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Post-fire structure and decomposition dynamics of coarse woody material in the western

Canadian continental boreal forest

by

Barbara Sander ©

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

of the requirements for the degree of Doctor of Philosophy

in Forest Biology and Management

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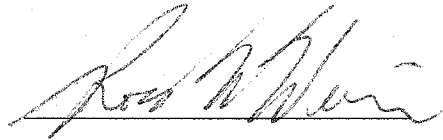T6E 2L6

January 2, 2003

Yet, poking around is a guaranteed way to learn. Ideas, after all, start with sense impressions; and all learning comes from making connections among observations and ideas. Insight is born of analogy. Everything interesting is complicated. Since truth is in the detail, seekers of truth should seek it there.

Kathleen D. Moore, Riverwalking: Reflections on moving water
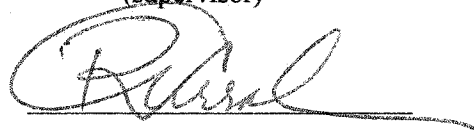
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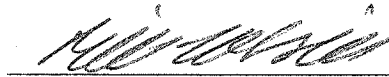
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Post-fire structure and decomposition dynamics of coarse woody material in the western Canadian continental boreal forest" submitted by Barbara Sander in partial fulfillment of the requirements for the degree of Doctor of Philosophy.
in Forest Biology and Management.

Dr. Ross W. Wein
(supervisor)

Dr. Randy S. Currah

Dr. William B. McGill

Dr. Donald J. Pluth

Dr. Cindy E. Prescott

January 6, 2003

Dedication

To my family: My parents, my husband and my children

Abstract

In the western Canadian continental boreal forest the structural properties and coarse woody material (CWM) fuel loads of different stages of early stand development (defined as tree seedling, tree sapling and young tree) were compared in aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) stands using a chronosequence approach. Stand ages ranged from 8 to 57 years. Decomposition of the fire-originated CWM was measured as changes in wood density over time.

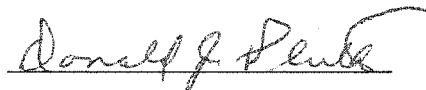Aspen sites had the highest average CWM fuel load of 21.4 Mg/ha. Jack pine had the lowest average fuel load of 2.65 Mg/ha. Black spruce stands had an average fuel load of 3.01 Mg/ha.

Weighted, nonlinear regression was used to estimate parameter values for linear, exponential and sigmoidal decomposition functions of CWM wood density. The performances of the functions were compared using a secondary Akaike Information Criterion (AIC_c). Post-fire standing dead trees did not decompose significantly. For aspen CWM the sigmoidal function had the best fit as indicated by the lowest AIC_c (-8.395), followed by the linear and the exponential function. For jack pine CWM the AIC_c of the linear and sigmoidal function were very similar (-10.978 and 10.551) and the exponential function had the highest value and the poorest fit. For black spruce CWM all equations performed poorly; the linear and exponential function had similar values of AIC_c (-20.732 and -19.876) whereas the sigmoidal function had the highest value.

Variables influencing the moisture content of CWM like distance of the CWM from the ground and an estimated climate moisture index affected decomposition dynamics differently: CWM close to the ground decomposed faster than CWM elevated

> 5 cm off the ground, the effect of the climate moisture index was most pronounced in jack pine increasing the lag-term for decomposition. Proposed conceptual decomposition models identify the need for more quantitative data to improve breakdown functions of snags and the vertical distribution of CWM during the first decades after fire.

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Without the support of Dr. Steve Cumming maximum likelihood estimation and nonlinear regression still would have been a daunting feat: Thank you, Steve, for all your time and patience. Dr. Simon Landhäusser offered constructive suggestions and support over the whole course of my program. Members of the Climate Change research group at the Northern Forestry Center, Edmonton, AB, provided the values for the climate moisture index.

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Many people had to put up with me and crazy schedules during the completion of this thesis; I would like to thank everyone living with us in Muse House during this time, my friends and fellow sufferers Maja and Karsten, and all my other friends (tall and small) who supported me in one way or the other; they kept me sane.

Finally, my greatest thanks and my love go to my husband Matthias and my children, who waited long enough for me to finish writing this "book".

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AIC, δAIC	Akaike information criterion, difference between two AIC values
AIC_c, δAIC_c	secondary Akaike information criterion, difference between two secondary AIC values
CI	confidence interval
CMI	climate moisture index
CWM	coarse woody material
DG	distance from the ground
D.f.	degrees of freedom
FSP	fiber saturation point
K	number of estimated parameters, plus one for the variance
LL	log-likelihood
MC	moisture content
Mg	Megagram (10^6g)
Pg	Petagram (10^{15}g)
RSS	residual sum of squares
σ^2	variance
SEM	standard error of the mean
SD	standard deviation
SOM	soil organic matter
W	weight, biomass
WD	wood density
V	volume

Chapter 1: Functions of coarse woody material in the boreal forest, a review

Introduction

Fire has been an important driving force of stand dynamics in the western Canadian boreal forest. Increased fire severity and longer fire seasons are predicted for the future of the Canadian boreal forest as part of climate change scenarios with increased temperature and precipitation (Li et al. 2000). One of the prominent legacies of a forest fire is the fire-killed trees that remain standing as snags until they fall over and become coarse woody material (CWM)(Hansen et al. 1991; Lee et al. 1995). Windthrow, diseases and insect infestations are additional disturbances that produce larger quantities of CWM. As about 30 % of the annual net primary production of a forest system accumulates as woody biomass, its decomposition is an integral part in ecosystem dynamics (Rayner and Boddy 1988).

CWM has multiple purpopses in the boreal forest, including energy for decomposers, habitat for wildlife, and fuel for a subsequent fire. From a fire management perspective research has focused on CWM quantity (e.g., Brackebush 1975, Dahms 1949). More recently, research focusing on wildlife and diversity evaluated the importance of CWM as structural habitat features (e.g., Kolström 1998, Stelfox 1995). The increasing discussion of the role of forests as carbon sinks has triggered research on carbon pools and fluxes, storage, decomposition dynamics and influencing factors (e.g. Sellers et al. 1997, Naesset 1999, Nalder and Wein 1999).

CWM as a structural element

Fuel

Large fuels (CWM diameter > 7.62 cm) contribute little to the spread of fire but much to the overall energy release (Agee and Huff 1987). With low moisture content large fuels prolong fire duration and increase the ecological impact through thermal energy release to the soil. The larger volume of coarse woody material in young and old stands (Agee and Huff 1987), might be one reason why these forests are more susceptible

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to wildfire than mid-aged forests. The importance of CWM as a fuel for wildfire is dependent on a range of factors that include regional climate and stand age.

Habitat features

Natural forest sites with abundant structural features like snags and CWM provide habitat for a variety of animal and plant species. In contrast, managed forests and plantations with a reduced structural legacy and few microhabitat features may not provide adequate environmental conditions required by many vertebrates (Hansen et al. 1991). In countries with a long record of managing forests for timber (e.g. Europe) many plant, animal, and microorganism species that are dependent on CWM habitat elements are threatened (e.g., Berg et al. 1994). In Canada, structural diversity has been associated with old-growth forest and the importance of snags has been highlighted by high-profile animal species like owls and woodpeckers. Forest species of nearly every group of organisms are dependent on CWM for food, shelter or reproduction (e.g., Crites and Dale 1995, Harmon et al. 1986, Roy et al. 1995). Frequently, decaying logs are a location of nitrogen input since nitrogen-fixing bacteria coexist with various wood decay fungi (Hendrickson 1991, Jurgensen et al. 1987, Larsen et al. 1978).

CWM as a carbon pool

There is still a certain amount of uncertainty regarding the residual terrestrial carbon sink, which is likely partitioned between the northern extra-tropics and the tropics (IPCC 2001). Since the 1990s this has sparked research in atmospheric carbon fluxes of the boreal forest (e.g., BOREAS (Trumbore and Harden 1997)). But instead of being a carbon sink boreal ecosystems might turn into a carbon source and contribute to climatic feedbacks under changing conditions (Bonan et al. 1992, Woodwell et al. 1998). Remaining uncertainties about the size of the sink, its mechanisms and its response to future changes have triggered efforts to increase the predictive power of carbon budget models (Apps et al. 1993). During the last decade efforts have been made to estimate the various fluxes of carbon, nitrogen and other nutrients, and models to predict these fluxes have been developed (Bonan 1990, Apps 1993, Apps et al. 1991, Kurz and Apps 1995,

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Kurz et al. 1995). Carbon budget work and estimation of long-term changes in forest carbon pools is frequently limited by the variability of site dynamics.

The main carbon pools in the boreal forest are live vegetation and soil organic matter, including litter and CWM (Apps et al. 1991). Most of the carbon accumulated in forests is stored in the aboveground tree mass and to a lesser extent in shrubs, ground vegetation and the forest floor (Nalder and Wein 1999). In natural stands, trees become CWM over time. Unfortunately, there are few quantitative data regarding CWM from long chronosequence studies (Harmon et al. 1990, Krankina and Harmon 1995, Laiho and Prescott 1999). A recent study by Nalder and Wein (1999) identified rotten logs as contributing 5- 14 % to the total forest floor carbon.

Forest fires cause direct and indirect carbon releases that range from 0.5 Pg C * $year^{-1}$ for the Russian boreal forest (Dixon and Krankina 1993) to 27 Pg C * $year^{-1}$ for the Canadian boreal forest (Amiro et al. 2001). The direct carbon release from combusted biomass is dependent on fire intensity (MacLean and Wein 1980). The indirect carbon dioxide emissions through the decomposition of uncombusted trees and soil respiration are estimated to account for three to six times the direct release (Auclair and Carter 1993, Dixon and Krankina 1993). Decomposition of the uncombusted tree biomass is a one of many processes in the recycling of tree mass after fire (Figure 1.1): It is preceded by the breakdown of standing dead trees or snags and followed by the incorporation of the biomass into the forest floor and the soil.

After fire, snags can remain standing for years before they fall to the forest floor (Dahms 1949), where they are more susceptible to decomposition. The decomposition rate of trees is species-specific since it is strongly influenced by anatomical as well as chemical properties (composition of hemicelluloses, lignin, and extractives) of the wood (Alban and Pastor 1993). Recently, studies suggested species-specific functional forms (linear, sigmoidal or exponential) for decomposition dynamics (Harmon et al. 2000, Laiho and Prescott 1999). Better understanding of long-term post-fire decomposition and a better quantification of decomposition processes of CWM will lead to greater accuracy of carbon estimates in the boreal forest carbon budget.

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Decomposition dynamics

The two main concurrent processes of CWM decomposition are fragmentation and mineralization (Harmon et al. 1986). Wood is a complex material consisting largely of cellulose and lignin. Wood mineralization is caused by bacteria, symbiotic protozoa in insects and fungi through enzymes that degrade the wood components. Insect and fungal activities are often associated since insects serve as vectors for fungal transmission.

Fungi are the most important wood decomposers (Zabel and Morrell 1992), although only a limited group of fungi are able to produce enzymes that can chemically modify or degrade lignin and at the same time tolerate chemical stresses like the presence of antifungal extractives in wood (Dix and Webster 1995). The chemical composition of the extractives differs not only between wood of gymnosperms and angiosperms but is species-specific as well. These attributes result in species-specific wood density, wettability and decomposition rates of wood. Nitrogen availability and lignin : nitrogen ratios are considered less restricting factors for wood decay than commonly assumed because wood decay fungi have adapted to a nitrogen poor environment by developing mechanisms to conserve nitrogen through hyphal autolysis and internal recycling (Zabel and Morrell 1992). Brown rot fungi also coexist with nitrogen-fixing bacteria (Larsen et al. 1978).

In general, decomposition is expressed as a decay parameter, coefficient or rate, which equals the fraction of biomass that is lost per unit time without implying that these fractions are approximately constant. Olson (1963) used a negative exponential function to calculate decay parameters for litter accumulation in an idealized forest. The negative exponential function assumes a constant fractional weight loss over time and has been used to calculate decay coefficients in various studies and models (e.g. Alban and Pastor 1993, Johnson and Greene 1991, Means et al. 1985, Naesset 1999, Sollins 1982). Lately, linear and sigmoidal mathematical functions have been used to describe the decomposition rate of CWM (e.g., Busse 1994, Laiho and Prescott 1999). Recently models that are able to adjust for variable decomposition rates over time have been hypothesized by Harmon et al. (2000).

Moisture and temperature greatly influence decomposition rates of wood (Boddy 1983a and 1983b, Marra and Edmonds 1996). In a low moisture environment like the

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continental boreal forest (Hogg 1994) the lack of moisture for wood decay organisms is likely a major controlling factor for decomposition rates.

Climatic factors

The catabolic processes and growth of wood decay fungi are mainly dependent on temperature and water as environmental factors (Griffin 1977). Even though studies provided accurate estimates of wood decomposition, few account for the seasonal and yearly difference in macroclimate and corresponding differences in wood microclimate (Rayner and Boddy 1988).

Temperature

Fungi are able to metabolize over a range of temperatures. Under experimental conditions beech branches showed a measurable amount of CO_2 release at 5° C (Boddy 1983) whereas the upper temperature limit for most wood decay fungi is around 40° C (Zabel and Morrell 1992). Under field conditions high temperatures seem to be less important than lower temperatures. Microclimate greatly influences wood temperatures, e.g., CWM decomposing in woodlands will experience lower temperature maxima and higher minima than wood decomposing in open lands (Rayner and Boddy 1988).

One effect of fire is an increase in soil thermal regimes (Fraser et al. 2002) that may lead to accelerated decomposition and mineralization (MacLean et al. 1983). In Bonan's model of the boreal forest system, woody biomass not consumed by fire is added to the annual litter pool and one factor controlling the decomposition of litter is soil temperature (Bonan 1990). These assumptions might not be valid for the coarse woody material in the continental climate of the Western Canadian boreal forest. After a fire of high severity the soil organic layers might be consumed and only a few of the fallen boles are in direct contact with the mineral soil. Most snags that fall after fire are elevated above the soil by their branches or by other fallen boles. Therefore, soil moisture and temperature might have less effect on decomposition than precipitation, air temperature and air humidity.

Moisture

Moisture content in CWM is directly influenced by water input, water-holding capacity and water output (Rayner and Boddy 1988). Water-holding capacity depends on available void space, which increases with decomposition. From a fungal perspective the four main water sources are precipitation, water vapor, translocation by mycelia, and metabolic water produced during decomposition.

Wood-decaying basidiomycetes are more sensitive to water stress than to varying temperatures since they require a free water source for the oxidation of the lignin (Zabel and Morrell 1992). The point where no free water exists in the cell lumina is referred to as the fiber saturation point; this represents the water content of the wood in equilibrium with a matric potential of about -0.1 MPa (Griffin 1977). The lowest water potential allowing measurable fungal growth lies between -5.0 and -7.0 Mpa; this is equivalent to 25-30% dry weight moisture content. Wood with less moisture is usually resistant to decay (Zabel and Morrell 1992). Generally, favourable moisture content is above 20% of the wood dry weight.

Low water potentials are caused by direct sun energy or lack of precipitation, either by drought or interception of rainfall by tree crowns (Dix and Webster 1995). After a stand replacement fire the tree canopy is removed and therefore exposure and precipitation are important factors for decomposition of CWM. The moisture content of CWM is affected by factors like diameter (Brackebush 1975) and distance between CWM and the ground (Erickson et al. 1985).

Objectives

The main objectives of this study are to: 1. evaluate the postfire changes in CWM fuel loads and of structural habitat features in the western continental boreal forest, and 2. quantify post-fire decomposition dynamics of aspen, jack pine and black spruce CWM and the influence of climatic factors.

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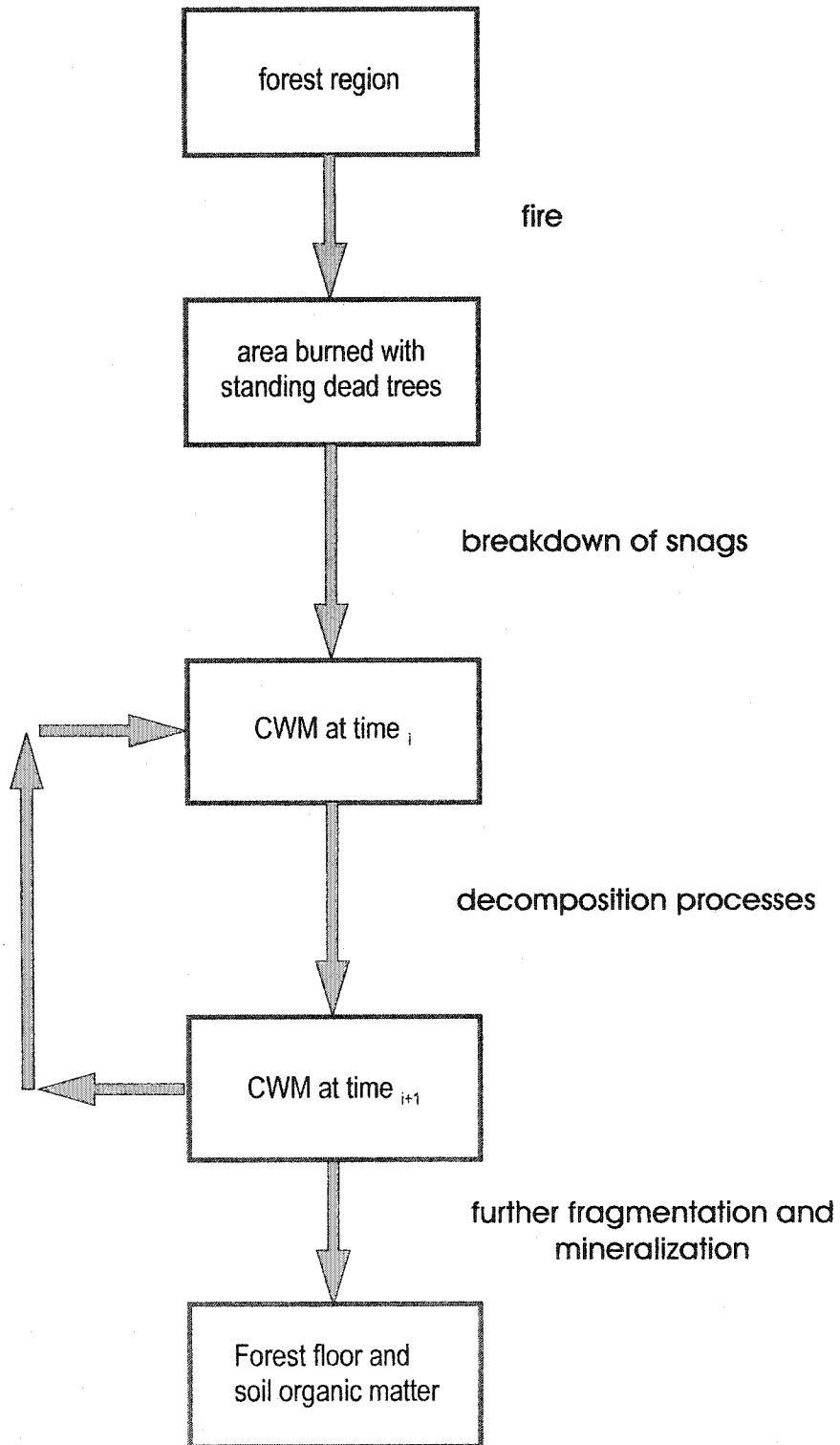
Figure 1.1: Processes involved in creating and mineralizing CWM. Dark gray arrows represent CWM decomposition dynamics. Time $_i$ represents years after fire.

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Chapter 2: General study area

Introduction

The study area extended from Lesser Slave Lake, Alberta in the south, to Wood Buffalo National Parkin the north, to Peace River in the west, and to Sandy Bay, Saskatchewan, in the east (Fig. 2.1). Climatically, the study area spans the mid boreal ecoclimatic region with only few sites bordering the high and low boreal regions (Ecoregion Working Group, 1989) Annual precipitation in the mid boreal ecoclimatic region ranges from 400 to 500 mm. Maximum precipitation (70 to 90 mm) and maximum temperature (15 to 18 °C) occur in July. Winters are cold (-18 to -25 °C) and last for 6 to 7 months, usually with persistent snow cover. Summers are cool and last about 5 months. Most study sites are located in a zone of decreasing moisture from east to west (Pojar 1996). The disturbance regime is characterized by stand-replacing wildfires (Dix and Swan 1971).

Study sites can be grouped into an eastern and western region (Figures 2.1 and 2.2): Sites in the eastern region (Region 1) are part of the Northern Coniferous Boreal Forest Region (B.22a, Rowe 1972). Sites in Alberta (Region 2) were mainly located in the Mixedwood Boreal Forest region (B.18a, Rowe 1972) with a few northern sites bordering the Hay River Boreal Forest region (B.18b, Rowe 1972). Sites in Region 1 were more closely grouped than sites in Region 2.

