AN ABSTRACT OF THE THESIS OF

Mikhail A. Yatskov for the degree of Doctor of Philosophy in Forest Science presented on March 1, 2016.

Title: The Impact of Disturbance on Carbon Stores and Dynamics in Forests of Coastal Alaska.

Abstract approved:

_____

Mark E. Harmon

Changes in climate caused by increased concentrations of carbon dioxide (CO_2) in the Earth's atmosphere have led land and ocean surface temperatures to increase by 0.85^oC and sea level to increase by 19 cm relative to preindustrial times. Global climate change will lead to further alterations in mean temperature and precipitation, as well as their extremes that are likely to influence disturbance regimes. Disturbance play an important role in forest dynamics and succession, by influencing forest ecosystems structure and function, reorganizing forests by reducing live and increasing dead matter, and thus affecting ecosystem carbon (C) balances. Under a changing climate disturbances are likely to cause widespread tree mortality across forested landscapes, creating vast amounts of coarse woody debris (CWD) that will emit C to the atmosphere to a degree that regional C balances and future C dynamics are likely to change.

C balance of forested regions depends on inputs in form of C sequestered by live components during growth and outputs in form of C emitted from dead components through decomposition and combustion. Live trees in many forest ecosystems represent the largest aboveground C pool and the dynamics of this pool, as controlled by growth and mortality, have been extensively

studied. In contrast, few have examined either the post-disturbance fate of CWD C or assessed C storage potential of salvaged biomass despite the occurrence of multiple recent large-scale disturbance events.

Biomass and C stores and their uncertainty were estimated in the Temperate and the Boreal ecoregions of Coastal Alaska using the empirical data from the Forest Inventory and Analysis (FIA) program, literature data, and modeling using standard methods employed by the FIA program. The average aboveground woody live (218.9±4.6 Mg/ha) and log (28.1±1.8 Mg/ha) biomass in the Temperate ecoregion were among the lowest in the Pacific Northwest, whereas snag biomass (30.5±1.0 Mg/ha) was among the highest. In the Boreal ecoregion, CWD biomass comprised almost 50% of the regional aboveground woody store (76.7±3.8 Mg/ha) with bark beetle damaged stands containing 82% of the total CWD biomass. In contrast, in the Temperate ecoregion, CWD comprised 20% of the regional aboveground woody store (277.5 ±5.4 Mg/ha) with 76% of total CWD biomass in undisturbed stands. Total C stores estimates in Coastal Alaska ranged between 1523.6 and 1892.8 Tg with the highest contribution from soils and the largest potential reductions in uncertainty related to the tree and soils C pools.

The impact of a large-scale spruce bark beetle (SBB) outbreak on aboveground dead wood C dynamics on the Kenai Peninsula was modeled utilizing data from the FIA program and CWD decomposition rate-constants from a chronosequence and decomposition-vectors analysis. Decomposition rate-constants from the chronosequence ranged between -0.015 yr^{-1} and -0.022 yr^{-1} for logs and -0.003 yr^{-1} and +0.002 yr^{-1} for snags. Decomposition rate-constants from the

decomposition-vectors ranged between -0.045 yr^{-1} and +0.003 yr^{-1} among decomposition phases and -0.048 yr^{-1} and +0.006 yr^{-1} among decay classes. Relative to log generating disturbances those creating snags delayed C flux from CWD to the atmosphere, produced a smaller magnitude C flux, and had the potential to store 10% to 66% more C in a disturbed system over time.

The effect of several management strategies ranging from "leave-as-is" to "salvage-and-utilization" on C stores and emissions following SBB outbreak on Kenai Peninsula, Alaska was evaluated. A forest with immediate post-disturbance regeneration reached pre-disturbance C stores faster than one with delayed regeneration. Lack of regeneration, representing a loss of tree cover on the disturbed portion of the landscape, caused a permanent decrease in wood C stores. Among the "salvage-and-utilization" scenarios considered, biomass fuel production with substitution for fossil fuels created the largest long-term C storage assuming the substitution was permanent. Given that reduction in near-term emissions may be a more robust strategy than long-term ones, the "leave-as-is" scenarios may represent the most feasible way to mitigate global climate change following disturbance.

The Impact of Disturbance on Carbon Stores and Dynamics in Forests of Coastal Alaska

by
Mikhail A. Yatskov

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented March 1, 2016
Commencement June 2016

Doctor of Philosophy thesis of <u>Mikhail A. Yatskov</u> presented on <u>March 1, 2016</u>.

APPROVED:

_____

Major Professor, representing Forest Science

_____

Head of the Department of Forest Ecosystems and Society

_____

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

_____

Mikhail A. Yatskov, Author

ACKNOWLEDGEMENTS

The volume of this thesis would be insufficient to thank all the people who were part of my life over the course of nearly a decade that I have been working on this project. To list them all individually and express my gratitude on pages of this document would be a daunting task. I value your friendship, your support, your encouragement, and your belief in me. Each of you individually, in your own way, helped me persevere in the difficult times and reach the successful completion of this endeavor. My deepest bow and warmest thanks to all of you!!!

I express my deep gratitude to my graduate committee members. This work would not be possible without your patience, support, and guidance. Thanks to my major professor Dr. Mark Harmon who I have had a pleasure to work with for over 20 years. Under no circumstances this theses would have been finished if it wasn't for your subtle but persistent leadership. If I ever work with the students, I would like to adopt your ways of setting a sparkle of knowledge and love for the science in them. Thanks to Dr. Olga Krankina who served part of the term as my major professor. You have built my character like nobody else. There is no obstacle that could stop me or a problem that could discourage me now. Thanks to Dr. Tara Barrett, whose active involvement throughout all the stages of FIA data compilation, analysis, and manuscript writing secured the success of this project. Your readiness to help and timely and thoughtful responses to my requests were invaluable. Thanks to Dr. Tom Spies whose constructive criticism helped me prepare for the preliminary re-examination. Thank you for your thorough manuscript revisions. Thanks to Dr. Staci Simonich who served as my graduate school representative. Your gentle approach after my failure of the preliminary exam put me into the right mindset that led to the

successful re-examination and completion of the project. Thank you all for playing a key role in my becoming a scientist. I am forever grateful to you for being my mentors.

I would like to thank the former and current faculty, staff, and fellow-students of the OSU Forestry Department for their support, encouragement, and companionship. Thanks to Kimberly Wallin who severed as a departmental graduate representative at the early stages of my PhD work. If it was not for your initial encouragement to start a PhD program, I would most likely passed this opportunity and would never stepped outside my comfort zone. I would like to thank Dr. Lisa Ganio, Manuela Huso, and Ariel Muldoon for their support and statistical advice. Thanks to Drs. Temesgen Hailemariam, John Bailey, Klaus Puettmann, David Shaw, Richard Warring, Kermit Cromack, Bruce Shindler, Lech Muszyński, Darrell Ross, Ed Jensen and John Sessions for expressing genuine interest in my progress as a student and forestry professional. Thanks to my friend, Dr. Harold Zald who was a constant source of advice and optimism, as well as a companion in philosophical, scientific, and social discussions. Your positive attitudes, thoughtful recommendations, knowledge of ecosystem ecology and FIA procedures, ability to think outside the box and see far into the future inspired me to continue my project when I ran out of steam. Thanks to my friend Leif Mortenson for sharing with me the burden of the long hours spent in the computer lab and for being my walking companion and a partner in conversations. My thanks also go to Drs. Doug Maguire, Carlos Sierra, Alan Tepley, Jenny Dauer, James Johnston, Garrett Meigs, Chris Dunn, Claire Phillips, Tara Hudiburg, Dirk Pflugmacher, and Bianca Eskelson for their support and help with preliminary exam preparations.

CONTRIBUTION OF AUTHORS

Dr. Mark Harmon was involved in the design, data and sample collection, data analysis, and writing of this manuscript in its entirety, provided tools and laboratory space for sample processing and data analysis, and was valuable source of guidance, information, and assistance in every aspect of this study. Dr. Olga Krankina was actively involved in the design, data analysis, results interpretation, and writing of Chapter 2, provided revisions for Chapters 3 and 4, and was a constant source of valuable advice and information throughout this study. Dr. Tara Barrett provided invaluable assistance at every stage of Chapter 2, was constant source of advice on data analysis, compilation, results interpretation, and manuscript writing, and provided revisions for Chapters 3 and 4. Kevin Dobelbower provided assistance and advice with data analysis and compilation for Chapter 2. Dr. Andy Gray provided assistance and advice with data analysis and results interpretation for Chapter 2. Becky Fasth conducted sample processing, data management, analysis, and compilation for Chapter 3. Lori Trummer was involved in securing project funding, assisting with organization of the field season, and helping with the field data and sample collection for Chapter 3. Jay Sexton led the data and sample collection and processing for Chapter 3. Toni Hoyman assisted with data and sample collection and processing for Chapter 3. Chana Dudoit assisted with data and sample collection and processing for Chapter 3. Thomas Heutte provided data and valuable information for Chapter 4 and was actively involved in manuscript writing.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF TABLES

The Impact of Disturbance on Carbon Stores and Dynamics in Forests of Coastal Alaska

CHAPTER 1 -- INTRODUCTION

Carbon dioxide (CO_2) is a greenhouse gas (GHG) whose presence in Earth' atmosphere created climatic conditions favoring life on the planet. However, increased concentrations of CO_2 in the atmosphere caused by human activities over the course of the past 250 years, that include land use change, fossil fuel burning, and cement production, have led to climatic changes manifested in land and ocean surface temperature increase by 0.85ºC and sea level increase by 19 cm relative to preindustrial times (Pachauri et al. 2014). Global climate change will lead to further alterations in temperature, precipitation and their extremes (Karl et al. 1996), as well as shifts in timing, longevity, and intensity of dry and wet seasons (McCarthy 2001) that have been linked to changes in disturbance occurrence and regime (Dale et al. 2001, Soja et al. 2007).

Disturbances play an important role in forest dynamics and succession (Christensen 1989, Pickett and White 1985), influence forest ecosystems structure and function, and affect ecosystem carbon (C) balance. Their role varies dramatically across the landscape (Foster and Boose 1992) and depends on disturbance type, magnitude, frequency and severity. Based on a combination of these four factors, forests could serve as C sinks, C sources, or be C neutral (Smithwick et al. 2002). Disturbances reorganize forests, reducing the live and increasing dead matter, hence altering the C balance.

Forests play a key role in the C cycle (Dixon et al. 1994), comprising much of the terrestrial C stores with the amounts being dependent on natural and anthropogenic disturbance regime. The

extent, frequency, and severity of multiple disturbances including fires (Flannigan et al. 2000, Stocks at al. 2002, Westerling et al. 2006), bark beetle outbreaks (Williams and Liebhold 2002, Carroll et al. 2003, Werner at al. 2006, Bentz et al. 2010, Cudmore et al. 2010), drought events (Allen et al. 2010), and others (Dale et al. 2001) have been on the rise. These disturbances are likely to continue to cause widespread tree mortality across forested landscapes controlling the ratio between live and dead biomass pools (Franklin et al. 2002, Krankina et al. 2005).

Live and dead biomass pools within forest ecosystems represent two major interrelated components, where live biomass includes all parts of live trees as well as other plants, and dead biomass or woody detritus includes standing and downed boles, dead roots, dead branches, and stumps. Both components serve a number of functions in forests ranging from storage and cycling of energy (Odum 1968), C (Pregitzer and Euskirchen 2004), water (Waring and Schlesinger 1985, Waring and Running 2010, Chapin et al. 2011), and nutrients (Odum 1969, Vitousek and Reiners 1975); soil formation (McFee and Stone 1966) and stabilization (Oades 1993, Bronick and Lal 2005); wildlife habitat (Hansen 1991, Freedman et al. 1996); and seedbed for plants (Harmon and Franklin 1989). The size of these two pools is controlled by the factors influencing inputs and outputs (Olson 1963). Live pool size depends on biomass production controlled by tree species composition, site productivity, length of growing season, regeneration rate following disturbance, tree mortality rate and the disturbance regime (i.e., type, magnitude, frequency, and severity). Dead pool size depends on the input from the live pool, associated with disturbance and mortality, and on the decomposition rate controlled by the quality of substrate, type of decomposing organisms, and substrate moisture and temperature (Harmon et al. 1986,

Harmon et al. 2011a). The C in live and dead pools comprises about 50% of the dry biomass (Barrett and Christensen 2011).

In recent decades, high latitude forests have been identified as hotspots of the global climate change (Stocks et al. 1998, Giorgi 2006). The climatic changes taking place in high latitudes impact stores and overall C dynamics (Goetz et al. 2007). Coastal Alaska is a vast region in the northern latitudes of the northern hemisphere with forest area of 6.2 million ha (Barrett and Christensen 2011) which has been of interest due to large C stores in live and dead biomass as well as in soils (Birdsey and Heath 1995, Heath et al. 2011, Goodale et al. 2002). These forests contain considerable aboveground biomass (Bormann and Sidle 1990, Leighty et al. 2006, Barrett and Christensen 2011) and substantial amount of soil organic matter (SOM) (Leighty et al. 2006, Johnson et al. 2011, Mishra and Riley 2012) and thus represent a potentially large C pool. Their future role in C cycling depends on a legacy of past disturbances, current conditions, as well as future climate, disturbance, and management regimes.

Coastal Alaska is characterized by an array of disturbances, both natural and anthropogenic. Disturbance types range from small-scale gap dynamics with short return interval and low severity, where each gap is formed through mortality of three or fewer overstory trees (Nowacki and Kramer 1998), characteristic to southeast Alaska, to large-scale spruce bark beetle outbreaks (Wittwer 2004, USDA 2005, Werner et al. 2006) with longer return interval (Berg et al. 2006) and high spruce mortality (Werner et al. 2006), characteristic of the Kenai Peninsula. Cascading disturbances where one type of disturbance alters conditions for another type also take place

(Holsten et al. 2000, Ross et al. 2001, Flint and Haynes 2006). Disturbance types differ in the legacy they leave behind, from severe windthrows where most of the live biomass is transferred to the CWD pool and left on site to clearcuts where most of the aboveground biomass is removed from the site for processing (Alaback 1982, Veblen and Alaback 1996). In temperate and boreal forests CWD serves as a long-term C storage (Spies et al. 1988, Smithwick et al. 2002, Janisch and Harmon 2002). The absolute amounts of CWD (Spies et al. 1988, Smithwick et al. 2002) vary by forest and disturbance types and successional stages of stand development (Janisch and Harmon 2002). The large-scale mortality associated with frequent and severe disturbances could temporarily increase CWD stores which combined with elevated decomposition rates resulting from warmer climate could lead to increased CO_2 fluxes to the atmosphere.

Forest management strategies provide avenues for mitigating global climate change through curbing CO_2 emissions and storing C in forest sector (Brown et al. 1995). Salvage and utilization of CWD created by disturbance could store C long-term in forest products (Kurz et al. 1992) or prevent fossil fuels C from being used via production and substitution by biomass fuels (Mitchell et al. 2012).

This study examines how C stores and dynamics in the forest ecosystems of Coastal Alaska are controlled by the disturbances and evaluates C storage management options in forest sector following disturbances. In Chapter 2 we examine the current above- (live tree, snag, log, FWD, and understory vegetation) and belowground (live and dead roots and soils) biomass and C stores in the forests of Coastal Alaska, assess uncertainty in estimates of these stores and evaluate

impact of different types of disturbance on three major aboveground (live, snag, and log) biomass pools. In Chapter 3 we investigate the effects of large-scale disturbance on CWD dynamics in spruce-dominated forests of Kenai Peninsula, Alaska. We use a chronosequence approach (Harmon et al. 1987, Harmon and Sexton 1996) to determine and compare decomposition rate-constants of snags and logs, a decomposition-vectors analysis (Harmon et al. 2000) to examine and compare early, intermediate, and late stages in terms of CWD decomposition rates, and utilize a simulation model to examine the effect on CWD dynamics of disturbances caused by bark beetles versus windthrow. In Chapter 4 we estimate the changes in tree bole-related C on the Kenai Peninsula following a major spruce bark beetle outbreak. Using model simulations, we evaluate the effect of several management strategies on C stores ranging from a "leave-as-is" scenario to salvage logging. Chapter 5 summarizes the findings of this study and makes recommendations.

CHAPTER 2 -- CARBON POOLS AND BIOMASS STORES IN THE FORESTS OF COASTAL ALASKA: UNCERTAINTY OF ESTIMATES AND IMPACT OF DISTURBANCE

Mikhail A. Yatskov, Mark E. Harmon, Olga N. Krankina, Tara M. Barrett, Kevin R. Dobelbower, and Andrew N. Gray

ABSTRACT

Forests provide significant long-term carbon (C) storage but have potential to increase future C emissions with a changing climate. Aboveground biomass, C stores, and the effect of disturbance were examined using forest inventory data collected across all ownerships on 6.2 million ha in Coastal Alaska. We modelled six C pools using empirical data, estimated two others using the literature, and quantified estimate uncertainty. The average aboveground live (218.9±4.6 Mg/ha) and log (28.1±1.8 Mg/ha) biomass in the Temperate ecoregion were among the lowest in the Pacific Northwest, whereas snag biomass (30.5±1.0 Mg/ha) was among the highest. In the Boreal ecoregion, coarse woody debris (CWD) biomass comprised almost 50% of the regional average (76.7±3.8 Mg/ha) with bark beetle damaged stands containing 82% of the total CWD biomass. In contrast, in the Temperate ecoregion, CWD comprised 20% of the regional aboveground woody average (277.5 ±5.4 Mg/ha) with 76% of total CWD biomass in undisturbed stands. Total C stores estimates in Coastal Alaska ranged between 1523.6 and 1892.8 Tg with the highest contribution from soils. The largest potential reductions in uncertainty are related to the tree and soils C pools. Disturbance determines total biomass amounts in the system and controls the ratio between live and dead biomass pools and thus has the ability to shift forest stands into C source to the atmosphere.

INTRODUCTION

Biomass in forest ecosystems has been of interest, initially as a source of timber and fuel but more recently as a potentially significant store of C (Dixon et al. 1994, Harmon et al. 2001, Smithwick et al. 2002, Goodale et al. 2002). The latter is associated with the fact that live (Whittaker and Likens 1973, Woodwell et al. 1978) and dead (McFee and Stone 1966, Triska and Cromack 1980) woody plant tissues retain C long-term, thus preventing it from re-entering atmosphere in the form of carbon dioxide (CO_2). CO_2 is a greenhouse gas (GHG), and its increased concentration in the atmosphere has been linked to the rise in global temperatures (Arrhenius 1896, Post et al. 1990, IPCC 2013) and other phenomena related to global climate change (IPCC 2013). Use of forests as C sinks is a possible way to reduce atmospheric CO_2 (Iverson et al. 1993, Marland 2000, IPCC 2001, Millar et al. 2007).

Live and dead biomass pools within forest ecosystems represent two major interrelated components, where live biomass includes all parts of live trees as well as other plants, and dead biomass or woody detritus includes standing and downed boles, dead roots, dead branches, and stumps. Both components serve a number of functions in forests ranging from storage and cycling of energy (Odum 1968), C (Pregitzer and Euskirchen 2004), water (Waring and Schlesinger 1985, Waring and Running 2010, Chapin et al. 2011), and nutrients (Odum 1969, Vitousek and Reiners 1975); soil formation (McFee and Stone 1966) and stabilization (Oades 1993, Bronick and Lal 2005); wildlife habitat (Hansen 1991, Freedman et al. 1996); and seedbed for plants (Harmon and Franklin 1989). The size of these two pools is controlled by the factors influencing inputs and outputs (Olson 1963). Live pool size depends on biomass production

controlled by tree species composition, site productivity, length of growing season, regeneration rate following disturbance, tree mortality rate and the disturbance regime (i.e., type, magnitude, frequency, and severity). Dead pool size depends on the input from the live pool, associated with disturbance and mortality, and on the decomposition rate controlled by the quality of substrate, type of decomposing organisms, and substrate moisture and temperature (Harmon et al. 1986, Harmon et al. 2011a). Among these factors disturbance is one of the most important in controlling the ratio between live and dead biomass pools (Franklin et al. 2002, Krankina et al. 2005), as disturbances, particularly those characterized by high severity, transfer large amounts of live biomass into dead biomass thus shifting forest stands into source phase.

Disturbances play an important role in forest dynamics and succession (Christensen 1989, Pickett and White 1985), influence forest ecosystems structure and function, and affect ecosystem C balance. Disturbances are characterized by the disturbance regime, which is governed by state factors such as climate, topography, parent material, potential biota, and time (Chapin et al. 2002) and affected by ecosystem processes, such as primary production, decomposition, and trophic interactions. Their role varies dramatically across the landscape (Foster and Boose 1992) and depends on disturbance type, magnitude, frequency and severity. Based on changes in the relationship among these four factors, forests could become C sinks, C sources, or C neutral (Smithwick et al. 2002). Climate change has been linked to increased disturbance magnitude, frequency, and severity especially in forests in northern latitudes (Stocks at al. 2002, Werner at al. 2006, Soja et al. 2007). Therefore, feedback mechanisms (Houghton 1995, Schimel 1995, Bonan 2008) acting thorough disturbance (Dixon and Krankina 1993,

Flannigan et al. 1998, Kurz et al. 2008) may escalate the CO_2 flux to the atmosphere from forest ecosystems thus increasing the rate of global climate change.

In recent decades, high latitude forests have been identified as hotspots of the global climate change (Stocks et al. 1998, Giorgi 2006). The climatic changes taking place in high latitudes impact stores and overall C dynamics (Goetz et al. 2007). Coastal Alaska is a vast region in the northern latitudes of the northern hemisphere with forest area of 6.2 million ha (Barrett and Christensen 2011) which has been of interest due to large C stores in live and dead biomass and in soils (Birdsey and Heath 1995, Heath et al. 2011, Goodale et al. 2002). These forests contain considerable aboveground biomass (Bormann and Sidle 1990, Leighty et al. 2006, Barrett and Christensen 2011) and substantial amount of soil organic matter (SOM) (Leighty et al. 2006, Johnson et al. 2011, Mishra and Riley 2012) and thus represent a potentially large C store. Their future role in C cycling depends on a legacy of past disturbances, current conditions, as well as future climate, disturbance, and management regimes.

Coastal Alaska is characterized by an array of disturbances, both natural and anthropogenic. Disturbance types range from small-scale gap dynamics with short return interval and low severity, where each gap is formed through mortality of three or fewer overstory trees (Nowacki and Kramer 1998), characteristic to southeast Alaska, to large-scale spruce bark beetle outbreaks (Wittwer 2004, USDA 2005, Werner et al. 2006) with longer return interval (Berg et al. 2006) and high spruce mortality (Werner et al. 2006), characteristic of Kenai Peninsula. Cascading disturbances where one type of disturbance alters conditions for another type also take place

(Holsten et al. 2000, Ross et al. 2001, Flint and Haynes 2006). Disturbance types differ in the legacy they leave behind, from severe windthrows where most of the live biomass is transferred to the dead biomass pool and left on site to clearcuts where most of the aboveground biomass is removed from the site for processing (Alaback 1982, Veblen and Alaback 1996). Interactions among the disturbances, local growing conditions, and climatic factors within Coastal Alaska can lead to complex ecosystem dynamics (Nowacki and Kramer 1998, Ott and Juday 2002).

The objectives in this study were to examine the current above- (live tree, snag, log, FWD, and understory vegetation) and belowground (live and dead roots and soils) biomass and C stores in the forests of Coastal Alaska, assess uncertainty in estimates of these stores and examine impact of different types of disturbance on three major live and dead aboveground biomass pools. We identified eight C pools in the forest ecosystems of Coastal Alaska, modelled six of these pools from Forest Inventory and Analysis (FIA) data, and used literature data to estimate the size of the remaining two C pools. We conducted uncertainty analysis of the C pools to understand major contributors and recognize ways of reducing uncertainty in C estimates. The main four questions of the study were: 1) how biomass was distributed by ecoregion, forest type, and disturbance type in Coastal Alaska; 2) to what degree does disturbance affect live and dead aboveground biomass; 3) how total C stores were distributed among eight C pools; and 4) what is the size and source of uncertainty associated with C pool estimates? To answer these questions we used data collected in Coastal Alaska by the FIA project over the period between 1995 and 2003.

METHODS

Study area

The field measurements used in this study were collected by the FIA program in the Coastal

Alaska region, which includes two ecological provinces: Coastal Temperate Rainforest and

Boreal Forest (hereafter referred to as the Temperate and the Boreal ecoregions) (Figure 2.1).

The Temperate ecoregion consists of Kodiak Island, the Gulf of Alaska Coast, and the Alexander

Archipelago (Nowacki et al. 2002). It is a mountainous region with thousands of densely forested

islands, glacially carved fjords, long U-shaped river valleys with steep deeply incised sidewalls,

estuaries, tidal flats and wide floodplains (Murphy and Witten 2006). The climate is

characterized by cool summers with abundant precipitation, frequent fog and low clouds, and

mild winters (Farr and Hard 1987). Snow is usually temporary at lower elevations in the southern

part of the coast, but accumulates along the northern coast. Mean annual temperature in the

Temperate ecoregion (Southeast and South Coast) for the period between 1995 and 2003 was

5ºC (NOAA 2014). Annual precipitation was highly variable locally due to differences in terrain

and over the period between 1995 and 2003 was as light as 418 mm or as heavy as 6,753 mm

(NOAA 2014). Extended periods without precipitation are rare. Temperate rain forests of

western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce (*Picea sitchensis* (Bong.)

Carr.) cover the shorelines and mountain slopes where soil drainage allows. Open and forested

wetlands occur on poorly drained soils, especially on compacted glacial tills, marine terraces,

and gentle slopes. These poorly drained low productivity sites support forest stands represented

by mixture of western hemlock, mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.), Sitka

spruce, lodgepole pine (*Pinus contorta* Dougl. ex. Loud.), Alaska yellow-cedar (*Chamaecyparis*

nootkatensis (D. Don) Spach), and western redcedar (*Thuja plicata* Donn ex D. Don.). Mountain

hemlock dominates higher elevations. On upper slopes forests progressively give way to

shrublands and alpine tundra (Nowacki et al., 2002).

The natural disturbance regime in the Temperate ecoregion is characterized mainly by high

frequency, low-intensity disturbance events creating stands with complex multi-aged multi-story

structure (Brady and Hanley 1984, Nowacki and Kramer 1998, Deal 2007). A variety of natural

disturbance agents shape these coastal forests. Occasional severe fall winds of hurricane force

(Harris and Farr 1974) along with ice storms cause blowdown of various sizes. Root disease

when combined with wind represents a common causal agent for the blowdown. High

precipitation, winter snow accumulation, and steep terrain lead to landslides and avalanches.

Floods, insect and disease outbreaks, and animal browsing are also present (Harris and Farr

1974, Rogers 1996). The mortality associated with the spruce bark beetle outbreaks can be

significant. For example, the outbreak of the 1940s resulted in mortality of 0.08 million cubic

meters of timber (Hard 1974), whereas outbreak of 1950s killed 0.004 million cubic meters of

timber (Zogas and Holsten 2002). Yellow cedar decline, a disturbance unique to southeast

Alaska, where decline-related tree mortality has been observed for the past 130 years (Hennon et

al. 1990), has affected over 0.2 million ha of forest (Hennon and Shaw 1997, USDA 2010).

Wildfires are rare (Harris et al. 1974). Some of these disturbance agents, such as grazing insects

(Hard 1974) and non-aggressive diseases and parasitic plants (Laurent 1974) often lead only to a

growth decline, while others, such as large-scale wind disturbance events (Harris and Farr 1974),

spruce bark beetle outbreaks (Werner et al. 2006), or rare fires (Potkin 1997) cause large scale tree mortality.

Timber harvest is the main anthropogenic disturbance by extent and severity in the Temperate ecoregion (Veblen and Alaback 1996, Barbour 2005). Partial harvest was common from the 1800s to 1950 (Deal 2007). Cutting intensity varied within and among stands ranging from 26% to 96% of the original basal area (Deal et al. 2010). The large-scale timber operations using clear-cutting became a common practice in coastal forests of southeast Alaska in the early 1950s (Harris and Farr 1974) with nearly 262.6 thousand ha of old-growth forest on all ownerships in southeast Alaska clearcut harvested over the next 50 years (Barbour 2005). Logging on an industrial scale peaked in the early 1990s (Veblen and Alaback 1996), and harvest levels in coastal Alaska decreased from 5.3 million cubic meters in the mid-1990s to 1.9 million cubic meters in 2001 (Campbell et al. 2004, 2005). Most of the harvest decline in Alaska has occurred on national forest ownership, resulting in an increasing proportion of harvest from private lands (Brackley et al. 2009). By 2005 the Tongass National Forest (NF) accounted for 24 percent of the 1.1 million cubic meters annual harvest volume in southeast Alaska (Halbrook et al. 2009), although the national forest has 83 percent of timberland in southeast Alaska (van Hees 2003).

The Boreal ecoregion is represented by Cook Inlet Basin on the western side of the Kenai Peninsula (Figure 2.1). It is a lowland covered with numerous lakes, ponds, and wetlands. The climate combines features of maritime and continental climates with moderate fluctuations of seasonal temperature and abundant precipitation. Mean annual temperature in the Cook Inlet for

the period between 1995 and 2003 was 2ºC (NOAA 2014). Precipitation over the period between

1995 and 2003 ranged between 262 mm and 2,516 mm depending on location and distance from

the coast (NOAA 2014). Wet organic soils support black spruce (*Picea mariana* (Mill.) B. S. P.)

forests and woodlands on flat to gently-sloping terrain. Mixed forests of white spruce (*Picea*

glauca (Moench) Voss), Sitka spruce, and Lutz spruce (*Picea X lutzii* Little), a hybrid between

white and Sitka spruce, trembling aspen (*Populus tremuloides* Michx.), and paper birch (*Betula*

papyrifera Marsh.) grow on better-drained more productive sites on hills and knolls. These

forests transition into black cottonwood (*Populus balsamifera* ssp. *trichocarpa* L.) stands or

alder-willow (*Alnus-Salix*) shrub communities in riparian areas along the river corridors and

around wetlands (Potkin 1997, Van Pattern 2000).

Main natural disturbances in the Boreal ecoregion include catastrophic fires (Potkin 1997, Berg

et al. 2006, Anderson et al. 2006) and spruce bark beetle outbreaks (Holsten et al. 2000), which

are extensive in south-central Alaska. For example, 100 thousand ha of white spruce forest on

the Kenai peninsula were infested annually by spruce bark beetles between 1976 and 1981

(Werner and Holsten 1983), and the outbreak that took place between 1989 and 2004 caused

extensive spruce mortality over 1.2 million ha of forest in south-central Alaska (USDA 2005,

Berg et al. 2006).

Anthropogenic disturbance (timber harvest) in the Boreal ecoregion began with sporadic harvest

of accessible old-growth spruce stands in the mid-1700s (Van Pattern 2000); in recent decades,

harvest has included more extensive clear felling and salvage logging in spruce stands affected

by beetle attacks (Flint 2006) with individual harvest units ranging from ~16 ha to over 400 ha and often being adjoined, creating continuous patches of disturbance (Van Pattern 2000).

Inventory sampling and plot design

Between 1995 and 2003, an equal-probability sample of field plots was established throughout the forests of southeast and south-central Alaska by the U.S. Forest Service Pacific Northwest Region's FIA program. The sampling area consisted of 4.8 million ha of accessible forest land across all ownerships and forest types. The forest land designated as wilderness study area within the Chugach and Tongass national forests as well as the entire Glacier Bay National Park comprising together 1.4 million ha were excluded from the inventory (Barrett and Christensen 2011, Figure 2.1). The measurements and observations used for estimating biomass were collected in field-visited plots. For the purposes of the inventory, forest land was defined as land currently having at least 10% tree crown cover by trees of any size, including cut, burned over, or flooded areas with the evidence of formerly having at least 10% tree cover. This definition excluded lands that have never supported forests and lands formerly forested on which current land use prohibits establishment of forests (USDA 2000).

Forest inventory plots included four 7.3-meter fixed-radius subplots located in a pattern where subplot two was 36.6 meters north (360º magnetic) of subplot one and subplots 3 and 4 were 36.6 meters from subplot one at an azimuth of 120º and 240º, respectively (Figure 2.2). Each plot included at least one forested stand (referred to as "polygon" in FIA literature prior to 2004 and "condition class" later on) represented by an area no less than 0.4 ha and continuous width of at

least 36.6 m. Such an area was characterized by the unique combination of Forest Type (assigned to a species representing a majority of stocking in a stand) or Vegetation Type (where forest was absent), Forest Density Class (percent ground area covered by tree crowns), Forest Stand Size (stand descriptor indicating which size-class of trees constituted the majority of stocking in the stand), and Forest Stand Origin (indication whether the forest stand has been artificially regenerated/manipulated or not) (USDA 2003). Among these stand characteristics, Forest Type (Table 2.1) was at the top of the hierarchy list due to its importance in stand delineation. Stocking was defined by FIA as the relative degree of occupancy of land by trees (USDA 2014b).

Disturbance types and characteristics for each stand were derived from field observations. Disturbance included infestation level for bark beetle outbreak, blowdown condition, root disease severity, clearcut (areas ≥2 ha where >75% of the trees have been cut), partial harvest (areas other than clearcuts where 25% to 75% of trees have been cut or damaged by tree removal), fire, flooding, earth movement/avalanche (for areas >0.3 ha), and others. The lack of disturbance in the stand was also recorded. Such stands (hereafter referred to as undisturbed) may have experienced disturbance but were not allocated to disturbed stands based on disturbance size or severity thresholds. Observed tree damage or mortality from bark beetles (*Dendroctonus rufipennis* or *Ips* spp.) was recorded under infestation level. Sixty percent of spruce trees attacked was used as a threshold between high and moderate severity of beetle attack. Blowdown was recorded only when extensive evidence of broken or uprooted trees in an area > 1 ha in or around the subplot was encountered. The levels of root disease ranged from

minor to severe (recorded when disease was obvious on exposed roots, root disease conks were observed growing near ground or on roots, or root disease was observed on broken boles or other exposed wood). Occurrence of clearcuts and selective cuts (partial harvest) was recorded.

The protocols for collecting disturbance data were slightly different for southeast and south-central Alaska. In southeast Alaska the disturbance (in areas subjected exclusively to clearcutting/logging and blowdown) was recorded when it affected polygons >0.4 hectares in size in and around the subplot center. The time limit for the disturbance was only specified for clearcut areas (up to 25 years). The disturbance was coded with a single code for areas being clearcut/logged or blown down with the type of disturbance being recorded in notes. Other types of disturbance (fire, bark beetle, logging damage reflecting harvest activities other than clearcutting, and others) could only be determined indirectly from tree damage codes. In south-central Alaska, to be recorded the area affected by disturbance had to be ≥1 ha and contain the subplot center. The disturbance protocol for south-central Alaska was focused only on disturbances that occurred within 10 years prior to the date of the visit.

The stand age was in general determined from 3 trees that were aged by counting annual rings on the core extracted with the increment borer. The trees selected for this purpose were representative of the age of each stand characterized by unique combination of forest type, stand size class, and other stand delineating variables (USDA 2003).

Live tree and snag biomass estimation

Field procedures

Live trees and snags with a diameter at breast height (d.b.h. – diameter at 1.37 m from the

ground level on the uphill side or from the root collar) of at least 12.5 cm were measured in 7.3-

meter fixed radius subplots (Figure 2.2). Live saplings (trees with the d.b.h. greater or equal to

2.5 cm and less than 12.5 cm) were measured in 2.0-meter fixed radius microplots.

Measurements and observations used in this study include tree species, d.b.h., total height (tree

or snag vertical length from the tree base to the tip of existing or reconstructed top), actual height

(tree or snag vertical length from the tree base to the break point), and snag deterioration stage

(decay class based on a 5-decay class system). Snags that were severed from the base or intact

and leaning less than 15° from the horizontal plane were considered logs (USDA 2000).

Live tree and snag biomass calculations

Total aboveground live tree biomass included bole wood, bark, branches, twigs and foliage. Live

tally trees and snags with d.b.h. $\geq$ 12.5 cm and live tally saplings with d.b.h. $\geq$ 2.54 cm were

included in biomass calculations, yielding 67,913 individual tree records. Biomass calculations

for each individual live tree, sapling, and snag were based on published species-specific direct

biomass equations (see Appendix 1, p. 117 in Barrett and Christensen (2011) for a full list of

citations).

Unlike earlier biomass estimates reported in Andersen (2011), our biomass estimates did account

for broken tops on live trees and snags and reduced density of snags due to decay. When trees or

snags had missing tops > 1.2 meters (4 feet) long, their biomass was calculated as a difference

between the intact aboveground tree biomass and the biomass of broken portion. To account for

reduced wood density in snags, we used field records of decay classes assigned to snags and

average density reduction factors for standing dead trees by species group

(hardwoods/softwoods) (Table 6, pg. 12 in Harmon et al. 2011b). Andersen (2011) ran snag

biomass calculations omitting the biomass adjustments associated with broken tops and density

loss over time. To test the impact of methods used by Andersen (2011), we also ran biomass

calculations without adjustments for broken tops and density reduction.

Log biomass estimation

Field procedures

Down Woody Material (DWM) (hereafter termed as logs), is defined as dead boles, portions of

dead boles, and primary branches severed from their bases, and rooted boles with a lean angle

less than 15º from horizontal plane and the diameter greater or equal to 2.5 cm at the large end

and length of at least 1 m. Logs were measured on either one, two, or sometimes three forested

subplots (depending on a number of forest stands within plot perimeter) in each plot using three

11.28-meter transects (Figure 2.2). The tally included tree pieces if their central axis crossed the

transect line. For each tallied piece, tree species, diameter at the large end, diameter at the small

end, length, and decay class were recorded. When advanced decay prevented the identification of

tree species, log pieces were assigned to either undetermined conifers or undetermined

hardwoods. Complete absence of log pieces on any of the transects was also recorded (USDA

2000).

Log biomass calculations

The volume of each individual log piece was calculated using a conic-paraboloid formula (Fraver et al. 2007):

$$V_m = l/12 * (5*A_L + 5*A_S + 2*(A_L*A_S)^{1/2}), \text{ where} \qquad (1)$$

V_m is the individual log volume (m), A_L is the cross-sectional area at the large end (m^2), A_S is the cross-sectional area at the small end (m^2), and l is the log length (m).

Volume estimates for logs in Decay Class 5 (DC-5) were adjusted to account for their elliptical shape. Only a single diameter measurement (i.e., maximum diameter) was taken in the field at each log end during the log inventory. DC-5 log pieces, however, commonly have elliptical cross-section of the trunk and using only the maximum diameter in calculations would overestimate the biomass of DC-5 logs. For a more realistic biomass estimate we adjusted the DC-5 log volume calculations by determining the minimum diameter and utilizing both the maximum and the minimum diameters for calculations of log cross section area. For that purpose we used data from Harmon (2011, data sets TD12 and TD35) for DC-5 logs. We utilized 12,806 paired (max/min) diameter records to determine average min-to-max diameter ratios in 20 cm diameter classes from 1-20 to > 120 cm. Then, we tested these ratios for differences among each other (Tukey-Kramer comparison of the means per diameter class) and for being different from 1 (at alpha 0.05 – T-test of the means per diameter class). The results indicated that most of the mean ratios were statistically different from each other and all of them were statistically different

from 1. We applied the diameter reduction factors to all DC-5 log pieces to calculate minimum

base and top diameters from the maximum diameters collected in the field (Table A2.1).

The mass of each individual log piece was calculated using the volume and the specific wood

density depending on species and decay class (Harmon et al. 2005, 2008). For pieces allocated in

the field to unknown hardwood or unknown softwood categories, we determined wood density

for each of these categories as an average based on densities from Harmon et al. (2008) weighted

by the number of log pieces with known species and decay class within each of two categories in

our log dataset.

Mass of log per unit area was calculated for each subplot containing log data using a formula

from Waddell (2002):

$$M_{UA} = (\pi/2L) * \Sigma(M_L/l), \text{ where} \tag{2}$$

M_{UA} is the mass per unit area (Mg/ha), L is the total length of the transect line in the area being

sampled (m), M_L is the mass per individual log (Mg), and l is the individual log length (m)

Then, the average mass per unit area was calculated for each Plot/Stand combination as the mean

of log mass per unit area in subplots within the same stand.

Mean aboveground biomass and sampling error calculations

From the field data, live, snag, log, CWD (snag and log combined) biomass pools and total woody (live, snag, and log) biomass were calculated. Out of the total of 6,844 plots in the Coastal Alaska FIA sample, most of the "access-denied" plots (1,808) were in the Glacier Bay National Park and NF System wilderness, where plot access using helicopters was not allowed, therefore these plots were not included in the calculations. Among 5,036 remaining plots measured between 1995 and 2003, 149 were access denied or hazardous and were excluded from the analysis. Mean biomass per ha and sampling error as well as estimates of population totals and associated sampling errors were calculated using the standard national method for FIA of combined ratio estimation with post-stratification and the plot as the sampling unit (see Bechtold and Patterson 2005). The number of accessible (both measured and not measured) plots was 4,887, among them 1,969 plots were field-measured forested. For 65 forested plots the log measurements were not collected in the field due to time limitation, weather conditions, ground cover phenology, snow on plot, or other reasons. Therefore, 1,904 plots (represented by 2,093 stands) contained measurements on all three biomass pools (live tree, snags, and logs) and estimates of aboveground biomass were based on these plots. Among these, 269 plots were in the Boreal ecoregion and 1,635 plots in the Temperate ecoregion.

The results were aggregated by ecoregion (2), forest type (8), and disturbance type (8). To allow for sufficient precision and meaningful estimates of the means and standard errors, in addition to unique forest types within each ecoregion, we combined some forest types into groups (Table 2.1). White and Sitka spruce forest types in Boreal ecoregion were combined into

a Boreal Spruce category, given the small number of observations for Sitka spruce, the fact that both species occur in the same habitat, hybridize to produce viable offspring, Lutz spruce (Viereck and Little 1972, Harris 1990), are subject to the same main disturbance agents, and finally, both forest types within Boreal ecoregion have compatible amounts of live, snag, and log biomass. In both ecoregions we also calculated averages for all hardwood and softwood forest types in aggregate.

Live and dead biomass in plots where different types of disturbance were recorded was examined as well as the contribution of different disturbance types to the total regional CWD stores (Figures 2.3, 2.4). Out of 1,904 forested plots, disturbance was recorded in 434 plots. The majority of these (215 plots) were damaged by spruce bark beetle, including 123 plots of high and 96 of moderate severity. Because some plots had multiple disturbance types, the counts of disturbed plots were not additive. Fire damaged stands were represented by a sample of 9 plots (Table 2.2). The disturbance type "Other" included various disturbances such as root disease (10 plots in Boreal and 9 in Temperate ecoregion), flooding (8 plots in the Temperate ecoregion), yellow cedar decline (7 plots in the Temperate ecoregion), corridors created along railroads, power lines, gas lines, and canals (3 plots in the Boreal ecoregion), one drained plot in the Boreal ecoregion, and one land slide plot in the Temperate ecoregion. We combined these in "Other" category due to the fairly low number of observations.

Carbon pools and uncertainty estimates

We assessed the total C stores in the forests for the Boreal, the Temperate and both ecoregions combined. To convert aboveground biomass to C, we assumed 50% of the biomass was C (Barrett and Christensen 2011) and applied it to our field estimates of live tree, snag (standing woody material – SWM), and log (DWM) biomass pools. To get a more complete estimate of C stores we calculated five additional C pools in the forests of Coastal Alaska: Live Roots, Dead Roots, Fine Woody Debris (FWD), Understory Vegetation, and Soils. Three pools (Live Roots, Dead Roots, and FWD) were estimated as a proportion of either live (Live Tree) or dead (CWD) pools due to lack of FIA data for these pools. Two pools (Understory Vegetation and Soils) were based on published data because understory data collected by FIA were never converted to biomass or C and soils data were not collected by FIA in Alaska prior to 2004 and after 2009. To estimate the mean values and uncertainty in these modeled C pools we used the Stochastic Uncertainty Estimator – SUE (Goodman 2002). SUE utilizes the Monte Carlo method to simulate repeated sampling, in our case for 10,000 runs from which the means and the uncertainty were calculated.

We defined uncertainty as a lack of confidence in a single value (Harmon et al. 2007). Uncertainty was represented as a range of values calculated using three main approaches: utilizing standard error (SE) of the mean from the forest inventory data (Live Wood and CWD pools), using SUE (FWD and Live and Dead Roots pools), and utilizing SE of the mean from literature data (Understory Vegetation and Soils pools).

To estimate Live Roots C pool and associated uncertainty we used belowground-to-aboveground biomass ratios from the literature. We assumed Live Roots C pool to be on average 20% of aboveground Live Tree C pool with a range of 15 to 26% (Santantonio 1977, Cairns et al. 1997, Hamburg et al. 1997, Leighty et al. 2006). To estimate uncertainty in Live Roots C pool, we used a uniform distribution defined by the range of the below-to-aboveground C pools ratio. The uncertainty for this pool was 6.4% ranging from 13.6% to 26.4% expressed as a percent of Live Tree C pool.

The dead Roots C pool was calculated from the CWD C pool using a ratio of steady-state masses for these pools. We partitioned aboveground C pool among components given that CWD contains only the bole component. From the Alaska 2004-2012 FIA tree (aboveground live and standing dead) database we selected trees with the d.b.h. at least 2.5 cm (1 inch) and determined that on average aboveground biomass consists of roughly 70 percent tree boles and 30 percent live and dead branches and foliage. By applying 20% Live Root to aboveground Live Tree C ratio to these percentages, live root biomass was determined to be equivalent to ~14% of total live bole biomass. Finally, to estimate belowground portion of CWD (snags and logs) C pool we adjusted the live root component's proportion to account for differential decomposition of above and belowground dead tree portions (Harmon et al. 2004) which with time may lead to change in the initial proportion of roots (14%). To do this we assumed both pools (Dead Root and CWD) to be in a steady-state where the store equals to the ratio of input and the decomposition rate-constant (Olson 1963). This implies that for a given annual input (tree mortality) the ratio of steady-state stores is in inverse proportion to the ratio of decomposition rates in these stores; in

other words – if decomposition rate of dead roots is higher than decomposition rate of boles then the ratio of dead roots to CWD is lower than the ratio of live roots to live bole. We assumed the bole decomposition rate-constant to be 0.04 per year based on SUE calculations using a triangular distribution with a minimum 0.007 per year, a mode of 0.029 per year, and a maximum of 0.083 per year. The mode rate-constant was determined as an average of 23 species-specific decomposition rate-constants from prior decomposition studies in western Oregon, Washington and Alaska (HJA 2013, Janisch et al. 2005, Harmon et al. 2005, Busse 1994, Alban and Pastor 1993, Spies et al. 1988, Sollins et al. 1987, Fahey 1983, Graham 1982, Graham and Cromack 1982, Gosz 1980, Grier 1978). We estimated the root decomposition rate-constant to be 0.045 per year based on SUE calculations using triangular distribution with a minimum of 0.016 per year, a mode of 0.036 per year, and a maximum of 0.084 per year. The mode rate-constant was determined for roots between 0.5 cm and 15 cm in size as an average based on 18 species-specific decomposition rate-constants from prior decomposition studies in western Oregon, Washington, and Wyoming (Janisch et al. 2005, Chen et al. 2001, Yavitt and Fahey 1982). Based on this, the Dead Root-to-CWD steady-state C pools ratio equaled to 0.04/0.045*14% = 12.4% of CWD pool with an uncertainty of 5.2% and an interval of 7.2% to 17.6%.

Using a similar approach, FWD C pool was estimated based on the CWD C pool as a ratio of steady-state masses of the latter two pools. FWD C pool was assumed to consist of the branches resulting from whole tree mortality and excluded branches entering FWD pool as live or dead branches breaking off of live trees. Our method therefore underestimated the size of FWD C

pool, however a more complete estimate would have introduced many processes for which little information exists (e.g., branch pruning rates, rates live and dead branches break). Similarly to the Dead Root biomass ratio, we used 2004-2012 FIA tree database of trees >2.5 cm in d.b.h. and determined live and attached dead branch biomass to be ~25 % whereas bole biomass to be ~75% of aboveground woody tree biomass (stem, bark, and live and dead branches). Therefore for each tree that died 25% of the aboveground woody input would have been branches and 75% boles yielding a 0.33 branch-to-bole ratio. To estimate the FWD pool from the CWD pool, we adjusted the branch to bole ratio to account for the fact that FWD and CWD pools decompose at different rates (Harmon et al. 2004). As with Dead Roots, we assumed the bole decomposition rate-constant to be 0.04 per year. We assumed the branch (<0.6 cm to 8 cm in diameter) decomposition rate-constant to be 0.117 per year based on SUE calculations using triangular distribution with a minimum of 0.004 per year , a mode of 0.074 per year , and a maximum of 0.274 per year. The mode rate-constant was the average based on 80 data points (5 species, 5 size classes, three geographic locations, and two physical positions) rate-constants from studies conducted in western Oregon (Harmon 2010). The mean FWD-to-CWD C pools ratio was 0.04/0.117* (1/3) = 11.4% with an uncertainty of 4.8% and an interval of 6.6% and 16.2%.

Understory vegetation C pool and associated uncertainty were estimated based on understory biomass data from Alaback (1982) and the stand age distribution of the 2,093 forested stands from our study. From the 60 stands sampled by Alaback (1982) in southeast Alaska we determined average understory biomass and standard error in four stand age groups 1-100 years (41 stands), 101-200 (13 stands), 201-300 (2 stands), 300+ (4 stands). For biomass listed as <0.1

Mg/ha (15 out of 60 observations) we assumed a value of 0.1 Mg/ha. We determined the

distribution of 2,093 forested stands from our study by the same four age groups and used SUE

to calculate average understory biomass (later converted to C using a 1:2 C-to-biomass ratio)

weighted by the number of stands in an age group for the Temperate ecoregion. Since we were

unable to locate information on understory C pool in Boreal ecoregion, the same average was

applied in calculations of the Understory vegetation C pool for the Boreal ecoregion and both

ecoregions combined probably overestimating actual Boreal understory C stores. To estimate

uncertainty in Understory vegetation C pool, we used respective mean biomass and standard

error by four age classes (3.93 and 1.65 Mg/ha for class 1, 0.69 and 0.25 for class 2, 4.20 and

2.46 for class 3, and 0.60 and 0.06 for class 4).

As C stores in soils are not provided by FIA for Coastal Alaska we used mean stores reported by

Johnson et al. (2011), who utilized a variety of data sources to estimate soil carbon in Alaska.

For their data set of soil samples mean and standard error of organic carbon in the top 1 m of soil

was 250±13 Mg/ha in the Temperate rainforest ecoregion, whereas in the Alaska Range

Transition ecoregion (which the Boreal ecoregion is a part of), mean and standard error was

260±16 Mg/ha (Kristofer Johnson, personal communication 2013). To estimate regional total C

store in the upper 1m of soil and its uncertainty, we multiplied these ecoregion averages and SE

by the respective total areas of the Boreal and the Temperate ecoregions. We note these estimates

have several limitations: 1) the soil profile datasets used in Johnson et al. (2011) came from

various sources with differing sampling and lab analysis protocols; 2) the soil sampling design

from Johnson at al. (2011) differed from one used in FIA sampling, thus the soils estimates are

best combined with the FIA-based estimates at the ecoregional level and not the FIA plot level;

3) while the Coastal Rainforest province from Johnson et al. (2011) matched up well with our

Temperate ecoregion, our Boreal ecoregion represented by the western Kenai Peninsula is just a

part of the Alaska Range Transition ecoregion reported by Johnson et al. (2011). We

acknowledge these limitations but feel that providing some measure of uncertainty of the soils C

stores estimates is necessary in the total regional C stores assessment.

Overall total C stores within the ecoregions and for both ecoregions combined were calculated as

a sum of all eight component C pools listed above. We also determined the percentage each

component C pool contributed to the total C store. The uncertainty of our estimates was reflected

as the confidence interval with the lower and upper bounds calculated as plus/minus two

standard errors of the mean estimate.

RESULTS

Biomass distribution

As could have been expected given its lower productivity, the range and magnitude of total

(combined live and dead) aboveground biomass averages by forest types were lower in the

Boreal vs. the Temperate ecoregion (Table 2.1). The range of 43.2±4.3 Mg/ha to 136.7±18.9

Mg/ha associated with the Boreal ecoregion forest types was narrower than the range of

53.0±10.5 Mg/ha to 399.0±9.8 Mg/ha associated with the Temperate ecoregion forest types. Low

productivity forest types such as black spruce had similar total biomass stores in both ecoregions

with 43.2±4.3 Mg/ha in the Boreal and 53.0±10.5 Mg/ha in the Temperate ecoregions. At the

same time, the highest average biomass in the Boreal ecoregion with 136.7±18.9 Mg/ha found in black cottonwood forest type was almost 3 times lower than the highest average biomass in the Temperate ecoregion with 399.0±9.8 Mg/ha found in western hemlock forest type.

In contrast to total biomass stores, the CWD (snag and log) stores in forest types of the Boreal and the Temperate ecoregions had similar ranges (Table 2.1). At the low end, associated again with the black spruce forest type, the CWD stores in the Boreal ecoregion (8.3±1.7 Mg/ha) were similar to the stores in the Temperate ecoregion (7.1±4.0 Mg/ha). At the high end, the CWD stores found in Sitka spruce stands of the Boreal ecoregion (92.8±18.7 Mg/ha) were similar to the stores found in western hemlock stands of the Temperate ecoregion (86.9±3.1 Mg/ha).

