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Carbon pools and biomass stores in the forests of Coastal Alaska: Uncertainty of estimates and impact of disturbance

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ABSTRACT

Forests provide significant long-term carbon (C) storage, but have the 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 (± SE) aboveground live (218.9 ± 4.6 Mg/ha) and log (28.1 ± 1.8 Mg/ha) biomass in the Alaskan 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 Alaskan Boreal ecoregion, on the Kenai Peninsula, coarse woody debris (CWD) biomass comprised almost 50% of the regional average of aboveground woody biomass (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 forests 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 determined total biomass amounts in the system and controlled the ratio between live and dead biomass pools and thus has the ability to shift forest stands into a C source to the atmosphere.

1. 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 carbon (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. Carbon dioxide (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, serving a number of functions in forests including 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 et al., 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

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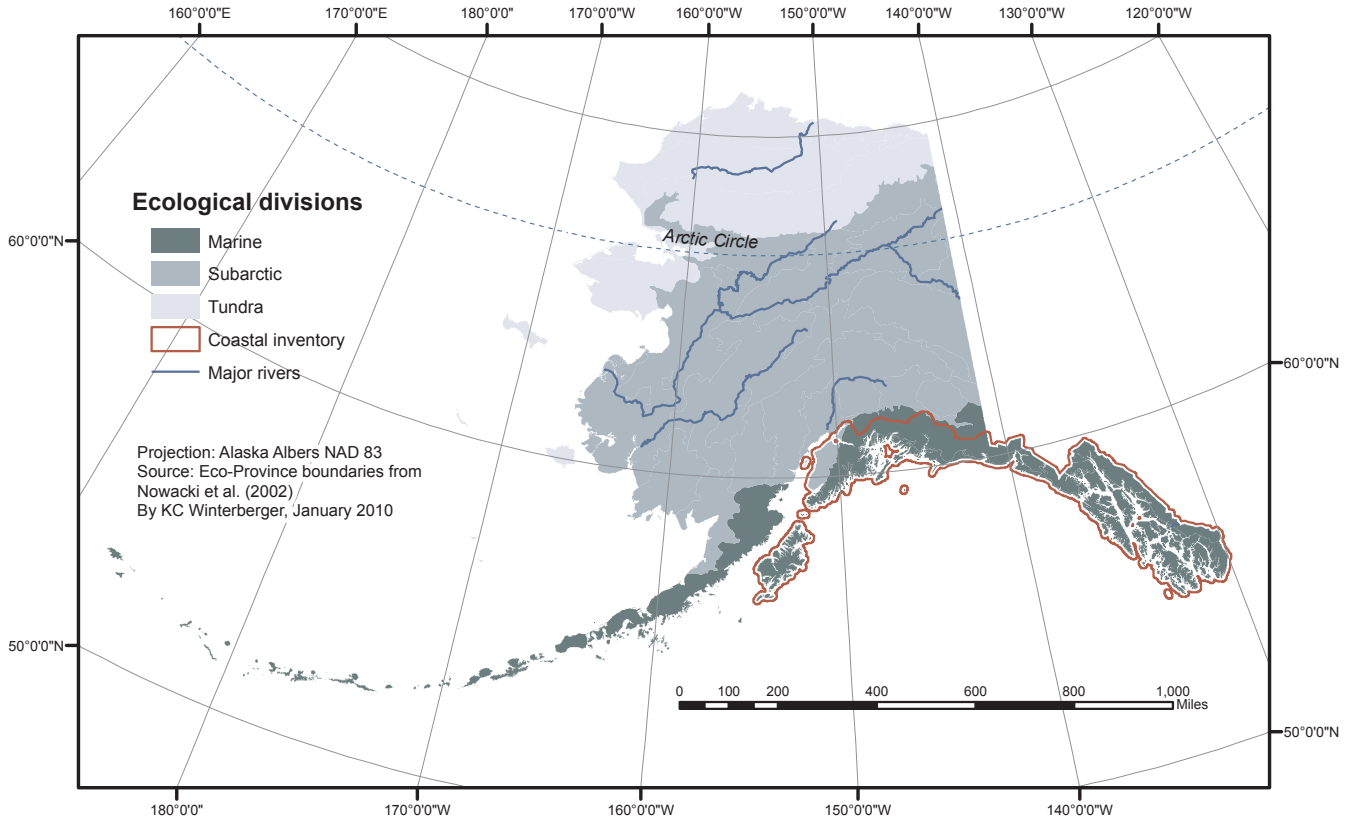


Fig. 1. Territory sampled by Coastal Alaska Forest Inventory and Analysis unit during the time period of 1995 to 2003 (after Nowacki et al., 2002).

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 sources of C to the atmosphere.

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. 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 and depending on the balance between the live and dead components, forests could become C sinks, C sources, or C neutral (Smithwick et al., 2002). Disturbance type and severity also have a significant effect on the CWD pool by partitioning between the snag and log components, diversifying the CWD decomposition trajectories because of differences in log and snag decomposition rates (Onega and Eickmeier, 1991; Yatskov et al., 2003; Harmon et al., 2005) and the lags associated with snag fall following the disturbance (Angers et al., 2010; Harmon et al., 2011a). Climate change has been linked to increased disturbance magnitude, frequency, and severity especially in forests in northern latitudes (Stocks et al., 2002; Werner et al., 2006; Soja et al., 2007). Therefore, feedback mechanisms (Houghton, 1995; Schimel, 1995; Bonan, 2008) acting through disturbance (Dixon and Krankina, 1993; Flannigan et al., 1998; Kurz et al., 2008a) may escalate the CO_2 flux to the atmosphere from forest ecosystems, at least over the short term, thus increasing the rate of global climate change.