Site selection

In western Canada, burned areas have been mapped since the 1940s; these records and forest inventory maps of burns greater than 1000 ha provided estimates for stand age in this chronosequence approach. Within these burns, sites were chosen to represent homogenous stands of a single tree species. Time since fire ranged from 7 to 56 years which was validated in the field from fire scars and the ages of three living trees (Appendix 2.1). Field selection included only single tree species forests (Figure 2.2):

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Aspen (*Populus tremuloides* Michx.,14 sites, 8 - 34 years) jack pine (*Pinus banksiana* Lamb., 22 sites, 7 - 44 years) and black spruce (*Picea mariana* (Mill.) BSP., 24 sites, 8 - 57 years). Older sites were rejected when nearly all CWM was overgrown by moss or covered by litter layer and therefore considered part of the soil system. The three tree species were associated with different site conditions, black spruce sites were chosen to represent hygric conditions with organic soils, aspen sites were chosen to represent mesic conditions on predominantly Gray Luvisols and jack pine sites were chosen to represent xeric site conditions on predominantly Brunisols. Individual non-identifiable fallen logs or fallen logs of a different species than the dominant tree species were not sampled.
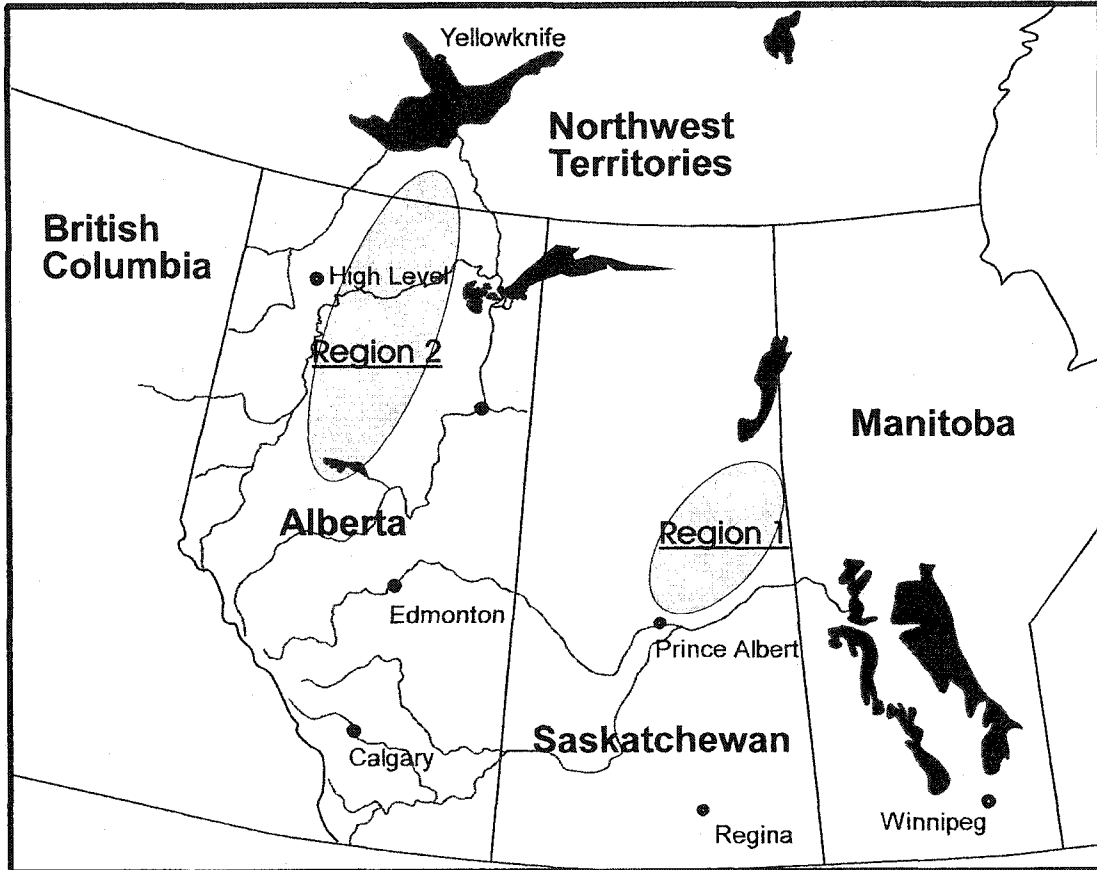
Figure 2.1: General study area of the Canadian prairie provinces showing Region 1 located in central Saskatchewan and Region 2 located in northern Alberta.

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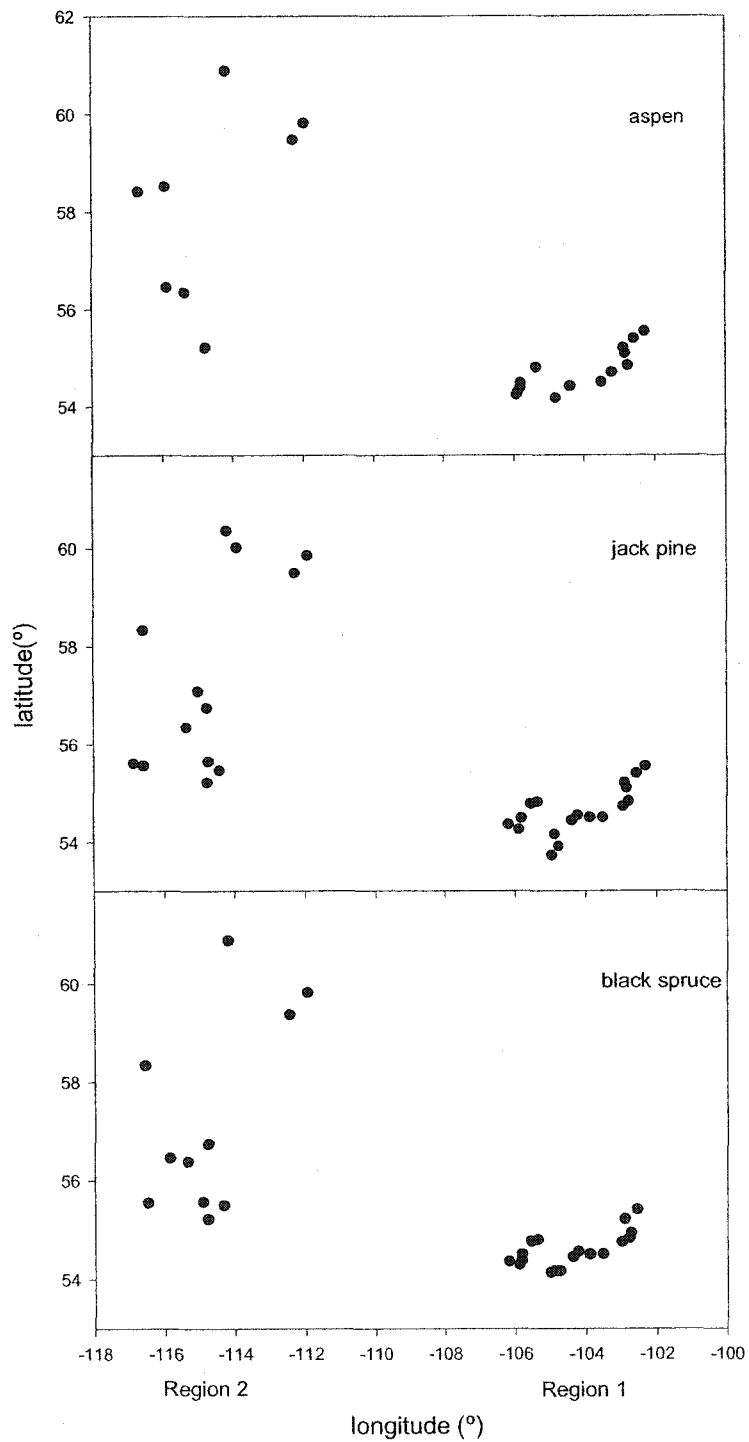
Figure 2.2: Distribution of 21 aspen, 33 jack pine and 30 black spruce sites by longitude and latitude. Sites were distinctly grouped into an eastern and western region.

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Appendix 2.1: Characteristics of aspen study sites.

Chosen sites were assigned a code identifying the region and age of the stands: The first number refers to the sampling region and the numbers after the dash indicate the number of years since the fire. Letters were used to identify different fires in a region that occurred in the same year, letters being assigned from south to north (e.g.,1-10a and 2-10b).

Location	species	province	site code	UTM longitude (W)	UTM latitude	stand age *	fire year#
Scherr Fire	AT	SK	1-8	-102.603	55.399	7+/-2	1989
Halfway Point	AT	SK	1-9a	-105.927	54.246	8+/-2	1988
Coffee Fire	AT	SK	1-9b	-104.411	54.421	7+/-2	1988
Lubicon Lake	AT	AB	2-15	-115.875	56.463	14+/-3	1982
Cherry Mountain	AT	AB	2-16	-112.276	59.477	15+/-3	1981
Pelican Narrows	AT	SK	1-17	-102.905	55.212	15+/-3	1980
McKenzie Fire	AT	SK	1-19	-105.376	54.807	16+/-4	1978
North Narrow Hills	AT	SK	1-20a	n.a.	n.a.	18+/-4	1977
Weyakwin	AT	SK	1-20b	-105.815	54.488	18+/-4	1977
Puskwakau Fire	AT	SK	1-20c	-103.515	54.505	16+/-5	1979
Slave Lake	AT	AB	2-29	-114.777	55.213	28+/-3	1968
RD 916	AT	SK	1-32	n.a.	n.a.	30+/-4	1965
Deschambault Fire	AT	SK	1-34a	-103.234	54.707	33+/-4	1963
Churchill River	AT	SK	1-34b	n.a.	n.a.	32+/-3	1963
Fort Vermillion	AT	AB	n.s.	n.a.	n.a.	33+/-4	
Pine Point	AT	NWT	n.s.	-114.188	60.889	33+/-4	1971?
Devil Lake	AT	AB	n.s.	-116.680	58.414	38+/-4	1960
Caribou River	AT	AB	n.s.	-115.926	58.523	40+/-2	1955
Candle Lake	At	SK	n.s.	-104.764	53.916	> 40	
Hwy 88	AT	AB	n.s.	-115.367	56.349	46+/-5	
RD135	AT	SK	n.s.	n.a.	n.a.	47+/-3	
Torch River RD	AT, SW	SK	n.s.	-105.072	53.728	50+/-6	
Lesser Slave Lake	AT	AB	n.s.	n.a.	n.a.	> 50	
south of Weyakwin	AT	SK	n.s.	-105.893	54.291	56+/-6	1940
RD135	AT	SK	n.s.	n.a.	n.a.	65+/-8	
south of Weyakwin	AT	SK	n.s.	-105.828	54.381	76+/-6	

n.s. = not sampled
n.a. = data not available due to technical problems with GPS
* stand age estimated in years by ring counts of regenerating trees and fire scars
# fire year from fire history maps

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Appendix 2.2: Characteristics of jack pine study sites.

Chosen sites were assigned a code identifying the region and age of the stands: The first number refers to the sampling region and the numbers after the dash indicate the number of years since the fire. Letters were used to identify different fires in a region that occurred in the same year, letters being assigned from south to north (e.g.,1-10a and 2-10b).

Location	species	province	site code	UTM longitude (W)	UTM latitude	stand age*	fire year #
Scherr Fire	PJ	SK	1-8	-102.567	55.405	7+/-2	1989
Halfway Point	PJ	SK	1-9a	-105.927	54.246	8+/-2	1988
Coffee Fire	PJ	SK	1-9b	-104.220	54.549	7+/-2	1988
Elaine Fire	PJ	SK	1-10a	-104.386	54.444	8+/-3	1987
Jackpine Natural Area	PJ	AB	2-10b	-116.579	55.566	10+/3-	1987
Loon River	PJ	AB	2-15	-115.026	57.081	13+/-4	1982
Cherry Mountain	PJ	AB	2-16	-112.267	59.497	16+/-3	1981
Pelican Narrows	PJ	SK	1-17	-102.910	55.216	15+/-4	1980
McKenzie Fire	PJ	SK	1-19	-105.368	54.819	16+/-4	1978
North Narrow Hills PP	PJ	SK	1-20a	n.a.	n.a.	18+/-5	1977
Weyakwin	PJ	SK	1-20b	-105.816	54.486	18+/-3	1977
Puskwakau Fire	PJ	SK	1-20c	-103.515	54.505	19+/-4	1979
Marten Hills	PJ	AB	2-25a	-114.422	55.465	22+-3	1972
Equisetum Lake	PJ	AB	2-25b	-114.770	56.742	22+-2	1972
Sass Lake	PJ	NWT	2-25c	-113.918	60.018	27+/-4	1970
Slave Lake	PJ	AB	2-29	-114.775	55.219	29+/-2	1968
Nyarling River	PJ	NWT	2-31	-114.196	60.362	29+/-4	1966
Emerald Pond	PJ	SK	1-32b	-105.552	54.780	27+/-5	1965
Herman Lake Fire	PJ	SK	1-32c	-103.880	54.500	29+/-4	1965
RD 916	PJ	SK	1-32a	-106.195		30+/-5	1965
Churchill River	PJ	SK	1-34b	-102.308	55.549	32+/-5	1963
Deschambault Fire	PJ	SK	1-34a	-102.933	54.730	33+/4-	1963
Salt River	PJ	AB	2-44	-111.915	59.859	44+/-6	1953
Hwy 5	PJ	NWT	n.s.	n.a.	n.a.		1955/66
Kathleen Fire	PJ	AB	n.s.	-116.870	55.610	38+/-4	1958
Hwy 88	PJ	AB	n.s.	-115.367	56.349	43+-3	
RD135	PJ	SK	n.s.	-102.854	55.101	46+-4	
close to PJ Nat. Area	PJ	AB	n.s.	-116.593	55.567	48+-3	
Torch River RD	PJ	SK	n.s.	-104.764	53.916	52+/-5	
Torch River RD	PJ	SK	n.s.	-104.962	53.726	52+/-5	
RD135	PJ	SK	n.s.	-102.786	54.830	53+-4	
Candle Lake	PJ	SK	n.s.	n.a.	n.a.	55+/-5	
north of Marten Hills	PJ	AB	n.s.	-114.734	55.647	55+-6	
south of Weyakwin	PJ	SK	n.s.	-105.893	54.291	56	1940
RD 913	PJ	SK	n.s.	-104.880	54.161	>100	
Machesis Lake	PJ	AB	n.s.	-116.580	58.331	120+/-15	

n.s. = not sampled
n.a. = data not available due to technical problems with GPS
* stand age estimated in years by ring counts of regenerating trees and fire scars
# fire year from fire history maps

Appendix 2.3: Characteristics of black spruce study sites.

Chosen sites were assigned a code identifying the region and age of the stands: The first number refers to the sampling region and the numbers after the dash indicate the number of years since the fire. Letters were used to identify different fires in a region that occurred in the same year, letters being assigned from south to north (e.g.,1-10a and 2-10b).

Location	species	province	site code	UTM longitude (W)	UTM latitude	stand age*	fire year #
Scherr Fire	SB	SK	1-8	-102.557	55.406	7+/-2	1989
Halfway Point	SB	SK	1-9a	-105.887	54.260	8+/-2	1988
Coffee Fire	SB	SK	1-9b	-104.219	54.557	7+/-2	1988
Elaine Fire	SB	SK	1-10a	-104.371	54.452	9+/-2	1987
Jackpine Natural Area	SB	AB	2-10b	-116.498	55.550	10+/-1	1987
Lubicon Lake	SB	AB	2-15	-115.869	56.462	13+/-3	1982
Cherry Mountain	SB	AB	2-16	-112.446	59.370	15+/-2	1981
Pelican Narrows	SB	SK	1-17	-102.906	55.215	15+/-4	1980
McKenzie Fire	SB	SK	1-19	-105.376	54.797	16+/-4	1978
North Narrow Hills PP	SB	SK	1-20a	-104.728	54.167	18+/-3	1977
Weyakwin	SB	SK	1-20b	-105.819	54.498	18+/-4	1977
Puskwakau Fire	SB	SK	1-20c	-103.525	54.511	16+/-5	1979
Marten Hills	SB	AB	2-25a	-114.326	55.498	24+-2	1972
Equisetum Lake	SB	AB	2-25b	-114.771	56.742	23+-4	1972
Slave Lake	SB	AB	2-29	-114.775	55.218	26+-3	1968
RD 916	SB	SK	1-32a	-106.195	54.359	30+/-4	1965
Emerald Pond	SB	SK	1-32b	-105.568	54.771	27+/-6	1965
Herman Lake Fire	SB	SK	1-32c	-103.889	54.501	32+/-3	1965-63
Deschambault Fire	SB	SK	1-34	-102.991	54.756	33+/-4	1963
Salt River	SB	AB	2-44	-111.942	59.827	43+/-3	1953
RD 913	SB	SK	1-51	-105.009	54.134	50+/-4	
RD135	SB	SK	1-56	-102.734	54.935	55+/-4	
south of Weyakwin	SB	SK	1-57	-105.889	54.295	55+/-6	
RD 913	SB	SK	n.s.	-104.880	54.161	95+/-8	
south of Weyakwin	SB	SK	n.s.	-105.828	54.381	>80	
Machesis Lake	SB	AB	n.s.	-116.568	58.342	134+/-10	
south of Weyakwin	SB	SK	n.s.	n.a.	n.a.	43+/-5	
RD135	SB	SK	n.s.	-102.786	54.832	60+/-5	
RD106	SB	SK	n.s.	-103.897	54.504	65+/-8	
north of Marten Hills	SB	AB	n.s.	-114.913	55.567	85+/-10	
Hwy 88	SB	AB	n.s.	-115.349	56.390	90+/-10	
Pine Point	SB	NWT	n.s.	-114.194	60.885	34+/-4	1971?

n.s. = not sampled
n.a. = data not available due to technical problems with GPS
* stand age estimated in years by ring counts of regenerating trees and fire scars
# fire year from fire history maps

Chapter 3: Structural features and fuel loads of coarse woody material in fire-originated stands in the western continental boreal forest

Introduction

Forest fires of all sizes have been an integral part of the western Canadian boreal forest ecosystem resulting in a mosaic of different vegetation and habitats over the landscape (e.g. Johnson 1992, Timoney and Wein 1991). Changing weather conditions during the fire event, topography and different fuel types create a variety of burning conditions that are reflected in a heterogeneous post-fire landscape with fire skips and stands that burned at different severities. The effects of fire are highly variable, depending on intensity (a function of heat yield and rate of consumption). In severe fires, most trees are killed by sufficient heat penetration through the bark to kill the cambial layers. For the first few decades after fire the primary source of coarse woody material (CWM) are the pre-disturbance trees (Hansen et al. 1991, Lee et al. 1995*b*).

Animal and plant species diversity is related to structural features of snags (standing dead trees killed by the last fire) and CWM (Berg et al. 1994, Hansen et al. 1991). Some vertebrates, such as bats and other small mammals, use snags and CWM for cover, feeding and reproduction (Crampton and Barclay 1995, Harmon et al. 1986, Roy et al. 1995). Managed natural forests and plantations have reduced structural diversity and microhabitat features, which may be below levels required by many vertebrates (Hansen et al. 1991). A number of threatened fungal species are positively correlated with CWM abundance, size, and stage of decay and negatively correlated with the amount of wood harvested (Bader et al. 1995). Providing CWM in various stage of wood decay is also an important factor for maintaining diversity of nonvascular plant species (Crites and Dale 1995).

Large diameter CWM contributes little to the rate of fire spread and is usually not incorporated into fire behavior prediction systems (e.g. Canadian forest fire behavior prediction system, Forestry Canada Fire Danger Group 1992). Nevertheless, big logs may represent over 50 % of the total CWM inventory (Hély et al. 2000), store a significant amount of carbon (Nalder and Wein 1999), and contribute significantly to the total

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energy release through fire or decomposition (Agee and Huff 1987). The amount of CWM in a stand can be expressed as biomass or volume concentration per unit area. These measurements represent slightly different ways of quantifying CWM since they are affected differently by decomposition processes. The distance CWM is suspended above the ground by other fallen trees influences the rate of decay (Sander 1995) and adds to the structural complexity of post-fire stands.

It has been proposed that in aspen mixedwood, structural features like the number of snags and the amount of CWM (biomass and volume) change during regeneration in a U-shaped pattern indicating that young and old stands have larger quantities of structural CWM (Lee et al. 1995a). In conifer stands, the pattern might be different since mortality and decay rates are dependent on the tree species (Alban and Pastor 1993) and coniferous trees tend to decompose more slowly than deciduous trees (Harmon et al. 1986). Factors like vegetation and fuel loads have a direct impact on the probability of a second fire. A second fire would obviously change the pattern.

The general objective of this study was to describe the structural properties (e.g. number of snags, tree regeneration, CWM weight and volume) during the breakdown period of snags in post-fire aspen, jack pine and black spruce stands.

Hypotheses

It was hypothesized that as post-fire age increases, the number of snags will decline until other processes (e.g. self-thinning, insect infestations, disease, a second fire) produce new snags. As snags fall on each other the distance of the boles from the ground, total weight and volume of CWM should increase until most snags have fallen over. Snag breakdown will be fastest for aspen and slowest for black spruce. Overall CWM accumulation (weight and volume) and distance from the ground will be faster for aspen than for the conifer species.

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Methods

The number of snags per hectare was based on all snags in a 10m equilateral triangle. The distance above ground (DG) of CWM was recorded as distance between ground surface and lower surface of the CWM. CWM 5 cm or closer to the ground was classified as downed and CWM more than 5cm off the ground was classified as elevated. Weight and volume of CWM was calculated using the line-intersect method (Van Wagner 1968, 1982). Since only horizontal CWM was measured and the diameter of the samples recorded, biases due to non-horizontal orientation and tallying (Brown and Roussopoulos 1974, Van Wagner 1982) should be of little concern. In aspen and jack pine stands only pieces with a diameter > 5cm were measured and sampled. For black spruce these standards were relaxed and all pieces > 1.5cm were measured and sampled. To correct for orientation biases randomly oriented equilateral triangles of 10m side length were used as sample lines. A total of 30 samples of CWM intersecting the line was collected. CWM crossing the line more than once were sampled only at the first intersection. The total length of the line needed (= sum of all sides of 1 to 4 triangles) was recorded. Volume and fuel load (weight) of CWM were calculated using the equations of the line-intersect method (Van Wagner 1968):

$$V = (k * \pi^2/8L) * \sum d^2$$

$$W = (G * k * \pi^2/8L) * \sum d^2$$

where V is volume per unit area ($m^3 * ha^{-1}$), W is weight per unit area ($Mg * ha^{-3}$), k is a unitless equation coefficient, d is piece diameter (cm) at intersection, L is length of sample line (m), and G is specific gravity. In the present study the mean wood density per site is used instead of specific gravity. The wood density was calculated based on oven dry weight and volume was based on diameter measured in the field and length measured in the lab. Length of the samples ranged from 2 to 15cm, samples with a smaller diameter tended to be longer than samples with a larger diameter. To calculate site-specific volume and weight, the average wood density of all CWM per site was used. The amount of carbon stored in CWM was calculated based on weight and reported carbon contents

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of 50 % for CWM (Laiho and Prescott 1999). Statistical analysis consisted of ANOVA using SPSS version 10.0 for Windows (SPSS Inc. 1989-1999)

Results

Structural development

During 7 to 57 years after the last stand replacing fire three different stages of structural stand development could be identified: the tree seedling stage, the tree sapling stage and the young tree stage (Table 3.1). Differences among these stages were related mainly to structural features like numbers of standing dead trees and DG of the CWM. At the tree seedling stage, regenerating trees were small and stands were dominated by snags, and CWM that was elevated above the ground. During the tree sapling stage regenerating trees were larger, and the number of snags and the average DG of the CWM declined. Very few snags remained standing during the young tree stage when young trees, close to maturity, started to dominate the stands and most CWM was close to the ground (Figure 3.1). As structural elements of CWM declined and the trees regenerated, the stands displayed more canopy closure and developed shrub and herb layers (Table 3.1).

In the three site types the average DG declined significantly as stands developed (Table 3.2, Figure 3.1). In aspen the DG declined significantly from the initial to the tree sapling and young tree stages. In jack pine the DG in the young stage was significantly lower than in the initial and establishing stage (Table 3.2). In black spruce the DG in the tree seedling stage was significantly higher than in the tree sapling and young tree stage. For all species the amount of CWM close to the ground (≤ 5 cm DG) increased with time (Figure 3.2); aspen showed the fastest and black spruce the slowest increase.

Fuel load and volume of coarse woody material

The average CWM weight of all aspen sites was 21.4 Mg·ha^{-1}. With an assumed carbon content of 50 % in wood the average carbon content of CWM per site was 10.7 Mg·ha^{-1}. The weight of CWM was not significantly different among the stages of aspen, jack pine and black spruce site development (Table 3.3). During early stand development

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the weight and volume of CWM peaked during the tree sapling stage (Figure 3.3, Table 3.3), but the maximum volume of 251 $m^3 \cdot ha^{-1}$ for site 2-29 did not coincide with the site of maximum fuel load (2-16) (Table 3.3). Low values for weight and volume in site 1-19 and 1-20a were very likely a result of salvage cutting close to the site and a heterogeneous species-composition of CWM that led to a higher number of CWM that were ignored. These sites were excluded from future analysis.