The aggregation of the results at the level of species group dominance provided for a direct comparison of ecoregion influences. In hardwood-dominated stands snag biomass in the Boreal ecoregion with 20.7±3.4 Mg/ha was twice as large as that in the Temperate ecoregion with 9.7±2.2 Mg/ha. At the same time in softwood-dominated stands, snag biomass in the Boreal ecoregion with 25.1±3.4 Mg/ha was smaller than snag biomass in the Temperate ecoregion with 31.8±1.1 Mg/ha. Log biomass had a different pattern and was similar between ecoregions in hardwood-dominated stands, 12.4±1.5 Mg/ha in the Boreal vs. 13.9±2.5 Mg/ha in the Temperate ecoregions, whereas in the softwood-dominated stands log biomass in the Boreal (11.2±2.6 Mg/ha) was less than half of that in the Temperate ecoregion (29.0±1.9 Mg/ha).

Biomass stores in the Boreal ecoregion play a minor role in total aboveground woody biomass stores of Coastal Alaska forests because of smaller area and generally lower stores in the Boreal ecoregion in comparison to the Temperate ecoregion (Tables 2.1, 2.3). Regional live and log biomass stores in the Boreal ecoregion were just slightly higher than the estimation error of corresponding biomass pools in the Temperate ecoregion. However, for the snag biomass pool the contribution of the Boreal ecoregion is more substantial due to disturbance. At the regional scale, CWD biomass in the Boreal ecoregion represented almost 46 percent of total (live and dead) aboveground woody biomass, whereas in the Temperate ecoregion CWD biomass represented about 21 percent of total aboveground woody biomass. In the Boreal ecoregion, 67 percent of CWD biomass consisted of snags compared to 52 percent in the Temperate ecoregion.

Disturbance

CWD stores differed between disturbed and undisturbed stands and varied among disturbance types (Table 2.2). Undisturbed stands contained on average 49.3±1.6 Mg/ha of CWD; most of it in snag form (29.6±1.0 Mg/ha or 60% of CWD total). Among disturbed stands, the highest amount of CWD was in Blowdown stands (143.6±17.1 Mg/ha). This disturbance type was also associated with the highest total (live+ dead) biomass (413.5±37.8 Mg/ha). The reason for high biomass is that blowdown primarily affects mature and old-growth stands in the Tempearte ecoregion containing high biomass. In contrast, the lowest CWD and total biomass stores with 19.3±7.8 Mg/ha and 27.3±8.4 Mg/ha, respectively, were associated with stands disturbed by fire. Low stores are potentially the outcome of fires mainly affecting stands in the Boreal ecoregion with relatively low biomass.

Disturbance regardless of type and severity increased the proportion of CWD in total (live + dead) aboveground biomass in the forests of Alaska when compared to undisturbed stands (Table 2.2). In undisturbed stands the CWD stores amounted to 17.8% of total biomass. The proportion of CWD in stands with natural (non-harvest) disturbance varied between 26.3% and 71.3%. The proportion of CWD in stands disturbed by harvest (clearcut and partial harvest) equaled 77.5% and 65.7%, respectively because of large input into CWD pool and the removal of live biomass from site by logging.

Disturbance type and severity had a significant effect on CWD pool partitioning between the snag and log components (Figure 2.3). Among the naturally disturbed stands the proportion of logs was the highest following blowdown (over 3 times more logs than snags). High severity SBB outbreaks increased the proportion of snags (snag biomass ~4 times higher than log biomass), whereas in fire damaged stands the shares of log and snag components were roughly equal. After clearcut and partial harvest the CWD stores were significantly skewed towards log component (33 and 6 times higher than snag biomass, respectively). In contrast, in undisturbed stands snag biomass was 1.5 times higher than log biomass.

The impact of disturbance type was strong enough to influence the average amounts of logs and snags in forest types. Historic clearcutting in the Temperate ecoregion affected the Sitka spruce forest type more than others and the average mass of snags in this type (18.7 ± 2.1 Mg/ha) was less than half the mass of logs (41.0 ± 9.0 Mg/ha), whereas in other major productive softwood forest types (western hemlock and western redcedar) the mass of snags was either similar to the

mass of logs or higher (Table 2.1). Bark beetle outbreaks in the Boreal ecoregion significantly increased the proportion of snags in spruce-dominated forests with snag mass being 3-5 times larger than log mass.

The contribution of different disturbance types to the total regional CWD stores varied between ecoregions of Alaska (Figure 2.4). Stands with high severity spruce bark beetle damage represented the largest fraction (69%) in overall CWD stores in the Boreal ecoregion. Stands with moderate severity spruce bark beetle damage represented the second largest fraction (13%) in CWD stores in the Boreal ecoregion, making spruce bark beetle outbreaks the disturbance type with the highest regional impact on CWD stores in the Boreal ecoregion. In the Temperate ecoregion the majority of CWD (76%) was in undisturbed stands, whereas Clearcuts represented the largest fraction (10 percent) in overall CWD stores among disturbed stands followed by blowdown stands (6 percent).

Carbon pools and uncertainty estimates

The total C stores in forests were 183 Tg (lower and upper bounds of 157 Tg to 209 Tg, respectively) for the Boreal, 1,525 Tg (1,362 Tg to 1,688 Tg) for the Temperate, and 1,708 Tg (1,523 Tg to 1,893 Tg) for both ecoregions combined. Even with the soil component included, the maximum Boreal C store estimate was ~6.5 times smaller than the minimum estimated C store in the Temperate ecoregion (Table 2.5) indicating the minor role of Boreal C stores in the total Coastal Alaska C stores.

Relative effect of the pools fractions on total C stores differed as these fractions were orders of magnitude apart. Soils C stores represented the largest portion (Table 2.5) and comprised 85%, 60%, and 63% of total C stores corresponding to 155 Tg (136 Tg to 174 Tg), 915 Tg (818 Tg to 1,012 Tg), and 1,070 Tg (954 Tg to 1,186 Tg) for the Boreal, the Temperate, and both ecoregions combined, respectively. Understory vegetation on the other hand represented the smallest portion of total C pool with percentages from total running at 0.4%, 0.3%, and 0.3% for the Boreal, the Temperate, and both ecoregions combined, respectively. Aboveground C stores as a percentage of total were 14% for the Boreal, 34% for the Temperate, and 32% for the region. Among total aboveground components live tree/sapling portion was the highest, representing 24% of the total C stores and the CWD component was at 7% from total C in both regions. However, live trees/saplings component varied between the ecoregions: in the Boreal ecoregion it comprised 7% of the total C pool and was similar to CWD component of 6%, whereas in the Temperate ecoregion it comprised 26% of the total. The combined live and dead root contribution to the total C was ~2% for the Boreal and ~6% for the Temperate ecoregions. Live and dead partitioning was 66% and 34% of the root C pool in the Boreal and 86% and 24% of the root C pool in the Temperate ecoregions, respectively (Table 2.5). FWD appeared to be fairly insignificant component comprising less than 1% of total C in both ecoregions. However, as a component of aboveground dead woody material (FWD + SWD + DWM C pools combined), FWD represented ~11% in each ecoregion (Table 2.5).

DISCUSSION

Biomass distribution

Our study contributed to better understanding of the average and total regional live and dead

biomass distribution in the forests of Coastal Alaska. Average live biomass estimates by forest

type obtained through our data analysis were consistent with those reported by other studies.

Biomass stores for different forest types in our study were within a standard error of those

reported by Barrett and Christensen (2011) with differences in population totals attributable to

the exclusion of NF wilderness (~4.4 million ha in Tongass and Chugach NF and Glacier Bay

wilderness areas; Barrett and Christensen 2011). Regional live biomass in Coastal Alaska of

1.23 ± 0.04 Pg was reported by Barrett and Christensen (2011) for live trees (≥ 2.5 cm at d.b.h.),

whereas our calculations resulted in 0.82 ± 0.02 Pg. This 1.5-fold difference in total biomass

corresponded well with the 1.5-fold difference in the forest area covered by each of the

inventories, where 6.197 million ha of forest were reported by Barrett and Christensen (2011)

which included NF wilderness and wilderness study areas, and 4.255 million ha of forest were

used in our calculations with NF wilderness and wilderness areas omitted.

We compared the results of our data analysis to the values calculated by FIA for western

Washington and Oregon, two regions within the United States that are located closest to Coastal

Alaska geographically, characterized by similar environmental conditions, and utilized the same

forest inventory sampling design and methodology of data analysis. Comparison of our estimates

of average live, snag, and log biomass by species groups (softwoods, hardwoods, and all species

combined) to the values calculated for western Washington and Oregon from PNW-FIADB

Annual Inventory Database 2001-2011 (USDA 2014a) indicated that both live and log biomass

estimates in Coastal Alaska were the lowest among these three regions in all species groups. At

the same time the snag biomass was the highest among three regions in softwoods and all species

combined. Upper bounds in live biomass values from Alaska (93 Mg/ha in black cottonwood

forests of Boreal ecoregion and 312 Mg/ha in western hemlock of Temperate ecoregion) were

also lower than values reported in other studies. For example, in the Pacific Northwest (PNW),

Smithwick et al. (2002) indicated upper bounds in live biomass (live and dead branch, foliage,

bole bark, and bole wood) to be 171 Mg/ha for eastside *Pinus*-dominated forests, and 929 Mg/ha

and 727 Mg/ha for coastal Sitka spruce – western hemlock old-growth forests in Oregon and

Washington, respectively. Hudiburg et al. (2009) reported upper live biomass limits (live bole,

branches, foliage, and coarse roots) in the range of 137-196 Mg/ha and 647-863 Mg/ha for the

East Cascades and Coast Range/Klamath Mountains, respectively. Low live biomass in our study

could be the indication of harsher growing conditions in Alaska with longer winters and shorter

summers as well as decreased vertical tree distribution with the tree line at lower elevations

when compared to western Oregon and Washington. The model simulation study conducted in

Oyster River watershed in British Columbia, Canada, a region with environmental conditions

similar to our Temperate ecoregion, also showed higher values for live aboveground biomass,

not only in undisturbed forests with assumed levels of 570 Mg/ha in 1920, but also in 2005

forests (recovering from disturbances of 1928-1949 and 1990) which contained 246 Mg/ha

(Chen et al. 2013). In part these differences could be attributed to the difference in species

composition with highly productive Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands

used in the Oyster River study.

Our estimates of CWD biomass were lower than those reported for other areas of the PNW coast. Acker et al. (2000) reported CWD biomass in 150-year old western hemlock – Sitka spruce stands of coastal Oregon range between 144 Mg/ha and 155 Mg/ha. Keenan et al. (1993) reported combined large and small log biomass range between 225.5 Mg/ha in 85-year old western hemlock – silver fir (*Abies amabilis*) stands and 362.6 Mg/ha in old growth western redcedar – western hemlock dominated stands of coastal British Columbia. Our CWD biomass estimates were 86.9±3.1 Mg/ha, 59.7±9.3, and 81.5±5.2 Mg/ha for western hemlock, Sitka spruce, and western redcedar forest types, respectively (Table 2.1). At the same time our CWD biomass estimates of 35.1±3.1 Mg/ha in the Boreal and 58.6±2.1 Mg/ha in the Temperate ecoregion, and 55.36±1.8 Mg/ha in Coastal Alaska (averages for stands of all ages) were at the higher end of the range of the estimates reported by Gould et al. (2008): 11.5 – 18.2 Mg/ha for the Boreal (Alaska and Minnesota) and 37.6 – 76.1 Mg/ha for the Temperate (Washington and Idaho) forests.

We also compared our results to the values from Russia, a region that is known to contain about 50% of the world's boreal forest (Kobak 1988) and where ecosystems are controlled by climatic factors and disturbance regimes similar to the boreal Alaska. Our CWD biomass estimates in general were at the higher end of the ranges published for forests in Russia. Krankina et al. (2002) reported that CWD biomass (snags, logs, and stumps) among seven studied regions in Russia was the highest in the Russian Far East at 13.9 Mg/ha (calculated as an overall average among the stands of all age groups). The highest overall biomass was reported in young stands in the Russian Far East at 24.4 Mg/ha. Stores modeled from tree mortality and decomposition rates

ranged between 14 Mg/ha and 42 Mg/ha in mature forests of the St.-Petersburg region (Tarasov

1999). A wider range of CWD stores, between 6.6 Mg/ha and 102 Mg/ha, was observed among

the old-growth spruce forest sites in St. Petersburg region (Shorohova and Shorohov 1999).

Other studies have estimated average CWD stores of a 7.4 Mg/ha for the European and 15 Mg/ha

for the Asian parts of Russia (Shvidenko and Nilsson 2000), with 34-40 Mg/ha for the entire

country (Moiseev et al. 2000). Our CWD estimates in most cases are higher when compared with

the studies utilizing or complementing Russian forest inventory data (Krankina et al. 2002,

Shvidenko and Nilsson 2000) but comparable to or lower than more localized estimates from the

Russian forests. This fact might be an indication that more localized studies that are based on

relatively small sets of plot measurements, tend to show higher biomass stores than studies based

on forest inventories, either FIA sampling (Bechtold and Patterson 2005) or wide-ranging visual

surveys in case of Russian forest inventory (Kukuev et al.1997). Another reason for our CWD

estimates being generally higher than those reported for Russian forests may be the difference in

methodology of CWD sampling and data analysis. We also hypothesize that the difference in

CWD amounts was due to differences in productivity of the Russian and the Coastal Alaskan

forests. However, comparison of the biomass stores between Russia and Coastal Alaska

indicated that no large differences exist. Live aboveground biomass stores in Russian forest

regions ranged between 43.3 Mg/ha and 245.2 Mg/ha (Krankina et al. 2005) with CWD stores

ranging between 5.7 Mg/ha and 13.9 Mg/ha (Krankina et al. 2002). In our study, live biomass

stores were slightly lower at 41.6 Mg/ha in the Boreal and 218.9 Mg/ha in the Temperate

ecoregions, and CWD stores were somewhat higher at 35.1 Mg/ha and 58.6 Mg/ha, for the

Boreal and the Temperate ecoregions, respectively.

High snag biomass in Alaska in comparison to the two PNW states (Oregon and Washington) could potentially be a result of high mortality rate of spruce-dominated forests damaged by the spruce bark beetle outbreak as well as snags resulting from the Alaska yellow cedar decline and potentially lower snag to log pools transfer rates (Figure 2.5). Relative similarity in CWD stores in three regions (55.3 Mg/ha in Coastal Alaska, 64.7 Mg/ha in western Washington, and 51.9 Mg/ha in western Oregon) and differences between snag and log pools may underline the disturbance type differences characteristic of these regions. The higher snag retention could also be linked to the proportion of timberland harvested in recent decades being smaller in Alaska while the area of old growth being 2-3 times larger than in Washington and Oregon (Donnegan et al. 2008, Campbell et al. 2010, Barrett and Christensen 2011). As our results indicate, harvested areas, especially clearcuts, tend to contain small amounts of snag biomass, whereas undisturbed areas contain relatively large amounts of snag biomass (Table 2.2). It could also be the combination of a smaller area harvested in Alaska and the legacy of previous management when close to 60% of live biomass during harvest events was removed from the forest leaving behind areas lacking large-diameter mature and old trees that represent the pool snag biomass pool gets replenished from.

The average snag biomass reported by Andersen (2011) for Coastal Alaska was higher than our average snag biomass. We compared the snag biomass calculation methods to those described in Andersen (2011) and ran the analysis using both methods, with biomass adjustments accounting for missing bole portions and density reduction due to decay and without these adjustments. This adjustment reduced our snag biomass estimates by as little as 5 and as much as 67 percent of the

unadjusted values for different forest types (Table 2.4). For the four individual forest types with

the highest snag biomass (western redcedar, western hemlock, Alaska yellow-cedar, and white

spruce), the adjustment reduced snag biomass estimates between 8 and 47 percent (Table 2.4),

whereas for all forest types combined the reduction of snag biomass estimate was 41 percent.

The main reason we ran the calculations using adjusted and unadjusted biomass was to determine

if the difference in estimates derived from data collected in previous inventory cycle suggested

change over time or just reflected difference in estimation methods. White spruce was the only

forest type with a substantial difference between 40.8±5.1 Mg/ha (unadjusted value from our

study) and 26.0±4.5 Mg/ha (Andersen 2011) and thus potentially showing the actual change over

time (Table 2.4). The similar trend was observed in white spruce forest type when we compared

our unadjusted snag biomass (40.8±5.1 Mg/ha) to the average snag biomass obtained from the

data collected during the 2004-2010 period (24.8±2.8 Mg/ha) (Table 2.4), i.e. over

approximately 9-year interval between the inventories. However, this difference was most

pronounced when comparison was done for combined White/Sitka spruce forest types in Boreal

ecoregion only, 50.1±5.8 Mg/ha vs. 29.6±3.6 Mg/ha (Table 2.4). Boreal ecoregion has

experienced an extensive spruce bark beetle outbreak between 1989 and 2004 (Berg et al. 2006).

The data in Boreal ecoregion for our study were collected in early 2000s, i.e. shortly after the

outbreak peak in 1995. The second set of data was collected between 2004 and 2010 (about 7-

year interval between inventories). Thus, the difference in snag biomass could be an indication of

snag fall as time since the spruce beetle outbreak increases. There is still a possibility that these

results are affected by the difference in protocols of CWD collection between two inventories.

However, it seems that other forest types were not affected by the protocol differences, therefore it is probably of a minor factor and the differences can be in fact attributed to transition of a large cohort of dead trees from snags into logs.

Total snag biomass from our study, calculated using average snag biomass adjusted for broken tops and density loss was 0.123±0.004 Pg, or 2.4 times lower than 0.29±0.01 Pg reported by Barrett and Christensen (2011). However, total snag biomass, calculated using average snag biomass by forest type unadjusted for broken portions and density loss was 0.21±0.01 Pg, or 1.4-fold lower than that reported by Barrett and Christensen (2011). This difference corresponds with the 1.5-fold difference in the land area covered by the periodic and annualized inventories.

Our results show that CWD pool is a significant component of biomass in forest ecosystems of Alaska sampled by FIA with regional CWD comprising 46 and 21 percent of Total Combined aboveground biomass in the Boreal and the Temperate ecoregions respectively (Table 2.3). Snags comprised 67 percent of CWD in the Boreal and 52 percent in the Temperate ecoregions (Table 2.3). Taking into account the biomass dynamics, these snags will eventually fall and become a part of log pool. These dynamics suggest the importance of collecting inventory data on all three (live, snags, and logs) biomass pools. Unfortunately, Coastal Alaska, one of the few regions among the vast territory inventoried by the PNW Research Station, has been deficient in that aspect, as the log inventory has been limited in annualized (2004 – 2013) survey. Log inventory using Line Intersect Method was confined to the plots visited as part of the National Forest Health Monitoring (FHM) protocol (1/16 of total field visited plots) and only conducted

from 2004 to 2009, after which the FHM protocol was dropped by FIA. Thus, only limited

information on log biomass has been collected in Coastal Alaska since 2004 field season, with

insufficient power for statistical analysis. This means first, that once these snags fall down they

are unaccounted for in the inventory; in terms of C stock estimation this translates into a

substantial underestimate. While theoretically it is possible to utilize log-to-live volume or

biomass ratios to estimate log biomass, such ratios may vary widely in post-disturbance young

forests precluding the calculation of meaningful estimates (Krankina et al. 2002). Second, the

stores and the dynamics of the entire and potentially large log biomass pool are overlooked.

Inferring log mass from estimates of other biomass pools is problematic as the proportion of logs

and snags varies among forest and disturbance types and among ecoregions (Tables 2.1 and 2.2).

Given that Coastal Alaska has the largest total biomass among all Pacific states, the uncertainty

in C stores and C fluxes will further delay the ability of scientific community to have a full

account of C stores in forest ecosystems as well as our understanding of C dynamics driven by

local disturbance regime. Log inventory using a "down wood lite" protocol resumed in Alaska

starting with the 2014 field season and executed on all field-visited plots (USDA 2014b).

Disturbance

Our estimates of CWD amounts in disturbed stands may not reflect adequately the impact of

disturbance because specific types of disturbance affect different categories of stands and are

associated with particular Forest Types or successional stages in stand development. In this

study, the CWD stores in stands with fire disturbance were low compared to undisturbed stands

(Table 2.2) even though fire most certainly increases the amount of CWD. This example

demonstrates the limitations of inventory as a method for estimating the impact of disturbance on CWD stores even though inventories are often used for this purpose (Barrett and Christensen 2011). Accounting for differences in stand characteristics associated with specific disturbance types and subsetting the plot measurements to approximate better pre-disturbance amounts of CWD can address this problem. In our case, the limited number of plots with recorded fire disturbance in the Boreal ecoregion (9) does not permit a robust characterization of fire impact on CWD.

All disturbance types had higher percent CWD in total (live+dead) aboveground biomass than for the Undisturbed category (Figure 2.3). However, there was nearly 10-fold difference in CWD biomass range among the disturbance types (Table 2.2). Biomass extremes in disturbed stands were associated with the Blowdown disturbance on one end and the Fire disturbance on the other. These results could be explained at least partially by the regional differences. Stands affected by Blowdown disturbance type were in most cases located in the Temperate ecoregion (southeast AK), where this type of disturbance was prevalent. Most Undisturbed stands were also located in the Temperate ecoregion, therefore the average biomass totals between Blowdown and Undisturbed stands should have been similar. It was not the case because Blowdown category contained mostly mature and old-growth stands, whereas Undisturbed category contained the stands of all age groups, therefore the total biomass in Blowdown stands was larger than in Undisturbed stands. However, when compared to biomass in forest types most often associated with the Blowdown disturbance, the average biomass in Blowdown stands (Table 2.2) was similar to the average biomass in western hemlock and 25% higher than biomass in Sitka spruce

forest types (Table 2.1). The difference with Sitka spruce total average biomass is mostly because of CWD pool size, which could be explained by historic logging in Sitka spruce stands. Fires in contrast to Blowdown disturbance, are a rare event in the Temperate ecoregion (McCullough et al. 1998, Harris 1999) but are more common in the Boreal ecoregion (De Volder 1999, Lynch et al. 2006, Berg et al. 2006). Therefore, the biomass averages from fire-damaged stands, while being 2-4 times lower (Table 2.2 versus Table 2.1), were similar to the averages from the Boreal forest types. Adjusting for age for the comparison between fire and other disturbance types would probably provide better understanding of the differences in the stores but small number of fire-damaged stands (9) precluded us from meaningful comparison. It is important to recognize that while disturbances increase the amount of CWD these amounts in disturbed stands are often associated with particular forest type or successional stage in stand development, thus do not reflect the average CWD stores, and should probably be used for the comparison in relative terms (as a ratio or percent of live or total biomass).

Disturbance type and severity also had a significant effect on CWD pool partitioning between the snag and log components thus diversifying the CWD decomposition trajectories. This diversity was a result of differences in log and snag decomposition rates (Onega and Eickmeier 1991, Yatskov et al. 2003, Harmon et al. 2005) as well as the variability in snag fall rate associated with the lag interval following the disturbance (Angers et al. 2010, Harmon et al. 2011a). The factors impacting the variability in the lag interval include environmental characteristics (climate), site characteristics (aspect, slope, soils, productivity, and exposure to disturbance agents), stand characteristics (history, disturbance regime, species composition, age, and

density), and tree characteristics (species, d.b.h., height, cause of death, and bole condition at time of death) (Harmon et al. 1986, Raphael and Morrison 1987, Garber et al. 2005).

The differences partitioning of CWD to snag and log categories could be linked to the disturbance types based on the nature of their agents (e.g., wind, fire, insects, etc.). When the CWD pool is examined, clearcuts and partially harvested stands tend to produce low snag and high log biomass, which corresponds with report by McCurdy and Stewart (2005) indicating that log volume almost doubled, whereas snag volume decreased 52 times to 0.5 m^3/ha following the clearcut harvesting, although the total pre- and postharvest CWD volume remained roughly the same.

High severity SBB outbreaks have an opposite effect, initially producing high snag and low log biomass with this proportion switching later in a stand history as snags fall. The reports of high spruce mortality rate (>80 percent) in many beetle-damaged stands (Hennon et al. 1995) are in line with our findings of high snag biomass as an outcome of SBB outbreak.

Allocation of biomass to CWD pool could be a characteristic feature of the disturbance types affecting the forests ecosystems. In Coastal Alaska, high severity SBB outbreaks and fire along with clearcuts and partial cuts produced relatively high percent of CWD from total (live+dead) aboveground biomass in contrast to relatively low percent of CWD produced by moderate severity SBB outbreaks and Blowdown (Figure 2.3). However, distinction should be made between harvest and non-harvest disturbance categories because often the biomass removed from

the forest is overlooked in the analysis. The average total biomass in clearcuts was 109.4±9.3 Mg/ha with the bulk (77%) in the CWD pool (Figure 2.3). Assuming all clearcut stands prior to disturbance were mature and old growth with total biomass equivalent or even higher than average biomass in undisturbed stands (277.2±5.7 Mg/ha), about 60% of total aboveground biomass was removed from the ecosystem as a result of clearcut harvesting. That left behind 40% of biomass partitioned between live and dead biomass pools. Partial Harvest with average total biomass of 187.3±81.3 Mg/ha (Table 2.2) removed about 32% of total biomass leaving on site 68% of biomass partitioned between live and dead pools. Higher CWD biomass amounts associated with certain disturbance types may outline the areas on the landscape that could serve as potential long-term C sources to the atmosphere until newly developed stands offset the emissions from CWD.

Comparison of the total regional CWD stores indicated that in the Boreal ecoregion spruce bark beetle outbreaks represent the disturbance type with the highest regional impact on CWD stores. Over 80% of total CWD in the Boreal ecoregion were associated with this type of disturbance. This corresponds with the effect of this type of disturbance in other boreal forests (Kurz et al. 2008a). The Temperate ecoregion was affected by disturbances to a lesser extent with most of CWD associated with undisturbed stands. Similar results were obtained through the simulation modeling study conducted in Oyster River watershed in British Columbia, Canada, an area adjacent geographically and environmentally similar to our Temperate ecoregion, where undisturbed stands in 1920 (assumed to be the initial condition) contained 412 Mg/ha of dead organic matter (DOM: forest floor litter, dead wood, and belowground dead roots). These stores

increased briefly through the period of intensive logging and fire disturbance between 1928 and 1949, but dropped to the lowest 106 Mg/ha in 1971 and increased, but not fully recovered, to 198 Mg/ha (half of the initial) by 2005 (Chen et al. 2013). Our results therefore are indicating that the Boreal and the Temperate ecoregions are governed by a different set of disturbances and may play vastly different roles in a future C budget under climate change conditions.

Carbon pools and uncertainty estimates

One of the objectives in this study was to examine the above (live tree, snag, log, FWD, and understory vegetation) and below ground (live and dead roots and soils) C stores in the forests of Coastal Alaska, and assess the main sources and contributions of the uncertainty in estimates of these stores. Three components important in uncertainty estimates are the size of the pool, the uncertainty associated with the pool, and the sources of this uncertainty (Harmon et al. 2007, Melson et al. 2011). Several sources of uncertainty were identified in previous studies: measurement error (quantifies uncertainty in physical measurements, such as tree d.b.h.), sampling error (associated with the fact that the parameter of interest could not be measured directly, thus requiring selection of a sample from the population), model prediction error (associated with any estimated regression relationship as well as the conversion factors from one physical quantity to another, such as biomass to C), and model selection error (introduced when one set of equations is used from an array of applicable relationships) (Harmon et al. 2007, Melson et al. 2011, Harmon et al. 2015).

The effect of the pool size and its uncertainty on overall uncertainty could be best seen through comparison of the largest and smallest C pools. Soils C pool is the largest among our C pool estimates. It accounts for over 60% in total ecosystem C for both ecoregions combined (Table 2.5) and in some biomes (Boreal forests) could exceed 80% of total ecosystem C (Malhi et al. 1999). When compared to the Understory C pool, the soils C pool is nearly 200 times larger (1069.7 Tg vs. 5.7 Tg) with the uncertainty that is 35 times larger (116 Tg vs. 3.3 Tg) . In fact, the uncertainty associated with the soils C pool is 20 times larger than the Understory C pool itself (116 Tg vs. 5.7 Tg) indicating that fairly small changes in soils C pool would lead to noticeable changes in the total C pool, whereas several-fold changes in the Understory C pool will have minor effect on the total C stores.

Some sources of uncertainty have a larger effect on individual C pool estimates than the others. Sampling error is likely high for soils and low for pools estimated by FIA. The highest standard error percent in relation to the estimated mean was associated with the understory vegetation data obtained from the literature (29 to 31%). FWD had the next highest followed by the dead and live roots. On the lower end of the SE percent were live tree C pool (2 to 7%) and surprisingly soils (5 to 6%). Given the high variation in soils C (Ping et al. 2002) and fairly low number of observations in our literature source (Johnson et al. 2011), we suspect that soils sample is potentially lacking a representative distribution, therefore such a low SE in soils C estimates underestimates actual uncertainty. Johnson et al. (2011) used 83 observations from the Alaska Range region (of which the Boreal ecoregion is part of) and 165 observations from the Coastal Rainforest region (corresponding to Temperate ecoregion in our study). The soils SE is the

representative of the sample and may not reflect the full variability in the soils C pool in the

Boreal and Temperate ecoregions. In contrast, aboveground C pools with systematic FIA

sampling have fairly large number of observations. Aboveground biomass data were collected by

FIA on 269 and 1635 plots in the Boreal and Temperate ecoregions, respectively, i.e., on nearly

10 times as many plots as soils data. Measurement error is probably low in both cases with

current quality control measures in place.

Model prediction error contributes to overall uncertainty through use of a one-for-all C-to-

biomass conversion factor. Heath and Smith (2000) assigned +/-15% uncertainty to their live tree

volume-to-C estimates. Melson et al. (2011) used +/-10% uncertainty of the midpoint estimate

(for live stem wood averaged across species) in volume-to-C conversion. This form of

uncertainty is probably also high for the modelled pools especially Dead Roots, FWD, and

Understory because of the general nature of the literature-derived ratios and numerous

assumptions that had to be made. Harmon et al. (2008) indicated that depending on volume

equation the uncertainty in CWD biomass for a well-sampled species ranged from ±4% to 7%

percent, whereas for a well-sampled genus, the uncertainty ranged from ±21% to 38%,

depending on the decay class volume distribution.

Model selection error was considered to be the main source of uncertainty of the live C estimates

(Melson et al. 2011) with stem wood volume uncertainty of 12% and stem wood biomass

uncertainty of 22% of the midpoint estimate. This form of uncertainty was also relatively high

for the CWD C estimates. High uncertainty is most likely associated with the inter-regional

application of biomass equations (Barrett and Christensen 2011, table of biomass citations, p. 117) and adaptation of the allometric equations used in biomass calculations for the range of tree diameters (Melson et al. 2001).

Measures to reduce uncertainty should probably be directed toward its greatest contributors (soils and aboveground live and dead tree C pools) and most significant sources (sampling and model selection errors among the uncertainty sources, respectively). Future efforts to reduce soils estimate uncertainty could be directed towards increasing the sample size. Ideally, the soil sampling should be done on FIA plots, so the same analytical methods could be used for the data analysis for above and belowground C stores. The problem with this scenario in Alaska is that only Coastal Alaska has been inventoried over the years leaving the largest portion of the state untouched. Nevertheless, soil sampling at the large scale should be expanded, systematized (possibly using stratification), its intensity should be increased, and same sampling and laboratory analysis methods should be utilized. For the tree biomass, the measures associated with model selection error may include subdividing biomass equations (by geographic distribution and size classes), inclusion of a form factor into biomass equations, developing new equations representative of the region where there is lack of such (Coastal Alaska), and developing equations for difficult-to-measure components (roots) (Melson et al. 2011).

CONCLUSIONS

This study provided estimates of aboveground live and dead stores and examined the effects of

disturbance on biomass stores in the Boreal and the Temperate ecoregions of Coastal Alaska. In

addition, above- and belowground live and dead C pools were estimated and uncertainty analysis

of these estimates was conducted to identify the type and sources of uncertainty to explore the

ways it could be decreased in future estimates.

Biomass values obtained from plot-level data were compared to those from other similar forested

regions. Both average aboveground live tree and log biomass in Coastal Alaska were lower than

the amounts reported for other neighboring coastal rainforest ecosystems in the PNW. At the

same time, snag biomass generally was higher. Overall CWD stores in Coastal Alaska were

lower than values reported from the coastal PNW and Canada but were higher than values

reported from Russia, another cold-climate forest region. At the regional scale, CWD biomass in

the Boreal ecoregion represented almost 46 percent of aboveground (live and dead tree) biomass

(67 percent of CWD consisted of snags) as compared to 21 percent in the Temperate ecoregion

(52 percent of CWD consisted of snags). For the Boreal ecoregion, the snag biomass pool was

more substantial due to disturbance.

Disturbances represented important events leading to reorganization of components within the

forest ecosystems of Coastal Alaska. Regardless of type and severity, disturbances increased the

proportion of CWD in total aboveground (live and dead tree) biomass in the forests of Alaska

when compared to undisturbed stands, likely changing the C balance and future C dynamics in

disturbed stands. The contribution of different disturbance types to the total regional CWD stores varied between ecoregions of Alaska with spruce bark beetle outbreaks having the highest regional impact on CWD stores in the Boreal ecoregion. In the Temperate ecoregion the highest CWD stores were found in stands deemed undisturbed but in reality subject to small-scale disturbances. Disturbance type and severity also had a significant effect on CWD pool partitioning between the snag and log components likely diversifying the CWD decomposition trajectories.

We examined the FIA plot-level data in the context of the whole ecosystem C by identifying and estimating the size of eight C pools within the forests of Coastal Alaska. Among these, the soils C pool was the largest, representing 62.6% of the total ecosystem C. It was followed by live aboveground, live root, snag, log, FWD, dead root, and understory vegetation C pools with the last representing <1% of the ecosystem C. Three C pools estimated from plot-level data measured by FIA in the field (live, snag, and log component) cumulatively represented 30.6% of the total ecosystem C or just half of that contributed by soils pool, emphasizing the importance of whole-ecosystem approach when assessing C stocks within the system. Such an approach allows for better understanding of the potential behavior of each C pool within the ecosystem context under changing disturbance regimes and changing climate.

Uncertainty of C estimates is essential in accurately determining the upper and lower bounds of forest C sources and sinks with the purpose of assessing forest C sequestration potential. In our study, the uncertainty of the individual pools (2xSE of the pool's mean estimate) was 10.8%,

4.2%, 6.4%, 6.5%, 12.0%, 4.8%, 5.2%, and 57.9% for the soils, live aboveground, live roots, snag, log, FWD, dead roots, and understory vegetation pool, respectively. The highest sources of uncertainty were associated with the belowground (soils) and the aboveground (live and dead) tree C pools (due to pools sizes) and most likely produced by the sampling and the model selection errors, respectively. To improve C estimates in soils and decrease uncertainty in this C pool more representative sampling should be undertaken across Coastal Alaska utilizing stratified, random, or systematic sampling techniques or their combinations. To reduce uncertainty in the aboveground live and dead C pools we recommend more attention be paid to the form of tree bole that is used in volume equations as differences in form and not necessarily the equations describing these shapes are likely introducing the most uncertainty.

FIGURES

Figure 2.1. Territory sampled by coastal Alaska Forest Inventory and Analysis unit (after Nowacki et al. 2002).
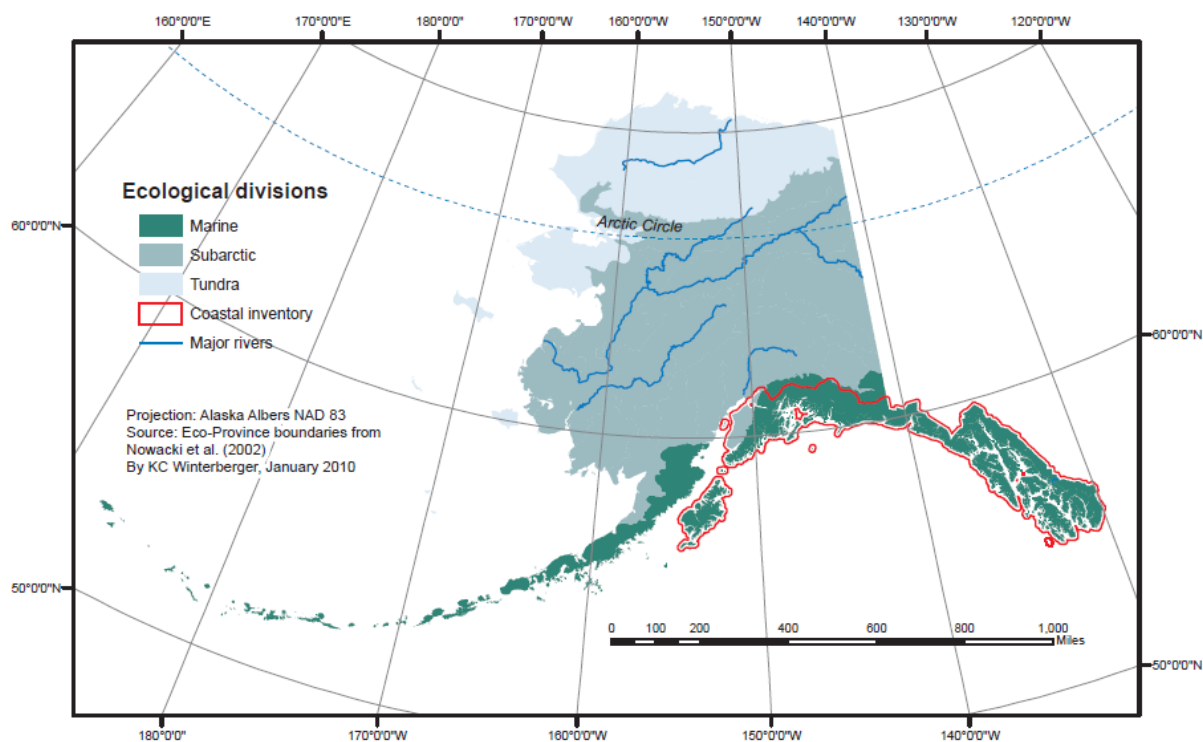
Figure 2.2. Periodic Alaska four-point FIA plot layout.

7.3-m fixed
radius subplot

2.1-m fixed
radius microplot

5.64-m HV
profile subplot

Three 11.28-m
DWM transects
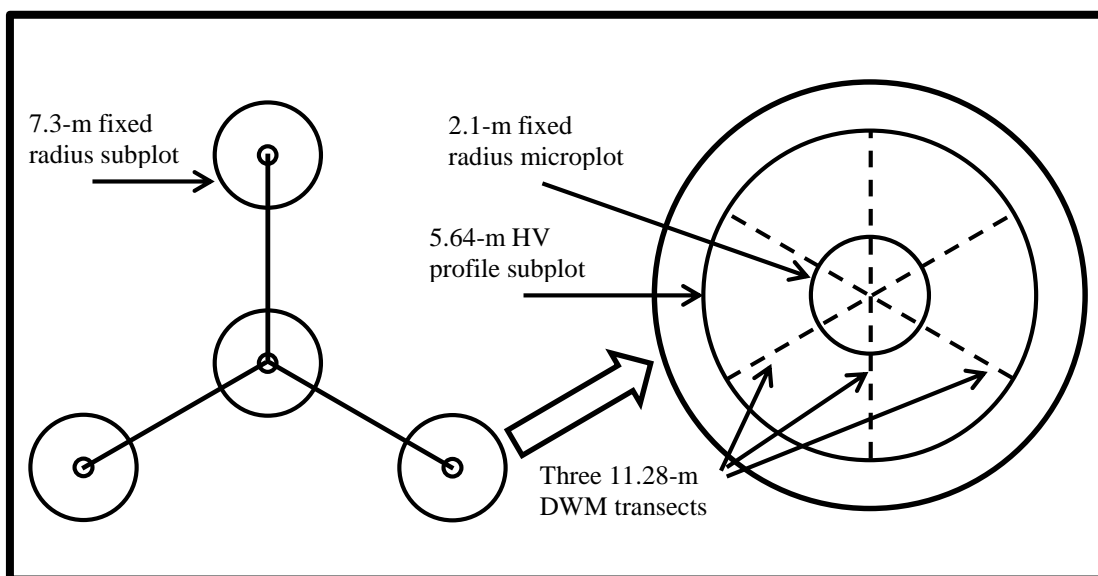
Figure 2.3. CWD as percent of aboveground woody (live and dead) biomass by disturbance type.
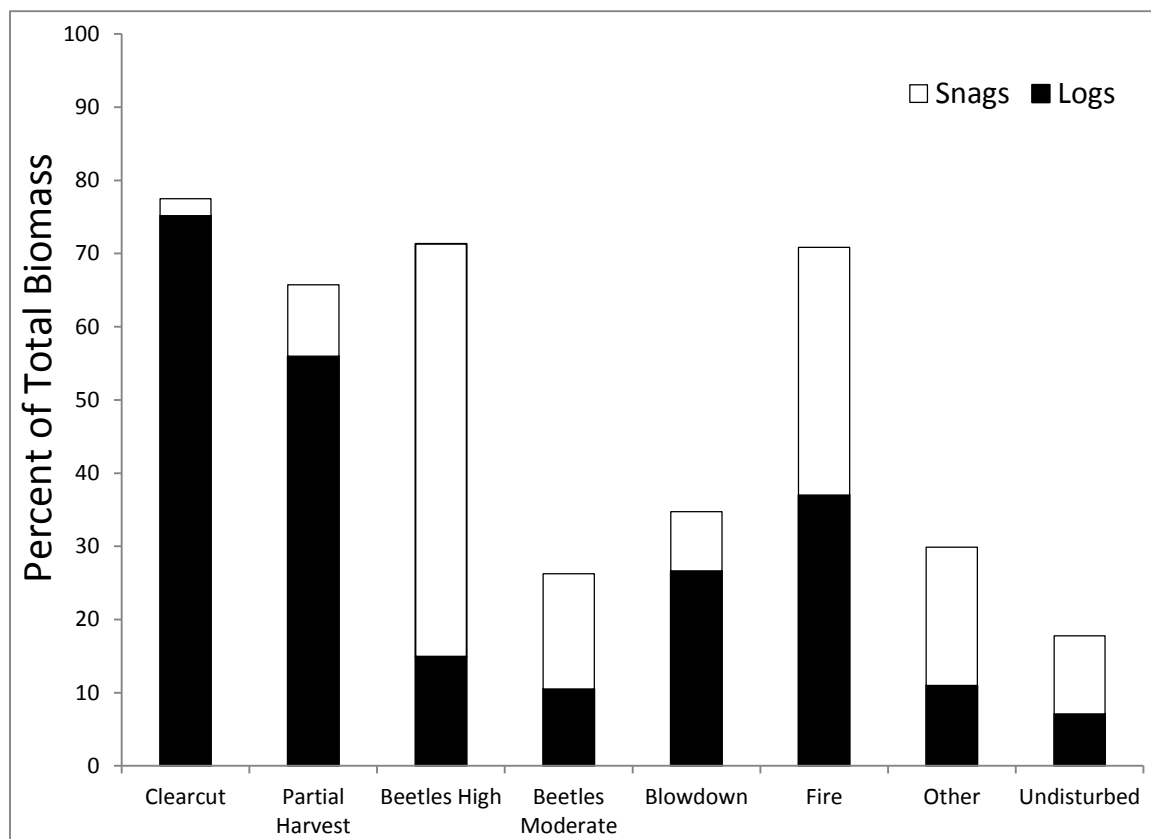
Figure 2.4. Contribution of disturbance types to regional CWD stores (% of total CWD mass in ecoregion).
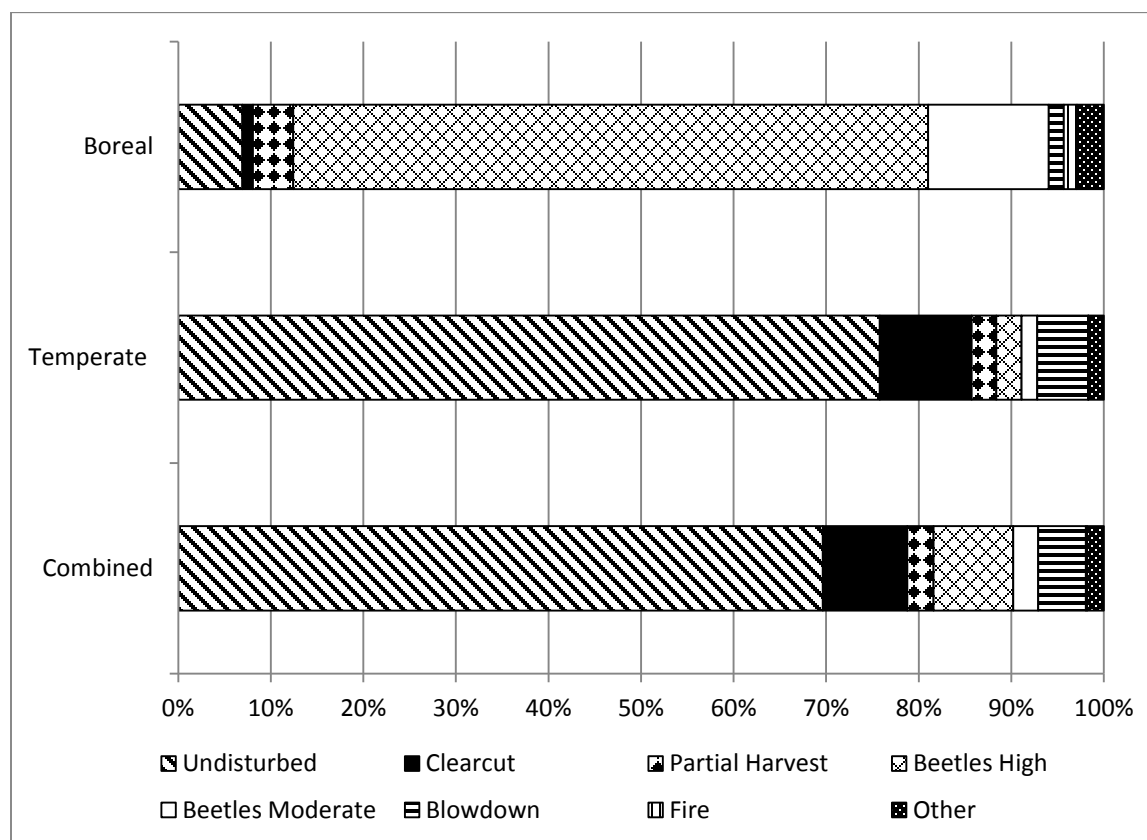
Figure 2.5. Comparison of the estimates of average snag (a) log (b) and live biomass (c) among Coastal Alaska and Wester Washington and Oregon in softwood (SFWD), hardwood (HDWD), and all forest type categories.
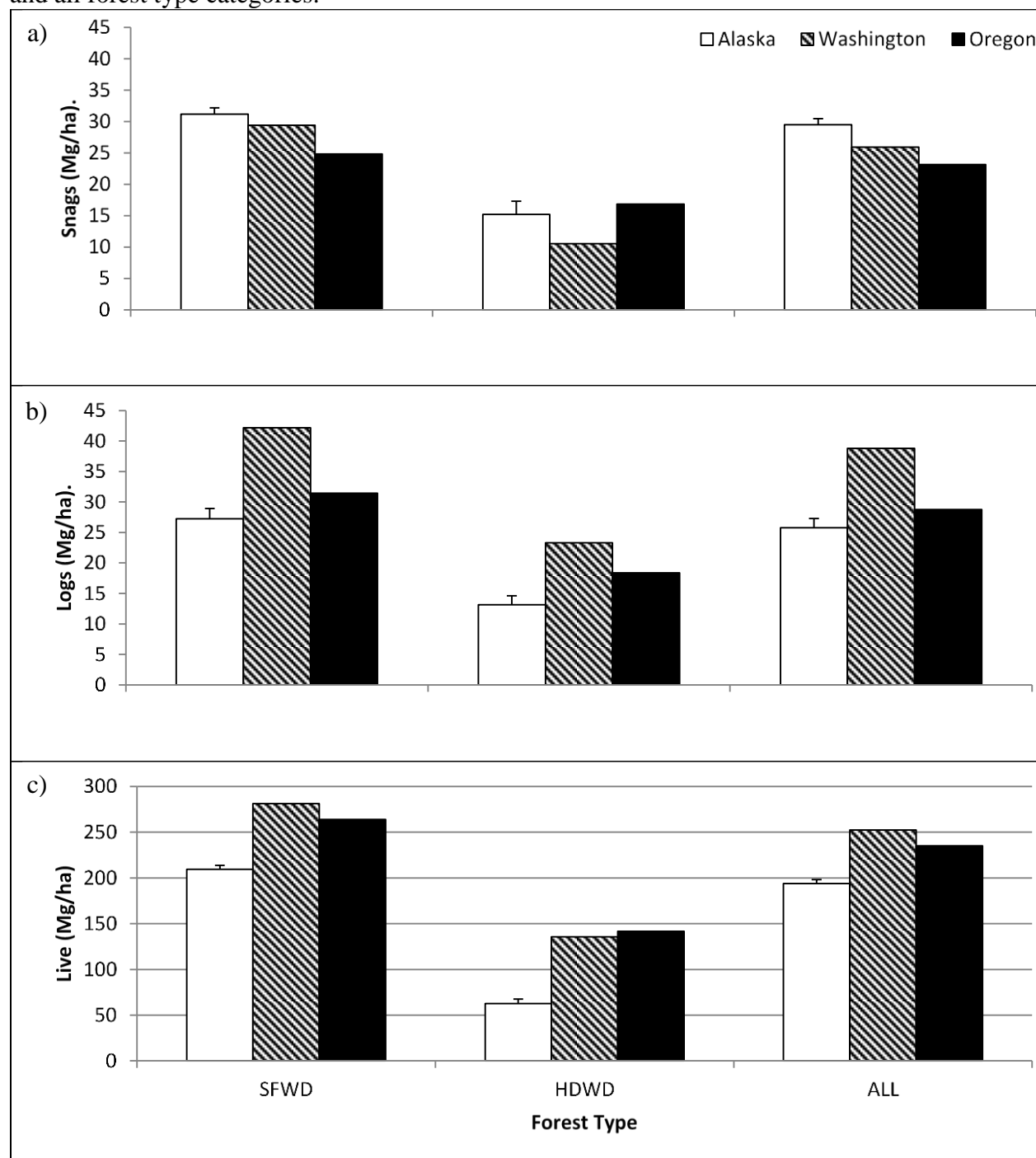
TABLES

Table 2.1. Estimates of average biomass and standard error (Mg/ha) by ecoregion and forest type in Coastal Alaska.

Ecoregion	Forest Type	# of plots[c]	Live x̄ (SE), Mg/ha	Snags (SE), Mg/ha	Logs x̄ (SE), Mg/ha	CWD x̄ (SE), Mg/ha	Total x̄ (SE), Mg/ha
Boreal	Black spruce	84	34.9 (3.5)	2.5 (0.9)	5.8 (1.3)	8.3 (1.7)	43.2 (4.3)
	Sitka spruce	11	16.8 (2.8)	77.4 (16.2)	15.4 (7.0)	92.8 (18.7)	109.5 (19.2)
	White spruce	80	23.9 (3.4)	41.0 (5.7)	16.2 (5.5)	57.2 (7.9)	81.1 (8.8)
	White/Sitka spruce[a]	91	22.9 (3.0)	46.2 (5.6)	16.1 (4.8)	62.4 (7.4)	85.2 (8.2)
	Mountain hemlock	2	63.5 (3.8)	5.7 (3.5)	15.9 (9.7)	21.6 (13.2)	85.1 (17.0)
	All Softwoods	174	29.0 (2.3)	25.1 (3.4)	11.2 (2.6)	36.3 (4.4)	65.3 (4.9)
	Black cottonwood	6	93.3 (20.3)	33.2 (19.5)	10.2 (3.7)	43.4 (19.7)	136.7 (18.9)
	Cottonwood /Willow[b]	3	56.1 (10.2)	11.9 (7.9)	6.1 (2.5)	18.0 (10.3)	74.2 (17.1)
	Paper birch	87	57.8 (5.5)	21.0 (3.8)	13.6 (1.8)	34.6 (4.2)	92.4 (6.2)
	Trembling aspen	13	81.5 (14.3)	14.2 (4.4)	7.0 (2.5)	21.1 (6.1)	102.6 (18.4)
	All Hardwoods	108	62.8 (5.0)	20.7 (3.4)	12.4 (1.5)	33.1 (3.7)	95.8 (5.6)
	All Boreal Forest Types	**269**	**41.6 (2.5)**	**23.5 (2.4)**	**11.7 (1.7)**	**35.1 (3.1)**	**76.7 (3.8)**
Temperate	Alaska yellow-cedar	233	163.4 (6.7)	31.8 (2.0)	13.7 (1.5)	45.5 (2.9)	208.9 (8.4)
	Black spruce	4	45.9 (10.8)	5.3 (3.4)	1.8 (1.3)	7.1 (4.0)	53.0 (10.5)
	Sitka spruce	284	254.1 (14.0)	18.7 (2.1)	41.0 (9.0)	59.7 (9.3)	313.7 (16.5)
	White spruce	19	37.6 (5.6)	20.9 (5.8)	13.0 (3.2)	33.9 (7.5)	71.4 (11.3)
	Lodgepole pine	90	44.8 (4.6)	10.0 (1.3)	3.9 (0.7)	14.0 (1.7)	58.7 (5.9)
	Mountain hemlock	307	140.3 (7.4)	16.4 (1.7)	9.3 (1.1)	25.7 (2.2)	166.0 (8.3)
	Western hemlock	579	312.1 (8.9)	44.4 (2.3)	42.5 (2.2)	86.9 (3.1)	399.0 (9.8)
	Western redcedar	113	238.5 (12.6)	52.4 (3.7)	29.1 (3.4)	81.5 (5.2)	319.9 (14.8)
	Softwoods	1552	229.1 (4.7)	31.8 (1.1)	29.0 (1.9)	60.8 (2.2)	289.9 (5.5)
	Black cottonwood	51	83.5 (14.3)	4.6 (1.6)	10.1 (2.8)	14.7 (3.7)	98.2 (15.7)
	Cottonwood /Willow[b]	1	28.8 (n/a)	47.3 (n/a)	100.4 (n/a)	147.7 (n/a)	176.5 (n/a)
	Paper birch	34	34.4 (6.3)	15.3 (5.0)	9.9 (2.4)	25.2 (6.6)	59.6 (9.6)
	Red alder	8	88.0 (10.0)	7.7 (5.8)	57.6 (25.3)	65.3 (30.2)	153.3 (33.7)
	Trembling aspen	4	48.3 (14.0)	12.3 (3.9)	22.1 (15.2)	34.4 (15.3)	82.7 (15.7)
	Hardwoods	97	62.7 (8.1)	9.7 (2.2)	13.9 (2.5)	23.6 (3.9)	86.4 (9.5)
	All Temperate Forest Types	**1635**	**218.9 (4.6)**	**30.5 (1.0)**	**28.1 (1.8)**	**58.6 (2.1)**	**277.5 (5.4)**

Table 2.1 (Continued). Estimates of average biomass and standard error (Mg/ha) by ecoregion and forest type in Coastal Alaska.

