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Topographic characteristics and plant community structure of fire residuals in Virginia Hills, Alberta

by

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Agnes Sze-Pui Wong

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
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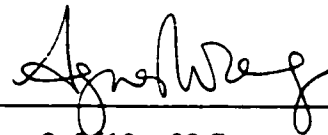
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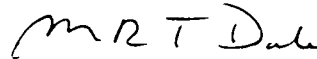
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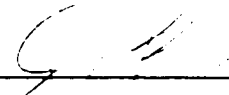
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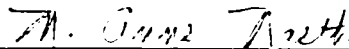
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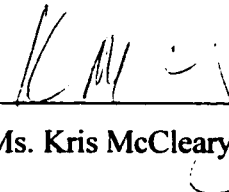
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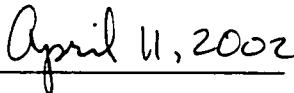
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ABSTRACT

In this thesis, I evaluated the characteristics of fire residuals, which are unburned islands within burned forest, from a 1998 fire in Virginia Hills, Alberta. My objectives were: 1) to determine whether residuals exhibit similar environmental and forest characteristics that contribute to residual formation and 2) to determine diversity of understory communities. Residuals contained significantly greater density of small-diameter black spruce, white spruce and larch than burned forest. Lower tree density in burned forest was not due to immolation. Ages of burned forest and residuals were not significantly different; however, burned forest was slightly older. Differences in environmental and forest characteristics were not due to burn condition but due to variability among site locations. Understory communities ranged from mesic woodlands to bogs. Residual formation was not influenced by topography but probably by tree species and general local moisture. Stochastic factors may have played a strong role in residual formation in this fire.

ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION

1.1 General Introduction

Natural wildfires play an important role in structuring forest stands and in maintaining habitat heterogeneity in the boreal forest (Heinselman 1971, Halpern and Spies 1995). Forest fires shape the boreal landscape by re-setting successional stages by decreasing dominant species, and competition for moisture, nutrients, heat and light. High intensity fires also provide suitable seedbeds for recolonization, triggering seed release from serotinous cones for stand regeneration and enhancing diversity of understory vascular plant species (Heinselman 1971).

Vegetation patterns on the boreal landscape are due to large, infrequent fires (Johnson 1992, Delong and Kessler 2000) resulting in a mosaic of differently aged forest stands (Heinselman 1971). Only a small proportion of fires that burn annually cause changes in the forest structure and composition (Kiil *et al.* 1986, Johnson 1992, Delong and Kessler 2000, Alberta Forest Protection 2001). In 1998, 64.2% of fires burned in Alberta were less than 1 hectare in size. Only 3.6% of fires exceeded an area of 500 hectares (Figure 1.1) but they accounted for 97.9% of total area burned (Alberta Forest Protection 2001). Similarly, Kiil *et al.* (1986) found less than 3% of fires in Alberta exceeded 200 hectares in size but accounted for 95% of annual area burned.

This study was conducted in Virginia Hills approximately 200 km north west of Edmonton, Alberta. In spring to late fall 1998, a fire burned through 163 138 ha of forest (Alberta Forest Protection 2001, Figure 2.2). The study area is classified as part of the Foothills natural region of Alberta (Kershaw *et al.* 2001). This area is composed of rolling topography and receives more precipitation than in the Boreal Forest Natural Region. Vegetation community types range from lodgepole pine forests with fire adapted understory in the upland to white spruce and aspen forests with a more diverse understory

in mesic sites to black spruce forests in muskegs and bogs (Kershaw *et al.* 2001, Beckingham *et al.* 1996).

1.2 Fire Residuals

Fires rarely kill all vegetation within their perimeters (Lyon *et al.* 1978), leaving a gradient of burn severity from severe to none, creating islands of unburned forest within the burned area (Foster *et al.* 1998, Turner *et al.* 1998). These islands are known as fire refugia, fire residuals, fire skips, or stringers (Quirk and Sykes 1971, Zackrisson 1977, Eberhart and Woodard 1987, Camp *et al.* 1997, Turner *et al.* 1998, Smyth 1999, Gandhi 1999, Bottorff 2001) and contain biological legacies (Franklin 1993, Foster *et al.* 1998, Hörnberg *et al.* 1998, Delong and Kessler 2000) such as old large diameter trees, snags and high amount of coarse woody debris (Franklin 1993, Delong and Kessler 2000). Although residuals have been acknowledged in earlier fire studies (Rowe and Scotter 1973, Heinselman 1971, Zackrisson 1977), there is a need for further research into their role in disturbed landscapes (Johnson 1992). Recently, research on residuals has gained popularity due to their ecological importance and incorporation into harvesting practices (Halpern and Spies 1995, Acker *et al.* 1998, Smyth 1999, Delong and Kessler 2000, Schieck and Hobson 2000, Bottorff 2001).

There are many factors that influence fire burning and residual formation. There are two types of factors that influence residual formation: stochastic and structural. Stochastic factors include local weather, temporal and seasonal effects. Structural factors are forest stand characteristics, spatial location, species composition, and topography.

Stochastic factors

Many studies suggest that climatic conditions, weather, duration of fire, seasonal and diurnal effects are the major fire controlling factors (Foster 1983, Eberhart and Woodard 1987, Turner and Romme 1994, Bessie and Johnson 1995, Delong and Kessler

2000). Several years of drought conditions and fuel accumulation can create ideal conditions for large-scale fire disturbances as demonstrated by the 1998 Yellowstone National Parks fires (Christensen *et al.* 1989). Meteorological conditions become increasingly important when fires burn for long duration due to exposure to daily variations in wind speed, wind direction and precipitation (Van Wagner 1983, Turner and Romme 1994). Eberhart and Woodard (1987) found a positive relationship between fire size and residual area. They suggest that as fire size increases, the probability of encountering natural fuel breaks also increases therefore creating greater number of residuals. Although meteorological conditions greatly influence fire behaviour (Bessie and Johnson 1995), a combination of structural and stochastic factors can contribute to residual formation.

Structural factors

Spatial location plays a major part in residual formation (Romme and Knight 1981, Romme 1982, Foster 1983, Bergeron and Brisson 1990, Bergeron 1991, Camp *et al.* 1997). Topography is a known factor in controlling fire behaviour (Quirk and Sykes 1971, Loope and Gruell 1973, Rowe and Scotter 1973, Zackrisson 1977, Romme and Knight 1981, Van Wagner 1983, Dansereau and Bergeron 1993, Takaoka and Sasa 1996, Ohlson *et al.* 1997, Taylor and Skinner 1998, Delong and Kessler 2000) due to its influence on moisture accumulation. Fires tend to burn uphill quickly because the head of the fire is near the ground layer, and pre-heating fuels. Moisture tends to accumulate in depressions or valleys and as a result, dampens ignition processes and slows fire spread (Samran *et al.* 1995, Whelan 1995).

Tree species composition is also known to have an effect on flammability due to differences in crown architecture (Smyth 1999). Coniferous trees can have long, dead lower branches which act like fuel ladders to promote crown fires while deciduous trees retain more moisture and have high crowns (Van Wagner 1983, Larsen 1997, Smyth 1999, Delong and Kessler 2000).

1.3 Importance of residuals

Residuals are important features in the boreal forest because they affect the early stages of succession (Turner *et al.* 1998) by functioning as a seed source for post-fire forest regeneration (Eberhart and Woodard 1987, Turner and Romme 1994, Asselin *et al.* 2001), influencing establishment rates of new colonizers, and producing propagules into disturbed areas (Alexander *et al.* 1983, Turner *et al.* 1998). Residuals also act as refugia for species diversity (Thomas *et al.* 1976, Halpern and Spies 1995, Camp *et al.* 1997, Kolstrom and Lumatjarvi 2000, Schieck and Hobson 2000, Tittler *et al.* 2001). Residuals can contain biological legacies and may be older than the surrounding landscape and can therefore support greater diversity of bryophytes, vascular plants, and insects (Franklin 1993, Segerström *et al.* 1994, Kuusinen 1996, Ohlson *et al.* 1997, Camp *et al.* 1997, Hörnberg *et al.* 1998, Gandhi 1999, Bottorff 2001). This high diversity in residuals is a result of habitat heterogeneity, moist conditions and the absence of large-scale disturbance (Hörnberg *et al.* 1998). In Sweden, residuals are extremely diverse in beetle, plant, fungi and bryophyte species (Hörnberg *et al.* 1998). In another study, a small proportion of residual swamp forest contained 33% of all of Sweden's known bryophyte species and 22 of those species are red-listed on endangered species lists (Segerström *et al.* 1994). There have been relatively few studies in North American boreal forests that focus on the characteristics of residuals and residuals as biodiversity refuges (Gandhi 1999, Smyth 1999, Delong and Kessler 2000, Bottorff 2001).

The growing conflicts between forestry, sustainability, and conservation is causing a shift from traditional clear cutting to less invasive methods such as green retention, and partial harvesting (Hunter 1993, Swanson and Franklin 1992, Delong and Tanner 1996, Fries *et al.* 1997, Halpern *et al.* 1999, Traut and Muir 2000). Such harvesting regimes try to mimic parameters of naturally disturbed landscapes to enhance habitat recovery, minimize time for forest regeneration and maximize sustainable yields from their forest management areas (Hobson and Schieck 1999). Presently, residual formation is poorly understood, providing the need for more research on characteristics

of residuals and their predictability. If these residual stands escape multiple fires, their plant communities may be considerably older than surrounding forest and can contain greater floristic diversity (Segerström *et al.* 1994, Hörnberg 1998, Bottorff 2001). Residuals represent a small proportion of the boreal landscape that provide unique habitat communities for flora and fauna (Delong and Kessler 2000), and play an important role in regeneration and should be considered in conservation plans.
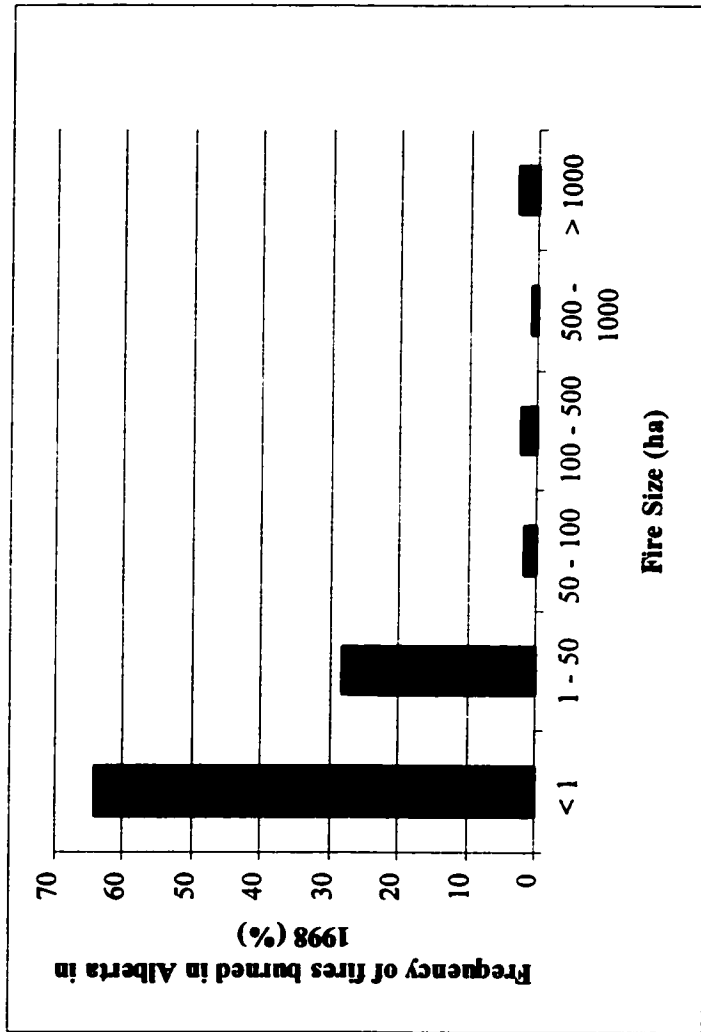
Figure 1.1: Frequency of fires burned in Alberta in 1998 (Alberta Forest Protection 2001).

1.4 Literature Cited

Acker, S.A., E.K. Zenner and W.H. Emmingham. 1998. Structure and yield of two-aged stands on the Willamette National Forest, Oregon: implications for green tree retention. Canadian Journal of Forest Research 20: 749-758.

Alberta Forest Protection. 2001. Historical Wildfire Information. Government of Alberta. http://envweb.env.gov.ab.ca/env/forests/fpd.

Alexander, M.E., B. Janz, and D. Quintilio. 1983. Analysis of extreme wildfire behavior in east-central Alberta: a case study. 7th Conference on Fire and Forest Meteorology. American Meteorological Society. Massachusetts, U.S.A.

Asselin, H., M.J. Fortin, and Y. Bergeron. 2001. Spatial distribution of late successional coniferous species regeneration following disturbance in south western Quebec boreal forest. Forest Ecology and Management 140: 29-37.

Beckingham, J.D., I.G.W. Corns, and J.H. Archibald. 1996. Field Guide to Ecosites of West-Central Alberta. Canadian Forest Service Special Report 9. Northern Forestry Centre, Edmonton, Alberta, Canada.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology 72: 1980-1992.

Bergeron, Y. and J. Brisson. 1990. Fire regime in red pine stands at the northern red pine stands at the northern limit of the species range. Ecology 71: 1352-1364.

Bessie, W.C. and E.A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology 76: 747-762.

Bottorff, Q.W. 2001. Fire skips and understory plant diversity in an upper foothills-subalpine forest in northwestern Alberta. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Camp, A., C. Oliver, P. Hessburg, and R. Everett. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. Forest Ecology and Management 95: 63-77.

Christensen, N.L., J.K.Agee, P.F. Brussard, J. Hughes, D.H. Knight, G.W.Minshall, J.M.

Peek, S.J. Pyne, F.J. Swanson, J.W. Thomas, S. Wells, S.E. Williams, and H.A. Wright. 1989. Interpreting the Yellowstone fires of 1998. Bioscience 39: 678-685.

Dansereau, P.R. and Y. Bergeron. 1993. Fire history in the southern boreal forest of northwestern Quebec. Canadian Journal of Forest Research 23: 25-32.

Delong, S.C. and W.B Kessler. 2000. Ecological characteristics of mature forest remnants left by wildfire. Forest Ecology and Management 131: 93-106.

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

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

Foster, D. R. 1983. The history and pattern of fire in the boreal forest of Southeastern Labrador. Canadian Journal of Botany 61: 2459-2471.

Foster, D.R., D.H. Knight, and J.F. Franklin. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbance. Ecosystems 1: 497-510.

Franklin, J.F. 1993. Lessons from old-growth. Journal of Forestry 91:10-13.

Fries, C., O. Johansson, B. Pettersson, and P. Simonsson. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. Forest Ecology and Management 94: 89-103.

Gandhi, K.J.K. 1999. The importance of fire skips as biotic refugia and the influence of forest heterogeneity on epigaeic beetles in pyrogenic stands in the northern Rocky Mountains. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Halpern, C.B., S.A. Evans, C.R. Nelson, D. McKenzie, D.A. Liguori, D.E. Hibbs and M.G. Halaj. 1999. Response of forest vegetation to varying levels and patterns of green tree retention: an overview of a long-term experiment. Northwest Science 73: 27-44.

Halpern, C.B. and T.A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5: 913-934.

Heinselman, M.L. 1971. The natural role of fire in northern conifer forests. In Fire in the Northern Environment: a Symposium. (Eds.) C.W. Slaughter, R.J. Barney and

G.M. Hansen. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon, U.S.A.

Hobson, K.A. and J. Schieck. 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. Ecological Applications 9: 849-863.

Hörnberg, G., O. Zackrisson, U. Segerström, B.W. Svensson, M. Ohlson, R.H.W. Bradshaw. 1998. Boreal swamp forests. Bioscience 48: 795-802.

Hunter, R.L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 9: 1041-1058.

Johnson, E. A. 1992. Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. Cambridge University Press, New York, U.S.A.

Kershaw, L., J. Gould, D. Johnson and J. Lancaster. 2001. Rare vascular plants of Alberta. The University of Alberta Press and The Canadian Forest Service. Alberta, Canada.

Kiil, A.D., D. Quintilio, and M.E. Alexander. 1986. Adaptation of a national system of fire danger rating in Alberta, Canada: a case study in technology transfer. Proceedings of the 18th IUFRO World Congress. Division 6: General Subjects. Ljubljana, Yugoslavia.

Kolstrom, M. and L. Lumatjarvi. 2000. Saproxylic beetles on aspen in commercial forests: a simulation approach to species richness. Forest Ecology and Management 126:113-120.

Kuusinen, M. 1996. Importance of spruce swamp forests for epiphyte diversity and flora on *Picea abies* in southern and middle boreal Finland. Ecography 19: 41-51.

Larsen, C.P.S. 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. Journal of Biogeography 24: 663-673.

Loope, L.L. and G.E. Gruell. 1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. Quaternary Research 3: 425-443.

Lyon, L.J., H.S. Crawford, E. Czuhai, R.L. Fredricksen, R.F. Harlow, L.J. Metz, and

H.A. Pearson. 1978. Fire effects on fauna: a state of knowledge review. U.S. Department of Agriculture, Forest Service General Technical Report WO-6.

Ohlson, M., L. Sodestrom, G. Hörnberg, O. Zackrisson and J. Hermansson. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth forests. Biological Conservation 81: 221-231.

Quirk, W.A. and D.J. Sykes. 1971. White spruce stringers in a fire-patterned landscape in interior Alaska. *In* Fire in the Northern Environment: a Symposium. (Eds.) C.W. Slaughter, R.J. Barney and G.M. Hansen. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon, U.S.A.

Romme, W.H. and D.H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62: 319-326.

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52: 199-221.

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

Samran, S., P.M. Woodard and R.L. Rothwell. 1995. The effect of soil water on ground fuel availability. Forest Science 41: 255-267.

Schieck, J. and K.A. Hobson. 2000. Bird communities associated with live residual tree patches within cutblocks and burned habitat in mixedwood boreal forests. Canadian Journal of Forestry 30: 1281-1295.

Segerström, U., R. Bradshaw, G. Hörnberg, and E. Bohlin. 1994. Disturbance history of a swamp forest refuge in northern Sweden. Biological Conservation 68: 189-196.

Smyth, C.L. 1999. Overstory composition of live residuals in fire affected landscapes of northern Alberta. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Swanson, F. J. and J.F. Franklin. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. Ecological Applications 2: 262-274.

Takaoka, S. and K. Sasa. 1996. Landform effects on fire behavior and post-fire

regeneration in the mixed forests of northern Japan. Ecological Research 11:339-349.

Taylor, A.H., and C.N. Skinner. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, U.S.A. Forest Ecology and Management 111: 285-301.

Thomas, J.W., R.J. Miller, H. Black, J.E. Rodiek and C. Maser. 1976. Guidelines for maintaining and enhancing wildlife habitat in forest management in the Blue Mountains of Oregon and Washington. Transactions of North American Wildlife and Natural Resources Conference 41: 452-476.

Tittler, R., S.J. Hannon and M.R. Norton. 2001. Residual tree retention ameliorates short-term effects of clear-cutting on some boreal songbirds. Ecological Applications 11: 1656-1666.

Traut, B.H. and P.S. Muir. 2000. Relationships of remnant trees to vascular undergrowth communities in the western Cascades: a retrospective approach. Northwest Science 74: 212-223.

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

Turner, M. G. and W.H. Romme. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology 9: 59-77.

Van Wagner. C.E. 1983. Fire behaviour in northern conifer forests and shrublands. *In* The Role of Fire in Northern Circumpolar Ecosystems. (Eds.) R.W. Wein and D.A. MacLean. John Wiley and Sons, New York, U.S.A.

Whelan, R.J. 1995. The Ecology of Fire. Cambridge Studies in Ecology. Cambridge University Press. New York, U.S.A.

Zackrisson, O. 1977. Influence of forest fires on the north Swedish boreal forest. Oikos 29: 22-32.

CHAPTER 2

THE EFFECT OF FOREST STAND CHARACTERISTICS ON RESIDUAL FORMATION

2.1 Introduction

In the past, fire has been the main agent of disturbance in the boreal forest (Delong and Tanner 1996). In North America, the natural disturbance cycle is estimated to be from 80 to 125 years (Johnson 1992) however the natural disturbance cycle has been modified and lengthened due to industrial activities and fire suppression (Heinselman 1978). The boreal forest is composed of a mosaic of differently aged forest stands. Past fires have caused this heterogeneity on the landscape, but within fires, the burn severity is also extremely patchy. Burn severity can range from severely burned areas with complete tree mortality and exposed mineral soil, to unburned forest patches. These patches, surrounded by burned forest, are known as fire residuals, fire skips, fire stringers, island remnants, or fire refugia (Quirk and Sykes 1971, Eberhart and Woodard 1987, Segerström et al. 1994, Camp et al. 1997, Hörnberg et al. 1998, Smyth 1999, Delong and Kessler 2000). For this thesis, they will be referred to as residuals. Residuals occur throughout fire-affected ecosystems including the boreal landscape in North America and Sweden, montane areas and South African fynbos (Quirk and Sykes 1971, Eberhart and Woodard 1987, Van Wilgen et al. 1990, Segerström et al. 1994, Camp et al. 1997, Hörnberg et al. 1998, Smyth 1999).

There have been few studies that focus on residuals in the boreal forest (Eberhart and Woodard 1987, Burgess 1997, Smyth 1999). In northern Alberta, Eberhart and Woodard (1987) found a positive relationship between fire area and residual area. They suggest larger fires could potentially reach firebreaks more often causing increased residual formation. Residuals occur mainly in valley bottoms, gullies, ridges, near waterbodies which have mesic environments (Quirk and Sykes 1971, Bergeron and

Brisson 1990, Whelan 1995, Camp *et al.* 1997). Now that emulating natural disturbance is being incorporated in harvesting practices (Halpern *et al.* 1999, Delong and Tanner 1996), there is a surprising lack of information on residual formation. This lack of understanding undermines the effort in simulating natural disturbance. In this thesis, I hope to provide further information on the residual characteristics and formation.

There are two types of factors that influence residual formation: stochastic and structural. Stochastic factors include meteorological conditions, variations in wind speed, wind direction, precipitation, local and regional weather (Foster 1983, Bessie and Johnson 1995, Delong and Kessler 2000). Structural factors include spatial location, forest characteristics, local topography and waterbodies (Camp *et al.* 1997, Smyth 1999). Stochastic variables in combination with structural variables can influence fire behaviour and residual formation (Whelan 1995).

Abiotic influences

Topography can create variation in local climate and natural fuel breaks which affects residual formation (Camp *et al.* 1997). The influence of topography on fire behaviour has been studied extensively (Rowe and Scotter 1973, Van Wagner 1983, Romme and Knight 1981, Takaoka and Sasa 1996, Camp *et al.* 1997). On uniform topography, fire spread depends on wind direction, wind speed, and fire intensity. Fires burn uphill very quickly because radiation from the head flames dries nearby fuel and increases ignition rates. The opposite is true when burning downhill because the head of the fire is farther from the ground. Moisture also accumulates in valley bottoms and depressions which also reduces fire intensity and ignition (Whelan 1995).

Soil moisture, a variable related to topography, can be extremely important for residual formation. High soil moisture reduces ignition, the rate of combustion, and the rate of fire spread as compared to more xeric and upland habitats (Samran *et al.* 1995, Whelan 1995). These abiotic characteristics such as topography, proximity to waterbodies or other natural fuel breaks help define the biotic characteristics of the forest and together they can influence residual formation.

Biotic influences

Certain tree species are more susceptible to burning due to their inherent characteristics. The degree of tree flammability ranges from low such as trembling aspen (*Populus tremuloides* Michx.) to high such as lodgepole pine (*Pinus contorta* Loudon). In general, deciduous trees contain higher moisture content and higher tree crowns than coniferous trees making them less flammable (Smyth 1999, Cumming 2001).

Stand age can also affect residual formation, though the response of fire to stand age is unclear (Van Wagner 1983, Foster 1983, Despain 1991). Older stands that have accumulated downed logs, coarse woody debris (CWD), and litter can be susceptible to fire. For example fire suppression in Yellowstone National Park allowed the forest to age and accumulate fuel. Along with several years of drought and high fire hazard climatic conditions, the conditions of the forest allowed the 1988 fires to burn with greater intensity than they might have otherwise (Despain 1991). Fire ignition depends on sufficient fuel accumulation and therefore will also have an effect on residual formation. Some studies have found that younger stands are effective fuel breaks due to the lack of sufficient fuels (Van Wagner 1983, Schimmel and Granström 1997). As well, some studies have found older stands may be more difficult to penetrate because older trees have thicker bark than younger trees (Foster 1983, Turner *et al.* 1999).

In this chapter, my objectives were: 1) to determine residual edge characteristics and their variability and 2) to determine whether residuals and burned forest exhibit similar stand-level characteristics of vegetation structure (tree density, age, DBH, and species) and topography (aspect, slope and slope position).

2.2 Methods

Study Site

Topography and climate

The general study area (~N54° 71', W116° 53') was situated in the Upper Foothills ecoregion (Beckingham *et al.* 1996) in Virginia Hills, Alberta (Figure 2.1). The topography was composed of strongly rolling ridges and elevation ranges from 900 to 1500 m (Beckingham *et al.* 1996). Study site elevations ranged from 1012 to 1166 m.

The climatic regime of this ecoregion is continental with a mean summer precipitation of 340 mm and mean annual precipitation of 540 mm. The mean May to September temperature is approximately 10 to 12°C (Sweetgrass Consultants 1997).

Vegetation

The forest vegetation of the Upper Uoothills of Alberta is composed of spruce-dominated, pine-dominated, and deciduous stands. Common tree species include lodgepole pine (*Pinus contorta* Loudon), black spruce (*Picea mariana* (Mill.) BSP.), white spruce (*Picea glauca* (Moench) Voss) and larch (*Larix laricina* (Du Roi) K. Koch) (Beckingham *et al.* 1996). Shrub layer vegetation consisted of common species such as green alder (*Alnus crispa* (Ait.) Pursh), Labrador tea (*Ledum groenlandicum* Oeder) and various ericaceous dwarf shrubs. Understory non-shrub vegetation included common boreal species such as bunchberry (*Cornus canadensis* L.) and palmate-leaved coltsfoot (*Petasites palmatus* (Ait.) A. Gray). Common bryophytes such as feather moss (*Pleurozium schreberi* (Brid.) Mitt.), Knight's plume (*Ptilium crista-cristensis* (Hedw.) De Not.), and stair step moss (*Hylocomium splendens* (Hedw.) B.S.G.) covered the ground layer.

Virginia Hills Fire

During May of 1998, a lightning-induced crown fire was ignited on flat topography of provincial land (N54° 71', W116° 53') and burned approximately 163,138 ha of boreal forest, leaving many forest residuals of varying sizes within the fire perimeter (Figure 2.2). Twenty-three sampling sites were established in randomly chosen

residuals within the fire. Sampling took place two years post-fire during May to August 2000.

Locating Residuals

Coverage maps of Alberta Vegetation Inventory (AVI), roads, cutlines, seismic lines, cutblocks, waterbodies and fire were obtained from the Foothills Model Forest prior to field data collection. Access maps were developed in ArcView GIS package and all residuals were located. Candidate residuals were limited to locations near vehicle and foot access routes. Salvage-logged areas and "cat-guarded" areas were also excluded from candidate residuals. "Cat-guarded" areas were forested areas that were bulldozed to create fuel breaks to help contain the fire. Study sites were randomly chosen from the remaining pool of candidate residuals therefore maintaining unbiased sampling. Of 54 candidate forest residuals, nine were randomly chosen. A range of residual sizes was selected (from 7.64 ha to 2,845.3 ha). Residuals were categorized as small or large based on relative area. To determine the cut-off between small and large residuals, the area of the largest residual (2,845.3 ha) was divided by two. In total, 4 small residuals and 5 large residuals were sampled.

Locating Transects

The contiguous quadrat transect method was used to characterize changes in forest structure and local topography across the fire edge. To improve efficiency in the field, transect locations were limited to within 1.0 km from an access route. Transects were limited to burn boundaries between completely burned to unburned forest. Other burn types such as partial burns and ground fire burns were omitted from potential transect locations. Transects were randomly placed perpendicularly across complete burn to unburned residual edges. For small (and large) residuals, 2 (and 3) transects were randomly laid out. Each transect was approximately 100 metres in length and 5 metres wide. The residual edge was defined based on complete tree mortality. Once the edge was defined, transects extended 50 metres into the burned matrix and 50 metres into the

unburned forest resulting in approximately 10 quadrats in each burn class. A transition zone between the burned and unburned sections was added if the fire boundary was unclear. Transects were divided into 5 m x 5 m contiguous quadrats, resulting in approximately 20 quadrats per transect (Figure 2.3). In total, 23 transects from 9 residuals were sampled.