The average weight of CWM in jack pine stands (2.65 $Mg \cdot ha^{-1}$, = 1.3 $MgC \cdot ha^{-1}$) was much lower than for aspen. The differences between fuel loads among stages of development were close to being significant (Table 3.2). Maximum fuel load and volume occurred during the tree sapling stage (Figure 3.3 , Table 3.4). Black spruce stands had a slightly higher average fuel load (3.01 $Mg \cdot ha^{-1}$, = 1.5 $MgC \cdot ha^{-1}$) than jack pine. There were no significant differences in weight or volume among the stages (Table 3.2). Contrary to the other two species fuel load and CWM volume peaked during the tree seedling stage (Figure 3.3, Table 3.5).

Aspen and jack pine exhibited a larger decrease of CWM weight than of volume: From the tree sapling to the young tree stage weight decreased by 59 % for aspen and 50 % for jack pine whereas volume decreased by 22 % and 28 % respectively (Figure 3.3). Black spruce showed a gradual decline; in the young stage only 49 % of the weight and 58 % of CWM volume remained (Figure 3.3).

Discussion

CWM dynamics depend on snag breakdown rates after fire. Reported lag times before the onset of snag breakdown range from 2 years for *Pinus contorta* (Lyon 1977) to 20 years for *Pseudotsuga* and *Tsuga* (McArdle 1931). In the present study snag breakdown continued for 30 years for aspen and jack pine and for 40 years for black spruce. Dahms (1949) reported that close to 50 % of all ponderosa pine snags remained standing 10 years after the fire and 22 % remained standing 22 years after the fire. Other half times for snag breakdown after fire range from 10 years for *Pinus contorta* (Lyon 1977) to 27 years for *Pseudotsuga* and *Tsuga* (McArdle 1931). Few long-term studies exist that quantify snag breakdown rates after fire for the western boreal forest.

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Overall densities of snags are variable, ranging from 19 stems·ha^{-1} at 22-26 years after fire (Lee et al. 1995b) for aspen mixedwood forests in Alberta, and 500 - 7000 stems·ha^{-1} at 32 years after fire in the southeastern mixedwood boreal in Quebec forest (Hély et al. 2000) to 2500 - 3000 stems·ha^{-1} at 11 years in the sub-boreal spruce forest of British Columbia (Clark et al. 1998). Differences in pre-fire tree densities, average diameter, different fire intensities and variable breakdown rates might be the main reasons for the reported range in snag densities.

Aspen fuel loads in the present study were within the range reported for other forest regions and tree species: The reported average biomass of CWM in young temperate forest stands was 14 Mg·ha^{-1} and ranged from 20-32 Mg·ha^{-1}for fir-stands to 7-11 Mg·ha^{-1} for mixed pine stands (Harmon et al. 1986). In the southeastern Canadian boreal forest fuel loads of CWM ranged from 22 to 28 Mg·ha^{-1} at age 32 (Hély et al. 2000). In the present study jack pine CWM fuel loads were generally lower than the reported 4.5 Mg·ha^{-1}at in a mature lodgepole pine forest in the Rocky Mountains (Delisle et al. 1988) with only three sites exceeding this value. Fuel loads in the tree seedling and tree sapling stage were similar and declined in the young stage. Fuel loads for black spruce were of the same magnitude and showed no obvious trends.

In a study of clearcut loblolly pine stands maximum amounts of slash or CWM occur directly after disturbance and showed a sharp decline (50 % weight) during the first 10 years (Barber and Van Lear 1984). In contrast, burnt areas provide considerable amounts of CWM for 30 years after fire. The differences in amount of CWM in harvested stands compared to burned stands have been illustrated by studies in eastern Canada (Pedlar et al. 2002) and Russia (Krankina et al. 2002). The relatively large amount of CWM in aspen sites of the present study underline the importance of recently disturbed aspen stands for wildlife. The effects of harvesting and removing structural features like snags and CWM have been discussed by Berg et al. (1994), Hansen et al. (1991) and Harmon et al. (1986).

Aspen stands generally have the highest volume of CWM in boreal forest stands. Values in the present study are comparable to the results of similar post-fire studies in the area: at age 23 to 26 years the reported volume was around 60 m^3/ha (Lee et al. 1995a),

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between 20 and 60 years volume in aspen-dominated stands ranged between 93 and 95 m^3/ha (Lee et al. 1997). In eastern Canada CWM concentrations in mature deciduous forests (105 m^3/ha) were significantly higher than for coniferous forests (18 m^3/ha) (Pedlar et al. 2002).Values for sub-boreal spruce mixedwood stands were larger: The overall CWM volume was larger than 100 m^3/ha at 11 years (Clark et al. 1998) and decreased until 200 years. Reported values for coniferous trees in temperate forests ranged from 90 - 130 m^3/ha in balsam fir-dominated stands and 30 - 55 m^3/ha for mixed pine stands (Harmon et al. 1986). Differences between proportional weight loss and volume loss are a result of a specific feature of wood decay.

All of the above features and fuel loads are depend on two main factors: the number of trees per area (or pre-fire stem densities) and the diameter of the trees. Sites that were relatively old when they burned will have lower stem densities and larger stem diameters. Since weight and volume are calculated on the base of the squared diameter, a few large trees have a large impact on the value. The greater the tree densities and the tree diameter the higher the probability that a fallen tree will be supported by other trees above the ground. Since stand age and diameter were not included in the analysis of the present study a large part of the variation could not be explained and F-values remained low.

Conclusions

During post-fire stand development, structural features change as snags fall over and CWM weight and volume increase. Weight and volume of CWM for aspen was considerably higher than for the conifer species but did not differ during three stages of stand development. Distance of CWM from the ground declined during development of aspen, jack pine and black spruce stands. Results from the present study serve as a baseline and guideline for further forest management and conservation decisions and provide the boundaries for modeling exercises of decomposition processes and carbon budgets.

Table 3.1: Structural properties of post-fire forest sites for three stages of stand development. The number of observations for the tree seedling, tree sapling and young tree stage are given as n_1, n_2 and n_3 respectively.

stage of structural development		tree seedling	tree sapling	young tree
Aspen	age (yr),	1-10	11-30	30- 40
(n_1 = 3)	height (m)	< 3 m	3-8 m	> 8
(n_2 = 8)	canopy closure (%)	< 50	> 50	> 50, variable
(n_3 = 3)	snags/ha	900 – 1500	230 - 900	-
	DG (cm)	19-29	9-23	< 6
	subcanopy	-	-	black and white spruce, paper birch
	shrublayer	resprouting Alnus sp.	Alnus sp. Viburnum edule	Alnus sp. Viburnum edule
	herblayer	high coverage Calamagrostis canadenssis Epilobium angustifolium few Ericaceae (mainly Linnea borealis) Vicia americana	medium/high coverage Rosa acicularis Cornus canadensis some mosses more different Ericaceae (Vaccinium sp.)	medium coverage, patchy increased litter thickness Actea/Spirea Pyrola asarifolia some Ericaceae Polytrichum sp. Dicranum sp.
jack pine	age (yr),	1-10	11-32	> 33
(n_1 = 5)	height (m)	< 2	2 - 5 m	> 5 m
(n_2 = 14)	canopy closure (%)	< 10 %	10-30 %	> 30 %
(n_3 = 3)	snags/ha	900 – 3500	230 - 900	-
	DG (cm)	15-30	2-30	< 12
	subcanopy	-	-	black spruce
	shrublayer	some Ericaceae (Vaccinium sp.)	Viburnum edule	-
	herblayer	low coverage, bare soil Polytrichum juniperinum Funaria hygrometrica Epilobium angustifolium Linnea borealis	low/medium coverage, less bare soil, increased needle litter, few lichen, Polytrichum juniperinum Vaccinium angustifolium V. vitis-idaea Rosa acicularis	low/medium coverage increased lichen, patchy thick moss layer Pleurozium schreberi) Vaccinium angustifolium V. vitis-idaea
black spruce	age (yr)	1 - 20	21- 40	> 40
(n_1 = 11)	height (m)	< 1 m	1 - 3 m	> 3 m
(n_2 = 7)	canopy closure (%)	n.a.	< 10 %	> 10 %
(n_3 = 4)	snags/ha	1,500 - 11,500	1,000 - 6,000	< 230
	DG (cm)	14-30	5-17	< 10
	subcanopy	-	-	-
	shrublayer	Ledum groenlandicum Salix sp.	Salix sp., Ledum groenlandicum Betula glandulosa	Salix sp., Alnus sp. Betula glandulosa Ledum spp.
	herblayer	Sphagnum sp. Rubus chamaemorus Vaccinium sp. Equisetum sp.	Sphagnum sp., Rubus chamaemorus Vaccinium sp. Equisetum sp. some lichen.	thick moss layer Sphagnum sp. Pleurozium schreberi Eriopherum scheuchzeri Vaccinium sp. more lichen

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Table 3.2: ANOVA for DG, weight and volume in the three stages of stand development: tree seedling, tree sapling and young tree stage.

Sites	Variable	D.f.	F-value	Significance (p)	Different stages*
Aspen	DG	13	30.8	< 0.001	1-2, 1-3, 2-3
	weight	9	1.51	> 0.1	
	volume	9	1.24	> 0.1	
Jack pine	DG	21	26.1	< 0.001	1-3,2-3
	weight	21	3.4	= 0.56	
	volume	21	0.9	> 0.1	
Black spruce	DG	21	11.6	= 0.001	1-2, 1-3
	weight	20	0.5	> 0.1	
	volume	20	0.4	> 0.1	

*Post hoc comparisons (Scheffé) revealed which stages of stand development were significantly different ($p < 0.05$)

Table 3.3: Post-fire aspen CWM fuel load (W) and volume (V) for aspen sites at three stages of stand development.

stage	tree seedling			tree sapling						young tree		
site-code	1-8	1-9a	1-9b	2-15	2-16	1-19	1-20a	1-20b	2-29	1-32	1-34a	1-34b
W (Mg*ha⁻¹)	6.27	20.18	30.39	39.45	46.51	12.61	16.74	26.30	23.67	16.88	12.49	5.80
W-lowCI*	6.06	19.25	27.72	37.05	43.93	10.64	14.24	22.99	17.30	14.38	10.23	4.98
W-upCI*	6.47	21.12	33.05	41.84	49.08	14.59	19.25	29.61	30.04	19.38	14.76	6.63
V (m³/ha)	15.39	55.54	97.83	122.37	139.03	44.59	67.53	125.69	250.74	117.11	97.53	48.22

* upper and lower confidence intervals (CI) for weight are based on the 95 % upper and lower limits of the average wood density

Table 3.4: Post-fire jack pine CWM fuel load (W) and volume (V) for jack pine sites at three stages of stand development.

stage	tree seedling					tree sapling														young tree		
site-code	1-8	1-9a	1-9b	1-10a	2-10b	2-15	2-16	1-17	1-19	1-20a	1-20b	1-20c	2-25a	2-25b	2-29	2-31	1-32a	1-32b	1-32c	1-34a	1-34b	2-44
W (Mg*ha⁻¹)	3.04	1.33	2.91	1.77	5.49	3.32	4.65	2.57	3.01	2.49	2.80	1.37	5.77	3.56	2.47	2.30	1.28	1.21	1.76	3.08	0.74	1.39
W-lowCI*	2.84	1.26	2.79	1.69	5.03	3.05	4.45	2.35	2.73	2.22	2.61	1.25	5.21	3.27	2.23	2.00	1.09	1.01	1.51	2.75	0.65	1.14
W-upCI*	3.23	1.39	3.03	1.85	5.95	3.58	4.85	2.79	3.29	2.76	2.98	1.49	6.33	3.84	2.71	2.60	1.46	1.29	2.02	3.41	0.83	1.64
V (m³/ha)	7.16	3.60	7.97	4.29	17.18	13.67	12.15	6.96	8.67	8.89	7.10	3.87	22.23	9.76	8.09	7.90	5.59	5.47	9.76	11.22	3.82	7.49

* upper and lower confidence intervals (CI) for weight are based on the 95 % upper and lower limits of the average wood density

Table 3.5: Post-fire black spruce CWM fuel load (W) and volume (V) for black spruce sites at three stages of stand development.

stage	tree seedling										tree sapling							young tree			
site-code	1-8	1-9a	1-10a	2-10b	2-15	1-17	1-19	1-20a	1-20b	1-20c	2-25a	2-25b	2-26	2-29	1-32a	1-32b	1-32c	2-44	1-51	1-56	1-57
W (Mg*ha⁻¹)	0.71	0.65	1.11	0.74	1.93	4.17	12.66	1.27	4.12	4.00	8.15	3.07	4.76	1.03	1.92	1.83	3.82	5.57	0.31	0.53	0.83
W-lowCI*	0.66	0.62	1.07	0.71	1.80	3.94	11.69	1.19	3.96	3.66	7.59	2.83	4.37	0.91	1.70	1.65	3.42	5.00	0.28	0.45	0.75
W-upCI*	0.72	0.67	1.15	0.77	2.07	4.40	13.63	1.34	4.27	4.34	8.71	3.30	5.16	1.14	2.13	2.01	4.21	6.14	0.34	0.61	0.91
V (m³/ha)	1.38	1.50	2.06	1.55	4.26	9.15	25.78	2.80	9.41	8.56	20.87	7.13	10.71	2.86	4.94	4.55	9.88	13.16	1.00	1.81	2.35

* upper and lower confidence intervals (CI) for weight are based on the 95 % upper and lower limits of the average wood density
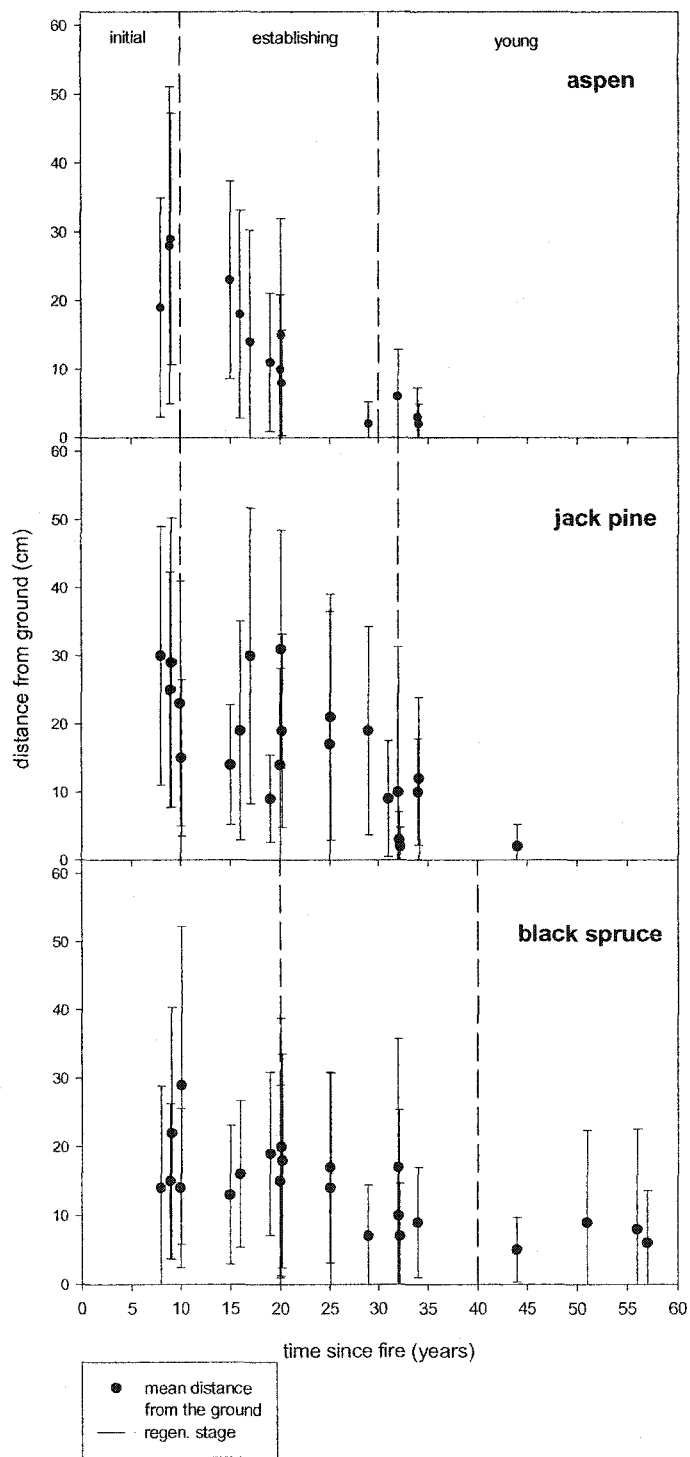
Figure 3.1: Mean distance from ground of aspen, jack pine and black spruce CWM 8-57 years after fire. Error bars represent the standard deviation (n= 30).

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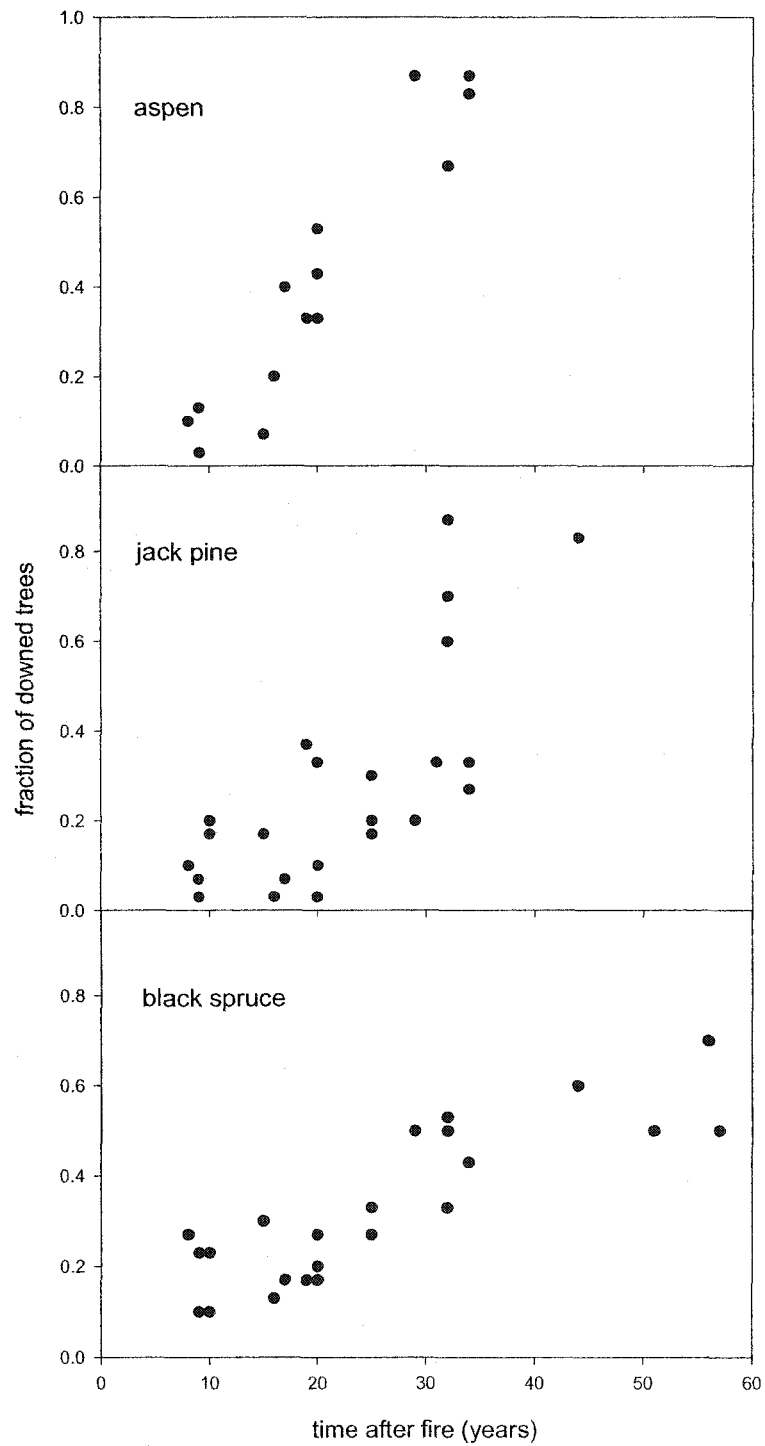
Figure 3.2: Fraction of downed aspen, jack pine and black spruce CWM ($\leq$ 5 cm off the ground) over time.

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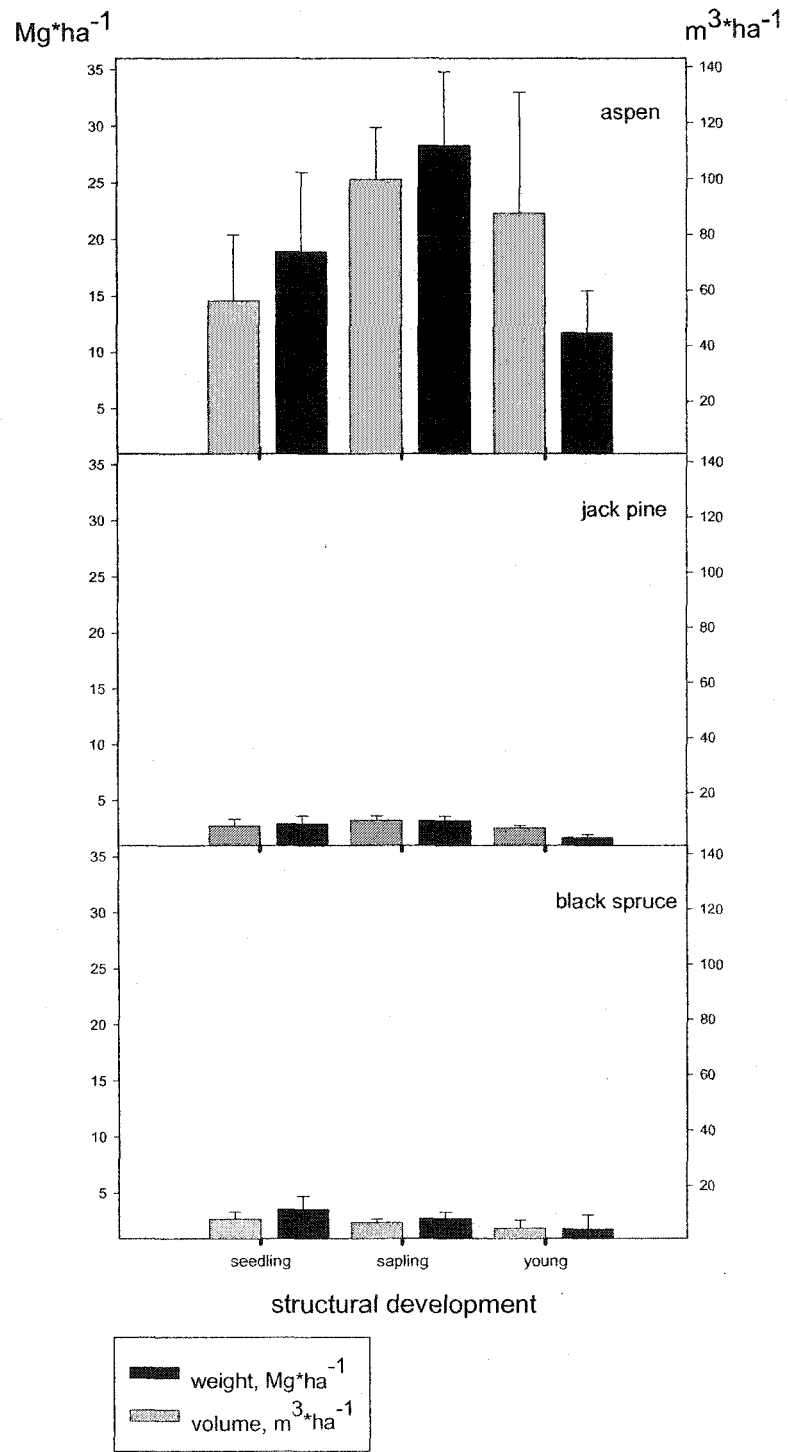
Figure 3.3: Mean weight and volume of aspen, jack pine and black spruce CWM in three regeneration stages (tree seedling, tree sapling and and young tree). Error bars represent the standard error of the mean.