Ecoregion	Forest Type	# of plots[c]	Live x̄ (SE), Mg/ha	Snags (SE), Mg/ha	Logs x̄ (SE), Mg/ha	CWD x̄ (SE), Mg/ha	Total x̄ (SE), Mg/ha
Combined	Softwoods	1726	209.3 (4.4)	31.2 (1.0)	27.3 (1.7)	58.4 (2.0)	267.7 (5.1)
	Hardwoods	205	62.8 (4.8)	15.2 (2.1)	13.2 (1.4)	28.4 (2.8)	91.1 (5.6)
	All Forest Types Combined	**1904**	**194.0 (4.1)**	**29.5 (1.0)**	**25.8 (1.5)**	**55.3 (1.8)**	**249.2 (4.8)**

[a] Forest type is formed by combining white and Sitka spruce forest types;

[b] Forest type with two prevalent species, cottonwood and willow;

[c] Some plots have multiple forest types, so numbers of plots are not additive; number of plots indicates plots with DWM.

Table 2.2. Estimates of average biomass and standard error (Mg/ha) by disturbance type in Coastal Alaska.

Disturbance Type	# of plots[c]	Live x̄ (SE), Mg/ha	Snags x̄ (SE), Mg/ha	Logs x̄ (SE), Mg/ha	CWD x̄ (SE), Mg/ha	Total x̄ (SE), Mg/ha
Clearcut	119	24.6 (3.8)	2.5 (0.8)	82.2 (8.7)	84.7 (8.7)	109.4 (9.3)
Partial Harvest	25	64.2 (14.7)	18.3 (6.6)	104.9 (80.8)	123.2 (80.8)	187.3 (81.3)
SBB[a] high	123	30.7 (3.3)	60.4 (4.9)	16.0 (3.6)	76.4 (6.1)	107.0 (7.2)
SBB[a] moderate	96	95.9 (8.7)	20.5 (4.3)	13.7 (1.9)	34.2 (4.9)	130.1 (11.8)
SBB[a] combined[b]	215	57.6 (4.7)	43.9 (3.7)	15.1 (2.2)	58.9 (4.4)	116.5 (6.5)
Blowdown	38	269.9 (32.6)	33.4 (9.3)	110.2 (15.6)	143.6 (17.1)	413.5 (37.8)
Fire	9	8.0 (5.2)	9.2 (5.5)	10.1 (3.8)	19.3 (7.8)	27.3 (8.4)
Other	39	134.2 (18.0)	36.2 (11.3)	21.0 (3.9)	57.2 (12.6)	191.4 (25.6)
Undisturbed	1502	227.9 (5.0)	29.6 (1.0)	19.7 (1.0)	49.3 (1.6)	277.2 (5.7)

[a] SBB – spruce bark beetle;

[b] "combined" includes both, high and moderate severity;

[c] Some plots have multiple disturbance types, so numbers of plots are not additive; number of plots indicates plots with DWM.

Table 2.3. Estimates of total ecoregion area (ha) and total biomass (Tg) by biomass pools in Coastal Alaska.

Ecoregion	Area	Live (SE)	Snags (SE)	Logs (SE)	CWD (SE)	Total (SE)
	Thousand ha	Tg	Tg	Tg	Tg	Tg
Boreal	595	24.6 (1.7)	13.9 (1.6)	6.9 (1.1)	20.8 (2.1)	45.4 (3.0)
Temperate	3660	790.5 (17.3)	110.0 (3.8)	101.4 (6.4)	211.4 (7.7)	1001.9 (20.6)
Combined	**4255**	**815.1 (17.3)**	**123.9 (4.0)**	**108.3 (6.5)**	**232.2 (7.9)**	**1047.3 (20.5)**

Table 2.4. Estimates of average snag biomass and standard error (Mg/ha) adjusted and unadjusted for broken top and density loss.

Forest Type	# of plots[c]	Average Adjusted Snag Biomass Mean (SE)	Average Unadjusted Snag Biomass Mean (SE)	Percent Difference	Average Snag Biomass after Andersen (2011)	Average Snag Biomass for the period 2004-2010
		Mg/ha	Mg/ha	%	Mg/ha	Mg/ha
Alaska yellow-cedar	233	31.8 (2.0)	49.5 (2.9)	36	47.0 (7.6)	43.1 (4.0)
Black spruce	88	2.6 (0.8)	3.1 (1.0)	15	3.6 (1.3)	---
Sitka spruce	295	21.3 (2.2)	37.1 (4.1)	43	44.8 (7.6)	34.6 (4.4)
White spruce	99	37.5 (4.9)	40.8 (5.1)	8	26.0 (4.5)	24.8 (2.8)
White/Sitka spruce[a]	394	25.3 (2.1)	38.0 (3.3)	34	---	---
White/Sitka spruce[a] Boreal Ecoregion		46.2 (5.6)	50.1 (5.8)	n/a	---	29.6 (3.6)
Lodgepole pine	90	10.0 (1.3)	13.3 (1.7)	24	10.8 (1.8)	12.4 (1.8)
Western redcedar	113	52.4 (3.7)	83.9 (5.9)	38	72.6 (9.4)	68.3 (7.1)
Western hemlock	579	44.4 (2.3)	84.3 (4.7)	47	85.6 (6.3)	95.8 (6.0)
Mountain hemlock	309	16.4 (1.7)	25.0 (2.5)	34	21.5 (2.7)	22.2 (2.7)
Softwoods	1726	31.2 (1.0)	53.2 (1.9)	41	---	---
Black cottonwood	57	7.6 (2.9)	10.7 (3.4)	29	7.6 (3.1)	5.0 (2.1)
Cottonwood /Willow[b]	4	23.0 (9.9)	24.3 (10.2)	5	---	---
Paper birch	121	19.1 (3.1)	22.8 (3.4)	16	18.8 (3.1)	16.1 (2.7)
Red alder	8	7.7 (5.8)	25.9 (17.0)	67	17.0 (10.8)	---
Trembling aspen	17	13.7 (3.5)	16.9 (4.1)	19	17.0 (4.5)	15.6 (5.8)
Hardwoods	205	15.4 (2.1)	18.8 (2.3)	18	---	---
All Forest Types Combined	**1904**	**29.5 (1.0)**	**49.6 (1.7)**	**41**	**---**	**---**

[a] Forest type is formed by combining white and Sitka spruce forest types;

[b] Forest type with two prevalent species, cottonwood and willow;

[c] Some plots have multiple forest types, so numbers of plots are not additive; number of plots indicates plots with DWM.

Table 2.5. Estimates of total carbon stores by ecoregion in Coastal Alaska.

C pools	Boreal			Temperate			Combined		
	$\bar{x}$, Tg	% Total	$\bar{x}\pm2SE$, Tg	$\bar{x}$, Tg	% Total	$\bar{x}\pm2SE$, Tg	$\bar{x}$, Tg	% Total	$\bar{x}\pm2SE$, Tg
Live Trees/Saplings[a]	12.3	6.7	10.6 - 14.0	395.2	25.8	377.9 - 412.6	407.5	23.8	390.3 - 424.8
Standing Woody Material[a]	6.9	3.8	5.3 - 8.5	55.0	3.6	51.2 - 58.8	61.9	3.6	57.9 - 66.0
Down Woody Material[a]	3.4	1.9	2.4 - 4.5	50.7	3.3	44.3 - 57.2	54.2	3.2	47.7 - 60.7
Fine Woody Debris[b]	1.3	0.7	0.9 - 1.8	13.7	0.9	8.9 - 18.6	15.1	0.9	9.8 - 20.4
Understory vegetation[c]	0.8	0.4	0.3 - 1.3	4.9	0.3	2.1 - 7.8	5.7	0.3	2.4 - 9.1
Total Aboveground	24.8	13.6	19.5 - 30.2	519.6	34.1	484.4 - 554.9	544.5	31.9	508.0 - 580.9
Live Roots[b]	2.5	1.3	1.7 - 3.2	79.0	5.2	53.8 - 104.3	81.5	4.8	55.4 - 107.6
Dead Roots[b]	1.1	0.6	0.7 - 1.6	11.6	0.8	7.4 - 15.9	12.8	0.7	8.1 - 17.4
Roots	3.6	2.0	2.4 - 4.8	90.7	5.9	61.2 - 120.2	94.3	5.5	63.6 - 125.0
Soils to 1m depth[c]	154.7	84.5	135.7 - 173.7	915.0	60.0	818.3 - 1011.7	1069.7	62.6	953.9 - 1185.5
Total	**183.1**	**100.0**	**157.5 - 208.7**	**1525.3**	**100.0**	**1363.8 - 1686.8**	**1708.4**	**100.0**	**1525.5 - 1891.4**

[a] Uncertainty calculated utilizing SE of the mean from the forest inventory data;

[b] Uncertainty calculated using Standard Uncertainty Estimator (SUE);

[c] Uncertainty calculated using SE of the mean from literature data.

REFERENCES

Acker, S.A., Harcombe, P.A., Harmon, M.E., and Greene, S.E. 2000. Biomass accumulation over the first 150 years in coastal Oregon *Picea-Tsuga* forest. Journal of Vegetation Science 11: 725-738.

Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce – western hemlock forests of southeast Alaska. Ecology 63(6): 1932-1948.

Alban, D.H. and Pastor, J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. 23: 1744–1749.

Andersen, H.-E. 2011. Biomass and Carbon. *In*: Barrett, T.M. and Christensen, G.A. (Tech. Eds.). 2011. Forest of southeast and south-central Alaska, 2004-2008: Five-year forest inventory and analysis report. Portland, OR: U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Research Station, Gen. Tech. Rep. PNW-GTR-835, pp. 13-22.

Anderson, R.S., Hallett, D.J., Berg, E.E., Jass, R.B., Toney, J.L., de Fontaine, C.S., and DeVolder, A.D. 2006. Holocene development of boreal forests and fire regimes on the Kenai lowlands of Alaska. The Holocene 16(6): 791- 803.

Angers, V.A., Drapeau, P., and Bergeron, Y. 2010. Snag degradation pathways of four North American boreal tree species. For. Ecol. Manage. 259(3): 246-256. DOI: 10.1016/j.foreco.2009.09.026

Arrhenius, S. 1896. On the influence of carbonic acid in the air upon the temperature of the ground. Philosophical Magazine 41: 237-276.

Barbour, R.J., Zaborske, R.R., McClellan, M.H., Christian, L., and Golnick, D. 2005. Young-stand management options and their implications for wood quality and other values. Landscape and Urban Planning 72(1): 79-94.

Barrett, T.M. and Christensen, G.A. (Tech. Eds.). 2011. Forest of southeast and south-central Alaska, 2004-2008: Five-year forest inventory and analysis report. Gen. Tech. Rep. PNW-GTR-835. Portland, OR: U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Research Station, 156 p.

Bechtold, W.A. and Patterson, P.L. (Eds.). 2005. The enhanced forest inventory and analysis program – national sampling design and estimation procedures. USDA Forest Service. Southern Research Station. Gen. Tech. Rep. GTR-SRS-80.

Berg, E.E., Henry, J.D., Fastie, C.L., De Volder, A.D., Matsuoka, S.M. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. For. Ecol. Manage. 227: 219-232.

Birdsey, R.A. and Heath, L.S. 1995. Carbon changes in US forests. *In*: Productivity of America's forests and climate change 271: 56-70.

Bonan, G.B. 2008. Forests and climate change: Forcing, feedbacks, and the climate benefits of the forests. Science 320(5882): 1444-1449. DOI: 10.1126/science.1155121

Bormann, B.T. and Sidle, R.C. 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. Journal of Ecology 78(3): 561-578.

Brackley, A.M., Haynes, R.W., and Alexander, S.J. 2009. Timber harvests in Alaska: 1910-2006. Res. Note PNW-RN-560. Portland, OR: U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Research Station, 24 p.

Brady, W. and T. Hanley. 1984. The role of disturbance in old growth forests: Some theoretical implications for Southeastern Alaska. *In*: Meehan, W., Merrell, T. Jr., and Hanley, T. (Eds.). Proceedings of the symposium on fish and wildlife relationships in old-growth forests. American Institute of Fishery Research Biologists, Juneau, AK, pp. 213–218.

Bronick, C.J. and Lal, R. 2005. Soil structure and management: A review. Geoderma 124(1): 3-22.

Busse, M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Science Society of America Journal 58(1): 221-227.

Cairns, M.A., Brown, S., Helmer, E.H., and Baumgardner, G.A. 1997. Root biomass allocation in the world's upland forests. Oecologia 111: 1-11.

Campbell, S., Waddell, K., Gray, A. (Tech. Eds.) 2010. Washington's forest resources, 2002-2006: Five-year Forest Inventory and Analysis report. Gen. Tech. Rep. PNW-GTR-800. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 189 p.

Campbell, S., van Hees, W.S., and Mead, B. 2005. South-Central Alaska forests: Inventory highlights. Gen. Tech. Rep. PNW-GTR-652. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 28 p.

Campbell, S., van Hees, W.S., and Mead, B. 2004. Southeast Alaska forests: Inventory highlights. Gen. Tech. Rep. PNW-GTR-609. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 20 p.

Chapin III, F.S., Chapin, M.C., Matson, P.A., and Vitousek, P. 2011. Principles of terrestrial ecosystem ecology. Springer.

Chapin, F.S., Matson, P., and Mooney, H. 2002. Principles of terrestrial ecosystem ecology. New York: Springer. 436 p. Chapter 6.

Chen, B., Arain, M.A., Khomik, M. Trofymow, J.A., Grant, R.F., Kurz, W.A., Yeluripati, J., and Wang, Z. 2013. Evaluating the impacts of climate variability and disturbance regimes on the historic carbon budget of a forest landscape. Agricultural and Forest Meteorology 180: 265– 280.

Chen, H., Harmon, M.E., and Griffiths, R.P. 2001. Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: A chronosequence approach. Can. J. For. Res. 31: 246–260.

Christensen, N.L. 1989. Landscape history and ecological change. Forest and Conservation History 33(3): 116-125.

De Volder, A. 1999. Fire and climate history of lowland black spruce forests, Kenai National Wildlife Refuge, Alaska. MS Thesis. Northern Arizona University.

Deal, R.L., Heithecker, T., and Zenner, E.K. 2010. Comparison of tree size structure and growth for partially harvested and even-aged hemlock-spruce stands in southeast Alaska. Journal of Forest Research 15(1): 31-37.

Deal, R.L. 2007. Management strategies to increase stand structural diversity and enhance biodiversity in coastal rainforests of Alaska. Biological Conservation 137(4): 520-532.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexier, M.C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. Science 263(5144): 185-190.

Donnegan, J., Campbell, S., and Azuma, D. (Tech. Eds.) 2008. Oregon's forest resources, 2001-2005: Five-year Forest Inventory and Analysis report. Gen. Tech. Rep. PNW-GTR-765. Portland, OR: U.S. Forest Service, Pacific Northwest Research Station, 186 p.

Fahey T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. Ecological Monographs 53: 51-72.

Farr, W.A. and Hard, J.S. 1987. Multivariate analysis of climate along the southern coast of Alaska--some forestry implications. Res. Paper PNW-372. Portland, OR: Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, 38 p.

Flint, C.G. 2006. Community perspectives on spruce beetle impacts on the Kenai Peninsula, Alaska. For. Ecol. Manage. 227(3): 207-218.

Flint, C.G. and Haynes, R. 2006. Managing forest disturbances and community responses: Lessons from the Kenai Peninsula, Alaska. J. For. 104(5): 269-275.

Foster, D.R. and Boose, E.R. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. Journal of Ecology, pp. 79-98.

Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C ., Bible, K., and Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155(1): 399-423.

Fraver, S., Ringvall, A., and Jonsson, B.G. 2007. Refining volume estimates of down woody debris. Can. J. For. Res. 37: 627-633.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Flemming, S., Forbes, G., Gerrow, J.S., Johnson, G., Woodley, S. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. 4: 238–265.

Garber, S.M., Brown, J.P., Wilson, D.S., Maguire, D.A., and Heath, L.S. 2005. Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. Can. J. For. Res. 35(4): 787-796.

Giorgi, F. 2006. Climate change hot-spots. Geophys. Res. Lett. 33(8), 4 p. http://dx.doi.org/10.1029/2006GL025734

Goetz, S.J., Mack, M.C., Gurney, K.R., Randerson, J.T., and Houghton, R.A. 2007. Ecosystem responses to recent climate change and fire disturbance at northern high latitudes: Observations and model results contrasting northern Eurasia and North America. Environmental Research Letters 2(4), 045031.

Goodale, C.L., Apps, M.J., Birdsey, R.A., Field, C.B., Heath, L.S., Houghton, R.A., Jenkins, J.C., Kohlmaier, G.H., Kurz, W., Liu, S., Nabuurs, G.-J., Nilsson, S., and Shvidenko, A.Z. 2002. Forest carbon sinks in the Northern Hemisphere. Ecological Applications 12(3): 891-899.

Goodman, J.R. 2002. HJ Andrews Experimental Forest. Long Term Ecological Research. SUE – Stochastic Uncertainty Estimator User's Guide. http://andrewsforest.oregonstate.edu/pubs/webdocs/models/sue.cfm

Gosz, J.R. 1980. Nutrient budget studies for forests along an elevational gradient in New Mexico. Ecology, pp.515-521.

Gould, W.A., Gonzalez, G., Hudak, A.T., Nettleton Hollingsworth, T., and Hollingsworth, J. 2008. Forest structure and Down Woody Debris in Boreal, Temperate, and Tropical forest fragments. USDA Forest Service. UNL Faculty Publication. Paper 176. http://digitalcommons.unl.edu/usdafsfacpub/176

Graham, R.L. 1982. Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range. Ph.D. thesis, Oregon State University, Corvallis, Oregon.

Graham, R.L. and Cromack, K. Jr. 1982. Mass, nutrient content, and decomposition rate of dead boles in rain forests of Olympic National Park. Can. J. For. Res. 12: 51 1-521.

Grier, C.C. 1978. A *Tsuga heterophylla-Picea sitchensis* ecosystem of coastal Oregon: Decomposition and nutrient balances of fallen logs. Can. J. For. Res. 8(2): 198-206.

Halbrook, J.M., Morgan, T.A., Brandt, J.P., Keegan, C.E., Dillon, T., and Barrett, T. 2009. Alaska's timber harvest and forest products industry, 2005. Gen. Tech. Rep. 787 PNW-681. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, 30 p. http://www.fs.fed.us/pnw/pubs/pnw_gtr787.pdf

Hamburg, S.P., Zamolodchikov, D.G., Korovin, G.N., Nefedjev, V.V., Utkin, A.I., Gulbe, J.I., Gulbe, T.A. 1997. Estimating the carbon content of Russian forests: A comparison of phytomass/volume and allometric projections. Mitigation and Adaptation Strategies of Global Change Netherlands: Springer 2: 247-265.

Hansen, A.J., Spies, T.A., Swanson, F.J., and Ohmann, J.L. 1991. Conserving biodiversity in managed forests. BioScience 41(6): 382-392.

Hard, J. 1974. The forest ecosystem of southeast Alaska. Forest Insects. USDA FS GTR, PNW-13. PNW forest and range experimental station. USDA, FS, Portland, Oregon.

Harmon, M.E., Fasth, B., Halpern, C.B., and Lutz, J.A. 2015. Uncertainty analysis: An evaluation metric for synthesis science. Ecosphere 6(4): 1-12.

Harmon, M.E. 2011. HJ Andrews Experimental Forest LTER Data Catalog. http://andrewsforest.oregonstate.edu/lter/data.cfm?frameURL=http://andlter.forestry.oregonstate.edu/ltermeta/ltersearch/DataCatalog.aspx?topnav=173. Andrews Experimental Forest LTER. Last accessed April 04, 2013.

Harmon, M.E., Bond-Lamberty, B., Tang, J., and Vargas, R. 2011a. Heterotrophic respiration in disturbed forests: A review with examples from North America. Journal of Geophysical Research: Biogeosciences, 116(G4). DOI:10.1029/2010JG001495.

Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., and Yatskov, M. 2011b. Differences between standing and downed dead tree wood density reduction factors: A comparison across decay classes and tree species. USDA Forest Service. Research Paper NRS-15.

Harmon, M.E. 2010. Branch decomposition study, unpublished data.

Harmon, M.E., Woodall, C.W., Fasth, B., and Sexton, J. 2008. Woody detritus density and density reduction factors for tree species in the United States: A synthesis. USDA Forest Service. GTR-NRS-29.

Harmon, M.E., Phillips, D.L., Battles, J.J., Rassweiler, A., Hall Jr, R.O., Lauenroth, W.K., Fahey, T.J., and Knapp, A.K. 2007. Quantifying uncertainty in net primary production measurements. Principles and standards for measuring primary production, pp. 238-260.

Harmon, M.E., Fasth, B., Yatskov, M., Sexton, J., and Trummer, L. 2005. The fate of dead spruce on the Kenai Peninsula: A preliminary report. USDA Forest Service. Tech. Rep. R10-TP-134. March 2005.

Harmon, M.E., Bible, K., Ryan, M.G., Shaw, D.C., Chen, H., Klopatek, J., and Li, X. 2004. Production, respiration, and overall carbon balance in an old-growth *Pseudotsuga-Tsuga* forest ecosystem. Ecosystems 7: 498-512.

Harmon, M.E., Krankina, O.N., Yatskov, M., and Matthews, E. 2001. Predicting broad-scale carbon stores of woody detritus from plot-level data. *In*: Lai, R., Kimble, J., and Stewart, B.A. (Eds.). Assessment methods for soil carbon. CRC Press, New York, pp. 533-552.

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

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133-302.

Harris, A.S. 1999. Wind in the forests of southeast Alaska and guides for reducing damage. USDA FS PNW-GTR-244. Portland, Oregon, 63 p.

Harris, A.S. 1990. *Picea sitchensis* (Bong.) Carr. Sitka spruce. *In*: Burns, R.M., Honkala, B.H. (Tech. Eds.). Silvics of North America. Volume 1. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service, pp. 260-267.

Harris, A.S. and Farr, W.A. 1974. The forest ecosystem of southeast Alaska. 7. Forest ecology and timber management. USDA For. Serv. Gen. Tech. Rep. PNW-25.

Harris, A.S., Hutchinson, O.K., Meehan, W.R., Swanston, D.W., Helmers, A.E., Hendee, J.C., and Collins, T.M. 1974. The forest ecosystem of southeast Alaska, 1: The setting. USDA For. Serv. Get. Tech. Rep. PNW-GTR-12.

Heath, L.S., Smith, J.E., Woodall, C.W., Azuma, D.L., and Waddell, K.L. 2011. Carbon stocks on forestland of the United States, with emphasis on USDA Forest Service ownership. Ecosphere 2(1), art6.

Heath L.S. and Smith J.E. 2000. An assessment of uncertainty in forest carbon budget projections. Environ. Sci. Policy 3: 73-82.

Hennon, P.E. and Shaw, C.G. III. 1997. The enigma of yellow cedar decline. What is killing these long-lived, defensive trees? J. For. 95(12): 3-10.

Hennon, P.E., Mask, R., and Holsten, E.H. 1995. Forest insect and disease conditions in Alaska, 1994. Forest Health Management Report R10-TP-51. State and Private Forestry, USDA, Forest Service, Juneau, AK, 42 p.

Hennon, P.E., Hansen, E.M., and Shaw, C.G. III. 1990. Dynamics of decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. Can. J. Bot. 68: 651-662.

HJA 2013. Bole decomposition rates of seventeen tree species in Western U.S.A. An on-line report prepared for the USDA USFS, Washington office. http://andrewsforest.oregonstate.edu/pubs/webdocs/reports/decomp/tables.htm. Accessed February 18, 2013.

Holsten, E.H., Thier, R.W., Munson, A.S., and Gibson, K.E. 2000. The spruce beetle. Forest Insect and Disease Leaflet 127. USDA Forest Service. http://www.na.fs.fed.us/spfo/pubs/fidls/sprucebeetle/sprucebeetle.htm

Houghton, R.A. 1995. Effects of land-use change, surface temperature, and CO_2 concentration on terrestrial stores of carbon. *In*: Woodwell, G.M. and Mackenzie, F.T. (Eds.). Biotic feedbacks in the global climatic system. Oxford University Press, New York, pp. 333-366.

Hudiburg, T., Law, B., Turner, D.P., Campbell, J., Donato, D., and Duane, M. 2009. Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. Ecological Applications 19(1): 163-180.

IPCC 2013. Hartmann, D.L., Klein Tank, A.M.G., Rusticucci, M., Alexander, L.V., Brönnimann, S., Charabi, Y., Dentener, F.J., Dlugokencky, E.J., Easterling, D.R., Kaplan, A., Soden, B.J. Thorne, P.W., Wild, M., and Zhai, P.M. 2013. Observations: Atmosphere and Surface. *In*: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., and Midgley, P.M. (Eds.). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC 2001. IPCC TAR WG3 (2001). Metz, B., Davidson, O., Swart, R., and Pan, J., (Eds.). Climate Change 2001: Mitigation. Contribution of Working Group III to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press. ISBN 0-521-80769-7. (pb: 0-521-01502-2)

Iverson, L.R., Brown, S., Grainger, A., Prasad, A. and Liu, D. 1993. Carbon sequestration in tropical Asia: An assessment of technically suitable forest lands using geographic information systems analysis. Clim. Res. 3: 23–38.

Janisch, J.E., Harmon, M.E., Chen, H., Fasth, B., and Sexton, J. 2005. Decomposition of coarse woody debris originating by clearcutting of an old-growth conifer forest. Ecoscience 12(2): 151-160. DOI: http://dx.doi.org/10.2980/i1195-6860-12-2-151.1

Johnson, K.D., Harden, J., McGuire, A.D., Bliss, N.B., Bockheim, J.G., Clark, M., Nettleton-Hollingsworth, T., Jorgenson, M.T., Kane, E.S., Mack, M., and O'Donnell, J. 2011. Soil carbon distribution in Alaska in relation to soil-forming factors. Geoderma 167: 71-84.

Keenan, R.J., Prescott, C.E., and Kmmins, J.P. 1993. Mass and nutrient content of woody debris and forest floor in western red cedar and western hemlock forests of northern Vancouver Island. Can. J. For. Res. 23: 1052-1059.

Kobak, K.I. 1988. Biotical compounds of carbon cycle. Gidrometeoizdat Publishers. Leningrad, Russia.

Krankina, O.N., Houghton, R.A., Harmon, M.E., Hogg, E.H., Butman, D., Yatskov, M., Huso, M., Treyfeld, R.F., Razuvaev, V.N., and Spycher, G. 2005. Effects of climate, disturbance, and species on forest biomass across Russia. Can. J. For. Res. 35(9): 2281-2293.

Krankina, O.N., Harmon, M.E., Kukuev, Y.A., Treyfeld, R.F., Kashpor, N.N., Kresnov, V.G., Skudin, V.M., Protasov, N.A., Yatskov, M., Spycher, G., and Povarov, E.D. 2002. Coarse woody debris in forest regions of Russia. Can. J. For. Res. 32: 768-778.

Krankina, O.N. and Harmon, M.E. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water, Air, and Soil Pollution 82: 227-238.

Kukuev, Y.A., Krankina, O.N., and Harmon, M.E. 1997. The forest inventory system in Russia. J. For. 95(9): 15-20.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., and Safranyik, L. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452(7190): 987-990.

Kurz, W.A., Stinson, G., Rampley, G.J., Dymond, C.C., and Neilson, E.T. 2008a. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. Proc. Natl. Acad. Sci. USA 105(5): 1551–1555. DOI: 10.1073/pnas.0708133105

Laurent, T.H. 1974. The forest ecosystems of southeast Alaska. Forest diseases. USDA Forest Service GTR PNW-23. Pacific Northwest Forest and Range Experimental Station. Portland, Oregon.

Leighty, W.W., Hamburg, S.P., and Caouette, J. 2006. Effects of management on carbon sequestration in forest biomass in Southeast Alaska. Ecosystems 9(7): 1051-1065.

Lynch, H.J., Renkin, R.A., Crabtree, R.L., and Moorcroft, P.R. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems 9: 1318–1327.

Malhi, Y., Baldocchi, D.D., and Jarvis, P.G. 1999. The carbon balance of tropical, temperate, and boreal forests. Plant Cell Environ. 22: 715–740. DOI: 10.1046/j.1365-3040.1999.00453.x

Marland, G. 2000. The future role of reforestation in reducing buildup of atmospheric CO_2. *In*: Wigley, T.M.L. and Schimel, D.S. (Eds.). The carbon cycle. Cambridge University Press, Cambridge, pp. 190–198.

McCullough, D.G., Werner, R.A., and Neumann, D. 1998. Fire and insect in northern and boreal forest ecosystems of North America. Annu. Rev. Entomol. 43: 107-27.

McCurdy, D. and Stewart, B. 2005. Changes in dead wood structure following clearcut harvesting in Nova Scotia softwood forests. Forest research report. Nova Scotia DNR. Forest managmenet planning. FOR 2005-1 No. 76.
http://www.gov.ns.ca/natr/library/forestry/reports/REPORT76.PDF

McFee, W.W. and Stone, E.L. 1966. The persistence of decaying wood in the humus layers of northern forests. Soil Science Society of America Journal 30(4): 513-516.

Melson, S.L., Harmon, M.E., Fried, J.S., and Domingo, J.B. 2011. Estimates of live-tree carbon stores in the Pacific Northwest are sensitive to model selection. Carbon Balance and Management 6(2): 1-16.

Millar, C.I., Stephenson, N.L., and Stephens, S.L. 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications 17: 2145–2151.
http://dx.doi.org/10.1890/06-1715.1

Mishra, U. and Riley, W.J. 2012. Alaskan soil carbon stocks: Spatial variability and dependence on environmental factors. Biogeosciences 9: 3637–3645. www.biogeosciences.net/9/3637/2012/, DOI:10.5194/bg-9-3637-2012

Moiseev, B.N., Alfiorov, A.M., and Strakhov, V.V. 2000. About the evaluation of carbon stores and increments in forests of Russia (in Russian). Lesnoye Khozyajstvo 4: 18-20.

Murphy, K.A. and Witten, E. 2006. Fire Regime Condition Classes (FRCC) Interagency Guidebook Reference Conditions (draft).

NOAA 2014. National Oceanic and Atmospheric Administration. NOAA Satellite and Information Service. National Climatic Data Center. US Department of Commerce.
http://www.ncdc.noaa.gov/IPS/cd/cd.html;jsessionid=4E5612C511E74A2687A84659B08AA18
7?_page=0&jsessionid=4E5612C511E74A2687A84659B08AA187&state=AK&_target1=Next+
%3E

Nowacki, G., Spencer, P., Fleming, M, Brock, T., and Jorgenson, T. 2002. Unified ecoregions of Alaska: 2001. U.S. Geological Survey Open-File Report 02-297 (map).
http://agdc.usgs.gov/data/usgs/erosafo/ecoreg/index.html

Nowacki, G.J. and Kramer, M.G. 1998. The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. Gen. Tech. Rep. PNW-GTR-421. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Station, 32 p.

Oades, J.M. 1993. The role of biology in the formation, stabilization and degradation of soil structure. Geoderma 56(1): 377-400.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164 (3877): 262-270.

Odum, E.P. 1968. Energy flow in ecosystems: A historical review. American Zoologist 8: 11-18.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in terrestrial ecosystems. Ecology 42: 322-331.

Onega, T.L. and Eickmeier, W.G. 1991. Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. Bull. Torrey Bot. Club 118: 52–57.

Ott, R.A. and Juday, G.P. 2002. Canopy gap characteristics and their implications for management in the temperate rainforests of southeast Alaska. For. Ecol. Manage. 159(3): 271-291.

Pickett, S.T.A. and White, P.S. 1985. Patch dynamics - a synthesis. *In*: Pickett S.T.A. and White, P.S. (Eds.). Ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, pp. 371-384.

Ping, C.L., Michaelson, G.J., Kimble, J.M., and Everett, L.R. 2002. Organic carbon stores in Alaska soils. *In*: Lal, R., Kimble, J.M., and Follet, R. (Eds.). Agricultural Practices and Policies of Carbon Sequestration in Soils, pp. 485-494.

Post, W.M., Peng, T.-H., Emanuel, W.R., King, A.W., Dale, V.H., and DeAngelis, D.L. 1990. The global carbon cycle. American Scientist 78: 310–326.

Potkin, M. 1997. Fire history disturbance study of the Kenai Peninsula mountainous portion of the Chugach National Forest. Draft. USDA Forest Service. Chugach National Forest. December 5, 1997. Anchorage, Alaska.

Pregitzer, S.P. and Euskirchen, E.S. 2004. Carbon cycling and storage in world forests: Biome patterns related to forest age. Global Change Biology 10(12): 2052-2077.

Raphael, M.G. and Morrison, M.L. 1987. Notes: Decay and dynamics of snags in the Sierra Nevada, California. Forest Science 33(3): 774-783.

Rogers, P. 1996. Disturbance ecology and forest management: A review of the literature. USDA Forest Service, Intermountain Research Station, Gen. Tech. Rep. INT GTR-336. (See also http://www.usu.edu/beetle/literature.htm)

Ross, D.W., Daterman, G.E., Boughton, J.L., and Quigley, T.M. 2001. Forest health restoration in South-Central Alaska: A problem analysis. USDA Forest Service. PNW Research Station. PNW-GTR-523, July 2001.

Santantonio, D., Hermann, R.K., and Overton, W.S. 1977. Root biomass studies in forest ecosystems. Pedobiologia 17: 1-31.

Schimel, D.S. 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1(1): 77-91.

Shorohova, E.V. and Shorohov, A.A. 1999. Characteristics of detritus decay classes for spruce, birch, and aspen in middle taiga spruce forests. St.-Petersburg Forestry Research Institute 1: 17-23.

Shvidenko, A.Z. and Nilsson, S. 2000. Fire and the carbon budget of Russian forests. *In*: Kasischke E.S. and Stocks, B.J. (Eds.). Fire, climate change, and carbon cycling in the boreal forests, pp. 289-311.

Smithwick, E.A.H., Harmon, M.E., Remillard, S.M., Acker, S.A., and Franklin, J.F. 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. Ecological Applications 12: 1303–1317. http://dx.doi.org/10.1890/1051-0761(2002)012[1303:PUBOCS]2.0.CO;2

Soja, A.J., Tchebakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., Chapin, F.S., and Stackhouse, P.W. 2007. Climate-induced boreal forest change: Predictions versus current observations. Global and Planetary Change 56(3): 274-296.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D., and Spycher, G. 1987. Patterns of log decay in old-growth Douglas-fir forests. Can. J. For. Res. 17(12): 1585-1595.

Spies, T.A., Franklin, J.F., and Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69(6): 1689-1702.

Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan, M.D., Hirsch, K.G., Logan, K.A., Martell, D.L., and Skinner, W.R. 2002. Large forest fires in Canada, 1959–1997. Journal of Geophysical Research: Atmospheres (1984–2012), 107(D1), FFR-5.

Stocks, B.J., Fosberg, M.A., Lynham, T.J., Mearns, L., Wotton, B.M., Yang, Q., Jin, J.-Z., Lawrence, K., Hartley, G.R., Mason, J.A., and McKenney, D.W. 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. Climatic Change 38(1): 1-13. http://dx.doi.org/10.1023/A%3A1005306001055

Tarasov, M.E. 1999. Role of coarse woody debris in carbon balance of forest ecosystems of Leningrad oblast' (in Russian). Candidate of biological sciences thesis. St.-Petersburg Institute of Scientific Research in Forestry.

Triska, F.J. and Cromack, K. Jr. 1980. The roles of wood debris in forests and streams. *In*: Waring, R.H. (Ed.). Forests: Fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis, Oregon, pp. 171-190.

USDA 2014a. PNW-FIADB. Pacific Northwest Annual Forest Inventory Database. Pacific Northwest Research Station, Forest Inventory and Analysis. http://www.fs.fed.us/pnw/rma/fia-topics/inventory-data/index.php

USDA 2014b. Field instructions for the annual inventory of Coastal Alaska 2014. Forest Inventory and Analysis program. PNW Research Station. USDA Forest Service.

USDA 2010. Southeast Forest Health Protection. State and Private Forestry. Alaska Region. http://www.fs.fed.us/r10/spf/fhp/sefhp/seycedar.htm.

USDA 2005. Forest health conditions in Alaska – 2004. A forest health protection report. USDA Forest Service. Alaska region R-10-PR-3. State of Alaska Natural Resources Division of Forestry. Compiled by Dustin Wittwer. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev2_038152.pdf

USDA 2003. Field procedures for the Coastal Alaska inventory 2003. USDA Forest Service, PNW Research Station – Forestry Sciences Lab and Region 10 – Alaska. http://www.fs.fed.us/pnw/fia/local-resources/pdf/field_manuals/ak/2003_coak_field_manual.pdf

USDA 2000. Field procedures for the southeast Alaska inventory 2000. USDA Forest Service, PNW Research Station – Forestry Sciences Lab and Region 10 – Alaska. http://www.fs.fed.us/pnw/fia/local-resources/pdf/field_manuals/ak/2000_seak_field_manual.pdf

Van Hees, W.W.S. 2003. Forest resources of southeast Alaska, 2000: Results of a single-phase systematic sample. Res. Paper PNW-RP-557. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Station, 96 p.

Van Pattern, D.J. 2000. Soil survey of lower Kenai Peninsula area, Alaska. USDA NRCS publication, 179 p.

Veblen, T.T. and Alaback, P.B. 1996. A comparative review of forest dynamics and disturbance in the Temperate rainforests of North and South America. *In*: Lawford, R.G., Alaback , P.B., and Fuentes, E. (Eds.). High-latitude rainforests and associated ecosystems of the West Coast of the Americas: Climate, hydrology, ecology, and conservation. Springer-Verlag New York, 409 p.

Viereck, L.A. and Little, E.L. Jr. 1972. Alaska trees and shrubs. Agric. Handb. 410. Washington, DC: U.S. Department of Agriculture, Forest Service, 265 p.

Vitousek, P.M. and Reiners, W.A. 1975. Ecosystem succession and nutrient retention: A hypothesis. Bioscience 25(6): 376-381. DOI: 10.2307/1297148.

Waddell, K.L. 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. Ecological Indicators 1: 139-153.

Waring, R.H. and Running, S.W. 2010. Forest ecosystems: Analysis at multiple scales. Elsevier.

Waring, R.H. and Schlesinger, W.H. 1985. Forest ecosystems. Concepts and management. Academic Press.

Werner, R.A., Holsten, E.H., Matsuoka, S.M., and Burnside, R.E. 2006. Spruce beetles and forest ecosystems in south-central Alaska: A review of 30 years of research. Forest Ecol. Manag. 227: 195–206.

Werner, R.A. and Holsten, E.H. 1983. Mortality of white spruce during a spruce beetle outbreak on the Kenai Peninsula in Alaska. Can. J. For. Res. 13: 246-250.

Whittaker, R.H. and Likens, G.E. 1973. Carbon in the biota. *In*: Woodwell, G.M. and Pecan, E.V. (Eds.) Carbon and the biosphere. Technical Information Center, Oak Ridge, TN, pp. 281-302.

Wittwer, D. (Compiler). 2004. Forest health conditions in Alaska—2003, a forest health protection report. U.S. For. Ser. Tech. Rep. R10-TP-113. Juneau, AK, USA.

Woodwell, G.M., Whittaker, R.H., Reiners, W.A., Likens, G.E., Delwiche, C.C. and Botkin, D.B. 1978. The biota and the world carbon budget. Science 199: 141-178.

Zogas, K. and Holsten, E.H. 2002. Bibliography Alaska region. Forest health protection 1919 – 2001. Tech. Rep. R10-TP-107. USDA Forest Service, S&PF. Anchorage, AK, 136 p. http://www.fsl.orst.edu/wfiwc/admin/history/ak-bibliography.pdf

Yatskov, M., Harmon, M.E., and Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. For. Res. 33: 1211-1226.

Yavitt, J.B. and Fahey, T.J. 1982. Loss of mass and nutrient changes of decaying woody roots in lodgepole pine forests, southeastern Wyoming. Can. J. For. Res. 12(4): 745-752.

CHAPTER 3 -- DECOMPOSITION DIFFERENCES BETWEEN SNAGS AND LOGS IN FORESTS OF KENAI PENINSULA, ALASKA FOLLOWING SPRUCE BARK BEETLE OUTBREAK

Mikhail A. Yatskov, Mark E. Harmon, Becky Fasth, Lori Trummer, Jay Sexton, Toni L. Hoyman, and Chana M. Dudoit

ABSTRACT

Progressive rise in temperatures in northern latitudes could potentially increase the frequency and severity of disturbances in forest ecosystems, transferring large amounts of live biomass to coarse woody debris (CWD) pools that emit carbon (C) in form of carbon dioxide (CO_2). The type of CWD created by these disturbances may determine the rate and amount of C transfer as well as the length of time the disturbed landscape remains a C source. We studied the effect of a large-scale disturbance on CWD dynamics in spruce-dominated forests of Kenai Peninsula, Alaska by determining CWD decomposition rate-constants using the chronosequence and decomposition-vectors approaches and modeling CWD dynamics after a hypothetical bark beetle outbreak versus a windthrow. Decomposition rate-constants from the chronosequence ranged between -0.015 yr^{-1} and -0.022 yr^{-1} for logs and -0.003 yr^{-1} and +0.002 yr^{-1} for snags. Decomposition rate-constants for logs from the decomposition-vectors ranged between -0.045 yr^{-1} and +0.003 yr^{-1} among decomposition phases and -0.048 yr^{-1} and +0.006 yr^{-1} among decay classes. The modeling exercise showed that relative to log generating disturbances those creating snags delayed C flux from CWD to the atmosphere, produced a smaller magnitude C flux, and have a potential to store 10% to 66% more C in the system over time.

INTRODUCTION

Forests comprise much of the terrestrial C store with the amounts being dependent on natural and anthropogenic disturbance regimes. Disturbances reorganize forests, reducing the live and increasing dead matter, hence altering the C balance. At larger extents of time and space, changes in disturbance regimes could lead to a long-term alteration in amount of C stored in forests which in turn could trigger changes in climatic feedbacks. With a relatively constant disturbance regime under stable climate, negative feedbacks could lead to long-term stability in C stores. Under changing climate the disturbance regime may become more intense creating a strong influx of C into CWD pool leading to possible positive feedbacks exacerbating alterations in climate.

CWD is an important, long-lasting element of forest ecosystems (McFee and Stone 1966, Triska and Cromack 1980) serving multiple roles from structural and functional components (Harmon et al. 1986, Franklin et al. 1987) to nutrient (Odum 1969, Vitousek and Reiners 1975, Lambert et al. 1980, Fahey 1983, Krankina and Harmon 1995) and energy (Odum 1968) cycling. In temperate and boreal forests CWD also serves as a long-term C storage (Spies et al. 1988, Smithwick et al. 2002, Janisch and Harmon 2002). The absolute amounts of CWD (Spies et al. 1988, Smithwick et al. 2002) vary by forest and disturbance types (Yatskov et al. - Chapter 2, Tables 2.1 and 2.2) and successional stages of stand development (Janisch and Harmon 2002)**. The large-scale mortality associated with frequent and severe disturbances could temporarily increase CWD stores which combined with elevated decomposition rates resulting from warmer climate could lead to increased CO_2 fluxes to the atmosphere. CO_2, a greenhouse gas, has rapidly

increasing atmospheric concentrations linked to the phenomena of the global climate change

(IPCC 2013). Decomposition of CWD is a major pathway for C stored in forest ecosystems to

get released as CO_2 to the atmosphere.

CWD decomposition rates are an integral part in the C cycling controlled by the quality of

substrate, type of decomposing organisms, and substrate moisture and temperature (Harmon et

al. 1986, Harmon et al. 2011a). CWD position (standing, i.e. snags vs. downed, i.e. logs) is a one

of the important characteristics having potential to influence the CWD decomposition rates due

to differences in microclimates with snags generally decomposing slower than logs (Harmon et

al. 1986, Onega and Eickmeier 1991, Yatskov et al. 2003, Jomura et al. 2008).

CWD decomposition rates have been studied extensively in the PNW of the U.S. (Triska and

Cromack 1980, Graham and Cromack 1982, Sollins 1982, Erickson et al. 1985, Harmon et al.

1994, Harmon et al. 1995, Janisch et al. 2005), Canada (Johnson and Greene 1991, Laiho and

Prescott 1999, Brais et al. 2006), Russia (Krankina and Harmon 1995, Tarasov 1999, Harmon et

al. 2000, Wirth et al. 2000, Shorohova and Shorohov 2001, Tarasov and Birdsey 2001, Yatskov

et al. 2003) and Europe (Naesset 1999, Shorohova et al. 2008). Alaska, a vast forested region

containing large C stores in live and dead biomass and in soils (Birdsey and Heath 1995, Heath

et al. 2011, Goodale et al. 2002), has been overlooked in these studies despite the fact that high

latitude forests in recent decades have been identified as hotspots of the global climate change

(Stocks et al. 1998, Giorgi 2006). These climatic changes impact stores and overall C dynamics

(Goetz et al. 2007). For our study we selected Kenai Peninsula located in south-central Alaska.

With little to no data on CWD decomposition, a total area of ~2.3 million ha (Schwartz and Franzmann 1991) a quarter of which are forested (Potkin 1997), and 429,000 ha of forest affected by spruce bark beetle infestation that took place between 1989 and 2004 (U.S. Forest Service 2004, M. Rude, Kenai Peninsula Spruce Bark Beetle Mitigation Program, unpublished data), Kenai Peninsula offered a great opportunity for research on this topic. As the disturbances of this type, severity, and magnitude might represent the future response of the forest ecosystems to climate change, we studied the CWD decomposition on Kenai Peninsula to understand the consequences of such disturbances for C balance and cycling within forest ecosystems.

The studies of CWD decomposition rates have mostly utilized four main methods including time series in which CWD pieces are tracked through time as they decompose (Edmonds and Eglitus 1989, Alban and Pastor 1993, Harmon et al. 1994, Harmon et al. 1995, Chueng and Brown 1995, Brown et al. 1996), input-to-biomass ratios in which the system is assumed to be in a steady-state (Lambert et al. 1980, Sollins 1982, Harmon and Chen 1991), chronosequences involving substitution of space for time allowing for simultaneous sampling of CWD that died at various times (Harmon et al. 1987, Krankina and Harmon 1995, Yatskov et al. 2003, Janisch et al. 2005), and decomposition-vectors analysis representing a hybrid between the time series and the chronosequence (Harmon et al. 2000). In our study we relied on the chronosequence and decomposition-vectors approaches which shared similarities in sampling methodology, took advantage of the dated disturbance events, obtained results in a relatively short period of time in contrast to time series, and dealt with bole-level measurements in disturbed stands as opposed to

input-to-biomass ratios which require systems in a steady-state and are based on stand-level measurements.

In formulating our hypothesis we utilized the knowledge of previous studies on snag and log decomposition. Several studies reported that the decomposition rate-constants of snags are lower than those of logs (Onega and Eickmeier 1991, Yatskov et al. 2003), with moisture and temperature being the causal factors (Harmon et al. 1987, Harmon and Chen 1991, Marra and Edmonds 1996, Chen 1999, Hicks 2000). The remaining mass of spruce logs was also shown to follow the reverse S-shaped pattern with three distinct (slow-fast-slow) phases (Harmon et al. 2000, Yatskov et al. 2003) as opposed to single-exponential curve (Olson 1963) often used to describe decomposition.

The overall objective of the study was to investigate the effects of large-scale disturbance on CWD dynamics in spruce-dominated forests of Kenai Peninsula, Alaska. We examined three hypotheses: 1) Snags decompose slower than logs, 2) CWD decomposition consists of three phases with distinctly different decomposition rate-constants, 3) Disturbances differing in the type of CWD created (snags vs. logs) affect C release from CWD. To address these we used: 1) a chronosequence approach to determine and compare decomposition rate-constants of snags and logs, 2) a decomposition-vectors analysis to examine and compare early, intermediate, and late stages in CWD decomposition associated with <30%, 30% - 70%, and >70% density, volume, or mass loss over time, and 3) a simulation model to examine the effect on CWD dynamics of disturbances caused by bark beetles vs. windthrow.

METHODS

Study area

The Kenai Peninsula covers 2.6 million ha in south central Alaska (latitude 60°N, longitude 150°W) (Peterson et al. 1984). The Peninsula is surrounded by Prince William Sound (east), Cook Inlet (west), Turnagain Arm, a semidiurnal hypertidal estuary (Greb and Archer 2007) (north), and Gulf of Alaska (south) and connected to mainland Alaska in the north by 16-km wide bridge made of land and ice (Peterson et al. 1984) (Figure 3.1).

The Peninsula can be divided into two distinct landforms. The eastern part is dominated by the snowcapped Kenai Mountains rising to 2,000 m above sea level, supporting major ice fields (Peterson et al. 1984, Schwartz and Franzmann 1992). The western part, formed by the Kenai lowlands, is represented by a rolling plateau with the elevation ranging from sea level to 500 m above sea level (Peterson et al. 1984) and covered by numerous lakes, ponds, and wetlands.

Long-term climatic records for the western and northern portions of the Kenai Peninsula representing our study area indicate a maritime climate with spring being the driest and fall being the wettest seasons (Table 3.1). The 30-year mean annual temperature (Table 3.2) over the period between 1979 and 2008 was 2.4°C with a low of 0.9°C (in 1996 and 1999) and a high of 3.9°C (in 2002) (NOAA 2014). The coldest month in the region was January with the 30-year mean temperature of -6.9°C. The hottest month was July with the 30-year mean of 12.8°C. Mean annual precipitation in this zone for the same time period was 584 mm with a low of 397 mm (in 1996) and a high of 816 mm (in 1981) (NOAA 2014).

The Kenai lowlands support variety of vegetation communities ranging from pure stands of black spruce (*Picea mariana* (Mill.) B. S. P.) on wet organic soils, to mixed forests containing either white spruce (*Picea glauca* (Moench) Voss), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), or Lutz spruce (*Picea* x *lutzii* Little), a viable hybrid between white and Sitka spruce, mixed with trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), or both of these hardwoods growing on drier more productive sites. Riparian areas along rivers and around wetlands are dominated by black cottonwood (*Populus balsamifera* ssp. *trichocarpa* L.) stands or alder-willow (*Alnus-Salix*) shrub communities (Potkin 1997, Van Pattern 2000).

Natural and anthropogenic disturbances have formed forests that are complex in age structure and their distribution of live and dead components. Natural disturbances that are most significant in extent, severity, and long-term effects on forest communities include catastrophic fires (Potkin 1997, De Volder 1999, Berg et al. 2006, Anderson et al. 2006) and spruce bark beetle outbreaks (Holsten et al. 2000, Werner et al. 2006). Anthropogenic disturbances historically were associated with selective harvest of accessible spruce stands (Van Pattern 2000), whereas more recently were attributable to salvage logging in beetle-damaged stands (Flint 2006). Interaction of the disturbance types on the Kenai creates a potential for the cascading disturbances when windthrow, fire, or harvest follow the spruce bark beetle outbreaks (Holsten et al. 2000, Ross et al. 2001, Flint and Haynes 2006), or when bark beetle outbreaks, windthrow, or harvest follow fires (McCullough 1998, Werner et al. 2006).

Experimental design

This project was an observational study using the CWD generated by disturbances taking place at various times across Alaska's Kenai Peninsula. CWD included spruce snags (i.e., standing dead boles) and logs (downed and dead boles) with minimum large-end diameter of 10 cm and minimum length of 3 m. Snags and logs, covering full range of decomposition stages, were treated as experimental units that were sampled during two sampling times (2002 and 2008) in a total of 21 plots within 13 sites across western and northern parts of the Peninsula (Figure 3.1). By utilizing a chronosequece approach, we substituted space for time by making an assumption that the sites and plots are similar in conditions controlling the decomposition process. The criteria for site selection included our ability to date the timing of disturbances causing tree mortality and presence of logs and snags suitable for sampling.