Field Data Collection

To assess forest structure of burned and unburned forest and to characterize the residual edge; tree and shrub species present, diameter at breast height (DBH), density, canopy cover and took increment cores from the 2-3 largest DBH trees were recorded in each quadrat. To ensure tree density was not influenced by immolation, stems with DBH greater than 10 cm were considered to be trees; stems with DBH less than 10 cm no matter what their height were not. Core samples were labeled and stored in straws and either taped or stapled at each end. Tree cookies were taken if high quality cores could not be extracted from the trees. A tree cookie sample, which is a cross section of the tree trunk, was taken near the base of the tree trunk to ensure the sample included a pith for more accurate ageing. Fire scars were not located in any of the trees measured.

Slope, slope position and aspect were recorded in each 5m x 5m quadrat to assess local topography of the residual edge. Slope along the transect was measured using a clinometer. Slope position was assessed using the definitions given in Beckingham *et al.* (1996). Percentage of coarse woody debris (CWD), percentage of litter (%), depth to mineral soil (cm), and depth to water (cm) were also recorded to give a general assessment of the environmental conditions along the transect. Coarse woody debris was defined as pieces of dead wood with diameter greater than 3 cm. Percent covers of coarse woody debris and litter were visually estimated in each 5m x 5m quadrat

Laboratory Methods

Increment core and tree cookie preparation

Samples were oven-dried at low heat for 24 hours. Mounting boards were constructed using 8" x 10" plywood and approximately 10 shallow channels were cut. Cores were mounted on these boards using wood glue. Each board was then sanded using 100-grit up to 600-grit sandpaper to achieve a fine grain on each core and exposing the cells of late and early wood (Varem-Sanders and Campbell 1996). Cookies were also oven-dried at low heat for two days to prevent cracking. Radial slices were cut from each cookie and sanded using the same methods as above. A total of 960 cores and cookies were examined.

Tree ageing

Trees were aged using both DendroScan version 4.53 software (Varem-Sanders and Campbell 1996) and by counting rings under a dissecting microscope. The number of tree rings was counted for each sample, and actual tree age was estimated if the pith was absent. Age estimation from simple ring counting followed the same methods used in the DendroScan software (Varem-Sanders and Campbell 1996).

2.3 Analyses

General analyses

Transects and residuals were analyzed separately to determine the range of variation among them. Relative tree species densities, tree species frequency and age for burned and unburned forests were calculated for each residual and transect. DBH class distributions were also produced for burned and unburned forests. Tree species and DBH size class frequencies in burned and unburned forests were compared using G tests for heterogeneity (Sokal and Rohlf 1995). A pooled and heterogeneity G test was calculated at the residual and transect level to account for any heterogeneity among them. The significance level was Bonferroni adjusted by dividing the p-values by the number of

transects (α" = α/k where k = number of transects) (Sokal and Rohlf 1995). Tree ages were estimated and summarized for burned and unburned forest. Average age for burned and unburned forest in each residual and transect was compared using t-tests. This permitted an assessment of forest structure and any coarse differences and variability between burned and unburned forest. All general analyses were performed using MS Excel and S-PLUS 2000.

Edge Detection analysis

Edge detection analysis was used to determine whether the fire edge could be correctly detected based on forest structure. Correctly identified fire edges may provide some information on factors contributing to residual formation. One method of edge detection is the split moving window technique where the difference between pairs of adjacent blocks is calculated along the entire length of the transect (Ludwig and Cornelius 1987, Legendre and Legendre 1998). The results are graphed and any peaks of high values indicate a possible edge. Block size is user defined and ranges from 1 (fine scale) to half of the total number of quadrats. Using a block size too small results in a high sample-to-sample noise whereas a block size too large results in too few data points for a practical interpretation (Ludwig and Cornelius 1987). To test for significant peaks, randomization procedure of the data was used (Manley 1997). Difference between pairs of adjacent blocks were randomly shuffled 999 times between and within species and quadrats and compared to observed data to determine whether actual data were significantly different from random data. Edge detection analysis was performed using software written in Quick Basic 4.

A mid-size block of 5 quadrats was used in order to minimize noise and maximize number of data points. To test whether fire preferentially burns through low density of large diameter trees or high density of small diameter trees, a ratio of basal area to tree count was calculated and used in the analysis. An increasing ratio indicates a trend towards a low density of large diameter trees while a decreasing ratio indicates a trend

towards a high density of small diameter trees. I would expect residuals to be composed of a high density of small trees due to insufficient fuel accumulation.

Ordination

Canonical Correspondence Analysis (CCA) was used to examine the relationships between site and species characteristics and relate the site and species data to environmental conditions. CCA is a direct ordination method, which locates species and sites in ordination space according to their similarities while being constrained by environmental variables (Ter Braak 1986, Ter Braak 1994, Palmer 1993). The advantages of CCA are that it can determine the relationship between species along an environmental gradient, analyse all environmental and species data simultaneously (Palmer 2000) and uncover patterns from a combination of environmental variables, which may not be observed if each variable was analysed individually. One weakness is that it assumes environmental variables sampled are important in structuring data. The objective of this analysis was two-fold: to determine the relationship between environmental conditions and tree species data, and to determine whether there is a difference in tree species characteristics and environmental conditions between burned and unburned sites.

Partial CCA was also used to partition the variance into variance explained by environmental variables, site location and both environmental variables and site location (Ter Braak 1990). This analysis was used to determine how much of the variance can be explained by differences among residuals rather than differences between burn condition.

Spatial Autocorrelation and Logistic Regression

The objective for the logistic regression analysis was to determine whether burned or unburned quadrats could be predicted by tree species, tree species density, total DBH and tree species DBH. Due to the method of data collection, the data violated the assumption of independence between observations. The contiguous quadrat transect layout used in this study caused each observation to be spatially autocorrelated, thus making tests of significance too liberal (Dale and Fortin *in press*).

Detecting spatial autocorrelation

Study transects were in close proximity to each other; therefore, I assumed the tree data exhibited a similar autoregressive structure. I sampled twenty-three transects in nine residuals which I treated as twenty-three realizations of the same autoregressive structure. Autocorrelation of DBH and tree density at each lag was averaged to obtain a general autoregressive structure of the data. Random transect datasets were created using this general autocorrelation structure to calculate mean autocorrelation and standard deviation at each lag. Confidence intervals were then calculated for autocorrelation at each lag and Bonferroni adjusted to account for each sampled transect. Autocorrelation in each transect was compared to the general autoregressive model and its confidence intervals to determine whether all transects follow this general autoregressive structure. If autocorrelation declines exponentially, i.e. a first order autoregression, it is possible to use a simple "effective sample size" correction to determine significance of each of the predictors in the logistic regression model (Cressie 1991).

Autocorrelation for each transect and variable was calculated in S-PLUS 2000 and graphed with 95% confidence intervals. If autocorrelation estimates do not exceed the confidence intervals, autocorrelation could be assumed to have no effect on statistical testing (S-PLUS 1999).

Cressie's correction for effective sample size (Cressie 1991) can be used to deflate sample size to compensate for liberal significance tests (Equation 1.1). However, this type of correction assumes the data fits a first order autoregressive model (Equation 1.2).

$$ n' = \frac{n}{\left[1 + 2 \left\{ \frac{\rho}{(1-\rho)} \right\} \left\{ 1 - \left(\frac{1}{n} \right) \right\} - 2 \left\{ \frac{\rho}{(1-\rho)} \right\}^2 \left(\frac{1 - \rho^{n-1}}{n} \right) \right]} \qquad \text{Equation 1.1} $$

Where: ρ = spatial autocorrelation at lag 1

n = sample size

$$x_i = \rho x_{i-1} + \varepsilon_i \qquad\qquad \text{Equation 1.2}$$

Where: ρ = spatial autocorrelation parameter

x = sample, i

ε_i are independent

Logistic regression

Logistic regression was performed on quadrats to determine whether burn class (burned, unburned) could be predicted by predictor variables such as tree species, density and DBH. For this analysis, each quadrat was nested within their respective transect and residual site to maintain proper degrees of freedom. Several models were produced in order to develop a stable model. A summary table of the models was produced to illustrate variability among the transects in direction and significance of the relationships.

Although discriminant function analysis (DFA) would have been appropriate in determining important variables responsible for burn condition, its assumptions are stricter than those of logistic regression and DFA is less robust than logistic regression because it is sensitive to departures from normality (Hosmer and Lemeshow 1989).

2.4 Results

General transect characteristics

Local topography along transects was generally flat (Figure 2.4b). Few transects exhibited any slope (Figure 2.4a-c). Overall, there were significantly greater tree frequencies of all species in the unburned quadrats than in the burned quadrats except for unidentified spruce and lodgepole pine (Figure 2.5). Black spruce and lodgepole pine dominated the burned and unburned forests (Figure 2.6b,d). Larch and white spruce were also common in unburned forests and transition areas and less common in burned forests

(Figure 2.6b-d). There were very few occurrences of trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), and balsam fir (*Abies balsamifera* (L.) Mill.) species in all classes (Figure 2.6a). Composition of burned and unburned forests was very similar with only minor differences in species abundance (Figure 2.6b-d). Unburned forest contained greater frequencies of small diameter trees (Figure 2.7a). Frequencies of larger trees were similar in unburned and burned forests (Figure 2.7). Average ages in burned and unburned forests were highly variable (Table 2.1). Age distributions of each residual were generally skewed to the right indicating that mean age was generally greater than the mode and median. Several substantially older trees could be contributing to an inflated average age. On average, burned forest was older than unburned forest in 5 residuals. Two residuals showed similar average age in both burned and unburned forest and unburned forest was older than burned forest in 2 residuals. Tree diameter was positively related to tree age ($r=0.343$, $\alpha = 0.01$) but age was highly variable in trees with small DBH (Figure 2.8).

Tree species and DBH size class frequency and age distributions in each residual

There was high variability in frequencies of tree species between burned and unburned quadrats in the transect and site levels (Table 2.2). In general, there were lower tree frequencies in burned forest than in unburned forests. Significant differences in tree frequencies between burned and unburned forest were found in 4 of 9 sites and 7 of 23 transects (Table 2.2). Significant heterogeneity ($G_{h\ transect} = 220.07$, $p = 0.0005$; $G_{h\ residual} = 42.15$, $p = 0.0005$) was found among sites and transects, indicating that both sites and transects exhibited extremely high variability (Table 2.2). These differences were not due to immolation because many burned small diameter trees (with DBH less than 10 cm) were still present in the burned forest. Since sampling took place two-years post-fire, it is unlikely the burned forest has begun to degrade or decompose.

Density of black spruce, lodgepole pine, larch and white spruce was highly variable among sites and transects (Tables 2.3-2.6). Both the transect and site levels indicated greater frequencies of black spruce, larch, white spruce and total frequency in

the unburned forest than in the burned forest, while lodgepole pine frequency had no consistent trend. Lodgepole pine frequency was inconsistent in burned and unburned forest resulting in an insignificant pooled G value (Table 2.4). As expected, unidentified spruce was found significantly more in burned forest than in unburned forest (Table 2.7) since some spruce trees were burned beyond proper identification.

In the 5 –15 cm diameter size class, there was high heterogeneity among sites (Table 2.8a, Figure 2.7). Pooled and individual residual G tests in 15 – 30 cm DBH size class were not significant except for residual 14 (Table 2.8b, Figure 2.7c). There was no significant difference in DBH size class greater than 30 cm between burned and unburned forest among sites (Table 2.8c, Figure 2.7d). The sample size of this 30cm DBH class was considerably less than the smaller size classes because there were only three sites that had trees with DBH larger than 30 cm. Due to low stem counts in the larger size class, data were not separated by transect and species.

There was very little age difference between burned and unburned forest (Table 2.1). Average age of burned forest was older than the unburned forest in one site and five transects. Only three transects found unburned forest to be older than the burned forest. In most transects, ages from burned and unburned forest were very similar. Mean age ranged from 50 – 121 years (Table 2.1).

Edge detection

Overall, fire edges were highly variable and its detection was sporadic (Figure 2.9a-c). High densities of small lodgepole pine and black spruce characterized areas near fire edges (Figure 2.10a). The presence of larch, balsam fir or low densities of large white spruce occurred near the fire edges (Figure 2.10a). Edges of larger residuals were correctly identified more often than edges of small residuals.

In 13 of 23 transects, the fire boundary was detected by the edge detection method (Figure 2.9a-b). Of these 13 transects, 10 transects showed significant peaks at the fire edge (Figure 2.9b). In general, basal area to stem count ratio of lodgepole pine and black spruce decreased from burned to unburned forest indicating a trend towards greater

densities of smaller diameter trees in the unburned forest (Figure 2.10a-b). Several transects (residual 7 transect 2, residual 8 transect 2, and residual 9 transect 2) exhibited increasing ratio of white spruce indicating greater densities of large diameter trees in the unburned forest (Figure 2.10a). For two transects (residual 3 transect 1 and residual 3 transect 3), larch was present at the fire boundary (Figure 2.10a).

If the probability of a large area escaping fire is less than a small area escaping fire then it is possible the residual was formed due to structural characteristics rather than stochastic factors. From the 10 transects where the edge was significantly detected, seven of those transects were from large residuals (3, 13, 14, 15) while three were from small residuals (7, 8) suggesting that the edge may be more defined in large residuals.

Ordination: Canonical Correspondence Analysis

Two ordinations were performed: one with all tree species and another with all spruce species lumped together (Figures 2.11, 2.13). The environmental axes explained very little variance in the dataset in both ordinations (Tables 2.9-2.10). No clear separation between burned and unburned quadrats was found but the burned quadrats tended to occur around the periphery of the triplot. Partial CCA analysis found that site location explained most of the variance, therefore quadrats from the same residual were more similar to each other than quadrats from other residuals (Figures 2.11, 2.13). None of the environmental variables sampled characterized burned and unburned quadrats (Tables 2.9, 2.10).

All tree species and all environmental variables

Axis 1 represented a depth to water (general local moisture), litter cover and south and west-facing gradient, whereas axis 2 represented an age, and north and east-facing gradient (Figure 2.11a, Table 2.9). There was also a black spruce to white spruce-lodgepole pine dominated forest gradient along the first axis and a black spruce to larch dominated forest gradient along the second axis. Axes 1-3 explained only 11.4% of variance in the species dataset (Table 2.11). There was no distinct separation between

burned and unburned quadrats. Unburned quadrats tended to be characterized by high local moisture sites with high depth to soil, east facing aspect and high density of black spruce, while burned quadrats tended to aggregate near the centre and lower half of the triplot (Figure 2.11a) and were characterized by unidentified spruce species, unknown species, older average forest age and high amount of litter.

By plotting axes 1 and 3, burned and unburned quadrats were distinguishable along depth to soil, general local moisture and age gradients (Figure 2.11b). Burned quadrats tended to occur around the periphery of the ordination, indicating that burned quadrats are likely to have more extreme environmental characteristics than the unburned quadrats such as more litter cover, shallower depth to soil and water. Many burned quadrats tended to have greater amounts of lodgepole pine than unburned quadrats.

A partial CCA was then used to partition the variances between environmental conditions and site location. In total, 42.67% was explained by the environment, site and environment and site together (Figure 2.12) while 7% of variance was explained only by the environmental variables and 31% of variance was explained by site.

Spruce tree species combined and all environmental variables

All *Picea* species were combined and analyzed again in case the trends seen in the previous ordination were misleading. Axis 1 represented a local moisture gradient and southwest-facing aspect gradient whereas axis 2 represented litter cover, depth to soil gradient, northeast-facing aspect and age gradient (Figure 2.13a, Table 2.10). These environmental gradients were not strong nor did they explain much of the variation in the species and site data (Table 2.11) however, this ordination provided much less spread in the triplot and explained considerably more variation (17.2%) in the species data set than the previous ordination. Most sites were aggregated near the centre, indicating both burned and unburned quadrats have similar environmental conditions (Figure 2.13a). Unburned sites were characterized by greater depth to soil, and were located on an east-facing aspect, whereas burned sites were more variable. Some burned sites had more lodgepole pine and unknown tree species, more litter, and older average forest age. By

plotting axes 1 and 3, burned and unburned quadrats were separated along an age, coarse woody debris cover, and litter cover gradients (Figure 2.13b).

In total, 31.11% of variance was explained by environment only, site only and both environment and site together. In contrast to the previous ordination, the environment explained 9% of variance, only 15% of variance was explained by site and 7% of variance was explained by both environment and site (Figure 2.14). Based on both ordinations, quadrats from the same residual tended to be more similar to each other than quadrats from other residuals indicating that there is high variability in species and environmental conditions among residuals (Figure 2.15).

Generalized Linear Modeling

Spatial autocorrelation did not have a significant effect on the statistical tests for density and DBH data (Figure 2.16). Greater density of small diameter spruce species was found in the burned quadrats while greater densities of large diameter larch and black spruce were found in the unburned quadrats. White spruce was not found to be important in any model. Lodgepole pine density as a predictor of burn class was inconclusive, and tree size could not be incorporated in any model due to instabilities it produced.

Effect of spatial autocorrelation

When autocorrelation was averaged among all transects, tree DBH and density were minimally autocorrelated at long lag distances (Figure 2.16). Both variables exhibited a first order autoregressive structure; neighboring quadrats were not highly correlated (0.09 and 0.17 for DBH and density respectively). Autocorrelation at longer distances were close to 0.00 and did not exceed ±0.08 indicating that spatial autocorrelation is weak in the data. An effective sample size was also calculated using Cressie's correction for effective sample size (Cressie 1991). With autocorrelation at 0.17 for the density dataset and 0.09 for the DBH dataset, the effective sample size was deflated from the original 460 quadrats to 324 quadrats and 377 quadrats, respectively.

Data were transformed to help normalize the data, however; transformed data was still skewed to the right. The lack of normality may compromise the fit of the model and should be taken into consideration for interpretation.

Effect of species density

Originally, I wanted to develop a model that incorporated all tree species' densities as predictors of burn class. This produced an instable model; therefore several smaller stable models were developed (Table 2.12). An instable model indicates there was a poor fit between the model and the data causing poor prediction of burn class. Black spruce and lodgepole pine were examined individually because together they introduced instabilities in the larger model. The trends in the data were highly variable and very few predictor coefficients were significant.

Density of unidentifiable spruce was a significant predictor of burned quadrats in 4 of 23 transects since most cindered spruce could not be identified to species (Table 2.12). Larch was significantly denser in unburned quadrats than burned quadrats in one transect. White spruce was not important in predicting burn class of the quadrats. This model explained 32.3% of the deviance in the dataset.

Black spruce density was significantly greater in unburned quadrats for 9 transects while lodgepole pine density was inconclusive (Table 2.12). Lodgepole pine density was significantly greater in burned quadrats in one transect and significantly lower in burned quadrats in another transect. Each model explained 24.7% and 11.9% of deviance respectively.

Effect of stem size

Several smaller DBH models were produced to model burned and unburned quadrats. Again, all species were found to be significant in predicting burn class except for white spruce and lodgepole pine (Table 2.12).

Burn class modeled by spruce species and black spruce explained the most deviance in the dataset (58.2%) where small diameter spruce species and large diameter black spruce were significant in predicting unburned quadrats.

Spruce size was generally smaller in residuals while white spruce size was not significant in predicting burn class of each quadrat. Large diameter larch was significant in predicting unburned quadrats in one transect. This model explained 30.4% of the deviance in the species dataset.

Lodgepole pine could not be included in any of the models because it caused instabilities in the models. Lodgepole pine frequency was greater in burned quadrats in some transects while frequency was lower in burned quadrats in other transects (Table 2.4).

Because not all spruce individuals could be identified to genus due to the fire, all spruce species were combined and used as a predictor in case trends from the previous analyses were misleading. Spruce density and DBH were very weak predictors of burn class where only two transects exhibited significantly greater density in residuals and three transects exhibited significantly smaller diameter stems in the residuals.

In summary, the effect of stem size and species density on burn class was weak but a high density of large diameter black spruce and larch and a low density of unidentified spruce trees characterized unburned quadrats.

2.5 Discussion

Effect of tree species on residual formation

Coniferous tree species can promote fire movement and crowning due to their architecture, which can provide a fuel ladder from tree base to the tree crown (Foster 1983, Johnson 1992). This effect can be more prevalent in older stands where trees have many dead low-hanging branches and needle litter, twigs and other fine fuels (Rowe and Scotter 1973). The continuity of ground fuels to crown fuels makes coniferous forests

much more susceptible to intense burning. In this study, tree species composition had a very weak effect on residual formation in the Virginia Hills fire. Black spruce and lodgepole pine were dominant among all sites and tree species composition was similar among sites (Figure 2.6). Because the burned and unburned sites were compositionally similar, tree species did not have an effect on residual formation. Black spruce density and total tree densities were greater in residuals than in the burned forest, and a high density of small diameter trees characterized the fire edge in most residuals (Figure 2.7) suggesting that a high density of small diameter and possibly young black spruce may be contributing to residual formation. This is surprising because black spruce is known to be a highly flammable forest type (Kiil 1975); however, the lack of fuel accumulation in young stands could inhibit successful ignition and burning (Schimmel and Granström 1997). Black spruce has highly variable habitat requirements, ranging from upland well-drained sites to lowland moist acidic environments and *Sphagnum* bogs (Lauriault 1989). Since residuals were generally characterized by higher local moisture conditions than burned forest, it is likely residuals formed in bog areas containing lowland black spruce (Figure 2.11, 2.13).

Overall, lodgepole pine density and frequency were inconsistent among sites. Lodgepole pine density and size were also unable to predict burn class of each quadrat. Although results from this study are inconclusive, lodgepole pine is highly flammable, and serves as fuel for both surface and crown fires (Van Wagner 1983). Lodgepole pine occurs over a wide range of soils and sites (Farrar 1995) but thrives in upland, drier boreal sites (Johnson *et al.* 1995). Rowe and Scotter (1973) have also found that lodgepole pine has the greatest crown and surface fire hazard or ignitability of all tree species in the boreal forest. Due to the flammability of lodgepole pine, it was surprising that lodgepole pine was not a good predictor of burned forest. This is a result of lodgepole pine occurring equally in burned and residual forest.

Although white spruce was rare throughout the study area, white spruce was found significantly more often in residuals than in burned areas but tree size was not a significant predictor (Table 2.6). Presence of white spruce in residuals is consistent with

previous studies that have found white spruce stringers within fire-affected areas (Quirk and Sykes 1971, Heinselman 1971, Viereck 1973). White spruce generally occurs in well drained to moist soils (Johnson *et al.* 1995) such as ravines, floodplains (Rowe 1970) and other natural firebreaks that help the formation of fire residuals.

Deciduous species may also have an effect on burn severity and can slow fire movement (Foster 1983, Van Wagner 1983, Cumming 2001). Some studies have found certain deciduous tree species are able to evade fire better than others, and can escape crowning due to their discontinuous fuels, high canopy and moisture retention (Johnson 1992, Smyth 1999, Cumming 2001). Although there were several transects that contained balsam poplar (*Populus balsamifera*), trembling aspen (*P. tremuloides*), and paper birch (*Betula papyrifera*), they were rare in the study sites and did not have any effect on the analyses. Larch, a deciduous conifer, is generally associated with bogs and mesic habitats (Johnson *et al.* 1995), however it occurred both in burned and unburned forests (Figure 2.6 and Table 2.5). The presence or increased density of larch occurred mainly near the fire edge and could reflect a change in fuel flammability, topography or a possible change in hydrology (Figure 2.10). There was evidence in one transect where a high density of large diameter larch occurred in the unburned quadrats. The lack of any clear trend is probably due to its relative rarity in comparison to black spruce or lodgepole pine.

Based on these results, the effect of tree species played a small role in the highly variable process of residual formation. It was difficult to determine whether tree species composition plays a large role in residual formation due to the relative homogeneity of forest stand composition within the study area.

Effect of Forest Structure on Residual Formation (forest density, tree size and tree age)

Total tree density along the fire boundary was a good predictor in determining burned and unburned forest (Table 2.12). Burned forest generally contained lower tree density than the residual. Low density of large diameter trees and high densities of small diameter trees characterized the fire edge and unburned forest respectively (Figure 2.10). Although it is possible that some of the small diameter trees were incinerated in the fire,

many small diameter trees (DBH less than 5 cm) were present in the burned areas and sampling took place within two years post-fire so the edges has not started to degrade. This provides some evidence that effect of total tree density is not likely to be an artefact from the fire. However these results contradict Delong and Kessler's study (2000) where residuals were found to contain lower density of large diameter trees.

Larger diameter black spruce and larch trees were weakly related to residuals (Table 2.12), but edge detection analyses showed greater density of small diameter trees in residuals and near fire edges. Schimmel and Granström (1997) found that recently burned forests or younger forests can act as firebreaks. It has been suggested that forests with high density of small diameter trees are younger in age and have not had the time to accumulate fuels (Romme 1982, Schimmel and Granström 1997, Johnson 1992), however average age in burned and unburned quadrats were highly variable and not significantly older than each other. CCA ordination showed an age gradient where burned quadrats were slightly older than unburned quadrats which provide some albeit weak evidence that younger forests can act as a fire break while older forests burn more frequently (Figure 2.11, 2.13). Older forests with low densities of large diameter trees with accumulated snags, duff, and litter are may be more susceptible to burning, but there has been contradicting evidence (Van Wagner 1983, Schimmel and Granström 1997, Delong and Kessler 2000). My data suggest that slightly younger forests that may have had insufficient fuel accumulation and high local moisture were contributing to residual formation.

Effect of topography and abiotic conditions

There were extremely small variations in topography between transects and most of the transects were on flat terrain. Local topography had a very small effect or no effect at all on burning patterns in the 1998 Virginia Hills fire. On flat topography, wind direction and speed can influence fire behaviour (Foster 1983, Whelan 1995). Only two transects, both from large residuals, exhibited slight downhill slopes (Figure 2.4), while transects from small residuals exhibited only flat terrain or slightly uphill slopes. Only

two transects from large residuals had extreme downhill slopes indicating that topography was highly variable and may not have contributed towards residual formation at small scales. Another influential factor in residual formation to consider is the characteristics of the fire itself.

General local moisture and depth to mineral soil were the main gradients that separated burned and unburned quadrats (Figure 2.11, 2.13). Again, this indicates that moisture may have an influence on residual formation (Samran *et al.* 1995). Moisture is related to topography, can affect species composition, dryness of ground fuels, and therefore affects the probability of successful fire ignition. The second most important gradient was found to be north and east facing aspects (Figure 2.11, 2.13). Although there was no clear separation between burn classes, some of the burned quadrats were characterized with north facing aspects. This pattern has been shown in previous studies where north-facing aspects burn with more intensity (Barrett 1988) because it can support greater tree growth and fuel accumulation due to its cooler and moister conditions (Zackrisson 1977). This contrasts other studies where north-facing sites burned less frequently than south facing sites (Francis 1996, Camp *et al.* 1997, Taylor and Skinner 1998). Inconsistencies among studies emphasize the variability of fires due to fire type, weather, climatic conditions, fire duration and geographic location.

General Conclusions

Lightning ignited the fire started on May 2, 1998 and it burned an area of 163,138 ha (Alberta Forest Protection 2001). The crown fire spread quickly on a relatively flat terrain and burned through a "boreal spruce" fuel type (Alberta Forest Protection 2001, Johnson 1992). A fire of this magnitude is rare because most fires are generally less than a hectare in size, but larger fires contribute most to disturbance and total area burned (Foster 1983, Agee 1993, Fryer and Johnson 1987).

Given the severity of the fire, it appears from my results that weather conditions and duration of burning, stand-level characteristics in forest structure and local topography are not likely to influence residual formation. However, residuals may play a

vital role in post-fire forest regeneration and serve as a seed source (Turner and Romme 1994, Turner *et al.* 1998) and refugia for later successional species (Rowe and Scotter 1973, Asselin *et al.* 2001). There was high variability in residual age and residuals may not persist over several fire cycles. Forest tree density and composition had a weak influence on residual formation, but other climatic or environmental factors were probably driving residual formation in the 1998 Virginia Hills fire. The trends among all transects were highly variable and may indicate the different environmental conditions before the disturbance, during disturbance and post-disturbance (Delong and Kessler 2000). This study draws attention the need for more research on residual formation in different fires.

Environmental and forest stand characteristics of fire residuals in this 1998 fire were highly variable among sites and could not predict burned forest from residual forest. However, moisture appeared to have some influence in residual formation. Some residuals were characterized by greater densities of black spruce and larch, which indicates that moisture may play a weak role in residual formation.

Table 2.1. Estimated age summary for burned and unburned forest in each residual.

Residual	Unburned				Burned			
	Mean	Median	Mode	Standard Deviation	Mean	Median	Mode	Standard Deviation
3	71.11	44	41	50.53	50.44	41	41	33.03
5	111.24	114	125	15.46	121.39	113	105	13.58
7	60.67	58	49	13.86	53.71	52	50	15.42
8	94.98	100	54	39.13	105.89	119	130	37.51
9	60.13	57	56	14.65	84.79	68	54	33.92
11	61.87	63	62	6.39	60.38	62	63	9.48
13	63.23	63	63	9.70	63.28	63	63	6.65
14	67.91	62	61	26.01	85.70	60	59	50.05
15	62.09	60	60	16.39	84.67	62	62	39.89

Table 2.2. G test summary of stem counts of burned and unburned trees species. Note: Transect notation indicates Residual number and Transect number. Df = degrees of freedom. Sig. = significant (alpha = 0.0005). "+" indicates greater stem count in unburned forest than burned forest. "-" indicates lower stem count in unburned forest than burned forest.