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Chapter 4: Post-fire decomposition dynamics of coarse woody material in the western continental boreal forest

Introduction

The main carbon pools in the boreal forest are the upland forests and peatland (Apps et al. 1991). In the upland forests, the carbon is stored in the live trees, the soil, and the coarse woody material (CWM). CWM can account for > 20% of the total carbon pool (Busse 1994, Kurz and Apps 1995). During the last decade the various fluxes of carbon, nitrogen and other nutrients have been measured and models to predict these have been developed (Apps 1993, Apps et al. 1991, Bonan 1990, Kurz and Apps 1995). Fire influences the carbon budget dynamics of the boreal forest in oxidizing the vegetation and soil organic matter. Post-fire snags and CWM are a legacy of the pre-fire tree generation and provide structural diversity, shelter and habitat for wildlife and a nutrient and carbon store (Berg et al. 1994, Harmon et al. 1986).

Several decades are required to measure decomposition in post-fire stands (Franklin et al. 1987) so we adopted a chronosequence approach using large areas with severe fires. Severe forest fires produce relative homogenous conditions, most of the vegetation and the forest floor is removed and only burnt trees remain standing for more than a decade without showing obvious signs of decomposition. In a pilot study in Wood Buffalo National Park, Canada, standing dead aspen, jack pine and white spruce trees killed by a severe fire showed no significant decomposition over a 13-year period (Sander 1995).

Decomposition rates of litter and of coarse woody material are usually modeled as an exponential decay process (Alban and Pastor 1993, Meentemeyer 1978). This function implies that the proportional rate of decay is constant over time and was initially used to evaluate the importance of substrate quality on decomposition processes (Olson 1963). This approach has been criticized because wood is a heterogeneous material with specific decomposition constants for its components, cellulose, hemicellulose and lignin (e.g.

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Harmon et al. 1986). Lately there have been indications that linear and sigmoidal dynamics might be involved (Harmon et al. 2000, Johnson and Greene 1991, Laiho and Prescott 1999).

In some cases a linear function provided a relatively good fit for wood decomposition processes (Brown et al. 1998, Laiho and Prescott 1999) and Harmon (1982) suggested incorporation of a lag time when modeling fragmentation rates. In a field study, Laiho and Prescott (1999) used a sigmoidal function to describe the decomposition of pine. Functional forms that belong to the sigmoidal family allow for varying decomposition rates over time. Decomposition rates increase with time and decrease when the remaining substrate consists mainly of the recalcitrant portions of the wood. Wood decomposition rates of are strongly species-specific (e.g., Harmon et al. 1986) and recently it has been suggested that the form of the function of decomposition over time varies with different species (Laiho and Prescott 1999). Factors include the species-specific anatomical and chemical structures of wood such as vessel and tracheid size and content of phenolic compounds (Zabel and Morrell 1992).

The objective of the present study was to uses a chronosequence approach to measure post-fire CWM decomposition for three widely distributed tree species and to evaluate the fit of a linear, exponential and sigmoidal function.

Hypotheses

It was hypothesized that until snags fall over there is minimal decomposition. A second hypothesis was that aspen (*Populus tremuloides* MICHX.) CWM will have the highest decomposition rate, and that jack pine (*Pinus banksiana* LAMB.) and black spruce *Picea mariana* (MILL.) B.S.P.) CWM will have lower decomposition rates as they represent more decay resistant tree species. A third hypothesis was that linear and sigmoidal functions are valid alternatives to the exponential function for describing CWM decomposition.

Methods

<u>Experimental design</u>

Within forested areas that burned between 1940 and 1990 relatively homogeneous aspen, jack pine and black spruce sites were chosen. At each site (see chapter 2) 30 samples of CWM were collected based on the line-intersect method sampling procedures (Van Wagner 1982). For each point of intersection, the bole diameter was recorded and disc samples of varying length (2 to 15 cm) were collected. For aspen and jack pine only pieces of bole > 5 cm in diameter were collected. CWM of black spruce was relaxed to include samples > 1.5 cm diameter. Heavily fragmented pieces were considered part of the forest soil and not measured. In cases where fragmentation was restricted to a small portion of the tree bole, the sample was taken as close to the point of intersection as possible. At every site, samples from 10 live trees were collected as controls for species and site variability in wood density. In addition, 10 standing dead trees were sampled. Discs from standing living and dead trees were collected at random locations along the stem.

Wood density (WD, $g*cm^{-3}$) was used as a measure for wood decomposition and calculated using the cylinder method described by Christensen (1984):

$$WD_t = W_t/V_t$$

where W_t is the dry weight (g) and V_t the volume (cm^3) at time t, which is expressed as years since the last fire. Volume was estimated based on the function of a regular cylinder:

$$V_t = \pi * r^2 * L$$

where r is the radius (cm) of the sample piece and L is the length (cm) of the sample piece. The radius of the sample piece was based on diameter measurements based on circumference and taken prior to sampling in the field. The length of every sample was measured in the lab at 4 evenly spaced points on the perimeter of the sample. Samples were considered dry when their weight did not change over 24 hours at 75° C. Wood density represents the nominal density of the sample at time t and includes fungal biomass inside the tree bole. Previous studies showed that for 39 % mass loss an

additional 39% was converted to fungal biomass (Swift 1973). A series of small experiments showed that using field diameter to estimate volume was comparable to volume estimates based on water immersion and using green diameter (Appendix 7.1).

Snags exhibited signs of shrinkage, indicating that moisture content was below the fiber saturation point. The extent of shrinkage was unknown so the density of all snag samples was converted to green density based on literature shrinkage values for ovendry density (Jessome 1977). This converted value was compared with the wood density of living trees based on green diameter and ovendry weight.

In the context of carbon budget modeling the differentiation between apparent mass loss (Jones and Worrall 1995) and wood mass loss is less important than in studies of fungal ecology. By taking a black box approach and looking at the apparent mass loss the focus was decomposition as carbon loss due to carbon dioxide release rather than processes in wood decay. Also by making all necessary dimensional measurements prior to sample removal, fragmentation was kept to a minimum. When pieces were missing from the CWM sample due to fragmentation the sample volume was adjusted accordingly, and it was assumed that the missing pieces had a similar density as remaining pieces. Overall, losses due to fragmentation were considered of minor impact since lag times for tree bole fragmentation range from 25 to 80 years depending on species (Harmon et al. 1986). This was confirmed by field observations: sampling methods only rarely needed to be adjusted for partially fragmented tree boles.

Statistical Analysis

Statistical outliers were removed from the data since samples might have come from incorrectly identified tree species, trees already dead before the fire or survivor trees that died considerably later than the burnt trees. Statistical analysis consisted of t-tests and ANOVA on means of estimated densities and weighted nonlinear constrained regression using SPSS 10.0 (SPSS 1999).

Analysis of variance was used to test for site effect on WD of living trees. The mean WD of living and standing dead trees were compared using paired t-tests with two-tailed significance levels. To compensate for the shrinkage of standing dead trees their

density was converted to green density using shrinkage values of 11.8 % for aspen, 9.6 % for jack pine and 11.1 % for black spruce (Jessome 1977).

Linear, exponential and sigmoidal models were used to calculate decomposition coefficients for each species. The mean of a recently (< 10 years) burnt site with the highest measured WD was used as the Y-intercept (A) since it represented "nearly undecayed" conditions (for aspen A = 0.41 cm^3, for jack pine A = 0.41 cm^3, and for black spruce A = 0.54 cm^3). The following functions as models of decay dynamics of each species were evaluated:

Linear	WD = A +(-B*time)	[1]
Exponential	WD = A *EXP(-B*time)	[2]
Sigmoidal	WD = A *(1-(1-EXP(-B*time))**C	[3]

In all equations wood density (g*cm^{-3}) is a function of time only. The sigmoidal form (Equation [3]) is an approximation of a true sigmoid function. It was adopted because the exponential form (Equation [2]) is nested within; exponential decay is a special case, with C = 1.0.

The density data for aspen and jack pine were heteroscedastic. During the first 15 years, variances were usually low, then they increased around 20 -30 years and decreased thereafter. To compensate for unequal variances the data were weighed by their respective variance (weighted least squares) (Huet et al. 1996). Since R-square values of nonlinear regressions might possess an inherent bias, goodness of fit is evaluated using the log-likelihood (LL) (Huet et al. 1996):

$$LL = - n/2 \log 2\pi - 0.5 \Sigma(\log \sigma_i^2 + (Y_i - y_i)^2/\sigma_i^2)$$

where n represents the number of sites,

σ_i^2 is the observed variance of the ith site,

Y_i is the observed mean density of the ith site,

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and y_i is the estimated mean density of the ith site.

For model selection Akaike's information criterion (AIC) and a second-order AIC (AIC_c) for small sample sizes were used (Burnham and Anderson 1998):

$$AIC = -2*LL_i + 2K$$
$$AIC_c = AIC + (2K (K+1))/(n-K-1),$$

where LL_i is the log-likelihood of the different regression models, K is the number of parameters (including the Y- intercept) in model plus one for σ^2, and n the sample size. Values of $\delta_i AIC$ and $\delta_i AIC_c$ were calculated subtracting the smallest value of AIC or AIC_c from the respective other models to allow easier interpretation of the nonoptimal values. Values for $\delta_i AIC$ and $\delta_i AIC_c$ larger than 2 roughly correspond to p values equal or smaller than 0.05. AIC is a relative term that evaluates which model is closest to the unknown mechanism that generated the data. It is based on information theory and Kullback-Liebler distance (Burnham and Anderson 1998).

Results

Wood density

The mean wood density for all living aspen sampled in the study area was 0.4 g/cm^3 (Table 4.1). A one-way ANOVA showed that the differences among sites were significant (Table 4.2). Post-hoc comparisons identified two sites in study Region 2 as having samples with a significant lower wood density (all reported significance levels are p< 0.05) than sites that are located in Region 1. The mean wood density for all samples of living jack pine in the study area was 0.382 g/cm^3 (Table 4.1). The mean wood density of the individual sites were significantly different from each other (Table 4.2). Sites of lower wood density tended to be found in Region 2. Scheffé- comparisons identified a homogenous subgroup (p= 0.05) existing of all sites but excluded site two sites in Region 2. The mean wood density for all sampled living black spruce trees was 0.428 g/cm^3

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(Table 4.1). The differences among sites were significant (Table 4.2). Post-hoc comparisons revealed that the wood density for samples form a site in Region 1 was significantly lower than most sites from Region 2.

The wood density of standing dead aspen and jack pine was not significantly different from living trees sampled on the same site (Table 4.3 and 4.4). On 16 black spruce sites the density did not differ significantly between living and standing dead trees (Table 4.5). The wood density of living trees exceeded that of snags on only one site (1-8) whereas the opposite relation occurred on another site (2-16).

Decomposition

Aspen had the highest decomposition rate regardless of the functions used, ranging from 0.008 $g \cdot cm^{-3} \cdot yr^{-1}$ for the linear model to 0.087 yr^{-1} for the sigmoidal model (Table 4.6). In comparison decomposition rates jack pine were 0.005 $g \cdot yr^{-1}$ in the linear model and 0.033 yr^{-1} in the sigmoidal model (Table 4.6). The linear decomposition coefficient of black spruce was one half than that of aspen (0.004 $g \cdot yr^{-1}$, Table 4.6). Decomposition coefficients of black spruce had a smaller range (0.004- 0.01, Table 4.6) than the other two species.

The performance of the three decay functions (Equations [1] to [3]) measured by the difference in AIC_c (δAIC_c) was different for each species (Table 4.7). For aspen the sigmoidal function had the best fit as measured by the AIC_c , for jack pine and black spruce the linear function had the lowest AIC_c. Overall function performance of aspen and jack pine followed a common pattern (Table 4.6 and 4.7, Figure 4.1): weighted RSS and δAIC_c values were always highest for the exponential functions indicating a relatively poor fit and wRSS values for the linear and sigmoidal functions were lower and relatively similar. The differences of the δAIC_c for aspen indicate that the sigmoidal function has a considerably better fit than the linear one, whereas in jack pine the linear function has the smallest AIC_c with the difference between the linear and the sigmoidal function being small (Table 4.8).

Differences between the δAIC_cs were most pronounced in aspen (Table 4.7). Differences in δAIC_cs decreased with the decomposition rates. The slower the decomposition of a species, the smaller were the differences in δAIC_c.

The relative performance of the three functions in black spruce was different; the differences in the weighted RSS were minimal (Table 4.6, Figure 4.1), but AIC_c values indicate that the linear function has the closest fit and the sigmoidal function the poorest fit (Table 4.7). The δAIC_c for the sigmoidal function was larger than 2 making it a poorer fit in comparison to the linear model.

To evaluate and compare the ecological implications of different parameter values the predicted time for 10 % remaining wood density were calculated for parameter values from this and other studies (Table 4.8). For aspen stands predicted times for 90% mass loss were less than 100 years and ranged from 44 years to 92 years. For jack pine more time was needed to decompose 90 %; the predicted time ranged from 74 to 164 years. For black spruce stands the predicted time ranged from 121 to 273 years (Table 4.8).

Discussion

After fire, snags remain standing in many ecosystems for several years. For example, post-fire snags in the southern Appalachian Mountains showed only limited decomposition (Harmon 1982). The present study confirmed that aspen, jack pine and black spruce snags showed minimal decomposition as well since wood densisty of living trees and snags were similar. A study on attached dead branchwood decomposition in Kent, England, indicated that precipitation and air humidity are the main controlling factors (Boddy 1983). Since snags showed signs of shrinkage indicating that their moisture content sank below the fiber saturation point, moisture might be limiting snag decomposition.

Density of wood

Wood density of living trees showed a wide range, differing among sites as well as between living trees and snags. The age of the living trees sampled ranged from

relatively young trees (ca. 20 years old) to mature survivor trees. Wood density changes with the age of a tree: in young trees the density is highest near the pith (slow seedling growth due to competition), whereas in older trees the outermost wood has lower density (Harmon et al. 1986). Since the present study did not control for age of living or burned trees, differences in tree age might contribute to the variability of wood density.

Varying wood density values in snags than in living trees can be a result of snags being much older than sampled living trees or caused by "case-hardening" shrinkage, which occurs predominantly in conifers under the influence of desiccation and UV-radiation. Significantly lower wood density of black spruce snags might be caused by converting the volume of snag samples to green volume. Since it is unlikely that the moisture content of standing dead trees was as low as oven-dry samples, the reported wood density values for snags might underestimate the actual density.

Wood density of living and dead standing trees differed among sites. Depending on stand age and geographical location wood density will vary between individual sites but mean wood densities for larger geographical areas (e.g. provinces) are similar (Singh 1984). The study (Singh 1984) reported values for mean living aspen, jack pine and black spruce wood densities from the prairie provinces that were higher than for the present study. This is mainly attributed to differences in stand age since for this study some of the stands were comprised of regenerating trees less than 40 years old.

Coarse woody material decomposition dynamics
Decomposition coefficients

In the present study the species effect on CWM decomposition was discernible in all functional forms that were evaluated. Other studies reported strongly species-specific decomposition rates as well (e.g. Alban and Pastor 1993, Prescott and Laiho 1998). Aspen wood is highly susceptible to decay because of larger vessels and less heartwood than jack pine and black spruce. Many aspen trees are already infected by heartrot while living (Hiratsuka and Loman 1984). For aspen trees felled and placed on the ground in northern Minnesota Alban and Pastor (1993) reported a decomposition rate of $k = 0.08 \, yr^{-1}$ based on an exponential function and Miller (1983) reported a decomposition rate of $k =$

0.015 yr^{-1} based on an linear function for the same region. Decomposition of aspen in the western Canadian continental boreal forest is slower than either value.

Conifer trees have lower decomposition rates than aspen. A study of jack pine decomposition gave a decomposition rate of k = 0.042 (calculated based on an exponential function) (Alban and Pastor, 1993) which is considerably higher than values from the present study. Decomposition rates of lodgepole pine (*Pinus contorta*) which has a similar wood structure and density to jack pine were very similar to the decomposition coefficient in the present study (Fahey 1983, Johnson and Greene 1991). Laiho and Prescott (1999) calculated the decomposition coefficient of lodgepole pine based on the sigmoidal model, and the value for the decomposition coefficient (0.082 yr^{-1}) is much higher than for jack pine (0.033 yr^{-1}) in this study.

Decomposition rates for black spruce CWM are less common. Studies on other species of spruce recorded decomposition rates of 0.071 yr^{-1} for white spruce (Alban and Pastor 1993) and 0.003 yr^{-1} for Engelmann spruce (Johnson and Greene 1991). The decomposition coefficients based on the exponential function for black spruce were much closer to values for Engelmann spruce than white spruce. Black and Engelmann spruce both grow slowly under extreme conditions, black spruce in wetlands and Engelman spruce in the subalpine zone.

Apart from anatomical reasons for species-specific decomposition rates the different site conditions might influence decomposition rates: most aspen sites (see Chapter 2) were moister and might be more favorable to wood decay than jack pine sites that were characterized by a dry moisture regime. In black spruce sites decomposition might be limited by the cold and wet soil conditions and in older sites the CWM is overgrown by *Sphagnum spp.* and saturated with water.

Modeling Decomposition

When modeling CWM decomposition it is important to consider that in addition to species-specific decomposition rates the functional forms of the dynamics can be species-specific as well. Harmon et al. (1986) suggested several models for decomposition but most of the attention has been paid to different exponential equations to describe decomposition (e.g., Alban and Pastor 1993, Busse 1994, Means et al. 1985,

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Meentemeyer 1978, Naesset 1999, Olson 1963). Lambert et al. (1980) reported equally well-fitting exponential and linear models, but preferred the exponential by theoretical considerations. One problema with the negative exponential model was that environmental factors like wood moisture content was a more important factor than remaining substrate (Erickson et al. 1985). In another study the single-exponential equation did not predict the initial lag in decomposition (Busse 1994). Recent evidence suggests that in some cases, an exponential model of decomposition is not appropriate (Harmon et al. 2000, Johnson and Greene 1991, Laiho and Prescott 1999). In a previous study of lodgepole pine and Engelmann spruce in the Rocky Mountains the R-squares values for the exponential model were only marginally higher than for the linear model (Johnson and Greene 1991).

The results of the present study have implications for the integration of state variables and forcing functions into carbon budget models rates in the western continental Canadian boreal forest. Post-fire decomposition is not constant over time, as assumed by the exponential model. The linear and sigmoidal functions, which are consistent with temporally variable decay rates are better fits to the data. For aspen and jack pine the negative exponential function explained less variation (as measured by a larger a difference > 2 in $\delta_i AIC_c$) than a linear or sigmoidal function. For the first two decades after fire the negative exponential model overestimated decomposition for aspen as well as for jack pine. After 20 and 30 years for aspen and jack pine, respectively, the linear and the sigmoidal model predicted faster decomposition than the exponential model. The negative exponential model overestimated long-term decomposition. Especially during the first few decades after fire, the amount of carbon still stored aspen and jack pine CWM might be larger than estimated. Later, decomposition might release carbon more quickly than previously assumed.

Decomposition for black spruce was very slow and all models had similar values of AIC_c. Field observations suggested that due to low decomposition rates the regrowth of peat moss is faster than decomposition of the tree boles. Around 70 years after fire the decaying tree boles were overgrown and integrated into the peat layer. At this time many tree boles were waterlogged as well. The high water content and acidic environment very

likely prevent decomposition of these black spruce tree boles and their biomass is stored in the accumulating peatlayer.

The different mathematical functions predict a wide range of years after fire at which 90% of the biomass would be lost. For aspen and jack pine the linear and sigmoidal model predicted a similar amount of time needed for a 90 % loss of the biomass. Like the exponential model the linear model overestimated decomposition rates during the first two decades. The exponential function seemed to overestimate the time needed for the decomposition of 90 % of the biomass. Field observations indicated that at around 50 years (aspen) and 80 years (jack pine) the fragmented tree boles are incorporated into the forest soils (Ian Nalder, personal communication). The inability of all three functions to predict the long-term losses of coarse woody material and the poor behavior of all three functions at low annual density losses indicate that in these cases most of the variation in density loss seems to be dependent on other factors.

Conclusions

Decomposition of snags is minimal, but when the boles fall and lie close to the soil, decomposition is measurable. Depending on the tree species the linear or sigmoidal function are preferred choices for modeling decomposition dynamics of CWM in the Canadian western continental boreal forest. During the first two decades after fire the negative exponential function is overestimating decomposition in aspen and jack pine. Decomposition for black spruce is slower and best represented by the linear or exponential function.

Table 4.1: Relative density and diameter of boles of living trees of three boreal tree species.

	Species	Mean	SEM	N	low CI (95%)	up CI (95%)	Min. mean	Max. mean
Density (g^*cm^{-3})	aspen	0.40	0.004	139	0.39	0.40	0.35	0.46
	jack pine	0.38	0.003	218	0.38	0.39	0.31	0.42
	black spruce	0.43	0.003	239	0.42	0.43	0.35	0.48
Diameter (cm)	aspen	8.6	0.195	139	8.2	9.0	6.3	11.1
	jack pine	9.3	0.229	218	9.3	10.2	7.2	12.0
	black spruce	6.2	0.176	239	5.8	6.5	4.3	7.9

Table 4.2: One way ANOVA of wood density and diameter of living trees among sites for all species.

	Species	D.f.	Significance	Hom.variance
Density (g^*cm^{-3})	aspen	13	< 0.001	0.003
	jack pine	21	< 0.001	0.001
	black spruce	22	< 0.001	0.033
Diameter (cm)	aspen	13	<0.001	0.006
	jack pine	21	0.005	0.006
	black spruce	22	0.05	0.030

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Table 4.3: Differences in stemwood density between living aspen and aspen snags.