In 2002, a total of 226 spruce trees including 69 snags, 146 logs and 11 live trees were sampled (Table 3.3). Among sampled live and dead trees the large-end diameters ranged between 10 and 70 cm and length ranged between 3.7 m and 25.7 m. Live trees and snags were felled to allow for sampling. Out of 215 CWD pieces, time since death (hereafter referred as CWD age) was determined for 195. All 69 snags and 126 logs were dated with snag ages ranging between 1 and 43 years and log ages ranging between 2 and 76 years (Table 3.3). Among the 146 logs, we sampled 20 that were not dated, thus did not determine CWD age. Eleven live trees were sampled to determine bark and wood initial (prior to decomposition) density and initial bark thickness and were assigned a CWD age of 0.

In 2008, a total of 253 CWD pieces were sampled including 29 new snags with ages ranging

between 5 and 44 years to replace ones that had been felled in 2002. In addition we sampled 2

new logs with the age of 24 years, resampled 202 logs (a legacy of 2002 sampling) with ages

ranging between 6 and 82 years, and resampled 20 logs that were not dated in 2002 (Table 3.3).

Field procedures

The field procedures included: dating CWD, assigning CWD to one of five decay classes,

measuring CWD dimensions (diameters, length, bark percent cover and wood fragmentation

losses), and sampling CWD bark and wood for density.

CWD dating determined the CWD age to be used in building chronosequences. In dating CWD

we utilized the permanent disturbance records (beetle outbreaks, fires, logging activities,

windthrow events), mortality information from long-term forest health monitoring plots, scars on

nearby live trees caused by tree or snag fall, age of regeneration following disturbance, and the

date of growth release from trees that survived the disturbance. The precision of these methods

varies with more recent disturbance events providing more accurate information on CWD age.

Among the sampled sites, Dry Gulch (Holsten 1984) and Resurrection Creek (Werner and

Holsten 1983) were permanent long-term health monitoring sites of spruce bark beetle activity

providing fairly accurate information on the timing of tree mortality (starting 1969 and 1976,

respectively). CWD cause of death was recorded: the majority of CWD pieces resulted from

mortality caused by spruce bark beetles (122) with fire being a second most common cause of

death (60), followed by cutting (17), windthrow (13), wind breakage (2), and other random miscellaneous causes including unknown (12).

A five decay-class system was utilized to generally describe the state of decomposition. After CWD pieces were selected, each was assigned to one of five decay classes based on visual characteristics developed in other studies (Triska and Cromack 1980, Graham and Cromack 1982, Sollins 1982, Harmon and Sexton 1996) and utilized extensively by the USDA Forest Inventory and Analysis (FIA) program to tally CWD (USDA 2014). These characteristics included indicators of structural integrity (presence of bark, sloughing of sapwood, ability of CWD piece to support its own weight, mobility of branch stubs, cross-sectional shape of the CWD pieces) as well as indicators of wood tissue deterioration by biotic factors (wood discoloration such as blue stain associated with the invasion of fungi, visible presence of white or brown rots, and/or presence of fungi fruiting bodies).

Two sets of measurements were taken to allow for CWD volume calculations necessary for building the chronosequences. The first set, used for current bole volume calculations, included base and top diameters, diameter at 1.37 m from the base referred to as diameter at breast height (d.b.h.), bole length, as well as diameters at the locations of tissue sampling. The second set, used for estimation of the initial bole volume, included stem diameters and length noted above along with measurements that allowed reconstruction of the missing bark and/or wood based on initial thickness, stem length missing from decay, and whether the current volume represented the whole tree vs. a partial tree. There were 24 logs recorded as partial trees and 7 logs without

an initial DBH reconstructed in the field. Most of these logs were used to calculate the decomposition rate-constants through the chronosequence analysis. Twenty logs that were missing the CWD age were used for analysis associated with decay classes and decomposition-vectors but not the chronosequence analysis.

Tissue density sampling necessary for CWD biomass calculations was performed on every snag and log (11 live trees sampled in 2002 included). As a general rule four discs (separated into bark and wood samples) were cut equidistant along the CWD bole with a chainsaw unless CWD pieces were relatively short in length. Diameter of each disc was measured in the field either with a steel Spencer logger tape or cloth diameter tape (for intact sections) or a ruler as minimum and maximum (for decomposed sections with elliptical cross-section) (to the nearest 0.1 cm). The distance of the sampling location from the base along the tree bole was measured with a Spencer tape (to the nearest 0.1 m) (see extensive sampling methods description in Harmon and Sexton 1996 and Yatskov 2000). Discs were wrapped with plastic film and placed inside plastic bags to prevent loss of material and moisture and transported to the field camp. Discs were stored for a day or occasionally for several days in a cool place before processing.

Lab procedures

Lab procedures determined bark and wood sample dimensions (diameters, longitudinal thickness, radial thickness, circumferential length) and weights, and measured the wood radial depth of decay. Diameters, longitudinal thickness, circumferential length, and radial depth of decay were measured to the nearest 0.1 cm, whereas the radial thickness was measured to the

nearest 0.1 mm. Sample dimensions were used to calculate tissue sample volume. Tissue weights divided by this volume produced bark and wood density. Wood radial depth of decay was measured to assess the rate of decay spread into logs and snags.

The sample dimensions taken depended on the physical condition of the discs: fully intact (intact bark and wood), fragmented bark and intact wood, or wood discs with elliptical cross-section. For the intact discs (those having no missing bark or wood) the outside-bark and the inside-bark (i.e., wood) diameters and disc longitudinal thickness at 4-6 equally spaced locations were measured. Diameters were measured with a cloth diameter tape, whereas longitudinal thickness was measured with a ruler or electronic caliper. For the discs with fragmented bark, bark circumferential length and longitudinal and radial thicknesses were measured. Bark circumferential length was measured either with a cloth tape or a ruler, longitudinal thickness was measured with a ruler, whereas radial bark thickness was measured with an electronic caliper. Average longitudinal thickness of bark and wood was based on at least four measurements with the number of measurements being dependent on the regularity of shape of each tissue. Radial bark thickness was measured on fragmented bark with an average based on at least four measurements. For wood discs having the elliptical cross-section characteristic of logs with advanced stages of decomposition, measurements of maximum and minimum diameters and wood longitudinal thickness were taken in the field with a ruler. Depth of decay was measured with a ruler on each quadrant of the cut face of each disc as the distance the decay advanced from the periphery of the disc towards the pith.

Total wet bark and wood sample weights for each disc were determined in the field office.

Weighing of bark and wood samples and subsamples was conducted using two types of

electronic scales. Ohaus Corporation NV-8100 scales with 8100 g capacity and readability to 0.5

g were used to weigh total bark and wood wet samples. Ohaus Corporation CT200 with 202 g

capacity and readability to 0.01 g were used to weigh the bark and wood wet and dry

subsamples. Wood and bark subsamples (50-150 g depending on the stage of deterioration) were

taken in the field office, weighed to determine the wet subsample weight, placed in cloth bags,

and air dried to reduce further decomposition. Subsample dry weight was determined at the

laboratory after oven drying at 55°C for up to two weeks until a stable weight was recorded.

Calculations

Calculations estimated CWD bole current and initial volume, density, and mass. These

calculations were done at two levels: for each disc and the entire bole.

Disc-level calculations

For the intact discs the outside-bark and the inside-bark (wood) volumes were calculated

utilizing the volume formula for a cylinder. Bark volume was determined as the difference

between outside-bark and inside-bark disc volumes. Bark volume for the discs with fragmented

bark was determined using formula for a rectangular cuboid utilizing three dimensions of the

fragmented bark. Volume of wood discs having the elliptical cross-section was determined

utilizing the formula for a volume of a cylinder with cross-section area based on an ellipse.

Subsample wet and dry weights were used to calculate the dry-to-wet weight ratio, which was multiplied by the total disc wood and bark wet weights to produce total sample wood and bark dry weights. Bark and wood sample densities were determined as the ratio of the sample bark and wood dry weights to corresponding volumes.

Percent disc cross-section area affected by decay was calculated using the inside bark disc diameter and the radial depth of decay. First, average depth of decay was calculated (in the lab during disc processing) as an average of at least four measurements. Second, the area affected by decay was determined as the difference between the total disc cross-section area and the disc cross-section area unaffected by decay. Third, the percent disc cross-section area affected by decay in relation to total disc cross-section area was calculated.

Bole-level calculations

To build chronosequences it was necessary to determine the initial (preceding decomposition) and current (as of time of sampling) volume, biomass, and density for each sampled snag and log with subsequent calculations of the proportion remaining volume, biomass, and density. We separated this process into four steps.

As a first step, current and initial CWD bole volumes were determined. Each bole was divided into segments where dimensions were represented by segment length and large- and small-end diameters (base diameter, d.b.h., cross-section diameters, and top diameter). In our calculations we utilized several pathways depending on the physical bole condition of the sampled snag or

log. For the fully intact segments, the outside and inside-bark (wood) segment volumes were determined using a formula for a frustrum of a cone:

$$V = \frac{l}{3} \times (A_L + A_S + \sqrt{A_L \times A_S}), \text{ where} \qquad \text{(Equation 1)}$$

V is segment volume (m³), l is segment length (m), A_L is basal area at the large end (m²), and A_S is basal area at the small end (m²). Bark segment volume was determined as a difference between the outside and the inside-bark segment volumes. In case of intact segments, the current and initial tissue volumes were assumed equal. In case of pieces with fragmented or absent bark and intact wood, segment wood volume was determined using equation 1. When bark was fragmented, radial bark thickness was utilized to calculate outside-bark segment diameters and to determine the segment initial bark volume (as the difference between outside and inside-bark segment volumes). Segment current bark volume was calculated as a product of the initial bark volume and the bole bark percent cover. For the segments where bark was completely absent, the initial bark volume was determined using the initial bark radial thickness from freshly felled trees. The initial radial bark thickness for each segment without bark was calculated in four steps and was based on 11 live trees sampled in 2002. First, for each sampled disk within the tree we determined the bark thickness-to-inside bark diameter ratio. Second, for each of 11 trees we determined average ratio weighed by the disc bark cross-section area. Third, we calculated the overall average ratio using 11 trees. Finally, the estimated bark thickness for the large- and small-end diameters in a segment was calculated using this ratio. For snags and logs with fragmented or missing wood, we utilized missing wood measurements (length and radial

thickness) to calculate the initial wood volume. Combined (bark and wood) current and initial segment volumes were calculated as the sum of segment bark and wood current and initial volumes, respectively. Total CWD bole current and initial volumes were calculated as the sum of segment volumes.

To estimate the initial volume of the logs recorded as partial as well as logs missing reconstructed DBH, first we estimated the initial DBH. We made an assumption that the initial DBH could not have been smaller than the largest diameter measured for a particular log in the field (either base diameter, diameter of any disk sampled, or top diameter). Second, we took the largest diameter assuming it was inside bark diameter and from it estimated the initial DBH by adding the missing initial bark radial thickness multiplied by two. Reconstruction of the initial DBH allowed us to estimate the initial volume at the time of death by using allometric volume equation developed based on 11 intact freshly cut trees and 52 intact Decay Class 1 (DC-1) and DC-2 snags and logs:

$$V = 0.4272 * DBH^{2.1036}, \text{ where} \qquad \text{(Equation 2)}$$

V is bole volume, and DBH is bole diameter at 1.37 m from the ground level.

The same 63 trees were used to develop allometric height equation to reconstruct the initial total tree length when the sampled log was not entire. The equation form was based on Garman et al. (1995):

$$H = 1.37 + 54 \times \left[1 - exp(-0.0136 \times DBH)^{0.885}\right], where \qquad \text{(Equation 3)}$$

H is total bole length in m, and ***DBH*** is bole diameter at 1.37 m from the ground level.

As second step, current and initial CWD bole biomasses were determined. Segment bark and wood biomass was calculated as a product of current and initial segment bark and wood volumes and corresponding current and initial bark and wood densities. For all segments within a CWD piece except the top one, current bark and wood densities associated with the upper disc in each segment were used. For the very top segment, current bark and wood densities associated with the lower disc in the segment were used. Initial bark and wood densities were obtained as an average weighted by the disc bark or wood area from 11 live trees sampled in 2002. Combined (bark and wood) current and initial segment biomasses were calculated as a sum of segment bark and wood current and initial biomasses, respectively. Total CWD bole current and initial biomasses were calculated as a sum of segment biomasses.

For the logs recorded as partial as well as logs missing reconstructed DBH the initial mass was calculated by multiplication of the allometrically determined initial volume and the initial bole density from 11 freshly cut trees.

As the third step, current and initial CWD bole densities were determined as the ratio of corresponding CWD bole biomasses to total CWD bole volumes.

As the final step, the proportion volume, mass, and density remaining was calculated for each individual CWD piece:

$$\boldsymbol{Proportion\ Remaining}\ (\boldsymbol{V}, \boldsymbol{D}, \boldsymbol{M}) = \frac{Current\ (V,D,M)}{Initial\ (V,D,M)}, \text{where} \qquad \text{(Equation 4)}$$

V is volume, *D* is density, and *M* is mass, **Current** represents snag/log volume, density, or mass at time of sampling in 2002 or 2008, **Initial** represents the estimate of initial snag/log volume, density, or mass at the time of tree death.

Percent disc cross-section area affected by decay at the bole level was calculated as the percent area weighted by the individual disc cross-section area.

Statistical analysis

Statistical analysis comprised of three independent steps: the decay class-specific characteristics analysis, the chronosequence analysis, and the decomposition-vectors analysis. Each analysis was performed for three CWD physical characteristics: volume, density, and mass. Once the snag and log decomposition rate-constants from the chronosequence and the decomposition-vectors were obtained, we modelled CWD stores and dynamics.

Decay class-specific characteristics

We calculated mean (± standard error, SE) CWD current density, percent bark cover, tissue moisture content, and percent disc cross-section area affected by decay by year of sampling, position, and decay class to generally describe the decomposition process. The trends in decomposition (changes in decay class-specific density, percent bark cover, moisture content, and percent disc cross-section area affected by decay) were compared between snags and logs.

Chronosequence analysis

We used three data sets to analyze decomposition rate-constants of CWD volume, mass, and density loss. Snags and logs in each of these data sets were analyzed as separate groups. The first data set was based on the 2002 CWD collection. It included 69 snags with the age range between 1 and 43 and 137 logs (excluding from general log data set 20 logs missing CWD age and including 11 logs cut as live trees) with the age range between 0 and 76 years (Table 3.3). The second data set was based on the 2008 CWD collection. It included 29 new snags (not sampled in 2002) with the age range between 5 and 44, 2 new logs aged at 24 years, and 205 logs (legacy of 2002 sampling including 69 snags and 136 logs) with the age range between 6 and 82 (Table 3.3). The third data set contained a mix of 2002 and 2008 CWD pieces with the purpose of increasing the number of data points in the chronosequence. To form a third data set from the 2002 and 2008 sets for snags we used all 98 snags (69 from 2002 and 29 from 2008) cumulatively having a CWD age range between 1 and 44. The log data set was constructed from several sources, namely, the logs sampled either in 2002 (count of one) or 2008 (count of two) and the 136 CWD that were sampled as logs in 2002 and re-sampled in 2008. To form a data set from the 136 re-sampled logs we determined the mean for CWD age, volume, mass, and density using log physical characteristics from the two sampling events. Therefore, the final data set included logs sampled either in 2002 or 2008, and re-sampled logs, and contained 139 CWD with the age range between 0 and 82 years. The 69 CWD sampled as snags in 2002 and re-sampled as logs in 2008 were excluded from this data set. Snags converted to logs had the decomposition rate-constant that was substantially lower than the pure log data set, thus when lumped with re-sampled logs, it significantly lowered the overall rate-constant.

We analyzed chronosequences for snags and logs in each of three data sets using single exponential equation (Olson 1963):

$$Y_t = Y_0 \times e^{-k \times t}, \text{ where} \qquad \text{(Equation 5)}$$

Y_t is the proportion volume, density, or mass remaining at time t (years), Y_0 is the proportion initial volume, density, or mass, i.e. 1.0, and k is decomposition rate per year constant (year^{-1}).

Linear regression (PROC MIXED procedure, SAS statistical software package, Version 7, SAS Institute, Cary, NC) was run after the proportion of volume, density, or mass remaining was transformed to natural logarithm:

$$ln(proportion\ V, D, M\ remaining) = -k \times t, \text{ where} \qquad \text{(Equation 6)}$$

V is volume, D is density, M is mass, k is decomposition rate per year constant (year^{-1}), and t is time (years).

We used equation 5 and checked whether intercept was greater than zero (Table A3.1) indicating a lag in decomposition and the need for a nonlinear equation. We also visually inspected each data set to examine the goodness of fit. In those cases when intercept was significantly different from zero or the model did not visually fit the data well the nonlinear regression (PROC NLIN procedure, SAS statistical software package, Version 7, SAS Institute, Cary, NC) was used to fit a lag exponential model:

$$Y_t = Y_0 \times (1 - (1 - e^{-k \times t}))^L, \text{ where} \qquad \text{(Equation 7)}$$

Y_t is the proportion volume, density, or mass remaining at time t (years), Y_0 is the proportion

initial volume, density, or mass, i.e. 1.0, k is decomposition rate per year constant (year^{-1}), and L

is a shape parameter causing a lag in decomposition.

Decomposition-vectors analysis

Several studies suggested that CWD decomposition process in some species consists of three

phases, initial-slow, intermediate-rapid, and final-slow (Harmon et al. 2000, Yatskov et al.

2003). To test this hypothesis we utilized the methodology from Harmon et al. 2000 for a

decomposition-vectors analysis.

To conduct the decomposition-vectors analysis a new data set was created. It included 225 CWD

pieces (i.e., 69 snags that became logs and 156 re-sampled logs) that were sampled during both

the initial (2002) and final (2008) sampling events (Table 3.3). Using this data set and the

equation from Harmon et al. (2000) we calculated k for each individual CWD piece:

$$k = -[ln(Initial) - ln(Final)]/t, \text{ where} \qquad \text{(Equation 8)}$$

k is the individual snag/log decomposition rate-constant, *Initial* is the individual snag/log

volume, density, or mass at time of sampling in 2002, *Final* is the individual log volume,

density, or mass at time of re-sampling in 2008, $t = 6$ years is time length between the sampling

events (2002 to 2008).

 To test the hypothesis of a three-phase decomposition process we divided CWD pieces into three groups based on percent density, volume, or mass lost: 1) up to 30%, 2) 30% to 70%, and 3) over 70% and calculated mean k for each of the groups. To observe the changes in k by decay class we used individual CWD decomposition rate-constants to calculate decay class-specific mean k. Then, we used Fisher's Protected Least Significant Difference (LSD) test (Cramer and Howitt 2004) to obtain pairwise comparison for k within the 3 groups and within the 6 (DC-0 included) decay classes.

Modeling CWD stores and dynamics

We used Stella-based simulation model (version 10.0.06 isee systems, Inc.) first, to test the effect of beetle-kill on CWD C fluxes and stores to the atmosphere, and second, to test if varying assumptions about the lag in snag fall-down rate and the log decomposition rate-constants would change the conclusions about the C dynamics.

The C dynamics of snag and log pools were simulated by having snags falling to become logs and both pools loosing C to the atmosphere via decomposition. To account for the lag in snag fall and gradual loss of snags once they began to fall we divided snags into five sub-pools, the first to account for the C transferred from live to snag C pool, the second to account for the lag in snag fall, and the remaining three to account for a gradual increase in the snag fall rate. Fluxes were associated with C transfer between snag sub-pools, C transfer from snags to logs (snag fall), and decomposition losses to the atmosphere and modeled as donor-controlled processes:

$$F = C_{DP} \times k, \text{ where} \hspace{3cm} \text{(Equation 9)}$$

F is a C flux, C_{DP} is the C store in donor pool, and k is rate-constant describing the proportion of the C store in donor pool removed annually. The rate-constants describing the transfer fluxes between snag sub-pools (k_{ST}) were set to:

$$k_{ST} = 1 - k_D - k_{SLT}, \text{where} \qquad \text{(Equation 10)}$$

k_D was the decomposition per year rate-constant, and k_{SLT} was snag-to-log transfer per year rate-constant. The k_{ST} rate was used to allow for a full transfer of C from one snag sub-pool to another once the residence time of a snag sub-pool had been reached. Initial snag and log pool stores as well as the amount of CWD added by disturbances were based on the forest inventory plot data for the white spruce stands, collected on Kenai Peninsula by the Forest Inventory and Analysis program (see Table 2.1 in Yatskov et al. - Chapter 2). Assuming 1:2 C-to-woody biomass ratio, the initial C store of log pool was 8 Mg C ha^{-1} with the input from live to either log (in case of windthrow) or snag (in case of beetle-kill) pools following disturbance of 32 Mg C ha^{-1}. A single snag decomposition rate-constant was from the chronosequence analysis, whereas log decomposition rate-constants were from the chronosequence and the decomposition-vectors analyses, described earlier in this chapter. Although we did not measure the snag-to-log transfer rate, our field observations indicated that it took approximately 10 years following the disturbance for snags to begin falling in numbers and that few snags remained standing after 40 years. We therefore assumed that snags would begin to fall 10 years after disturbance with 99% of the snags being on the ground by year 40 following the disturbance. To make the increase in snag fall gradual we doubled the transfer rate-constant every two years with each snag sub-pool until final transfer rate-constant was reached in snag sub-pool 5. Given that we could only

approximate the snag fall process, we performed sensitivity tests to see how varying the assumptions about the lag in snag fall-down rate would influence the results.

Two major simulation scenarios included: 1) windthrow, where C in CWD created by disturbance was fully allocated to logs, and 2) beetle-kill, where C in CWD created by disturbance was fully allocated to snags. Both scenarios were examined using two log decomposition rate-constants with a latter scenario having three sets of assumptions (as part of sensitivity test) about snag fall: 2a) snags have zero lag before beginning transfer from snag to log pool, 2b) a 5-year lag before beginning transfer from snag to log pool, and 2c) a 10-year lag before beginning transfer from snag to log pool.

RESULTS

Decay class-specific characteristics

The differences in decay class-specific characteristics corresponded well with the difference in CWD physical position. In the decay classes that both snags and logs occurred, snag decay class-specific densities were higher than corresponding log decay class-specific densities in both 2002 and 2008 data sets (Table 3.4a). The snags and logs also showed different trends in CWD density change with increasing decay class. Snag decay class-specific densities were available only for the DC-1 through DC-3 and DC-2 and DC-3 for the 2002 and 2008 data sets, respectively. For both 2002 and 2008 data sets, the snag decay class-specific density values were similar (the initial density of 0.380 ± 0.010 g/cm^3 versus 0.416 ± 0.023 g/cm^3 or 0.373 ± 0.009 g/cm^3 for DC-3 2002 or 2008 snags, respectively) (Table 3.4a). In contrast, log density progressively decreased

from the initial of 0.380 ± 0.010 g/cm^3 to a DC-5 density of 0.101 ± 0.003 g/cm^3, 0.119 ± 0.005, and 0.105 ± 0.004 g/cm^3 for the 2002, 2008, and combined (COMBO) data sets, respectively (Table 3.4a). The snag and log decay class-specific densities from 2008 data set were generally lower than those from the 2002 data set likely reflecting the longer period of decomposition.

Decomposition differences between snags and logs were also evident in the fraction of the disc cross-section area affected by decay. The highest percent area affected by decay in snags was reached in DC-3, the most advanced decay class we were able to sample, and equaled 20%, 23%, and 21% for 2002, 2008, and COMBO data sets, respectively. In comparison, the area affected by decay in DC-3 logs was approximately three times higher (Table 3.4b). The difference between snags and logs was also reflected through the way the disc cross-section area affected by the depth of decay changed from early to advanced decay classes. For 2002 snags the change between DC-1 and DC-2 was approximately three-fold, from 5% to 17%. For 2002 logs, the increase between DC-1 and DC-2 and between DC-2 and DC-3 was also approximately three-fold, but areas affected by decay were higher than in snags, from 9% to 26% and from 26% to 75%, respectively. For 2008 data set, the percent area affected by decay in DC-1 (47%) was 5 times higher than that in 2002 (9%) and the increase from DC-1 to DC-3 was more gradual, from 47% to 62% to 76%. The COMBO data set had more balanced increase in decay of 17% - 38% - 74% for DC-1 to DC-3 logs (Table 3.4b). Disc cross-section area affected by decay increased progressively in logs from 1% in DC-0 to 100%, 95%, and 96% in DC-5 for 2002, 2008, and COMBO data sets, respectively.

Trends in bark loss were similar between snags and logs. Both lost bark via similar pattern until DC-3, when bark cover percent in snags was about 40% lower than in logs (Table 3.4b). The bark cover percent values were very similar among all three data sets.

The snags were drier than logs decreasing in moisture content three-fold from 24% (DC-0) to 8% (DC-1) and maintaining low moisture content through DC-3. Logs moisture content dropped initially between DC-0 and DC-1, increasing to 28% - 39% by DC-3 and growing to 61% - 97% (depending on a data set).

Chronosequence analysis

In most cases the single exponential model (equation 5) worked well in fitting the snag and log proportion of volume, mass, and density for three data sets (2002, 2008, and combination) (Table A3.1). The lag exponential model (equation 7) was used for log volume (2002, 2008, and COMBO data sets) based on a visual examination of the residuals.

Snag density decomposition rate-constants of +0.002±0.001, 0.000±0.001, and +0.002±0.001 year^{-1} for 2002, 2008, and the COMBO data sets, respectively and R^2 ranging between 0.0000 and 0.1818 (Table 3.5), indicated little to no change of density with time for the first 44 years of *P. lutzii* snag decomposition (Table 3.3). Snag volume decomposition rate-constants were fairly low with the highest absolute value of k of -0.003±0.001 year^{-1} for 2008 data set and R^2 ranging between 0.2655 and 0.4839 (Table 3.5). Snag mass decomposition rate-constants (k) were

similar to those obtained for the density and volume (Table 3.5) with the data fitting the single exponential curve described by equation 5.

Log density decomposition rate-constants were very similar among the data sets (2002, 2008, and the COMBO) ranging between -0.013±0.002 year^{-1} and -0.017±0.002 year^{-1}. Log mass data sets showed higher k ranging between -0.020±0.002 year^{-1} and -0.022±0.002 year^{-1}. Log volume decomposition rate-constants ranged between -0.016±0.003 year^{-1} and -0.018±0.004 year^{-1} with a lag between 3.183±0.760 and 3.307±0.966 and R^2 ranging between 0.7043 and 0.8484 (Table 3.5). The duration of this lag in decomposition was between 10 and 20 years long (Figures 3.2d, 3.2e, and 3.2f). Besides the lag, the log volume decomposition rate-constants were similar to log density decomposition rate-constants (Table 3.5).

Decomposition-vectors analysis

The decomposition rate-constants from decomposition-vectors analysis varied widely depending on the type of variable used (density, volume, or mass), the type of k (phase-specific, or decay class-specific), and type of CWD decomposition trajectory (snag-to-log, or log-to-log). The phase-specific density, volume, and mass k's varied between -0.045 yr^{-1} and +0.020 yr^{-1}, and between -0.034 yr^{-1} and +0.003 yr^{-1} for re-sampled logs (L/L) and snags converted to logs (S/L), respectively (Table 3.6). Decay class-specific k's varied between -0.048 yr^{-1} and +0.026 yr^{-1}, and between -0.047 yr^{-1} and +0.006 yr^{-1} for L/L and S/L, respectively (Table 3.7). Overall L/L decomposition-vectors k was -0.038±0.002 yr^{-1}.

The decomposition-vectors analysis revealed a general and substantial (reflected by steep angle of the arrows) loss in CWD density by S/L as well as by L/L (Figures 3.3a, 3.3b). Both sets of pairs S/L and L/L showed significant density loss for the first 40 years of decomposition. The density decomposition rate (as indicated by the slope of the arrows) decreased by the CWD age of ~80 for L/L, whereas not decreasing for S/L (Figure 3.3a, 3.3b). The average density decomposition rate-constant from decomposition-vectors (S/L and L/L combined, Table 3.6) was higher than that determined from the log chronosequence for 2002, 2008, and both years combined (Table 3.5) (-0.024 yr^{-1} vs. a range from -0.013 yr^{-1} to -0.017 yr^{-1}, respectively). The average decomposition-vectors volume decomposition rate-constant was lower than the values from the chronosequence (-0.008 yr^{-1} vs. a range from -0.016 yr^{-1} to -0.018 yr^{-1}, respectively). Finally, the average mass k from the decomposition-vectors (S/L and L/L combined) was higher than that determined from the chronosequence (-0.031 yr^{-1} vs. a range from -0.020 yr^{-1} to -0.022 yr^{-1}, respectively).

The change in volume was not consistent for most ages, with some CWD pieces decreasing in volume, some increasing in volume, and some maintaining similar volume between the initial (2002) and final (2008) sampling events (Figures 3.3c, 3.3d). The only consistent decreasing trend in volume was observed in re-sampled logs (L/L) after 70 years of age (Figure 3.3c).

For mass in S/L a consistent loss could be observed first ~25 years followed by an inconsistent trend with some vectors indicating major losses and some indicating gains in general. Mass loss in L/L was high up to 40 years and low at age 80.

Fisher's Protected LSD pairwise comparisons for three decomposition phases (up to 30%, 30% to 70%, and over 70%) associated with percent mass, density, and volume loss showed consistent difference between phases 1 and 3 and 2 and 3 suggesting significantly slower decomposition rates once CWD loses 70% of its mass, density, or volume (Table 3.8). The only consistent difference in decay class-specific k comparison was between DC-5 and the rest of the decay classes (Table 3.9) again suggesting that decomposition slows down in the advanced stages of decay.

Modeling CWD stores and dynamics

For both major simulation scenarios (a windthrow with 32 Mg C ha^{-1} in disturbance-generated CWD fully allocated to logs and a beetle-kill with the same amount of C in disturbance-generated CWD fully allocated to snags and both having the initial log C pool of 8 Mg C ha^{-1}) we used two decomposition rate-constants. First rate-constant was based on chronosequence and was assumed to be -0.02 yr^{-1}, whereas second rate-constant was based on decomposition-vectors and was assumed to be -0.04 yr^{-1}.

As expected, disturbance caused a pulse (i.e., flux) of C to the atmosphere; however the shape, magnitude and timing of this pulse were influenced by whether snags were created as a result of disturbance and the timing of snag fall (Figure 3.4).

In the windthrow scenario the C flux was solely produced by log pool and reached a sharp peak after the disturbance and then declined following an exponential pattern. The magnitude of the pulse was 0.8 Mg C ha^{-1} yr^{-1} and 1.6 Mg C ha^{-1} yr^{-1} for the log decomposition rate-constants of 0.02 yr^{-1} and 0.04 yr^{-1}, respectively.

In the beetle-kill scenario, the creation of snags caused the C pulse to be spread out over time forming a hump (instead of a peak), decreased the pulse magnitude and delayed C pulse to the atmosphere by forming a "shelf" of low C flux associated with the lag time required for snags to start falling. For example, when there was no lag in snag fall, flux maximums of 0.6 Mg C ha^{-1} yr^{-1} and 1.01 Mg C ha^{-1} yr^{-1} were reached 14 and 11 years after disturbance for log decomposition rate-constants of -0.02 yr^{-1} and -0.04 yr^{-1}, respectively. Introduction of 5-yr lag for snag fall decreased the maximum flux to 0.57 Mg C ha^{-1} yr^{-1} and 0.92 Mg C ha^{-1} yr^{-1} and delayed maximum flux until 25 and 22 years passed disturbance for the rate-constants of -0.02 yr^{-1} and -0.04 yr^{-1}, respectively. Finally, 10-yr lag in snag fall lead to decrease in flux maximums to 0.55 Mg C ha^{-1} yr^{-1} and 0.9 Mg C ha^{-1} yr^{-1}, with peak fluxes occurring 31 and 27 years after disturbance for log decomposition rate-constants of -0.02 yr^{-1} and -0.04 yr^{-1}, respectively.

The form of mortality (logs vs. snags) also dictated the behavior, complexity, and magnitude of CWD C stores (Figure 3.5). Under the windthrow scenario the log C pool reached its maximum of 40 Mg C ha^{-1} immediately after the disturbance (8 Mg C ha^{-1} of legacy CWD plus 32 Mg C ha^{-1} transferred from live pool as a result of disturbance). Due to lack of any additional C input following the disturbance, this store declined following the negative exponential pattern with

95% of C gone in 150 years at a rate-constant of -0.02 year^{-1} or in 75 years at a rate-constant of -0.04 year^{-1}.

Under the beetle-kill scenario the stores in snag pool reached its maximum of 32 Mg C ha^{-1} immediately after the disturbance, whereas the stores in log pool reached its maximum of 27.5 Mg C ha^{-1} 30 years after disturbance or 22.2 Mg C ha^{-1} 27 years after disturbance for rate-constants of -0.02 yr^{-1} and -0.04 yr^{-1}, respectively. Without a lag in the start of snag fall, snag C stores curve showed a steady and relatively fast decline due to C loss to the log pool and the atmosphere. Simultaneously, the log pool showed a steady buildup of stores forming a hump until the pool outputs finally overweighed the inputs at which point the C stores curve showed a steady exponential decline. When the lag in snag fall was included, both snag and log stores became subject solely to decomposition-related losses with both curves forming a "shelf" showing little decline in stores over the duration of the lag. Thus, the process of snag pool decline and log pool buildup was delayed until the end of the lag in the start of snag fall. Total CWD C stores curve resembled a reverse S-shaped pattern indicating slow-fast-slow stages of decomposition. The first slow phase in CWD C stores became more pronounced with the increase in lag interval (from 0 to 5 to 10 years). Total CWD C stores after the windthrow having the same starting point as stores after the beetle-kill, were lower regardless of the duration of the snag fall lag over the course of 200 years following the disturbance.

DISCUSSION

The differing physical environment of decomposing snags and logs led to differences in their decomposition trajectories. Moisture and temperature have been shown to affect the wood decomposition in the field (Harmon et al. 1987, Marra and Edmonds 1996) and laboratory studies (Harmon and Chen 1991, Chen 1999, Hicks 2000). Excessive moisture reduces aeration (Harmon and Chen 1991) thus inhibiting decomposition. Similarly, moisture contents below wood fiber saturation point, 26-39% of dry weight depending on species (Scheffer and Cowling 1966), as well as temperatures outside the 15-40°C range (Zabel and Morrell 1992) constrain the activity of wood decomposing organisms. On the Kenai Peninsula, decomposition for both snags and logs is slowed by generally low temperatures throughout the year which rarely approach 15°C (NOAA 2014) and even less frequently reach the optimum for fungal activities of 25-30°C (Käärik 1974). The observed differences in decomposition of snags and logs (Table 3.4a, 3.4b) could at least partially be attributed to a milder temperature regime for logs under the cover of summer vegetation and winter snow. However, the key factor influencing different snag and log decomposition trajectories is probably moisture.

CWD moisture balance depends on the difference between inputs and outputs. Two major water inputs into CWD are canopy throughfall (Sexton and Harmon 2009) and metabolic production of water by fungi (Griffin 1977). The first one depends on precipitation amount, seasonality (Harmon and Sexton 1995), canopy cover and density, and an effective area of CWD. CWD effective area might be the key difference between the snag and log throughfall interception potential as surface area of an intact vertically-standing snag bole in the horizontal plane is

significantly smaller than that of a similarly sized log bole in horizontal position. The second one is a byproduct of decomposition in the amount sufficient enough (approximately 0.555 g of water from complete decomposition of 1.0 g of cellulose) to alter significantly the rate of decay (Griffin 1977). Thus, in logs the higher rate of byproduct water production could be associated with a positive feedback related to higher rates of decomposition. The outputs include runoff from the CWD surface, absorption, leachates from CWD bottom, and evaporation (Sexton and Harmon 2009). Log runoff has been found to be proportional to the throughfall (Harmon and Sexton 1995). While in absolute numbers water runoff is probably higher for logs due to higher log interceptive potential, as a fraction of throughfall it is likely higher for snags due to their vertical position, leaving less water for absorption, leaching, and evaporation. Absorption was found to be higher in more decayed wood (Gough et al. 2007) therefore is probably lower for snags due to their lower level of deterioration and as a fraction of throughfall interception. The proportion of canopy throughfall interception leaching through logs was reported to increase with log decomposition and suggested to be caused by increased tissue decay (Harmon and Sexton 1995). Given the extent of deterioration of snags in comparison to logs, their leachates are probably also lower. Besides keeping snag tissues at low moisture content, low levels of snag leaching also reduce removal of the inhibitors of decay such as essential oils, tannins, and phenolic substances (Scheffer and Cowling 1966, Panshin and de Zoew 1970, Marra and Edmonds 1996) from snag tissues. Long-term retention of the natural preservatives in snags along with low moisture could cause their slower decomposition in comparison to logs. Finally, evaporation in snags is probably higher than in logs given their direct exposure to sun and wind

as opposed to logs which are protected from the drying action of sun and wind under cover of

vegetation overtopping them.

The snags we sampled seemed to follow a similar deterioration pattern to those found in other

regions that experienced beetle-related spruce mortality. Low moisture appeared to limit snag

decomposition during *P. engelmanii* snag deterioration following a bark beetle outbreaks in Utah

(Mielke 1950) and Colorado (Hinds et al. 1965). In Utah relatively few snags fell in the first 10

years and 84% of the snags were still standing 25 years after the trees succumbed to mortality. In

Colorado, 8% and 28% of standing volume was windthrown 10 and 20 years after the time of

peak mortality. In Utah and Colorado snag fall was mainly caused by basal sap and root decay

(Mielke 1950, Hinds et al. 1965). Except for the bottom 4 feet representing the area of snag

failure with moisture content frequently ranging between 50 and 100% (Hinds et al. 1965), snag

trunks appeared to be too dry to develop decay with moisture contents generally below 22%

(Mielke 1950).

Decay class-specific density

The differences between snag and log decay class-specific densities (Table 3.4a) provided a

strong indication that snags were less decomposed than logs within corresponding decay classes.

In DC-2, density in snags increased from a fraction of a percent to 4%, whereas in logs density

dropped anywhere from 8% to 13% from the initial value of 0.380 g/cm^{-3}. In DC-3, snag density

either increased by 9% or dropped slightly from the initial by 2%, whereas the density of logs

dropped 22-32% from the initial value. Even more remarkable difference between the density of

snags and logs was observed when CWD age was considered. DC-3 snags and DC-4 logs had

comparable CWD ages (Table 3.4a) with density in DC-3 snags fluctuating close to the initial

compared to the density of DC-4 logs dropping 58% to 64% from the initial value.

The causes for the differences in density between snags and logs could include higher rate of

deterioration in logs vs. snags, tissue shrinkage in snags associated with low tissue moisture

content, snag volume loss to fragmentation, and the nature of snag selection for sampling. The

relative area affected by decay in snags and logs suggests decomposition in snags progressed

much slower than in logs. Within corresponding decay classes, the area affected by decay (Table

3.4b) in snags was constantly lower than that in logs, with the largest difference in DC-3, where

log disc area affected by decay was approximately threefold of that in snags. When CWD age

was considered, the difference was almost fourfold with ~20% of the snag disc area being

affected compared with tissues from DC-4 logs being almost entirely impacted by decay. Similar

to a number of other publications on spruce snags (Yatskov et al. 2003, Mäkinen et al. 2006,

Harmon et al. 2011) and logs (Graham and Cromack 1992, Shorohova and Shorohov 2001,

Yatskov et al. 2003, Mäkinen et al. 2006) deterioration, the current study showed little to no

change in snag density and a gradual decrease in log density with decay class. Despite the

differences in decay class-specific densities among individual studies, the density reduction

factors (the ratio of the decayed density of a piece of dead wood to its undecayed density) among

studies were fairly comparable and in general followed the sequence $1.0 \rightarrow 1.1 \rightarrow 1.1$ from DC-

1 through DC-3 snags and $1.0 \rightarrow 0.9 \rightarrow 0.7 \rightarrow 0.4 \rightarrow 0.3$ from DC-1 through DC-5 logs. Tissue

shrinkage associated with low moisture had a higher effect on snags than on logs. When moisture

content in spruce wood is reduced below fiber saturation point of ~30% (Stamm 1929), external

dimension volumetric shrinkage greater than 11% (Stamm 1934a) could occur. The percent

change in external dimensions could be 6-12% in tangential direction (tangent to the annual

rings), 3-7% in the radial direction (from the center to the periphery of the tree), and a fraction of

a percent in the longitudinal direction (parallel to the fibers) (Stamm 1934b). The higher density

in snags than in logs could also be attributed to the volume loss via fragmentation (Brown et al.

1996). Snags due to their vertical position could have lost decomposed tissues off the stem as

part of fragmentation process leaving behind less decomposed, drier, and denser core. This is

consistent with data on bark fragmentation: DC-3 snags retained approximately 2% of stem bark

compared to about 40% retained by DC-3 logs (Table 3.4b). However, since original bole

volume reconstruction techniques providing insight on wood fragmentation losses are associated

with a level of uncertainty, it is difficult to definitely say how much more the fragmentation

process affected snags in comparison to logs. Finally, the explanation for the higher density in

snags than in logs could be a sampling artifact. We sampled the snags that remained standing

because they were less affected by decay, therefore more structurally sound, whereas the more

decomposed snags fell to the ground.

Decomposition rate-constants

Decomposition rate-constants based on density, volume, and mass loss obtained via the

chronosequence method in our study were generally comparable to those reported by others

(Table 3.10). Similar to literature reported values, our snag k's showed little to no mass, volume,

or density loss over the span of 49 years following the tree mortality event. Our log k's were at

the lower end of the values reported for other studies conducted for spruce. One reason for low

k's could be the fact that we did not differentiate between the log diameter classes with k's

determined for the logs with the diameter 10-70 cm. Effect of log size (diameter) on

decomposition rate-constants have been discussed in literature (Harmon et al. 1986, Brown et al.

1996) and negative size-to-decay rate correlation have been demonstrated in some studies on

spruce decomposition. Based on k's determined by Tarasov and Birdsey (2001) half-life ($T_{0.5}$) of

P. abies logs was 12, 22, and 27 years for diameter classes 5-20 cm, 20-40 cm, and 40-60 cm,

respectively. Decomposition rate-constants provided by Holeksa et al. (2008) produce $T_{0.5}$ for *P.

abies* logs of 26, 27, and 43 years for the diameter classes 10-22 cm, 23-35 cm, and >35 cm,

respectively. There are, however, studies that either demonstrated an inconsistent effect of size

on spruce decomposition rate-constants (Foster and Lang 1982) or showed a positive size-to-

decay rate correlation (Graham and Cromack 1982, Naesset 1999). Results of these studies could

potentially be attributed to the fact that the decomposition rate-constants were based on density

loss as opposed to mass loss over time. The latter methodology incorporates density and volume

loss, both significant components in decomposition (Lambert et al. 1980, Graham 1982,

MacMillan 1988).

A number of studies showed that decomposition of some species, including spruce, follows

three-phase decomposition pattern with early slow phase followed by fast intermediate phase and

ending with slow late phase (Means et al. 1992, Laiho and Prescott 1999, Harmon et al. 2000,

Yatskov et al. 2003). Our hypothesis that the decomposition process consists of three distinct

phases was not supported for spruce logs (Table 3.8) sampled on the Kenai Peninsula as the

decomposition rate-constants in logs (based on fraction of density, volume, or biomass loss) were similar in first two phases with both being higher than the third phase. This implies a two-phase decomposition process in spruce logs on the Kenai. Similar results were obtained by running comparison of the decomposition rate-constants determined for the decay classes (Table 3.9). Unlike Hale and Pastor (1998) whose approach resulted in moderately slow decomposition rates for decay class 1 logs, slow for decay class 2, increased rates for decay class 3, and an even higher rates for decay class 4 logs, only DC-5 rate in our study was different from any other decay classes in terms of k. It is not clear why we were unable to detect a slower decomposition rate in the first phase of decomposition, or in early decay classes. Wood moisture content below 25%, considered to be the threshold for active decomposition by fungi (Hartley 1949), in DC-1 and DC-2 logs (Table 3.4b) suggests that decomposition at an early stage should be slower. It may be that our selection of the mass, density, and volume loss of 30% for the phase one combined slow and rapid decomposition phases. If that was the case, however, it seems that we should have seen a slow phase between the DC-0 and DC-1 or DC-0 and DC-2, which was not the case. It is also possible that we sampled logs that were already in the rapid phase of decomposition because the logs were inoculated quickly and extensively by fungal spores due to increased activity of wood-decomposing fungi in an area of substantial and reoccurring mortality. Three-phase decomposition process could potentially describe decomposition in snags better than in logs given the initial 10- to 40-year lag in decomposition while snags are standing, rapid decomposition after snags fall and moderately slow decomposition associated with advanced stages of stem decay.

Spruce decomposition rate-constants obtained through two methods differed despite the expectation they would be similar. The decomposition rate-constant determined via decomposition-vectors method based on 156 logs (approximately -0.04 yr^{-1}) was roughly twice that obtained using chronosequence (approximately -0.02 yr^{-1}). These results contrast with Harmon at al. (2000) who reported statistically similar decomposition rate-constants obtained via the decomposition-vectors over a 3-year resampling interval vs. one-time chronosequence methods. However, Harmon at al. (2000) noted that biomass decomposition rates from decomposition-vectors method were up to 69% higher than rates determined from one-time chronosequence. This difference could stem from multiple sources affecting the chronosequence decomposition rate-constant including dating the mortality and small number of observations of CWD in the advanced decomposition stages. Generally, there is a higher uncertainty associated with the estimates of timing of mortality for trees that have been dead longer periods of time. When combined with a limited number of such CWD pieces in advanced decomposition stages, the overestimate of time since tree death will likely produce a lower k whereas its underestimate will produce a higher k. At the same time, the differences in our results could potentially and at least partially be attributed to the climatic factors such as increased number of days per year with positive temperatures and a recent mean annual temperature increase. The 30-yr average between 1969 and 1998 (prior to our sampling) was 2.0ºC, whereas the 30-yr average between 1979 and 2008 (capturing the timing of sampling events 2002 and 2008) was 2.4ºC. At the same time, 6-year average between the dates of sample (2002 – 2008) was 2.7ºC (NOAA 2014). Applying Q$_{10}$ factor (Panshin and de Zoew 1970, Chen 1999, Hicks 2000), describing a rate of change in biological system with 10ºC increase in temperature, did not support this idea. With a

presumption that activity of fungi increases two-fold for every 10°C rise in temperature, the initial rate-constant of -0.020 yr^{-1}, and temperature change of 0.7°C , the decomposition-vectors rate-constant should have been -0.021 yr^{-1}, i.e. substantially lower than -0.04 yr^{-1} obtained in our analysis.

Modeling CWD stores

The form of mortality (snags vs. logs) can have an important impact on the temporal pattern of stores and fluxes of C given the decomposition rate-constants of snags are 20 to 40 times slower than that of logs. This difference is caused by two lags associated with beetle-kill. The first lag is associated with the time period that snags remain standing before they start to fall. This lag creates a "shelf" of low C flux corresponding in length to this lag, delaying the pulse of higher C flux associated with the snags moving into the log pool (Figure 3.4).The second lag is caused by the fact it takes time for all snags to fall. Because transfer of snags to logs is gradual, the buildup of the more rapidly decomposing log C pool is delayed as is the maximum flux from CWD C pool (Figure 3.4). The magnitude of the maximum flux is also lower after the beetle-kill than windthrow.

The slower C emissions associated with the formation of snag pool allow for higher C stores over time in beetle-kill vs. windthrow scenario. When total CWD C stores examined, the area between the total CWD curves (Figure 3.6) represents the amount of C stored in the ecosystem affected by the beetle-kill over one affected by the windthrow in the 200 years following disturbance. Windthrow curve follows an exponential decline, whereas beetle-kill curve follows

a reverse S-shaped pattern with the stores in both scenarios approaching 0 beyond year 200.

Except for several years immediately after the disturbance, the amount of C stored in beetle-kill

in any particular year is higher than that stored in windthrow, making it have higher long-term C

stores. At a minimum, beetle-kill with no lag in snag fall and log decomposition rate-constant of

-0.02 yr^{-1} stores about 10% more C than windthrow over a 200-year post-disturbance period. At

maximum, beetle-kill with 10-yr lag in snag fall and log decomposition rate-constant of -0.04 yr^{-1} stores about 66% more C than windthrow over a 200-year post-disturbance period. This

difference is similar to that between the windthrow and a clearcut that removes ~60% of total

aboveground biomass from the system (Yatskov et al. - Chapter 2): given the same

decomposition rates and no inputs, the windthrow stores 60% more C in CWD over a 200-year

period than the clearcut. The delay in C loss to the atmosphere may be long enough to allow for

new cohort of trees to establish, rebuilding the C sequestering capabilities of the system, thus

steering the ecosystem C balance after disturbance toward neutrality. Hence, given the same

recovery rate of live components, the beetle-kill system may become C neutral faster than the

windthrow system.

CONCLUSIONS

The effect of large-scale disturbance on CWD dynamics in spruce-dominated forests of Kenai

Peninsula, Alaska was examined in relation to type of CWD produced and differences between

snag and log decomposition. The chronosequence and decomposition-vectors approaches were

utilized to describe snag and log decomposition and a simulation model was used to examine the

effect of disturbance generated CWD type on C stores and fluxes.

A comparison between the snag and log decay class-specific density changes and differences in decomposition rate-constants based on density, volume, and mass loss indicated snags decomposed slower than logs. This was likely caused by differing environmental conditions (temperature and moisture regimes) associated with CWD physical position, with moisture potentially being the most important factor. Our hypothesis that the decomposition process consists of three distinct phases for the spruce logs (L/L) sampled on the Kenai Peninsula was not supported. Decomposition rate-constants for the first two phases based on the fraction of density, volume, and mass loss were similar to each other but different from the third phase implying two-phase spruce decomposition process. Two-phase process was also supported by comparison of decay class-specific decomposition rate-constants. Three-phase decomposition process could potentially describe decomposition in CWD that start out as snags (S/L) better than in logs (L/L) given the initial 10- to 40-year lag in decomposition while snags are standing, rapid decomposition after snags fall and become logs and moderately slow decomposition associated with advanced stages of stem decay in logs. Given the slower C release from snag C pool associated with lags delaying snag decomposition, disturbances producing significant amount of CWD in form of snags could create landscapes more effective at C storage than those producing logs. Not only would these landscapes emit less C over a time period, but also potentially revert faster to C neutrality.

The comparison between long-term decomposition rate-constant from chronosequence (-0.02 yr^{-1}) and short-term rate-constant from decomposition-vectors (-0.04 yr^{-1}) may indicate a trend of

increasing C fluxes from disturbed forest ecosystems in recent past. Warming climate could be creating conditions leading to the increase in disturbance frequency and severity and in CWD decomposition rate-constants which in turn, through positive feedbacks, lead to increase in C fluxes and further increase in temperature.