TESTS	df	G	Sig.	Stem Counts
Pooled	1	30.01	*	
Heterogeneity (transect)	22	220.07	*	
Total (transect)	23	250.08	*	
Heterogeneity (residual)	8	42.15	*	
Total (residual)	9	72.16	*	
Transect				
R3T1	1	42.36	*	-
R3T2	1	69.35	*	+
R3T3	1	13.17	*	-
R5T1	1	12.38	*	+
R8T1	1	24.91	*	+
R13T2	1	35.66	*	+
R14T1	1	16.71	*	+
Residual				
R5	1	10.27	*	+
R8	1	14.26	*	+
R13	1	14.40	*	+
R14	1	14.35	*	+

Table 2.3. G test summary of black spruce (*Picea mariana*) stem counts in burned and unburned forest. Note: Transect notation indicates Residual number and Transect number. Df = degrees of freedom. Sig. = significant (alpha = 0.0005). "+" indicates greater stem count in unburned forest than burned forest. "-" indicates lowerstem count in unburned forest than burned forest.

TESTS	df	G	Sig.	Stem counts
Pooled	1	78.97	*	
Heterogeneity (transect)	20	206.24	*	
Total (transect)	21	285.22	*	
Heterogeneity (residual)	7	102.27	*	
Total (residual)	8	181.25	*	
Transect				
R3T1	1	25.08	*	+
R3T2	1	34.14	*	+
R5T1	1	16.23	*	+
R5T2	1	20.34	*	+
R8T1	1	11.93	*	-
R8T2	1	28.27	*	-
R9T2	1	18.50	*	+
R13T2	1	35.79	*	+
R14T1	1	14.84	*	+
R15T2	1	24.09	*	+
Residual				
3	1	13.24	*	+
5	1	38.01	*	+
8	1	37.84	*	-
9	1	15.40	*	+
11	1	12.12	*	+
13	1	49.48	*	+
14	1	15.15	*	+

Table 2.4. G test summary of lodgepole pine (*Pinus contorta*) stem counts in burned and unburned forest. Note: Transect notation indicates Residual number and Transect number. Df = degrees of freedom. Sig. = significant (alpha = 0.0005). "+" indicates greater stem count in unburned forest than burned forest. "-" indicates lower stem count in unburned forest than burned forest.

TESTS	df	G	Sig.	Stem counts
Pooled	1	0.50		
Heterogeneity (transect)	14	248.32	*	
Total (transect)	15	248.81	*	
Heterogeneity (residual)	6	49.10	*	
Total (residual)	7	49.60	*	
Transect				
R3T1	1	136.96	*	-
R3T2	1	63.91	*	+
R5T1	1	11.28	*	+
R15T2	1	11.93	*	-
Residual				
3	1	9.00	*	-
5	1	16.57	*	+
13	1	8.47	*	+
15	1	11.20	*	-

Table 2.5. G test summary of larch (*Larix laricina*) stem counts in burned and unburned forest. Note: Transect notation indicates Residual number and Transect number. Df = degrees of freedom. Sig. = significant (alpha = 0.0005). "+" indicates greater stem count in unburned forest than burned forest.

TESTS	df	G	Sig.	Stem counts
Pooled (transect)	1	74.82	*	
Heterogeneity (transect)	3	59.94	*	
Total (transect)	4	134.77	*	
Pooled (residual)	1	71.51	*	
Heterogeneity (residual)	2	20.40	*	
Total (residual)	3	91.91	*	
Transect				
R8T1	1	86.86	*	+
R9T1	1	44.73	*	+
Residual				
8	1	76.58	*	+
9	1	15.19	*	+

Table 2.6. G test summary of white spruce (*Picea glauca*) stem counts in burned and unburned forest. Note: Transect notation indicates Residual number and Transect number. Df = degrees of freedom. Sig. = significant. "+" indicates greater stem count in unburned forest than burned forest.

TESTS	df	G	p value	Sig.	Stem counts
Pooled	1	10.30	0.0050	*	
Heterogeneity (transect)	3	5.32	0.0250	*	
Total (transect)	4	15.62	0.0050	*	
Heterogeneity (residual)	1	4.14	0.0500	*	
Total (residual)	2	14.44	0.0010	*	
Transect					
R9T1	1	6.86	0.0100	*	+
Residual					
9	1	11.64	0.0010	*	+

Table 2.7. G test summary of all spruce species (*Picea spp.*) stem counts in burned and unburned forest. Note: Transect notation indicates Residual number and Transect number. Df = degrees of freedom. Sig. = significant (alpha = 0.0005). "-" indicates lower stem count in unburned forest than burned forest.

TESTS	df	G	Sig.	Stem counts
Pooled (transect)	1	38.82	*	
Heterogeneity (transect)	6	59.13	*	
Total (transect)	7	97.96	*	
Pooled (residual)	1	83.02	*	
Heterogeneity (residual)	5	76.21	*	
Total (residual)	6	159.23	*	
Transect				
R5T2	1	12.12	*	-
R5T3	1	22.36	*	-
R13T3	1	52.79	*	-
Residual				
5	1	46.84	*	-
9	1	42.84	*	-
13	1	68.38	*	-

Table 2.8 a. G test summary of 5 - 15 cm size class stem counts of burned and unburned tree species.
Note: df = degrees of freedom. Sig. = significant (alpha at least 0.0005).
"+" indicates greater stem count in unburned forest than burned forest.

TESTS	df	G	Sig.	Residual	G	df	Sig.	Stem counts
Pooled (residual)	1	48.61	*	5	10.65	1	*	+
Heterogeneity	8	55.24	*	8	17.73	1	*	+
Total	9	103.85	*	9	16.31	1	*	+
				13	17.42	1	*	+
				14	27.65	1	*	+

Table 2.8 b. G test summary of 15 - 30 cm size class stem counts of burned and unburned tree species.
Note: df = degrees of freedom. Sig. = significant (alpha at least 0.02)
"-" indicates lower stem count in unburned forest than burned forest.

TESTS	df	G	Sig.	Residual	G	df	Sig.	Stem counts
Pooled (residual)	1	5.73	*	14	10.96	1	*	-
Heterogeneity	8	14.86						
Total	9	20.59	*					

Table 2.9. Interset correlations between environmental variables
and CCA axes for analysis using all tree species.

Variable	Axis 1	Axis 2	Axis 3
West aspect	0.495	0.116	0.412
Depth to soil (cm)	-0.442	0.415	0.213
South aspect	0.398	0.161	-0.083
Depth to water (cm)	-0.379	-0.180	0.121
Age (years)	-0.309	-0.596	-0.008
Litter (%)	0.245	-0.133	-0.704
Coarse Woody Debris (%)	-0.113	-0.037	-0.277
East aspect	-0.081	0.456	-0.563
North aspect	-0.008	-0.285	0.409

Table 2.10. Interset correlations between environmental variables
and CCA axes for analysis using combined spruce species.

Variable	Axis 1	Axis 2	Axis 3
West aspect	0.535	0.109	0.223
Depth to soil (cm)	-0.409	0.420	0.181
South aspect	0.404	0.171	-0.640
Depth to water (cm)	-0.372	-0.199	-0.073
Age (years)	-0.298	-0.594	-0.359
Litter (%)	0.179	-0.110	-0.594
East aspect	-0.149	0.457	-0.222
Coarse Woody Debris (%)	-0.128	-0.013	-0.328
North aspect	0.019	-0.316	0.450

Table 2.11. Canonical Correspondence Analysis Axes Summary Statistics (using Monte Carlo tests, all eigenvalues were found to be significant at p = 0.001).

Main dataset	Environmental dataset	Statistic	Axis 1	Axis 2	Axis 3
All species	All environmental variables	Eigenvalue	0.182	0.108	0.062
		% variance explained	5.9	3.5	2.0
		cumulative variance explained	5.9	9.4	11.4
		inertia	3.0766		
Combined spruce species	All environmental variables	Eigenvalue	0.177	0.107	0.023
		% variance explained	9.9	6.0	1.3
		cumulative variance explained	9.9	15.9	17.2
		inertia	1.7906		

Table 2.12. Logistic regression model summary of predictors of burn class and deviance explained ("~" = burn class modeled by, Sx = unidentified spruce species, Sw = white spruce, Lt = larch, Sb = black spruce, Pl = lodgepole pine).

Density Models	Null Deviance	Residual Deviance	Deviance Explained (%)	Independent variable	Significant Coefficients	
					Negative	Positive
~ Sx + Sw + Lt	625.1988	423.0174	32.3	Sx	4	0
				Sw	0	0
				Lt	0	1
~ Sx + Sw	625.1988	452.0771	27.7	Sx	4	0
				Sw	0	0
~ Sx + Lt	625.1988	468.0038	25.1	Sx	4	0
				Lt	0	1
~ Sb	625.1988	470.5013	24.7	Sb	2	9
~ Pl	625.1988	550.9481	11.9	Pl	1	1

DBH Models	Null Deviance	Residual Deviance	Deviance Explained (%)	Independent variable	Significant Coefficients	
					Negative	Positive
~ Sx + Sb	625.1988	364.1491	58.2	Sx	3	0
				Sb	0	4
~ Sx + Sw + Lt	625.1988	435.1630	30.4	Sx	4	0
				Sw	0	0
				Lt	0	1
~ Sx + Sw	625.1988	459.8479	26.4	Sx	4	0
				Sw	0	0
~ Sx + Lt	625.1988	474.2738	24.1	Sx	4	0
				Lt	0	1
~ Pl	625.1988	unstable model		Pl		

NOTE TO USERS

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UMI

50 m burned

Transition area
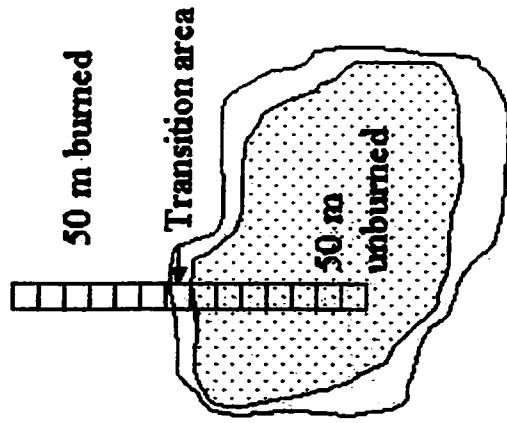
50 m unburned

NOTE: There will be 10 5m x 5m quadrats in burned and unburned areas.
Diagram not to scale.

Figure 2.3. Transect layout across residual edge.

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a. Extreme downhill topography

b. Relatively flat topography

c. Downhill topography

d. Uphill topography
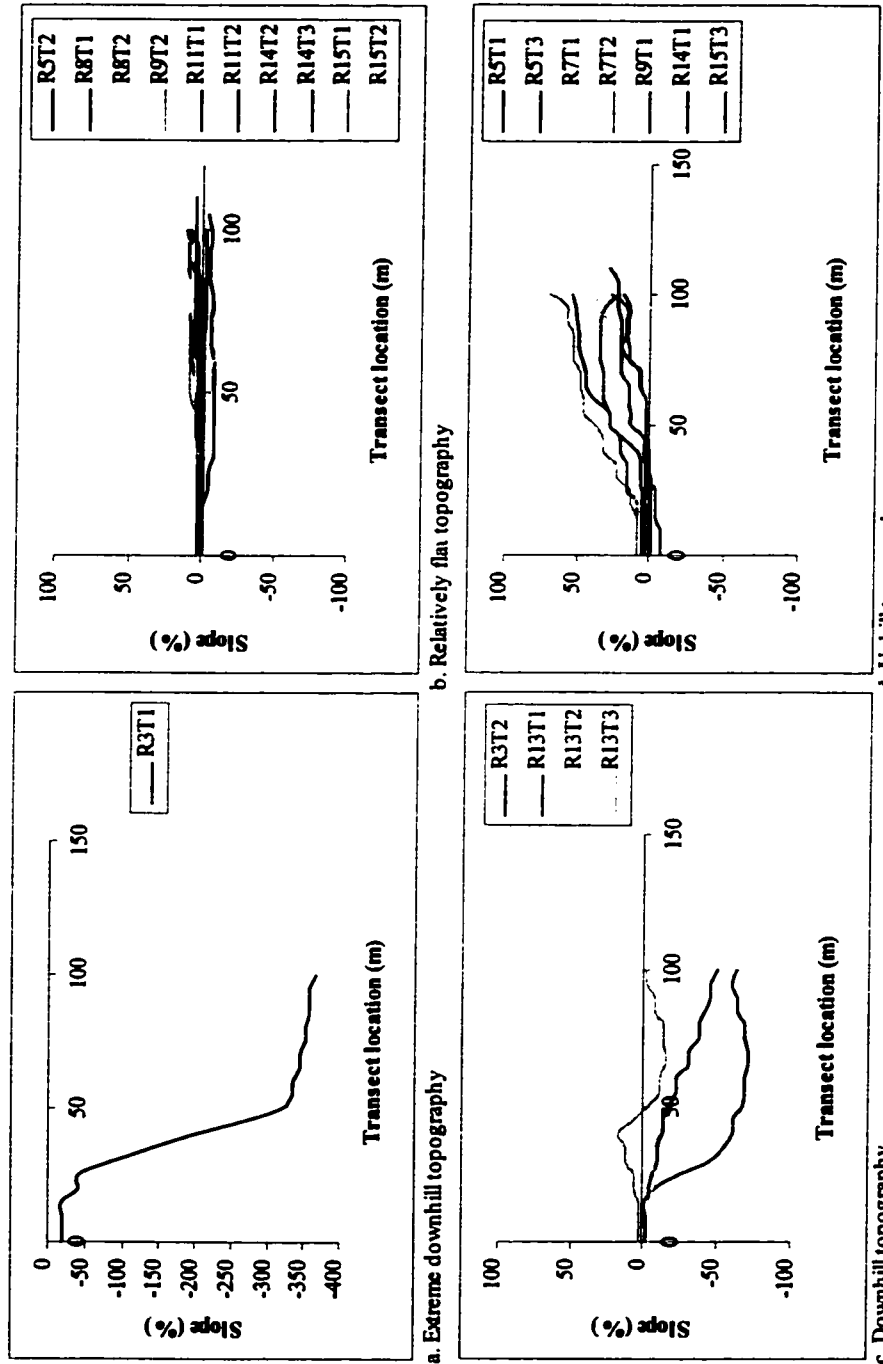
Figure 2.4. Topographical profile of each transect where left to right is burned to unburned forest.
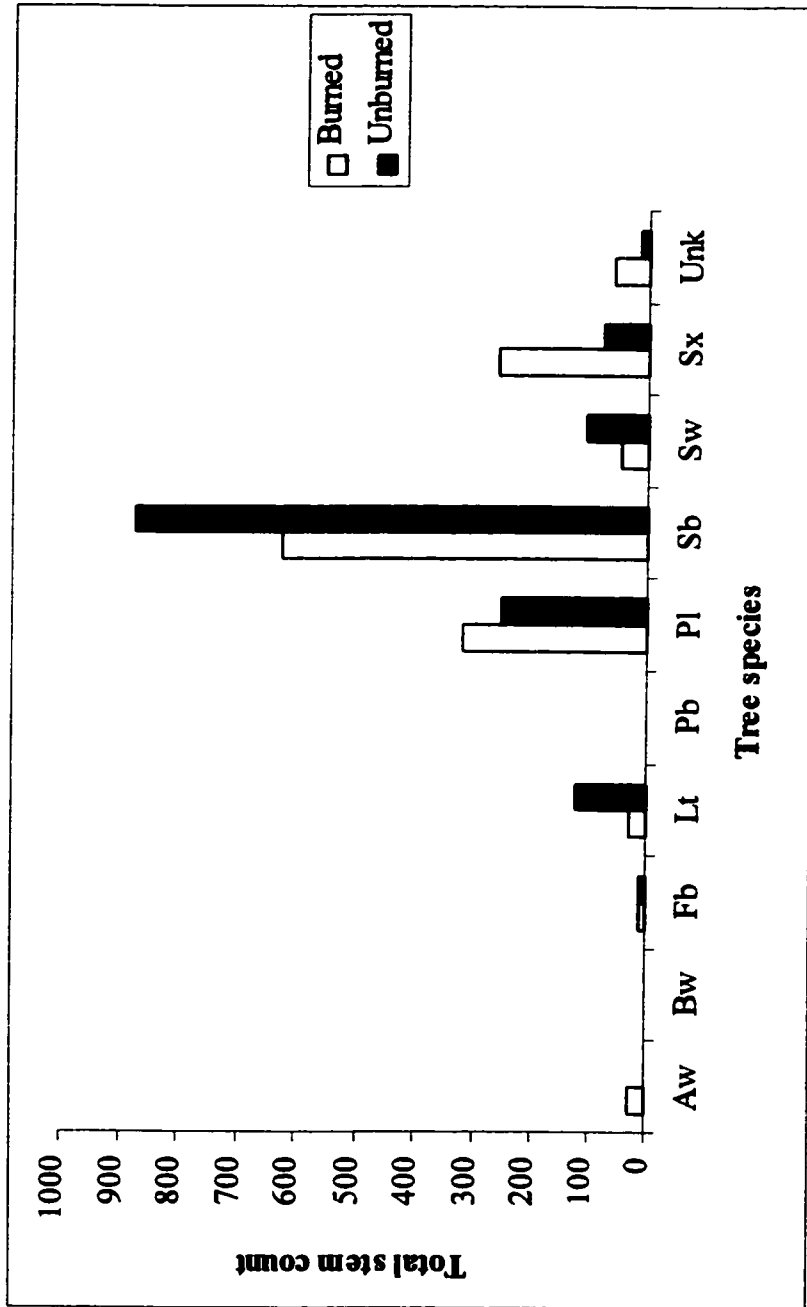
Figure 2.5. Frequency of all tree species in both burned and unburned forest. Where Aw = white aspen, Bw = white birch, Fb = balsam fir, Lt = larch, Pb = balsam poplar, Pl = lodgepole pine, Sb = black spruce, Sw = white spruce, Sx = spruce species, Unk = unknown species.
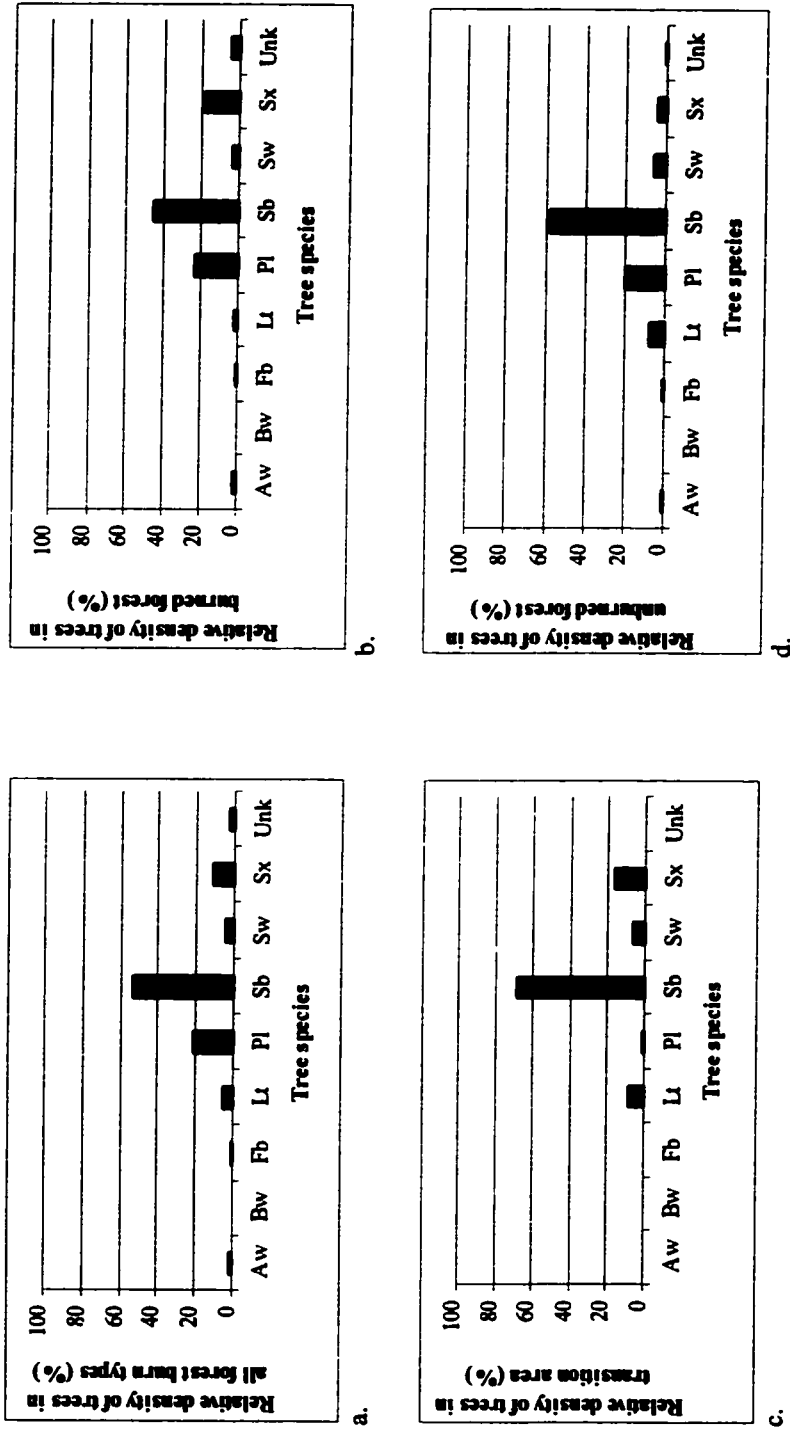
Figure 2.6 a-d. Relative densities of tree species in: a) all forest types, b) burned forest, c) transition area where fire boundary was unclear, d) unburned forest. Species abbreviations: Aw = trembling aspen, Bw = white birch, Fb = balsam fir, Lt = western larch, Pl = lodgepole pine, Sb = black spruce, Sw = white spruce, Sx = unidentified spruce species, Unk = unknown tree species.
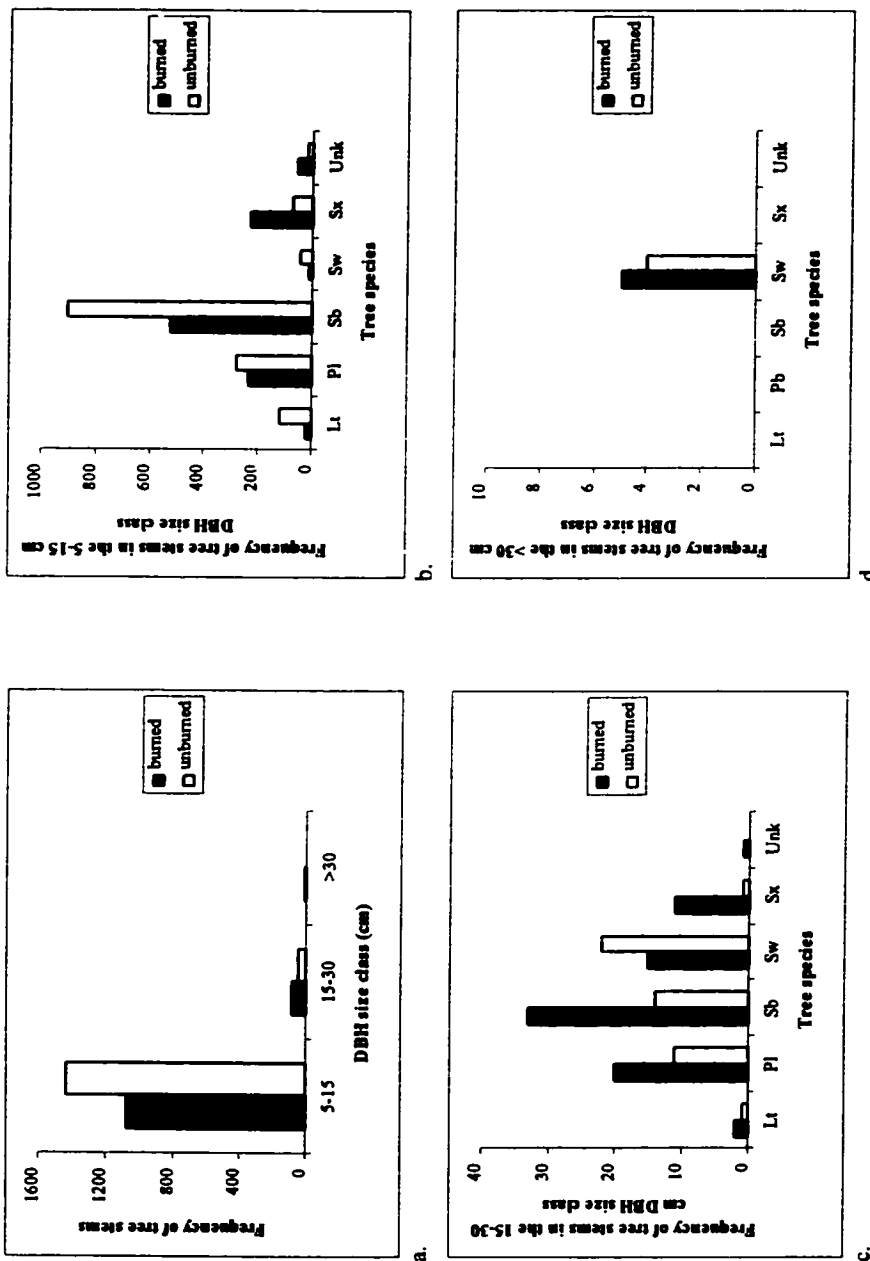
Figure 2.7. DBH size class frequency histograms of burned and unburned trees where Lt = larch, Pl = lodgepole pine, Sb = black spruce, Sw = white spruce, Sx = unidentified spruce, Unk = unknown tree species.
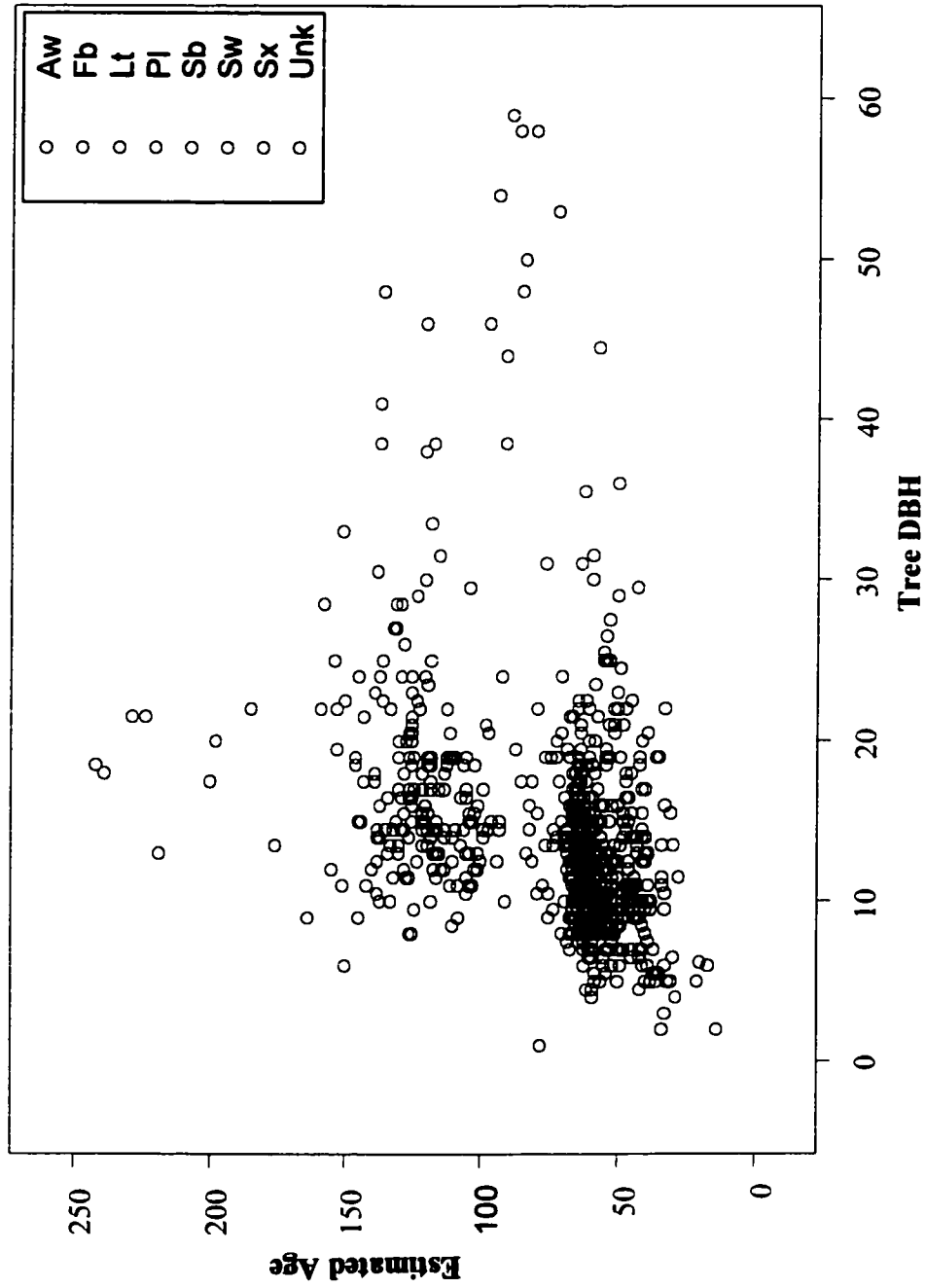
Figure 2.8. Relationship between tree size and age based on tree core samples.
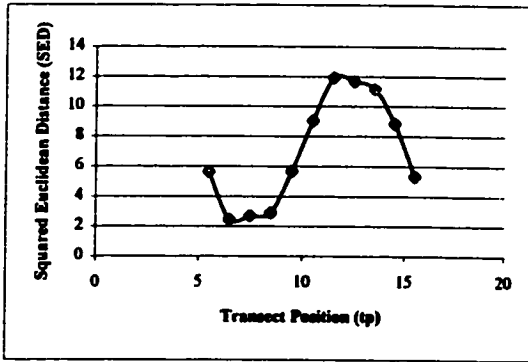
i. Residual 3 Transect 1 (n = 20, fire edge at tp 10-11)
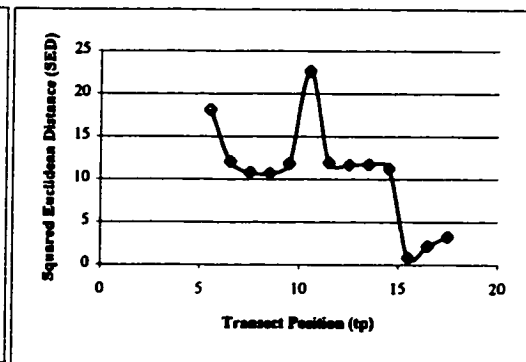
ii. Residual 3 Transect 3 (n = 21, fire edge at tp 9 - 10, 11 - 12)
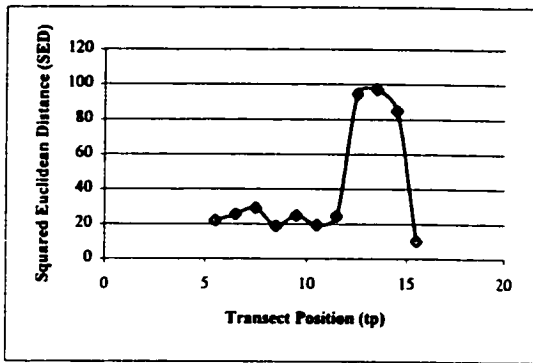
iii. Residual 7 Transect 2 (n = 20, fire edge at tp 10 - 11)
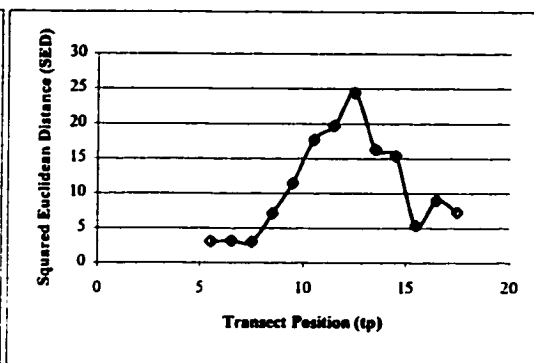
iv.Residual 8 Transect 2 (n=22, fire edge at tp 10-11, 12-13)
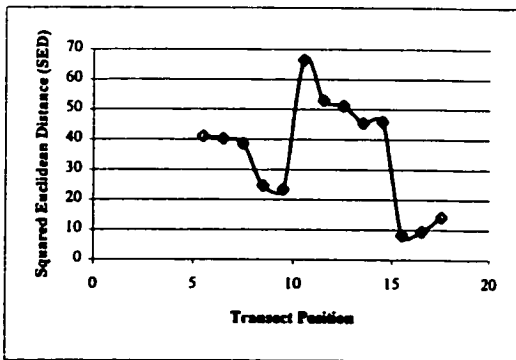
v. Residual 9 Transect 2 (n = 22, fire edge at tp 10 - 11, 12 - 13)
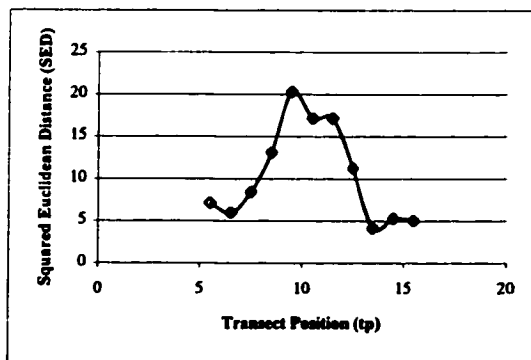
vi. Residual 13 Transect 1 (n = 20, fire edge at tp 10 - 11)