Sites	1-8	1-9a	1-9b
Mean density difference	0.08	0.04	-0.03
N	9	10	10
T-value	4.14	3.36	-1.51
Significance-level *	0.42	0.84	0.40

* two-tailed significance levels

Table 4.4: Differences in stemwood density between living jack pine and jack pine snags.

Sites	1-7	1-8a	1-8b	1-9	2-10	2-16
Mean density difference	0.003	0.05	0.008	0.01	0.003	0.04
N	10	10	10	10	9	10
T-value	0.25	2.07	0.51	0.87	0.17	2.58
Significance-level *	0.97	0.64	0.51	0.34	0.18	0.61

* two-tailed significance levels

Table 4.5: Differences in stemwood density between living black spruce and black spruce snags.

Sites	1-8	1-9a	1-9b	1-10a	2-10b	2-15	2-16	1-17	1-19	1-20a	1-20b	2-25a	2-25b	2-29	1-32a	1-32b	1-32c	1-34
Mean density difference	0.02	-0.08	0.02	-0.03	0.06	-0.06	-0.01	0.01	-0.02	-0.01	0.06	-0.01	-0.05	0.08	0.04	0.01	-0.04	0.04
N	10	10	10	10	9	10	10	10	10	10	10	10	10	10	10	10	10	10
T-value	3.21	-5.56	0.96	-2.37	1.63	-4.65	-0.42	8.55	-1.12	-1.96	2.96	-0.72	-3.7	2.84	1.9	0.41	-1.84	-3.75
Significance-level *	0.02	0.64	0.17	0.43	0.58	0.71	0.04	0.23	0.79	0.11	0.75	0.5	0.66	0.33	0.38	0.76	0.61	0.53

* two-tailed significance level

Table 4.6: Parameter values and confidence intervals (CI) for three different functions of post-fire wood density of CWM of three boreal tree species obtained by weighted nonlinear regression.

Species	Model	N	Weighted R-square	Weighted RSS	B	C
Aspen A= 0.41	linear	14	0.68	0.0001	0.008	
	95% CI				0.007-0.009	
	exponential	14	0.58	0.00013	0.025	
	95% CI				0.021-0.038	
	sigmoidal	14	0.77	0.00007	0.087	4.92
	95% CI				0.037-0.136	-0.45-10.29
Jack pine A=0.41	linear	23	0.56	0.00021	0.005	
	95% CI				0.004-0.006	
	exponential	23	0.51	0.00023	0.014	
	95% CI				0.012-0.017	
	sigmoidal	23	0.59	0.0002	0.033	2.18
	95% CI				0.010-0.56	0.336-4.015
Black spruce A= 0.54	linear	23	0.70	0.00014	0.004	
	95% CI				0.004-0.005	
	exponential	23	0.73	0.00013	0.01	
	95% CI				0.009-0.011	
	sigmoidal	23	0.74	0.00013	0.008	0.889
	95% CI				0.003-0.013	0.530-1.247

A= Y-intercept, highest measured CWM mean site density, $g*cm^{-3}$

Table 4.7: Log-likelihoods, AIC, secondary AIC (AIC$_c$) and their relative performance expressed as the respective differences (δ_iAIC and δ_iAIC$_c$) and subsequent ranking for three competing models (linear, exponential and sigmoidal)

Species	Model	K	LL	AIC	δ_iAIC	AIC$_c$	δ_iAIC$_c$	Ranking
Aspen	linear	2	2.08	- 0.17	10.62	0.92	9.32	2
	exponential	2	- 4.17	12.34	23.14	13.43	21.83	3
	sigmoidal	3	8.4	- 10.8	0	- 8.4	0	1
Jack pine	linear	2	7.79	- 11.58	0.24	- 11.0	0	1
	exponential	2	6.6	- 9.2	2.62	- 8.6	2.38	3
	sigmoidal	3	8.91	- 11.81	0	- 10.55	0.43	2
Black spruce	linear	2	12.67	- 21.332	0	- 20.73	0	1
	exponential	2	12.24	- 20.48	0.86	- 19.88	0.86	2
	sigmoidal	3	12.64	- 19.28	2.05	- 18.02	2.71	3

Table 4.8: Time since fire in years to 90% loss of CWM mass by species as predicted using the parameter estimates of Table 4.6, and data from Alban and Pastor (1993) and Laiho and Prescott (1999).

Species	Linear	Exponential	Sigmoidal	Alban and Pastor	Laiho and Prescott
Aspen	46	92	44.	16	
Jack Pine	73	164	93	30	20*
Black Spruce	121	230	273	18	30**

* lodgepole pine, similar wood density to jack pine
** Engelmann spruce
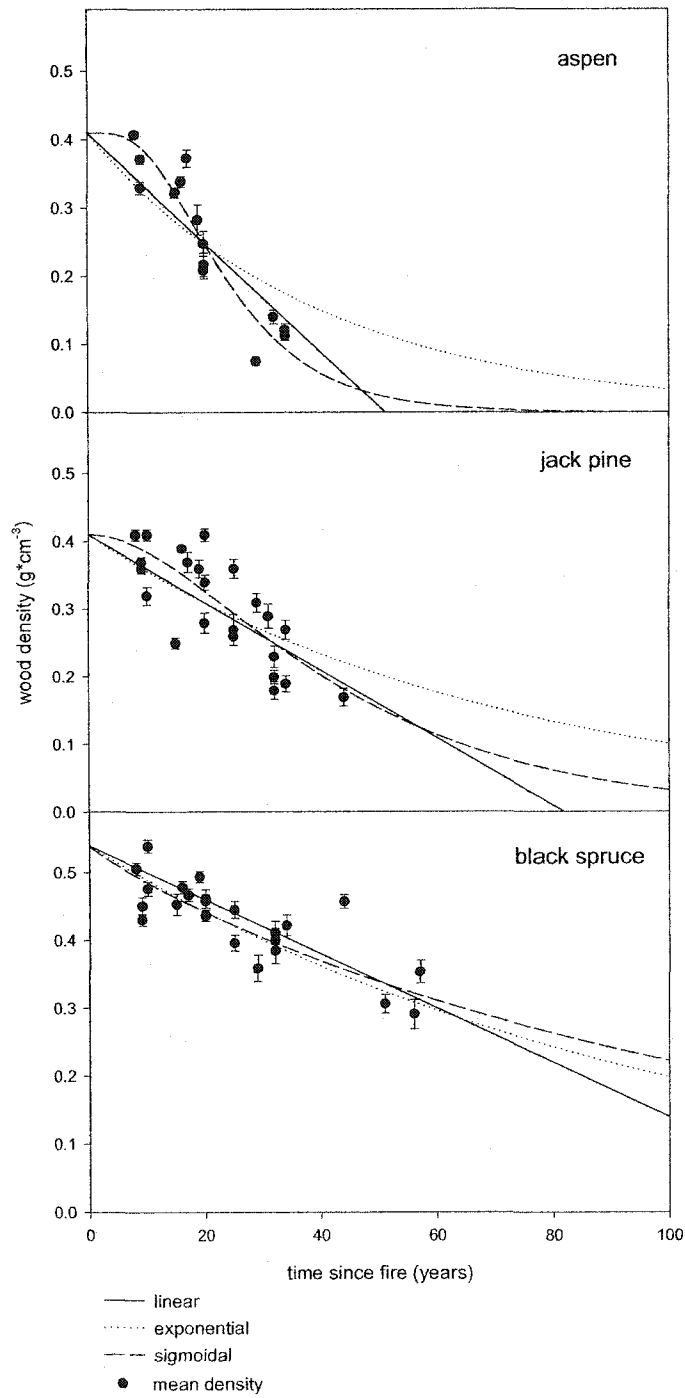
Fig. 4.1: Mean wood density of aspen, jack pine, and black spruce CWM and modeled estimates using equation 1-3. Error bars represent the standard error of the mean.

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Chapter 5: Influence of moisture-related variables on decomposition processes of coarse woody material in the western Canadian continental boreal forest

Introduction

Water is a crucial factor in decomposition processes of wood and it is well known that too much or too little water will inhibit decomposition. For decomposer organisms water is available in voids of the substrate (e.g., Boddy 1986) (from precipitation, adsorption from the air and then translocated to the organisms) and metabolic water. Water losses from wood occur through drainage, translocation and then evaporation. A direct measure of water availability is the water potential (Griffin 1977). Water potential values relate to equilibrium conditions which can be achieved in laboratory settings. Many studies relating to natural substrates express moisture content as percentage of oven-dry weight. The limiting moisture content (MC) for most wood-decay organisms is about 30 %, which corresponds to - 40 bar matric potential and is referred to as the fiber saturation point (FSP) (Griffin 1977).

Observations of coarse woody material (CWM) in Wood Buffalo National Park indicated that the most abundant fungi on jack pine and white spruce CWM were the yellow-red gill polypore (*Gloeophyllum sepiarium* (Fr.) Kar.) and the common split gill (*Schizophyllum commune* Fr.) on aspen CWM (Sander 1995). These fungi have been reported to be adapted to drought stress (Childs 1939, Loman 1959). This might be an indication that in the western continental boreal forest lack of water is an important factor limiting wood decomposition. This is in contrast to the limit of the process by an excess of water in forests of western Oregon (Progar et al. 2000).

CWM decomposition processes can be studied at the scale of the individual log. It is generally accepted that the water content of CWM is influenced primarily by the diameter of the bole and the vertical height of the bole above the ground. Water content increases rapidly in small diameter and therefore high surface area to volume ratio boles.

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Large diameter samples absorb water more slowly, but once wet, they will retain water longer. The common theory is that small diameter CWM will decay faster because of more rapid water uptake, faster microorganism colonization and a smaller amount of decay-resistant heartwood (Graham and Cromack 1982, Sollins 1982, Harmon et al. 1986). A few other studies reported faster decay rates of larger boles (Erickson et al. 1985, Naesset 1999) while Busse (1994) did not identify any effect of diameter in decomposition rates. In addition to diameter, vertical location influences the MC because CWM lying on the ground is exposed to higher air humidity and less movement of air than suspended CWM. Loman (1959) observed that suspended slash had fewer sporocarps than slash that was in contact with the ground. Field observations indicate that suspended CWM is much more exposed to high temperatures, wind and UV radiation especially during early stages after fire when canopy closure and shading is low. Decomposition of elevated boles was slower than for CWM close to the ground (Busse 1994, Erickson et al. 1985). It is hypothesized that in the western continental boreal forest, low moisture levels are a stress factor for decomposition organisms and larger diameter CWM as well as CWM close to the ground should have a higher MC and more rapid decomposition rates.

CWM decomposition can also be studied at the landscape level. Precipitation is the most important water source for wood-decay fungi and evaporation is the major driving force for water losses. Methods have been developed to estimate climatic gradients over landscapes using a climate moisture index (CMI) (Hogg 1994, Hogg and Schwarz 1997, Hutchinson and Gessler 1994, Nalder and Wein 1998, Price et al. 2000). Childs (1939) demonstrated regional and climatic effects on decomposition and observed that winters in Oregon were usually cold enough to retard decay even though moisture conditions were favorable; during most of the summer CWM was exposed to sun and wind and was too dry to decay. Understanding the influence of varying moisture regimes and local and regional climate on the CWM carbon pool is important when trying to assess the impact of changing climate (e.g. more annual precipitation and higher annual temperatures predicted for the continental boreal forest (IPCC 2001)).

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Hypotheses

It was hypothesized that individual tree bole characteristics like diameter and distance from the ground will influence the moisture content of CWM; large CWM or CWM close to the ground will have a higher MC than small or suspended CWM. Differences in precipitation and temperature estimated by a CMI or climatic differences between Region 1 and 2 will reduce decomposition rates for the stands and region with less precipitation or higher temperatures.

Methods

Study area

The study was based on the same set of samples described in the previous chapters. Study sites located in Saskatchewan were identified as Region 1 and sites located in Alberta and the Northwest Territories were identified as Region 2.

Wood moisture content and vertical position

During the May - August 1997 field season, fresh weights of the tree bole samples were used to estimate the moisture content (MC).

$$MC\ (\%) = weight\ of\ water*100/ovendry\ sample\ weight$$

The moisture content was log-transformed (logMC), and to determine the relationship between sample diameter and moisture content the samples were classified into two diameter classes. Class limits were selected to create subsets of approximately equal sample size (aspen: class 1 $\leq$ 12 cm, class 2 > 12cm, jack pine: class 1 $\leq$ 9 cm, class 2 > 9 cm, black spruce : class 1 $\leq$ 4 cm, class 2 > 4 cm). Means of MC were compared using independent samples t-test (for aspen equal variances were not assumed). Due to the division of the data, diameter was not considered as a variable for further statistical analysis.

Distance from the ground of each sample was measured in the field as the distance between the ground and the lower surface of the tree bole and identified as distance above the ground (DG). Samples were grouped into five distance classes: class 1< 10, class 2 = 10 to 19.9, class 3 = 20 to 29.9, class 4 = 30 to 39.9, and class 5 ≥ 40 cm above the ground. Differences of mean MC between distance classes were evaluated using SPSS 10.0, Scheffé's t-test for homogeneous variances (aspen) and Tamhane's T2-test for heterogeneous variances (jack pine and black spruce). To test the effect of ground contact on decomposition processes samples were divided into two data sets per species: downed (distance above ground ≤ 5 cm) and elevated (distance above ground > 5cm).

Climate moisture index (CMI)

To describe climatic differences among the sites an annual climate moisture index was used that reflected differences in precipitation as well as evaporation. This index is based on the sum of the differences between mean monthly precipitation and potential evapotranspiration (Hogg 1994, 1997). Potential evapotranspiration was calculated using the Jensen-Haise method. The climate moisture index based on the Jensen-Haise method was spatially interpolated using ANUSPLIN (Hutchinson 1991, 1999, Price et al. 2000). ANUSPLIN is an elevation-dependent interpolation of climatic data. The Jensen-Haise climate moisture index was preferred to other indices (Hogg 1997) because it is independent of input parameters and determined by elevation, temperature and solar radiation of the individual climate station. The annual climate moisture index is expressed in cm of precipitation. In the statistical analysis the LOG 10 of the climate moisture index was used.

Weighted nonlinear regression

An approach similar to stepwise regression was used to link variables in linear, exponential and sigmoidal equations. Equation performance was compared between downed and elevated data sets. The climate moisture index was treated as a continuous variable whereas region was introduced into the regression as a categorical variable. Regional and climate effects were tested on undivided data sets as well as on data sets representing downed and elevated samples.

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Variables were inserted into the best fitting equation from a previous analysis. In cases where differences between the performance of equations were small, both equations were used for further analysis. Weighted constrained nonlinear regression (SPSS 10.0) was used for parameter estimation and calculation of the likelihood (Huet et al. 1996). The second order Akaike Information Criterion (AIC_c) was used for comparison of equation performance to avoid any bias related to too many parameters in relation to sample size (Burnham and Anderson 1998).

The following equations were used for parameter estimation:

	equation	No.	K*
linear	Y= A+(-B*time)	[1.1]	2
linear, CMI	Y= A+(-(B+C*LOG(CMI)*time)	[1.2]	3
linear, region	Y= A+(-(B+C*region)*time)	[1.3]	3
exponential	Y= A*(1-(1-EXP(-B*time)))	[2.1]	2
exponential, CMI	Y= A*(1-(1-EXP(-(B+C*LOG(CMI)*time)))	[2.2]	3
exponential, region	Y= A*(1-(1-EXP(-(B+C*region)*time)))	[2.3]	3
sigmoidal	Y= A*(1-(1-EXP(-B*time))**D)	[3.1]	3
sigmoidal, rateterm	Y= A*(1-(1-EXP(-(B+C*LOG(CMI))*time))**D)	[3.2]	4
sigmoidal, lagterm	Y= A*(1-(1-EXP(-B*time))**(D+E*CMI))	[3.3]	4
sigmoidal, region	Y= A*(1-(1-EXP(-(B+C*region)*time))**(D+E*region))	[3.4]	5

* K= number of estimated parameters in model plus one for σ^2.

The highest measured mean wood density of a recently burned site was used to represent minimally decayed conditions and Y-intercept (for aspen and jack pine A= 0.41 g*cm^{-3}, for black spruce A= 0.54 g*cm^{-3}). For equation performance several options were evaluated. The parameter values with the smallest AIC_c values from a previous analysis were set as fixed parameter values for calculation of the likelihood. Then weighted constrained nonlinear regression procedures estimated new parameter values for different equations. Only likelihood and AIC_c values that are calculated on the same data set are comparable. The lowest AIC_c generally indicated the best fit and differences in AIC_c

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(δAIC_c) larger than 2 are considered as evidence for a poorer fit of the respective model (Burnham and Anderson 1998).

Results

Coarse woody material moisture content

Of the three species, aspen CWM had the highest average moisture content of 135 % (range from 42 % to 315 %). The average MC for all jack pine CWM was 71 % (range from 41 to 140 %). Black spruce boles had the lowest average MC with only 31 % (range of 16 % to 52 %). For all species the MC of large diameter CWM was higher than of small diameter CWM (Table 5.1, Figure 5.1). In aspen and jack pine the log of the moisture content of large diameter CWM was significantly greater than the log of the moisture content of small diameter CWM (Table 5.1)

The relationship between distance from the ground and MC (Table 5.2, Figure 5.2) was similar for all three species. In aspen sites CWM that was elevated more than 30 cm off the ground (i.e. 30 % of samples) had a mean MC of less than 30 % (Table 5.2, Fig. 5.2). For jack pine only CWM that was elevated more than 40 cm off the ground (13 % of samples) had a mean MC below 30%. For black spruce only boles that were on the ground or less than 10 cm off the ground (15 % of samples) had a MC of more than 30 % (Table 5.2, Figure 5.2). For all three species the decrease in MC upward along the vertical profile approximated the shape of a negative exponential curve (Fig. 5.2)

For aspen, ANOVA (variances homogenous) showed that the mean log of moisture content between distance classes was significantly different ($p < 0.001$, Table 5.3). Post-hoc comparisons revealed that the CWM nearest to the ground were moister than those elevated over the ground ($p < 0.001$). The log of moisture content of distance class 2 was significantly higher than the MC of distance class 5 ($p = 0.013$). In jack pine and black spruce, distance classes 1 and 2 were significantly different ($p < 0.01$, Table 5.3) from each other and all other values. The values for distance classes 2-4 were not significantly different.

Effect of moisture-related variables on decomposition

Dividing the data sets into downed (distance above ground ≤ 5 cm) and elevated (distance above ground > 5 cm) CWM showed faster decomposition for the downed CWM. The decomposition rate (B) of downed CWM increased compared to the rate of the undivided data set (fixed parameters, Table 5.4, Figure 5.3). Only for downed jack pine the difference ($\delta_1 AIC_c$) between the fixed and estimated function was smaller than two (Table 5.4) showing no evidence for differences between data sets. The decomposition rate of elevated CWM decreased compared to the overall rate of the undivided data set (fixed parameters, Table 5.4, Figure 5.3). The difference in AIC_c values between fixed and estimated parameters ($d_1 AICc$) ranged from 1.618 to 8.536 (Table 5.4) indicating that the lower estimated parameter provide a better fit for the data. The δAIC_c for the sigmoidal function for elevated jack pine did not confirm this trend. In this case the AIC_c for the fixed parameter function was smaller than for the elevated one. Lag parameters (D) for the sigmoidal equations did not change for downed and elevated aspen and jack pine.

For downed aspen CWM the linear equation with the estimated parameters provided the best fit as measured by the AIC_c, $\delta_2 AIC$ values exceeded 2 (Table 5.4). For elevated aspen the sigmoidal equation with estimated parameters had the lowest AIC_c, with $\delta_2 AIC$ values exceeding five. For jack pine the linear equation with estimated parameters had the lowest AIC_c for downed and elevated CWM, but differences between AIC_c values were small: $\delta_2 AIC_c$ of the linear equation with fixed parameters and the sigmoidal equation with estimated parameters were smaller than two. For elevated jack pine the AIC_c values for the sigmoidal equation were considerably higher than for the AIC_c for the linear equation showing a considerably poorer fit. Downed and elevated black spruce samples had the lowest AIC_c for the exponential function with estimated parameters (Table 5.4). For downed black spruce the $\delta_2 AIC_c$ exceeded two whereas for elevated black spruce the $\delta_2 AIC_c$ between the exponential and linear equation with estimated parameters was very small.

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Climate moisture index and region

For the undivided data set of aspen CWM introducing the logarithm of the climate moisture index to the sigmoidal function did not improve the AIC_c (Table 5.5). The AIC_c value for downed aspen showed an increase with the introduction of the logarithm of the climate moisture index to the linear equation, indicating a poorer fit. AIC_c values for the different equations in elevated aspen were very similar. The effect of climate moisture index on the lag term (equation 3.3) was very small. Aspen was the only species where the amount of residual variation seemed to increase with increasing climate moisture index.

Introducing region as a categorical variable to the linear and sigmoidal equations did not improve the AIC_c of downed and elevated CWM (Table 5.6). For the undivided data set including region into the linear equation resulted in a considerably smaller AIC_c, $dAIC_c$ were larger than five. The parameter value for B increased from 0.008 to 0.009. Downed CWM showed a similar increased parameter values of C.

Since previous performance of the linear and sigmoidal equations for jack pine were similar for the undivided and downed data sets both sets of equations were evaluated. For the undivided data set the introduction of the logarithm of the climate moisture index to the linear equation did not improve the AIC_c (Table 5.7). Incorporating the climate moisture index into the lag- and rate-term of the sigmoidal function lead to a decrease in AIC_c values. Adding the climate moisture index to the lag-term resulted in the smallest AIC_c value, the difference to other AIC_c values was larger than two. The pattern for downed jack pine was similar. Adding the climate moisture index to the lag-term of a sigmoidal function resulted in the lowest AIC_c value, the difference in AIC_c between the linear-fixed parameter and the sigmoidal-lagterm equation (equation 3.4.) was slightly smaller than two (Table 5.7). For elevated CWM the unchanged linear equation with fixed parameters had the lowest AIC_c values. Introducing region to the linear and sigmoidal equation did not improve the AIC_c. The equations without the additional variable had the smallest AIC_c (Table 5.8).

For black spruce introducing the logarithm of the climate moisture index in the linear and exponential equation generally led to smaller AIC_c values (Table 5.9). The pattern for the undivided data set and elevated CWM was similar: incorporating the

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logarithm of the climate moisture index into the equations led to a decrease in AIC_c values. Including the logarithm of the climate moisture index into the linear equation resulted in the lowest AIC_c values. The differences between AIC_c values were more pronounced in elevated black spruce than in the undivided data set. Downed black spruce CWM deviated from this pattern: the exponential equation had lower AIC_c values than the linear equation, including the LOG(climate moisture index) into the exponential equation resulted in the lowest AIC_c (Table 5.9). Introducing region into the linear and exponential equation did not improve the AIC_c. The equations without the additional variable had the smallest AIC_c (Table 5.10).