FIGURES

Figure 3.1. The Kenai Peninsula map showing sampling sites.
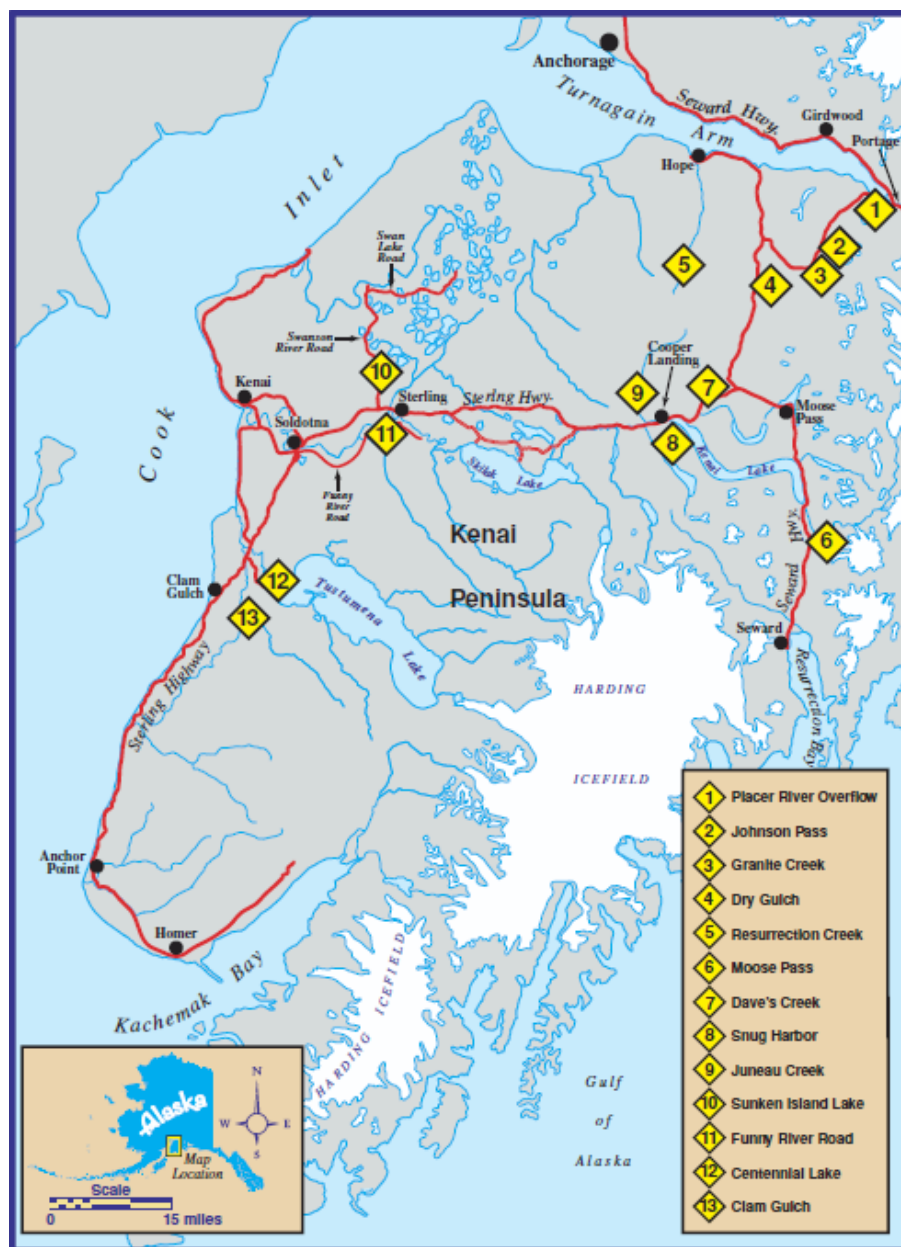
Figure 3.2. Snag and log decomposition curves based on negative single exponential and lag models.
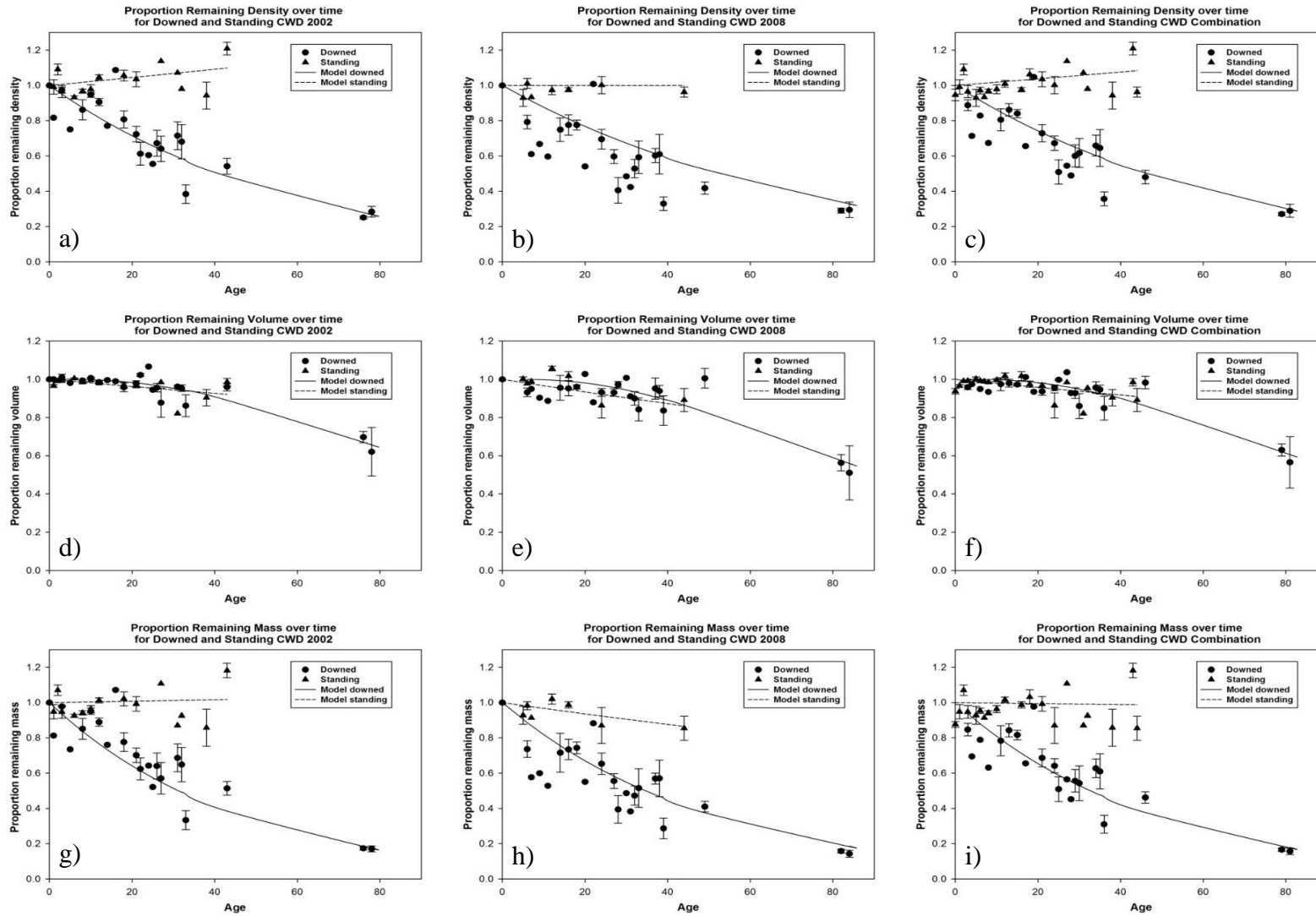
Figure 3.3. CWD volume, mass, and density proportion remaining for initial (2002) and final (2008) sampling events portrayed by decomposition vectors.
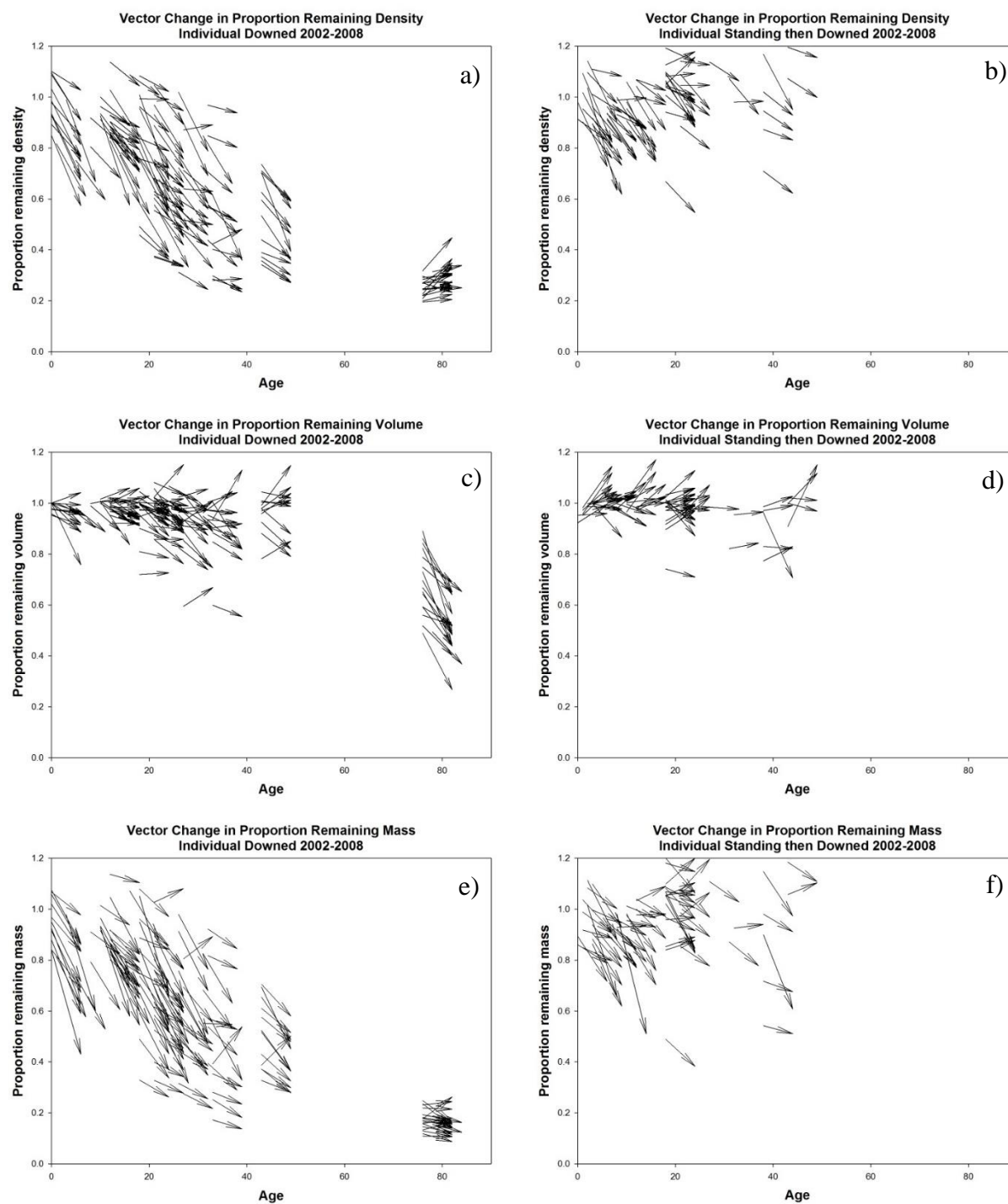
Figure 3.4. C flux (Mg C ha^{-1} yr^{-1}) from CWD for the windthrow (no snags) and beetle-kill (no lag in snag fall, 5-year lag in snag fall, and 10-year lag in snag fall) scenarios at log decomposition rate-constant of -0.04 year^{-1} and pre-disturbance flux of 0.32 Mg C ha^{-1} yr^{-1}.
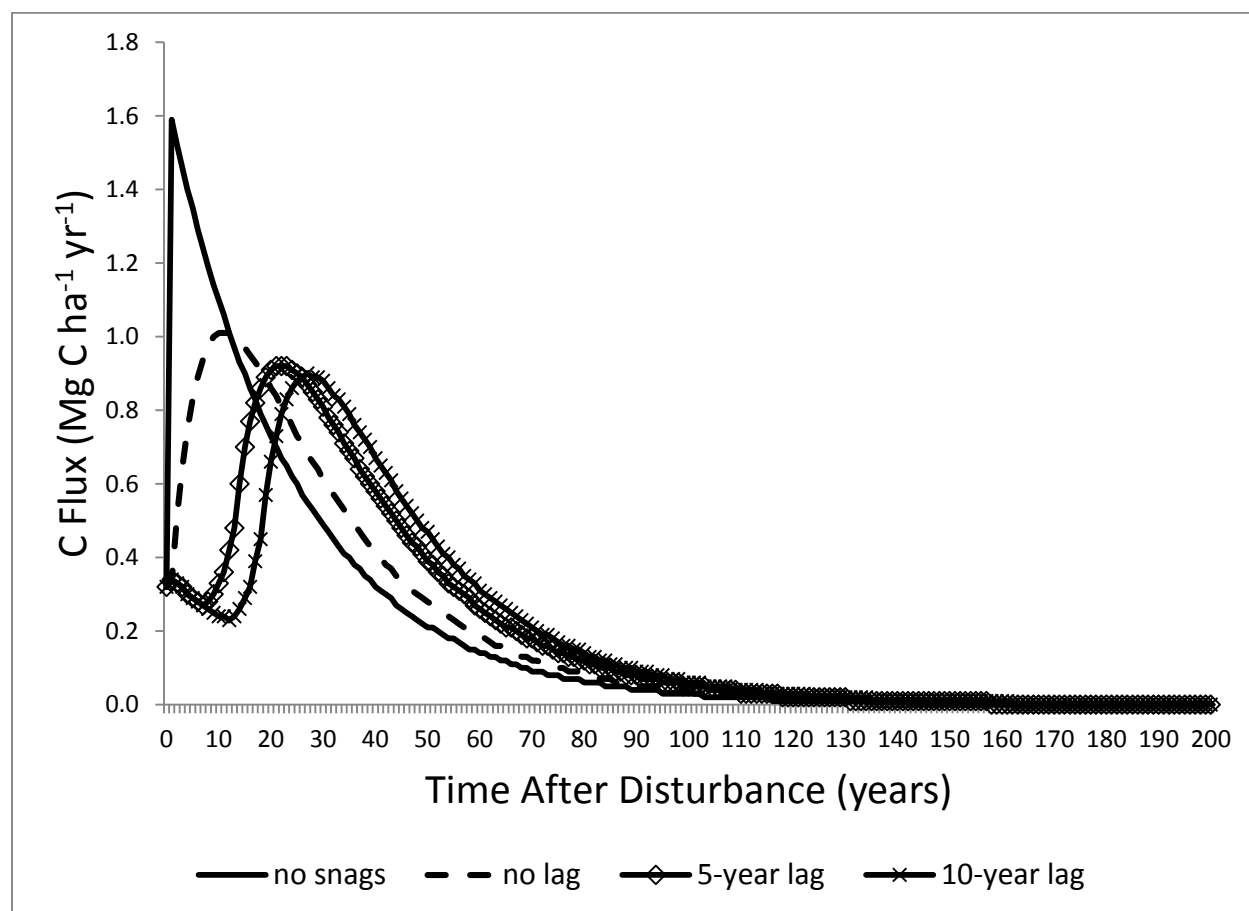
Figure 3.5. C Stores (Mg C ha^{-1}) for log, snag, and total CWD pools for the windthrow (no snags) and beetle-kill (10-year lag in snag fall) scenarios at log decomposition rate-constant of -0.04 year^{-1}, pre-disturbance log C pool of 8 Mg C ha^{-1}, and disturbance generated mortality of 32 Mg C ha^{-1}.
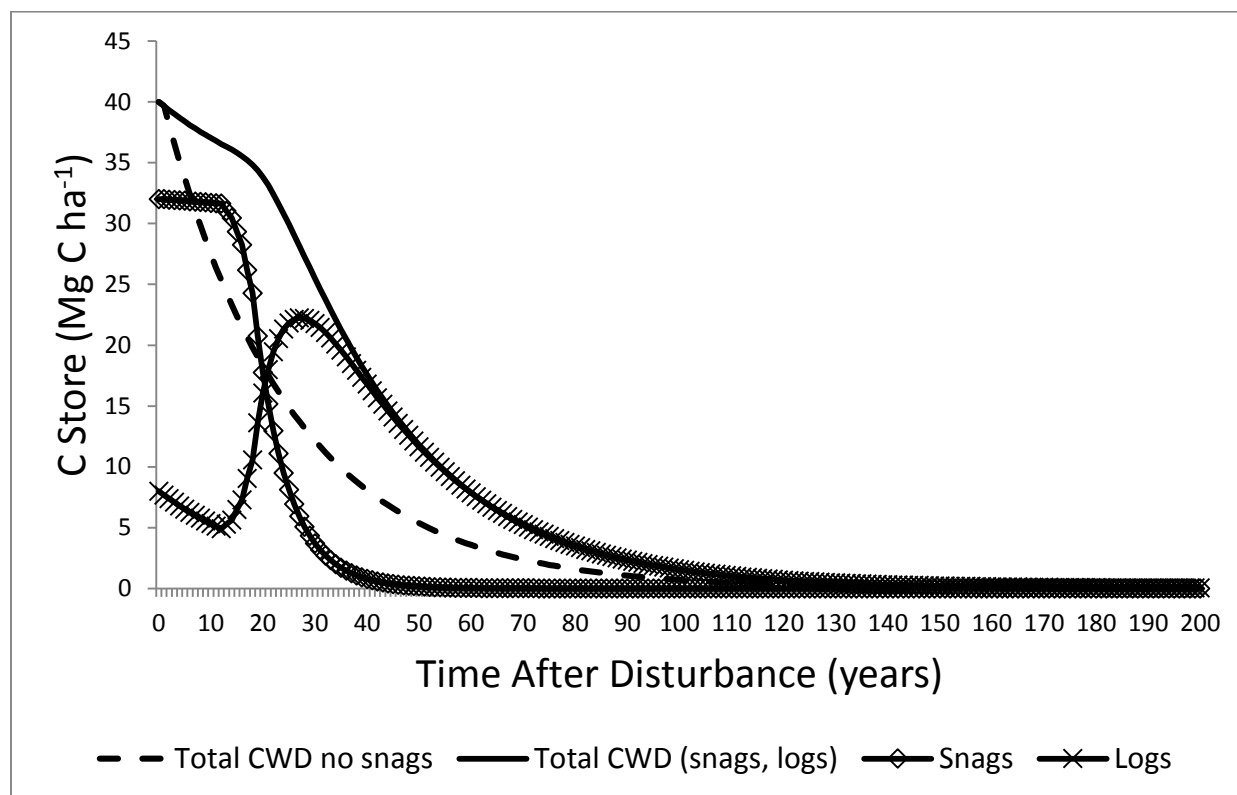
Figure 3.6. Total C Stores (Mg C ha^{-1}) windthrow (no snags) and beetle-kill (10-year lag in snag fall) scenarios at log decomposition rate-constant of -0.04 year^{-1}.
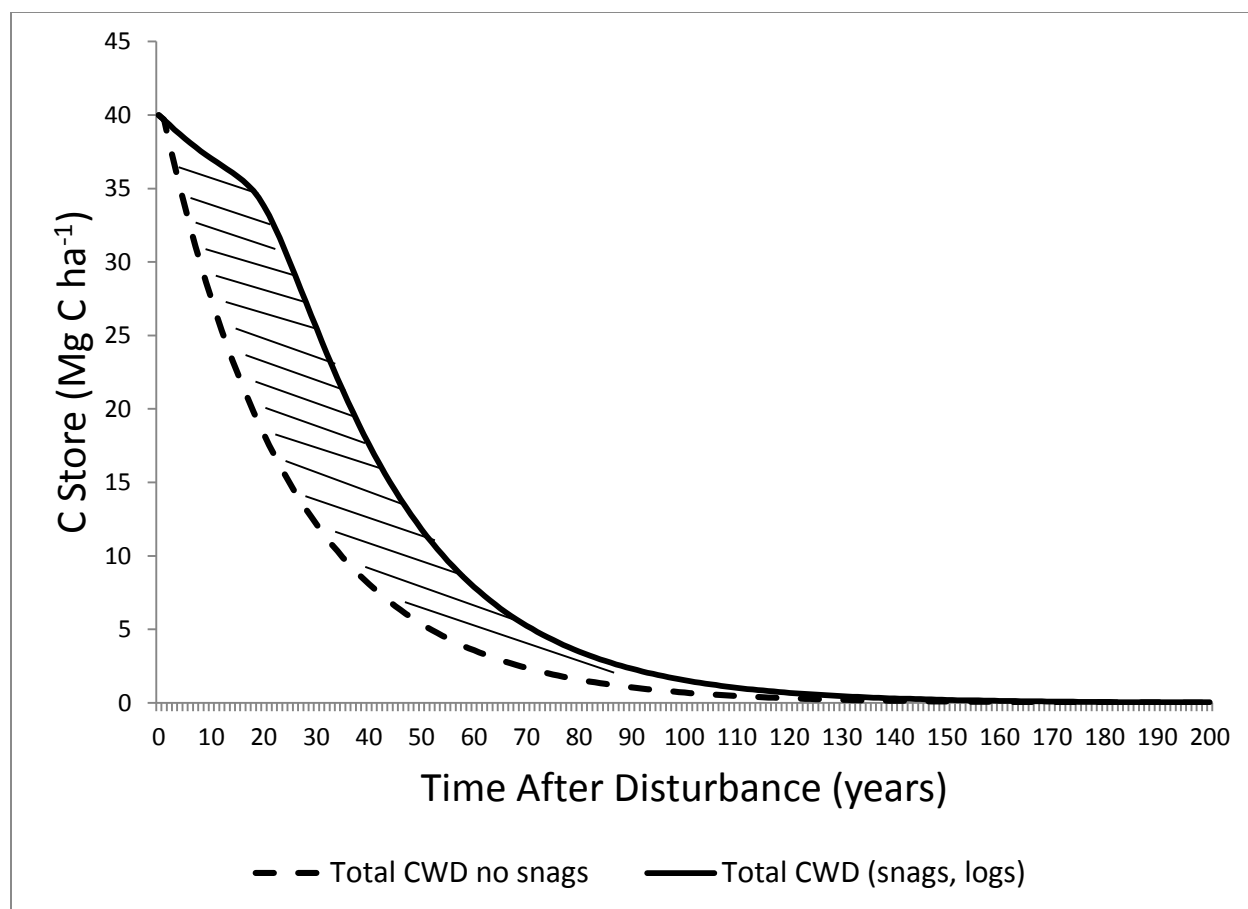
TABLES

Table 3.1. Monthly 30-year average (1979-2008) climatic data for the western and northern Kenai Peninsula.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Temperature, ºC	-6.9	-5.6	-2.7	2.0	6.8	10.6	12.8	12.1	8.3	1.9	-3.8	-6.1
Precipitation, mm	47	37	28	23	23	27	46	67	90	76	60	61

Table 3.2. Annual average 30-year (1979-2008) period climatic data for the western and northern Kenai Peninsula.

	Precipitation (mm)/Year	Temperature (ºC)/Year	January (ºC)/Year	July (ºC)/Year
30-year mean	584/---	2.4/---	-6.9/---	12.8/---
30-year max	816/1981	3.9/2002	0.6/1981	14.6/2004
30-year min	397/1996	0.9/1996, 1999	-15.8/1989	11.4/1982

Table 3.3. CWD count and age range by year of sampling.

2002 sampling			2008 sampling		
CWD type	Number	CWD age range	CWD type	Number	CWD age range
Live	11	0	Logs	11	6
Snags	69	1 - 43	Logs	68	7 - 49
Logs	126	2 - 78	Logs	123	8 - 84
Logs	20	No age	Logs	20	No age
Snags	---	---	Snags	29	5 - 44
Logs	---	---	Logs	2	24
Total	226	---	Total	253	---

Table 3.4. Decay class-specific snag and log characteristics for 2002, 2008, and COMBO data sets.

a)

	Decay	CWD count			CWD age (years): Mean (SE)			Density (g/cm^3): Mean (SE)		
		2002	2008	COMBO[a]	2002	2008	COMBO	2002	2008	COMBO
Initial	0	11	---	---	0 (0.0)	---	0 (0.0)	0.380 (0.010)	---	
Snags	1	21	---	21	4 (1.0)	---	4 (1.0)	0.383 (0.007)	---	0.383 (0.007)
	2	38	24	62	16 (1.1)	13 (1.5)	15 (1.5)	0.398 (0.006)	0.379 (0.007)	0.391 (0.005)
	3	10	5	15	41 (0.8)	40 (4.0)	40 (1.4)	0.416 (0.023)	0.373 (0.009)	0.401 (0.016)
Logs	1	6	1	2	7 (2.0)	6 (0.0)	3 (0.0)	0.366 (0.018)	0.352 (0.000)	0.378 (0.008)
	2	32	68	30	14 (1.0)	15 (0.9)	11 (1.3)	0.350 (0.006)	0.330 (0.007)	0.343 (0.006)
	3	59	97	66	26 (1.0)	28 (1.0)	25 (1.0)	0.258 (0.009)	0.277 (0.009)	0.295 (0.008)
	4	24	34	21	40 (1.7)	40 (1.9)	37 (2.0)	0.150 (0.006)	0.137 (0.007)	0.161 (0.010)
	5	25	27	20	76 (0.1)	82 (0.1)	79 (0.1)	0.101 (0.003)	0.119 (0.005)	0.105 (0.004)

[a] COMBO snag count is a cumulative number of snags sampled in 2002 and 2008; COMBO in log count represents a sum of 136 logs sampled in 2002 and resampled in 2008, 1 log sampled only in 2002, and 2 logs sampled only in 2008.

b)

	Decay	% disc area affected by decay: Mean (SE)			% bark cover: Mean (SE)			Moisture %: Mean (SE)		
		2002	2008	COMBO	2002	2008	COMBO	2002	2008	COMBO
Initial	0	0.81 (0.81)	---		100.0 (0.0)	---		24.3 (3.4)	---	
Snags	1	5.43 (3.04)	---	5.43 (3.04)	95.0 (2.1)	---	95 (2.1)	7.5 (0.8)	---	7.5 (0.8)
	2	17.25 (4.38)	13.29 (4.30)	14.93 (3.09)	81.3 (4.6)	81.0 (5.9)	82 (3.5)	5.9 (0.6)	6.6 (0.5)	6.2 (0.4)
	3	19.85 (9.85)	23.19 (15.08)	20.96 (7.96)	2.2 (2.0)	2.2 (0.8)	2 (1.3)	7.2 (1.3)	10.9 (0.9)	8.5 (1.0)
Logs	1	8.55 (2.66)	46.54 (0.00)	17.29 (10.41)	98.5 (0.7)	100.0 (0.0)	100 (0.5)	18.5 (5.5)	11.6 (0.0)	11.4 (0.3)
	2	26.35 (5.56)	62.26 (4.65)	37.88 (3.90)	80.0 (5.4)	82.0 (2.8)	86 (3.5)	12.7 (1.7)	23.2 (1.9)	22.1 (2.5)
	3	75.34 (3.99)	75.91 (3.47)	73.95 (3.25)	41.0 (4.3)	36.6 (3.2)	43 (3.8)	27.8 (2.4)	39.3 (2.6)	33.9 (2.5)
	4	99.53 (0.14)	98.18 (1.31)	96.86 (1.85)	5.3 (2.5)	6.2 (2.2)	12 (4.6)	81.7 (6.3)	87.9 (5.5)	74.8 (7.7)
	5	99.98 (0.06)	94.74 (3.37)	96.47 (2.25)	0.6 (0.6)	0.6 (0.6)	0 (0.0)	60.6 (7.5)	96.8 (9.6)	83.2 (9.2)

Table 3.5. Snag and log decomposition rate-constants based on CWD chronosequences.

LOGS

YEAR	VARIABLE	K	INTERCEPT[a]	LAG[b]	R2	N
2002	PRM[c]	-0.022 (0.002)	1.063 (0.062)	---	0.8635	137
2002	DEN[d]	-0.017 (0.002)	0.996 (0.054)	---	0.8242	137
2002	VOL[e]	-0.016 (0.003)	---	3.183 (0.760)	0.8484	137
2008	PRM	-0.020 (0.002)	0.893 (0.079)	---	0.7913	138
2008	DEN	-0.013 (0.002)	0.827 (0.075)	---	0.6470	138
2008	VOL	-0.018 (0.004)	---	3.307 (0.966)	0.7043	138
COMBO	PRM	-0.021 (0.002)	0.954 (0.072)	---	0.8305	137
COMBO	DEN	-0.015 (0.002)	0.891 (0.064)	---	0.7519	137
COMBO	VOL	-0.017 (0.003)	---	3.266 (0.806)	0.7994	137

SNAGS

YEAR	VARIABLE	K	INTERCEPT[a]	LAG[b]	R2	N
2002	PRM	0.000 (0.002)	0.974 (0.036)	---	0.0044	70
2002	DEN	0.002 (0.001)	0.988 (0.028)	---	0.1818	70
2002	VOL	-0.002 (0.001)	0.996 (0.019)	---	0.2674	70
2008	PRM	-0.003 (0.001)	0.988 (0.027)	---	0.4935	29
2008	DEN	0.000 (0.001)	0.973 (0.018)	---	0.0000	29
2008	VOL	-0.003 (0.001)	1.020 (0.028)	---	0.4839	29
COMBO	PRM	0.000 (0.002)	0.957 (0.034)	---	0.0018	98
COMBO	DEN	0.002 (0.001)	0.972 (0.024)	---	0.1394	98
COMBO	VOL	-0.002 (0.001)	0.995 (0.019)	---	0.2655	98

[a] Chronosequences based on a linear regression of a model $Y_t = Y_0 \times e^{k \times t}$;

[b] Chronosequences based on a lag exponential regression of a model $Y_t = Y_0 \times (1 - (1 - e^{k \times t}))^L$;

[c] Mass;

[d] Density;

[e] Volume.

Table 3.6. Decomposition phase-specific snag-to-log and log-to-log decomposition rate-constants based on CWD decomposition-vectors analysis.

Logs-to-logs						
Phase[a]	Variable[b]	N	k	Min k	Max k	SE
1	DEN	74	-0.034	-0.096	0.004	0.002
2	DEN	58	-0.032	-0.099	0.057	0.004
3	DEN	24	0.020	-0.040	0.122	0.008
1	VOL	137	-0.010	-0.101	0.063	0.002
2	VOL	19	-0.035	-0.100	0.059	0.008
1	MASS	67	-0.039	-0.112	0.017	0.003
2	MASS	57	-0.045	-0.155	0.052	0.004
3	MASS	32	-0.022	-0.083	0.081	0.007
Snags-to-logs						
1	DEN	69	-0.021	-0.082	0.016	0.002
2	DEN	1	-0.034	-0.034	-0.034	N/A
1	VOL	70	0.003	-0.075	0.039	0.002
1	MASS	68	-0.017	-0.109	0.032	0.003
2	MASS	2	-0.025	-0.041	-0.010	0.015
Combined Snags/Logs-to-logs						
	DEN	226	-0.024	-0.099	0.122	0.002
	VOL	226	-0.008	-0.101	0.063	0.002
	MASS	226	-0.031	-0.155	0.081	0.002

[a] Density, Volume, or Mass loss over time: 1 – <30% loss, 2 – 30-69% loss, 3 – >=70% loss;
[b] Variable type: DEN – density, VOL – volume, MASS – mass.

Table 3.7. Decay class-specific snag-to-log and log-to-log decomposition rate-constants based on CWD decomposition-vectors analysis.

Logs-to-logs						
Decay class	Variable[a]	N	k	Min k	Max k	SE
0	DEN	11	-0.037	-0.066	-0.011	0.005
1	DEN	5	-0.031	-0.066	-0.009	0.011
2	DEN	32	-0.028	-0.079	0.004	0.003
3	DEN	59	-0.038	-0.096	0.021	0.003
4	DEN	24	-0.036	-0.099	0.004	0.005
5	DEN	25	0.026	-0.024	0.122	0.007
0	VOL	11	-0.010	-0.046	0.007	0.004
1	VOL	5	-0.004	-0.016	0.009	0.005
2	VOL	32	-0.007	-0.031	0.013	0.002
3	VOL	59	-0.006	-0.031	0.031	0.002
4	VOL	24	-0.012	-0.094	0.063	0.007
5	VOL	25	-0.040	-0.101	0.059	0.007
0	MASS	11	-0.047	-0.112	-0.015	0.008
1	MASS	5	-0.035	-0.082	-0.005	0.015
2	MASS	32	-0.035	-0.078	0.017	0.004
3	MASS	59	-0.044	-0.095	0.052	0.003
4	MASS	24	-0.048	-0.155	0.043	0.008
5	MASS	25	-0.014	-0.081	0.081	0.007
Overall	MASS	156	-0.038	-0.155	-0.081	0.002
Snags-to-logs						
0	DEN	11	-0.037	-0.066	-0.011	0.005
1	DEN	21	-0.033	-0.082	-0.004	0.004
2	DEN	39	-0.015	-0.045	0.016	0.002
3	DEN	10	-0.016	-0.034	-0.006	0.003
0	VOL	11	-0.010	-0.046	0.007	0.004
1	VOL	21	0.006	-0.024	0.026	0.002
2	VOL	39	0.001	-0.075	0.025	0.003
3	VOL	10	0.005	-0.051	0.039	0.008
0	MASS	11	-0.047	-0.112	-0.015	0.008
1	MASS	21	-0.026	-0.073	0.009	0.004
2	MASS	39	-0.014	-0.109	0.018	0.004
3	MASS	10	-0.011	-0.065	0.032	0.008

[a] Variable type: DEN – density, VOL – volume, MASS – mass.

Table 3.8. Fisher's Protected LSD pairwise comparisons for percent mass, density, and volume loss categories of *k*.

Phases[a]		Mass				Density				Volume			
		S/L[b]		L/L[c]		S/L		L/L		S/L		L/L	
		p-value	difference[d]	p-value	difference	p-value	difference	p-value	difference	p-value	difference	p-value	difference
1	2	0.60	No	0.25	No	0.43	No	0.74	No	---	---	<0.0001	Yes
1	3	---	---	0.01	Yes	---	---	<0.0001	Yes	---	---	---	---
2	3	---	---	0.0004	Yes	---	---	<0.0001	Yes	---	---	---	---

[a] Phases used in pairwise comparison of *k*: 1 for <30% loss, 2 for 30%-70% loss, and 3 for >70% loss;
[b] CWD sampled as snags in 2002 and as logs in 2008;
[c] CWD sampled as logs in both 2002 and 2008;
[d] Differences are significant at $\alpha=0.05$.

Table 3.9. Fisher's Protected LSD pairwise comparisons for decay class k.

Decay Classes[a]		Mass				Density				Volume			
		S/L[b]		L/L[c]		S/L		L/L		S/L		L/L	
		p-value	difference[d]	p-value	difference	p-value	difference	p-value	difference	p-value	difference	p-value	difference
0	1	---	---	0.45	No	---	---	0.64	No	---	---	0.60	No
0	2	---	---	0.24	No	---	---	0.25	No	---	---	0.73	No
0	3	---	---	0.75	No	---	---	0.92	No	---	---	0.59	No
0	4	---	---	0.96	No	---	---	0.85	No	---	---	0.78	No
0	5	---	---	0.002	Yes	---	---	<0.0001	Yes	---	---	0.0002	Yes
1	2	0.04	Yes	0.99	No	<0.0001	Yes	0.75	No	0.26	No	0.74	No
1	3	0.07	No	0.51	No	0.004	Yes	0.54	No	0.85	No	0.82	No
1	4	---	---	0.38	No	---	---	0.71	No	---	---	0.44	No
1	5	---	---	0.14	No	---	---	<0.0001	Yes	---	---	0.00	Yes
2	3	0.07	No	0.16	No	0.89	No	0.05	Yes	0.51	No	0.81	No
2	4	---	---	0.11	No	---	---	0.22	No	---	---	0.41	No
2	5	---	---	0.01	Yes	---	---	<0.0001	Yes	---	---	<0.0001	Yes
3	4	---	---	0.61	No	---	---	0.68	No	---	---	0.26	No
3	5	---	---	<0.0001	Yes	---	---	<0.0001	Yes	---	---	<0.0001	Yes
4	5	---	---	<0.0001	Yes	---	---	<0.0001	Yes	---	---	<0.0001	Yes

[a] Decay classes used in pairwise comparison of k;
[b] CWD sampled as snags in 2002 and as logs in 2008;
[c] CWD sampled as logs in both 2002 and 2008;
[d] Differences are significant at $\alpha=0.05$.

Table 3.10. Comparison of spruce decomposition rate-constants determined in this study with published values from other regions.

Species	Location	CWD Type[a]	Diameter, (cm)	CWD property[b]	Intercept and rate-constant		Period (years)	Study Type[d]	Source
					Y_0	k/ k_{100}[c],(yr^{-1})			
Picea abies	SE Norway	L	7-9 10-15 16-20 21-25 >25 All	D	unknown	0.0275 0.0342 0.0435 0.0391 0.0412 0.0330	32	CS	Naesset 1999
	St. Petersburg Region, NW Russia	S LN L S/LN/L	>4	M	1.000	0.008 0.009 0.015 0.016[f]	0-50	CS	Shorohova and Shorohov 2001
		L	5-20 20-40 40-60	D	1.000	0.059 0.032 0.026	0-71	CS	Tarasov and Birdsey 2001
		S L S/L	11-20	M	1.184 0.825 unknown	0.044/0.014 0.026/0.032 0.028/0.036	2-7 2-73 2-73	CS	Yatskov et al. 2003
	St. Petersburg and Novgorod Regions, NW Russia	S/L/ST	>10	D	unknown	0.034	0-12	CS	Krankina and Harmon 1995
		S/L	>10	M D V	unknown	0.033 0.013 0.027	1-54	CS	Harmon et al. 2000
	Carpathians, Poland	L	10-22 23-35 >35	V	unknown	0.027 0.026 0.016	10	VRDC	Holeksa et al. 2008
P. ajanensis	Khabarovsk Region, Russian Far East	S L	17-47 15-63	M	1.252 0.966	0.035/0.031 0.028/0.029	1-71 2-77	CS	Yatskov et al. 2003
P. engelmannii	Canadian Rockies	S/L	1-18	D	unknown	0.0054 0.0025	35 100	CS	Johnson and Greene 1991

Table 3.10 (Continued). Comparison of spruce decomposition rate-constants determined in this study with published values from other regions.

Species	Location	CWD Type[a]	Diameter, (cm)	CWD property[b]	Intercept and rate-constant		Period (years)	Study Type[d]	Source
					Y_0	k/k_{100}[c],(yr^{-1})			
P. glauca	Northcentral Minnesota	L	5-22	D	unknown	0.071	14-17	TS	Alban and Pastor 1993
	Southwestern Alberta, Canada	S/L	~15	M	unknown	0.0271	14	TS	Laiho and Prescott 1999
	Abitibi Region, Northern Quebec	L	>10	D	unknown	0.038	64	CS	Brais et al. 2006
P. lutzii	Kenai Peninsula, Alaska	S	17-70 19-49	2002 M 2008M M[e] 2002 V 2008 V V[e] 2002 D 2008 D D[e]	0.974 0.988 0.957 0.996 1.020 0.995 0.988 0.973 0.972	0.000 0.003 0.000 0.002 0.003 0.002 -0.002 0.000 -0.002	0-43 6-49	CS	This study
		L	10-61 10-70	2002 M 2008 M M[e] 2002 D 2008 D D[e]	1.063 0.893 0.954 0.996 0.827 0.891	0.022 0.020 0.021 0.017 0.013 0.015	0-76 6-82	CS	This study
P. mariana	Manitoba, Canada	L	>=5	M	unknown	0.060 0.050		DR CSST	Bond-Lamberty and Gower 2008
	NW Quebec	S	>=5	D	unknown	0.0058	~30	CS	Angers et al. 2012
P. obovata	Krasnoyarsk Region, Russia	S L	17-47 15-63	M	0.985 1.106	-0.0006/0.0006 0.049/0.045	2-15 0-33	CS	Yatskov et al. 2003
P. rubens	White Mountain NF, New Hampshire	L	10 – 15 15 – 25 25-40	D	unknown	0.033[g] 0.027[g] 0.032[g]	0-64	CS	Foster and Lang 1982

Table 3.10 (Continued). Comparison of spruce decomposition rate-constants determined in this study with published values from other regions.

Species	Location	CWD Type[a]	Diameter, (cm)	CWD property[b]	Intercept and rate-constant		Period (years)	Study Type[d]	Source
					Y_0	k/k_{100}[c],(yr^{-1})			
P. sitchensis	Olympic NP, Hoh River, Washington	L	<60 >60 All	D	unknown	0.0119 0.0096 0.0111	4-68	CS	Graham and Cromack 1982

[a] CWD type: S – snags, L – logs, LN – leaning CWD, ST – stump;

[b] CWD property: D – density, V – volume, M – mass;

[c] Decomposition rate-constant with intercept 100;

[d] Study type: CS – chronosequence, CSST – chronosequence of stands, DR – direct respiration, TS – time series, VRDC – volume reduction in decay classes;

[e] Mass, volume, and density for combined 2002/2008 data set;

[f] Rate-constant for all CWD types including naturally created stumps with the decomposition rate-constant of 0.021 yr^{-1};

[g] Rate-constants were based on stem wood density loss excluding bark.

REFERENCES

Alban, D.H. and Pastor, J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. 23: 1744–1749.

Anderson, R.S., Hallett, D.J., Berg, E.E., Jass, R.B., Toney, J.L., de Fontaine, C.S., and DeVolder, A.D. 2006. Holocene development of boreal forests and fire regimes on the Kenai lowlands of Alaska. The Holocene 16 (6): 791-803.

Angers, V.A., Drapeau, P., and Bergeron, Y. 2012. Mineralization rates and factors influencing snag decay in four North American boreal tree species. Can. J. For. Res. 42: 157-166. DOI:10.1139/X11-167

Berg, E.E. and Anderson R.S. 2006. Fire history of white and Lutz spruce forests on the Kenai Peninsula, Alaska, over the last two millennia as determined from soil charcoal. For. Ecol. Manage. 227: 275–283.

Berg, E.E., Henry, J.D., Fastie, C.L., De Volder, A.D., Matsuoka, S.M. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. For. Ecol. Manage. 227: 219-232.

Birdsey, R.A. and Heath, L.S. 1995. Carbon changes in US forests. *In*: Productivity of America's forests and climate change 271: 56-70.

Bond-Lamberty, B. and Gower, S.T. 2008. Decomposition and fragmentation of coarse woody debris: Re-visiting a boreal black spruce chronosequence. Ecosystems 11(6): 831-840.

Brais, S., Paré D., and Lierman, C. 2006. Tree bole mineralization rates of four species of the Canadian eastern boreal forest: Implication for nutrient dynamics following stand-replacing disturbances. Can. J. For. Res. 36: 2331-2340.

Brown, S., Mo, J., McPherson, J.K., and Bell, D.T. 1996. Decomposition of woody debris in Western Australian forests. Can. J. For. Res. 26: 954–966.

Chen, H. 1999. Root decomposition in three coniferous forests: Effects of substrate quality, temperature, and moisture. PhD dissertation. Oregon State University, Corvallis, Oregon.

Chueng, N., and Brown, S. 1995. Decomposition of silver maple (*Acer saccharinum* L.) woody debris in central Illinois bottomland forest. Wetlands 15: 232–241.

Cramer, D. and Howitt, D. (Eds.). 2004. Fisher's LSD (Least Significant Difference) or protected test. The SAGE Dictionary of Statistics. London, England: SAGE Publications, Ltd., 2004. 67. SAGE Research Methods. Web. 13 Aug. 2015.

De Volder, A. 1999. Fire and climate history of lowland black spruce forests, Kenai National Wildlife Refuge, Alaska. MS Thesis. Northern Arizona University.

Edmonds, R.L. and Eglitis, A. 1989. The role of Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. Can. J. For. Res. 19: 853–859.

Erickson, H.E., Edmonds, R.L., and Peterson, C.E. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. Can. J. For. Res. 15: 914-921.

Fahey T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. Ecological Monographs 53: 51-72.

Flint, C.G. 2006. Community perspectives on spruce beetle impacts on the Kenai Peninsula, Alaska. For. Ecol. Manage. 227(3): 207-218.

Flint, C.G. and Haynes, R. 2006. Managing forest disturbances and community responses: Lessons from the Kenai Peninsula, Alaska. J. For. 104(5): 269-275.

Foster, J.R. and Lang, G.E. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Can. J. For. Res. 12(3): 617-626.

Franklin J.F., Shugart H.H., and Harmon M.E. 1987. Tree death as an ecological process. BioScience 37: 550-556.

Garman, S.L., Acker, S.A., Ohman, J.L., and Spies, T.A. 1995. Asymptotic height-diameter equations for twenty-four tree species in western Oregon. Research Contribution 10. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, 22 p.

Giorgi, F. 2006. Climate change hot-spots. Geophys. Res. Lett. 33(8), 4 p. http://dx.doi.org/10.1029/2006GL025734

Goetz, S.J., Mack, M.C., Gurney, K.R., Randerson, J.T., and Houghton, R.A. 2007. Ecosystem responses to recent climate change and fire disturbance at northern high latitudes: Observations and model results contrasting northern Eurasia and North America. Environmental Research Letters 2(4), 045031.

Goodale, C.L., Apps, M.J., Birdsey, R.A., Field, C.B., Heath, L.S., Houghton, R.A., Jenkins, J.C., Kohlmaier, G.H., Kurz, W., Liu, S., Nabuurs, G.-J., Nilsson, S., and Shvidenko, A.Z. 2002. Forest carbon sinks in the Northern Hemisphere. Ecological Applications 12(3): 891-899.

Gough, C.M., Vogel, C.S., Kazanski, C., Nagel, L., Flower, C.E., and Curtis, P. S. 2007. Coarse woody debris and the carbon balance of a north temperate forest. For. Ecol. Manage. 244(1): 60-67. DOI:10.1016/j.foreco.2007.03.039

Graham, R.L. 1982. Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range. Ph.D. thesis, Oregon State University, Corvallis, Oregon.

Graham, R.L. and Cromack, K. Jr. 1982. Mass, nutrient content, and decomposition rate of dead boles in rain forests of Olympic National Park. Can. J. For. Res. 12: 51 1-521.

Greb, S.F. and Archer, A.W. 2007. Soft-sediment deformation produced by tides in a meizoseismic area, Turnagain Arm, Alaska. Geology 35 (5): 435-438. Geological Society of America. DOI: 10.1130/G23209A.

Griffin, D.M. 1977. Water potential and wood-decay fungi. Ann. Rev. Phytopathol. 15: 319-329.

Hale, C.M. and Pastor, J. 1998. Nitrogen content, decay rates, and decompositional dynamics of hollow versus solid hardwood logs in hardwood forests of Minnesota, USA. Can. J. For. Res. 28(9): 1276-1285.

Harmon, M.E., Bond-Lamberty, B., Tang, J., and Vargas, R. 2011a. Heterotrophic respiration in disturbed forests: A review with examples from North America. Journal of Geophysical Research: Biogeosciences, 116(G4). DOI:10.1029/2010JG001495

Harmon, M.E., Krankina, O.N., and Sexton, J. 2000. Decomposition vectors: A new approach to estimating woody detritus decomposition dynamics. Can. J. For. Res. 30: 76–84.

Harmon, M.E. and Sexton, J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. U. S. LTER Publication No. 20.

Harmon, M.E. and Sexton, J. 1995. Water balance of conifer logs in early stages of decomposition. Plant and Soil 172: 141-152.

Harmon, M.E., Whigham, D.F., Sexton, J., and Olmsted I. 1995. Decomposition and mass of woody detritus in the dry tropical forests of the Northeastern Yucatan Peninsula, Mexico. Biotropica 27(3): 305-316.

Harmon, M.E., Sexton, J., Caldwell, B.A., and Carpenter, S.E. 1994. Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. Can. J. For. Res. 24: 1883–1893.

Harmon, M.E. and Chen, H. 1991. Coarse woody debris dynamics in two old-growth ecosystems. BioScience, pp. 604-610.

Harmon, M.E., Cromack K. Jr., and Smith, B.G. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Can. J. For. Res. 17(10): 1265-1272.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr., and

Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133-302.

Hartley, C. 1949. Fungi and wood. Yearbook of Agriculture, pp. 630-633.

Heath, L.S., Smith, J.E., Woodall, C.W., Azuma, D.L., and Waddell, K.L. 2011. Carbon stocks on forestland of the United States, with emphasis on USDA Forest Service ownership. Ecosphere 2(1), art6.

Hicks, W.T. 2000. Modeling nitrogen fixation in dead wood. PhD dissertation. Oregon State University, Corvallis, Oregon.

Hinds, T.E., Hawksworth, F.G., and Davidson, R.W. 1965. Beetle-killed Engelmann spruce: Its deterioration in Colorado. J. For. 63: 536-542.

Holeksa, J., Zielonka, T., and Zywiec, M. 2008. Modeling the decay of coarse woody debris in a subalpine Norway spruce forest of the West Carpathians, Poland. Can. J. For. Res. 38: 415-428. DOI:10.1139/X07-139

Holsten, E.H., Thier, R.W., Munson, A.S., and Gibson, K.E. 2000. The spruce beetle. Forest Insect and Disease Leaflet 127. USDA Forest Service. http://www.na.fs.fed.us/spfo/pubs/fidls/sprucebeetle/sprucebeetle.htm

Holsten, E.H. 1984. Factors of susceptibility in spruce beetle attack on white spruce in Alaska. Journal of the Entomological Society of British Columbia 81: 39-45.

IPCC 2013. Hartmann, D.L., Klein Tank, A.M.G., Rusticucci, M., Alexander, L.V., Brönnimann, S., Charabi, Y., Dentener, F.J., Dlugokencky, E.J., Easterling, D.R., Kaplan, A., Soden, B.J. Thorne, P.W., Wild, M., and Zhai, P.M. 2013. Observations: Atmosphere and Surface. *In*: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., and Midgley, P.M. (Eds.). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Janisch, J.E., Harmon, M.E., Chen, H., Fasth, B., and Sexton, J. 2005. Decomposition of coarse woody debris originating by clearcutting of an old-growth conifer forest. Ecoscience 12(2): 151-160. DOI: http://dx.doi.org/10.2980/i1195-6860-12-2-151.1

Janisch, J.E. and Harmon, M.E. 2002. Successional changes in live and dead wood carbon stores: Implications for net ecosystem productivity. Tree Physiology 22(2-3): 77-89.

Johnson, E.A. and Greene, D.F. 1991. A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia − Picea engelmannii* forests. Journal of Vegetation Science 2: 523-530.

Jomura, M., Kominami, Y., Dannoura, M., and Kanazawa, Y. 2008. Spatial variation in respiration from coarse woody debris in a temperate secondary broad-leaved forest in Japan. Forest Ecol. Manag. 255(1): 149-155.

Käärik, A.A. 1974. Decomposition of wood. *In*: Dickinson, C.H. and Pugh, G.J.F. (Eds.). Biology of Plant Litter Decomposition. London, Academic Press, pp. 129-174.

Krankina O.N. and Harmon M.E. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water, Air and Soil Pollution 82: 227-238.

Laiho, R. and Prescott, C.E. 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. Can. J. For. Res. 29: 1592-1603.

Lambert R.L., Lang G.E., and Reiners, W.A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61: 1460-1473.

MacMillan, P.C. 1988. Decomposition of coarse woody debris in an old-growth Indiana forest. Can. J. For. Res. 18: 1353-1362.

Mäkinen, H., Hynynen, J., Siitonen, J., and Sievänen, R. 2006. Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. Ecological Applications 16(5): 1865-1879.

Marra, J.L. and Edmonds, R.L. 1996. Coarse woody debris and soil respiration in a clearcut on the Olympic Peninsula, Washington, U.S.A. Can. J. For. Res. 26: 1337-1345.

McCullough, D.G., Werner, R.A., and Neumann, D. 1998. Fire and insect in northern and boreal forest ecosystems of North America. Annu. Rev. Entomol. 43: 107-27.

McFee, W.W. and Stone, E.L. 1966. The persistence of decaying wood in the humus layers of northern forests. Soil Science Society of America Journal 30(4): 513-516.

Means, J.E., MacMillan, P.C., and Cromack, K. Jr. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest. Can. J. For. Res. 22: 1536-1546.

Mielke, J.L. 1950. Rate of deterioration of beetle-killed Engelmann spruce. J. For. 48: 882-888.

Naesset, E. 1999. Decomposition rate-constants of *Picea abies* logs in southeastern Norway. Can. J. For. Res. 29: 372-381.

NOAA 2014. National Oceanic and Atmospheric Administration. Satellite and Information Service. National Climatic Data Center. US Department of Commerce. http://www.ncdc.noaa.gov/IPS/cd/cd.html;jsessionid=4E5612C511E74A2687A84659B08AA18

7?_page=0&jsessionid=4E5612C511E74A2687A84659B08AA187&state=AK&_target1=Next+%3E

Odum, E.P. 1969. The strategy of ecosystem development. Science 164 (3877):262-270.

Odum, E.P. 1968. Energy Flow in Ecosystems: A Historical Review. American Zoologist 8: 11-18.

Odum, E.P. and Biever, L.J. 1984. Resource quality, mutualism, and energy partitioning in food chains. American Naturalist, pp.360-376.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in terrestrial ecosystems. Ecology 42: 322-331.

Onega, T.L., and Eickmeier, W.G. 1991. Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. Bull. Torrey Bot. Club 118: 52–57.

Panshin, A.J. and de Zoew, C. 1970. Textbook of wood technology. Vol. 1. McGraw-Hill Book Co., New York.

Peterson, R.O., Woolington, J.D., and Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88: 3-52.

Potkin, M. 1997. Fire history disturbance study of the Kenai Peninsula mountainous portion of the Chugach National Forest. Draft. USDA Forest Service. Chugach National Forest. December 5, 1997. Anchorage, Alaska.

Ross, D.W., Daterman, G.E., Boughton, J.L., and Quigley, T.M. 2001. Forest health restoration in South-Central Alaska: A problem analysis. USDA Forest Service. PNW Research Station. PNW-GTR-523, July 2001.

Scheffer, T.C. and Cowling, E.B. 1966. Natural resistance of wood to microbial deterioration. Annu. Rev. Phytopathol. 4(1): 147-168.

Schwartz, C.C. and Franzmann, A.W. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. The Journal of Wildlife Management, pp.426-431.

Schwartz, C.C. and Franzmann, A.W. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs 113: 3-58.

Sexton, J.M. and Harmon, M.E. 2009. Water dynamics in conifer logs in early stages of decay in the Pacific Northwest, USA. Northwest Science 83(2): 131-139.

Shorohova, E., Kapitsa, E., and Vanha-Majamaa, I. 2008. Decomposition of stumps in a chronosequence after clear-felling vs. clear-felling with prescribed burning in a southern boreal forest in Finland. For. Ecol. Manage. 255(10): 3606-3612.

Shorohova, E.V. and Shorohov A.A. 2001. Coarse woody debris dynamics and stores in a boreal virgin spruce forest. Ecol. Bul. 49: 129-135. http://www.jstor.org/stable/20113270

Smithwick, E.A.H., Harmon, M.E., Remillard, S.M., Acker, S.A., and Franklin, J.F. 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. Ecological Applications 12(5): 1303–1317. http://dx.doi.org/10.1890/1051-0761(2002)012[1303:PUBOCS]2.0.CO;2

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Can. J. For. Res. 12: 18-28.