Figure 2.9 a. Edge detection summary of transects which correctly identifies a significant peak of difference near or at the fire boundary.
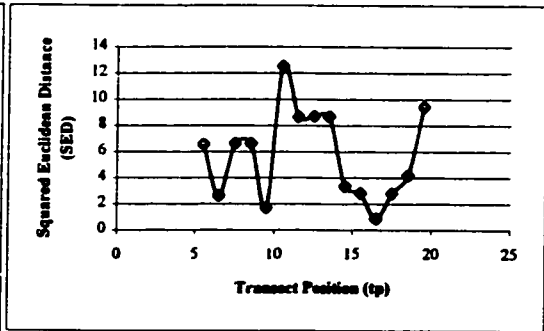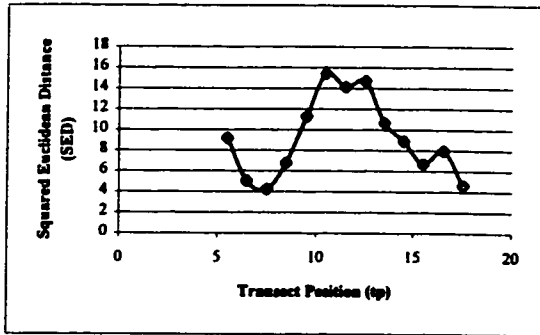
vii. Residual 14 Transect 2 (n = 22, fire edge at tp 10 - 11, 12-1   viii. Residual 14 Transect 3 (n=24, fire edge at tp 10-11, 14-15)
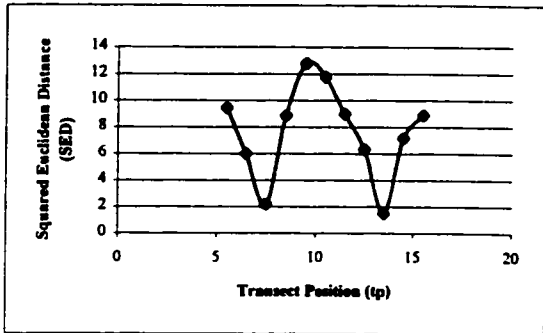
ix. Residual 15 Transect 3 (n = 20, fire edge at tp 10 - 11)   x. Residual 15 Transect 2 (n=22, fire edge at tp 10-11, 12-13)
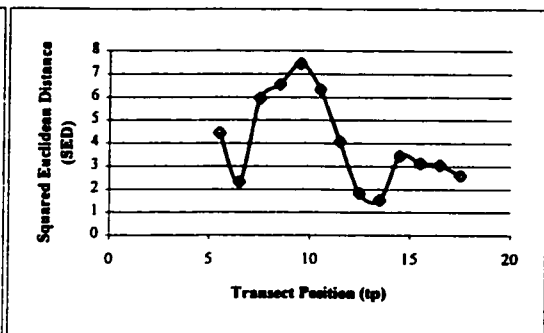
Figure 2.9 a cont'd. Edge detection summary of transects which correctly identifies a significant
peak of difference near or at the fire boundary.
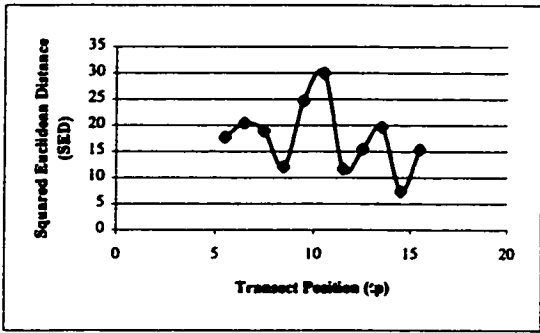
i. Residual 7 Transect 1 (n = 20, fire edge at tp 10 - 11)
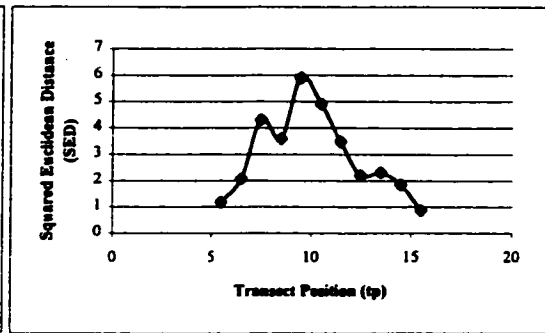
ii. Residual 13 Transect 3 (n = 20, fire edge at tp 10 - 11)
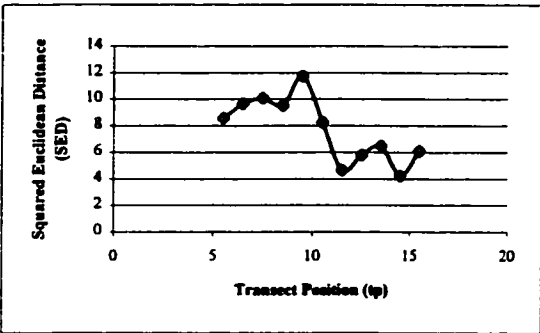
iii. Residual 5 Transect 3 (n = 20, fire edge at transect position 10-11)

Figure 2.9 b. Edge detection summary of transects which correctly identifies a peak of difference near or at the fire boundary.
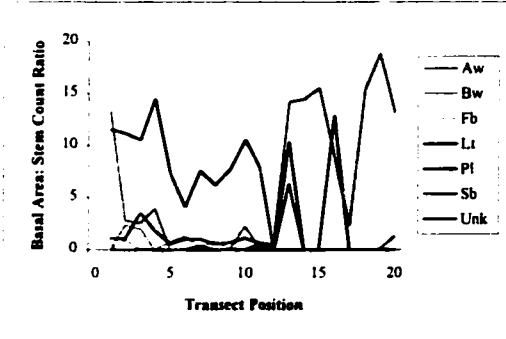
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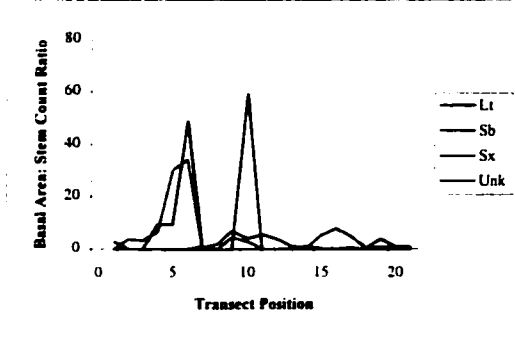
b. Residual 3 Transect 3
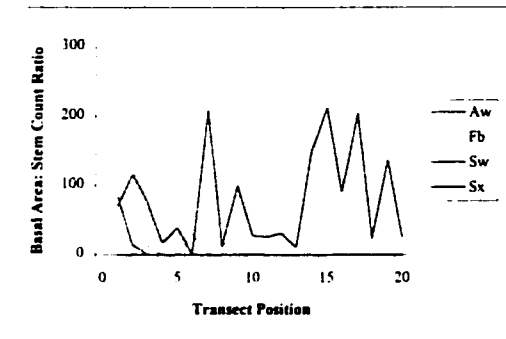
c. Residual 7 Transect 2
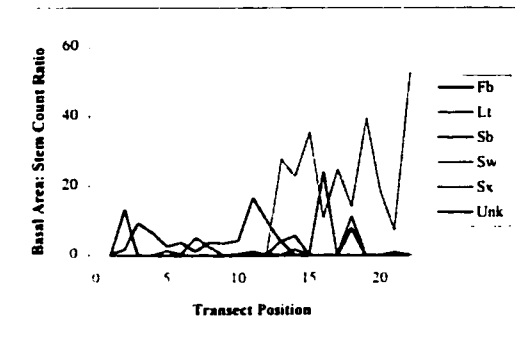
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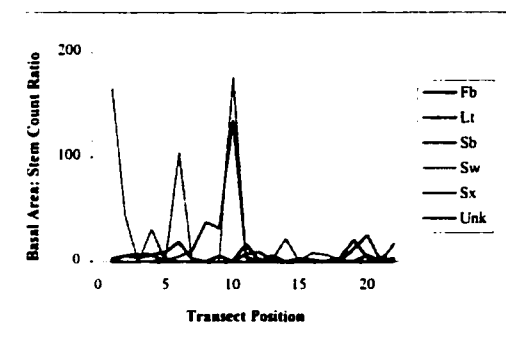
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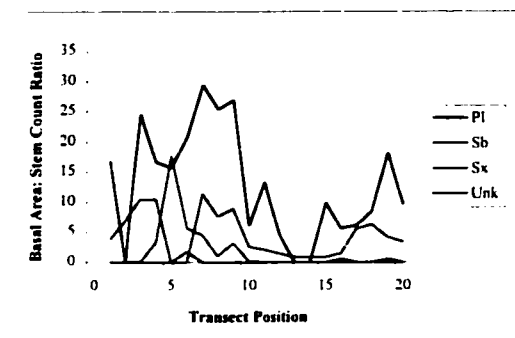
f. Residual 13 Transect 1

Figure 2.10 a. Basal Area: Stem Count ratio for each transect which correctly identifies a significant peak of difference near or at the fire boundary.
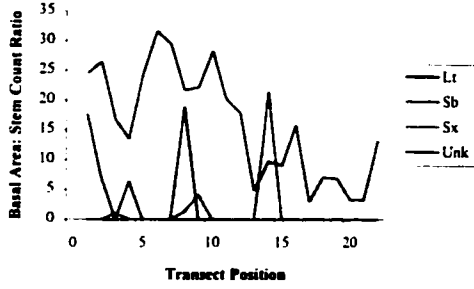
g. Residual 14 Transect 2
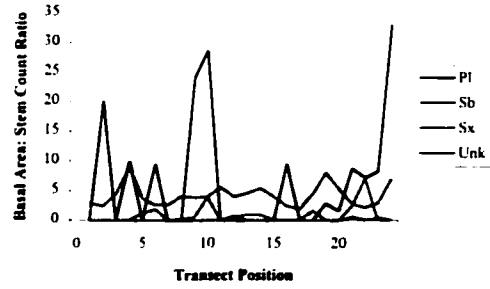
h. Residual 14 Transect 3
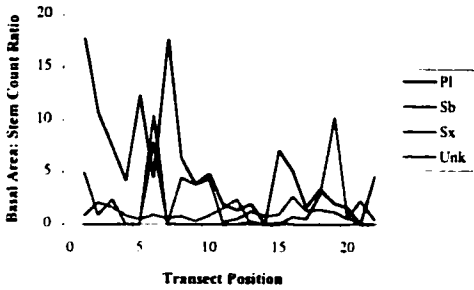
i.Residual 15 Transect 2
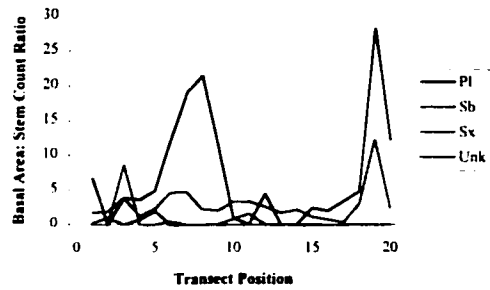
j. Residual 15 Transect 3

Figure 2.10 a cont'd. Basal Area: Stem Count ratio for each transect which correctly identifies a significant peak of difference near or at the fire boundary.
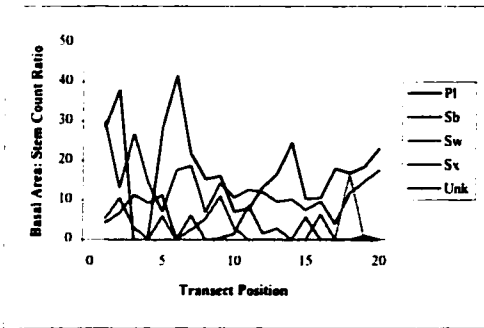
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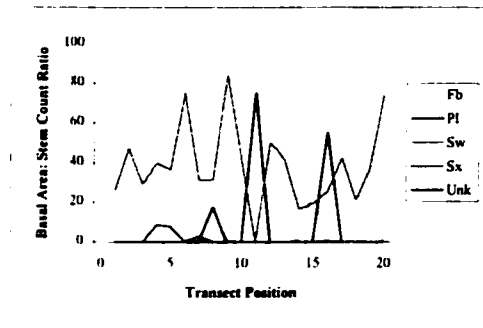
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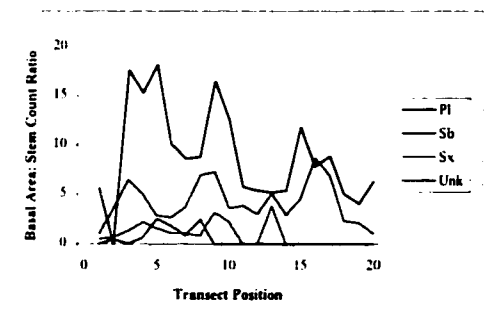
c. Residual 13 Transect 3