Discussion

Substrate moisture content directly influences decomposition. Lab experiments showed that maximum CO_2 evolution rates for wood samples occurred at more than 100% MC (Boddy 1983). Usually a MC between 80 and 100 % optimizes decay and moisture contents below 30% usually inhibit decomposition (Zabel and Morrell 1992). Results from the present study show that the MC of small CWM as well as elevated CWM was considerably lower than large or downed CWM. For black spruce the MC of most samples was less than 30 %.

Brackebush (1975) observed that drying occurred from the surface inward, with a low increase of moisture in the outer portions of a tree bole, and a steep increase towards the moist center of the tree bole. Contrary to the common assumption that larger tree boles take longer to dry, diameter had no large effect on the MC of tree boles on the ground. Only smaller elevated tree boles showed a diameter effect: they had a longer period of low (< 30%) MC during the summer (Brackebush 1975). In a more recent study, the MC of CWM was generally lower in smaller residues, during periods in the summer the MC was too low for decomposition (Erickson et al. 1985). The results of the present study point in the same direction; during summer, larger tree boles had a higher MC, and smaller tree boles had a lower than optimal MC for decomposition.

Various effects of diameter on decomposition have been previously reported. Studies on white fir, western hemlock and Douglas-fir showed that small diameter wood

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decays faster (Graham and Cromack 1982, Harmon et al. 1986, Sollins 1982). Another study reported higher decay parameters for larger boles (> 15 cm) of Norway spruce (Naesset 1999). In one study the higher decay rates for larger boles of Douglas-fir and western hemlock occurred together with higher MC of the tree boles (Erickson et al. 1985). Other studies found no effect of diameter on decomposition of red spruce (Foster and Lang 1982), western hemlock and Douglas-fir (Marra and Edmonds 1996). Busse (1994) hypothesized that for lodgepole pine a generally dry climate and low MC of the tree boles might preclude the effect of diameter on decomposition. These contradicting results from other studies emphasize that effects of diameter might be influenced by other factors, e.g., height above ground, tree species and study region. The experimental design of this study did not allow inferences on the effect of diameter on decomposition. Follow-up studies controlling for different diameters are needed to close this gap.

The effect of distance above ground in the present study concurs with a study on large fuels that found that tree boles placed on a rack were drier and had a longer period of MC below 30 % than tree boles on the ground (Brackebush 1975). One possible reason for the differences is that tree boles on the ground absorb water from the soil which would support the view that water uptake is mainly determining MC. Another possible reason is that elevated tree boles have a lower MC than tree boles on the ground because of larger water losses due to greater exposure to wind and solar radiation. Tree boles close to the ground would be more protected by regenerating trees and a developing herb layer.

In a study of dead beech branchwood after heavy rainfall the MC increased until one day after a rain event, but then drying processes predominated: Six days after a major rain event the branchwood had MC below 30%, even with small intermittent amounts of rain (Boddy 1983). All this suggests that drying rather than wetting processes might control the MC of CWM. Factors that directly influence the drying of the tree bole like diameter, distance from the ground and evaporation are central for understanding CWM decomposition processes.

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Effect of moisture related variables on decomposition

In all species studied CWM that was located on or close to the ground decayed faster than the overall average decomposition rate. These results were independent of the functional form used to represent the decomposition dynamics. A similar effect has been noticed previously for pine logging slash in contact with the ground, which decayed 50 % faster than aerial slash (Barber and Van Lear 1984). Similar effects have been observed in previous studies: relatively sound samples that were elevated above the soil surface did not decompose (Busse 1994), and in the Douglas-fir region elevated residues decomposed slower than residue on the ground (Erickson et al. 1985). In a study with a modeling approach ground contact and soil moisture had significant effects on spruce boles' decomposition rates (Naesset 1999). One of the factors strongly influenced by the level of elevation of the tree bole is its MC (Figure 5.2). The observations from the present study support the hypothesis that on an individual tree bole level MC is a critical factor for decomposition in the western boreal forest.

Many aspen trees are infested with heart rot while living, and this would preclude any lag time caused by fungal colonization (Hiratsuka and Loman 1984), which might be one reason why downed aspen CWM showed no lag time. Also, as wood starts to decompose, pore space and water holding capacity increase resulting in a potentially higher MC of well decayed tree wood (Zabel and Morrell 1992). The average distance from the ground of CWM declined over time (Figure 3.1). The dynamic processes influencing height above ground, like settling of the CWM and the point at which an elevated CWM turns into downed CWM could not be accounted for in this study. They need to be taken into consideration when evaluating the linear functions for the undivided data sets and elevated CWM: Decay rates and dynamics would be different over time including these processes. As a result, other functional forms than the ones considered in the present study might be preferred to describe these dynamics. Regardless, height above ground seems to be a factor influencing decomposition rates and important to consider when focusing on decomposition processes.

On aspen sites only the lag time of elevated CWM seemed to be affected by climate moisture index. Yet differences in AIC_c were very small indicating that

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decomposition of elevated CWM was either too slow to show any major effects, or that the fast regrowth of aspen is providing more forest-like and less exposed conditions. Overall there was no evidence that the climatic factors represented by the climate moisture index were influencing decomposition on mesic aspen sites. The increasing amount of residual variation with increasing climate moisture index might indicate that either climate moisture index is confounded or is interacting with other variables. The change in parameter values after introducing study region into the linear function indicates that overall decomposition in Alberta is faster than in Saskatchewan. This trend is not supported by the downed or elevated data set where introducing region to the linear and exponential function did not lead to improvements of function performance. At this point the differences in study region for the undivided data set might as well be an artifact of the considerable differences in the number of study sites: only 3 of the 14 sites are located in Alberta.

Jack pine was the only species that was clearly affected in decomposition by the climate moisture index. Introducing the climate moisture index changed performance of the different functions; the sigmoidal function had the lowest AIC_c. The undivided data set and downed CWM showed an increase in the lag term of the sigmoidal function with increasing climate moisture index. This contradicted the initial hypotheses that lower climate moisture index values would relate to either lower decomposition rates or longer lag times. Introducing climate moisture index into the linear function did not improve AIC_c values for elevated jack pine. Since CWM on these sites was usually fairly exposed, even in later stages of the regeneration process, decomposition rates were relatively low. In this case the low rates might preclude any effect the climatic variables represented by the climate moisture index might have on the decomposition. Differentiating between the study regions in Saskatchewan and Alberta did not lead to any improvements in performance of the functions in any data set. This might be an indication that similarities on a site level, e.g., sandy soils with good drainage, are more important for decomposition than regional differences like fire history, variation in tree populations or regional weather patterns.

In black spruce, introducing the climate moisture index to the linear and exponential function always lowered the AIC$_c$ values. Differences in AIC$_c$ values between the linear and exponential equations including climate moisture index were small for the undivided data set and elevated CWM. This might be an indication that elevated CWM dominates the undivided data set which is supported by the fact that more CWM was classified into the elevated than into the downed category. Differences between the performance of the various functions was more pronounced in downed CWM. The parameter values for black spruce supported the initial hypothesis that sites with low climate moisture index also have lower decomposition rates. Decomposition rates and dynamics in all black spruce data sets were not affected by regional differences. Considering that conditions that give rise to peatlands across climatic regions are usually similar and that the burnt black spruce CWM gets incorporated into the peat layer, differences in decomposition rates or dynamics, if any, are probably very small.

Overall, different species seem to be affected differently by the climate moisture index as no general pattern emerged: For aspen sites effects were minimal, in jack pine climate moisture index seemed to increase the lag time for decomposition, and black spruce sites with a higher climate moisture index had higher decomposition rates as well. This leads to the question; Is climate moisture index an appropriate indicator for climatic variables influencing decomposition rates? The climate moisture index is based on annual precipitation (Hogg 1994, 1997). In Utah, two main factors determined how dry a tree bole will become, the MC at the beginning of the summer desiccation period (after spring rain) and the duration of the desiccation period (Brackebush 1975). This situation is different for the western continental boreal forest where precipitation maxima usually occur in June-July (Ecoregions Working Group, 1989). In a study on litter decomposition in Canadian forests summer precipitation was one of the important variables (Trofymov et al. 2002). The situation for CWM might be different since short rainfall penetrates only the top half of a tree bole (Brackebush 1975). Summer rain events of high intensity might not be a major source of moisture for decay fungi. Runoff from elevated CWM would be considerable and high temperatures would lead to high evaporation rates. Snow or winter precipitation would mainly affect the downed CWM since it would provide a moisture

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source in spring. This suggests that seasonal moisture indices, e.g., spring and summer precipitation and evaporation, might be more suitable variables for analysis.

Conclusions

Without strong support for the influence of climatic variables on decomposition of CWM it is impossible to extrapolate how predicted climatic change, e.g., increased annual precipitation and higher temperatures (IPCC 2001) might influence decomposition rates or dynamics. Nevertheless, on a individual tree bole level the low MC of CWM suspended more than 30 cm above the ground and lower decomposition rates for elevated CWM indicate that MC might be limiting decomposition and changes in precipitation might well lead to changes in decomposition dynamics. Considering only increased precipitation in the future, lag times for decomposition might decrease and decomposition rates increase resulting in shorter turnover times and a reduction of carbon stored in CWM.

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Table 5.1: Mean moisture content of small and large diameter CWM for three tree species.

Species	Class#	N	Mean diameter (cm)	Mean MC (%)	Mean LOG(MC)	SD LOG(MC)	Mean diff.	T	Sign. (2-tailed)
Aspen	1	47	7.9	61	1.57	.39			
	2	43	17.2	216	2.09	.52	-.53	-5.36*	< 0.001*
Jack pine	1	117	6.9	59	1.64	.33			
	2	139	12.7	81	1.77	.36	-.13	-3.60	0.002
Black spruce	1	116	2.6	28	1.32	.31			
	2	121	6.1	34	1.39	.31	-.07	-1.75	0.09

Class 1 represents diameter samples ≤ 12 cm for aspen, ≤ 9 cm for jack pine, ≤ 4 cm for black spruce and class 2 represents larger diameter samples.
*equal variances not assumed

Table 5.2: Mean moisture content of CWM along a vertical profile for three tree species.

Species	Class#	N	Mean MC (%)	Mean LOG(MC)	SD
Aspen	1	29	265	2.42	.28
	2	16	51	1.71	.31
	3	17	37	1.57	.35
	4	10	28	1.44	.22
	5	17	22	1.34	.25
Jack pine	1	48	109	2.04	.27
	2	71	62	1.79	.35
	3	65	40	1.6	.28
	4	37	37	1.56	.31
	5	34	28	1.45	.23
Black spruce	1	36	57	1.76	.32
	2	81	25	1.40	.29
	3	64	17	1.22	.21
	4	29	15	1.18	.15
	5	27	15	1.18	.14

Class 1 represents logs elevated < 10 cm, class 2 = 10- 19.9, class 3 =20- 29.9, class 4 =30-39.9 and class 5 ≥ 40 cm off the ground.

Table 5.3: ANOVA of mean LOG(MC) of CWM among different elevation classes.

		Sum of Squares	D.F.	Mean Square	F	Sign.
Aspen	Between Groups	17.27	4	4.32	51.64	.000
	Within Groups	7.02	84	0.08		
	Total	24.29	88			
Jack pine	Between Groups	9.61	4	2.40	26.98	.000*
	Within Groups	22.26	250	0.09		
	Total	31.87	254			
Black spruce	Between Groups	8.96	4	2.24	36.08	.000*
	Within Groups	14.41	232	0.06		
	Total	23.36	236			

*equal variances not assumed

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Table 5.4: Likelihood and AIC_c values of a linear, exponential and sigmoidal function for downed and elevated CWM wood density of aspen, jack pine and black spruce.

Species		Equation	B	D	LL	AIC_c	$\delta_1 AIC_c$	$\delta_2 AIC_c$
Aspen	downed	1.1-fixed	0.008		1.728	1.877	7.39	7.390
A = 0.41		1.1	0.009		5.423	-5.513	0	0
		3.1-fixed	0.087	4.92	4.924	-0.841	2.19	4.672
		3.1	0.098	4.92	6.051	-3.031	0	2.482
	elevated	1.1-fixed	0.008		3.194	-1.187	1.939	7.570
		1.1	0.007		4.163	-3.126	0	5.632
		3.1-fixed	0.087	4.92	5.674	-2.682	6.075	6.075
		3.1	0.077	4.92	8.712	-8.757	0	0
Jack pine	downed	1.1-fixed	0.005		3.687	-2.669	1.485	1.486
A = 0.41		1.1	0.006		4.430	-4.154	0	0
		3.1-fixed	0.033	2.18	-1.388	10.275	12.48	14.43
		3.1	0.039	2.18	4.851	-2.202	0	1.953
	elevated	1.1-fixed	0.005		6.556	-8.512	1.618	1.618
		1.1	0.004		7.356	-10.13	0	0
		3.1-fixed	0.033	2.18	6.594	-5.926	0.769	4.204
		3.1	0.029	2.18	6.210	-5.157	0	4.973
Black spruce	downed	1.1-fixed	0.004		2.359	-0.118	4.632	10.065
A = 0.54		1.1	0.005		4.670	-4.741	0	5.443
		2.1-fixed	0.01		6.299	-7.998	2.185	2.185
		2.1	0.011		7.392	-10.183	0	0
	elevated	1.1-fixed	0.004		11.514	-18.429	2.887	3.076
		1.1	0.0036		12.958	-21.316	0	0.189
		2.1-fixed	0.01		8.785	-12.970	8.536	8.536
		2.1	0.008		13.053	-21.506	0	0

$\delta_1 AIC_c$ gives the difference in AIC_c between the fixed and estimated parameter values using the same equation.

$\delta_2 AIC_c$ gives the overall difference in AIC_c with regard to the lowest AIC_c value calculated for the data set.

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Table 5.5: Likelihood and AIC_c values for linear and sigmoidal functions including the CMI for aspen CWM wood density.

Data	Equ.	B	C	D	E	LL	AIC_c	δAIC_c
Undivided	3.1-fixed	0.087		4.92		8.397	-8.395	0
	3.2	0.105	-0.018	4.92		7.454	-2.463	5.931
	3.3	0.098		4.92	0.131	7.62	-2.796	5.599
Downed	1.1-fixed	0.009				5.423	-5.513	0
	1.2	0.023	-0.012			-6.698	19.346	22.396
Elevated	3.1-fixed	0.077		4.92		8.712	-8.757	0.498
	3.2	0.082	-0.05	4.92		8.724	-8.724	0.474
	3.3	0.077		4.92	0.001	8.961	-9.255	0

Table 5.6: Likelihood and AIC_c values for linear and sigmoidal functions including the study region for aspen CWM wood density.

Data	Equ.	B	C	D	E	LL	AIC_c	δAIC_c
Undivided	3.1-fixed	0.087		4.92		8.397	-9.317	5.668
	1.3	0.009	-0.0006			12.23	-14.063	0
	3.4	0.9	-0.003	4.92	-0.0005	8.611	0.279	14.341
Downed	1.1-fixed	0.009				5.423	-5.513	0
	1.3	0.011	-0.001			5.84	-2.679	2.833
	3.4	0.1	-0.002	4.92	0.00003	6.06	7.88	13.392
Elevated	3.1-fixed	0.077		4.92		8.712	-8.757	0
	1.3	0.005	0.002			4.678	-0.689	8.069
	3.3	0.074	-0.003	4.92	0.00002	8.734	1.103	9.86

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Table 5.7: Likelihood and AIC_c values for linear and sigmoidal functions including the CMI for jack pine CWM wood density.

Data	Equ.	B	C	D	E	LL	AIC_c	δAIC_c
Undivided	1.1-fixed	0.005				7.789	-10.987	3.189
	1.3	0.006	-0.001			8.799	-10.334	3.833
	3.1-fixed	0.033		2.18		8.907	-10.551	3.616
	3.2	0.40	-0.007	2.18		9.705	-12.148	2.019
	3.2	0.033		1.69	0.047	10.715	-14.167	0
Downed	1.1-fixed	0.006				4.430	-4.154	1.597
	1.3	0.006	-0.0004			4.529	-1.558	4.193
	3.1-fixed	0.039		2.18		4.851	1.952	7.704
	3.2	0.043	-0.005	2.18		5.056	0.554	6.305
	3.3	0.029		1.25	0.033	8.202	-5.751	0
Elevated	1.1-fixed	0.004				7.365	-10.13	0
	1.2	0.005	-0.001			8.146	-9.028	1.102

Table 5.8: Likelihood and AIC_c values for linear and sigmoidal functions including the study region for jack pine CWM.

Data	Equ.	B	C	D	E	LL	AIC_c	δAIC_c
Undivided	1.1-fixed	0.005				7.789	-10.987	0
	1.3	0.005	-0.0003			8.248	-9.234	1.744
	3.4	0.034	-0.002	2.18	0.001	9.251	-6.972	4.933
Downed	1.1-fixed	0.006				4.430	-4.154	0
	1.3	0.006	-0.0007			5.337	-3.173	0.981
	3.4	0.021	0.017	1.02	1.27	5.388	3.51	7.664
Elevated	1.1-fixed	0.004				7.356	-10.13	0
	1.3	0.004	-0.0003			7.894	-8.524	1.606
	3.4	0.030	-0.001	2.18	0.00002	6.417	0.696	10.826

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Table 5.9: Likelihood and AIC_c values for linear and exponential functions including the CMI for black spruce CWM wood density.

Data	Equ.	B	C	LL	AIC_c	δAIC_c
Undivided	1.1-fixed	0.004		12.683	-20.676	1.756
	1.2	0.0001	0.003	14.848	-22.432	0
	2.1-fixed	0.01		12.229	-19.856	2.575
	2.2	0.002	0.007	14.732	-22.201	0.232
Downed	1.1-fixed	0.005		4.670	-4.741	7.076
	1.2	0.008	0.004	6.879	-6.484	5.322
	2.1-fixed	0.011		7.392	-10.183	1.633
	2.2	0.002	0.009	9.534	-11.816	0
Elevated	1.1-fixed	0.004		12.985	-21.316	3.599
	1.2	0.001	0.002	16.109	-24.955	0
	2.1-fixed	0.008		13.053	-21.506	3.45
	2.2	0.002	0.005	16.089	-24.915	0.04

Table 5.10: Likelihood and AIC_c values for linear and exponential functions including the study region for black spruce CWM wood density.