Spies, T.A., Franklin, J.F., and Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69(6): 1689-1702.

Stamm, A.J. 1934a. Swelling of wood. USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin in cooperation with the University of Wisconsin. R1061, 15 p.

Stamm, A.J. 1934b. Effect of inorganic salts upon the swelling and the shrinking of wood. Journal of the American Chemical Society 56: 1195-1204. DOI: 10.1021/ja01320a063

Stamm, A.J. 1929. The fiber-saturation point of wood as obtained from electrical conductivity measurements. USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin in cooperation with the University of Wisconsin. R859, 11 p.

Stocks, B.J., Fosberg, M.A., Lynham, T.J., Mearns, L., Wotton, B.M., Yang, Q., Jin, J.-Z., Lawrence, K., Hartley, G.R., Mason, J.A., and McKenney, D.W. 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. Climatic Change 38(1): 1-13. http://dx.doi.org/10.1023/A%3A1005306001055

Tarasov M.E. and Birdsey R.A. 2001. Decay rate and potential storage of coarse woody debris in the Leningrad region. Ecological Bulletin, 49.

Tarasov, M.E. 1999. Role of coarse woody debris in carbon balance of forest ecosystems of Leningrad oblast'. Ph.D. thesis, St. Petersburg Forestry Research Institute Publishers, St. Petersburg, Russia. [In Russian].

Triska, F.J. and Cromack, K. Jr. 1980. The roles of wood debris in forests and streams. *In*: Waring, R.H. (Ed.). Forests: Fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis, Oregon, pp. 171-190.

Van Pattern, D.J. 2000. Soil survey of lower Kenai Peninsula area, Alaska. USDA NRCS publication, 179 p.

Vitousek, P.M. and Reiners, W.A. 1975. Ecosystem succession and nutrient retention: A hypothesis. Bioscience 25(6):376-381. DOI: 10.2307/1297148.

Werner, R. A., Holsten, E. H., Matsuoka, S. M., and Burnside, R. E. 2006. Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research Forest Ecol. Manag. 227:195–206.

Werner, R.A. and Holsten, E.H. 1983. Mortality of white spruce during a spruce beetle outbreak on the Kenai Peninsula in Alaska. Can. J. For. Res. 13: 246-250.

Wirth, C., Schulze, E.-D., and Luhker, B. 2000. How fire exerts control over carbon balances in Siberian Scots pine forests. *In*: Apps, M.J. and Marsden, J. (Eds.). The role of boreal forests and forestry in the global carbon budget. Abstracts of International Science Conference, 8-12 May 2002, Edmonton, Alberta. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, 77 p.

USDA 2014. Field instructions for the annual inventory of Coastal Alaska 2014. Forest Inventory and Analysis program. PNW Research Station. USDA Forest Service. Anchorage, Alaska.

Yatskov, M., Harmon, M.E., and Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. For. Res. 33: 1211-1226.

Yatskov, M. 2000. A chronosequence of wood decomposition in the boreal forests of Russia. MS thesis. Oregon State University, Corvallis, Oregon, 168 p.

Zabel, R.A. and Morrell, J.J. 1992. Factors affecting the growth and survival of fungi in wood (Fungal Ecology), pp. 102-115. *In*: Wood microbiology: Decay and its prevention. Academic Press, Inc. Harcourt Brace Jovanovich, Pubs.

CHAPTER 4 -- MODELING CARBON DYNAMICS IN SPRUCE-DOMINATED FORESTS OF KENAI PENINSULA, ALASKA FOLLOWING THE SPRUCE BARK BEETLE OUTBREAK OF THE 1990S

Mikhail A. Yatskov, Mark E. Harmon, and Thomas M. Heutte

ABSTRACT

Climate-related changes in disturbance regimes in forest ecosystems could create future landscapes that are a long-term carbon (C) source to the atmosphere. Post-disturbance forest management strategies provide avenues for mitigating global climate change through curbing carbon dioxide emissions and storing C in forests or forest products. Using model simulations, we evaluated the effect of several management strategies on C stores and emissions following a spruce bark beetle outbreak on Kenai Peninsula, Alaska for three possible tree regeneration scenarios including no-, immediate, and delayed regeneration. System C storing potential was assessed under delayed regeneration for management ranging from "leave-as-is" to "salvage-and-utilization". Immediate tree regeneration led to the recovery of disturbed areas to steady-state pre-disturbance C stores of 49.27 Mg C ha^{-1} 25 years earlier than regeneration delayed by 25 years. Lack of regeneration, representing a permanent loss of tree cover on disturbed portion of the landscape, caused a permanent decrease in wood C stores to a lower steady-state level of 31.51 Mg C ha^{-1}. The "leave-as-is" management stored more C in the short-run, whereas "salvage-and-utilization" management stored more C in the long-run. Among the "salvage-and-utilization" scenarios, biomass fuels with fossil fuel substitution provided larger C storage assuming the substitution is permanent. Because a reduction in near-term emissions may be a more robust strategy than reducing long-term emissions, the "leave-as-is" scenarios may offer more immediate contribution to mitigation of global climate change.

INTRODUCTION

Global climate change will lead to alterations in temperature, precipitation and their extremes (Karl et al. 1996), as well as shifts in timing, longevity, and intensity of dry and wet seasons (McCarthy 2001) that have been linked to changes in disturbance occurrence and regime (Dale et al. 2001, Soja et al. 2007). The extent, frequency, and severity of multiple disturbances including fires (Flannigan et al. 2000, Stocks at al. 2002, Westerling et al. 2006), bark beetle outbreaks (Williams and Liebhold 2002, Carroll et al. 2003, Werner at al. 2006, Bentz et al. 2010, Cudmore et al. 2010), drought events (Allen et al. 2010), and others (Dale et al. 2001) have been on the rise. These disturbances are likely to continue to cause widespread tree mortality across forested landscapes creating vast amounts of coarse woody debris (CWD) that emit C to the atmosphere to a degree that regional C balance and future C dynamics are likely to change.

C balance of forested regions depends on inputs (C sequestered by live components during growth) and outputs (C emitted from dead components through decomposition or combustion) (Janisch and Harmon 2002, Houghton 2005). Live trees in many forest ecosystems represent the largest aboveground C pool (Grier and Logan 1977, Smithwick et al. 2002, Yatskov et al. - Chapter 2), therefore live tree C dynamics associated with growth and mortality have been extensively studied (Everham and Brokaw 1996, McMahon et al. 2010, Meddens et al. 2012, Hansen 2014). In contrast, despite multiple recent large-scale disturbance events (Potter et al. 2005, Berg et al. 2006) few have examined the post-disturbance fate of CWD C (Harmon et al. 2005, Kurz at al. 2008, Hansen 2014).

The Kenai Peninsula, Alaska, provides a rare opportunity to examine C dynamics following a recent spruce bark beetle (SBB) outbreak (Berg et al. 2006, Werner et al. 2006). Estimates of C stores (Barrett 2014, Yatskov et al. – Chapter 1) as well as information on regeneration (Boucher and Mead 2006, Barrett 2014) in disturbed areas are available from the Forest Inventory and Analysis (FIA) Program (USDA 2015a). Tree mortality data associated with SBB activity for the 1989-2015 time period were obtained from the aerial surveys conducted by the Forest Health Protection (FHP) Program (USDA 2015b). CWD decomposition rate-constants and parameters for the model of CWD-related C dynamics were acquired from a chronosequence and decomposition-vectors analysis of CWD (Yatskov et al. – Chapter 2). Thus, Kenai represents a region, where the development of a major disturbance could be examined by utilizing existing information on disturbance severities, forest inventory plot data information, and empirically derived CWD decomposition rate-constants, to provide estimates and projections of long-term C dynamics.

Our main objective in this analysis was to utilize available information to estimate the balance of tree bole-related C on the Kenai Peninsula following a major spruce bark beetle outbreak. Using model simulations, we evaluated the effect of several management strategies on C stores ranging from a "leave-as-is" scenario to salvage logging and utilization. We hypothesized that the management strategies associated with the least removal of bole biomass from disturbed forest will provide the highest ecosystem C storage. This is because the C losses associated with relatively slow CWD decomposition can be lower than those associated with the harvesting, transportation, and processing of harvested bole biomass (Apps et al. 1999). Hence, the "leave-

as-is" management strategy could lead to more C stored in the forest in comparison to management strategies when bole biomass is harvested as a biogenic energy source (Kurz et al. 1992, Mitchell et al. 2012).

METHODS

Study area

The Kenai Peninsula is located in south central Alaska (latitude 60°N, longitude 150°W) and covers land area of 2.6 million ha (Peterson et al. 1984). The Peninsula is surrounded by water bodies including Prince William Sound (east), Cook Inlet (west), Turnagain Arm, a semidiurnal hypertidal estuary (Greb and Archer 2007) (north), and Gulf of Alaska (south) and connected to mainland Alaska in the north by 16-km wide land and ice bridge (Peterson et al. 1984).

The Peninsula can be divided into two distinct landforms. The eastern part is dominated by the Kenai Mountains rising to 2,000 m above sea level, supporting major ice fields (Peterson et al. 1984, Schwartz and Franzmann 1992). The western part, the Kenai lowlands, is dominated by a rolling plateau with the elevation ranging from sea level to 500 m above sea level (Peterson et al. 1984) and covered by numerous lakes, ponds, and wetlands.

The study area encompassing the western and northern portions of the Kenai Peninsula has a maritime climate with spring being the driest and fall being the wettest seasons (Table 4.1). The 30-year mean annual temperature over the period between 1979 and 2008 was 2.4°C (Table 4.2) with a low of 0.9°C (in 1996 and 1999) and a high of 3.9°C (in 2002) (NOAA 2014). The coldest

month in the region was January with the 30-year mean temperature of -6.9°C. The hottest month was July with the 30-year mean of 12.8°C. Mean annual precipitation in this zone for the same time period was 584 mm with a low of 397 mm (in 1996) and a high of 816 mm (in 1981) (NOAA 2014).

The Kenai lowlands support variety of vegetation communities ranging from pure stands of black spruce (*Picea mariana* (Mill.) B. S. P.) on wet organic soils, to mixed forests containing either white spruce (*Picea glauca* (Moench) Voss), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), or Lutz spruce (*Picea x lutzii* Little), a viable hybrid between white and Sitka spruce, mixed with trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), or both of these hardwoods growing on drier more productive sites. Riparian areas along rivers and around wetlands are dominated by black cottonwood (*Populus balsamifera* ssp. *trichocarpa* L.) stands or alder-willow (*Alnus-Salix*) shrub communities (Potkin 1997, Van Pattern 2000).

Natural and anthropogenic disturbances have formed forests that are complex in age structure and their distribution of live and dead components. Natural disturbances that are most significant in extent, severity, and long-term effects on forest communities include spruce bark beetle outbreaks (Holsten et al. 2000, Werner et al. 2006) and fires (Potkin 1997, De Volder 1999, Berg et al. 2006, Anderson et al. 2006). The long-term average return interval for beetle outbreaks was estimated at 52 years (Berg et al. 2006). Fire return interval depends on the forest community. In black spruce-dominated stands the mean fire return interval (MFRI) was estimated either at 89±43 (mean ± SD) years (De Volder 1999) or 130±66 years (Anderson et al. 2006), using

dendrochronology or sedimentary charcoal analysis, respectively. In white/Lutz spruce-dominated stands the MFRI was estimated either at 81±41 years (Anderson et al. 2006) or 515±355 years (Berg and Anderson 2006), using lake sedimentary charcoal or radiocarbon-dated soils charcoal samples, respectively. Anthropogenic disturbances historically were associated with selective harvest of accessible spruce stands (Van Pattern 2000), whereas more recently were attributable to salvage logging in beetle-damaged stands (Flint 2006).

Data sources for the study

This analysis took advantage of existing information on C stores, rates of decomposition, rates of growth, and mortality rates for Kenai Peninsula forests. The estimates of pre-disturbance C stores in white/Lutz spruce-dominated stands as well as average-sized tree C and tree growth rates were obtained from the data provided by FIA program. Empirically derived spruce CWD decomposition rate-constants were obtained from a chronosequence and decomposition-vectors analysis of spruce CWD. Finally, spruce tree mortality rates were estimated from the aerial annual surveys conducted between 1989 and 2015 by the FHP program. Coupling the information from these sources we modelled C dynamics in spruce-dominated forests of the Kenai Peninsula following the outbreak of the 1990s and projected C dynamics 200 years into the future to examine several management scenarios.

Inventory sampling and plot design

In 2001 and 2002, an equal-probability sample of field plots was established throughout the forests of Kenai Peninsula as part of the south-central Alaska forest inventory by the U.S. Forest

Service Pacific Northwest Region's FIA program (USDA 2015a). The sampling area consisted of accessible forest land across all ownerships and forest types. The forest land designated as a wilderness study area within the Chugach national forest was excluded from the inventory (Barrett and Christensen 2011). The measurements and observations used for estimating biomass were collected in field-visited plots. For the purposes of the inventory, forest land was defined as land currently having at least 10% tree crown cover by trees of any size, including cut, burned over, or flooded areas with the evidence of formerly having at least 10% tree cover. This definition excluded lands that have never supported forests and lands formerly forested on which current land use prohibits establishment of forests (USDA 2000).

Forest inventory plots included four 7.3-meter fixed-radius subplots located in a pattern where subplot two was 36.6 meters north (360º magnetic) of subplot one and subplots 3 and 4 were 36.6 meters from subplot one at an azimuth of 120º and 240º, respectively. Each plot contained at least one forest stand represented by an area of at least 0.4 ha and continuous width of at least 36.6 m. Such an area was characterized by the unique combination of variables including Forest Type (assigned to a species representing a majority of stocking in a stand), Forest Stand Size (stand descriptor indicating which size-class of trees constituted the majority of stocking in the stand), and many others (USDA 2003). Among these stand characteristics, Forest Type was at the top of the hierarchy list due to its importance in stand delineation. Stocking was defined by FIA as the relative degree of occupancy of land by trees (USDA 2014).

Disturbance types and characteristics for each stand were derived from field observations. To be recorded the area affected by disturbance had to be ≥1 ha and contain the subplot center. The disturbance protocol was focused only on disturbances that occurred within 10 years prior to the date of the visit. Recorded disturbance characteristics included infestation level for bark beetle outbreaks, blowdown condition, root disease severity, as well as presence of clearcut, partial harvest, fire, flooding, earth movement/avalanche, and others. The lack of recent disturbance in the stand was also recorded. Observed tree damage or mortality from bark beetles (*Dendroctonus rufipennis* or *Ips* spp.) was recorded under infestation level. Sixty percent of spruce trees being attacked was used as a threshold between high and moderate severity of beetle attack.

The stand age was in general determined from 3 trees that were aged by counting annual rings on the core extracted with the increment borer. The trees selected for this purpose were representative of the age of each stand characterized by unique combination of forest type, stand size class, and other stand delineating variables (USDA 2003).

Live tree and CWD biomass estimation

Field procedures

Live trees and snags with a diameter at breast height (d.b.h. – diameter at 1.37 m from the ground level on the uphill side or from the root collar) of at least 12.5 cm were measured in 7.3-meter fixed radius subplots. Live saplings (trees with the d.b.h. greater or equal to 2.5 cm and less than 12.5 cm) were measured in 2.0-meter fixed radius microplots. Measurements and observations used in this study included tree species, d.b.h., total height (tree or snag vertical

length from the tree base to the tip of existing or reconstructed top), actual height (tree or snag

vertical length from the tree base to the break point), and snag deterioration stage (decay class

based on a 5-decay class system). Snags that were severed from the base or intact and leaning

less than 15° from the horizontal plane were considered logs, i.e. not a snag tally (USDA 2000).

Down Woody Material (DWM) (hereafter termed as logs), is defined as dead boles, portions of

dead boles, and primary branches severed from their bases, and rooted boles with a lean angle

less than 15° from horizontal plane and the diameter greater or equal to 2.5 cm at the large end

and length of at least 1 m. Logs were measured on either one, two, or sometimes three forested

subplots (depending on a number of forest stands within plot perimeter) in each plot using three

11.28-meter transects. The tally included tree pieces if their central axis crossed the transect line.

For each tallied piece, tree species, diameter at the large end, diameter at the small end, length,

and decay class were recorded. When advanced decay prevented the identification of tree

species, log pieces were assigned to either undetermined conifers or undetermined hardwoods

(USDA 2000).

Live tree and CWD biomass calculations

Total aboveground live tree biomass included bole wood, bark, branches, twigs and foliage. Live

tally trees and snags with d.b.h. ≥ 12.5 cm and live tally saplings with d.b.h. ≥ 2.54 cm were

included in biomass calculations. Biomass calculations for each individual live tree, sapling, and

snag were based on published species-specific direct biomass equations (see Appendix 1, p. 117

in Barrett and Christensen (2011) for a full list of citations). Our biomass estimates accounted for

broken tops on live trees and snags and reduced density of snags due to decay (Yatskov et al. –

Chapter 2). To account for reduced wood density in snags, we used field records of decay classes

assigned to snags and average density reduction factors for standing dead trees by species group

(hardwoods/softwoods) (Table 6, pg. 12 in Harmon et al. 2011b).

The mass of each individual log piece was calculated using the volume and the specific wood

density depending on species and decay class (Harmon et al. 2005, 2008). To calculate the

individual log piece volume we used a conic-paraboloid formula (Fraver et al. 2007). Volume

estimates for logs in Decay Class 5 (DC-5) were reduced to account for their elliptical shape (see

Yatskov et al. - Chapter 2 for more details). For pieces allocated in the field to unknown

hardwood or unknown softwood categories, we determined wood density for each of these

categories as an average based on densities from Harmon et al. (2008) weighted by the number

of log pieces with known species and decay class within each of two categories in our log

dataset. Mass of log per unit area was calculated for each subplot containing log data using a

formula from Waddell (2002). The average mass per unit area was calculated for each Plot/Stand

combination as the mean of log mass per unit area in subplots within the same stand.

Mean pre-disturbance aboveground biomass by age class

For modeling the pre-disturbance conditions in the stands we utilized the FIA dataset to estimate

live, snag, and log biomass stores in spruce-dominated stands prior to SBB outbreak. From the

field data, mean undisturbed stand biomass in Mg ha^{-1} was calculated using the standard national

method for FIA (see Bechtold and Patterson 2005). Out of the 209 at least partially forested FIA

plots with 237 unique stands identified during the 2001/2002 Kenai inventory, we selected 132 spruce dominated stands in 121 plots. These included 54 stands with white spruce forest type (11 undisturbed, 27 with high, and 16 with moderate disturbance severity), stands of various forest types with recorded spruce bark beetle outbreak disturbance (21 stands with high and 40 stands with moderate severity), and 17 stands that were neither white spruce forest type nor disturbed but had a significant spruce component ($\geq$30% of spruce trees from total by tree count).

The calculations of mean stand biomass differed between stands marked by the FIA field crews as undisturbed vs. disturbed. Mean pre-disturbance live biomass in undisturbed stands was based on live tally tree and sapling biomass only, whereas in stands marked as disturbed the mean pre-disturbance live biomass was based on a sum of live and DC-1 and DC-2 spruce snag biomass with the assumption that these snags represented the mortality from the recent SBB outbreak. Similarly, mean pre-disturbance snag biomass was calculated differently for the disturbed and undisturbed stands. Mean pre-disturbance snag biomass in undisturbed stands was based on total snag tally biomass, whereas in stands marked as disturbed the mean pre-disturbance snag biomass was based on a difference between the total snag tally biomass and DC-1 and DC-2 spruce snag tally biomass. Log biomass was calculated as a tally biomass regardless of the presence/absence of disturbance.

A total of 132 stands (123 plots) including 28 undisturbed, 56 moderately disturbed, and 48 highly disturbed stands (26, 53, and 44 plots, respectively) with the stand ages ranging from 0 to 163 years were assigned to a 20-year stand age classes (20 through 120). Age class 20 included 0

to 20-year old stands, age class 40 included 21 to 40-year old stands, and so on, except age class 120 included stands older than 100 years. The mean pre-disturbance biomass was aggregated by stand age classes.

Model calibration

Pre-disturbance live, snag, and log C stores by stand age classes were determined via biomass-to-C conversion using 1:2 C-to-biomass ratio (Barrett and Christensen 2011). To calibrate our simulation model to the landscape level, we calculated average C stores in three pools (live, snag, and log) weighted by number of stands in the stand age classes (Table A4.1). These were 36.28 Mg C ha^{-1}, 2.37 Mg C ha^{-1}, and 7.15 Mg C ha^{-1} for pre-disturbance live, snag, and log C pools, respectively. These C stores were assumed to represent a pre-outbreak stores.

To determine the background mortality rate we utilized the adjusted C stores and fluxes reported for the forests of Kenai Peninsula (Barrett 2014). The stores in Kenai Peninsula were reported at 59.2 Mg C ha^{-1}, 8.5 Mg C ha^{-1}, and 8.8 Mg C ha^{-1} for live, snag, and log pools (Barrett 2014, Table 16, pg. 23). The inventory period included the outbreak, therefore snag pool could have been inflated (comparing to pre-disturbance conditions associated with relatively low background mortality) because it contained both background and outbreak mortality. In turn, the live pool was probably decreased by the C that was transferred into snag pool as a result of the outbreak. From our pre-disturbance stand C store calculations we determined pre-disturbance snag-to-log C pool ratio (2.37 / 7.15 = 0.331) and applied that ratio to the values from Barrett (2014) reconstructing pre-disturbance live, snag, and log C stores to 64.8 Mg C ha^{-1}, 2.9 Mg C

ha^{-1}, and 8.8 Mg C ha^{-1}, respectively. To calculate woody NPP for the Kenai Peninsula based on the inventory, we summed C fluxes from Barrett (2014) including growth (0.852 Mg C ha^{-1} yr^{-1}), recruitment (0.084 Mg C ha^{-1} yr^{-1}), and mortality (0.156 Mg C ha^{-1} yr^{-1}), which amounted to 1.092 Mg C ha^{-1} yr^{-1}. Finally, the pre-disturbance (background) mortality rate was calculated as a ratio of the NPP (input) to live C store assuming steady-state conditions (i.e., 1.092 / 64.8 = 0.0169 yr^{-1}).

Biomass related to beetle mortality

To estimate annual tree biomass losses to beetle-related mortality we utilized the information from the FHP aerial detection survey (ADS). ADS represents one of the methods of collecting and reporting data on insect and disease outbreaks as well as other types of forest disturbances across state, private, and federal lands (FHTET 2015). It employs a technique known as digital aerial sketch-mapping to observe and monitor disturbance-related changes in the forest. The process involves annual aerial surveys which are supported by the ground surveys serving as ground truthing (DASM 2015).

The aerial surveys are conducted with use of survey aircraft typically flying at a speed of 110 miles per hour (m.p.h.) and altitude of 1,000 feet above ground level. Forest damage information is sketched at nominal 1:63,000 scale on a United States Geological Survey (USGS) quadrangle paper maps or maps displayed on touch-screen monitors or tablets. The sketch-map information is then post-processed using standard Geographic Information System (GIS) technology for storage, retrieval, and forest mortality and damage map production (DASM 2015).

The aerial survey observers are trained to recognize and associate damage patterns, discoloration, tree species and other clues to distinguish particular types of forest damage from surrounding undamaged forest. Despite the fact that bark beetle mortality is relatively easy to recognize compared to other types of damage (e.g., hardwood defoliation), low clouds, precipitation, smoke, and poor light conditions can inhibit the detection of damage signatures, or prevent some areas from being surveyed altogether due to safety concerns. Surveys do not cover the entire affected area each year; however, in the 1990s aerial surveys covered most of the spruce-dominated forests on the Kenai Peninsula due to the high interest in the spruce beetle outbreak.

The aerial survey data set covered time span between 1989 and 2015. Collected data consisted of geospatial vector polygon files indicating areas of spruce beetle damage. For the time period between 1989 and 1995, the area annually damaged by SBB was recorded. For the 1996-2000 period, damaged stands were subjectively grouped into polygons by the observer and classified as damaged/killed trees per acre (TPA) or trees per hectare (TPH) into Low with 2-10 TPA (5-25 TPH), Medium with 11-30 TPA (26-74 TPH), or High with >25 TPA (>74 TPH) damage severity classes. Mortality below 2 TPA (5 TPH) was considered endemic. Except for 2008, the damage extent for the 2000-2015 time period was determined as a count of damaged/killed trees per unit area. There was no SBB damaged area provided for 2008 because Kenai Peninsula was flown minimally that year.

To overcome the differences in mortality data collection techniques several approaches were used. To determine the upper bound of the high disturbance severity level we used the DC-1 and DC-2 spruce snag count in disturbed stands surveyed by the FIA program. On average, there were 126±13 (Mean ± SE) DC-1 and DC-2 spruce snags per ha which we assumed to reflect disturbance mortality. Therefore, the upper bound of the high disturbance severity class was assumed to equal 126 TPH. Then, to get a consistent data set over the entire disturbance period, mortality data from 2000-2015 period were reclassified as high, medium and low to match 1996-2000 classification. To fill in the missing area by severity values in 2008, data from 2007 and 2009 were averaged.

Aerial survey data collected over 1989-2015 time period were utilized to calculate annual C flux associated with beetle-related mortality. We converted TPH to C to determine C flux associated with the outbreak mortality. For that purpose, we calculated average spruce snag C amounts in 2-inch diameter classes using stands damaged by outbreak. A number of pre-disturbance live trees by diameter class and the killed-to-live trees proportion were utilized to account for the probability of trees by size being killed in disturbance. Using Monte Carlo methods in SAS (SAS statistical software package, Version 7, SAS Institute, Cary, NC), we made 10,000 runs to calculate C values represented by the severity level boundaries. These values combined with the proportion of the area by damage severity level from the aerial survey program were used to calculate annual mortality by making 10,000 runs using Monte Carlo simulator in Stochastic Uncertainty Estimator – SUE (Goodman 2002). To mimic the distribution of trees by size, in SUE we used triangular distribution for low and high severity levels (with rising and falling

hypotenuse, respectively) and uniform distribution for moderate disturbance severity level. The mortality flux was calculated this way for 1996-2015. The annual mortality flux for the period from 1990 to 1995 was calculated using the ratio of the area annually affected by outbreak between 1990 and 1995 and the area affected by outbreak in 1996 (the year with the highest mortality flux). We calculated 1989 mortality C flux as an average between the background mortality C flux and 1990 mortality C flux because the area ratio approach used to calculate 1990-1995 mortality fluxes yielded C flux value for 1989 that was below the background mortality.

Modeling approach to match the FIA and aerial survey data

Our preliminary analysis indicated that the amount of outbreak mortality estimated by aerial survey (64.82 Mg C ha^{-1}) was higher than pre-disturbance live C stores provided by the FIA program (36.28 Mg C ha^{-1}). Since this is not possible, we constrained the analysis within the upper and lower C store limits. To provide the lower limit in C stores, we decreased the ADS-based mortality to match FIA data. To provide the upper limit in C stores, we increased the initial live biomass from FIA to match the ADS-based mortality. From disturbed stands we calculated a ratio of mortality C to pre-disturbance live C (0.29). Based on this ratio we assumed that live C store value after disturbance period did not drop below ~71% of the initial live steady-state C stores. For the lower limit in C stores, we decreased the annual outbreak mortality values 5-fold to maintain post-disturbance live C stores at ~25.76 Mg C ha^{-1} (36.28*0.71). For the upper limit in C stores, we increased pre-disturbance live C stores 6-fold to maintain post-disturbance live C stores at ~154.55 Mg C ha^{-1} (36.28*6*0.71).

Modeling C stores and dynamics

We used a Stella-based simulation model (version 10.0.06 isee systems, Inc.) to test the effect of

beetle-related spruce mortality on live and CWD C fluxes and stores and to examine C dynamics

driven by different management regimes. To examine disturbance effects on C stores, we used

200-yr time frame capturing the 27-yr disturbance and 173-yr post-disturbance periods. Given

the uncertainty in timing, dynamics, and tree mortality levels of potential future outbreaks, we

restricted our modeling to long-term impact of the 1989-2015 outbreak period with data provided

by FHP ADS program. This assumed that post-disturbance period was only subject to

background mortality, and although this is unrealistic, it allowed us to follow the impact of the

1989-2015 mortality pulse.

Live C stores and dynamics

The live C stores and dynamics were simulated by creating a Live Wood (**LW**) C pool. Inputs to

LW pool were associated with Net Primary Production (NPP). NPP was assumed to increase as a

function of **LW** and was determined by the formula:

$$\boldsymbol{NPP} = \boldsymbol{NPP_{max}} * (\boldsymbol{1} - \boldsymbol{e}^{-k_G * LW}), \text{ where} \qquad \text{(Equation 1)}$$

NPP was a Net Primary Production C flux (Mg C ha^{-1} yr^{-1}), **NPP$_{max}$** was a maximum NPP, $\boldsymbol{k_G}$

was the proportional growth rate of NPP after disturbance (yr^{-1}), and **LW** was the live wood C

pool size (Mg C ha^{-1}) controlling the growth of NPP.

NPP_{max} (the input) was determined from maximum size of the Live Wood C pool LW_{max} (the store) and tree mortality rate k_M assuming the steady-state conditions (input = output) using formula:

$$NPP_{max} = LW_{max} * k_M, \text{where} \quad \text{(Equation 2)}$$

LW_{max} was the pre-disturbance live C store, and k_M was the background tree mortality.

The growth rate k_G for the equation 3 provided a positive feedback until 10% of LW_{max} was reached and was determined from formula:

$$k_G = \frac{Ln(0.05)}{0.1 * LW_{max}}, \text{where} \quad \text{(Equation 4)}$$

$Ln(0.05)$ represented 95% of biomass accumulated by the LW pool, and LW_{max} was maximum size of the Live Wood C pool.

Outputs from LW C pool were associated with mortality, calculated as product of tree mortality rate and the size of LW pool, and were partitioned into three C fluxes namely branch-twig-foliage (BTF), snag, and log fluxes. From the Alaska 2004-2012 FIA tree (aboveground live and standing dead) database we selected trees on Kenai Peninsula with the d.b.h. at least 2.5 cm (1 inch) and determined that on average aboveground biomass consisted of roughly 70% tree boles and 30% live and dead branches and foliage. Therefore, 30% of the annual mortality C was transferred to BTF pool. The subsequent data analysis only involved bole C. To calculate the background mortality, the annual mortality flux was partitioned between snag (25%) and log (75%) C. To calculate the beetle-caused outbreak mortality, the snag flux was determined as a

product between the *LW* C pool and annual outbreak mortality. The log C flux was determined

as a remainder of *LW* C pool multiplied by the log mortality rate.

CWD C stores and dynamics

The C dynamics of snag and log pools were simulated by having snags falling to become logs

and both pools losing C to the atmosphere via decomposition. To account for the lag in snag fall

and gradual loss of snags once they began to fall we divided snags into five sub-pools, the first to

account for the C transferred from live to snag C pool, the second to account for the lag in snag

fall, and the remaining three to account for a gradual increase in the snag fall rate. Fluxes were

associated with C transfer between snag sub-pools, C transfer from snags to logs (snag fall), and

decomposition losses to the atmosphere and modeled as donor-controlled processes:

$$F = C_{DP} \times k, \text{ where} \qquad \text{(Equation 5)}$$

F was a C flux, C_{DP} was the C store in donor pool, and k was rate-constant describing the

proportion of the C store in donor pool removed annually. The rate-constants describing the

transfer fluxes between snag sub-pools (k_{ST}) were set to:

$$k_{ST} = 1 - k_D - k_{SLT}, \text{ where} \qquad \text{(Equation 6)}$$

k_D was the decomposition per year rate-constant, and k_{SLT} was snag-to-log transfer per year rate-

constant. The k_{ST} rate was used to allow for a full transfer of C from one snag sub-pool to

another once the residence time of a snag sub-pool had been reached. Although we did not

measure the snag-to-log transfer rate, our field observations indicated that it took approximately

10 years following the disturbance for snags to begin falling in numbers and that few snags

remained standing after 40 years. We therefore assumed that snags would begin to fall 10 years after disturbance with 99% of the snags being on the ground by year 40 following the disturbance. To make the increase in snag fall gradual we doubled the transfer rate-constant every two years with each snag sub-pool until final transfer rate-constant was reached in snag sub-pool 5.

Decomposition-related losses to the atmosphere from the snag and log C pools were modeled as donor-controlled processes and were dependent on C stores in donor pools and the decomposition rate-constants. Spruce snag (-0.001 yr^{-1}) and log (-0.04 yr^{-1}) decomposition rate-constants were based on an empirical study of beetle-killed spruce decomposition on the Kenai Peninsula and were determined using chronosequence and decomposition-vectors approaches, respectively (Yatskov et al. – Chapter 3). The decomposition rate-constant k of -0.04 yr^{-1} obtained from the decomposition-vectors analysis was selected over the lower k of -0.02 yr^{-1} from the chronosequence analysis for several reasons. The decomposition-vectors analysis provided a more recent short-term (2002-2008) as opposed to a chronosequence long-term (i.e., 1924-2008) decomposition rate-constant. Decomposition-vectors k, unlike a chronosequence k, was not affected by bias associated with dating the mortality and to a lesser degree was affected by a small number of observations of CWD in the advanced decomposition stages, it accounted for a recent climatic changes and provided a parameter value that offered a more realistic model fit to reflect pre-disturbance live-to-dead and snag-to-log C pool ratios based on FIA data.

Modeling scenarios

Three main simulation scenarios included: 1) SBB outbreak with immediate regeneration in disturbed stands, 2) SBB outbreak with no regeneration in disturbed stands, 3) and SBB outbreak with 25-year delay in regeneration, as intermediate between scenarios 1 and 2. For the latter scenario we ran simulation with several management treatments: 3a) with 90% (to reflect <100% efficiency of salvage harvest) of killed biomass salvaged for fuel production, 3b) with 90% of killed biomass salvaged for paper production, and 3c) with 90% of killed biomass salvaged for long-term wood products (building material) manufacturing.

The regeneration rate for the simulations was assumed to influence the wood-related NPP. Background NPP as well as immediate regeneration scenario utilized NPP of 0.613 Mg C ha^{-1} yr^{-1}, whereas NPP for the no regeneration and delayed regeneration scenarios was calculated as a difference between the background NPP and the NPP proportion associated with annual C flux lost to mortality. Fuels were assumed to be immediately utilized with the displacement C values used from Mitchell et al. (2009, Appendix B) of 0.7816 and 0.3884 for biomass and ethanol fuels, respectively. For the paper production simulation we assumed 55% of the harvested outbreak mortality C being converted to paper products (Harmon et al. 1996). The loss (rate-constant) from this paper products pool was assumed to be -0.3 yr^{-1} with 10-year life span, where 50% of the flux went into the landfill and other 50% went to the atmosphere in form of emissions related to decomposition and combustion (Harmon et al. 1996). The loss (rate-constant) from the landfill pool was assumed to be -0.005 yr^{-1} with a life span of 600 years (Harmon et al. 1996). For the long-term wood products scenario we assumed 65% of the harvested outbreak mortality

C being converted to building material (75% manufacturing efficiency with some losses associated with decay and insect damage) (Harmon et al. 1996). The loss (rate-constant) from this pool was assumed to be -0.02 yr^{-1} with a 150-year life span, which was partitioned between the flux to the atmosphere (with rate-constant of -0.01 yr^{-1}) and flux to landfills (with rate-constant of -0.01 yr^{-1}). As with disposed paper, loss (rate-constant) from the landfill pool was assumed to be -0.005 yr^{-1} (Harmon et al. 1996).

RESULTS

Our estimates of the C flux associated with the 27-year SBB outbreak differed 5-fold (13.09 Mg C ha^{-1} vs. 64.82 Mg C ha^{-1}). These corresponded to the low and high estimates of pre-disturbance live C stores of 36.28 Mg C ha^{-1} and 217.68 Mg C ha^{-1}, respectively. Since our higher estimate of C stores was unrealistic given the FIA values, we utilized the lower C estimate in our subsequent analysis and used the upper C stores estimate only for the sake of comparison and uncertainty assessment.

Whether there was regeneration following the disturbance and whether it was delayed had a long-term effect on combined aboveground wood (live, snag, and log) C stores. When there was regeneration (immediate or delayed), there was a temporary decrease in wood C stores with a subsequent recovery to pre-disturbance levels (Figure 4.1). Under the no-regeneration scenario (representing a loss of tree cover on disturbed portion of the landscape), there was a permanent decrease in wood C stores. Aboveground wood C stores decreased to 43.98 Mg C ha^{-1} and 39.75 Mg C ha^{-1} for the immediate and delayed regeneration scenarios, respectively. In 200 years

counting from the initial disturbance year, these C stores recover to ~98% and ~97% of the pre-disturbance levels of 49.27 Mg C ha^{-1} for the immediate and delayed regeneration scenarios, respectively. When there was a drop in tree cover caused by no-regeneration, C stores decreased permanently to a new steady-state of 31.51 Mg C ha^{-1}. The differences in aboveground wood C dynamics between the immediate and delayed regeneration scenarios were mainly driven by the behavior of live C pool (Figure 4.2). The maximum difference in annual live C stores between these two scenarios was 3.9 Mg C ha^{-1} or 8%. C stores in snag and log pools between two scenarios were relatively similar with immediate-regeneration scenario stores being slightly higher after disturbance.

The timing of regeneration after disturbance had a major effect on annual net C change in the combined (live, snag, and log) C pool (Figure 4.3). All scenarios showed a decline in net C change during the disturbance period. The magnitude of this decline was the most significant under delayed and no-regeneration scenarios due to lack of regeneration with the lowest value of net C of -0.44 Mg C ha^{-1} yr^{-1}. The decline was less pronounced under immediate regeneration scenario with the lowest value of net C of -0.28 Mg C ha^{-1} yr^{-1}. Net C change turned positive 53 and 66 years after the start of disturbance period under delayed and immediate regeneration scenarios, respectively, but there was no positive phase under the no-regeneration scenario, eventually recovering to zero. The immediate and no-regeneration scenarios had complex net C post-disturbance response with a dip after initial increase (Figure 4.3) formed as a result of overlap between reduced post-disturbance input into CWD C pool and declined input into live C pool (Figure 4.4a). In contrast, net C under delayed regeneration scenario had a "linear" recovery

caused by strong positive input into the live C pool (Figure 4.4b) that was significant enough to counteract the reduction in post-disturbance input into CWD C pool.

When regeneration was delayed, the "leave-as-is" and "salvage-and-utilization" management scenarios caused an initial decline in combined aboveground (live, snag, log, and fuels substitution) C during and immediately after the disturbance period with a subsequent recovery (Figure 4.5). In general, the lowest stores were reached ~15 years earlier and often had a more pronounced decline under "salvage-and-utilization" vs. "leave-as-is" scenarios. The disturbance caused ~18% C stores decline from the pre-disturbance level in "leave-as-is" scenario, whereas post-disturbance management associated with salvage and utilization led to C stores decline by ~18% to 26%. The time period for post-disturbance C stores under "salvage-and-utilization" scenarios to reach the "leave-as-is" level was as short as ~40 years (i.e., production of biomass fuel with substitution) to as long as ~75 years (i.e., paper production with substitution) from the beginning of disturbance period. In 200 years counting from the initial disturbance year, "leave-as-is", paper, and building material C stores recovered to ~97%, ~99%, and 100% of the pre-disturbance levels of 49.27 Mg C ha^{-1}, respectively. The recovery to pre-disturbance C stores occurred 153 and 110 years from the beginning of disturbance period for the ethanol with substitution and biomass fuel with substitution production, respectively. Production of ethanol and biomass fuel with substitutions reached new steady-state of 52 Mg C ha^{-1} and 55.39 Mg C ha^{-1}, respectively, assuming these substitutions were permanent.

C emissions from the ecosystem under "salvage-and-utilization" peaked sharply during the 27-year disturbance period, whereas emissions under "leave-as-is" scenarios rose more gradually with a maximum occurring ~15 years after the disturbance period ended (Figure 4.6). Except for the no-regeneration scenario, CWD-related C emissions declined after the peak with subsequent recovery to pre-disturbance levels ~300 years from the beginning of the disturbance period. CWD-related C emissions for the no-regeneration scenario reached new, lower-than-previous steady-state level due to reduction in CWD associated with lower forest area. Among "salvage-and-utilization" scenarios, fuels production was associated with the highest C emissions followed by paper and building materials scenarios ranging at their peak between 0.68 Mg C ha^{-1} yr^{-1} and 1.04 Mg C ha^{-1} yr^{-1}, with "leave-as-is" scenario peaking at 0.51 Mg C ha^{-1} yr^{-1} (Figure 4.6).

Fuels production under the "salvage-and-utilization" stored the most C in the forest long-term assuming substitutions were permanent (Figure 4.7). Biomass fuel and ethanol production with substitution led to a sharp rise of the C stores during the disturbance period until reaching the level of long-term permanent stores. Similarly, building material with landfill as well as paper with landfill scenarios showed sharp increase in C stores during the disturbance period but the peak in these scenarios was followed by stores deterioration associated with decomposition and combustion. Despite this decline, C stores under the building material with landfill scenario were higher than those under the ethanol production with substitution the first 73 years from the beginning of disturbance period cumulatively exceeding them by 54.43 Mg C ha^{-1} over 73-year period. Between the non-fuel scenarios, on the annual basis the C stores in building materials (including corresponding landfill) were ~1.5 to 2 times higher than in paper (including

corresponding landfill) over the first 200 years from the beginning of disturbance period (Figure 4.7).

DISCUSSION

We assumed that the results of our study apply to the spruce forests of Kenai Peninsula damaged by the spruce bark beetle outbreak of the 1990s, however our CWD decomposition sampling sites were not systematically or randomly established across affected area. Our CWD sampling was generally limited to the road-accessible low-elevation sites that were subject to previous disturbances potentially due to some specific site or pre-disturbance stand characteristics. Therefore, the pre-disturbance stand characteristics as well as factors controlling the snag fall-down rates and/or decomposition process at these sites could have been vastly different from the spruce stands located closer to the coast or at higher elevation.

Large uncertainty associated with the FHP ADS outbreak mortality C estimates precluded direct use of C estimates from ADS in model simulations. The difference between the FIA C store estimates and mortality C flux estimates obtained from the FHP ADS created difficulties in merging the two data sets. Making adjustments to one of these estimates to match the other was necessary to model the long-term C dynamics during and after the 1989-2015 SBB outbreak period. Despite the fact that FHP ADS data have been utilized extensively for the analysis of spatial infestation patterns (Dodds et al. 2006), evaluation of the remote-sensing mapping of insect outbreaks (de Beurs and Townsend 2008), and the assessment of the interactions between SBB outbreaks and fires (Lynch et al. 2006, Kulakowski and Veblen 2007, Bond et al. 2009, and

Preisler et al. 2010), there are large uncertainties in ADS mortality estimates associated with the assumptions in the ADS methods, lack of complete coverage by surveys, and their subjective nature (Meddens et al. 2012). The ADS analysis in the conterminous United States using spatial data (Meddens et al. 2012) reported to underestimate the mortality in these surveys by a factor of 3-20. In our analysis, the assumption that unadjusted ADS mortality C estimates were accurate would suggest that the FIA underestimated aboveground woody C stores by a factor of 6, which conflicts with the reliable and statistically robust previously published FIA C stores estimates (Barrett and Christensen 2011, Barrett 2014, Yatskov et al. – Chapter 2). When limited by the FIA C stores estimates, the ADS overestimated outbreak-related mortality C by a factor of 5, which increases their previously assessed margin of uncertainty. To reduce the uncertainly of the ADS mortality estimates these estimates should go through a rigorous ground truthing procedure and be linked to the FIA or another reliable ground data source.

Lags represent an important component in ecosystem processes affecting the outcomes of the ecosystem C dynamics. Two major lags influencing C inputs and outputs in forested landscapes affected by the SBB outbreak were associated with live and dead components. The regeneration response to disturbance has a profound effect on C inputs and could determine the long-term recovery trajectory of C stores in the system. In turn, the low rate of snag decomposition, delay in the initiation of snag fall, and the gradual rate of snag-to-log transfer postpone the major C emissions from the CWD to the atmosphere following the SBB outbreak disturbance (Yatskov et al. – Chapter 2). The studies conducted on the Kenai Peninsula following the spruce bark beetle infestation indicated a range of regeneration levels from little to no regeneration (Holsten et al.

1995, LaBau 2004) to no evidence of widespread regeneration reduction from pre-disturbance

levels (van Hees 2005, Boucher and Mead 2006, Boggs et al. 2008). While variation in

regeneration levels and timing creates a landscape with diverse stand age structure, if C storage

is the main management objective, shortening or eliminating the regeneration lag with an

immediate and sufficient regeneration may be necessary to rebuild photosynthetic capacity and

quickly return the system to pre-disturbance conditions. The combination of early and successful

regeneration and delays in CWD C emissions caused by lags in CWD decomposition may speed

up ecosystem recovery to C neutrality. At the same time, delays in regeneration may put the

regeneration sequestration capacity and the peak of CWD-related C emissions out of synchrony,

keeping the system a C source to the atmosphere over a longer period of time. Lack of

regeneration and conversion of forests to shrub- (Allen et al. 2006) or grassland may lead to

reduction in forest land and as a result decreased C storage potential of the system and permanent

net C flux to the atmosphere.

Forest management strategies provide avenues for mitigating global climate change through

curbing CO_2 emissions and storing C in the forest sector (Brown et al. 1995). The views on

timing of the emissions reduction and associated policy and action implementation to meet the

emissions stabilization targets vary (IPCC 2007a) from those in support of early actions (Azar

and Dowlatabadi 1999, Van Vuuren and De Vries 2001) to those in favor of delayed response

(Wigley et al. 1996, Tol 2000). However, delayed response could mean a higher uncertainty in

future atmospheric CO_2 level estimates that may render the currently planned future mitigation

strategies incomplete or ineffective, thus requiring more abrupt and costly actions at a later date

to achieve a given stabilization targets (Preston and Jones 2006, IPCC 2007b). In our analysis, the "salvage-and-utilization" scenarios stored more C in the system than "leave-as-is" scenario in the long-term (Figure 4.5). However, in the short-term (up to 50 years) "salvage-and-utilization" scenarios were lower than the "leave-as-is" scenario in terms of C storage (Figure 4.5) and earlier in occurrence and higher in magnitude C emissions (Figure 4.6). Since the reduction in near-term emissions may be a more robust strategy than delay (Preston and Jones 2006, IPCC 2007b) the "leave-as-is" scenario could be the preferred management strategy in mitigating global climate change (Fargione 2008).

Production of fuels from tree biomass salvaged after disturbance to substitute for fossil fuels use also seemed to be an effective strategy to store C in the system (Figure 4.7). However, it is not clear how permanent the fossil fuel substitutions provided by biomass and ethanol utilization actually will be. Because the fossil fuels substitutions are virtual rather than physical their perpetuity seems questionable. When a tract of land gains reserved status (USDA 2014), that means the land is permanently withdrawn from the active management use and is protected by law or deed. There is no similar law or deed to physically protect the fossil fuels in the ground by permanently closing the coal mines or oil fields in certain locations. Given such physical location protection is lacking, any entity is theoretically able to tap into these fossil fuels reserves, should the necessity such as immediate lack or shortage of energy sources arise, thus causing leakage. Such leakage is likely to occur earlier than later in time while the alternative sources of energy are in the development stage yet demand for cheap and accessible energy keeps growing. Under such a scenario the forest management associated with creating substitutions via production and

utilization of fuels from biomass may prove to be counterproductive, as a leakage of fossil fuels substitutions at a relatively low rate of ~2.7% yr^{-1} would cause substitution depletion within 200 years from the initial disturbance event (Figure 4.8) with 50% of substitution C transferred to the atmosphere (i.e., half-life) in form of CO_2 in 26 years after the disturbance period is over.

Restricting our modeling to a single disturbance event allowed us to study the impact of the 1989-2015 SBB outbreak mortality pulse on long-term C dynamics. However, it represented an unrealistic long-term scenario given the long-term average return interval for SBB outbreaks is estimated at 52 years. Adjusting NPP, mortality, and decomposition parameters for a 52-year period capturing the 1989-2015 SBB outbreak indicated a long-term reduction in total, live, and CWD C stores by ~18%, ~25%, and ~6% respectively suggesting a loss of C to the atmosphere from the system in form of CO_2. The assessment of the long-term history and characteristics of past outbreaks could provide the understanding of the long-term effects of the future reoccurring outbreaks on landscape-level C stores and dynamics.

CONCLUSIONS

This study utilized available information to estimate the balance of tree bole-related C on the Kenai Peninsula following a major spruce bark beetle outbreak. C store and growth rate estimates in spruce-dominated stands were obtained using the data from the FIA program. Empirically derived spruce CWD decomposition rate-constants were obtained from a chronosequence and decomposition-vectors analysis of spruce CWD. Spruce tree mortality rates were estimated from the aerial surveys by the FHP ADS program. Using model simulations, we

evaluated the effect of several management strategies on C stores under "leave-as-is" and "salvage-and-utilization" scenarios.

The mismatch between the FIA based C estimates and the FHP ADS outbreak mortality C estimates prevented direct use of C estimates from ADS in model simulations. When limited by the FIA C stores estimates, the ADS overestimated outbreak-related mortality C by a factor of 5, which increased their previously assessed margin of uncertainty. To reduce the uncertainly of the ADS mortality estimates these estimates should go through a more rigorous ground truthing procedure and be linked to the FIA or another reliable ground data source.

Lags represented an important component in ecosystem processes affecting the outcomes of the ecosystem C dynamics by controlling the timing of the C inputs associated with regeneration and outputs related to CWD decomposition. The combination of immediate regeneration and delays in CWD C emissions may speed up ecosystem recovery to C neutrality. Delays in regeneration may put the C input peak and CWD C flux peak out of synchrony, keeping the system a C source to the atmosphere over a longer period of time. Finally, lack of regeneration in disturbed portion of the landscape and conversion of forests to shrub- or grassland may reduce forest land, decreasing C storage potential of the system via a permanent net C flux to the atmosphere.

The management strategies not removing bole biomass from disturbed forest provided the highest short-term ecosystem C storage. Moreover, the "leave-as-is" scenarios had lower C emissions with a less pronounced and more gradual and delayed peak than the "salvage-and-

utilization" scenarios. In the long-run, 40 to 75 years after the beginning of disturbance period, more C was stored under the "salvage-and-utilization" vs. "leave-as-is" scenarios as long as substitutions are permanent.

Assuming no leakage, management strategies associated with fuels production stored more C than the "leave-as-is" or building materials and paper production strategies. However, due to lack of legal protective mechanisms the permanence of C stores related to substitution are questionable.