Figure 2.10 b. Basal Area: Stem Count ratio for each transect which correctly identifies a peak of difference near or at the fire boundary.
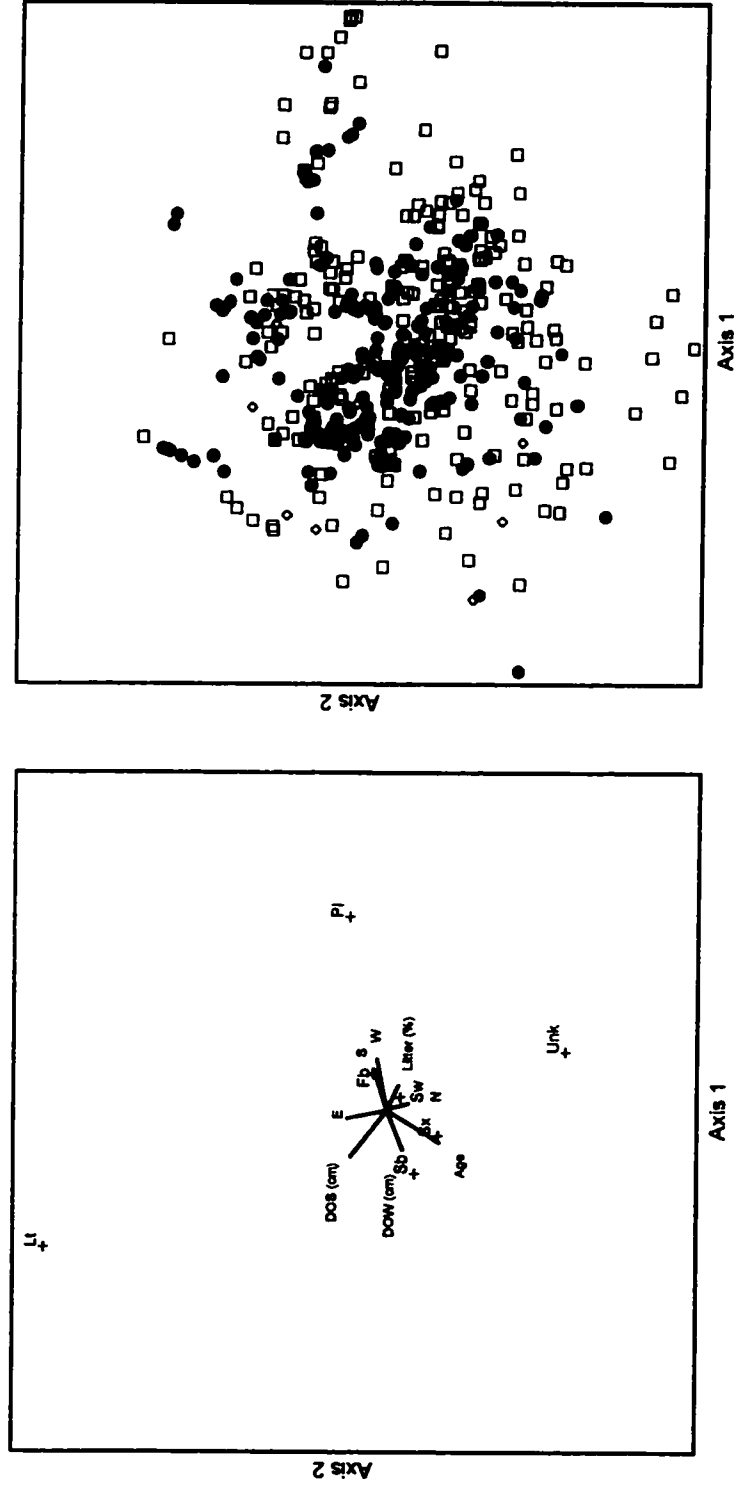
Figure 2.11a. Species and environmental gradients (left) and site (right) ordination scores of axis 1 and 2 from a Canonical Correspondence Analysis using all tree data.
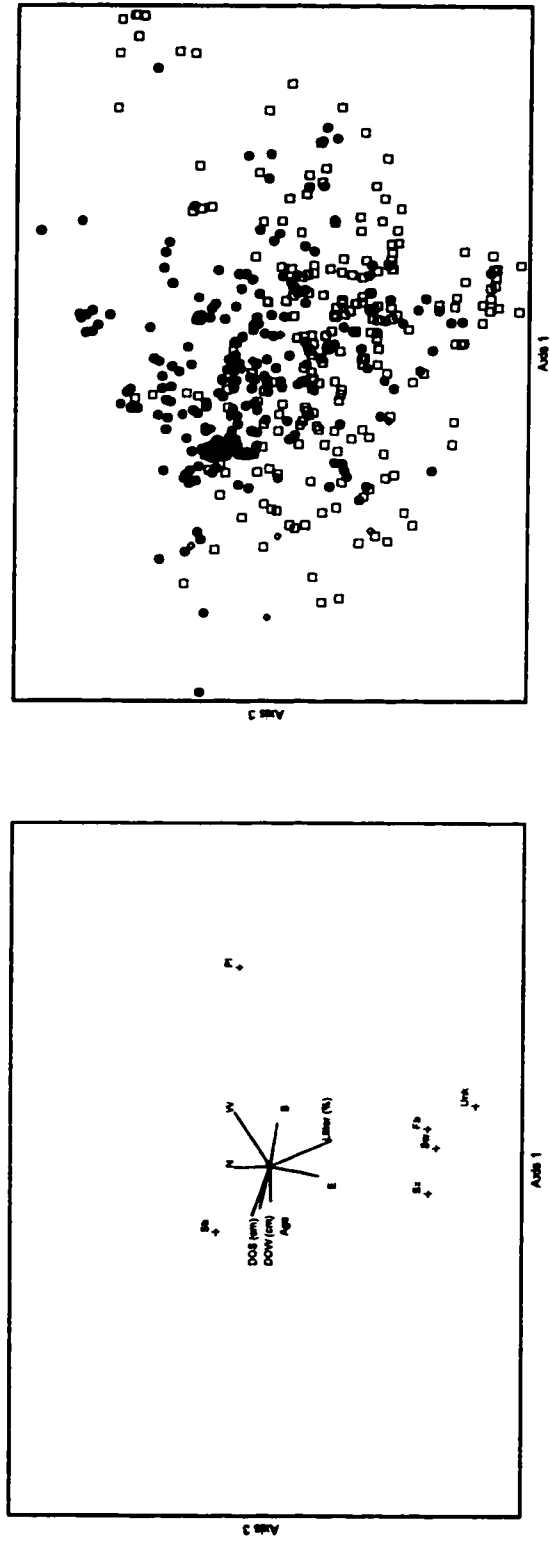
Figure 2.11b. Species and environmental gradients (left) and site (right) ordination scores of axis 1 and 3 from a Canonical Correspondence Analysis using all tree data.
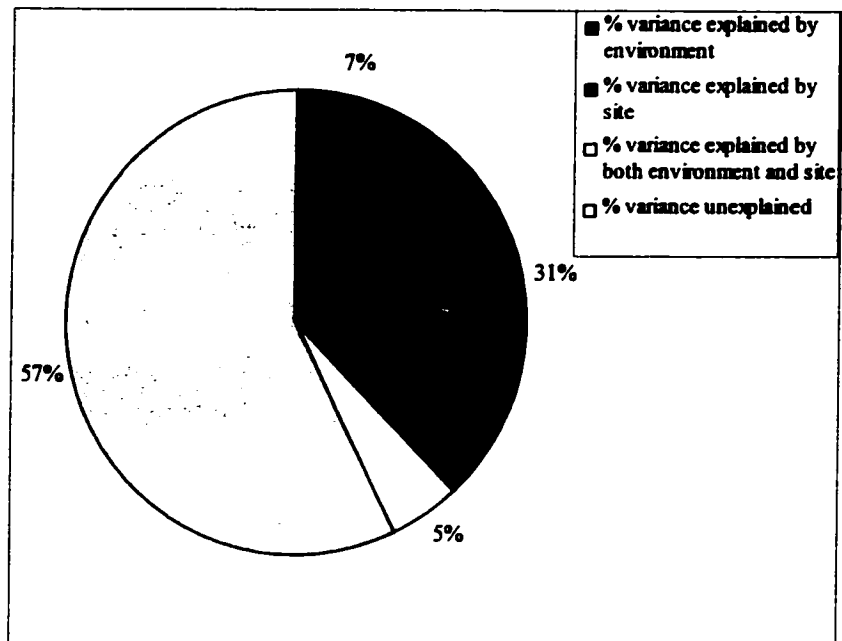
Figure 2.12. Percent of variation explained by environmental variables, site location, both environment and location and unexplained variance for ordination using the full tree species dataset.
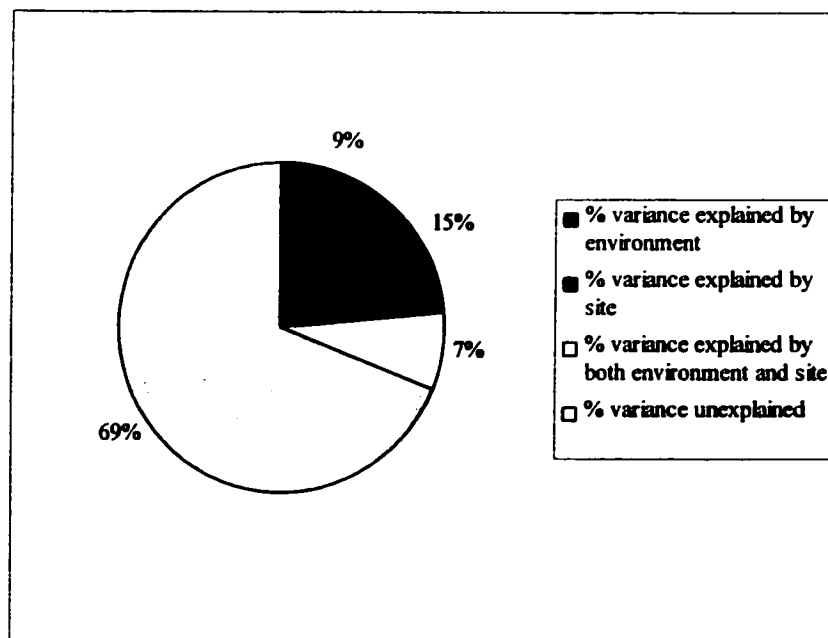
Figure 2.14. Percent of variation explained by environmental variables, site location, both environment and location and unexplained variance for ordination using the lumped spruce species dataset.
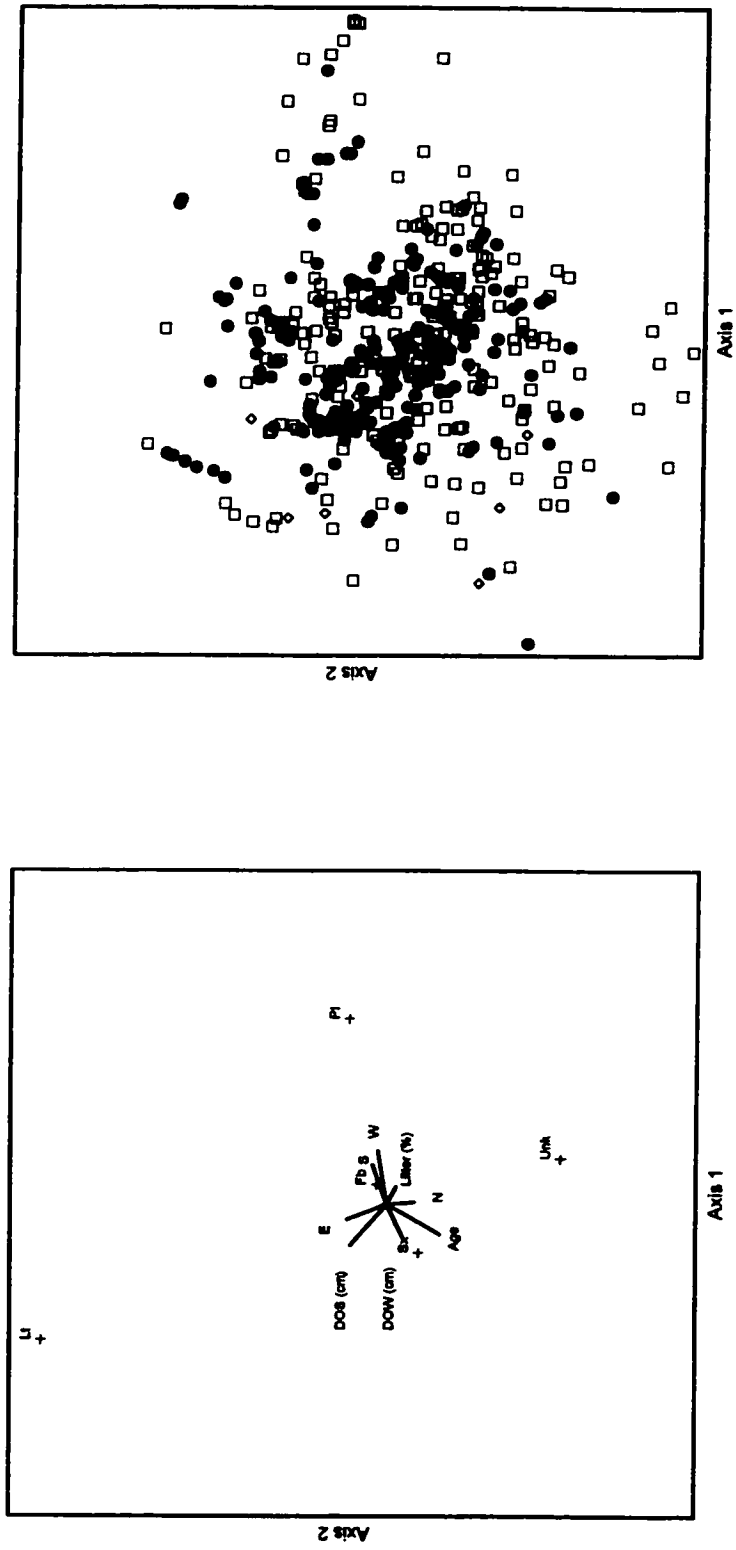
Figure 2.13a. Species and environmental gradients (left) and site (right) ordination scores of axis 1 and 2 from a Canonical Correspondence Analysis using combined spruce species data.
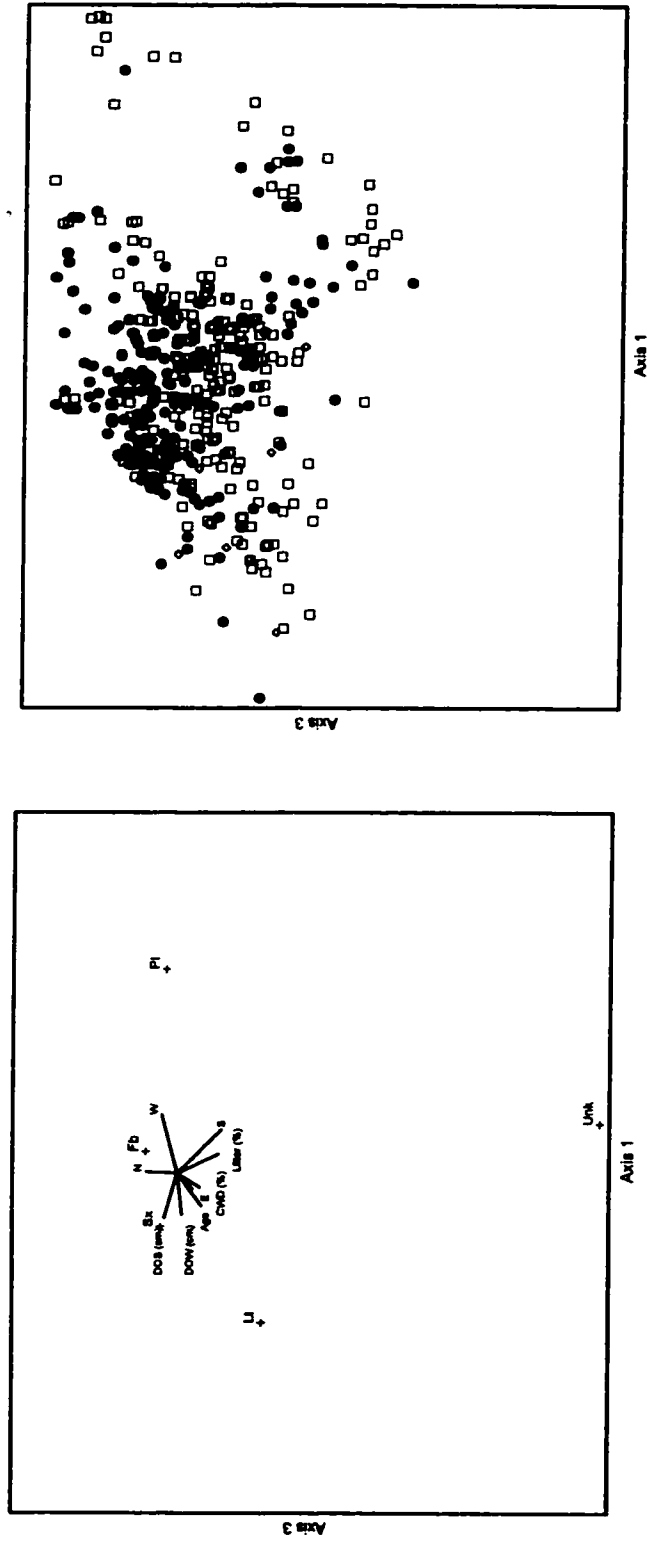
Figure 2.13b. Species and environmental gradients (left) and site (right) ordination scores of axis 1 and 3 from a Canonical Correspondence Analysis using combined spruce species data.
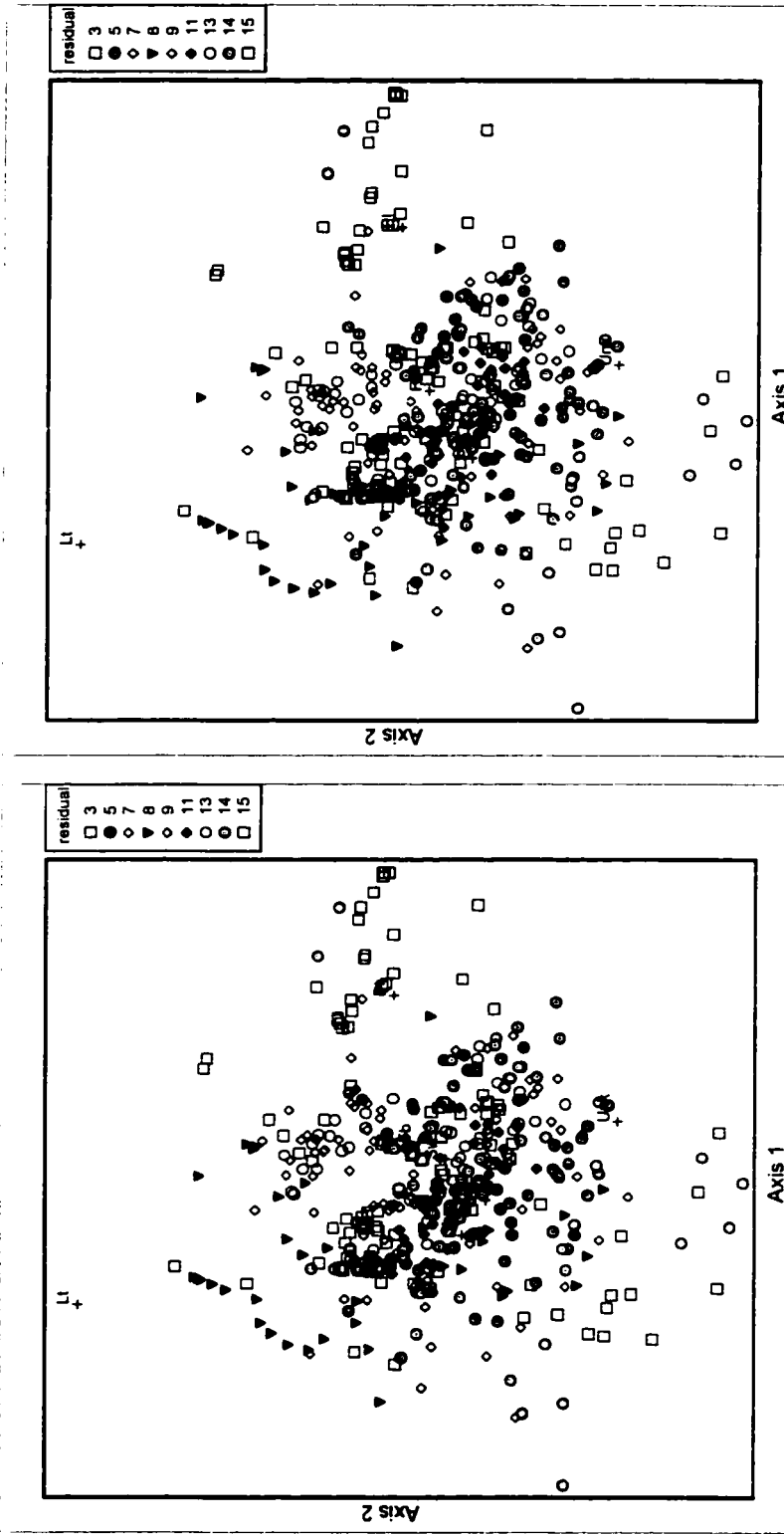
Figure 2.15. Canonical Correspondence Analysis residual site scores from all tree species (left) and spruce species combined (right).
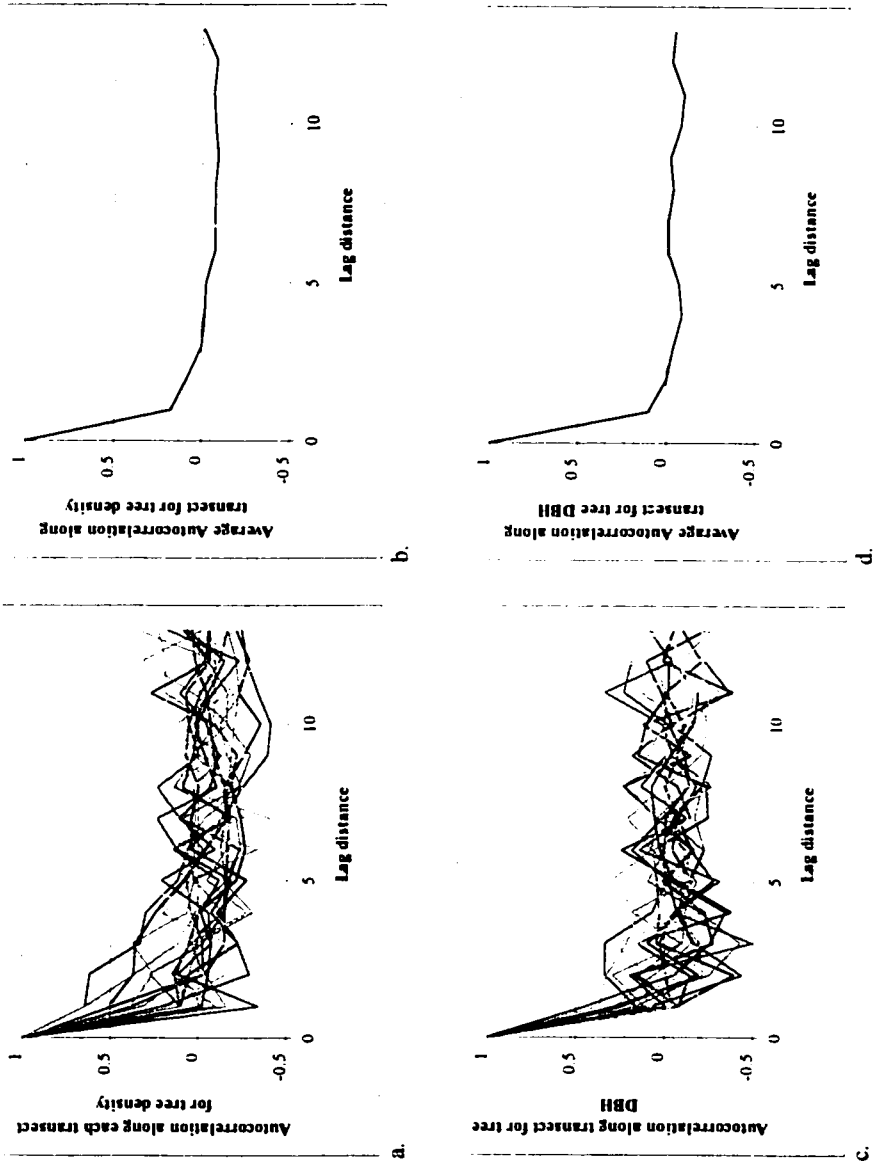
Figure 2.16. Autocorrelation at each lag distance for tree density and DBH along each transect (left) and average autocorrelation of tree density and DBH (right).

2.6 Literature Cited

Acker, S.A., E.K. Zenner and W.H. Emmingham. 1998. Structure and yield of two-aged stands on the Willamette National Forest, Oregon: implications for green tree retention. Canadian Journal of Forest Research 20: 749-758.

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island, Washington DC, U.S.A.

Alberta Forest Protection. 2001. Historical Wildfire Information. Government of Alberta. http://envweb.env.gov.ab.ca/env/forests/fpd/

Asselin, J., M.J. Fortin, and Y. Bergeron. 2001. Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Quebec boreal forest. Forest Ecology and Management 140: 29-37.

Barrett, S.W. 1988. Fire suppression's effects on forest succession within a central Idaho wilderness. Western Journal of Applied Forestry 3: 76 – 80.

Beckingham, J.D., I.G.W. Corns, and J.H. Archibald. 1996. Field Guide to Ecosites of West-Central Alberta. Canadian Forest Service Special Report 9. Northern Forestry Centre, Edmonton, Alberta, Canada.

Bergeron, Y. and J. Brisson. 1990. Fire regime in red Pine stands at the northern limit of the species' range. Ecology 71: 1352-1364.

Bessie, W.C. and E.A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology 76: 747-762.

Burgess, C.J. 1997. Forested landscape patterns in the western boreal mixedwood forest of Alberta: Riparian forests, fire history, canopy composition and topography. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Camp, A., C. Oliver, P. Hessburg, and R. Everett. 1997. Predicting late-successional fire refugia pre-dating European settlement ir the Wenatchee Mountains. Forest Ecology and Management 95: 63-77.

Cressie, N.A. 1991. Statistics for Spatial Data. *In* Statistics for Spatial Data. John Wiley and Sons, New York, U.S.A.

Cumming, S.G. 2001. Forest type and wildfire in the Alberta boreal mixedwood: what do fires burn? Ecological Applications 11: 97-110.

Dale, M.R.T. and M.J. Fortin. 2002. Spatial autocorrelation and statistical tests in ecology. Ecoscience *in press*.

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

Delong, S.C. and W.B. Kessler. 2000. Ecological characteristics of mature forest remnants left by wildfire. Forest Ecology and Management 131: 93-106.

Despain, D.G. 1991. Yellowstone Vegetation: Consequences of Environment and History in a Natural Setting. Roberts Rinehart Publishing. Colorado, U.S.A..

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

Farrar, J.L. 1995. Trees in Canada. Fitzhenry and Whiteside Limited and Canadian Forest Service. Ontario, Canada.

Foster, D.R. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. Canadian Journal of Botany 61: 2459-2471.

Francis, S.R. 1996. Linking Landscape Pattern and Forest Disturbance: Fire History of the Shakwak Trench, Southwest Yukon Territory. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Fries, C., O. Johansson, B. Pettersson, and P. Simonsson. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. Forest Ecology and Management 94: 89-103.

Fryer, G.I. and E.A. Johnson. 1987. Reconstructing fire behavior and effects in a subalpine forest. Journal of Applied Ecology 25: 1063-1072.

Halpern, C.B., S.A. Evans, C.R. Nelson, D. McKenzie, D.A. Liguori, D.E. Hibbs, and M.G. Halaj. 1999. Response of forest vegetation to varying levels and patterns of

green-tree retention: an overview of a long-term experiment. Northwest Science 73: 27-44.

Heinselman, M.L. 1978. Fire intensity and frequency as factors in the distribution and structure of northern forests. *In* Proceedings of the Conference Fire Regimes and Ecosystem Properties. US Department of Agriculture. General Technical Report WO-26.

Hörnberg, G., O. Zackrisson, U. Segerström, B.W. Svensson, M. Ohlson, R.H.W. Bradshaw. 1998. Boreal swamp forests. Bioscience 48: 795-802.

Hosmer, D.W. and S. Lemeshow. 1989. Applied Logistic Regression. John Wiley and Sons, New York, U.S.A.

Johnson, D., L. Kershaw, A. MacKinnon and J. Pojar. 1995. Plants of the Western Boreal Forest and Aspen Parkland. Lone Pine Publishing and Canadian Forest Service. Alberta, Canada.

Johnson, E.A. 1992. Fire and vegetation dynamics: Studies from the North American Boreal Forest. Cambridge University Press, New York, U.S.A.

Kiil, A.D. 1975. Fire spread in a black spruce stand. Canadian Forest Service Bi-Monthly Research Notes 31: 2-3.

Lauriault, J. 1989. Identification Guide to the Trees of Canada. Fitzhenry and Whiteside Limited. Ontario, Canada.

Legendre, P., and L. Legendre. 1998. Numerical Ecology 2nd edition. Elsevier Science. Amsterdam, Netherlands.

Ludwig, J.A. and J.M. Cornelius. 1987. Locating discontinuities along ecological gradients. Ecology 68: 448-450.

Manley, B.F.J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology. 2nd edition. Chapman and Hall. New York, U.S.A.

Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74: 2215-2230.

Palmer, M.W. 2000. The Ordination Webpage.

http://www.okstate.edu/artsci/botany/ordinate. Oklahoma State University, Oklahoma, U.S.A.

Quirk, W.A. and D.J. Sykes. 1971. White spruce stringers in a fire-patterned landscape in interior Alaska. *In* Fire in the Northern Environment: a Symposium. (Eds.) C.W. Slaughter, R.J. Barney and G.M. Hansen. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon, U.S.A.

Romme, W.H. and D.H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62: 319-326.

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52: 199-221.

Rowe, J.S. 1970. Spruce and fire in northwest Canada and Alaska. *In* Proceedings of the Tenth Annual Tall Timbers Fire Ecology Conference. Tallahassee, Florida, U.S.A.

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

Samran, S., P.M. Woodard and R.L. Rothwell. 1995. The effect of soil water on ground fuel availability. Forest Science 41: 255-267.

Schimmel, J. and A. Granstrom. 1997. Fuel succession and fire behavior in the Swedish boreal forest. Canadian Journal of Forest Research 27:1207-1216.

Segerström, U., R. Bradshaw, G. Hörnberg, and E. Bohlin. 1994. Disturbance history of a swamp forest refuge in northern Sweden. Biological Conservation 68: 189-196.

Smyth, C.L. 1999. Overstory composition of live residuals in fire affected landscapes of northern Alberta. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry 3rd edition. W.H. Freeman and Company, New York, U.S.A.

S-PLUS. 1999. Guides to Statistics, Volume 2. Data Analysis Products Division. Math

Soft, Inc. Washington, U.S.A.

Sweetgrass Consultants. 1997. Environmentally Significant Areas of Alberta. Prepared
by Sweetgrass Consultants Ltd. Calgary, Alberta, Canada.

Takaoka, S. and K. Sasa. 1996. Landform effects on fire behavior and post-fire
regeneration in the mixed forests of northern Japan. Ecological Research 11:339-
349.

Taylor, A.H. and C.N. Skinner. 1998. Fire history and landscape dynamics in a late-
successional reserve, Klamath Mountains, California, U.S.A. Forest Ecology and
Management 111: 285-301.

Ter Braak, C.F.S. 1986.Canonical correspondence analysis: a new eigenvector technique
for multivariate direct gradient analysis. Ecology 67:1167-1179.

Ter Braak, C.F.S. 1990. Update notes: CANOCO Version 3.10. Agricultural
Mathematics Group, Wageningen, The Netherlands.

Ter Braak, C.F.S. 1994. Canonical community ordination. Part I: Basic theory and linear
methods. Ecoscience 1: 127-140.

Turner, M.G., W.H. Romme, and R.H. Gardner. 1999. Prefire heterogeneity, fire severity
and early postfire plant reestablishment in subalpine forests of Yellowstone
National Park, Wyoming. International Journal of Wildland Fire 9: 21-36.

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

Turner, M.G. and W.H. Romme. 1994. Lanscape dynamics in crown fire ecosystems.
Landscape Ecology 9: 59-77.

Van Wagner. C.E. 1983. Fire behaviour in northern conifer forests and shrublands. In
The Role of Fire in Northern Circumpolar Ecosystems. (Eds.) R.W. Wein and
D.A. MacLean. John Wiley and Sons, New York, U.S.A.

Van Wilgen, B.W., K.B. Higgins, and D.U. Bellstedt.1990. The role of vegetation

structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. Journal of Ecology 78: 210-222.

Varem-Sanders, T.M.L. and I.D. Campbell.1996. Dendroscan: a tree-ring width and density measurement system. UBC Press, Vancouver, British Columbia, Canada.

Viereck, L.A. 1973. Wildfire in the taiga of Alaska. Quaternary Research 3: 465 – 495.

Whelan, R.J. 1995. The Ecology of Fire (Cambridge Studies in Ecology). Cambridge University Press, New York, U.S.A.

Zackrisson, O. 1977. Influence of forest fires on the north Swedish boreal forest. Oikos 29: 22-32.

CHAPTER 3

UNDERSTORY VASCULAR PLANT DIVERSITY IN RESIDUALS OF DIFFERENT SIZES AND AGES

3.1 Introduction

The boreal forest is composed of a mosaic of differently aged stands created from past forest fires and other natural disturbances. In any one year, many fires can occur within a landscape but only a small proportion will be extensive enough to cause large-scale changes in forest stand age and composition (Turner and Romme 1994). Burn intensity can range from severe to none resulting in a patchwork of unburned islands within the burned forest. These islands, known as fire residuals, contain unique habitat in the disturbed landscape (Delong and Kessler 2000). Because these areas are less disturbed than surrounding areas, they are able to support greater floristic diversity (Turner et al. 1998, Franklin 1993, Hörnberg et al. 1998). Residuals are commonly found in mesic areas, depressions, and ravines where topographical features and moisture regime can act as a natural fuel break (Foster 1983, Quirk and Sykes 1971). In previous studies, fire residuals were generally composed of late successional forests, with large diameter trees and have relatively old stand age compared to surrounding forest (Quirk and Sykes 1971, Hörnberg et al. 1998, Delong and Kessler 2000). This study found high inter-site variability in forest stand structure and local topography among residuals but there was weak evidence that residuals were composed of greater densities of black spruce and larch and may be slightly younger than burned forest.

Presence and spatial pattern of residuals are important features in a disturbed landscape and are especially important in large infrequent disturbances (Turner et al. 1998, Foster et al. 1998). They provide refugia for taxa that require late-successional habitats such as ungulates (Thomas et al. 1976, Euler 1981, Gasaway and Dubois 1985),

birds (Schieck and Hobson 2000, Hoyt 2000) and invertebrates (Gandhi 1999). Fire residuals have been studied extensively in the Swedish boreal forest (Hörnberg *et al.* 1998, Kuusinen 1996, Segerström *et al.* 1994), and are known as 'biological hotspots' of the boreal forest (Hörnberg *et al.* 1998). In Swedish boreal forests, less than two hectares of residual forest can contain over a third of the total number of bryophytes and many red-listed fungi species (Ohlson *et al.* 1997). These residuals cover only 5% of the forest landscape but contain more than 50% of the forest vascular species diversity (Ohlson *et al.* 1997). Hörnberg *et al.* (1998) and Segerström *et al.* (1994) attribute this phenomenon to the wide range of hydrotopography, and ecological niches within a limited area. Despite the growing interest in biological legacies, there have been very few diversity studies in residuals and whether they can be considered 'biological hotspots' in Canada's boreal landscape (Gandhi 1999, Bottorff 2001).

Fire residuals act as refugia for plant species diversity (Zackrisson 1977, Ohlson *et al.* 1997), and are important in facilitating re-colonization of the burned areas (Turner and Romme 1994). They are especially important in large infrequent disturbances where seed and vegetative dispersal from surrounding unburned forest is limited (Franklin 1993, Turner *et al.* 1994, Turner and Romme 1994, Halpern and Spies 1995, Turner *et al.* 1998, Asselin *et al.* 2001). Residuals that escape several fires results in later successional forest patches containing a range of tree sizes, environmental conditions, greater amount of snags and coarse woody debris within the burned forest (Hörnberg *et al.* 1998, Delong and Kessler 2000). This creates increased habitat heterogeneity which can lead to distinctive or greater floristic diversity (Franklin 1993) in residuals. If residuals continue to persist within a fire-affected landscape, their ecological role becomes increasingly important.

In this chapter, my objectives were: 1) to determine variability of vascular understory biodiversity and whether residuals have similar understory community composition, and 2) to compare vascular understory diversity and species richness with

residual average age and residual size. The probability of a large area to randomly escape fire is less than a small area therefore I would expect large residuals to have similar environmental conditions that influence residual formation. If residual formation is not random, they may have similar environmental conditions resulting in similar floristic compositions. If residuals are older than the surrounding forest matrix, they should also be able to support greater diversity of understory species than younger stands, due to increased habitat heterogeneity.

3.2 Methods

Please see Chapter 2 Section 2.2 for information on study site, residual and transect locations.

Field Data Collection

In each residual, sixty random $1m^2$ quadrats were used to sample understory vascular plants. A 50 m buffer from the fire edge was maintained throughout data collection to avoid immediate edge effects. Understory vascular species percent cover, tree canopy percent cover, water cover, litter and coarse woody debris percent cover were visually estimated. Canopy cover estimates were not collected for four of nine residuals. Residual forest age estimates were obtained from the unburned forest resulting in a total of 20-30 tree cores per residual (please see Chapter 2 Section 2.2 for coring and ageing methods).

Species Identification

Vascular species identification was performed in the field using field guides and floras (Johnson *et al.* 1995, Moss 1994). Unknown species were collected, dried and pressed. These specimens were identified and compared with known specimens in the

University of Alberta Vascular Plant Herbarium. Nomenclature followed the Flora of Alberta (Moss 1994).

3.3 Analyses

General analyses

Data summaries of species richness, evenness, Shannon's diversity index and Simpson's index of diversity for quadrats and averages for each residual were calculated using PC-Ord 4.14 software (McCune and Mefford 1999).

Box plots of diversity, evenness and species richness of each residual were used to illustrate any trends in the data. Kruskal-Wallis rank sum tests (S-PLUS 1999, Sokal and Rohlf 1995) were used to determine whether there were significant differences in quadrat diversity and species richness between residuals. Multiple comparison analysis was also used for residual pairwise comparisons of understory diversity (S-PLUS 1999). Average diversities of large and small residuals were then compared using two-sample t-test (Sokal and Rohlf 1995). S-PLUS 2000 was used for all general statistical analyses.

Figures were plotted in MS Excel to visualize the relationships among species diversity, species richness, average residual age and residual size.

Cluster Analysis

Cluster analysis was performed to identify common species groups, and to detect relationships between communities and environment. This method can provide information on community types and the range of communities within residuals. For this understory dataset, I used a hierarchical clustering method with average linkage clustering and the Sorensen (Bray and Curtis) distance measure. These options were chosen for their popular use in ecology and robustness to outliers (Jongman et al. 1995, McCune and Mefford 1999). PC-Ord 4.14 software was used for cluster analysis. Cluster

groups were then categorized based on the habitat requirements of vascular species found in Moss (1994) and Johnson *et al.* (1995).

Ordination

Some residuals were highly diverse in understory vascular species however, some species occurred only once among the residuals. Ordination methods are known to be sensitive to rare species and outliers therefore can produce unclear results (Jongman *et al.* 1995). For that reason, only species occurring in more than 5% of quadrats were used in the ordination analyses. Outlier analysis was performed on both datasets and removed for the analyses. Indirect ordination analysis was used on the entire dataset because canopy data was not recorded for four of the nine residuals. The objective was to determine similarities in species composition among residuals so that environmental conditions could be inferred. Reciprocal Averaging (RA) was used to determine whether certain species groups occur throughout all residuals (Hill 1973, Hill and Gauch 1980). Presence-absence data was used for this analysis because it produced clearer trends in the ordination. Direct gradient analysis was used for the five residuals that had canopy data. Canonical Correspondence Analysis (CCA) was used to determine the relationship between understory composition and diversity and environmental characteristics (Ter Braak 1986, 1994). Abundance data was used for this analysis. PC-Ord 4.14 software was used for all ordination and outlier analyses (McCune and Mefford 1999).

Ecosite Classification

Canopy and understory species composition and abundance were used to classify the ecosite type of each residual based on Beckingham *et al.* (1996). The objectives of using this subjective method were to determine community types that characterize residuals, to determine compositional community similarities between residuals and to infer general environmental conditions.