Data	Equ.	B	C	LL	AIC_c	δAIC_c
Undivided	2.1-fixed	0.01		12.238	-19.876	0
	1.3	0.005	-0.00007	11.405	-16.810	4.311
	2.3	0.011	-0.001	11.959	-16.655	3.203
Downed	2.1-fixed	0.011		7.392	-10.183	0
	1.3	0.006	-0.002	3.552	0.16	10.343
	2.3	0.014	-0.003	6.797	-6.33	3.853
Elevated	2.1-fixed	0.008		13.053	-21.506	0
	1.3	0.004	-0.0003	12.308	-17.353	4.153
	2.3	0.008	-0.003	12.858	-18.453	3.053
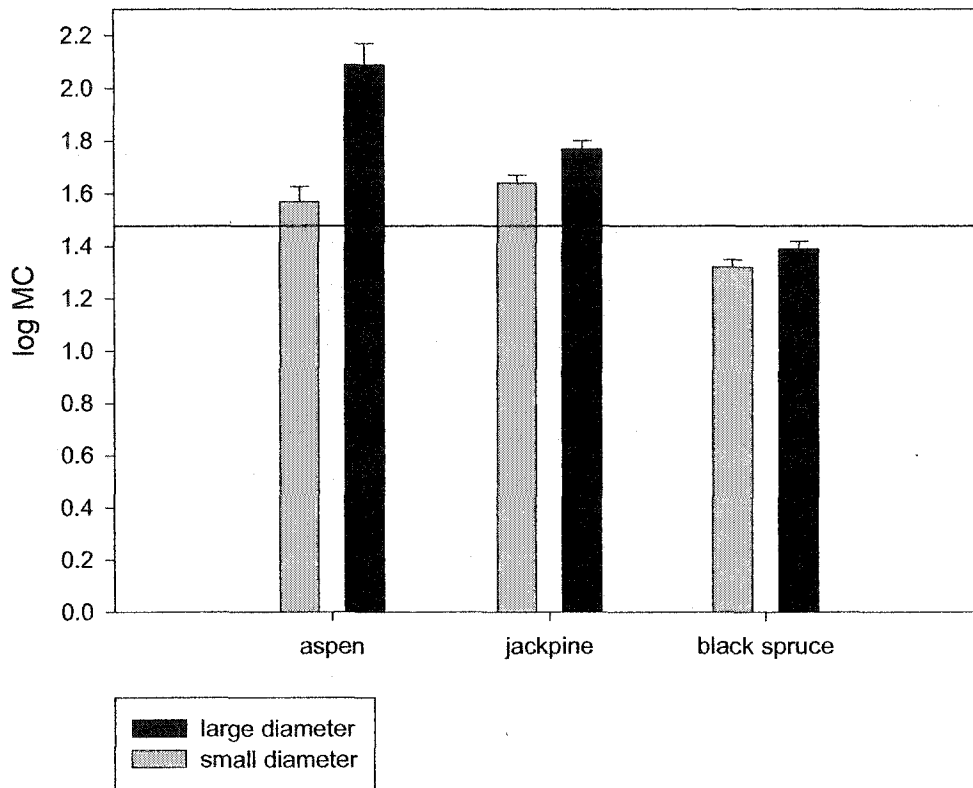
Figure 5.1: Mean moisture content of aspen, jack pine and black spruce CWM in the two diameter classes. Error bars represent the standard error of the mean. Diameter classes are as follows: Aspen: small ≤ 12cm, large > 12cm, jack pine: small ≤ 9 cm, large > 9 cm, black spruce: small ≤ 4 cm, large > 4 cm. The solid line represents 30% moisture content.
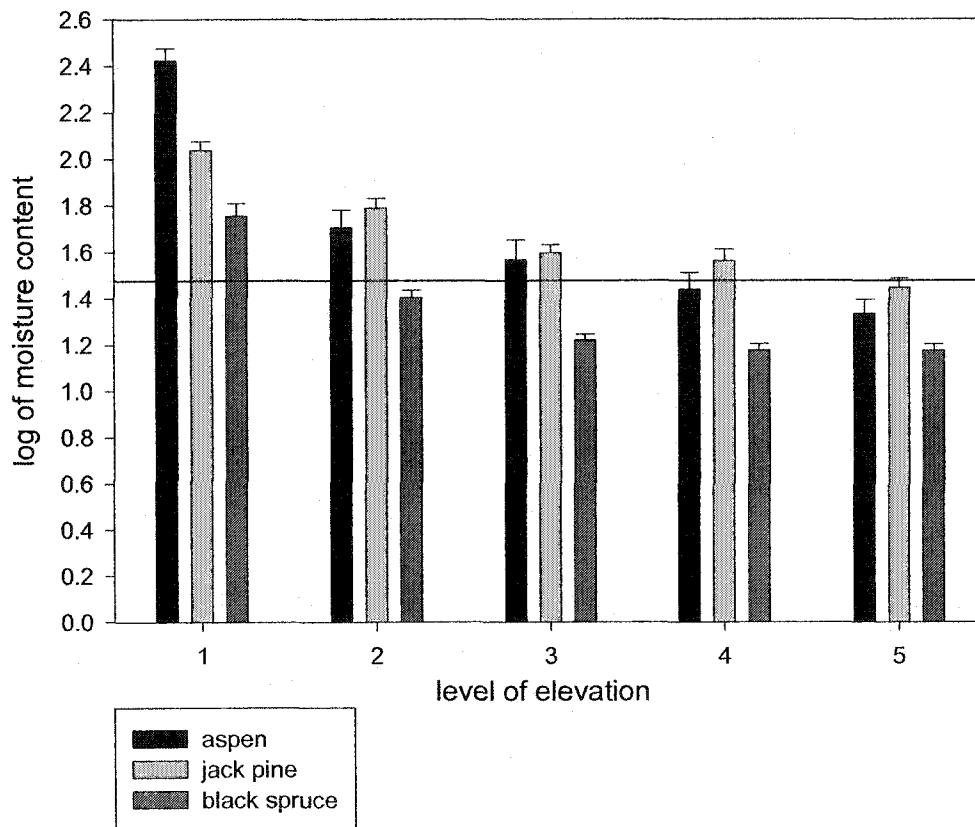
Figure 5.2: Mean moisture content of aspen, jack pine and black spruce CWM at different levels of elevation. Error bars represent the standard error of the mean. Elevation levels are: Level 1= 1-10 cm, level 2= 10.1-20 cm, level 3= 20.1-30 cm, level 4= 30.1-40 cm and level 5= > 40.1 cm raised above the ground. The solid line represents 30 % moisture content.
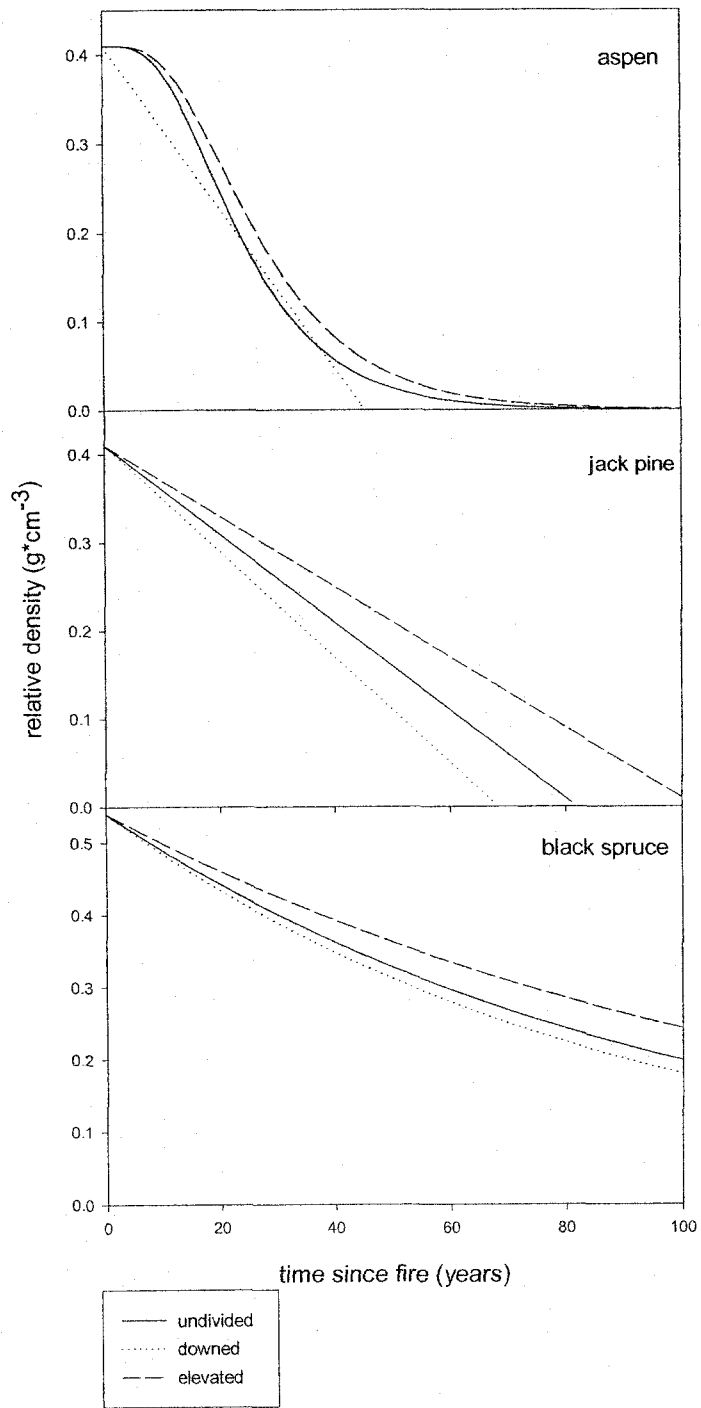
Figure 5.3: Best fitting functional forms for wood density of undivided, downed and elevated data sets of aspen, jack pine and black spruce CWM.

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Appendix 5.1: Estimated climate moisture index for aspen, jack pine and black spruce sites, provided by Dr. E Hogg and M. Siltanen, Northern Forestry Center.

Aspen		Jack pine		Black spruce	
Site	CMI	Site	CMI	Site	CMI
1-8	17.24	1-8	18.1	1-8	18.1
1-9a	8.38	1-9a	8.38	1-9a	8.38
1-9b	16.51	1-9b	12.84	1-9b	12.84
1-17	15.69	1-10a	16.51	1-10a	16.51
1-19	10.64	1-16	15.69	1-17	15.69
1-20a	11.02	1-19	10.64	1-19	10.64
1-20b	12.23	1-20a	10.48	1-20a	11.02
1-20c	9.35	1-20b	12.23	1-20b	12.23
1-32	9.39	1-20c	9.77	1-20c	9.35
1-34a	11.29	1-32a	9.39	1-32a	9.39
1-34b	16.83	1-32b	10.36	1-32b	10.36
2-15	6.64	1-32c	10	1-32c	10
2-16	4.23	1-34a	11.45	1-34	12.26
2-29	14.77	1-34b	18.02	1-51	10.73
		2-10b	9.01	1-56	13.25
		2-15	4.27	1-57	8.38
		2-17	3.87	2-10b	8.31
		2-25a	11.2	2-15	6.64
		2-25b	12.46	2-16	4.68
		2-25c	4.95	2-25a	14.5
		2-29	14.77	2-25b	12.46
		2-31	5.44	2-29	14.77
		2-44	1.42	2-44	1.42

Chapter 6: Improving decomposition models for the boreal forest: Hypotheses

Introduction

Northern forests are an important part of the global carbon cycle, mainly due to their large areal extent (Dixon et al. 1994) and high detrital carbon density. In recent years major efforts have been undertaken to understand and model carbon and other fluxes in the boreal forest (e.g., BOREAS: e.g., Baldocchi et al. 2000, Trumbore and Harden 1997; or CBM-CFS2: Kurz and Apps 1995). There is still uncertainty if the boreal forest currently serves as a carbon sink: its performance as sink or source depends on annually changing climatic variables (Arain et al. 2002, Barr et al. 2002). Within a boreal forest stand soil organic matter (SOM) and coarse woody material (CWM) account for 40 % of carbon (Barford et al. 2001). Studies focusing on CWM volume and using a qualitative decay class system (Lee et al. 1997, Stone et al. 1998, Pedlar et al. 2002) are difficult to link with overall biomass estimates (Krankina et al. 2002). To address this problem the present study focused on relative wood density over time as a measure of CWM decomposition. To link relative wood density of CWM with a broader context of boreal forest carbon fluxes, two conceptual models are presented.

For easier comparison between sites, the present study did not take into account differences in prefire stand conditions, which are important for initializing stand-level decomposition models. The assumption underlying the following synthesis is that functions describing relative density ($g*cm^{-3}$) loss of CWM are transferable to describing biomass ($kg*m^{-2}$) of CWM as calculated by the line-intersect method (Van Wagner 1982). Depending on the spatial scale of interest, two modeling approaches for CWM decomposition might be used.

For process-oriented questions regarding the stand-level a detailed approach is required. For questions regarding forest management or carbon budget estimation at the regional level, a coarse filter approach might be appropriate.

Without improving the existing models few implications for climatic change can be made beyond the very general statement that increased precipitation very likely will

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lead to faster decomposition. Without identifying important climatic variables no predictions can be made about the impact of changing temperature and precipitation and their interaction on the CWM carbon pool.

The objective of this chapter is to present two conceptual models for post-fire CWM decomposition in upland forests and to illustrate how results from the present study fit within the context of studies that have been focusing on carbon budgets and climate change of the western Canadian continental boreal forest.

Stand model (Figure 6.1)

The model focuses on burned upland forests since the present study shows that stands of lowland black spruce decompose extremely slowly and the CWM decomposition rate is likely controlled by the growth rate of *Sphagnum* spp. On a stand level input for the model would require stand data like standing tree biomass ($Mg*ha^{-1}$), tree density ($stems*ha^{-1}$) and composition, average diameter at breast height and age of the stand. These data should be available from existing data sets, from permanent sample plots and recent studies such as BOREAS (Sellers et al. 1997) and the ENFOR program (Nalder, unpublished data)

Fire function

Assuming disturbance by a severe fire, most of the trees in a stand would be killed by heat exposure. A factor that might need to be considered in terms of biomass loss is how much needle, branch and bark biomass would be oxidized during the fire. Models to represent fire behavior and areal extent have been developed as part of the Canadian Forest Fire Behavior Prediction System (CFFBPS, Forestry Canada Fire Danger Group 1992).

Breakdown function

As previous studies have shown (Harmon 1982, Sander 1995), snags decompose more slowly than boles near the soil surface. Biomass of bark, which most dead trees lose

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while standing contributes to the decomposition pool. As snags break down, they become available for accelerated decomposition rates. The description of the structural properties of aspen, jack pine and black spruce sites (Chapter 3) confirmed that breakdown rates are species specific. Hypothesized dynamics for post-fire snag breakdown (Figure 6.3 a) are loosely based on post-fire snag densities presented in Chapter 3; snag densities from the most recently burned sites (8 and 9 years since fire) were assumed to represent 100 %. The graphs (Figure 6.2 a) illustrate that functional forms for snag breakdown might range from negative exponential to sigmoidal ones. Field observations indicate that breakdown functions might be a combination of lag time during the first couple of years after the fire, an increase in breakdown rate due to a general weakening of the root system and the tree base, and stochastic weather events like major storms. Important variables influencing snag breakdown are diameter and height of the tree. More quantitative data on the breakdown rates after fire are needed to estimate varying breakdown rates over time.

Vertical distribution function

As the present study has shown, the distance of CWM from the ground influenced the performance of the three different functional forms as well as the rate of decomposition. Once a snag falls over it has a certain probability of falling on the ground or falling on top of other CWM. The vertical distribution function determines annually if a CWM would be put into the downed or elevated pool to assign the appropriate decomposition function. The overall probabilities of trees falling on the ground will be determined by prefire stand characteristics like tree density, diameter and average height of the trees.

CWM in the downed category either fell over directly after the fire when chances of falling directly on the ground were still high, or the trees were elevated at first and fell on CWM that fragmented or decomposed over time. For CWM in the elevated pool the probability of being categorized as downed increases over time. Since the present study did not differentiate between the two processes the fraction of downed CWM as described as part of the structural stand properties can only provide coarse estimates for the overall distribution of downed vs. elevated CWM in a stand. Based on numbers from

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Chapter 3 and on the assumption that directly after the fire (1 year) nearly all boles (0.9) that fell would be classified as downed it is hypothesized that the relative amount of downed CWM follows a u-shaped function (Figure 6.2 b).

More data for the vertical distribution during the first decade after fire are needed since the present study included only a few sites 7-10 years after the fire.

Decomposition function

Decomposition functions and the parameter values are based on tree species and vertical location: Linear functions describe downed aspen CWM, and sigmoidal functions describe downed and elevated jack pine as well as elevated aspen CWM. Further studies are needed to account for the effect of diameter and to identify appropriate climatic variables. A climate moisture index based on summer precipitation and temperature as in other decomposition studies (e.g., Trofymow et al. 2002) might be more appropriate for modeling CWM decomposition processes than an annual index (Hogg 1994).

Further fragmentation and mineralization

CWM would be considered part of the soil organic matter pool if more than half of the log is embedded by litter, or overgrown by mosses and heavily invaded by roots of vascular plants. These features are mostly qualitative since it would require different sampling techniques to determine the relative density of disintegrating logs. CWM is an important part of the forest floor carbon (Nalder and Wein 1999) and the dynamics of forest soil organic matter (SOM) have been characterized in other studies such as Bhatti et al. (2002) and Nalder and Wein (1999).

Landscape model (Figure 6.3)

On a landscape level the input for a CWM decomposition model would be initialized by the estimates of standing tree mass. These type of data are accessible through forest inventories or research surveys such as Sellers et al. (1997).

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Fire function

The size of the fire and the amount of trees killed depend on tree species distribution, characteristics of the fire and time of the fire. The result of the disturbance would be a mosaic of burned and unburned stands. A severe fire would kill most trees while low intensity fires would kill fewer trees. Input to the model would be mass per area.

Breakdown function

Breakdown of CWM after fire likely depends on tree species, tree diameter, and major storm events. Research is needed to provide quantitative data for breakdown rates of tree species of the western Canadian boreal forest. Estimates of annual breakdown rates and how they might be influenced by climatic variables are necessary to provide the annual input to the CWM pool.

Decomposition function

For evaluating decomposition dynamics on a landscape level at present climatic conditions, a more general approach to post-fire decomposition dynamics as described in chapter 4 is appropriate. Depending on the species distribution in the area burnt, parts of the CWM pool would undergo faster decomposition as described by the sigmoidal function for aspen CWM, or slower decomposition as described by the linear or sigmoidal function for jack pine. Further research is needed to determine how other tree species, especially white spruce, respond. The functions derived from the undivided data sets (chapter 4) are considered an adequate description for downed as well as elevated CWM since, as previously illustrated, modeling results are usually close to field measurements of the downed and elevated functions.

Further fragmentation and mineralization

Criteria for CWM to enter the SOM pool and associated problems with quantification would be the same as described above for the stand model.

Based on average fuel loads for the CWM (Figure 3.3), it is hypothesized that the functional form for total CWM biomass over time should follow a bell-shaped curve, with rapidly accumulating CWM during snag breakdown. Decomposition processes should determine the functional form of CWM decline (Figure 6.2 c)

Simulation

An early attempt to simulate the conceptual models has been made based on an aspen stand described from the southern study area of the BOREAS project with a stem density of approximately 2000 stems/ha and a standing above-ground biomass of approximately 90 Mg/ha (Halliwell et al. 1995). Directly after fire these values would translate into 2000 snags/ha with total biomass of 90 Mg/ha.

Fitting a linear function to data presented in Figure 6.3 a ($Y= 1-0.03*time$) provided an estimate for snag breakdown rate and the total CWM mass as input for the stand and landscape conceptual models. For simulating the stand model this pool was divided into downed and elevated CWM using a vertical distribution function obtained by fitting a quadratic function to the data presented in Figure 6.3 b ($Y= 0.62-0.005*time+0.002*time^2$). A linear decomposition function was used for the downed CWM pool and a sigmoidal decomposition function for the elevated CWM pool. The sum of downed and elevated aspen CWM provided the total stand CWM mass (total mass 1, Figure 6.4). For simulating the landscape model a sigmoidal function was used to decompose the input from the snag breakdown function.

The simulated data followed a bell shaped curve similar to the one presented for aspen CWM in Figure 6.2 c. Values for maximum CWM mass were comparable, 28.6 $Mg\cdot ha^{-1}$ for the simulated CWM mass based on the stand model, 24.8 $Mg\cdot ha^{-1}$ for simulated mass based on the landscape model and 28.3 $Mg\cdot ha^{-1}$ for the mean aspen CWM mass in the tree sapling stage. But simulated CWM mass declined faster than measured data from the present study indicate. The landscape model provided the lowest estimates for CWM mass and accumulation and decomposition of elevated CWM seemed to strongly influence the CWM biomass dynamics.

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Results from the present study were linked to stand data from other studies. But to move beyond simulation based on curve-fitting of data the post-fire breakdown rates of snags and the vertical distribution function need to be studied.

Conclusions

The conceptual models presented in the present study successfully simulated CWM weight over time. Not accounting for different decomposition rates and dynamics of downed and elevated CWM resulted in lower estimates of total CWM weight emphasizing the need for more quantitative data for the vertical distribution of CWM.

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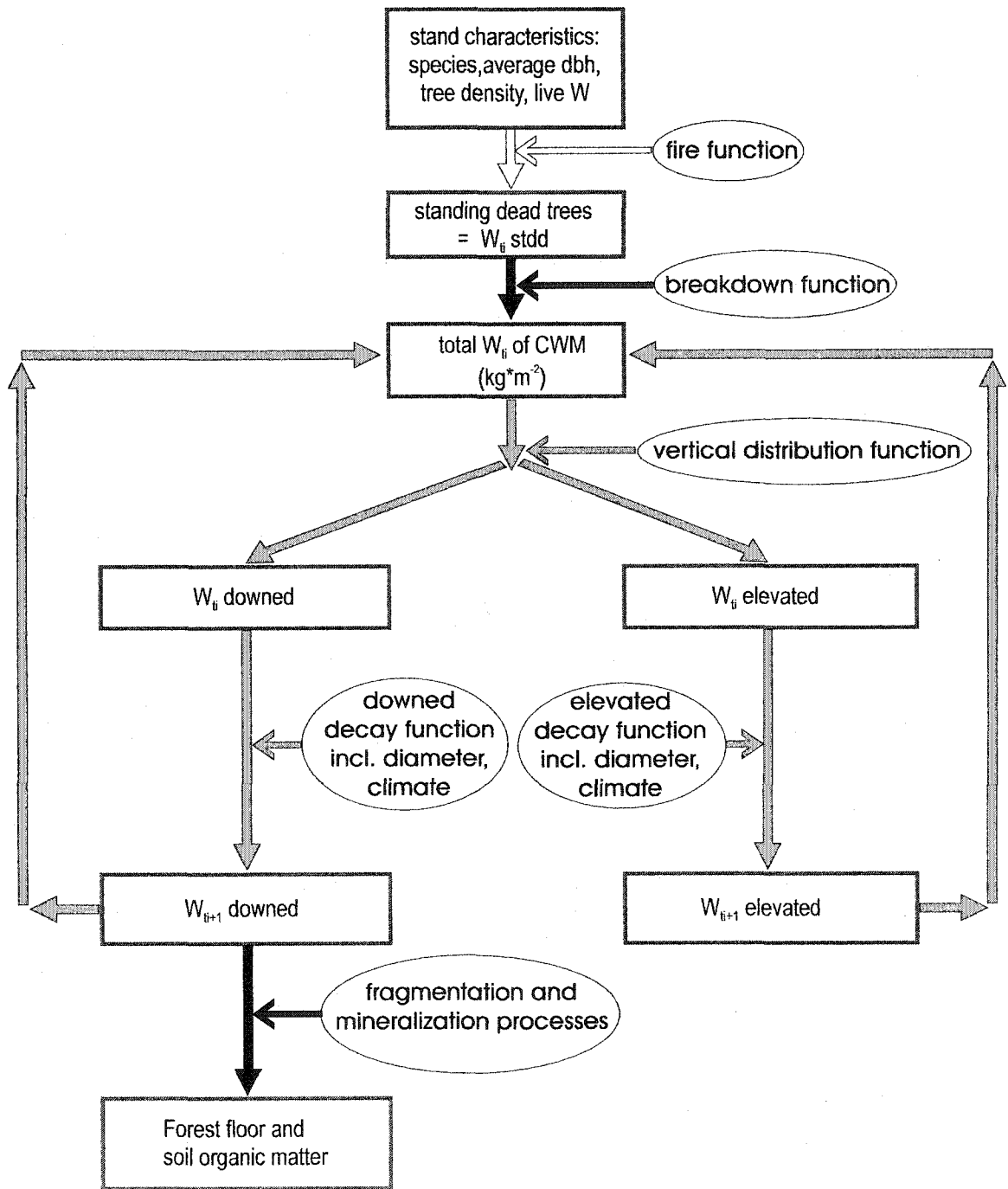
Figure 6.1: Conceptual model of CWM decomposition processes at the stand level. Biomass pools are presented in boxes whereas disturbance and decomposition processes are presented in ovals. White arrows represent processes described in other studies, gray arrows represent processes described in the present study, black arrows indicate a need for more quantitative data. dbh stands for tree diameter at breast height, W represents biomass expressed as weight per area $(kg*m^{-2})$ at time t at the i-th year after fire calculated based on the line intersect method (Van Wagner 1982).
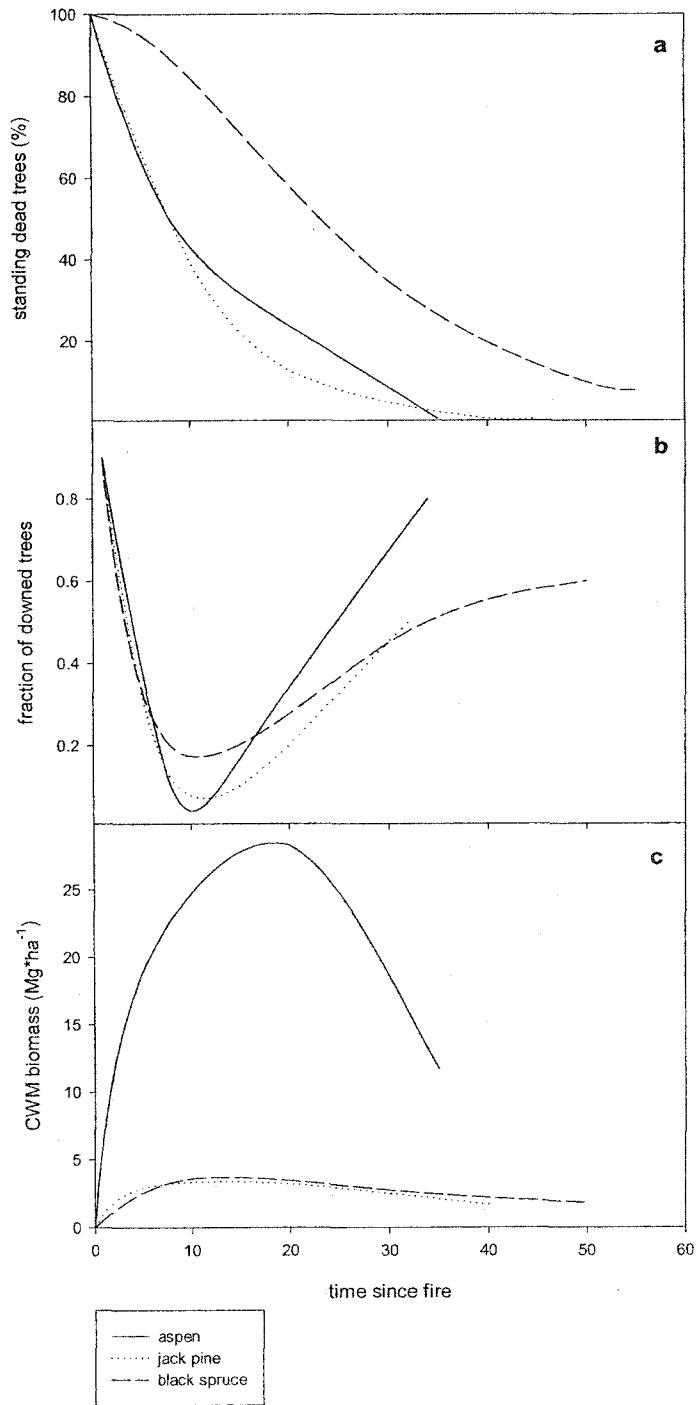
Figure 6.2: Hypothesized post-fire dynamics of aspen, jack pine and black spruce snag breakdown (a), fraction of downed CWM (b) and CWM mass (c).

