a single decayed log and soil microsite class respectively.

Early Successional Stands

	Decayed Log Microsites					
		Wildfire			Salvage	
	Benson	Chard	Mena	Cowper	Fawcett	Philomena
Total species richness	17	27	15	31	25	19
Vascular plant cover (%)	32.1 ± 9.7	68.7 ± 6.5	31.4 ± 10.1	49.9 ± 4.9	40.0 ± 6.4	38.3 ± 6.7
Bryophyte cover	32.9 ± 6.0	37.0 ± 5.9	38.6 ± 18.8	33.1 ± 7.1	1.0 ± 0.0	20.5 ± 15.9
Species richness	3.2 ± 0.4	5.6 ± 0.3	4.4 ± 0.4	4.1 ± 0.3	5.3 ± 0.8	5.0 ± 0.8
Bryophyte depth (cm)	22.1 ± 3.5	22.8 ± 3.0	27.0 ± 4.7	9.4 ± 1.2	0.0 ± 0.0	8.1 ± 2.5
Litter depth	0.4 ± 0.1	0.3 ± 0.1	0.5 ± 0.3	0.4 ± 0.1	0.0 ± 0.0	1.4 ± 0.6
N (g cm^{-3}) x 10^{-4}	7.0 ± 0.8	6.8 ± 9.7	8.1 ± 1.2	7.6 ± 1.1	7.2 ± 0.7	9.3 ± 0.7
C (g cm^{-3}) x 10^{-4}	512.0 ± 13.1	835.4 ± 4.9	497.2 ± 12.0	520.8 ± 6.6	525.7 ± 5.1	512.0 ± 4.6
P (g cm^{-3}) x 10^{-4}	0.44 ± 0.04	2.51 ± 0.69	0.60 ± 0.09	0.51 ± 0.08	0.48 ± 0.05	0.62 ± 0.04

	Soil Microsites					
		Wildfire			Salvage	
	Benson	Chard	Mena	Cowper	Fawcett	Philomena
Total species richness	18	19	19	22	25	20
Vascular plant cover (%)	50.4 ± 12.3	66.7 ± 10.4	40.6 ± 9.9	49.3 ± 11.9	90.3 ± 13.8	50.1 ± 10.7
Bryophyte cover	25.6 ± 8.1	18.6 ± 6.1	31.7 ± 14.5	9.5 ± 3.0	24.7 ± 12.7	6.0 ± 2.1
Species richness	4.5 ± 0.7	5.0 ± 0.5	5.0 ± 0.6	4.8 ± 0.9	6.9 ± 0.7	4.6 ± 1.1
Bryophyte depth (cm)	0.6 ± 0.1	0.1 ± 0.11	0.7 ± 0.3	0.2 ± 0.1	0.06 ± 0.06	0.2 ± 0.1
Litter depth (cm)	0.6 ± 0.6	0.2 ± 0.11	0.9 ± 0.4	3.0 ± 0.7	1.2 ± 0.5	1.2 ± 0.5
Canopy closure (%)	17.8 ± 6.1	13.1 ± 5.3	19.5 ± 2.6	2.7 ± 1.9	3.1 ± 1.3	6.4 ± 2.0
Soil compaction (kg/cm^2)	1.1 ± 0.2	1.2 ± 0.2	1.7 ± 0.3	1.4 ± 0.3	2.1 ± 0.4	1.4 ± 0.1
NO_3 (ppm in soil)	-	1.2 ± 0.1	1.3 ± 0.2	1.5 ± 0.3	1.2 ± 0.1	1.1 ± 0.2
NH_4 (ppm in soil)	-	5.4 ± 0.9	5.9 ± 1.0	7.7 ± 1.7	9.7 ± 2.0	5.2 ± 0.8
% N	-	0.11 ± 0.03	0.09 ± 0.01	0.41 ± 0.17	0.25 ± 0.06	0.09 ± 0.01
% C	-	2.4 ± 0.6	1.7 ± 0.3	1.8 ± 1.8	4.4 ± 1.1	1.6 ± 0.3

Mid-Successional Stands

	Decayed Log Microsites			
	Wildfire		Salvage	
	Calling L	Flattop	Kinuso	Slave
Total species richness	30	27	30	26
Vascular plant cover (%)	69.6 ± 11.1	50.4 ± 6.9	56.8 ± 9.8	65.2 ± 9.1
Bryophyte cover	63.4 ± 6.9	60.4 ± 5.8	59 ± 4.5	52.3 ± 6.6
Species richness	6.4 ± 0.45	6.3 ± 0.38	6.0 ± 0.40	6.6 ± 0.54
Bryophyte depth (cm)	2.3 ± 0.3	3.8 ± 0.6	3.8 ± 0.6	2.3 ± 0.6
Litter depth	77.2 ± 1.3	83.1 ± 1.2	82.4 ± 1.3	83.9 ± 1.0
Canopy closure (%)	78.4 ± 2.0	81.9 ± 2.3	84.8 ± 1.0	84.6 ± 1.2
N (g cm^{-3}) x 10^{-4}	7.2 ± 1.0	7.6 ± 0.5	8.8 ± 1.3	10.2 ± 1.0
C (g cm^{-3}) x 10^{-4}	615.4 ± 52.8	536.9 ± 27.2	542.8 ± 39.8	541.62 ± 38.1
P (g cm^{-3}) x 10^{-4}	0.43 ± 0.06	0.46 ± 0.05	0.51 ± 0.07	0.55 ± 0.05

	Soil Microsites			
	Wildfire		Salvage	
	Calling L	Flattop	Kinuso	Slave
Total species richness	26	29	30	27
Vascular plant cover (%)	80.5 ± 11.9	81.8 ± 13.1	93.3 ± 9.2	105.3 ± 8.5
Bryophyte cover	5.8 ± 2.2	0.25 ± 0.1	5.3 ± 1.6	0.45 ± 0.3
Species richness	6.8 ± 0.35	7.8 ± 0.72	7.8 ± 0.51	6.4 ± 0.40
Bryophyte depth (cm)	1.1 ± 0.4	0.3 ± 0.2	0.64 ± 0.2	0.11 ± 0.1
Litter depth (cm)	14.9 ± 8.1	5.0 ± 0.7	3.9 ± 0.3	5.4 ± 0.5
Canopy closure (%)	77.5 ± 2.4	82.6 ± 2.5	84.6 ± 1.3	84.9 ± 1.4
Soil compaction (kg/cm^2)	1.3 ± 0.2	1.0 ± 0.1	2.0 ± 0.2	1.7 ± 0.2
Soil moisture (% volumetric water capacity)	9.8 ± 2.0	25.1 ± 4.0	16.5 ± 1.0	11.8 ± 0.8
NO$_3$ (ppm in soil)	6.2 ± 2.5	11.8 ± 7.6	2.4 ± 0.1	4.4 ± 1.2
NH$_4$ (ppm in soil)	21.9 ± 5.0	11.9 ± 2.5	11.6 ± 1.5	17.9 ± 5.5
% N	0.44 ± 0.08	0.26 ± 0.03	0.34 ± 0.09	0.44 ± 0.12
% C	6.7 ± 1.2	4.9 ± 0.8	6.04 ± 1.5	8.9 ± 2.6