Linear Regression Analyses

Linear regression was used to determine the relationship of average residual age and size on understory species richness and diversity. The objective of this analysis was to determine whether species richness and diversity could be predicted based on average residual age and size. Residual area was log transformed while average residual age was transformed using arcsinh y (Legendre and Legendre 1998). Analyses were performed using data from each quadrat and averages from each residual. S-PLUS 2000 was used for all analyses.

3.4 Results

Average ages in unburned quadrats were highly variable ranged from 60 to 111 years (Table 2.1). Species richness, evenness and diversity varied considerably between residuals (Figure 3.1). There were significant differences in species richness, evenness, and diversity in quadrats among residuals but the differences were not significant when comparing average species richness, evenness and diversity among residuals (Table 3.1). There was no apparent relationship between average residual age, residual size and diversity (Figure3.3). Species groups were arranged along a moisture gradient from open woodland communities to bog communities (Figure 3.5-3.7, Table 3.4). Understory in residuals was governed by canopy type and local moisture conditions (Figure 3.7, Table 3.4). Ecosite classification also supported these findings where all sites were generally mesic to hygric in nature (Table 3.6). Residual size was weakly but positively related to species diversity while residual average age was negatively related to species diversity and richness (Figures 3.8-3.13).

General Analyses

Burned quadrats (mean age = 78.6 years) were slightly older than unburned (mean age = 72.9 years) residual quadrats (t = 2.5091, d.f. = 926, p = 0.0123) however, unburned quadrat average ages ranged from 60 to 111 years (Table 2.1).

A total of 80 vascular plant species were identified to species, 40 vascular taxa were identified only to genus and 13 vascular specimens were unidentifiable (Appendix Table A.1) for a total of 133 "species". Some specimens could not be identified due to immaturity of the plant or lack of vegetative or reproductive structures. Each residual contained a range of 14 – 55 vascular species (Appendix Table A.2). There were significant differences in species richness, evenness, Simpson's diversity index and Shannon's diversity index among quadrats (Table 3.1).

Although there was high variability in diversity and species richness in quadrats within residuals (Figure 3.1), the differences between average diversity, average species richness, Simpson's diversity and Shannon's diversity among residuals (Table 3.1) were not significant. Twelve residual pair combinations had significantly different diversities (Figure 3.4). Residual 3 was different from most residuals while residual 7 was different from 9, 11, 13, and 14. No visible trends in species diversity and average residual age (Figure 3.2) and in species diversity and residual size were detected (Figure 3.3). Mean diversity of small and large residuals was not significantly different (t = 0.7582, d.f. = 7, p = 0.4731).

Cluster Analysis

To determine the range of community types within residuals, species composition was classified using eight groups to establish common species groups and associations. Species composition was arbitrarily broken down into eight groups so that generalizations could be made about each community type. Species groups ranged from open woodland species, such as *Epilobium angustifolium* and *Linnaea borealis*, to moist woodland species, such as *Moneses uniflora* and *Mitella nuda*, to acidic boggy type species, such as *Oxycoccus microcarpus*, *Rubus chamaemorus* and *Ledum*

groenlandicum (Figure 3.5). Although the number of species in each group varied considerably (1 to 15 species), all species groups require mesic to wet habitats which suggests that species groups are arranged along a moisture gradient.

Indirect Ordination (Reciprocal Averaging)

Ordination demonstrated understory species groups similar to the cluster analysis results. Most sites were clustered near bog indicator species such as *Vaccinium vitis-idaea, Ledum groenlandicum, Empetrum nigrum* and *Gaultheria hispidula* (Figure 3.6a). Residual 7 was different in species composition from the rest of the residuals and isolated from them (Figure 3.6a). Canopy type in residual 7 was dominated by white spruce whereas black spruce dominated the canopy in the other residuals.

The first three ordination axes explained 28.31% of the variance in the species data set (Table 3.2). Along the first axis, species ranged from *E. nigrum* to *Galium boreale*. Along the second axis, species ranged from *Rubus chamaemorus* to *Viburnum edule*. There was a trend from bog, moist habitats to more open forested, moist meadow habitats (Figure 3.6b).

Direct Ordination (Canonical Correspondence Analysis)

There were two main gradients that structured the vascular understory data (Figure 3.7a, Table 3.4). The first three ordination axes explained 19.6% of the variance in the dataset (Table 3.3). The main gradient explained 11.7% of the species dataset (Table 3.3) and represented a gradient of canopy type and deciduous litter cover (Table 3.4). By inferring habitat requirements of these tree species, the main gradient could be expressed as a topographical gradient ranging from lowland bog dominated by black spruce to upland white spruce forest. Most sites were associated near bog species and ericaceous low shrubs (Figure 3.7). Again, quadrats from residual 7 was segregated from the rest of the others due to its different canopy type, moisture conditions and understory species such as *Viburnum edule, Calamagrostis canadensis,* and *Mitella nuda*. The

second gradient represented an average residual age and local moisture gradient (Table 3.4). Since average residual age was used for each residual, it produced the linear features shown in the ordination triplot (Figure 3.7). Most residuals exhibited similar species composition such as high black spruce cover, ericaceous low shrubs and other species which all require mesic to hygric conditions.

Ecosite Classification

Using Beckingham *et al.*'s (1996) ecosite classification, each residual was classified based on most abundant tree and understory species composition (Tables 3.5-3.6). Environmental conditions of each residual were inferred from the types of species present in each residual to determine similarities between residuals. All residuals were classified into four ecosite types: "Labrador tea – mesic Pl-Sb", "tall bilberry / arnica Sw", "Labrador tea – subhygric Sb-Pl" and "Labrador tea / horsetail Sb-Sw" (Table 3.6). These ecosite types are characterized by moist moisture regimes and relatively poor nutrient regimes.

Linear regression

Relationships between residual area and species richness in quadrats and average species richness in each residual were weak (Table 3.7, Figure 3.8). There was a weak positive relationship between understory species diversity in quadrats for both Shannon's diversity index, H', (R^2 = 0.011, coefficient = 0.061, Pr = 0.017) and Simpson's diversity index, D, (R^2 = 0.007, coefficient = 0.019, Pr = 0.054, Figures 3.9-3.10). A positive relationship between average H' and average D with residual area was more pronounced (Figure 3.9-3.10) indicating slightly greater diversity in larger residuals.

In general, species richness, H' and D at quadrat and residual levels were negatively related to average residual age (Figures 3.11-3.13). The strength of the relationship varied between models (Table 3.7). Species richness and H' in each quadrat significantly decreased as average stand age increased (S, regression coefficient = -5.966,

Pr = 0.00; H', regression coefficient = -0.397, Pr = 0.019). In summary, average species richness, average H' and average D increased as residual size increased and as average residual age decreased.

A quadratic term was added to the models to increase deviance explained by residual average age and area. None of the quadratic models were significantly different from the linear models and the deviance explained by residual average age and area remained less than 7%.

3.5 Discussion

All residuals sampled had similar floristic composition containing mostly ericaceous dwarf shrubs, and other common boreal mesic species. Although there was high variability of different community types found among the nine residuals studied, community types were governed by moisture and ranged from open woodland to acidic bog communities (Figures 3.5-3.7). These community types were expected since ground moisture has a major influence on fire behaviour (Samran *et al.* 1995). Most of the residuals studied are classified as wet forest types from the Upper Foothills natural subregion that are mainly dominated by black spruce with organic and mineral soils and the understory is comprised of *Ledum groenlandicum*, *Betula* spp., *Equisetum* spp., *Mitella nuda*, and *Linnaea borealis* (Kershaw *et al.* 2001).

Areas with greater general moisture can act as a fire barrier by inhibiting ignition (Samran *et al.* 1995, Whelan 1995) and occur in depressions (Whelan 1995). All residuals contained common species that require mesic to wet habitats. As well, the results (Figures 2.20, 2.22) from chapter two also suggested greater general local moisture in residuals. Many of the species groups indicated mesic conditions, however there were several species groups containing *Epilobium angustifolium* or *Arctostaphylos uva-ursi* which indicates these areas were relatively recently disturbed or have drier conditions (Foster 1985). Although quadrats were limited to 50 m beyond the fire edge, it

is possible that certain quadrats were influenced by edge effects. Edge effects can influence the microenvironment from 0 to 137 metres into the forest, however it can vary dramatically depending on variable of interest (Chen *et al.* 1992). Foster (1985) found *Empetrum nigrum* and *Gaultheria hispidula*, two species commonly found together, to be good indicators of older forests (Figures 3.5-3.7) contradicting earlier results where residual forests were slightly younger than burned forest. Although the age difference was not large, this demonstrates how variable residual formation can be.

In the Virginia Hills fire, older residuals did not contain greater floristic diversity and the relationship between understory diversity and average residual age was not strong. Residuals sampled were unlikely to have persisted over several fire episodes since the residual age was relatively young (Table 2.1). Diversity decreased as average residual age increased (Figures 3.12-3.13), which was unexpected because older forests can contain greater niche heterogeneity and species diversity (Spies and Franklin 1988). In the boreal forest, diversity is high in early post-fire succession, and decreases as the canopy closes but diversity does not increase with increasing age (De Grandpre *et al.* 1993, Shafi and Yarranton 1973, Tonteri 1994, Taylor *et al.* 1987, Foster 1985). It was possible that sampling 60 quadrats from each residual regardless of total residual area may not be enough to document the full range of habitat types.

None of the vascular species sampled were considered to be rare (ANHIC 2001). Residuals are not equivalent to Swedish residuals in that they are not biological hotspots for understory vascular species. Only 18% of Alberta's rare vascular plant species occur in the foothills (Kershaw *et al.* 2001). However, vascular species diversity was only assessed once during the growing season so it is possible that species or certain habitats were missed. As well, many of the sedges and grasses could not be identified because their reproductive structures were absent.

General Conclusions

Understory communities among residuals varied along a moisture gradient indicating high inter-site variability. Again, moisture appears to play a role in characterizing residuals and may possible play a role in residual formation. There was a positive relationship between residual area and species diversity and was probably due to increased range of habitats. Average residual age had a negative effect on both species diversity and species richness indicating that older residuals are not comparable to the biological hotspots of the Swedish boreal forest. Historical differences, environmental and industrial, between Swedish and North American residuals could also result in this difference. But for now, residuals formed from this fire can act as a seed source and refugia for understory species richness and diversity until the next fire.

Table 3.1. Kruskal-Wallis rank sum results summary of understory vascular data.

Variable	Grouping variable	degrees of freedom	Kruskal Wallis chi-square	p value
species richness per quadrat	Residual	8	104.59	0.00
evenness per quadrat	Residual	8	46.34	0.00
Simpson's diversity (H') per quadrat	Residual	8	57.05	0.00
Shannon's diversity (D) per quadrat	Residual	8	43.04	0.00
average species richness	Residual	8	8.00	0.43
average evenness	Residual	8	8.00	0.43
average H'	Residual	8	8.00	0.43
average D	Residual	8	8.00	0.43

Table 3.2. Reciprocal Averaging ordination axis summary
statistics for presence-absence vascular understory data from all residuals.

	Axis		
	1	2	3
Eigenvalue	0.43	0.37	0.22
Variance in species data			
% of variance explained	11.99	10.23	6.09
Cumulative % explained	11.99	22.22	28.31
Total inertia	3.62		

Table 3.3. Canonical Correspondence Analysis ordination axis summary
statistics for abundance vascular undestory data from residuals 5, 7, 8, 9 and 13.

	Axis		
	1	2	3
Eigenvalue	0.51	0.24	0.11
Variance in species data			
% of variance explained	11.70	5.40	2.50
Cumulative % explained	11.70	17.10	19.60
Total inertia	4.38		

Table 3.4. Canonical Correspondence Analysis correlation summary of environmental variables.

| Variable | Correlations | | |
	Axis 1	Axis 2	Axis 3
Picea glauca	0.876	0.138	0.032
Deciduous litter	0.567	-0.198	0.660
Coniferous litter	0.441	0.024	-0.374
Alnus crispa	0.399	-0.056	0.030
Abies balsamifera	0.396	-0.075	-0.162
Picea mariana	-0.316	-0.382	-0.082
Populus tremuloides	0.275	-0.066	0.127
Average stand age	-0.251	-0.734	0.029
Snag cover (%)	0.195	0.039	0.127
Coarse woody debris cover (%)	0.141	0.054	0.158
Pinus contorta	-0.131	-0.384	-0.217
Larix laricina	-0.127	0.248	0.110
Water cover (%)	-0.077	0.459	0.383
Salix spp	-0.008	0.187	0.093

Table 3.5. Ecosite summary of the most common species in each residual (Beckingham et al. 1996).
Where x = present, Pl = lodgepole pine, Sb = black spruce, Sw = white spruce.

d1.2 Labrador tea - mesic Pl-Sb

Residual	5
Canopy	
Pinus contorta	x
Picea mariana	x
Understory	
Ledum groenlandicum	x
Picea mariana	x
Cornus canadensis	x
Rubus pedatus	x
Vaccinium membraneceum	
Vaccinium vitis-idaea	
Vaccinium myrtilloides	
Linnaea borealis	
Vaccinium caespitosum	
Rosa acicularis	

e3.3 tall bilberry / arnica Sw

Residual	7	8
Canopy		
Picea glauca	x	x
Pinus contorta	x	x
Picea mariana		x
Populus tremuloides		
Understory		
Linnaea borealis	x	x
Cornus canadensis	x	x
Ledum groenlandicum		x
Vaccinium myrtilloides		x
Vaccinium vitis-idaea		x
Alnus crispa	x	
Abies lasiocarpa		
Picea mariana		
Rosa acicularis		

h1.2 Labrador tea - subhygric Sb-Pl

Residual	3	11	13	14	15
Canopy					
Pinus contorta	x	x	x	x	x
Picea mariana	x	x	x	x	x
Understory					
Ledum groenlandicum	x	x	x	x	x
Vaccinium vitis-idaea	x	x	x	x	x
Cornus canadensis	x	x	x	x	x
Petasites palmatus	x	x	x	x	x
Vaccinium myrtilloides	x		x	x	
Picea mariana					x
Rosa acicularis			x		
Equisetum sylvaticum					

e3.1 tall bilberry / arnica Sw

Residual	7
Canopy	
Picea glauca	x
Pinus contorta	x
Picea mariana	
Populus tremuloides	
Understory	
Alnus crispa	x
Linnaea borealis	x
Epilobium angustifolia	x
Cornus canadensis	x
Picea glauca	
Aster conspicuus	
Mertensia paniculata	

i1.1 Labrador tea / horsetail.Sb-Sw

Residual	9
Canopy	
Picea mariana	x
Picea glauca	x
Understory	
Ledum groenlandicum	x
Vaccinium vitis-idaea	x
Equisetum arvense	x
Equisetum pratense	x
Cornus canadensis	x
Petasites palmatus	x
Equisetum scirpoides	
Linnaea borealis	
Lonicera involucrata	
Rosa acicularis	
Equisetum sylvaticum	
Salix spp.	

Table 3.6. Ecosite classification of each residual based on Beckingham et al. (1996).

Residual	Edatope	Ecosite Type	Moisture Regime	Nutrient Regime
5	d1.2	Labrador tea - mesic Pl-Sb	Mesic	Poor
7	e3.1	Tall bilberry / arnica Sw	Mesic	Medium
7	e3.3	Tall bilberry / arnica Sw	Mesic	Medium
8	e3.3	Tall bilberry / arnica Sw	Mesic	Medium
3	h1.2	Labrador tea - subhygric Sb-Pl	Hygric	Poor
11	h1.2	Labrador tea - subhygric Sb-Pl	Hygric	Poor
13	h1.2	Labrador tea - subhygric Sb-Pl	Hygric	Poor
14	h1.2	Labrador tea - subhygric Sb-Pl	Hygric	Poor
15	h1.2	Labrador tea - subhygric Sb-Pl	Hygric	Poor
9	i1.1	Labrador tea / horsetail Sb-Sw	Hygric	Medium

Table 3.7. Summary of linear regression analyses on vascular understory data from all residuals. (* indicates significance)