ACKNOWLEDGEMENT

FIGURES

Figure 4.1. Aboveground wood C stores dynamics in three regeneration scenarios.
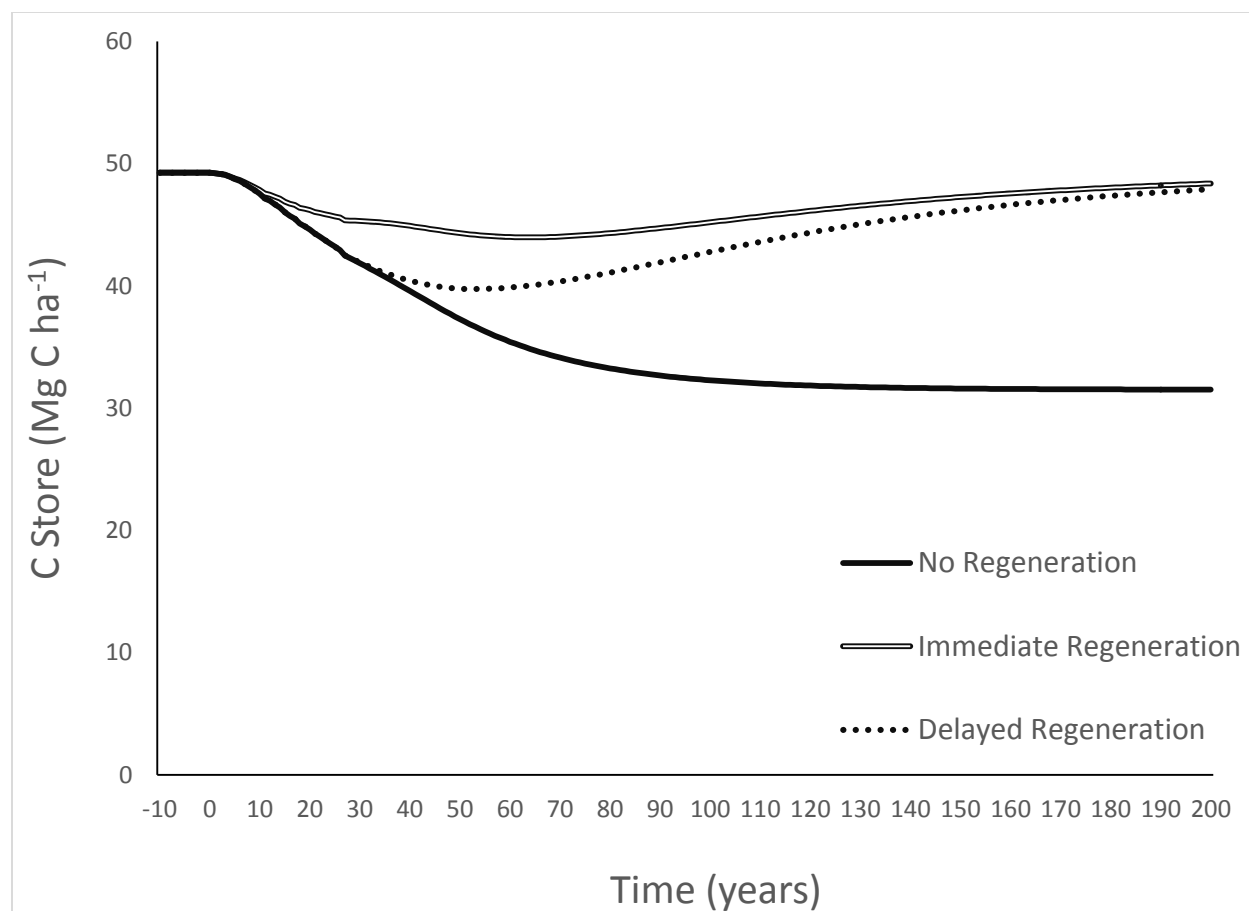
Figure 4.2. Carbon dynamics in four C pools under immediate (IR) and delayed (DR) regeneration scenarios.
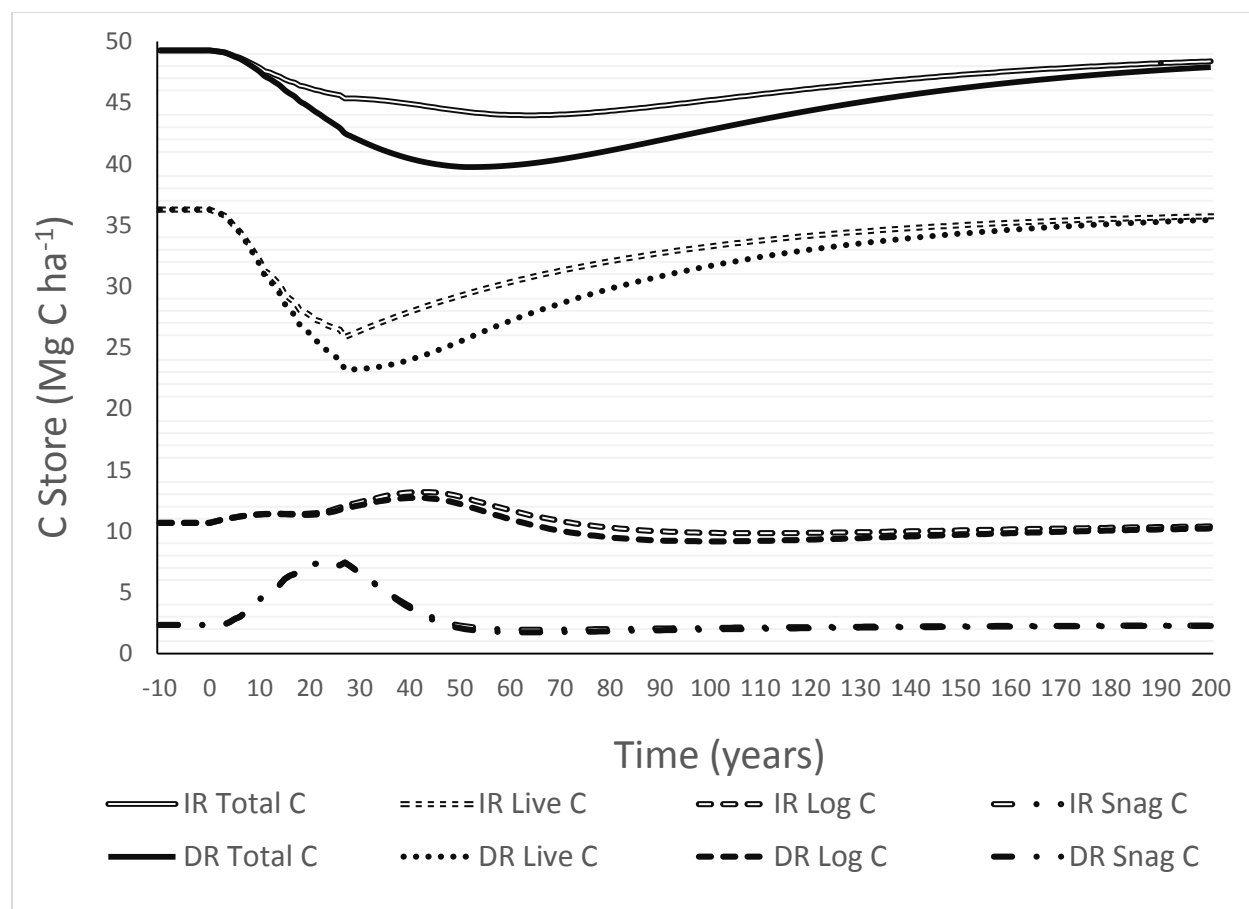
Figure 4.3. Annual combined (live, snag, and log) pool carbon net change for three regeneration scenarios.
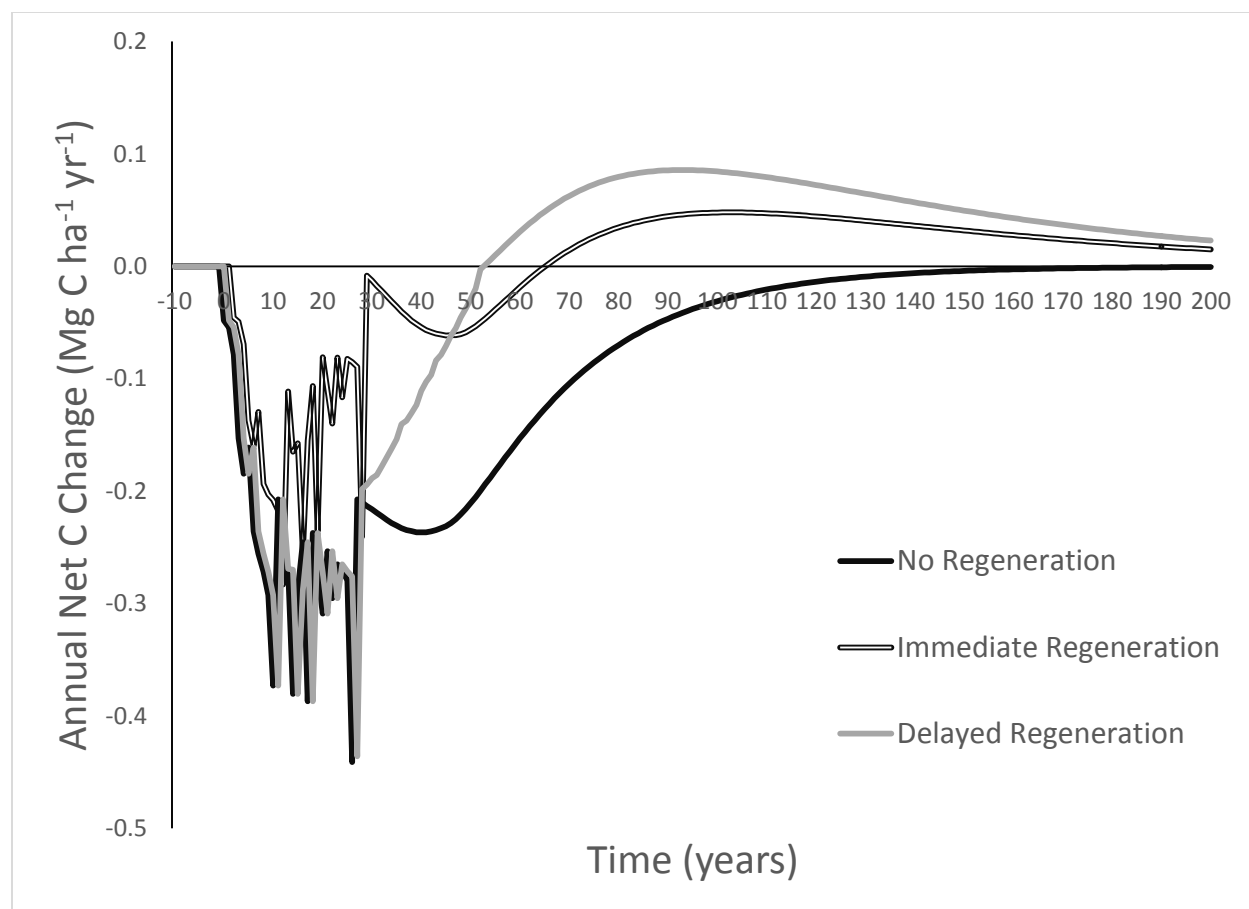
Figure 4.4. Net carbon change in live, CWD, and combined carbon pools for immediate and delayed regeneration scenarios.
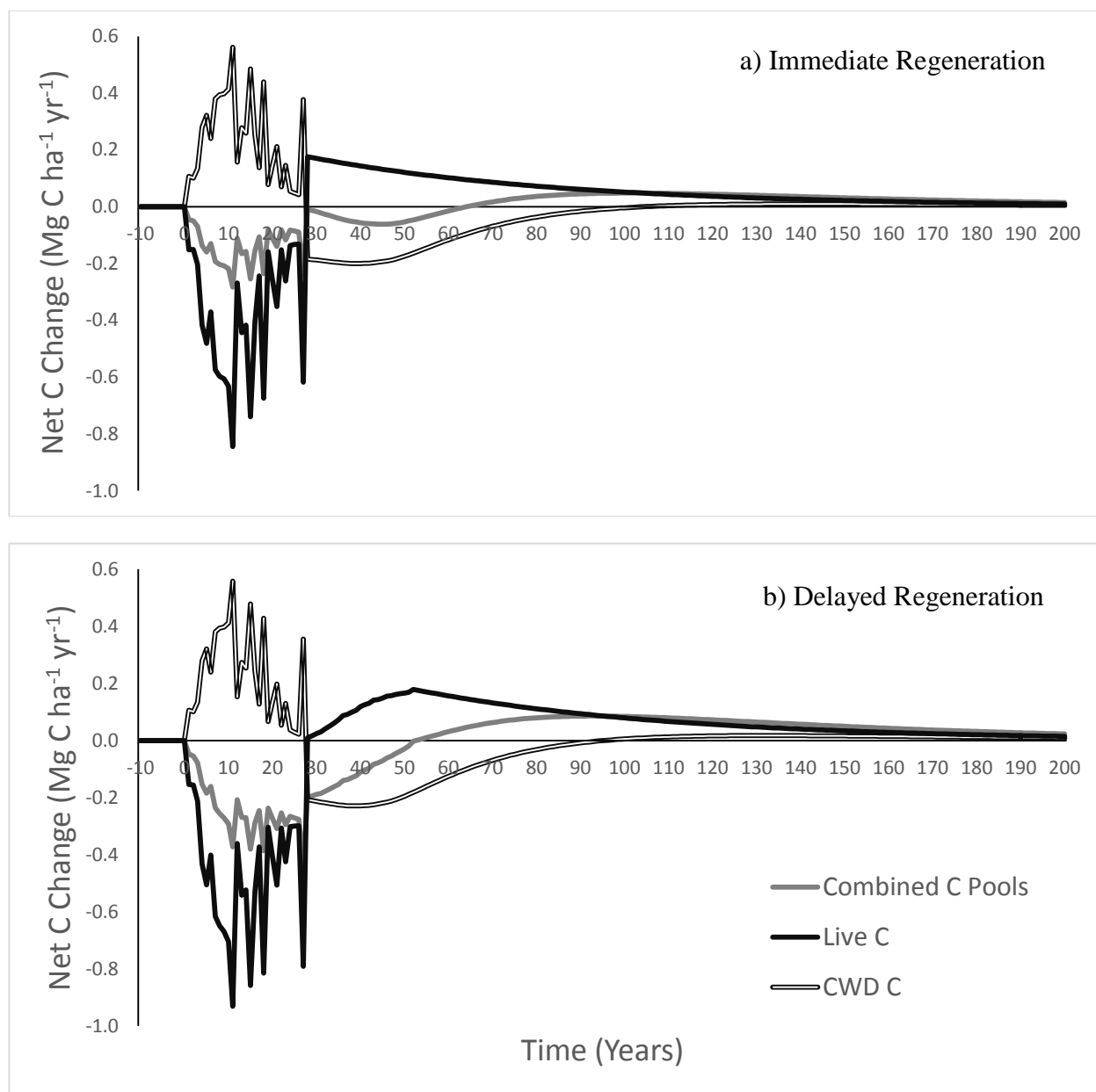
Figure 4.5. Effect of the management approach on aboveground wood carbon dynamics for "Leave-As-Is" and "Salvage-and-Utilization" scenarios.
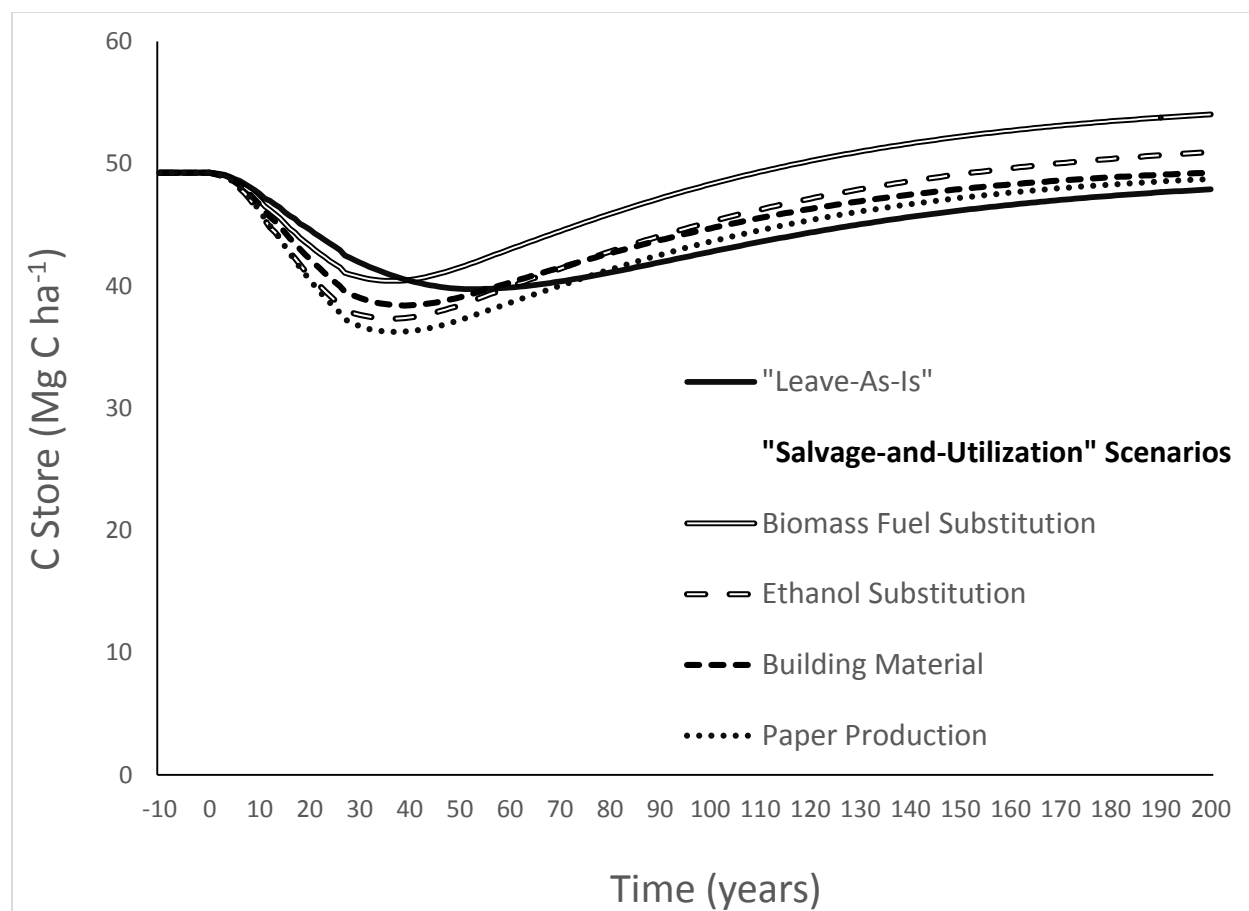
Figure 4.6. CWD-related carbon emissions for "Leave-As-Is" and "Salvage-and-Utilization" scenarios.
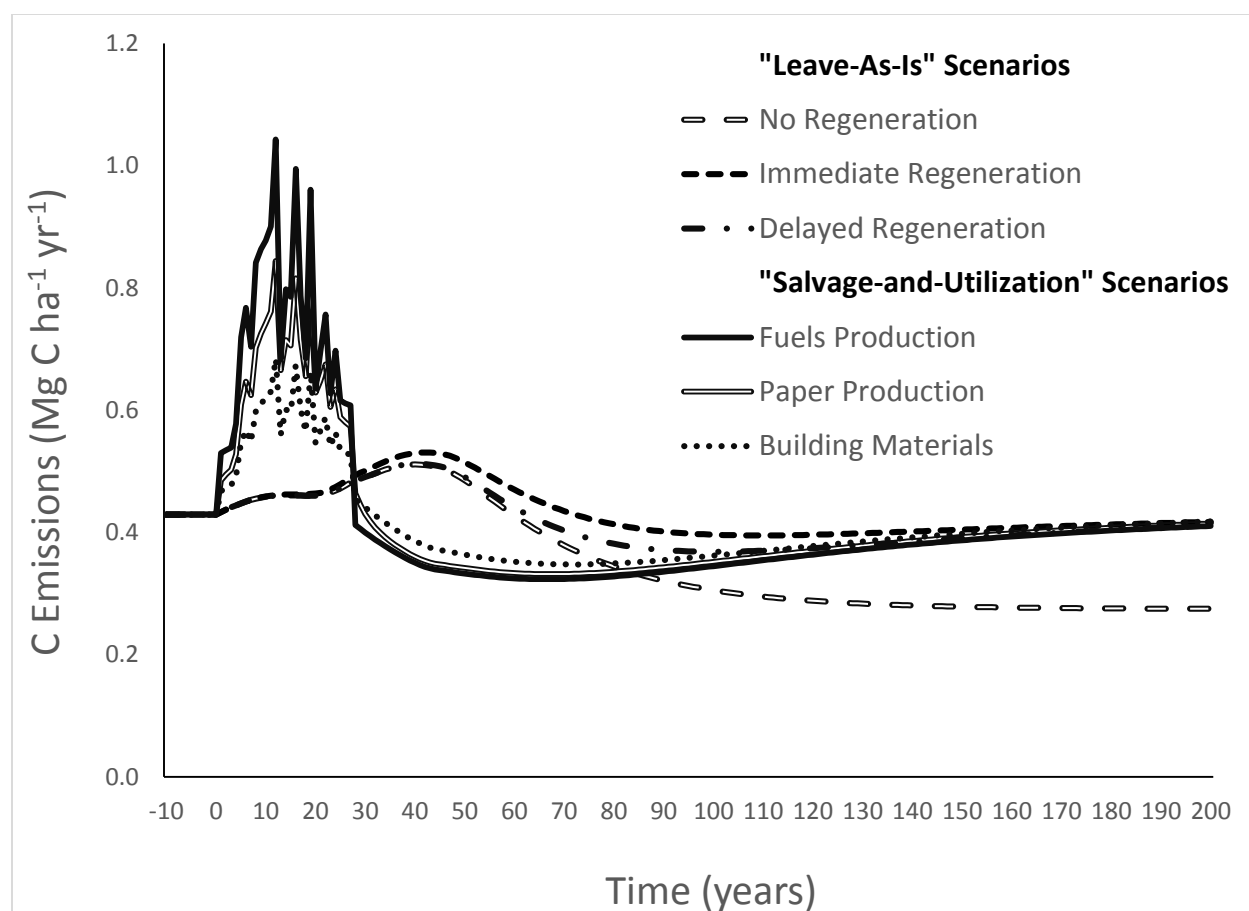
Figure 4.7. Carbon stores comparison for management approaches for "Salvage-and-Utilization" scenario with permanent substitution.
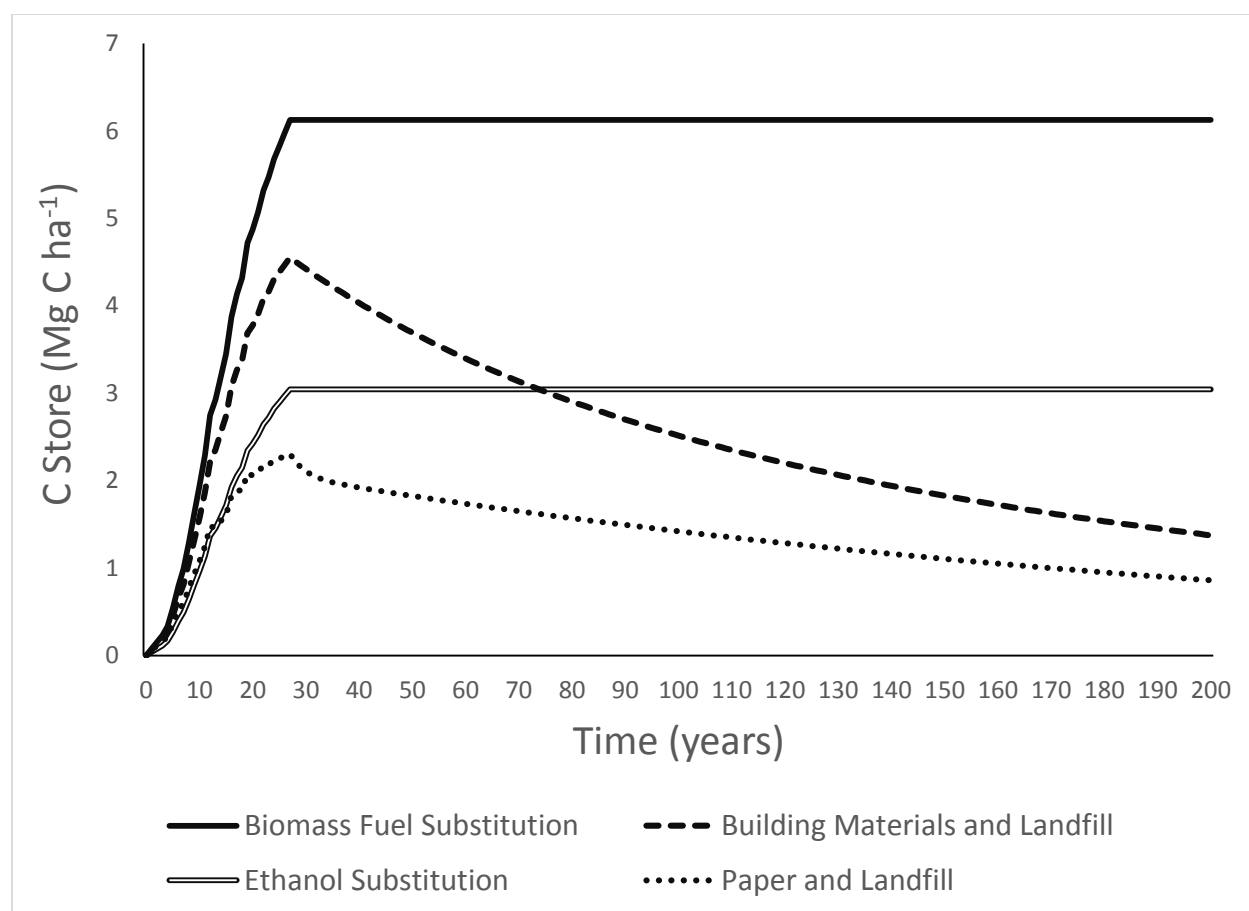
Figure 4.8. Carbon stores comparison for management approaches for "Salvage-and-Utilization" scenario with leakage of substitution.
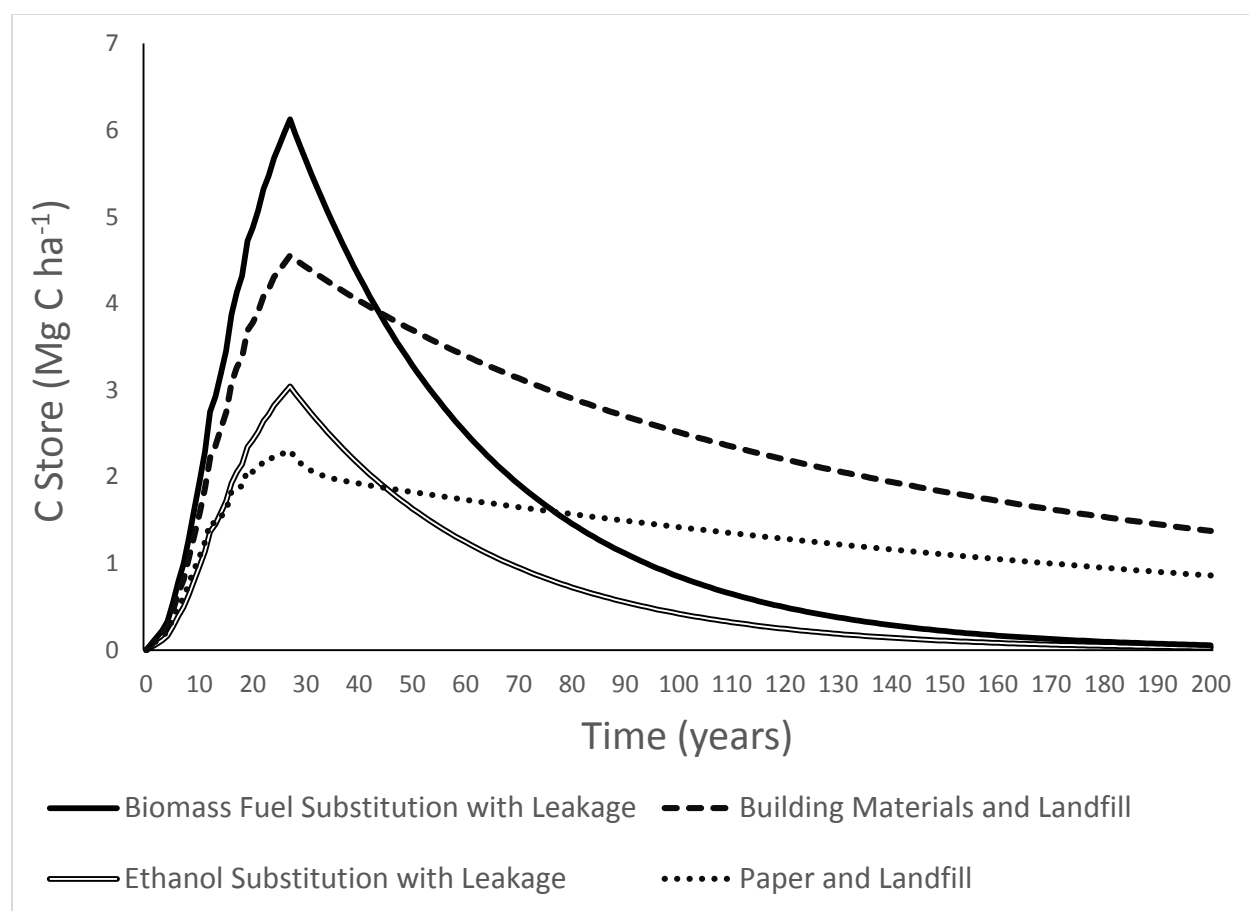
TABLES

Table 4.1. Monthly 30-year average (1979-2008) climatic data for the western and northern Kenai Peninsula.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
Temperature, ºC	-6.9	-5.6	-2.7	2.0	6.8	10.6	12.8	12.1	8.3	1.9	-3.8	-6.1
Precipitation, mm	47	37	28	23	23	27	46	67	90	76	60	61

Table 4.2. Annual average 30-year (1979-2008) period climatic data for the western and northern Kenai Peninsula.

	Precipitation (mm)/Year	Temperature (ºC)/Year	January (ºC)/Year	July (ºC)/Year
30-year mean	584/---	2.4/---	-6.9/---	12.8/---
30-year max	816/1981	3.9/2002	0.6/1981	14.6/2004
30-year min	397/1996	0.9/1996, 1999	-15.8/1989	11.4/1982

REFERENCES

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.T. and Gonzalez, P. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259(4): 660-684.

Allen, J.L., Wesser, S., Markon, C.J., Winterberger, K.C. 2006. Stand and landscape level effects of a major outbreak of spruce beetles on forest vegetation in the Copper River Basin, Alaska. For. Ecol. Manage. 227: 257-266.

Anderson, R.S., Hallett, D.J., Berg, E.E., Jass, R.B., Toney, J.L., de Fontaine, C.S., and DeVolder, A.D. 2006. Holocene development of boreal forests and fire regimes on the Kenai lowlands of Alaska. The Holocene 16 (6): 791- 803.

Apps, M.J., Kurz, W.A., Beukema, S.J., and Bhatti, J.S. 1999. Carbon budget of the Canadian forest product sector. Environmental Science and Policy 2(1): 25-41.

Azar, C. and Dowlatabadi, H. 1999. A review of technical change in assessment of climate policy. Annual Review of Energy and the Environment 24: 513-544.

Barrett, T.M. 2014. Storage and flux of carbon in live trees, snags, and logs in the Chugach and Tongass National Forests. Gen. Tech. Rep. PNW-GTR-889. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 44 p.

Barrett, T.M. and Christensen, G.A. (Tech. Eds.). 2011. Forest of southeast and south-central Alaska, 2004-2008: Five-year forest inventory and analysis report. Gen. Tech. Rep. PNW-GTR-835. Portland, OR: U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Research Station, 156 p.

Bechtold, W.A. and Patterson, P.L. (Eds.). 2005. The enhanced forest inventory and analysis program – national sampling design and estimation procedures. USDA Forest Service. Southern Research Station. Gen. Tech. Rep. GTR-SRS-80.

Bentz, B.J., Christopher, J.R., Fettig, J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., and Seybold, S.J. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. BioScience 60(8): 602-613.

Berg, E.E., Henry, J.D., Fastie, C.L., De Volder, A.D., and Matsuoka, S.M. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. For. Ecol. Manage. 227(3): 219-232.

Boggs, K., Sturdy, M., Rinella, D.J. and Rinella, M.J. 2008. White spruce regeneration following a major spruce beetle outbreak in forests on the Kenai Peninsula, Alaska. For. Ecol. Manage. 255(10): 3571-3579.

Bond, M.L., Lee, D.E., Bradley, C.M., and Hanson, C.T. 2009. Influence of pre-fire tree mortality on fire severity in conifer forests of the San Bernardino Mountains, California. Open Forest Science Journal 2: 41–47.

Boucher, T.V. and Mead, B.R. 2006. Vegetation change and forest regeneration on the Kenai Peninsula, Alaska following a spruce beetle outbreak, 1987–2000. For. Ecol. Manage. 227(3): 233-246.

Brown, S., Sathaye, J., Cannell, M., and Kauppi, P.E. 1995. Management of forests for mitigation of greenhouse gas emissions. Cambridge University Press.

Carroll, A.L., Taylor, S.W., Regniere, J., and Safranyik, L. 2003. Effect of climate change on range expansion by the mountain pine beetle in British Columbia. The bark beetles, fuels, and fire bibliography. Paper 195: 223-232. http://digitalcommons.usu.edu/barkbeetles/195

Cudmore, T.J., Björklund, N., Carroll, A.L., and Staffan Lindgren, B. 2010. Climate change and range expansion of an aggressive bark beetle: Evidence of higher beetle reproduction in naive host tree populations. Journal of Applied Ecology 47(5): 1036-1043.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., and Simberloff, D. 2001. Climate Change and Forest Disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. BioScience 51(9): 723-734.

DASM 2015. Digital aerial sketch mapping overview. USDA Forest Service. Website. Retrieved November 1, 2015 from http://www.fs.fed.us/foresthealth/technology/pdfs/dasm_detailed_overview.pdf

De Beurs, K.M. and Townsend, P.A. 2008. Estimating the effect of gypsy moth defoliation using MODIS. Remote Sensing of Environment 112: 3983–3990.

De Volder, A. 1999. Fire and climate history of lowland black spruce forests, Kenai National Wildlife Refuge, Alaska. MS Thesis. Northern Arizona University.

Dodds, K.J., Garman, S.L., and Ross, D.W. 2006. Landscape analyses of Douglas-fir beetle populations in northern Idaho. For. Ecol. Manage. 231: 119–130.

Everham, E.M. and Brokaw, N.V. 1996. Forest damage and recovery from catastrophic wind. The Botanical Review 62(2): 113-185.

Fargione, J., Hill, J., Tilman, D., Polasky, S., and Hawthorne, P. 2008. Land clearing and the biofuel carbon debt. Science 319(5867): 1235-1238.

FHTET 2015. Forest Health Technology Enterprise Team, USDA Forest Service. Website. Retrieved October 30, 2015 from http://www.fs.fed.us/foresthealth/technology/ads_standards.shtml

Flannigan, M.D., Stocks, B.J., and Wotton, B.M. 2000. Climate change and forest fires. Science of the Total Environment 262(3): 221-229.

Flint, C.G. 2006. Community perspectives on spruce beetle impacts on the Kenai Peninsula, Alaska. For. Ecol. Manage. 227(3): 207-218.

Fraver, S., Ringvall, A., and Jonsson, B.G. 2007. Refining volume estimates of down woody debris. Can. J. For. Res. 37: 627-633.

Goodman, J.R. 2002. HJ Andrews Experimental Forest. Long Term Ecological Research. SUE – Stochastic Uncertainty Estimator User's Guide. http://andrewsforest.oregonstate.edu/pubs/webdocs/models/sue.cfm

Greb, S.F. and Archer, A.W. 2007. Soft-sediment deformation produced by tides in a meizoseismic area, Turnagain Arm, Alaska. Geology 35 (5): 435-438. Geological Society of America. DOI: 10.1130/G23209A.

Grier, C.C. and Logan, R.S. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. Ecological Monographs, pp. 373-400.

Hansen, E.M. 2014. Forest development and carbon dynamics after mountain pine beetle outbreaks. Forest Science 60(3): 476-488.

Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., and Yatskov, M. 2011b. Differences between standing and downed dead tree wood density reduction factors: A comparison across decay classes and tree species. USDA Forest Service. Research Paper NRS-15.

Harmon, M.E., Woodall, C.W., Fasth, B., and Sexton, J. 2008. Woody detritus density and density reduction factors for tree species in the United States: A synthesis. USDA Forest Service. GTR-NRS-29.

Harmon, M., Fasth, B., Yatskov, M., Sexton, J., and Trummer, L. 2005. The fate of dead spruce on the Kenai Peninsula: A preliminary report. USDA Forest Service Technical Report R10-TP-134, 23 p.

Harmon, M.E., Harmon, J.M., Ferrell, W.K., and Brooks, D. 1996. Modeling carbon stores in Oregon and Washington forest products: 1900-1992. Climatic Change 33: 521-550.

Holsten, E.H., Thier, R.W., Munson, A.S., and Gibson, K.E. 2000. The spruce beetle. Forest Insect and Disease Leaflet 127. USDA Forest Service. http://www.na.fs.fed.us/spfo/pubs/fidls/sprucebeetle/sprucebeetle.htm

Holsten, E.H., Werner, R.A., DeVelice, R. 1995. Effects of a spruce beetle (Coleoptera: Scolytidae) outbreak and fire on Lutz spruce in Alaska. Environmental Entomology 24: 1539–1547.

Houghton, R.A. 2005. Aboveground forest biomass and the global carbon balance. Global Change Biology 11(6): 945-958.

IPCC 2007a. Intergovernmental Panel on Climate Change Forth Assessment Report: Climate change 2007: Working group III: Mitigation of climate change. Section 3.3.5.1 Emissions reduction and timing. https://www.ipcc.ch/publications_and_data/ar4/wg3/en/ch3s3-3-5-1.html

IPCC 2007b. Intergovernmental Panel on Climate Change Forth Assessment Report: Climate change 2007: Working group III: Mitigation of climate change.

Janisch, J.E. and Harmon, M.E. 2002. Successional changes in live and dead wood carbon stores: Implications for net ecosystem productivity. Tree Physiology 22(2-3): 77-89.

Karl, T.R., Knight, R.W., Easterling, D.R., and Quayle, R.G. 1996. Indices of climate change for the United States. Bulletin of the American Meteorological Society 77(2): 279-292.

Kulakowski, D. and Veblen, T.T. 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88: 759–769.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., and Safranyik, L. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452(7190): 987-990.

Kurz, W.A., Apps, M.J., Webb, T.M., and McNamee, P.J. 1992. The carbon budget of the Canadian forest sector: Phase I. Vol. 326. Forestry Canada, Northern Forestry Centre, 1992.

LaBau, J. 2004. Synthesis of ENRI findings from5 years of study of the spruce bark beetle on the Kenai Peninsula (abstract). *In*: A changing Alaskan ecosystem (symposium cd-rom), 2004 Feb. 24–26, Homer, Alaska. Kenai Peninsula Borough, Kenai Peninsula (AK), Spruce Beetle Mitigation Program.

Lynch, H.J., Renkin, R.A., Crabtree, R.L., and Moorcroft, P.R. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems 9: 1318–1327.

McCarthy, J.J. 2001. Climate change 2001: Impacts, adaptation, and vulnerability: Contribution of Working Group II to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

McMahon, S.M., Parker, G.G., and Miller, D.R. 2010. Evidence for a recent increase in forest growth. Proceedings of the National Academy of Sciences 107(8): 3611-3615.

Meddens, A.J., Hicke, J.A., and Ferguson, C.A. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecological Applications 22(7): 1876-1891.

Mitchell, S.R., Harmon, M.E., and O'Connell, K.E. 2012. Carbon debt and carbon sequestration parity in forest bioenergy production. GCB Bioenergy 4(6): 818-827. DOI: 10.1111/j.1757-1707.2012.01173.x

NOAA 2014. National Oceanic and Atmospheric Administration. Satellite and Information Service. National Climatic Data Center. US Department of Commerce. http://www.ncdc.noaa.gov/IPS/cd/cd.html;jsessionid=4E5612C511E74A2687A84659B08AA187?_page=0&jsessionid=4E5612C511E74A2687A84659B08AA187&state=AK&_target1=Next+%3E

Peterson, R.O., Woolington, J.D., and Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88: 3-52.

Potkin, M. 1997. Fire history disturbance study of the Kenai Peninsula mountainous portion of the Chugach National Forest. Draft. USDA Forest Service. Chugach National Forest. December 5, 1997. Anchorage, Alaska.

Potter, C., Tan, P.N., Kumar, V., Kucharik, C., Klooster, S., Genovese, V., Cohen, W., and Healey, S. 2005. Recent history of large-scale ecosystem disturbances in North America derived from the AVHRR satellite record. Ecosystems 8(7): 808-824.

Preisler, H.K., Ager, A.A., and Hayes, J.L. 2010. Probabilistic risk models for multiple disturbances: An example of bark beetles and wildfire. *In*: Pye, J.M., Rauscher, H.M., Sands, Y., Lee, D.S., and Beatty, J.S. (Tech. Eds.). Advances in threat assessment and their application to forest and rangeland management. Gen. Tech. Rep. PNW-GTR-802. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA, pp. 371–380. www.fs.fed.us/pnw/pubs/pnw_gtr802a.pdf

Preston, B.L. and Jones, R.N. 2006. Climate change impacts on Australia and the benefits of early action to reduce global greenhouse gas emissions. Canberra: CSIRO, 41 p.

Rauscher, H.M., Sands, Y., Lee, D.S., and Beatty, J.S. (Tech. Eds.). Advances in threat assessment and their application to forest and rangeland management. Gen. Tech. Rep. PNW-

GTR-802. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA. www.fs.fed.us/pnw/pubs/pnw_gtr802a.pdf

Schwartz, C.C. and Franzmann, A.W. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. The Journal of Wildlife Management, pp.426-431.

Smithwick, E.A.H., Harmon, M.E., Remillard, S.M., Acker, S.A., and Franklin, J.F. 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. Ecological Applications 12(5): 1303–1317. http://dx.doi.org/10.1890/1051-0761(2002)012[1303:PUBOCS]2.0.CO;2

Soja, A.J., Tchebakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., Chapin, F.S., and Stackhouse, P.W. 2007. Climate-induced boreal forest change: Predictions versus current observations. Global and Planetary Change 56(3): 274-296.

Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan, M.D., Hirsch, K.G., Logan, K.A., Martell, D.L. and Skinner, W.R. 2002. Large forest fires in Canada, 1959–1997. Journal of Geophysical Research: Atmospheres (1984–2012), 107(D1), FFR-5.

Tol, R.S.J. 2000. Timing of greenhouse gas emission reduction. Pacific and Asian Journal of Energy 10(1): 63-68.

USDA 2015a. http://www.fs.fed.us/pnw/rma/fia-topics/index.php. Last modified 10/27/2014. Accessed October 26, 2015.

USDA 2015b. http://www.fs.usda.gov/main/r10/forest-grasslandhealth/. Accessed October 25, 2015.

USDA 2014. Field instructions for the annual inventory of Coastal Alaska 2014. Forest Inventory and Analysis program. PNW Research Station. USDA Forest Service. http://www.fs.fed.us/pnw/rma/fia-topics/documentation/field-manuals/documents/Annual/2014_AFSL_FIA_Field_Manual_FINAL.pdf

USDA 2003. Field procedures for the Coastal Alaska inventory 2003.USDA Forest Service, PNW Station – Forestry Sciences Lab and Region 10 – Alaska. http://www.fs.fed.us/pnw/fia/local-resources/pdf/field_manuals/ak/2003_coak_field_manual.pdf

USDA 2000. Field procedures for the southeast Alaska inventory 2000. USDA Forest Service, PNW Station – Forestry Sciences Lab and Region 10 – Alaska. http://www.fs.fed.us/pnw/fia/local-resources/pdf/field_manuals/ak/2000_seak_field_manual.pdf

Van Hees, W.S. 2005. Spruce reproduction dynamics on Alaska's Kenai Peninsula, 1987–2000. USDA Forest Pacific Northwest Research Station, Portland (OR). Res. Pap. PNW-RP-563, 18 p.

Van Pattern, D.J. 2000. Soil survey of lower Kenai Peninsula area, Alaska. USDA NRCS publication, 179 p.

Van Vuuren, D.P. and de Vries, H.J.M. 2001. Mitigation scenarios in a world oriented at sustainable development: The role of technology, efficiency and timing. Climate Policy 1(2): 189-210.

Waddell, K.L. 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. Ecological Indicators 1: 139-153.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., and Swetnam, T.W. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313(5789): 940-943.

Werner, R.A., Holsten, E.H., Matsuoka, S.M., and Burnside, R.E. 2006. Spruce beetles and forest ecosystems in south-central Alaska: A review of 30 years of research. For. Ecol. Manage. 227(3): 195-206.

Wigley, T.M.L., Richels, R. and Edmonds, J.A. 1996. Economic and environmental choices in the stabilization of atmospheric CO_2 concentrations. Nature 379(6562): 240-243.

Williams, A.M. and Liebhold, A.M. 2002. Climate change and the outbreak ranges of two North American bark beetles. Agricultural and Forest Entomology 4: 87–99.

CHAPTER 5 -- CONCLUSIONS

This study examined C stores and dynamics in the forest ecosystems and in the forest sector of Coastal Alaska and how they are controlled by disturbances and subsequent management. In addition, above- and belowground live and dead C pools were estimated and uncertainty analysis was conducted to identify the ways uncertainty could be decreased in future estimates. The effect of large-scale disturbance on CWD dynamics in spruce-dominated forests of Kenai Peninsula, Alaska was examined in relation to the type of CWD produced and differences between snag and log decomposition. Chronosequence and decomposition-vectors analyses were utilized to describe snag and log decomposition and a simulation model was used to examine the effect of spruce bark beetle disturbance generated CWD on C stores and fluxes. Using model simulations and available information on live and dead C stores and dynamics, we evaluated the effect of several management strategies on woody C stores for "leave-as-is" and "salvage-and-utilization" scenarios.

Both average aboveground live tree and log biomass in Coastal Alaska were lower than the amounts reported for other neighboring coastal rainforest ecosystems in the PNW. At the same time, snag biomass generally was higher. Overall CWD stores in Coastal Alaska were lower than values reported from the coastal PNW and Canada, but were higher than values reported from Russia, another cold-climate forest region. At the regional scale, CWD biomass in the Boreal ecoregion represented almost 46 percent of aboveground (live and dead tree) biomass (67 percent of CWD consisted of snags) as compared to 21 percent in the Temperate ecoregion (52

percent of CWD consisted of snags). For the Boreal ecoregion, the snag biomass pool was more

substantial due to disturbance, related to a recent spruce bark beetle outbreak.

Disturbances represented important events leading to reorganization of components within the

forest ecosystems of Coastal Alaska. Regardless of type and severity, disturbances increased the

proportion of CWD in total aboveground (live and dead tree) biomass in the forests of Alaska

when compared to undisturbed stands, likely changing the C balance and future C dynamics in

disturbed stands. The contribution of different disturbance types to the total regional CWD stores

varied between ecoregions of Alaska with spruce bark beetle outbreaks having the highest

regional impact on CWD stores in the Boreal ecoregion. In the Temperate ecoregion, the highest

CWD stores were found in stands deemed undisturbed but in reality were subject to small-scale

disturbances. Disturbance type and severity also had a significant effect on CWD pool

partitioning between the snag and log components likely diversifying CWD decomposition

trajectories.

We examined the FIA plot-level data in the context of the whole ecosystem C by identifying and

estimating the size of eight C pools within the forests of Coastal Alaska. Among these, the soils

C pool was the largest, representing 62.6% of the total ecosystem C. It was followed by live

aboveground, live root, snag, log, FWD, dead root, and understory vegetation C pools with the

last representing <1% of the ecosystem C. Three C pools estimated from plot-level data

measured by FIA in the field (live, snag, and log components) cumulatively represented 30.6%

of the total ecosystem C or just half of that contributed by the soils pool, emphasizing the

importance of whole-ecosystem approach when assessing C stocks within the system. Such an approach allows for better understanding of the potential behavior of each C pool within the ecosystem context under changing disturbance regimes and changing climate.

Uncertainty of C estimates is essential in accurately determining the upper and lower bounds of forest C sources and sinks with the purpose of assessing forest C sequestration potential. In our study, the uncertainty of the individual pools (2xSE of the pool's mean estimate) was 10.8%, 4.2%, 6.4%, 6.5%, 12.0%, 4.8%, 5.2%, and 57.9% for the soils, live aboveground, live roots, snag, log, FWD, dead roots, and understory vegetation pool, respectively. The highest sources of uncertainty in total C stores were associated with the soils and the live and dead tree C pools (due to pools sizes) and most likely produced by sampling and model selection errors, respectively. To decrease uncertainty in the soil C pool more representative sampling should be undertaken across Coastal Alaska utilizing stratified, random, or systematic sampling techniques or their combinations. To reduce uncertainty in the aboveground live and dead C pools we recommend more attention be paid to the form of tree bole that is used in volume equations as differences in stem form are likely introducing the most uncertainty.

A comparison between the snag and log decay class-specific density changes and differences in decomposition rate-constants based on density, volume, and mass loss indicated snags decomposed slower than logs. This was likely caused by differing environmental conditions (temperature and moisture regimes) associated with the CWD physical position, with differences in moisture (i.e., snags were drier than logs) potentially being the most important factor. Our

initial hypothesis that the decomposition process consists of three distinct phases for the spruce logs sampled on the Kenai Peninsula was not supported. Decomposition rate-constants for the first two phases based on the fraction of density, volume, and mass loss were similar to each other but different from the third phase implying a two-phase spruce decomposition process. A two-phase process was also supported by comparison of decay class-specific decomposition rate-constants. A three-phase decomposition process could potentially describe decomposition in snags better than in logs given the initial 10- to 40-year lag in decomposition while snags are standing, rapid decomposition after snags fall and moderately slow decomposition associated with advanced stages of stem decay. Given the slower C release from snag C pool associated with lags delaying snag decomposition, disturbances producing significant amount of CWD in form of snags could create landscapes with larger C storage than those producing logs. Not only would these landscapes emit less C over a time period, but also potentially revert more quickly to C neutrality.

Comparison between long-term decomposition rate-constant for logs from chronosequences (-0.02 yr^{-1}) and short-term rate-constant from decomposition-vectors (-0.04 yr^{-1}) may indicate increased rates of CWD decomposition in the recent past. Warming climate could be creating conditions leading to the increase in disturbance frequency and severity as well as an increase in CWD decomposition rate-constants which in turn, through positive feedbacks, lead to increase in C fluxes to the atmosphere and further increase in temperatures.

The mismatch between the FIA based C estimates and the FHP ADS outbreak mortality C estimates prevented direct use of C estimates from ADS in model simulations. When not limited by the FIA C stores estimates, the ADS overestimated outbreak-related mortality C by a factor of 5, which increased their previously assessed margin of uncertainty. To reduce the uncertainly of the ADS mortality estimates aerial estimates should be calibrated with a rigorous ground truthing procedure and be linked to the FIA or another reliable ground data source.

Lags represented an important aspect of ecosystem processes, affecting ecosystem C dynamics by controlling the timing of the C inputs associated with regeneration and outputs related to CWD decomposition. The combination of immediate regeneration and delays in CWD C emissions may speed up ecosystem recovery to C neutrality. Delays in regeneration may place the C input peak and CWD C flux peak out of synchrony, keeping the system a C source to the atmosphere over a longer period of time. Finally, lack of regeneration and conversion of forests to shrub- or grassland may reduce forest land, decreasing C storage potential of the system via a permanent net C flux to the atmosphere.

The management strategies not removing bole biomass from disturbed forest landscapes provided the highest short-term (up to 50 years) ecosystem C storage. Moreover, these "leave-as-is" scenarios had lower C emissions with a less pronounced and more gradual and delayed peak than the "salvage-and-utilization" scenarios. Beyond 50 years after the beginning of disturbance period, more C was stored under the "salvage-and-utilization" versus "leave-as-is" scenarios when fuel-related substitution was considered (with the caveat the substitution is permanent).

Assuming no leakage, management strategies associated with fuels production stored more C than the "leave-as-is" or building materials and paper production strategies. However, due to lack of legal protective mechanisms the permanence of C stores related to substitution are uncertain.

As part of the Forest Carbon Accounting Framework (Woodall et al. 2015) the FIA program supplies forest C estimates that serve multiple essential purposes, i.e. forest C management, C credit trading, national reporting of GHG inventories to the United Nations Convention for Climate Change, calculating estimates for the Montreal Process criteria and indicators for sustainable forest management, registering forest-related activities for the national 1605(b) Voluntary Reporting of GHG Program, and other GHG registries for the States and regions (USDA 2016). Therefore, the FIA program serves as part of the solution in assessing and curbing GHG emissions from the U.S. forests. At the same time, given the extent and type of transportation employed by the FIA Data Collection Team (trucks, boats, helicopters, airplanes, and float planes), the C footprint of the FIA program is probably relatively large, thus contributing to the problem of climate change. We feel that the reduction of C emissions from the transportation use should be on the FIA priority list. More extensive use of alternative sampling methods (i.e., remote sensing, LIDAR, etc.), alternative types of transportation (hybrid or electrical vehicles), reduction in driving and flight time, as well as any other technology and activities reducing C emissions to the atmosphere by the FIA operations should be encouraged and rewarded.

Given the dynamic nature of the forest ecosystems driven by disturbances increasing in extent, frequency, and severity under changing climate and the relatively long (especially in the West) FIA plot re-measurement cycles (5 to 10 years) we recommend that in addition to the conventional long-term inventory plot monitoring system to have a disturbance-response inventory that would allow field crews to re-measure the plots within the perimeter of recent disturbances (fires, beetle outbreaks, etc.). Such program would allow a deeper understanding of the short- and long-term disturbance effects on disturbance-driven C dynamics.

Our analysis indicated that some of the major C pools were overlooked in the previous years of FIA sampling. To improve the accuracy and insure the biological and statistical robustness of the C estimates by FIA program, we recommend revising the FIA protocol to include the sampling of all major above- and belowground C pools in the system, namely soils, live, snag, log, ground cover (mosses and lichens), and understory vegetation on all FIA plots.

To fully understand landscape-level forest C stores and dynamics, it is important to have representative inventory sample of all areas across the landscape. Specifically for Alaska, the forest land designated as wilderness study area within the Chugach and Tongass national forests as well as the entire Glacier Bay National Park comprising together 1.4 million ha have been excluded from the inventory. The lack of data from such a large area increases the uncertainty in C stores estimates by FIA, but also the wilderness represents the area where human involvement into natural ecosystem processes has been minimal, thus providing an opportunity to monitor C

dynamics under "leave-as-is" management scenario. Thus, the importance of inventorying the Alaska wilderness is difficult to overemphasize. Given the new obligations by the U.S. on C accounting arena (Leggett 2015) we encourage a constructive dialogue between the FIA program and the wilderness managing agencies to allow the long-term monitoring program in the Alaskan wilderness.

For deeper understanding of C dynamics we recommend more work to be done studying the decomposition of CWD, FWD, and coarse roots in Alaska. Given the latitudinal and elevational variations of Alaskan forests, the effects of position, temperature, moisture, aspect, elevation, and other factors on C pools dynamics in Alaska need to be better understood.

We were unable to fully explain the differences in spruce log decomposition rate-constants as studied by chronosequence and decomposition-vectors approaches in Chapter 3. These differences may represent an actual effect of changing temperature on log decomposition or may just reflect the methodological issues between two approaches that do not conclusively demonstrate change. Therefore, further work is necessary in this area to fully understand the CWD dynamics on the Kenai Peninsula following large-scale disturbance events.