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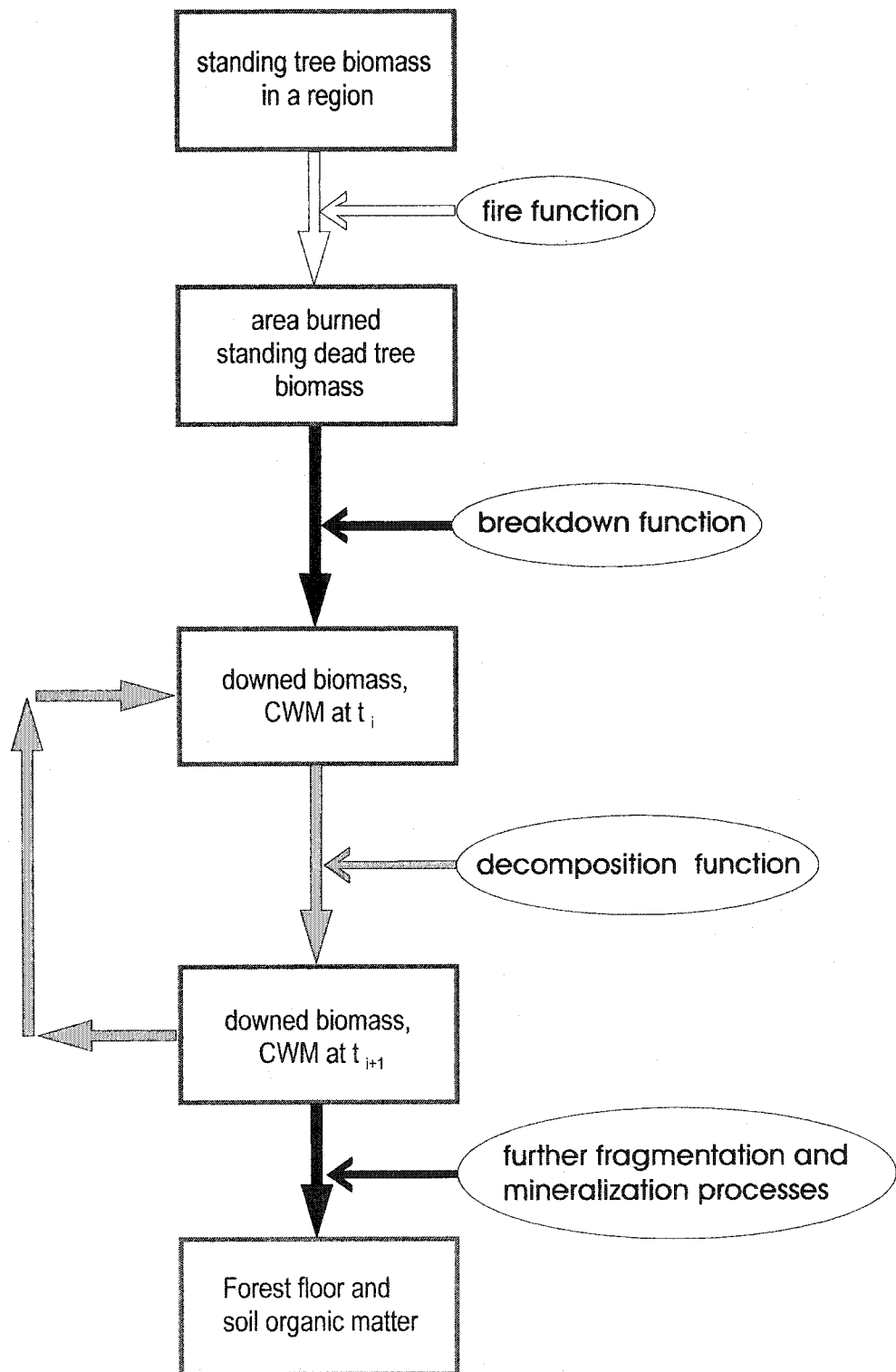
Figure 6.3: Conceptual model of CWM decomposition processes at a regional level. Biomass pools are presented in boxes whereas disturbance and decomposition processes are presented in ovals. White arrows represent processes described in other studies; gray arrows represent processes described in the present study, black arrows indicate a need for more quantitative data. Time t represents the i-th year after fire.
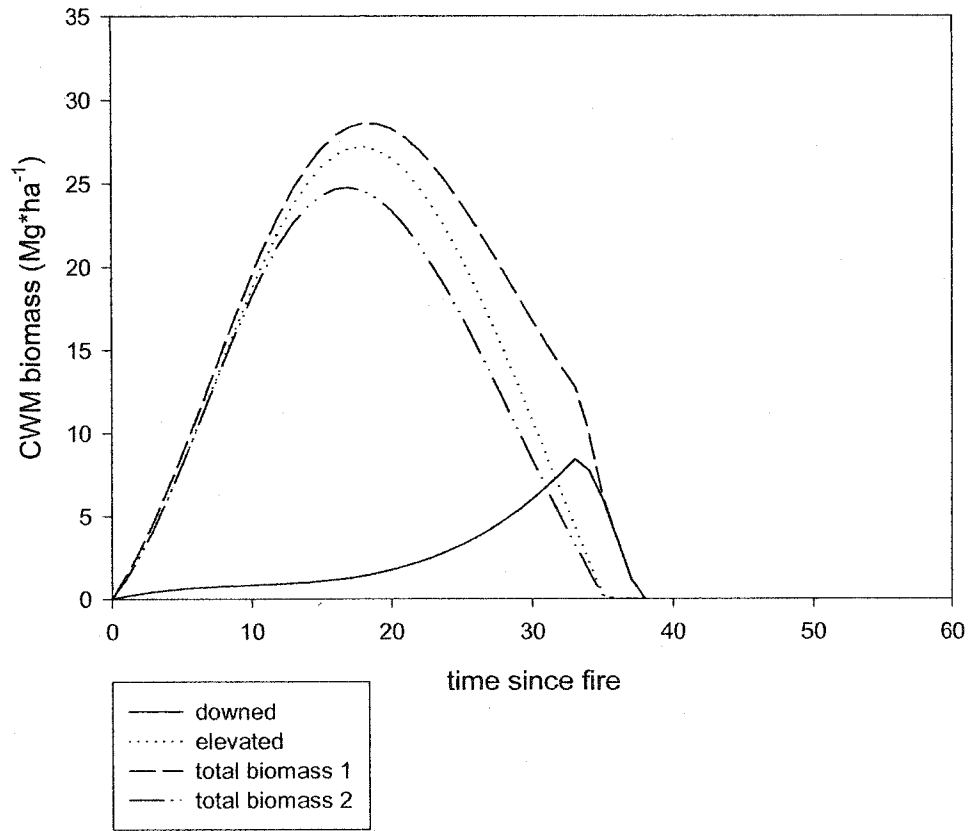
Figure 6.4: Simulated downed, elevated and total aspen CWM decomposition after fire. Total biomass 1 refers to simulated aspen CWM biomass from the stand model, and total biomass 2 refers to simulated aspen CWM biomass based on the landscape model.

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7. Appendices

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Appendix 7.1: A comparison of techniques used to measure volume of wood pieces

Introduction

Wood density and specific gravity are used as indicators for mechanical and physical properties of wood. The specific gravity of wood is calculated based on oven dry weight and weight of water displaced. Density is based on wood mass and the unit volume at a specific moisture content (Zabel and Morrell 1992). Wood density can relate to either green, ovendry or nominal wood density. Green density is based on green weight and volume of a sample, ovendry density is based on ovendry weight and volume, and nominal density is based on ovendry weight and volume when tested (Society of American Foresters 1971). The volume is either calculated based on diameter and length measurements or measured using water immersion techniques. Calculated values for irregular pieces are approximations of bulk volume whereas water immersion will give the actual bulk volume. At moisture contents below the fiber saturation point wood is highly hygroscopic. Therefore dried wood is usually coated with paraffin wax previous to immersion in water to avoid an uptake of water. In wood pieces with a water content over the fiber saturation point, spaces between the microfibrils, smaller voids and pores are filled with water. The wood has reached maximum volume and is less affected by exposure to water.

In long-term decomposition studies dealing with heavily decayed and fragmenting wood, immersing coated or uncoated wood pieces in water is not possible. Measuring diameter or circumference in situ before sampling in the field is possible.

Objective

The objective was to determine if volume estimates based on diameter measurements taken in the field before sampling are comparable to other methods of volume.

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Methods

Sound pieces from 27 black spruce snags and CWM and ten stem pieces of living jack pine trees were measured for diameter to the nearest mm in the field. All pieces were oven dried, cooled, and a second diameter and length measurement taken. Length of each sample was determined with four measurements at compass points. Uncoated samples were soaked in water over night to raise moisture contents above the fiber saturation point before a third measurement of diameter and length was taken. After excess water from the surface of the samples was removed, samples were submersed in water in a beaker and weighed.

The following methods to measure volume were compared:

A= Volume measurements were performed using water replacement (uncoated wet pieces of wood).

B= Volume calculated based on diameter and length of wet wood

C= Volume calculated based on diameter measured in the field and length measured on a wet piece

D= Volume calculated based on diameter taken in the field and length measured on an oven dry piece

The calculation of the volume of the samples was based on the assumption that all wood pieces were cylindrical. The volume was calculated by multiplying the cross-sectional area with the length of the sample. The different techniques were compared using paired T-tests (SPSS 10.0). Absolute rather than relative volume measurements were used since there was no indicator as to what number would constitute 100 %.

Results

Black spruce and jack pine samples showed a similar pattern: Calculating the volume based on wet diameter and wet height (B) usually resulted in the smallest numbers of average volume (black spruce = 145 cm^3, jack pine = 362 cm^3). Immersing the samples in water (A) provided higher values. Calculating the volume based on

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diameter measurements taken in the field (C and D) usually resulted in the largest average volume (average volume for black spruce C = 148 cm^3 and jack pine D = 404 cm^3). For black spruce CWM these differences were not significant (Table 7.1.1) whereas for living jack pine all differences but between C and D were significant (Table 7.1.2).

Table 7.1.1: Differences in volume for black spruce CWM.

	mean difference, cm^3	n	t	sign. (p, 2-tailed)
A-B	2.8411	28	1.18	0.25
A-C	-1.01	28	-0.46	0.65
A-D	-0.823	28	-0.36	0.72
B-C	-3.86	28	-1.57	0.13
B-D	-3.66	28	-1.44	0.16
C-D	0.191	28	0.55	0.59

Table 7.2.2: Differences in volume for living jack pine

	mean difference, cm^3	n	t	sign. (p, 2-tailed)
A-B	14.33	10	2.55	0.03
A-C	-18.04	10	-3.09	0.03
A-D	-27.69	10	-5.08	0.003
B-C	-32.37	10	-5.87	<0.001
B-D	-42.02	10	-4.24	0.002
C-D	-9.65	10	-1.34	0.21

Discussion

Differences in water content of wood and the associated shrinking and swelling affect mainly the tangential and radial planes of a sample (Zabel and Morrell 1992). Absorbed water molecules increase the distance between the microfibrils resulting in an increased diameter of a stem- disk: The diameter in field measurements was considerably larger than diameter measured in the lab either wet or dry. For pieces of black spruce CWM these differences were within the variability of each technique. Volume based on

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calculations with different height measurements (C and D) were not significantly different for pieces of black spruce or jack pine.

For jack pine the differences in volume were significant because the samples were taken from living trees. Green wood that has not been dried has a higher initial desorption curve (= higher % moisture at given relative humidity) than previously dried material. Therefore the difference between field diameter and wet diameter would be more pronounced in the pine samples that in the spruce samples.

Each technique has different sources of bias:

Method A: The water immersion technique introduces variability with the mechanical handling of the samples: Different amounts of water might be transported with the sample into the beaker, and the submerging devicewill be immersed to different degrees. Partly fragmented samples would have been impossible to measure with this technique. The water immersion will always give a low value for the volume since the water will fill voids left by insects or even cells that have been partly decomposed by fungi. These processes of decomposition introduce error.

Method B: Calculating the volume of the samples based on the diameter on the wet pieces introduces potential losses of softer pieces due to handling during oven drying and soaking prior to measuring the diameter. Any problems due to measuring diameter during adsorption (which gives the lowest % moisture at a given relative humidity) should have been avoided by soaking the pieces in water for several hours because water content should be over the fiber saturation point.

Methods C and D: By using field diameter any problems resulting from drying processes for living trees were avoided. Wood density of living trees is based on the green volume. For pieces from snags and CWM using field diameter introduces a certain variability since the pieces were sampled under varying conditions and were at different equilibrium moisture contents. For all pieces with a moisture content over the fiber saturation point (ca. 30 % MC.) the field diameter is close to green conditions . Since the samples were subjected to several annual cycles of drying and wetting, differences associated with sorption were much smaller than for green wood. Any losses due to handling and sawing was avoided since the diameter was taken previous to cutting the sample.

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Conclusions

Snag and CWM volume measurements of bole samples based on field diameter were comparable to other techniques.

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Appendix 7.2: Distance from the ground, bark cover and insect activity for aspen, jack pine and black spruce CWM

Table 7.2.1: DG, bark cover* and insect activity** of aspen CWM at three different stages of stand development.

stage	tree seedling			tree sapling								young tree		
site	1-8	1-9a	1-9b	2-15	2-16	1-17	1-19	1-20a	1-20b	1-20c	2-29	1-32	1-34a	1-34b
average DG (cm)	19	28	29	23	18	14	11	10	15	8	2	6	3	2
bark class 1	30	13	50	93	100	100	97	100	97	87	100	100	100	100
2	10	30	27	7	0	0	3	0	3	0	0	0	0	0
3	7	20	13	0	0	0	0	0	0	7	0	0	0	0
4	37	20	7	0	0	0	0	0	0	3	0	0	0	0
5	17	17	3	0	0	0	0	0	0	3	0	0	0	0
av. bark class	3.04	2.98	1.86	1.07	1	1	1	1	1.03	1.45	1	1	1	1
insect activity (%*)	7	10	17	53	73	57	57	50	80	73	100	87	97	93

* % of CWM in bark cover classes 1 to 5, class 1 = 1-20 %, 2 = 21-40 %, 3 =41-60 %, 4 = 61-80%, 5= 81-100 % bark cover
** % of CWM that showed signs of insect activity

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Table 7.2.2: DG, bark cover* and insect activity** of jack pine CWM at three different stages of stand development

stage	tree seedling					tree sapling														young tree		
site	1-8	1-9a	1-9b	1-10a	2-10b	2-15	2-16	1-17	1-19	1-20a	1-20b	1-20c	2-25a	2-25b	2-29	2-31	1-32a	1-32b	1-32c	1-34a	1-34b	2-44
average DG (cm)	30	25	29	23	15	14	19	30	9	14	31	19	12	21	19	9	10	3	2	10	12	3
bark cover class 1	43	17	3	70	57	100	93	96	97	87	93	100	94	100	100	100	100	100	100	100	100	100
2	13	40	13	30	13	0	7	4	3	10	7	0	4	0	0	0	0	0	0	0	0	0
3	23	23	33	0	7	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
4	20	13	30	0	23	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
5	0	7	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
av. bark class	2.81	2.63	3.48	1.3	1.96	1	1.03	1.04	1.03	1.16	1.07	1	1.06	1	1	1	1	1	1	1	1	1
insect activity (%*)	40	17	95	63	44	60	63	46	43	30	3	47	67	40	80	87	80	89	23	93	97	53

* % of CWM in bark cover classes 1 to 5, class 1 = 1-20 %, 2 = 21-40 %, 3 =41-60 %, 4 = 61-80%, 5= 81-100 % bark cover
** % of CWM that showed signs of insect activity

Table 7.2.3: DG, bark cover* and insect activity** of black spruce logs at three different stages of stand development

stage	tree seedling											tree sapling							young tree			
site	1-8	1-9a	1-9b	1-10a	2-10b	2-15	2-16	1-19	1-20a	1-20b	1-20c	2-25a	2-25b	2-29	1-32a	1-32b	1-32c	1-34	2-44	1-51	1-56	1-57
average DG (cm)	14	15	22	14	29	13	22	19	15	20	18	17	14	7	17	10	7	9	5	9	8	6
bark cover class 1	63	0	3	83	57	40	75	73	100	97	100	100	100	100	100	100	100	100	100	97	100	93
2	17	17	0	10	37	20	8	10	0	3	0	0	0	0	0	0	0	0	0	3	0	0
3	3	30	7	3	3	10	7	17	0	0	0	0	0	0	0	0	0	0	0	0	0	3
4	7	37	3	3	3	10	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	10	17	87	0	0	20	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
av. bark class	1.78	3.57	4.71	1.24	1.52	2.5	1.54	1.44	1	1.03	1	1	1	1	1	1	1	1	1	1.03	1	1.17
insect activity (%*)	3	5	17	0	13	63	45	3	n.a.	3	20	35	10	28	18	17	23	20	47	37	17	40

* % of CWM in bark cover classes 1 to 5, class 1 = 1-20 %, 2 = 21-40 %, 3 =41-60 %, 4 = 61-80%, 5= 81-100 % bark cover
** % of CWM that showed signs of insect activity

8. Glossary

air-dry density* density based on the weight an volume of wood in equilibrium with atmospheric conditions

basic density* density based on oven dry weight and green volume of wood

bole# a trunk or main stem of a tree.

bulk density* weight per unit of bulk volume, at specified moisture tension, i.e. of solid material plus pore space

coarse woody debris (CWD)# any piece(s) of dead woody material, e.g., dead boles, limbs and large root masses, on the ground in forest stands or streams

coarse woody material (CWM) used interchangeably with CWD. **In the present study** Trees that have been killed by the last fire and have fallen over, lying on the ground or horizontal to the ground.

fiber saturation point (FSP)# the point at which all the liquid water has been removed from the cell but the cell wall is still saturated

green* a loose term applied **1.** To wood of living trees, standing or freshly felled, or wood still containing most of the moisture present at the time of felling i.e. still above the fiber saturation point **2.** To unseasoned wood , i.e. above the fiber saturation point

green density* density based on the weight and volume of wood when green

nominal density* density based on oven-dry weight and the volume when tested – commonly when the wood is green or at 50 or 12 % moisture content

ovendry density* density based on the weight and volume of wood when oven-dry

snag# **1.** A standing generally unmerchentable dead tree from which the leaves and most of the branches have fallen **2.** A standing section of the stem of a tree, broken off usually below the crown **3.** A sunken log or a submerged stump or tree **4.** The projecting base of a broken ore cut branch on a tree stem. **In the present study** A standing dead tree killed by the last fire

specific gravity# the ratio of the density (weight per unit volume) of an object to the density of water at 4 °C

water potential# **1.** the free energy level or ability of water to do work **2.** a measure of plant water status

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9. Curriculum vitae

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Education

1995 to present	Ph.D. - Department of Renewable Resources, University of Alberta
1987-1995	Diplom in Biologie (equivalent to M.Sc.): Major: Botany Minors: Zoology, Genetics and Public Law Universität Tübingen, F. R. Germany

M. Sc.- Thesis title:
Decomposition of *Pinus banksiana* LAMB., *Picea glauca* (MOENCH) VOSS, and *Populus tremuloides* MICHX. in Wood Buffalo National Park after the Cherry Mountain Burn in 1981

Ph.D. Dissertation Topic (Forest Biology)

Post-fire structure and decomposition dynamics of coarse woody material in the western Canadian continental boreal forest

Scholarships and Awards

1999	Graduate Students' Association Graduate Student Service Award
1998	Graduate Research Assistantship
1995-1996	University of Alberta Ph.D. Scholarship
1995-1996	Government of Canada Award, International Council of Canadian Studies

1993	Scholarship from the Stipendienstiftung der Universität Tübingen, F. R. G.
1990	Integrated Study Program Abroad, (Scholarship of the German Academic Exchange Service for studying at the Universities of Turku and Oulu, Finland)

Research Experience

1995 to present	Research on Ph.D project
1993-1995	Field research in Wood Buffalo National Park and lab analysis for master's thesis
1992-1994	Prepared and analyzed fossils of the early Eocene from the Messel Pit, F. R. G.
1992	Assisted in the research project: "Significance of fragmentation, habitat size and quality for the survival of plant and animal populations on drought sites", Research Centre for Ecology, Halle-Leipzig, F.R.G.
1991	Summer research assistant to S.M. Landhäußer, Ph.D., on his project "climatic change and the arctic treeline" in Inuvik, N.W.T.
1989	Vegetation mapping of the area Doxbrunnen-Steinach, Altheim, F. R. G. for a survey of a planned nature reserve, Nature Protection Department, Baden Württemberg, F.R.G.

Publications

Sander, B., K. Athen, S. Billmann and A. Strubelt. 1993. Preparation and analysis of fossil leaf-cuticles of the fossil deposit of the Messel Pit, F.R.G. (translated title). Der Präparator **39**: 16-18.

Teaching Experience

1995-1998	Teaching assistant for classes in botany and forest ecology
1990-1994	Laboratory instructor (preparing course material, demonstrating and marking of

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assignments) in plant evolution, anatomy and adaptation

1992-1994	Laboratory instructor in plant ecology (systematics, communities and evolution
1992-1994	Field trip leader for students in Botany and Paleontology
1991-1993	Lectured and instructed a seminar and lab course (included design of seminar and course structure and content) on the paleoecology of the Messel Pit, Early Eocene, F. R. G.

Administrative Experience .

1998-2000	General Manager for the Assiniboia Community Housing Cooperative
1995-1999	Representative of the Graduate Students' Association at the University of Albertan in the Graduate Students Negotiation Committee, the Graduate Assistantship Policy Committee and the Taskforce on Graduate Student Employment
1987-1991	Active member Student Association, Faculty of Biology, Universität Tübingen, F. R. G
1989-1990	Member of the faculty of Biology's advisory commission on the development of undergraduate and graduate programs, Universität Tübingen, F. R. G.
1988-1989	Student associations' representative Universität Tübingen, Senate