Independent Variable	Dependent Variable	Coefficient	t value	Pr	R^2
Residual area (m², log)	Species richness (S)	0.045	0.253	0.800	0.000
	Average species richness (S)	0.040	0.060	0.954	0.001
	Simpson's index of diversity (D)	0.019	1.929	0.054*	0.007
	Average Simpson's index of diversity (D)	0.020	0.907	0.395	0.105
	Shannon diversity index (H')	0.061	2.400	0.017*	0.011
	Average Shannon diversity index (H')	0.062	0.905	0.395	0.105
Average Stand Age (years, transformed)	Species richness (S)	-5.966	-5.169	0.00*	0.049
	Average species richness (S)	-5.803	-1.480	0.182	0.239
	Simpson's index of diversity (D)	-0.062	-0.926	0.355	0.002
	Average Simpson's index of diversity (D)	-0.063	-0.411	0.694	0.024
	Shannon diversity index (H')	-0.397	-2.356	0.019*	0.010
	Average Shannon diversity index (H')	-0.390	-0.853	0.424	0.094
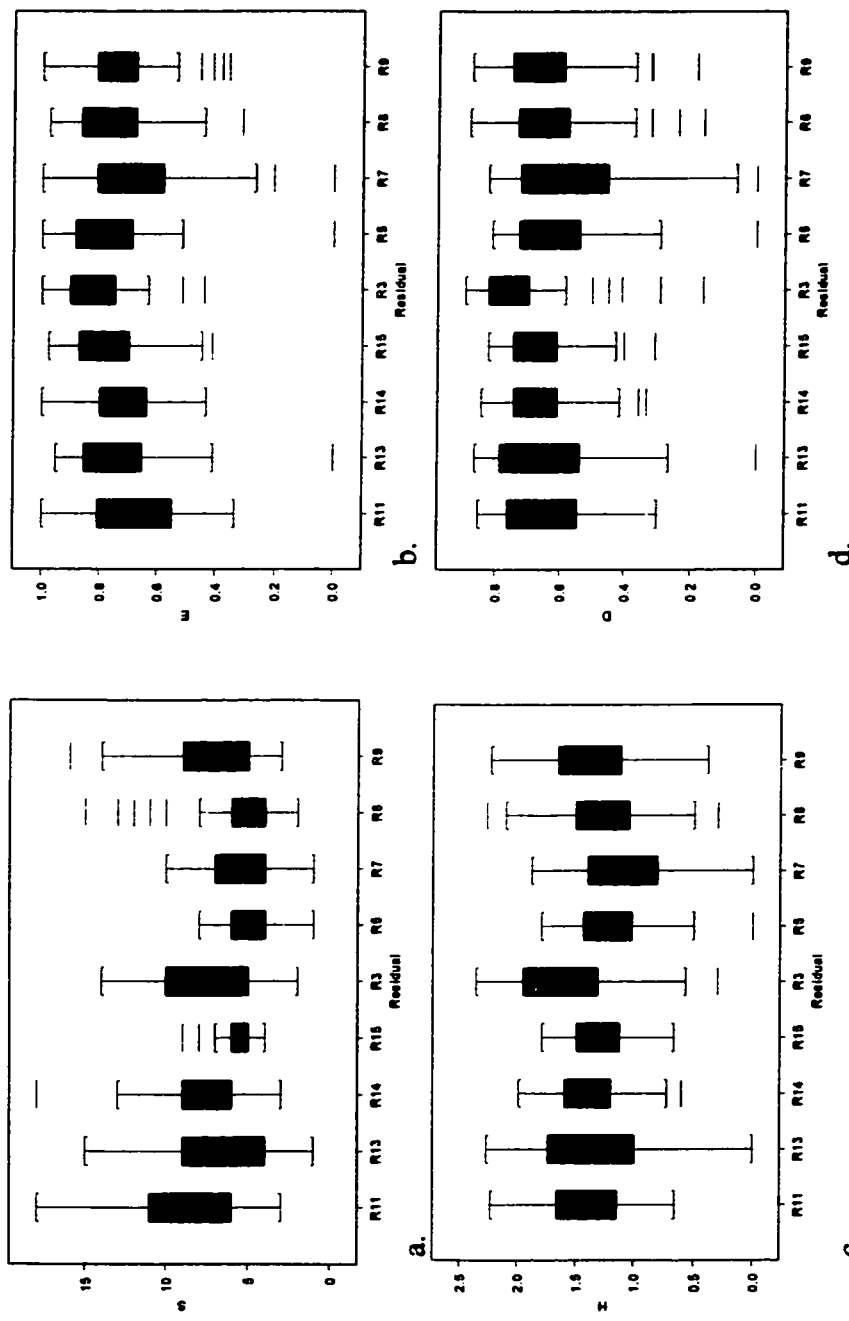
Figure 3.1a – d. Boxplots of species richness (S), species evenness (E), Shannon's diversity index (H') and diversity Simpson's index (D) for each residual.
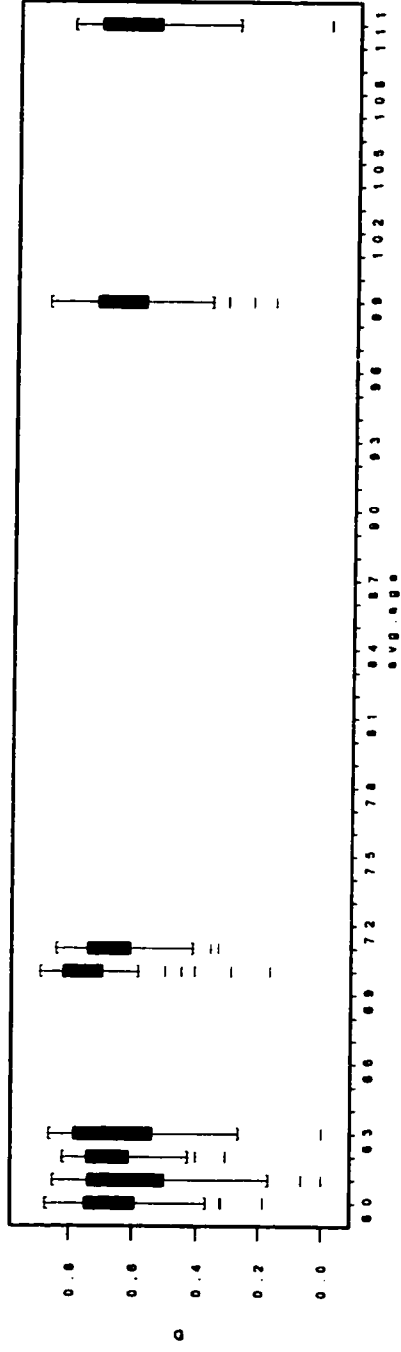
Figure 3.2. The relationship between understory species diversity and average stand age.
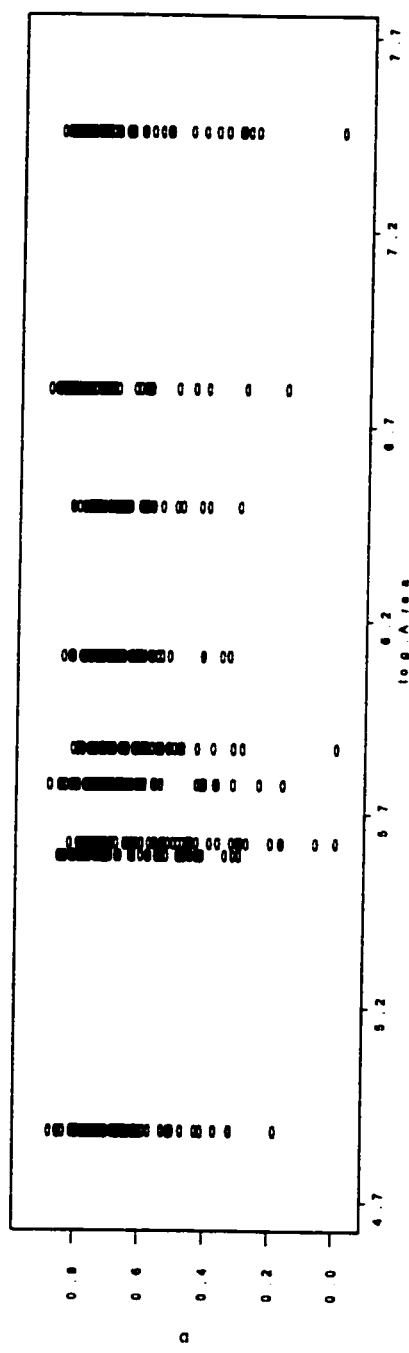
Figure 3.3. The relationship between understory species diversity and residual size.
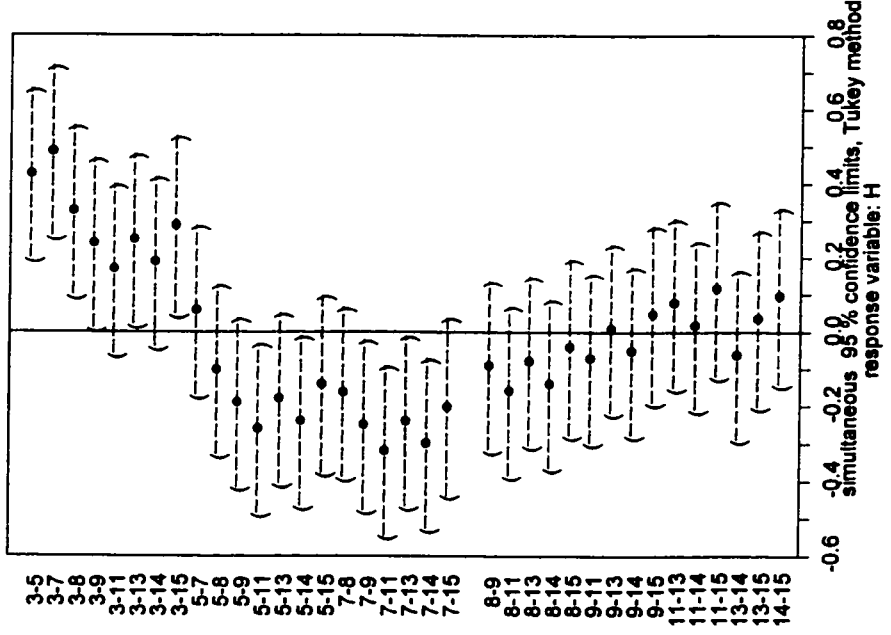
Figure 3.4. Pairwise comparisons of understory diversity (Simpson's diversity index, H) between pairs of residuals.
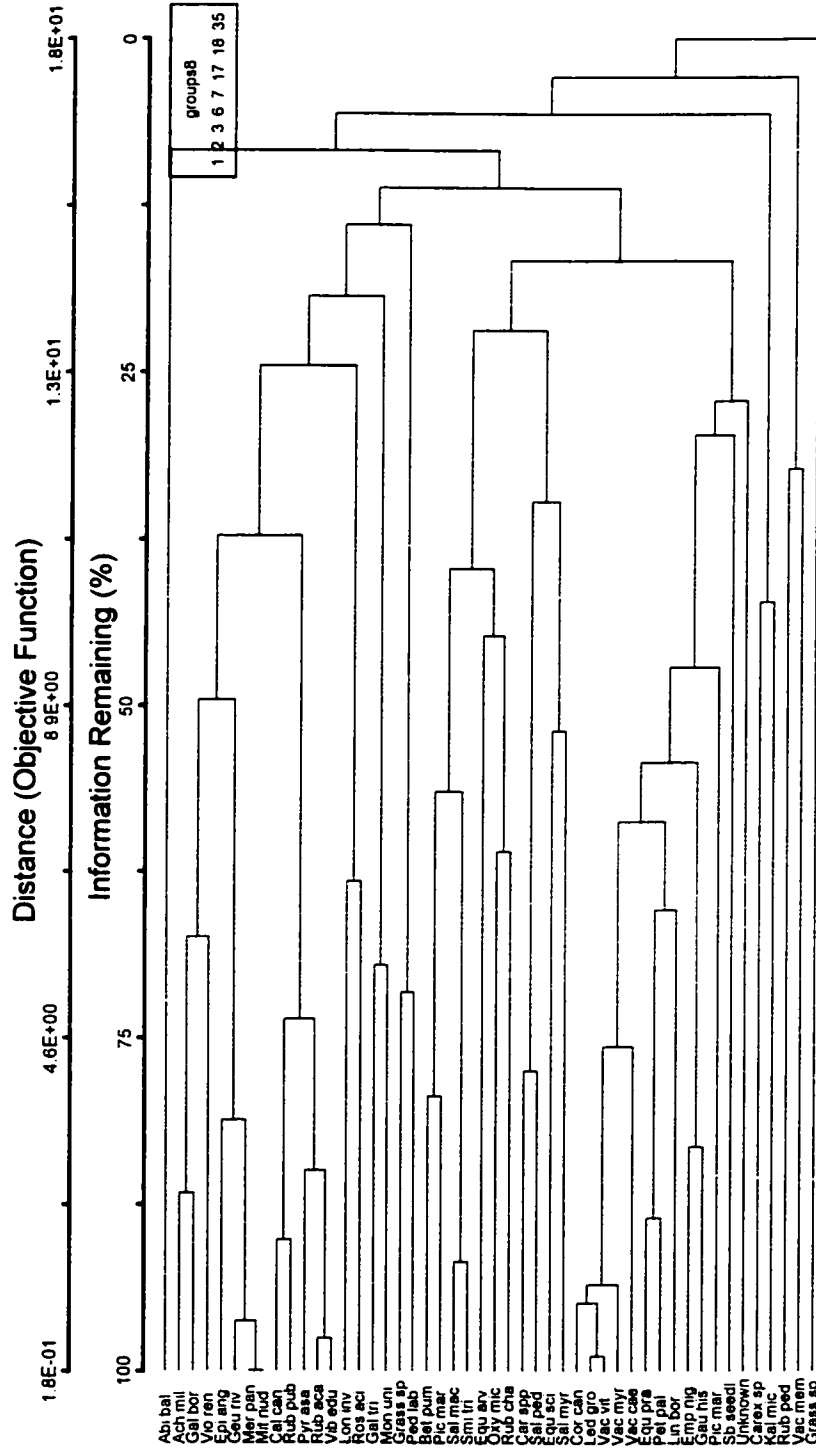
Figure 3.5. Cluster Analysis on understory abundance data (8 groups) using average linkage clustering and Sorensen (Bray-Curtis) distance measure.
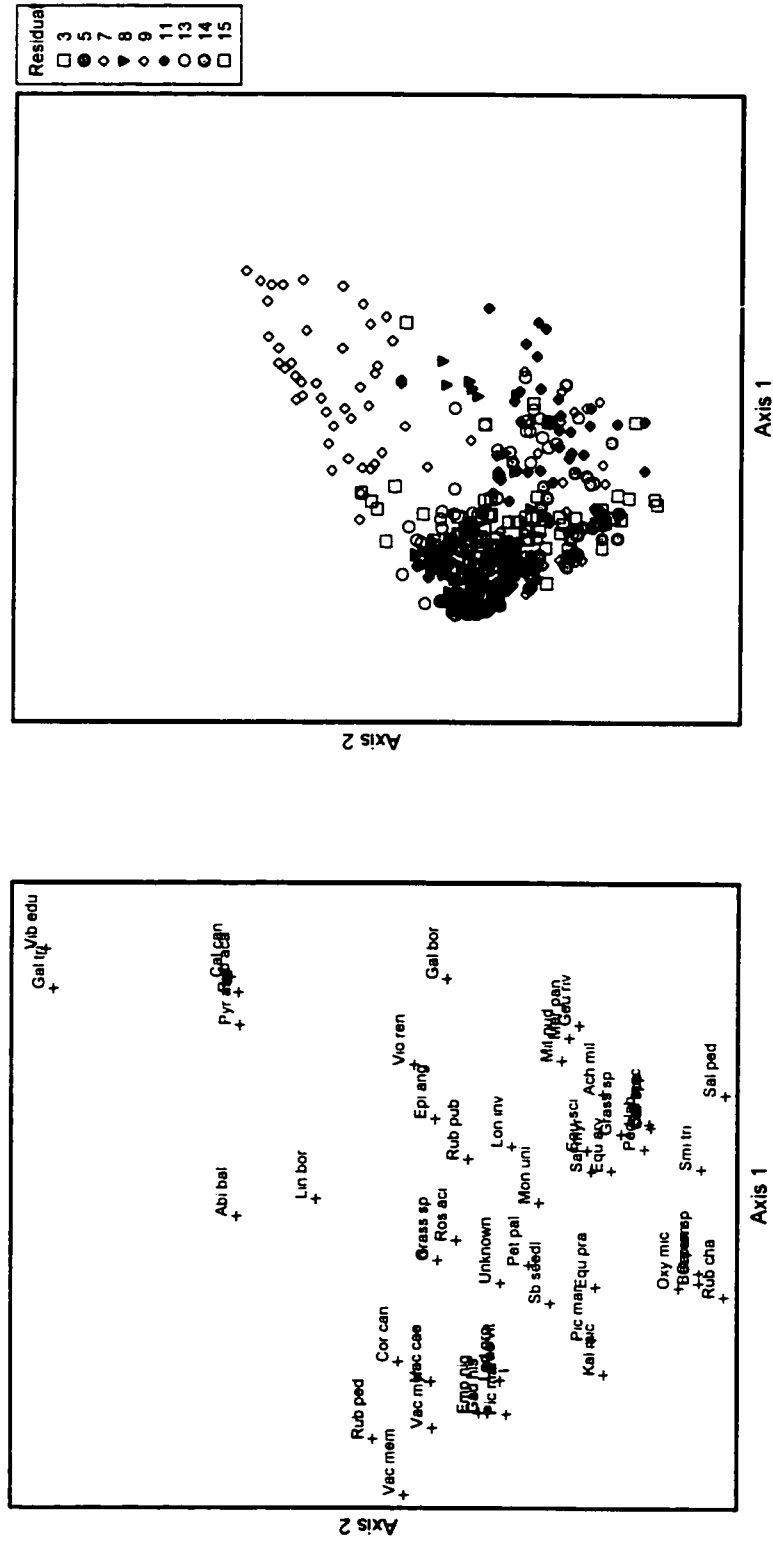
Figure 3.6. Species (left) and site (right) ordination scores for axis 1 and 2 from a Reciprocal Averaging ordination using presence-absence data (with outliers omitted). Species abbreviations are listed in Appendix Table A.3.
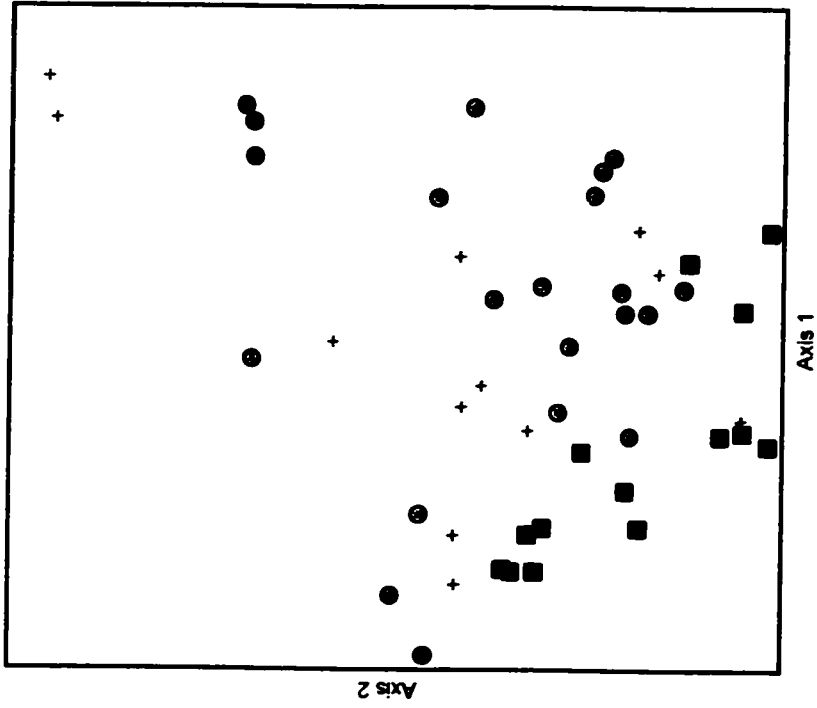
Figure 3.6 cont'd. Species ordination scores for axes 1 and 2 from a Reciprocal Averaging using presence-absence data. Squares indicate boggy species, circles indicate moist species, and crosses indicate open woodland species.
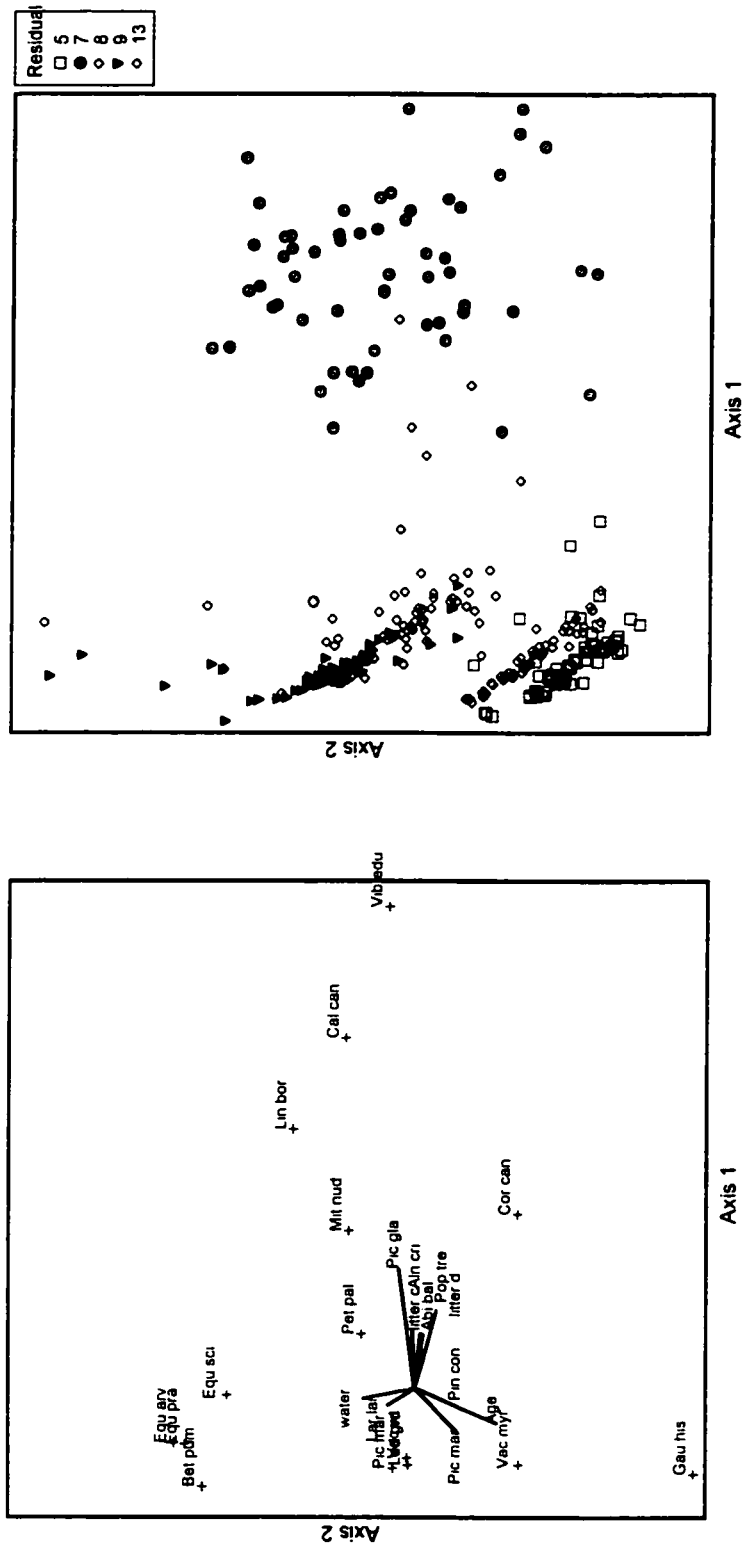
Figure 3.7. Species (left) and site (right) ordination scores for axes 1 and 2 from a Canonical Correspondence Analysis of understory data from residuals 5, 7, 8, 9, and 13 using abundance data (rare species were downweighted and outliers were omitted.) Species abbreviations are listed in Appendix Table A.3.
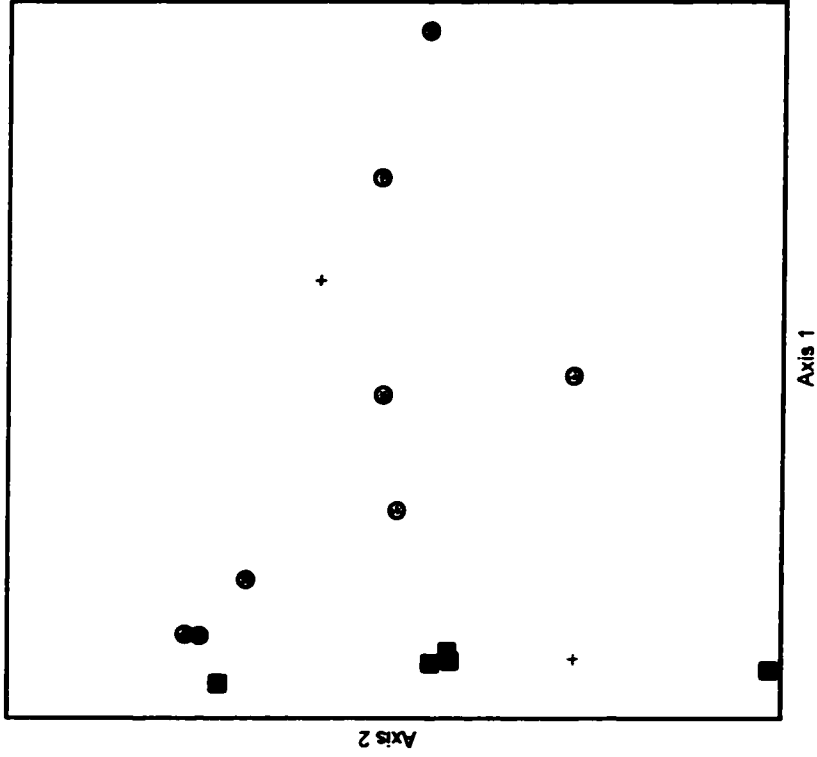
Figure 3.7 cont'd. Species ordination scores for axes 1 and 2 from a Canonical Correspondence Analysis of understory data from residuals 5, 7, 8, 9, and 13 using abundance data. Squares indicate boggy species, circles indicate moist species, and crosses indicate open woodland species.
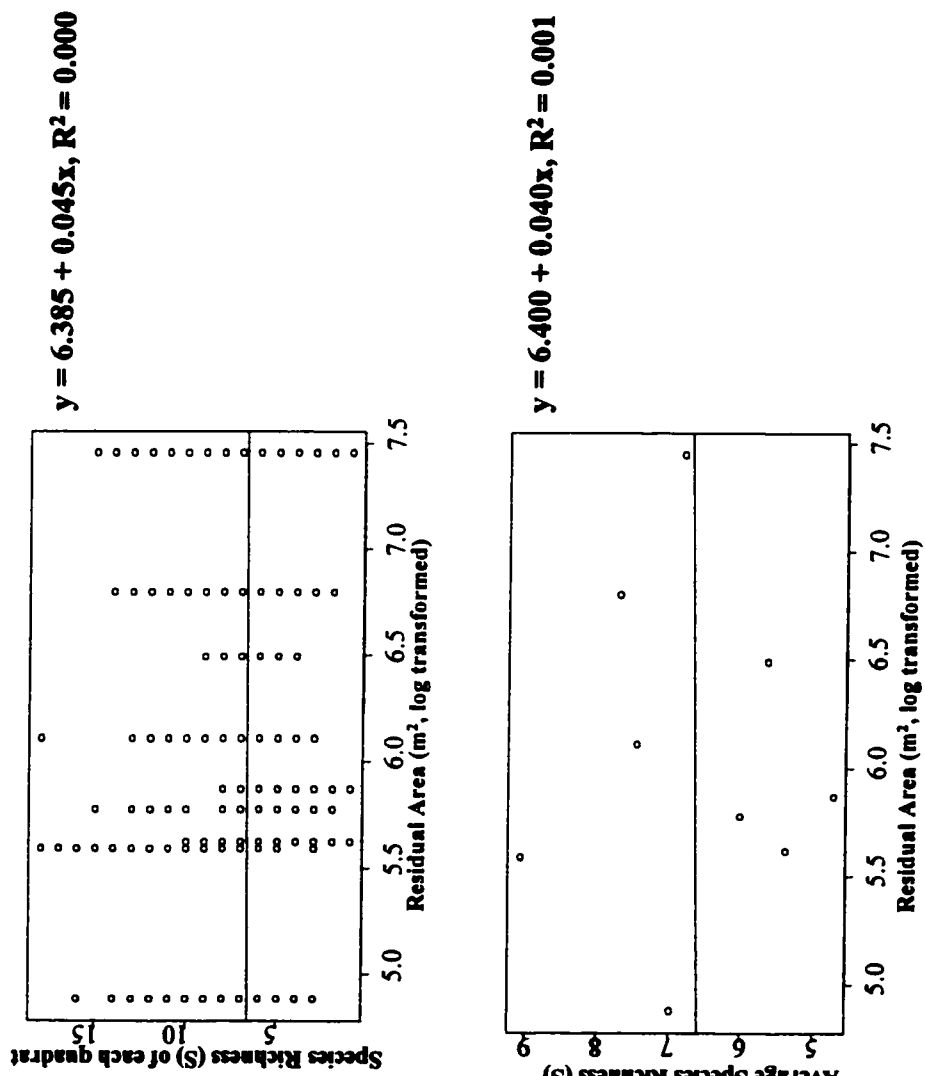
Figure 3.8. Relationship of quadrat species richness (top) and average residual species richness (bottom) with residual area (log transformed).

$y = 0.526 + 0.019x, R^2 = 0.007$

$y = 0.522 + 0.020x, R^2 = 0.105$
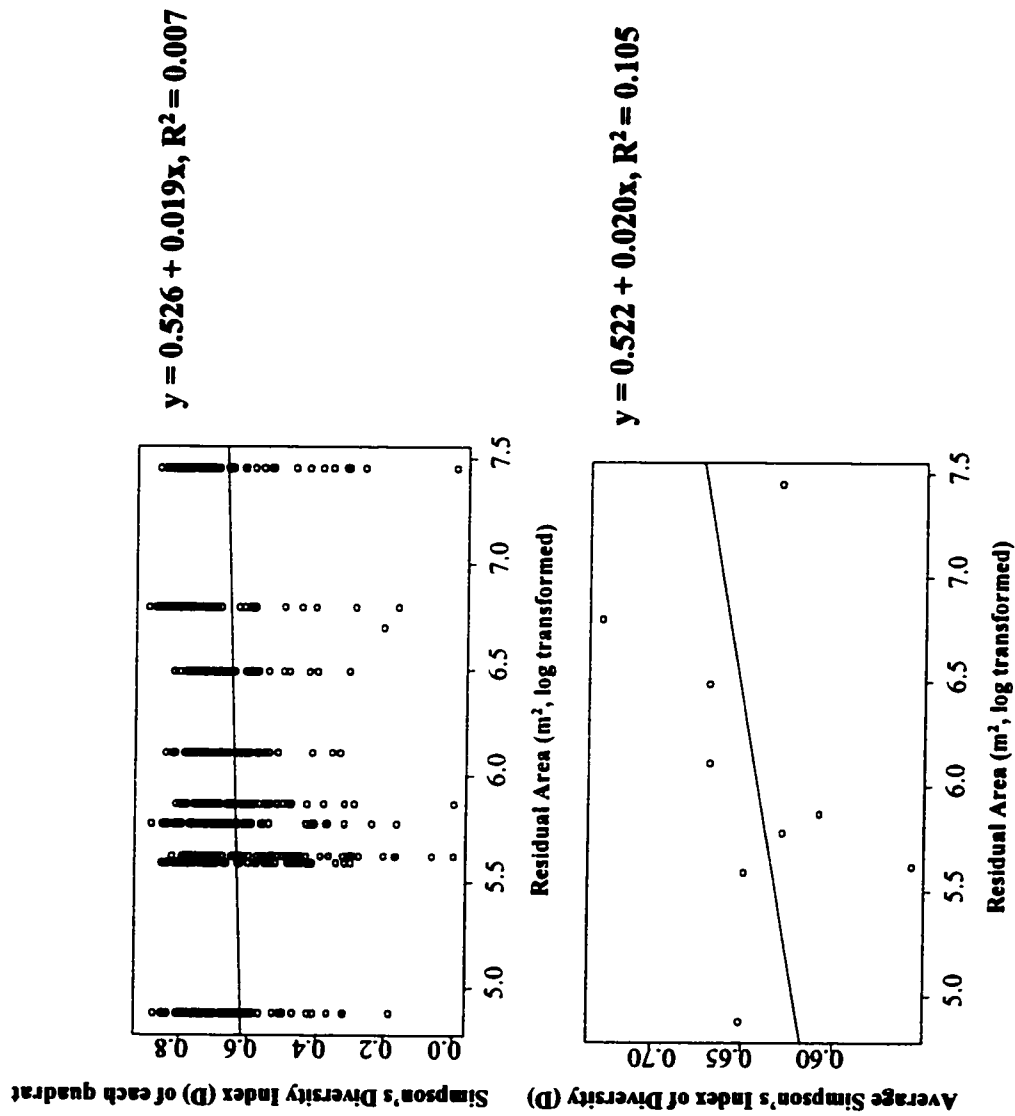
Figure 3.9. Relationship of quadrat Simpson's diversity (top) and average residual Simpson's diversity (bottom) with residual area (log transformed).
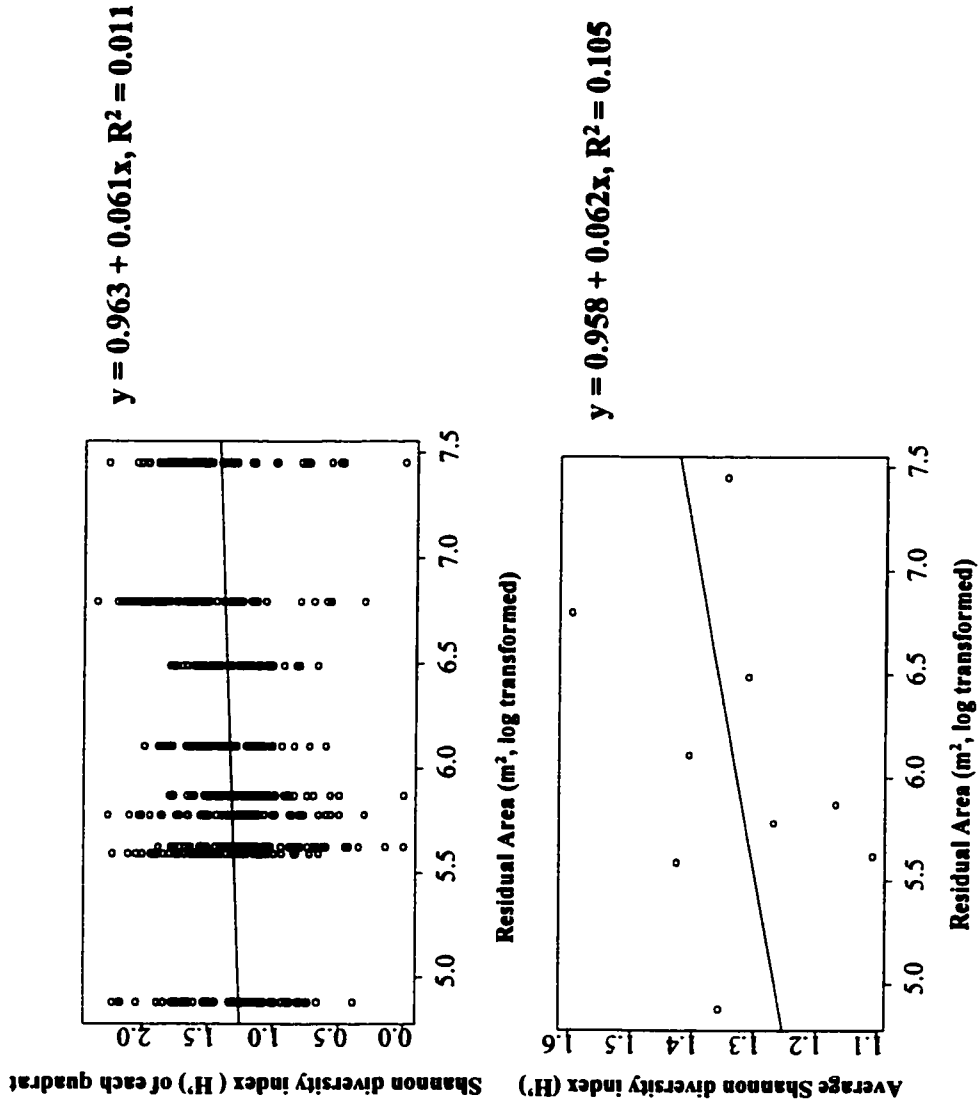
Figure 3.10. Relationship of quadrat Shannon's diversity (top) and average residual Shannon's diversity (bottom) with residual area (log transformed).