The possible positive future feedback involving disturbance regimes, carbon, and climate will continue as long as the susceptible host, pest, and environmental conditions favoring outbreaks are present. The future research should concentrate on how the intensity of this feedback changes, its duration, as well as the potential ability of this feedback to influence neighboring

landscapes. Answering these important questions will provide a scientific basis for making

informed decisions to manage the forests of the future.

BIBLIOGRAPHY

Acker, S.A., Harcombe, P.A., Harmon, M.E., and Greene, S.E. 2000. Biomass accumulation over the first 150 years in coastal Oregon *Picea-Tsuga* forest. Journal of Vegetation Science 11: 725-738.

Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce – western hemlock forests of southeast Alaska. Ecology 63(6): 1932-1948.

Alban, D.H. and Pastor, J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. 23: 1744–1749.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.T., and Gonzalez, P. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259(4): 660-684.

Allen, J.L., Wesser, S., Markon, C.J., and Winterberger, K.C. 2006. Stand and landscape level effects of a major outbreak of spruce beetles on forest vegetation in the Copper River Basin, Alaska. For. Ecol. Manage. 227: 257-266.

Andersen, H.-E. 2011. Biomass and Carbon. *In*: Barrett, T.M. and Christensen, G.A. (Tech. Eds.). 2011. Forest of southeast and south-central Alaska, 2004-2008: Five-year forest inventory and analysis report. Portland, OR: U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Research Station, Gen. Tech. Rep. PNW-GTR-835, pp. 13-22.

Anderson, R.S., Hallett, D.J., Berg, E.E., Jass, R.B., Toney, J.L., de Fontaine, C.S., and DeVolder, A.D. 2006. Holocene development of boreal forests and fire regimes on the Kenai lowlands of Alaska. The Holocene 16 (6): 791- 803.

Angers, V.A., Drapeau, P., and Bergeron, Y. 2012. Mineralization rates and factors influencing snag decay in four North American boreal tree species. Can. J. For. Res. 42: 157-166. DOI:10.1139/X11-167

Angers, V.A., Drapeau, P., and Bergeron, Y. 2010. Snag degradation pathways of four North American boreal tree species. For. Ecol. Manage. 259(3): 246-256. DOI: 10.1016/j.foreco.2009.09.026

Apps, M.J., Kurz, W.A., Beukema, S.J., and Bhatti, J.S. 1999. Carbon budget of the Canadian forest product sector. Environmental Science and Policy 2(1): 25-41.

Arrhenius, S. 1896. On the influence of carbonic acid in the air upon the temperature of the ground. Philosophical Magazine 41:237-276.

Azar, C. and Dowlatabadi, H. 1999. A review of technical change in assessment of climate policy. Annual Review of Energy and the Environment 24: 513-544.

Barbour, R.J., Zaborske, R.R., McClellan, M.H., Christian, L., and Golnick, D. 2005. Young-stand management options and their implications for wood quality and other values. Landscape and Urban Planning 72(1): 79-94.

Barrett, T.M. 2014. Storage and flux of carbon in live trees, snags, and logs in the Chugach and Tongass National Forests. Gen. Tech. Rep. PNW-GTR-889. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 44 p.

Barrett, T.M. and Christensen, G.A. (Tech. Eds.). 2011. Forest of southeast and south-central Alaska, 2004-2008: Five-year forest inventory and analysis report. Gen. Tech. Rep. PNW-GTR-835. Portland, OR: U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Research Station, 156 p.

Bechtold, W.A. and Patterson, P.L. (Eds.). 2005. The enhanced forest inventory and analysis program − national sampling design and estimation procedures. USDA Forest Service. Southern Research Station. Gen. Tech. Rep. GTR-SRS-80.

Bentz, B.J., Christopher, J.R., Fettig, J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., and Seybold, S.J. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. BioScience 60(8): 602-613.

Berg, E.E. and Anderson R.S. 2006. Fire history of white and Lutz spruce forests on the Kenai Peninsula, Alaska, over the last two millennia as determined from soil charcoal. For. Ecol. Manage. 227: 275–283.

Berg, E.E., Henry, J.D., Fastie, C.L., De Volder, A.D., and Matsuoka, S.M. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. For. Ecol. Manage. 227(3): 219-232.

Birdsey, R.A. and Heath, L.S. 1995. Carbon changes in US forests. *In*: Productivity of America's forests and climate change 271: 56-70.

Boggs, K., Sturdy, M., Rinella, D.J. and Rinella, M.J. 2008. White spruce regeneration following a major spruce beetle outbreak in forests on the Kenai Peninsula, Alaska. For. Ecol. Manage. 255(10): 3571-3579.

Bonan, G.B. 2008. Forests and climate change: Forcing, feedbacks, and the climate benefits of the forests. Science 320(5882): 1444-1449. DOI: 10.1126/science.1155121

Bond, M.L., Lee, D.E., Bradley, C.M., and Hanson, C.T. 2009. Influence of pre-fire tree mortality on fire severity in conifer forests of the San Bernardino Mountains, California. Open Forest Science Journal 2: 41–47.

Bond-Lamberty, B. and Gower, S.T. 2008. Decomposition and fragmentation of coarse woody debris: Re-visiting a boreal black spruce chronosequence. Ecosystems 11(6): 831-840.

Bormann, B.T. and Sidle, R.C. 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. Journal of Ecology 78(3): 561-578.

Boucher, T.V. and Mead, B.R. 2006. Vegetation change and forest regeneration on the Kenai Peninsula, Alaska following a spruce beetle outbreak, 1987-2000. For. Ecol. Manage. 227(3): 233-246.

Brackley, A.M., Haynes, R.W., and Alexander, S.J. 2009. Timber harvests in Alaska: 1910-2006. Res. Note PNW-RN-560. Portland, OR : U.S. Dept. of Agriculture, Forest Service, Pacific Northwest Research Station, 24 p.

Brady, W. and T. Hanley. 1984. The role of disturbance in old growth forests: Some theoretical implications for Southeastern Alaska. *In*: Meehan, W., Merrell, T. Jr., and Hanley, T. (Eds.). Proceedings of the symposium on fish and wildlife relationships in old-growth forests. American Institute of Fishery Research Biologists, Juneau, AK, pp. 213–218.

Brais, S., Paré D., and Lierman, C. 2006. Tree bole mineralization rates of four species of the Canadian eastern boreal forest: Implication for nutrient dynamics following stand-replacing disturbances. Can. J. For. Res. 36: 2331-2340.

Bronick, C.J. and Lal, R. 2005. Soil structure and management: A review. Geoderma 124(1): 3-22.

Brown, S., Mo, J., McPherson, J.K., and Bell, D.T. 1996. Decomposition of woody debris in Western Australian forests. Can. J. For. Res. 26: 954–966.

Brown, S., Sathaye, J., Cannell, M., and Kauppi, P.E. 1995. Management of forests for mitigation of greenhouse gas emissions. Cambridge University Press.

Busse, M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Science Society of America Journal 58(1): 221-227.

Cairns, M.A., Brown, S., Helmer, E.H., and Baumgardner, G.A. 1997. Root biomass allocation in the world's upland forests. Oecologia 111: 1-11.

Campbell, S., Waddell, K., Gray, A. (Tech. Eds.). 2010. Washington's forest resources, 2002-2006: Five-year Forest Inventory and Analysis report. Gen. Tech. Rep. PNW-GTR-800. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 189 p.

Campbell, S., van Hees, W.S., and Mead, B. 2005. South-Central Alaska forests: Inventory highlights. Gen. Tech. Rep. PNW-GTR-652. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 28 p.

Campbell, S., van Hees, W.S., and Mead, B. 2004. Southeast Alaska forests: Inventory highlights. Gen. Tech. Rep. PNW-GTR-609. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 20 p.

Carroll, A.L., Taylor, S.W., Regniere, J., and Safranyik, L. 2003. Effect of climate change on range expansion by the mountain pine beetle in British Columbia. The bark beetles, fuels, and fire bibliography. Paper 195: 223-232. http://digitalcommons.usu.edu/barkbeetles/195

Chapin III, F.S., Chapin, M.C., Matson, P.A., and Vitousek, P. 2011. Principles of terrestrial ecosystem ecology. Springer.

Chapin, F.S., Matson, P., and Mooney, H. 2002. Principles of terrestrial ecosystem ecology. New York: Springer. 436 p. Chapter 6.

Chen, B., Arain, M.A., Khomik, M. Trofymow, J.A., Grant, R.F., Kurz, W.A., Yeluripati, J., and Wang, Z. 2013. Evaluating the impacts of climate variability and disturbance regimes on the historic carbon budget of a forest landscape. Agricultural and Forest Meteorology 180: 265– 280.

Chen, H., Harmon, M.E., and Griffiths, R.P. 2001. Decomposition and nitrogen release from decomposing woody roots in coniferous forests of the Pacific Northwest: A chronosequence approach. Can. J. For. Res. 31: 246–260.

Chen, H. 1999. Root decomposition in three coniferous forests: Effects of substrate quality, temperature, and moisture. PhD dissertation. Oregon State University, Corvallis, Oregon.

Christensen, N.L. 1989. Landscape history and ecological change. Forest and Conservation History 33(3): 116-125.

Chueng, N., and Brown, S. 1995. Decomposition of silver maple (*Acer saccharinum* L.) woody debris in central Illinois bottomland forest. Wetlands 15: 232–241.

Cramer, D. and Howitt, D. (Eds.). 2004. Fisher's LSD (Least Significant Difference) or protected test. The SAGE Dictionary of Statistics. London, England: SAGE Publications, Ltd., 2004. 67. SAGE Research Methods. Web. 13 Aug. 2015.

Cudmore, T.J., Björklund, N., Carroll, A.L., and Staffan Lindgren, B. 2010. Climate change and range expansion of an aggressive bark beetle: Evidence of higher beetle reproduction in naive host tree populations. Journal of Applied Ecology 47(5): 1036-1043.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., and Simberloff, D. 2001. Climate Change and Forest Disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. BioScience 51(9): 723-734.

DASM 2015. Digital aerial sketch mapping overview. USDA Forest Service. Website. Retrieved November 1, 2015 from
http://www.fs.fed.us/foresthealth/technology/pdfs/dasm_detailed_overview.pdf

De Beurs, K.M. and Townsend, P.A. 2008. Estimating the effect of gypsy moth defoliation using MODIS. Remote Sensing of Environment 112: 3983–3990.

De Volder, A. 1999. Fire and climate history of lowland black spruce forests, Kenai National Wildlife Refuge, Alaska. MS Thesis. Northern Arizona University.

Deal, R.L., Heithecker, T., and Zenner, E.K. 2010. Comparison of tree size structure and growth for partially harvested and even-aged hemlock-spruce stands in southeast Alaska. Journal of Forest Research 15(1): 31-37.

Deal, R.L. 2007. Management strategies to increase stand structural diversity and enhance biodiversity in coastal rainforests of Alaska. Biological Conservation 137(4): 520-532.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexier, M.C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. Science 263(5144): 185-190.

Dodds, K.J., Garman, S.L., and Ross, D.W. 2006. Landscape analyses of Douglas-fir beetle populations in northern Idaho. For. Ecol. Manage. 231: 119–130.

Donnegan, J., Campbell, S., and Azuma, D. (Tech. Eds.). 2008. Oregon's forest resources, 2001-2005: Five-year Forest Inventory and Analysis report. Gen. Tech. Rep. PNW-GTR-765. Portland, OR: U.S. Forest Service, Pacific Northwest Research Station, 186 p.

Edmonds, R.L. and Eglitis, A. 1989. The role of Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. Can. J. For. Res. 19: 853–859.

Erickson, H.E., Edmonds, R.L., and Peterson, C.E. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. Can. J. For. Res. 15: 914-921.

Everham, E.M. and Brokaw, N.V. 1996. Forest damage and recovery from catastrophic wind. The Botanical Review 62(2): 113-185.

Fahey T.J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (*Pinus contorta* ssp. *latifolia*) ecosystems, southeastern Wyoming. Ecological Monographs 53: 51-72.

Fargione, J., Hill, J., Tilman, D., Polasky, S., and Hawthorne, P. 2008. Land clearing and the biofuel carbon debt. Science 319(5867): 1235-1238.

Farr, W.A. and Hard, J.S. 1987. Multivariate analysis of climate along the southern coast of Alaska--some forestry implications. Res. Paper PNW-372. Portland, OR: Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, 38 p.

FHTET 2015. Forest Health Technology Enterprise Team, USDA Forest Service. Website. Retrieved October 30, 2015 from http://www.fs.fed.us/foresthealth/technology/ads_standards.shtml

Flannigan, M.D., Stocks, B.J., and Wotton, B.M. 2000. Climate change and forest fires. Science of the Total Environment 262(3): 221-229.

Flint, C.G. 2006. Community perspectives on spruce beetle impacts on the Kenai Peninsula, Alaska. For. Ecol. Manage. 227(3): 207-218.

Flint, C.G. and Haynes, R. 2006. Managing forest disturbances and community responses: Lessons from the Kenai Peninsula, Alaska. J. For. 104(5): 269-275.

Foster, D.R. and Boose, E.R. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. Journal of Ecology, pp. 79-98.

Foster, J.R. and Lang, G.E. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Can. J. For. Res. 12(3): 617-626.

Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C ., Bible, K., and Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155(1): 399-423.

Franklin J.F., Shugart H.H., and Harmon M.E. 1987. Tree death as an ecological process. BioScience 37: 550-556.

Fraver, S., Ringvall, A., and Jonsson, B.G. 2007. Refining volume estimates of down woody debris. Can. J. For. Res. 37: 627-633.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Flemming, S., Forbes, G., Gerrow, J.S., Johnson, G., Woodley, S. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. 4: 238–265.

Garber, S.M., Brown, J.P., Wilson, D.S., Maguire, D.A., and Heath, L.S. 2005. Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. Can. J. For. Res. 35(4): 787-796.

Garman, S.L., Acker, S.A., Ohman, J.L., and Spies, T.A. 1995. Asymptotic height-diameter equations for twenty-four tree species in western Oregon. Research Contribution 10. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, 22 p.

Giorgi, F. 2006. Climate change hot-spots. Geophys. Res. Lett. 33(8), 4 p. http://dx.doi.org/10.1029/2006GL025734

Goetz, S.J., Mack, M.C., Gurney, K.R., Randerson, J.T., and Houghton, R.A. 2007. Ecosystem responses to recent climate change and fire disturbance at northern high latitudes: Observations and model results contrasting northern Eurasia and North America. Environmental Research Letters 2(4), 045031.

Goodale, C.L., Apps, M.J., Birdsey, R.A., Field, C.B., Heath, L.S., Houghton, R.A., Jenkins, J.C., Kohlmaier, G.H., Kurz, W., Liu, S., Nabuurs, G.-J., Nilsson, S., and Shvidenko, A.Z. 2002. Forest carbon sinks in the Northern Hemisphere. Ecological Applications 12(3): 891-899.

Goodman, J.R. 2002. HJ Andrews Experimental Forest. Long Term Ecological Research. SUE – Stochastic Uncertainty Estimator User's Guide. http://andrewsforest.oregonstate.edu/pubs/webdocs/models/sue.cfm

Gosz, J.R. 1980. Nutrient budget studies for forests along an elevational gradient in New Mexico. Ecology, pp.515-521.

Gough, C.M., Vogel, C.S., Kazanski, C., Nagel, L., Flower, C.E., and Curtis, P. S. 2007. Coarse woody debris and the carbon balance of a north temperate forest. For. Ecol. Manage. 244(1): 60-67. DOI:10.1016/j.foreco.2007.03.039

Gould, W.A., Gonzalez, G., Hudak, A.T., Nettleton Hollingsworth, T., and Hollingsworth, J. 2008. Forest structure and Down Woody Debris in Boreal, Temperate, and Tropical forest fragments. USDA Forest Service. UNL Faculty Publication. Paper 176. http://digitalcommons.unl.edu/usdafsfacpub/176

Graham, R.L. 1982. Biomass dynamics of dead Douglas-fir and western hemlock boles in mid-elevation forests of the Cascade Range. Ph.D. thesis, Oregon State University, Corvallis, Oregon.

Graham, R.L. and Cromack, K. Jr. 1982. Mass, nutrient content, and decomposition rate of dead boles in rain forests of Olympic National Park. Can. J. For. Res. 12: 51 1-521.

Greb, S.F. and Archer, A.W. 2007. Soft-sediment deformation produced by tides in a meizoseismic area, Turnagain Arm, Alaska. Geology 35 (5): 435-438. Geological Society of America. DOI: 10.1130/G23209A.

Grier, C.C. 1978. A *Tsuga heterophylla-Picea sitchensis* ecosystem of coastal Oregon: Decomposition and nutrient balances of fallen logs. Can. J. For. Res. 8(2): 198-206.

Grier, C.C. and Logan, R.S. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. Ecological monographs, pp. 373-400.

Griffin, D.M. 1977. Water potential and wood-decay fungi. Ann. Rev. Phytopathol. 15: 319-329.

Halbrook, J.M., Morgan, T.A., Brandt, J.P., Keegan, C.E., Dillon, T., and Barrett, T. 2009. Alaska's timber harvest and forest products industry, 2005. Gen. Tech. Rep. 787 PNW-681. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, 30 p. http://www.fs.fed.us/pnw/pubs/pnw_gtr787.pdf

Hale, C.M. and Pastor, J. 1998. Nitrogen content, decay rates, and decompositional dynamics of hollow versus solid hardwood logs in hardwood forests of Minnesota, USA. Can. J. For. Res. 28(9): 1276-1285.

Hamburg, S.P., Zamolodchikov, D.G., Korovin, G.N., Nefedjev, V.V., Utkin, A.I., Gulbe, J.I., Gulbe, T.A. 1997. Estimating the carbon content of Russian forests: A comparison of phytomass/volume and allometric projections. Mitigation and Adaptation Strategies of Global Change Netherlands: Springer 2: 247-265.

Hansen, E.M. 2014. Forest development and carbon dynamics after mountain pine beetle outbreaks. Forest Science 60(3): 476-488.

Hansen, A.J., Spies, T.A., Swanson, F.J., and Ohmann, J.L. 1991. Conserving biodiversity in managed forests. BioScience 41(6): 382-392.

Hard, J. 1974. The forest ecosystem of southeast Alaska. Forest Insects. USDA FS GTR, PNW-13. PNW forest and range experimental station. USDA, FS, Portland, Oregon.

Harmon, M.E., Fasth, B., Halpern, C.B., and Lutz, J.A. 2015. Uncertainty analysis: An evaluation metric for synthesis science. Ecosphere 6(4): 1-12.

Harmon, M.E. 2011. HJ Andrews Experimental Forest LTER Data Catalog. http://andrewsforest.oregonstate.edu/lter/data.cfm?frameURL=http://andlter.forestry.oregonstate.edu/ltermeta/ltersearch/DataCatalog.aspx?topnav=173. Andrews Experimental Forest LTER. Last accessed April 04, 2013.

Harmon, M.E., Bond-Lamberty, B., Tang, J., and Vargas, R. 2011a. Heterotrophic respiration in disturbed forests: A review with examples from North America. Journal of Geophysical Research: Biogeosciences, 116(G4). DOI:10.1029/2010JG001495

Harmon, M.E., Woodall, C.W., Fasth, B., Sexton, J., and Yatskov, M. 2011b. Differences between standing and downed dead tree wood density reduction factors: A comparison across decay classes and tree species. USDA Forest Service. Research Paper NRS-15.

Harmon, M.E. 2010. Branch decomposition study, unpublished data.

Harmon, M.E., Woodall, C.W., Fasth, B., and Sexton, J. 2008. Woody detritus density and density reduction factors for tree species in the United States: A synthesis. USDA Forest Service. GTR-NRS-29.

Harmon, M.E., Phillips, D.L., Battles, J.J., Rassweiler, A., Hall Jr, R.O., Lauenroth, W.K., Fahey, T.J., and Knapp, A.K. 2007. Quantifying uncertainty in net primary production measurements. Principles and standards for measuring primary production, pp.238-260.

Harmon, M., Fasth, B., Yatskov, M., Sexton, J., and Trummer, L. 2005. The fate of dead spruce on the Kenai Peninsula: A preliminary report. USDA Forest Service Technical Report R10-TP-134, 23 p.

Harmon, M.E., Bible, K., Ryan, M.G., Shaw, D.C., Chen, H., Klopatek, J., and Li, X. 2004. Production, respiration, and overall carbon balance in an old-growth *Pseudotsuga-Tsuga* forest ecosystem. Ecosystems (2004) 7: 498-512.

Harmon, M.E., Krankina, O.N., Yatskov, M., and Matthews, E. 2001. Predicting broad-scale carbon stores of woody detritus from plot-level data. *In*: Lai, R., Kimble, J., and Stewart, B.A. (Eds.). Assessment methods for soil carbon. CRC Press, New York, pp. 533-552.

Harmon, M.E., Krankina, O.N., and Sexton, J. 2000. Decomposition vectors: A new approach to estimating woody detritus decomposition dynamics. Can. J. For. Res. 30: 76–84.

Harmon, M.E. and Sexton, J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. U. S. LTER Publication No. 20.

Harmon, M.E., Harmon, J.M., Ferrell, W.K., and Brooks, D. 1996. Modeling carbon stores in Oregon and Washington forest products: 1900-1992. Climatic Change 33: 521-550.

Harmon, M.E. and Sexton, J. 1995. Water balance of conifer logs in early stages of decomposition. Plant and Soil 172: 141-152.

Harmon, M.E., Whigham, D.F., Sexton, J., and Olmsted I. 1995. Decomposition and mass of woody detritus in the dry tropical forests of the Northeastern Yucatan Peninsula, Mexico. Biotropica 27(3): 305-316.

Harmon, M.E., Sexton, J., Caldwell, B.A., and Carpenter, S.E. 1994. Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. Can. J. For. Res. 24: 1883–1893.

Harmon, M.E. and Chen, H. 1991. Coarse woody debris dynamics in two old-growth ecosystems. BioScience, pp. 604-610.

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

Harmon, M.E., Cromack K. Jr., and Smith, B.G. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Can. J. For. Res. 17(10): 1265-1272.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133-302.

Harris, A.S. 1999. Wind in the forests of southeast Alaska and guides for reducing damage. USDA FS PNW-GTR-244. Portland, Oregon, 63 p.

Harris, A.S. 1990. *Picea sitchensis* (Bong.) Carr. Sitka spruce. *In*: Burns, R.M., Honkala, B.H. (Tech. Eds.). Silvics of North America. Volume 1. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture, Forest Service, pp. 260-267.

Harris, A.S. and Farr, W.A. 1974. The forest ecosystem of southeast Alaska. 7. Forest ecology and timber management. USDA For. Serv. Gen. Tech. Rep. PNW-25.

Harris, A.S., Hutchinson, O.K., Meehan, W.R., Swanston, D.W., Helmers, A.E., Hendee, J.C., and Collins, T.M. 1974. The forest ecosystem of southeast Alaska, 1: The setting. USDA For. Serv. Get. Tech. Rep. PNW-GTR-12.

Hartley, C. 1949. Fungi and wood. Yearbook of Agriculture, pp. 630-633.

Heath, L.S., Smith, J.E., Woodall, C.W., Azuma, D.L., and Waddell, K.L. 2011. Carbon stocks on forestland of the United States, with emphasis on USDA Forest Service ownership. Ecosphere 2(1), art6.

Heath L.S. and Smith J.E. 2000. An assessment of uncertainty in forest carbon budget projections. Environ. Sci. Policy 3: 73-82.

Hennon, P.E. and Shaw, C.G. III. 1997. The enigma of yellow cedar decline. What is killing these long-lived, defensive trees? J. For. 95(12): 3-10.

Hennon, P.E., Mask, R., and Holsten, E.H. 1995. Forest insect and disease conditions in Alaska, 1994. Forest Health Management Report R10-TP-51. State and Private Forestry, USDA, Forest Service, Juneau, AK, 42 p.

Hennon, P.E., Hansen, E.M., and Shaw, C.G. III. 1990. Dynamics of decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. Can. J. Bot. 68: 651-662.

Hicks, W.T. 2000. Modeling nitrogen fixation in dead wood. PhD dissertation. Oregon State University, Corvallis, Oregon.

Hinds, T.E., Hawksworth, F.G., and Davidson, R.W. 1965. Beetle-killed Engelmann spruce: Its deterioration in Colorado. J. For. 63: 536-542.

HJA 2013. Bole decomposition rates of seventeen tree species in Western U.S.A. An on-line report prepared for the USDA USFS, Washington office. http://andrewsforest.oregonstate.edu/pubs/webdocs/reports/decomp/tables.htm. Accessed February 18, 2013.

Holeksa, J., Zielonka, T., and Zywiec, M. 2008. Modeling the decay of coarse woody debris in a subalpine Norway spruce forest of the West Carpathians, Poland. Can. J. For. Res. 38: 415-428. DOI:10.1139/X07-139

Holsten, E.H., Thier, R.W., Munson, A.S., and Gibson, K.E. 2000. The spruce beetle. Forest Insect and Disease Leaflet 127. USDA Forest Service. http://www.na.fs.fed.us/spfo/pubs/fidls/sprucebeetle/sprucebeetle.htm

Holsten, E.H., Werner, R.A., DeVelice, R. 1995. Effects of a spruce beetle (Coleoptera: Scolytidae) outbreak and fire on Lutz spruce in Alaska. Environmental Entomology 24: 1539–1547.

Holsten, E.H. 1984. Factors of susceptibility in spruce beetle attack on white spruce in Alaska. Journal of the Entomological Society of British Columbia 81: 39-45.

Houghton, R.A. 2005. Aboveground forest biomass and the global carbon balance. Global Change Biology 11(6): 945-958.

Houghton, R.A. 1995. Effects of land-use change, surface temperature, and CO_2 concentration on terrestrial stores of carbon. *In*: Woodwell, G.M. and Mackenzie, F.T. (Eds.). Biotic feedbacks in the global climatic system. Oxford University Press, New York, pp. 333-366.

Hudiburg, T., Law, B., Turner, D.P., Campbell, J., Donato, D., and Duane, M. 2009. Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. Ecological Applications 19(1): 163-180.

IPCC 2013. Hartmann, D.L., Klein Tank, A.M.G., Rusticucci, M., Alexander, L.V., Brönnimann, S., Charabi, Y., Dentener, F.J., Dlugokencky, E.J., Easterling, D.R., Kaplan, A., Soden, B.J. Thorne, P.W., Wild, M., and Zhai, P.M. 2013. Observations: Atmosphere and Surface. *In*: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., and Midgley, P.M. (Eds.). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC 2007a. Intergovernmental Panel on Climate Change Forth Assessment Report: Climate change 2007: Working group III: Mitigation of climate change. Section 3.3.5.1 Emissions reduction and timing. https://www.ipcc.ch/publications_and_data/ar4/wg3/en/ch3s3-3-5-1.html

IPCC 2007b. Intergovernmental Panel on Climate Change Forth Assessment Report: Climate change 2007: Working group III: Mitigation of climate change.

IPCC 2001. IPCC TAR WG3 (2001). Metz, B., Davidson, O., Swart, R., and Pan, J., (Eds.). Climate Change 2001: Mitigation. Contribution of Working Group III to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press. ISBN 0-521-80769-7. (pb: 0-521-01502-2)

Iverson, L.R., S. Brown, A. Grainger, A. Prasad and D. Liu. 1993. Carbon sequestration in tropical Asia: An assessment of technically suitable forest lands using geographic information systems analysis. Clim. Res. 3:23–38.

Janisch, J.E., Harmon, M.E., Chen, H., Fasth, B., and Sexton, J. 2005. Decomposition of coarse woody debris originating by clearcutting of an old-growth conifer forest. Ecoscience 12(2):151-160. DOI: http://dx.doi.org/10.2980/i1195-6860-12-2-151.1

Janisch, J.E. and Harmon, M.E. 2002. Successional changes in live and dead wood carbon stores: Implications for net ecosystem productivity. Tree Physiology 22(2-3): 77-89.

Johnson, K.D., Harden, J., McGuire, A.D., Bliss, N.B., Bockheim, J.G., Clark, M., Nettleton-Hollingsworth, T., Jorgenson, M.T., Kane, E.S., Mack, M., and O'Donnell, J. 2011. Soil carbon distribution in Alaska in relation to soil-forming factors. Geoderma 167: 71-84.

Johnson, E.A. and Greene, D.F. 1991. A method for studying dead bole dynamics in *Pinus contorta* var. *latifolia − Picea engelmannii* forests. Journal of Vegetation Science 2: 523-530.

Jomura, M., Kominami, Y., Dannoura, M., and Kanazawa, Y. 2008. Spatial variation in respiration from coarse woody debris in a temperate secondary broad-leaved forest in Japan. Forest Ecol. Manag. 255(1): 149-155.

Käärik, A.A. 1974. Decomposition of wood. *In*: Dickinson, C.H. and Pugh, G.J.F. (Eds.). Biology of Plant Litter Decomposition. London, Academic Press, pp. 129-174.

Karl, T.R., Knight, R.W., Easterling, D.R., and Quayle, R.G. 1996. Indices of climate change for the United States. Bulletin of the American Meteorological Society 77(2): 279-292.

Keenan, R.J., Prescott, C.E., and Kmmins, J.P. 1993. Mass and nutrient content of woody debris and forest floor in western red cedar and western hemlock forests of northern Vancouver Island. Can. J. For. Res. 23: 1052-1059.

Kobak, K.I. 1988. Biotical compounds of carbon cycle. Gidrometeoizdat Publishers. Leningrad, Russia.

Krankina, O.N., Houghton, R.A., Harmon, M.E., Hogg, E.H., Butman, D., Yatskov, M., Huso, M., Treyfeld, R.F., Razuvaev, V.N., and Spycher, G. 2005. Effects of climate, disturbance, and species on forest biomass across Russia. Can. J. For. Res. 35(9): 2281-2293.

Krankina, O.N., Harmon, M.E., Kukuev, Y.A., Treyfeld, R.F., Kashpor, N.N., Kresnov, V.G., Skudin, V.M., Protasov, N.A., Yatskov, M., Spycher, G., and Povarov, E.D. 2002. Coarse woody debris in forest regions of Russia. Can. J. For. Res. 32: 768-778.

Krankina O.N. and Harmon M.E. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water, Air and Soil Pollution 82: 227-238.

Kukuev, Y.A., Krankina, O.N., and Harmon, M.E. 1997. The forest inventory system in Russia. J. For. 95(9): 15-20.

Kulakowski, D. and Veblen, T.T. 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88: 759–769.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., and Safranyik, L. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452(7190): 987-990.

Kurz, W.A., Stinson, G., Rampley, G.J., Dymond, C.C., and Neilson, E.T. 2008a. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. Proc. Natl. Acad. Sci. USA 105(5): 1551–1555. DOI: 10.1073/pnas.0708133105

Kurz, W.A., Apps, M.J., Webb, T.M., and McNamee, P.J. 1992. The carbon budget of the Canadian forest sector: Phase I. Vol. 326. Forestry Canada, Northern Forestry Centre, 1992.

LaBau, J. 2004. Synthesis of ENRI findings from5 years of study of the spruce bark beetle on the Kenai Peninsula (abstract). *In*: A changing Alaskan ecosystem (symposium cd-rom), 2004 Feb. 24–26, Homer, Alaska. Kenai Peninsula Borough, Kenai Peninsula (AK), Spruce Beetle Mitigation Program.

Laiho, R. and Prescott, C.E. 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. Can. J. For. Res. 29: 1592-1603.

Lambert R.L., Lang G.E., and Reiners, W.A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61: 1460-1473.

Laurent, T.H. 1974. The forest ecosystems of southeast Alaska. Forest diseases. USDA Forest Service GTR PNW-23. Pacific Northwest Forest and Range Experimental Station. Portland, Oregon.

Leighty, W.W., Hamburg, S.P., and Caouette, J. 2006. Effects of management on carbon sequestration in forest biomass in Southeast Alaska. Ecosystems 9(7): 1051-1065.

Leggett, J.A. 2015. Greenhouse gas pledges by parties to the United Nations Framework Convention on Climate Change. Congressional Research Service 7-5700. R44092. https://www.fas.org/sgp/crs/misc/R44092.pdf.

Lynch, H.J., Renkin, R.A., Crabtree, R.L., and Moorcroft, P.R. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems 9: 1318–1327.

MacMillan, P.C. 1988. Decomposition of coarse woody debris in an old-growth Indiana forest. Can. J. For. Res. 18: 1353-1362.

Mäkinen, H., Hynynen, J., Siitonen, J., and Sievänen, R. 2006. Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. Ecological Applications 16(5): 1865-1879.

Malhi, Y., Baldocchi, D.D., and Jarvis, P.G. 1999. The carbon balance of tropical, temperate, and boreal forests. Plant Cell Environ. 22: 715–740. DOI:10.1046/j.1365-3040.1999.00453.x

Marland, G. 2000. The future role of reforestation in reducing buildup of atmospheric CO_2. *In*: Wigley, T.M.L. and Schimel, D.S. (Eds.). The carbon cycle. Cambridge University Press, Cambridge, pp. 190–198.

Marra, J.L. and Edmonds, R.L. 1996. Coarse woody debris and soil respiration in a clearcut on the Olympic Peninsula, Washington, U.S.A. Can. J. For. Res. 26: 1337-1345.

McCarthy, J.J. 2001. Climate change 2001: Impacts, adaptation, and vulnerability: Contribution of Working Group II to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

McCullough, D.G., Werner, R.A., and Neumann, D. 1998. Fire and insect in northern and boreal forest ecosystems of North America. Annu. Rev. Entomol. 43: 107-27.

McCurdy, D. and Stewart, B. 2005. Changes in dead wood structure following clearcut harvesting in Nova Scotia softwood forests. Forest research report. Nova Scotia DNR. Forest managmenet planning. FOR 2005-1 No. 76.
http://www.gov.ns.ca/natr/library/forestry/reports/REPORT76.PDF

McFee, W.W. and Stone, E.L. 1966. The persistence of decaying wood in the humus layers of northern forests. Soil Science Society of America Journal 30(4): 513-516.

McMahon, S.M., Parker, G.G., and Miller, D.R. 2010. Evidence for a recent increase in forest growth. Proceedings of the National Academy of Sciences 107(8): 3611-3615.

Means, J.E., MacMillan, P.C., and Cromack, K. Jr. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest. Can. J. For. Res. 22: 1536-1546.

Meddens, A.J., Hicke, J.A., and Ferguson, C.A. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecological Applications 22(7): 1876-1891.

Melson, S.L., Harmon, M.E., Fried, J.S., and Domingo, J.B. 2011. Estimates of live-tree carbon stores in the Pacific Northwest are sensitive to model selection. Carbon Balance and Management 6(2): 1-16.

Mielke, J.L. 1950. Rate of deterioration of beetle-killed Engelmann spruce. J. For. 48: 882-888.

Millar, C.I., Stephenson, N.L., and Stephens, S.L. 2007. Climate change and forests of the future: Managing in the face of uncertainty. Ecological Applications 17:2145–2151.
http://dx.doi.org/10.1890/06-1715.1

Mishra, U. and Riley, W.J. 2012. Alaskan soil carbon stocks: Spatial variability and dependence on environmental factors. Biogeosciences 9: 3637–3645. www.biogeosciences.net/9/3637/2012/. DOI:10.5194/bg-9-3637-2012

Mitchell, S.R., Harmon, M.E., and O'Connell, K.E. 2012. Carbon debt and carbon sequestration parity in forest bioenergy production. GCB Bioenergy 4(6): 818-827. DOI: 10.1111/j.1757-1707.2012.01173.x

Moiseev, B.N., Alfiorov, A.M., and Strakhov, V.V. 2000. About the evaluation of carbon stores and increments in forests of Russia (in Russian). Lesnoye Khozyajstvo 4: 18-20.

Murphy , K.A. and Witten, E. 2006. Fire Regime Condition Classes (FRCC) Interagency Guidebook Reference Conditions (draft).

Naesset, E. 1999. Decomposition rate-constants of *Picea abies* logs in southeastern Norway. Can. J. For. Res. 29: 372-381.

NOAA 2014. National Oceanic and Atmospheric Administration (NOAA). Satellite and Information Service. National Climatic Data Center. US Department of Commerce. http://www.ncdc.noaa.gov/IPS/cd/cd.html;jsessionid=4E5612C511E74A2687A84659B08AA187?_page=0&jsessionid=4E5612C511E74A2687A84659B08AA187&state=AK&_target1=Next+%3E

Nowacki, G., Spencer, P., Fleming, M, Brock, T., and Jorgenson, T. 2002. Unified ecoregions of Alaska: 2001. U.S. Geological Survey Open-File Report 02-297 (map). http://agdc.usgs.gov/data/usgs/erosafo/ecoreg/index.html

Nowacki, G.J. and Kramer, M.G. 1998. The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. Gen. Tech. Rep. PNW-GTR-421. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Station, 32 p.

Oades, J.M. 1993. The role of biology in the formation, stabilization and degradation of soil structure. Geoderma 56(1): 377-400.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164 (3877):262-270.

Odum, E.P. 1968. Energy Flow in Ecosystems: A Historical Review. American Zoologist 8: 11-18.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in terrestrial ecosystems. Ecology 42: 322-331.

Onega, T.L., and Eickmeier, W.G. 1991. Woody detritus inputs and decomposition kinetics in a southern temperate deciduous forest. Bull. Torrey Bot. Club 118: 52–57.

Ott, R.A. and Juday, G.P. 2002. Canopy gap characteristics and their implications for management in the temperate rainforests of southeast Alaska. For. Ecol. Manage. 159(3): 271-291.

Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., Church, J.A., Clarke, L., Dahe, Q., Dasgupta, P. and Dubash, N.K. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.

Panshin, A.J. and de Zoew, C. 1970. Textbook of wood technology. Vol. 1. McGraw-Hill Book Co., New York.

Peterson, R.O., Woolington, J.D., and Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88: 3-52.

Pickett, S.T.A. and White, P.S. 1985. Patch dynamics - a synthesis. *In*: Pickett S.T.A. and White, P.S. (Eds.). Ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, pp. 371-384.

Ping, C.L., Michaelson, G.J., Kimble, J.M., and Everett, L.R. 2002. Organic carbon stores in Alaska soils. *In*: Lal, R., Kimble, J.M., and Follet, R. (Eds.). Agricultural Practices and Policies of Carbon Sequestration in Soils, pp. 485-494.

Post, W.M., Peng, T.-H., Emanuel, W.R., King, A.W., Dale, V.H., and DeAngelis, D.L. 1990. The global carbon cycle. American Scientist 78: 310–326.

Potkin, M. 1997. Fire history disturbance study of the Kenai Peninsula mountainous portion of the Chugach National Forest. Draft. USDA Forest Service. Chugach National Forest. December 5, 1997. Anchorage, Alaska.

Potter, C., Tan, P.N., Kumar, V., Kucharik, C., Klooster, S., Genovese, V., Cohen, W., and Healey, S. 2005. Recent history of large-scale ecosystem disturbances in North America derived from the AVHRR satellite record. Ecosystems 8(7): 808-824.

Pregitzer, S.P. and Euskirchen, E.S. 2004. Carbon cycling and storage in world forests: Biome patterns related to forest age. Global Change Biology 10(12): 2052-2077.

Preisler, H.K., Ager, A.A., and Hayes, J.L. 2010. Probabilistic risk models for multiple disturbances: An example of bark beetles and wildfire. *In*: Pye, J.M., Rauscher, H.M., Sands, Y., Lee, D.S., and Beatty, J.S. (Tech. Eds.). Advances in threat assessment and their application to forest and rangeland management. Gen. Tech. Rep. PNW-GTR-802. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA, pp. 371–380. www.fs.fed.us/pnw/pubs/pnw_gtr802a.pdf

Preston, B.L. and Jones, R.N. 2006. Climate change impacts on Australia and the benefits of early action to reduce global greenhouse gas emissions. Canberra: CSIRO, 41 p.

Raphael, M.G. and Morrison, M.L. 1987. Notes: Decay and dynamics of snags in the Sierra Nevada, California. Forest Science 33(3): 774-783.

Rogers, P. 1996. Disturbance ecology and forest management: A review of the literature. USDA Forest Service, Intermountain Research Station, General Technical Report, INT GTR-336. (See also http://www.usu.edu/beetle/literature.htm)

Ross, D.W., Daterman, G.E., Boughton, J.L., and Quigley, T.M. 2001. Forest health restoration in South-Central Alaska: A problem analysis. USDA Forest Service. PNW Research Station. PNW-GTR-523, July 2001.

Santantonio, D., Hermann, R.K., and Overton, W.S. 1977. Root biomass studies in forest ecosystems. Pedobiologia 17: 1-31.

Scheffer, T.C. and Cowling, E.B. 1966. Natural resistance of wood to microbial deterioration. Annu. Rev. Phytopathol. 4(1): 147-168.

Schimel, D.S. 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1(1):77-91.

Schwartz, C.C. and Franzmann, A.W. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. The Journal of Wildlife Management, pp.426-431.

Schwartz, C.C. and Franzmann, A.W. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs 113: 3-58.

Sexton, J.M. and Harmon, M.E. 2009. Water dynamics in conifer logs in early stages of decay in the Pacific Northwest, USA. Northwest Science 83(2): 131-139.

Shorohova, E.V. and Shorohov, A.A. 1999. Characteristics of detritus decay classes for spruce, birch, and aspen in middle taiga spruce forests. St.-Petersburg Forestry Research Institute 1: 17-23.

Shorohova, E., Kapitsa, E., and Vanha-Majamaa, I. 2008. Decomposition of stumps in a chronosequence after clear-felling vs. clear-felling with prescribed burning in a southern boreal forest in Finland. For. Ecol. Manage. 255(10): 3606-3612.

Shorohova, E.V. and Shorohov A.A. 2001. Coarse woody debris dynamics and stores in a boreal virgin spruce forest. Ecol. Bul. 49: 129-135. http://www.jstor.org/stable/20113270

Shvidenko, A.Z. and Nilsson, S. 2000. Fire and the carbon budget of Russian forests. *In*: Kasischke E.S. and Stocks, B.J. (Eds.). Fire, climate change, and carbon cycling in the boreal forests, pp. 289-311.

Smithwick, E.A.H., Harmon, M.E., Remillard, S.M., Acker, S.A., and Franklin, J.F. 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. Ecological Applications 12(5): 1303–1317. http://dx.doi.org/10.1890/1051-0761(2002)012[1303:PUBOCS]2.0.CO;2

Soja, A.J., Tchebakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., Chapin, F.S., and Stackhouse, P.W. 2007. Climate-induced boreal forest change: Predictions versus current observations. Global and Planetary Change 56(3): 274-296.

Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D., and Spycher, G. 1987. Patterns of log decay in old-growth Douglas-fir forests. Can. J. For. Res. 17(12): 1585-1595.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Can. J. For. Res. 12: 18-28.

Spies, T.A., Franklin, J.F., and Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69(6): 1689-1702.

Stamm, A.J. 1934a. Swelling of wood. USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin in cooperation with the University of Wisconsin. R1061, 15 p.

Stamm, A.J. 1934b. Effect of inorganic salts upon the swelling and the shrinking of wood. Journal of the American Chemical Society 56: 1195-1204. DOI: 10.1021/ja01320a063

Stamm, A.J. 1929. The fiber-saturation point of wood as obtained from electrical conductivity measurements. USDA Forest Service, Forest Products Laboratory, Madison, Wisconsin in cooperation with the University of Wisconsin. R859, 11 p.

Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan, M.D., Hirsch, K.G., Logan, K.A., Martell, D.L. and Skinner, W.R. 2002. Large forest fires in Canada, 1959–1997. Journal of Geophysical Research: Atmospheres (1984–2012), 107(D1), FFR-5.

Stocks, B.J., Fosberg, M.A., Lynham, T.J., Mearns, L., Wotton, B.M., Yang, Q., Jin, J.-Z., Lawrence, K., Hartley, G.R., Mason, J.A., and McKenney, D.W. 1998. Climate change and forest fire potential in Russian and Canadian boreal forests. Climatic Change 38(1): 1-13. http://dx.doi.org/10.1023/A%3A1005306001055

Tarasov M.E. and Birdsey R.A. 2001. Decay rate and potential storage of coarse woody debris in the Leningrad region. Ecological Bulletin, 49.

Tarasov, M.E. 1999. Role of coarse woody debris in carbon balance of forest ecosystems of Leningrad oblast'. Ph.D. thesis, St. Petersburg Forestry Research Institute Publishers, St. Petersburg, Russia. [In Russian].

Tol, R.S.J. 2000. Timing of greenhouse gas emission reduction. Pacific and Asian Journal of Energy 10(1): 63-68.

Triska, F.J. and Cromack, K. Jr. 1980. The roles of wood debris in forests and streams. *In*: Waring, R.H. (Ed.). Forests: Fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis, Oregon, pp. 171-190.

USDA 2016. http://www.fia.fs.fed.us/forestcarbon/. Accessed February 13, 2016.

USDA 2015a. http://www.fs.fed.us/pnw/rma/fia-topics/index.php. Last modified 10/27/2014. Accessed October 26, 2015.

USDA 2015b. http://www.fs.usda.gov/main/r10/forest-grasslandhealth/. Accessed October 25, 2015.

USDA 2014. Field instructions for the annual inventory of Coastal Alaska 2014. Forest Inventory and Analysis program. PNW Research Station. USDA Forest Service. Anchorage, Alaska. http://www.fs.fed.us/pnw/rma/fia-topics/documentation/field-manuals/documents/Annual/2014_AFSL_FIA_Field_Manual_FINAL.pdf

USDA 2014a. PNW-FIADB. Pacific Northwest Annual Forest Inventory Database. Pacific Northwest Research Station, Forest Inventory and Analysis. http://www.fs.fed.us/pnw/rma/fia-topics/inventory-data/index.php

USDA 2014b. Field instructions for the annual inventory of Coastal Alaska 2014. Forest Inventory and Analysis program. PNW Research Station. USDA Forest Service.

USDA 2010. Southeast Forest Health Protection. State and Private Forestry. Alaska Region. http://www.fs.fed.us/r10/spf/fhp/sefhp/seycedar.htm.

USDA 2005. Forest health conditions in Alaska – 2004. A forest health protection report. USDA Forest Service. Alaska region R-10-PR-3. State of Alaska Natural Resources Division of Forestry. Compiled by Dustin Wittwer. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev2_038152.pdf

USDA 2003. Field procedures for the Coastal Alaska inventory 2003.USDA Forest Service, PNW Station – Forestry Sciences Lab and Region 10 – Alaska. http://www.fs.fed.us/pnw/fia/local-resources/pdf/field_manuals/ak/2003_coak_field_manual.pdf

USDA 2000. Field procedures for the southeast Alaska inventory 2000. USDA Forest Service, PNW Station – Forestry Sciences Lab and Region 10 – Alaska. http://www.fs.fed.us/pnw/fia/local-resources/pdf/field_manuals/ak/2000_seak_field_manual.pdf

Van Hees, W.S. 2005. Spruce reproduction dynamics on Alaska's Kenai Peninsula, 1987–2000. USDA Forest Pacific Northwest Research Station, Portland (OR). Res. Pap. PNW-RP-563, 18 p.

Van Hees, W.W.S. 2003. Forest resources of southeast Alaska, 2000: Results of a single-phase systematic sample. Res. Paper PNW-RP-557. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Station, 96 p.

Van Pattern, D.J. 2000. Soil survey of lower Kenai Peninsula area, Alaska. USDA NRCS publication, 179 p.

Van Vuuren, D.P. and de Vries, H.J.M. 2001. Mitigation scenarios in a world oriented at sustainable development: The role of technology, efficiency and timing. Climate Policy 1(2): 189-210.

Veblen, T.T. and Alaback, P.B. 1996. A comparative review of forest dynamics and disturbance in the Temperate rainforests of North and South America. *In*: Lawford, R.G., Alaback , P.B., and Fuentes, E. (Eds.). High-latitude rainforests and associated ecosystems of the West Coast of

the Americas: Climate, hydrology, ecology, and conservation. Springer-Verlag New York, 409 p.

Viereck, L.A. and Little, E.L. Jr. 1972. Alaska trees and shrubs. Agric. Handb. 410. Washington, DC: U.S. Department of Agriculture, Forest Service, 265 p.

Vitousek, P.M. and Reiners, W.A. 1975. Ecosystem succession and nutrient retention: A hypothesis. Bioscience 25(6): 376-381. DOI: 10.2307/1297148.

Waddell, K.L. 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. Ecological Indicators 1 (2002) 139-153.

Waring, R.H. and Running, S.W. 2010. Forest ecosystems: Analysis at multiple scales. Elsevier.

Waring, R.H. and Schlesinger, W.H. 1985. Forest ecosystems. Concepts and management. Academic Press.

Werner, R.A., Holsten, E.H., Matsuoka, S.M., and Burnside, R.E. 2006. Spruce beetles and forest ecosystems in south-central Alaska: A review of 30 years of research Forest Ecol. Manag. 227:195–206.

Werner, R.A. and Holsten, E.H. 1983. Mortality of white spruce during a spruce beetle outbreak on the Kenai Peninsula in Alaska. Can. J. For. Res. 13: 246-250.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., and Swetnam, T.W. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313(5789): 940-943.

Whittaker, R.H. and Likens, G.E. 1973. Carbon in the biota. *In*: Woodwell, G.M. and Pecan, E.V. (Eds.) Carbon and the biosphere. Technical Information Center, Oak Ridge, TN, pp. 281-302.

Wigley, T.M.L., Richels, R. and Edmonds, J.A. 1996. Economic and environmental choices in the stabilization of atmospheric CO_2 concentrations. Nature 379(6562): 240-243.

Williams, A.M. and Liebhold, A.M. 2002. Climate change and the outbreak ranges of two North American bark beetles. Agricultural and Forest Entomology 4: 87–99.

Wirth, C., Schulze, E.-D., and Luhker, B. 2000. How fire exerts control over carbon balances in Siberian Scots pine forests. *In*: Apps, M.J. and Marsden, J. (Eds.). The role of boreal forests and forestry in the global carbon budget. Abstracts of International Science Conference, 8-12 May 2002, Edmonton, Alberta. Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, 77 p.

Wittwer, D. (Compiler). 2004. Forest health conditions in Alaska—2003, a forest health protection report. U.S. For. Ser. Tech. Rep. R10-TP-113. Juneau, AK, USA.

Woodall, C.W., Coulston, J.W., Domke, G.M., Walters, B.F., Wear, D.N., Smith, J.E., Andersen, H.-E., Clough, B.J., Cohen, W.B., Griffith, D.M., Hagen, S.C., Hanou, I.S., Nichols, M.C., Perry, C.H., Russell, M.B., Westfall, J.A., and Wilson, B.T. 2015. The U.S. forest carbon accounting framework: Stocks and stock change, 1990-2016. GTR-NRS-154. Forest Service, Northern Research Station.

Woodwell, G.M., Whittaker, R.H., Reiners, W.A., Likens, G.E., Delwiche, C.C. and Botkin, D.B. 1978. The biota and the world carbon budget. Science 199: 141-178.

Yatskov, M. 2000. A chronosequence of wood decomposition in the boreal forests of Russia. MS thesis. Oregon State University, Corvallis, Oregon, 168 p.

Yatskov, M., Harmon, M.E., and Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. For. Res. 33: 1211-1226.

Yavitt, J.B. and Fahey, T.J. 1982. Loss of mass and nutrient changes of decaying woody roots in lodgepole pine forests, southeastern Wyoming. Can. J. For. Res. 12(4): 745-752.

Zabel, R.A. and Morrell, J.J. 1992. Factors affecting the growth and survival of fungi in wood (Fungal Ecology), pp. 102-115. *In*: Wood microbiology: Decay and its prevention. Academic Press, Inc. Harcourt Brace Jovanovich, Pubs.

Zogas, K. and Holsten, E.H. 2002. Bibliography Alaska region. Forest health protection 1919 – 2001. Tech. Rep. R10-TP-107. USDA Forest Service, S&PF. Anchorage, AK, 136 p. http://www.fsl.orst.edu/wfiwc/admin/history/ak-bibliography.pdf

APPENDIX

Table A2.1. Diameter reduction factors by diameter class for Decay Class 5 DWM pieces

Diameter class	Reduction factor
10	0.8092
30	0.6489
50	0.5506
70	0.4679
90	0.4123
110	0.4183
130	0.3228

Table A3.1. P-values in a test of the y-intercept in the equation 5 being different from zero

logs	2002 p-value	2008 p-value	combo p-value
mass	0.4665	0.7484	0.5169
density	0.7968	0.1317	0.0885
volume	**0.0082**	**0.0055**	**0.0308**

snags			
mass	0.2375	0.6767	0.2102
density	0.4458	0.1183	0.2447
volume	0.4721	0.4862	0.7719

p-values are significant at $\alpha < 0.05$.

Table A4.1. Pre-disturbance carbon stores in live, snag, and log carbon pools by stand age classes

Stand Age Class	# of Stands	Live (Mean ±SE)	Snag	Log
20	8	7.59 ± 2.78	5.65 ± 3.35	8.92 ± 3.79
40	13	24.44 ± 5.62	0.95 ± 0.42	5.75 ± 1.89
60	41	30.69 ± 2.68	0.64 ± 0.18	5.00 ± 3.56
80	15	34.29 ± 7.05	3.10 ± 1.36	9.76 ± 3.84
100	24	44.15 ± 4.18	2.54 ± 0.68	8.69 ± 2.74
120	31	50.94 ± 3.87	3.91 ± 1.33	7.67 ± 1.34
Average Weighted by # of Stands		36.28 ± 4.02	2.37 ± 0.89	7.15 ± 2.77