$$y = 23.554 - 5.966x, \ R^2 = 0.049$$

$$y = 23.069 - 5.803x, \ R^2 = 0.239$$
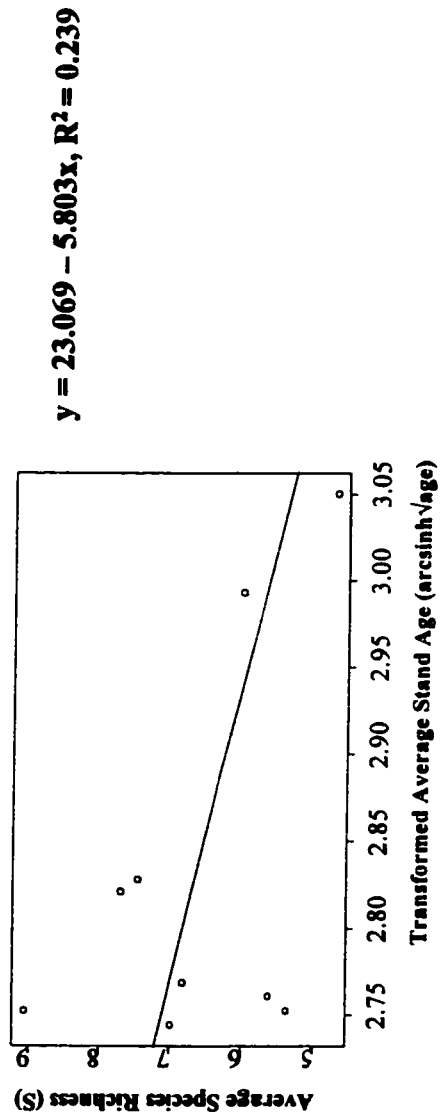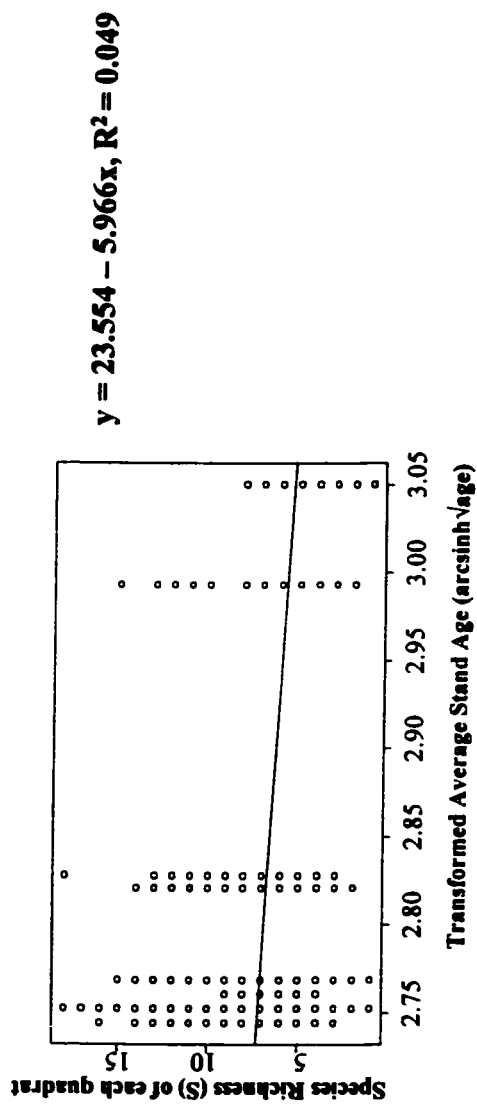
Figure 3.11. Relationship of quadrat species richness (top) and average residual species richness (bottom) with average stand age of the residual (transformed).
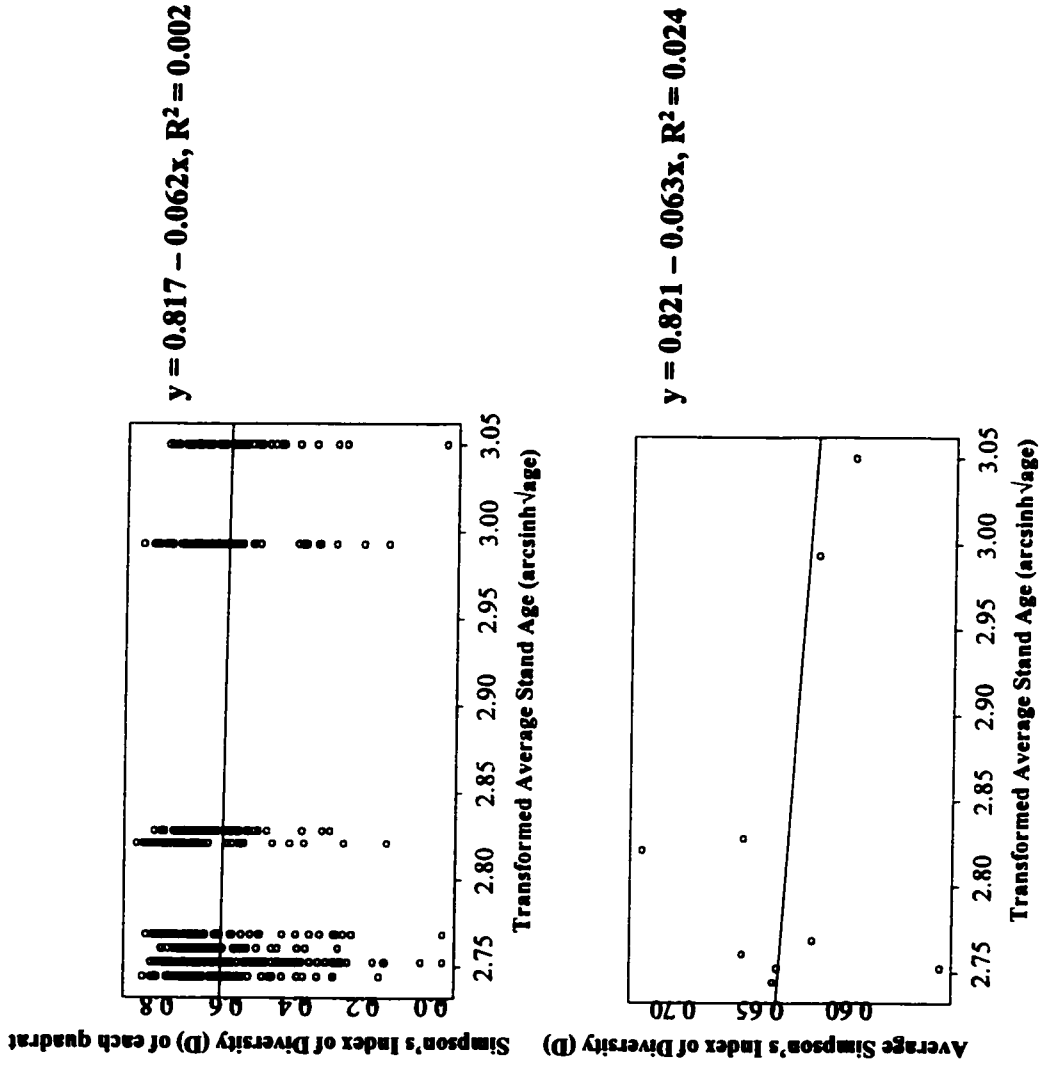
Figure 3.12. Relationship of quadrat Simpson's diversity (top) and average residual Simpson's diversity (bottom) with average stand age of the residual (transformed).
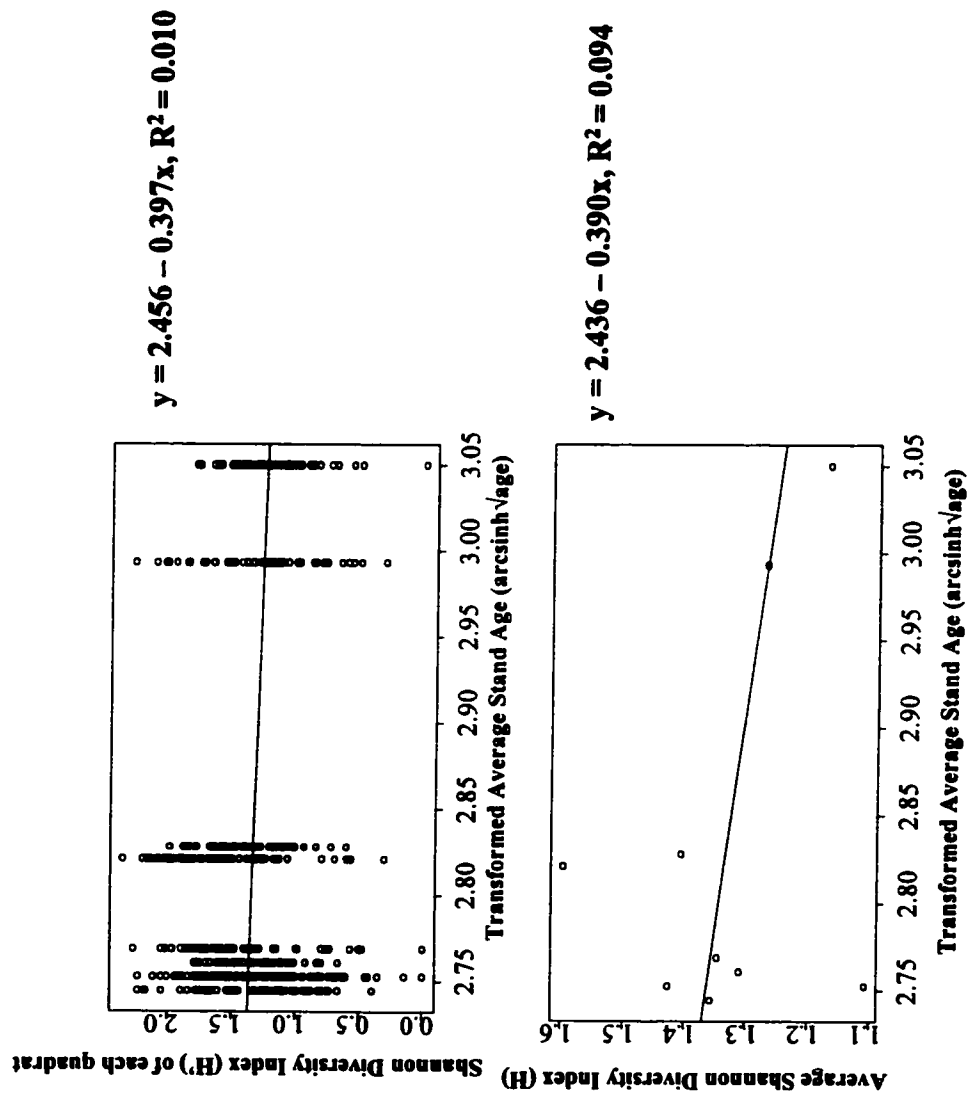
Figure 3.13. Relationship of quadrat Shannon's diversity (top) and average residual Shannon's diversity (bottom) with average stand age of the residual (transformed).

3.6 Literature Cited

Alberta Natural Heritage Information Centre (ANHIC). November 2001. Lists of Tracked Vascular Plants. Parks and Protected Areas, Alberta Community Development. Edmonton, Alberta.

Asselin, J., M.J. Fortin, and Y. Bergeron. 2001. Spatial distribution of late-successional coniferous species regeneration following disturbance in south western Quebec boreal forest. Forest Ecology and Management 140: 29-37.

Beckingham, J.D., I.G.W. Corns, and J.H. Archibald. 1996. Field Guide to Ecosites of West-Central Alberta. Canadian Forest Service Special Report 9. Northern Forestry Centre, Edmonton, Alberta, Canada.

Bottorff, Q. W. 2001. Fire skips and understory plan diversity in an upper foothills-subalpine forest in northwestern Alberta. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Chen, J., J.F. Franklin, and T.A. Spies. 1992. Vegetation responses to edge environment in old-growth Douglas-Fir forests. Ecological Applications 2: 387-396.

De Grandpre, L., D. Gagnon and Y. Bergeron. 1993. Changes in the understory of Canadian southern boreal forest after fire. Journal of Vegetation Science 4: 803-810.

Delong, S.C. and W.B Kessler. 2000. Ecological characteristics of mature forest remnants left by wildfire. Forest Ecology and Management 131: 93-106.

Euler, D. 1981. A moose habitat strategy for Ontario. Alces: 17: 180-192.

Foster, D. R. 1983. The history and pattern of fire in the boreal forest of Southeastern Labrador. Canadian Journal of Botany 61: 2459-2471.

Foster, D.R. 1985. Vegetation development following fire in *Picea mariana* (black spruce) – *Pleurozium* forest of southeastern Labrador, Canada. Journal of Ecology 73: 517-534.

Foster, D.R., D.H. Knight, and J.F. Franklin. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems 1: 487-510.

Franklin, J.F. 1993. Lessons from old-growth. Journal of Forestry 91:10-13.

Gandhi, K.J. 1999. The importance of fire skips as biotic refugia and the influence of forest heterogeneity on epigaeic beetles in pyrogenic stands in the northern Rocky Mountains. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Gasaway, W.C. and S.D. DuBois. 1985. Initial response of moose to a wildfire in interior Alaska. Canadian Field Naturalist 99: 135-140.

Halpern, C.B. and T.A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5: 913-934.

Heinselman, M.L. 1978. Fire intensity and frequency as factors in the distribution and structure of northern forests. *In* Proceedings of the Conference Fire Regimes and Ecosystem Properties. U.S. Department of Agriculture. General Technical Report WO-26.

Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. Journal of Ecology 61: 237-249.

Hill, M.O. and H.G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42: 47-58.

Hörnberg, G., O. Zackrisson, U. Segerström, B.W. Svensson, M. Ohlson, and R.H.W. Bradshaw. 1998. Boreal swamp forests. Bioscience 48: 795-802.

Johnson, D., L. Kershaw, A. MacKinnon and J. Pojar. 1995. Plants of the Western Boreal Forest and Aspen Parkland. Lone Pine Publishing and Canadian Forest Service. Alberta, Canada.

Jongman, R.H.G., C.J.F. Ter Braak, and O.F.R. Van Tongeren. 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press. New York, U.S.A.

Kershaw, L., J. Gould, D. Johnson and J. Lancaster. 2001. Rare vascular plants of

Alberta. The University of Alberta Press and The Canadian Forest Service. Alberta, Canada.

Kuusinen, M. 1996. Importance of spruce swamp forests for epiphyte diversity and flora on *Picea abies* in southern and middle boreal Finland. Ecography 19: 41-51.

Legendre, P. and L. Legendre. 1998. Numerical Ecology 2nd English Edition. Elsevier, New York, U.S.A.

McCune, B. and M.J. Mefford. 1999. Multivariate Analysis of Ecological Data, Version 4.14. MjM software, Glenedon Beach, Oregon, U.S.A.

Moss, E.H. 1994. Flora of Alberta, 2nd edition. *(Ed.)* J.G. Packer. University of Toronto Press, Ontario, Canada.

Ohlson, M., L. Sodestrom, G. Hörnberg, O. Zackrisson and J. Hermansson. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth forests. Biological Conservation 81: 221-231.

Oliver, C.D. and B.C. Larson. 1996. Forest Stand Dynamics. John Wiley and Sons, New York, U.S.A.

Quirk, W.A. and D.J. Sykes. 1971. White spruce stringers in a fire-patterned landscape in interior Alaska. *In* Fire in the Northern Environment: a Symposium. (Eds.) C.W. Slaughter, R.J. Barney and G.M. Hansen. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon, U.S.A.

S-PLUS. 1999. Guides to Statistics, Volume 1. Data Analysis Products Division. Math Soft, Inc. Washington, U.S.A.

Samran, S., P.M. Woodard, and R.L. Rothwell. 1995. The effect of soil water on ground fuel availability. Forest Science 41: 255-267.

Schieck, J., and K.A. Hobson. 2000. Bird communities associated with live residual tree patches within cutblocks and burned habitat in mixedwood boreal forests. Canadian Journal of Forest Research 30: 1281-1295.

Segerström, U., R. Bradshaw, G. Hörnberg, and E. Bohlin. 1994. Disturbance history of a

swamp forest refuge in northern Sweden. Biological Conservation 68: 189-196.

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

Sokal, R.R. and F.J. Rohlf. 1995. Biometry 3rd Edition. W.H. Freeman and Company, New York, U.S.A.

Spies, T.A. and J.F. Franklin. 1988. Old growth and forest dynamics in the Douglas fir region of western Oregon and Washington. Natural Areas Journal 8: 190-201.

Taylor, S.J., T.J. Carleton and P. Adams. 1987. Understory vegetation change in a *Picea mariana* chronosequence. Vegetatio 73: 63-72.

Ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

Ter Braak, C.J.F. 1994. Canonical community ordination. Part I: Basic theory and linear methods. Ecoscience 1: 127-140.

Thomas, J.W. and R.J. Miller, H. Black, J.E. Rodiek, and C. Maser. 1976. Guidelines for maintaining and enhancing wildlife habitat in forest management in the Blue Mountains of Oregon and Washington. Transactions of North America Wildlife and Natural Resources Conference 41: 452-476.

Tonteri, T. 1994. Species richness of boreal understory forest vegetation in relation to site type and successional factors. Annales Zoologici Fennici 31: 53-60.

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

Turner, M. G. and W.H. Romme. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology 9: 59-77.

Turner, M.G., W.W. Hargrove, R.H. Gardener and W.H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. Journal of Vegetation Science 5: 731-742.

Van Wagner, C.E. 1983. Fire behaviour in northern conifer forests and shrublands. *In*

The Role of Fire in Northern Circumpolar Ecosystems. (Eds.) R.W. Wein and D.A. MacLean. John Wiley and Sons, New York, U.S.A.

Zackrisson, O. 1977. Influence of forest fires on the north Swedish boreal forest. Oikos 29: 22-32.

CHAPTER 4

CONCLUSIONS AND FUTURE RESEARCH

In this thesis, I examined the characteristics and variability of fire residuals from a 1998 fire in Virginia Hills, Alberta. I was interested determining whether fire residuals can be predicted based on similar environmental and forest structural characteristics. Fire residuals are known to act as seed sources and biodiversity refugia on the landscape (Turner and Romme 1994, Delong and Kessler 2000, Bottorff 2001, Asselin *et al.* 2001). There are suggestions that residuals can remain disturbance free on the landscape over several fire cycles (Rowe and Scotter 1973, Hörnberg *et al.* 1998). If these suggestions are true, fire residuals can be important late-successional features on the landscape, and should be considered when managing forests to emulate natural disturbance (Delong and Tanner 1996, Halpern and Spies 1995, Traut and Muir 2000).

4.1 Effect of topography and forest structure on residual formation

My objectives for this part of the thesis were: 1) to characterize the residual edge based on local topography, forest tree density and composition, 2) to determine whether environmental and forest stand structure and composition are similar among all residuals and 3) to determine whether residual forests are older than burned forest.

Local topography in the 1998 Virginia Hills fire had little influence on residual formation. Although the study site was situated in the Upper foothills regions, there may not have been enough topographical variation to affect fire behavior. However, Quirk and Sykes (1971) have found small topographical features in residuals can be significantly different from burned areas. In quadrats with perceptible aspect, burned quadrats

occurred more often on north facing sites. This contradicts previous findings where south facing sites tended to burn more frequently than sites with a north aspect due to quicker fuel accumulation, greater temperatures and drier conditions (Quirk and Sykes 1971, Zackrisson 1977, Francis 1996, Camp *et al.* 1997).

In this study, residuals occurred on relatively mesic or boggy sites which indicate general local moisture has some influence on residual formation (Samran *et al.* 1995). Black spruce and larch occurred more often in residuals than in burned forest, which demonstrates residuals were associated with mesic and boggy sites. Residuals contained a greater density of small diameter trees and were slightly younger than burned forest. Residual formation in this study may be due to the lack of fuel accumulation (Schimmel and Granström 1997) and moisture retention in younger residual forest (Cumming 2001). However, in large fires such as the Virginia Hills fire, random weather conditions may play a stronger role than structural factors in fire behavior and residual formation.

4.2 Fire residuals as understory biodiversity refugia

My objectives for this part of the thesis were: 1) to determine the range of understory vascular community types that occur in residuals, and 2) to determine understory diversity and its relationship with residual size and age.

Understory vascular communities ranged from open woodland types, which were dominated by *Linnaea borealis*, *Epilobium angustifolium*, to bog-mesic types, that were dominated by *Oxycoccus microcarpus*, *Rubus chamaemorus* and *Ledum groenlandicum*. Although these communities were similar in environmental conditions, communities among the residuals studied were highly variable. Understory diversity was negatively related to average residual age while positively related to residual size where larger residuals contained greater numbers of species.

Residuals are not similar to the 'biodiversity hotspots' in Sweden (Hörnberg *et al.* 1998), however they do represent relatively rare habitat in the post-fire landscape and are important for regeneration, and colonization into the burned forest (Delong and Kessler 2000, Turner and Romme 1994).

4.3 Future research and conclusions

In this study, fire residuals could not be predicted solely from topographical and forest structural characteristics. Certain ecosite types may have tendencies to form residuals due to mesic or bog-like conditions. Future research could be directed towards determining forest types that have a high affinity towards residual formation. Residual formation may also be dependent on fire type, fire severity and forest type, as a result these factors should also be considered when choosing study sites. Studies at a larger scale may be useful since it is unlikely that stand-level characteristics can have a major influence on fire behaviour and residual formation. Other research could be determining the importance of moisture on residual formation by comparing waterbody and residual distributions and sampling from a range of different fires.

Although residuals may be formed randomly, they are still important features in the post-fire landscape since they act like seed sources, refugia for flora and fauna and may be a source of biodiversity for the regenerating burned forest (Delong and Kessler 2000). As a result, they should be considered for conservation and incorporated in partial harvesting and green retention regimes.

In conclusion, the factors controlling residual formation and characterizing residuals could not be determined based only on local topography and stand-level characteristics. Factors controlling residual formation may be occurring at a larger scale and it is unlikely for stand level characteristics to have an influence on fire behaviour. Patterns in forest structure and environmental conditions among residuals were highly

variable but results suggested that moisture has a weak influence on residual formation. Residual understory vascular communities were structured along a moisture gradient ranging from open woodlands to acidic bogs. Again, there was high inter-site variation among residuals but most residuals exhibited moist conditions.

4.4 Literature Cited

Asselin, J., M.J. Fortin, and Y. Bergeron. 2001. Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Quebec boreal forest. Forest Ecology and Management 140: 29-37.

Bottorff, Q. W. 2001. Fire skips and understory plant diversity in an upper foothills-subalpine forest in northwestern Alberta. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Camp, A., C. Oliver, P. Hessburg, and R. Everett. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. Forest Ecology and Management 95: 63-77.

Cumming, S.G. 2001. Forest type and wildfire in the Alberta boreal mixedwood: what do fires burn? Ecological Applications 11: 97-110.

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

Delong, S.C. and W.B Kessler. 2000. Ecological characteristics of mature forest remnants left by wildfire. Forest Ecology and Management 131: 93-106.

Francis, S.R. 1996. Linking Landscape Pattern and Forest Disturbance: Fire History of the Shakwak Trench, Southwest Yukon Territory. M.Sc. Thesis. University of Alberta, Edmonton, Alberta, Canada.

Halpern, C.B. and T.A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5: 913-934.

Hörnberg, G., O. Zackrisson, U. Segerström, B.W. Svensson, M. Ohlson, and R.H.W. Bradshaw. 1998. Boreal swamp forests. Bioscience 48: 795-802.

Quirk, W.A. and D.J. Sykes. 1971. White Spruce stringers in a fire-patterned landscape in interior Alaska. In Fire in the Northern Environment: a Symposium. (Eds.) C.W. Slaughter, R.J. Barney and G.M. Hansen. Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon, U.S.A.

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APPENDIX

Appendix Table A.1. Compiled Species List for Virginia Hills Summer 2000. Nomenclature follows Moss (1983).

Identified to species (80)	Identified to genus (40)	Unidentified (13)
Abies balsamifera	*Anemone spp.*	*Unk - 3 leaflet wet*
Achillea millefolium	*Aster spp.*	*Unk 1*
Actaea rubra	*Carex sp 'tiny'*	*Unk 4 - 5 leaflet wet*
Alnus crispa	*Carex spp*	*Unk 7*
Arctostaphylus uva-ursi	*Carex spp*	*Unk Salix 1 low*
Arnica cordifolia	*Carex spp*	*Unk Salix 3 toothed*
Aster ciliolatus	*Carex spp*	*Unk8 heart shaped*
Betula pumila	*Carex spp*	*Unknown 11 alt small wavy oblong (M)*
Calamagrostis canadensis	*Carex spp*	*Unknown 12 seedling (M)*
Carex aquatilis	*Carex spp.*	*Unknown 13- alt white spots*
Carex disperma	*Carex spp.*	*Unknown 2 3&3*
Carex globular	*Grass 1 spp*	*Unknown 5 toothy oblong lge (M)*
Carex interior	*Grass 1 spp*	*Unknown 6 tooth egg*
Carex media	*Grass 2 spp*	
Coptis trifolia	*Grass sp*	
Corallorhiza trifida	*Grass sp 1*	
Cornus canadensis	*Grass spp.*	
Danthonia californica	*Grass spp.*	
Delphinium glaucum	*Picea spp*	
Dryopteris assimilis	*Polygonum spp*	
Empetrum nigrum	*Rubus spp.*	
Epilobium angustifolium	*Rubus spp.*	
Equisetum arvense	*Rubus spp.*	
Equisetum pratense	*Salix #2*	
Equisetum scirpoides	*Salix #3 trunk*	
Fragaria virginiana	*Salix #4 trunk*	
Galium boreale	*Salix 1 spp*	
Galium triflorum	*Salix 2 spp*	
Gaultheria hispidula	*Salix spp.*	
Geum rivale	*Salix spp.*	
Goodyera repens	*Senecio spp.*	
Gymnocarpium dryopteris	*Smilacina spp.*	
Habenaria hyperborea	*Smilacina spp.*	
Kalmia microphylla	*Solidago spp*	
Larix laricina	*Stellaria spp*	
Lazula parviflora	*Stellaria spp*	
Ledum groenlandicum	*Unk 13 Salix spp*	
Linnaea borealis	*Unk 3 Carex spp*	
Listera cordata	*Unk 5 low willow*	
Lonicera involucrata	*Veronica spp.*	

Appendix Table A.1 cont'd. Compiled Species List for Virginia Hills Summer 2000. Nomenclature follows Moss (1983).

Identified to species (80)	Identified to genus (40)	Unidentified (13)
Maianthemum canadense		
Mertensia paniculata		
Mitella nuda		
Moneses uniflora		
Oxycoccus microcarpa		
Parnassia parviflora		
Pedicularis labradorica		
Petasites palmatus		
Petasites saggittus		
Picea glauca		
Picea mariana		
Pinus contorta		
Poa pratensis		
Populus tremuloides		
Pyrola asarifolia		
Ribes glandulosum		
Ribes hudsonianum		
Ribes triste		
Rosa acicularis		
Rubus acaulis		
Rubus chamaemorus		
Rubus idaeus		
Rubus pedatus		
Rubus pubescens		
Salix boothii		
Salix glauca		
Salix maccalliana		
Salix myrtillifolia		
Salix pedicellaris		
Senecio triangularis		
Senecio trifida		
Smilacina stellata		
Smilacina trifolia		
Sorbus stichensis		
Vaccinium caespitosum		
Vaccinium membranaceum		
Vaccinium myrtilloides		
Vaccinium vitis-idaea		
Viburnum edule		
Viola renifolia		

Appendix Table A.2. Vascular understory species list for each residual sampled in Virginia Hills fire area. Nomenclature follows Moss (1983).

Species	3	5	7	8	9	11	13	14	15
Abies balsamifera		x	x	x		x			x
Achillea millefolium	x				x	x	x	x	
Actaea rubra	x								
Alnus crispa	x		x	x		x			
Anemone spp.								x	
Arctostaphylus uva-ursi									x
Arnica cordifolia			x				x		
Aster ciliolatus						x			x
Aster spp.							x		
Betula pumila	x				x	x		x	x
Calamagrostis canadensis			x	x	x		x		
Carex aquatilis				x	x				
Carex disperma						x			
Carex globular				x					
Carex interior						x			
Carex media						x			
Carex spp	x		x	x	x	x	x	x	x
Carex spp					x			x	
Coptis trifolia			x						
Corallorhiza trifida						x			
Cornus canadensis	x	x	x	x	x	x	x	x	x
Danthonia californica							x		
Delphinium glaucum						x	x		
Dryopteris assimilis			x						
Empetrum nigrum	x	x		x	x			x	
Epilobium angustifolium	x		x	x	x	x	x		x
Equisetum arvense				x	x	x	x	x	x
Equisetum pratense	x			x	x	x	x	x	
Equisetum scirpoides	x			x	x	x	x		
Fragaria virginiana	x			x	x		x		x
Galium boreale			x	x	x	x	x		
Galium triflorum	x		x						
Gaultheria hispidula	x	x		x	x	x	x	x	x
Geum rivale						x			
Goodyera repens			x						

Appendix Table A.2 cont'd. Vascular understory species list for each residual sampled in Virginia Hills fire area. Nomenclature follows Moss (1983).

Species	3	5	7	8	9	11	13	14	15
Grass 1 spp	x		x			x	x	x	x
Grass 2 spp			x						
Gymnocarpium dryopteris	x		x						
Habenaria hyperborea	x					x			
Kalmia microphylla								x	x
Larix laricina seedling	x			x	x	x			
Lazula parviflora						x			
Ledum groenlandicum	x	x		x	x	x	x	x	x
Linnaea borealis	x		x	x	x	x	x		x
Listera cordata	x			x		x			
Lonicera involucrata	x			x	x	x	x		
Maianthemum canadense									x
Mertensia paniculata	x		x	x	x	x	x		
Mitella nuda	x		x	x	x	x	x	x	
Moneses uniflora	x		x			x	x	x	
Oxycoccus microcarpus	x				x	x	x	x	x
Parnassia parviflora	x								
Pedicularis labradorica	x				x		x		x
Petasites palmatus	x		x	x	x	x	x	x	x
Petasites saggittus								x	
Picea mariana	x	x	x	x	x	x	x		x
Picea mariana				x	x			x	
Picea spp								x	
Pinus contorta		x	x	x	x	x	x	x	x
Poa pratensis	x					x			
Polygonum spp						x			
Populus tremuloides			x						
Pyrola asarifolia	x		x		x	x		x	
Ribes glandulosum			x			x			
Ribes hudsonianum					x				
Ribes triste	x		x	x				x	
Rosa acicularis	x		x	x	x	x	x		x
Rubus acaulis	x		x			x		x	
Rubus chamaemorus	x				x	x		x	x
Rubus idaeus			x						
Rubus pedatus	x	x	x			x			

Appendix Table A.2 cont'd. Vascular understory species list for each residual sampled in Virginia Hills fire area. Nomenclature follows Moss (1983).

Species	3	5	7	8	9	11	13	14	15
Rubus pubescens	x		x	x	x		x	x	
Rubus spp.				x		x			x
Salix #2	x			x	x		x	x	
Salix 2 spp	x			x	x			x	
Salix spp.- Unk 5 low willow	x			x	x				
Salix boothii				x					
Salix maccalliana						x			
Salix myrtillifolia				x		x	x	x	
Salix pedicellaris						x			
Senecio triangularis						x	x		
Senecio trifida								x	
Senecio spp.							x		
Smilacina spp.				x	x				
Smilicina stellata			x						x
Smilacina trifolia	x			x	x	x	x	x	x
Solidago spp						x			
Sorbus stichensis		x							
Stellaria spp			x						
Vaccinium caespitosum	x	x		x		x	x	x	x
Vaccinium membranaceum		x					x		
Vaccinium myrtilloides	x	x	x	x	x		x		
Vaccinium vitis-idaea	x	x	x	x	x	x	x	x	x
Veronica spp.								x	
Viburnum edule	x	x	x	x			x		
Viola renifolia			x		x	x	x		

Table A.3. Vascular understory species names and their abbreviated names used in ordination analyses 120
(Nomenclature follows Moss 1983).

Abbreviated Name	Species Name	Abbreviated Name	Species Name
Abi bal seedling	*Abies balsamifera*	*Smi tri*	*Smilacina trifolia*
Ach mil	*Achillea millefolium*	Unknown 5	Unknown species
Bet pum	*Betula pumila*	*Vac cae*	*Vaccinium caespitosum*
Cal can	*Calamagrostis canadensis*	*Vac mem*	*Vaccinium membranaceum*
Car spp 1	*Carex* spp.	*Vac myr*	*Vaccinium myrtilloides*
Carex spp 2	*Carex* spp.	*Vac vit*	*Vaccinium vitis-idaea*
Cor can	*Cornus canadensis*	*Vib edu*	*Viburnum edule*
Emp nig	*Empetrum nigrum*	*Vio ren*	*Viola renifolia*
Epi ang	*Epilobium angustifolium*		
Equ arv	*Equisetum arvense*		
Equ pra	*Equisetum pratense*		
Equ sci	*Equisetum scirpoides*		
Gal bor	*Galium boreale*		
Gal tri	*Galium trifolium*		
Gau his	*Gaultheria hispidula*		
Geu riv	*Geum rivale*		
Grass sp 1	Grass sp 1		
Grass sp 2	Grass sp 2		
Kal mic	*Kalmia microphylla*		
Led gro	*Ledum groenlandicum*		
Lin bor	*Linnaea borealis*		
Lon inv	*Lonicera involucrata*		
Mer pan	*Mertensia paniculata*		
Mit nud	*Mitella nuda*		
Mon uni	*Moneses uniflora*		
Oxy mic	*Oxycoccus microcarpus*		
Ped lab	*Pedicularis labradorica*		
Pet pal	*Petasites palmatus*		
Pic mar sapling	*Picea mariana* sapling		
Pic mar seedling	*Picea mariana* seedling		
Pyr asa	*Pyrola asarifolia*		
Ros aci	*Rosa acicularis*		
Rub aca	*Rubus acaulis*		
Rub cha	*Rubus chamaemorus*		
Rub ped	*Rubus pedatus*		
Rub pub	*Rubus pubescens*		
Sal mac	*Salix maccalliana*		
Sal myr	*Salix myrtillifolia*		
Sal ped	*Salix pedicellaris*		