In recent decades, high latitude forests have been identified as hotspots of 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. A legacy disturbance currently influencing C dynamics includes an extensive spruce bark beetle outbreak in south-central Alaska prior and during the forest inventory cycle of 1995–2003 (Holsten et al., 2000). Specifically, spruce bark beetles infested 100 thousand ha of white spruce forest on the Kenai peninsula annually between 1976 and 1981 (Werner and Holsten, 1983) and caused an extensive spruce mortality over 1.2 million ha of forest in south-central Alaska over the period between 1989 and 2004 (USDA, 2005; Berg et al., 2006).

The objectives in this study were to examine the current above- (live tree, snag, log, fine woody debris (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 the impact of different types of disturbance on three major live and dead aboveground biomass pools. The study was guided by four questions: (1) how is biomass 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 are total C stores 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 Forest Inventory and Analysis (FIA) project over the period between 1995 and 2003. We identified eight C pools in the forest ecosystems of Coastal Alaska, modelled six of these pools from FIA data, and used literature data to estimate the size of the remaining two C pools (understory vegetation and soils). We conducted uncertainty analysis of the C pools to understand major contributors and recognize ways of reducing uncertainty in C estimates.

2. Methods

2.1. 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) (Fig. 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 5 °C (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 6753 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).

Coastal Alaska is influenced by an array of disturbances, both natural and anthropogenic. Disturbance types range from small-scale gap dynamics with short return interval and low severity, characteristic to southeast Alaska, where each gap is formed through mortality of three or fewer overstory trees (Nowacki and Kramer, 1998), 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 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 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 including severe winds, landslides and avalanches, floods, insects and diseases, parasitic plants, browsing, decline complexes, and fires. 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 et al., 2005). Partial harvest was common from the 1800s to 1950 (Deal, 2007) with cutting intensity from 26% to 96% of the original basal area (Deal et al., 2010). The large-scale clearcutting timber operations 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 et al., 2005). Clearcut 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-1990 s 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% of the 1.1 million cubic meters annual harvest volume in southeast Alaska (Halbrook et al., 2009), although the national forest has 83% of timberland in southeast Alaska (van Hees, 2003).

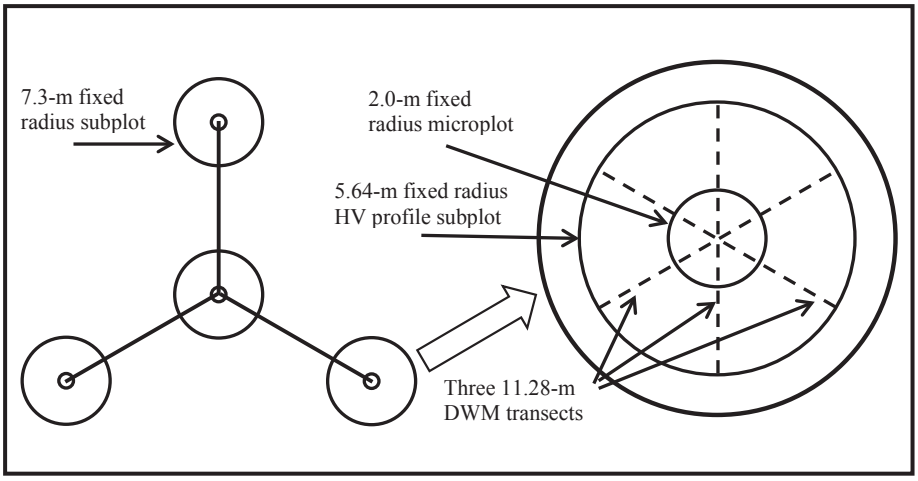
The Boreal ecoregion is represented by Cook Inlet Basin on the western side of the Kenai Peninsula (Fig. 1). It is a lowland covered with numerous lakes, ponds, and wetlands. The climate combines features of maritime and continental climates with moderate fluctuations of seasonal temperature and abundant precipitation. Mean annual temperature in the Cook Inlet for the period between 1995 and 2003 was 2 °C (NOAA, 2014). Precipitation over the period between 1995 and 2003 ranged between 262 mm and 2516 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* × *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). Both disturbances are extensive in south-central Alaska.

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).

2.2. 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, Fig. 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 areas with the evidence of formerly having at least 10% tree cover. Lands that have never supported forests and lands formerly forested on which



HV – Horizontal/Vertical vegetation profile subplot;
DWM – Down Woody Material.

Fig. 2. Periodic Alaska four-point FIA plot layout.

current land use prohibits establishment of forests (USDA, 2000) were excluded.

Forest inventory plots included four 7.3-meter fixed-radius subplots (Fig. 2) spaced 36.6 m between the subplot 1 center and centers of subplots 2, 3 and 4. 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 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). 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 using disturbance protocols that differed slightly between southeast and south-central Alaska (see Supplementary Materials section for details). 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 recent (within 10 years from the field visit) 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 timing, size or severity thresholds. Observed tree damage or mortality from bark beetles (*Dendroctonus rufipennis* or *Ips* spp.) was recorded under infestation level with 60% of spruce trees attacked 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 greater than 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 stand age was generally determined from 3 trees that were aged by counting annual rings on cores extracted with an 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).

2.3. Live tree and snag biomass estimation

2.3.1. 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 (Fig. 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).

2.3.2. 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. ≥ 12.5 cm and live tally saplings with d.b.h. ≥ 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 m (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.

2.4. Log biomass estimation

2.4.1. Field procedures

Downed 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 (Fig. 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 the transects was also recorded (USDA, 2000).

2.4.2. Log biomass calculations

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

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

where 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 (see Supplementary Materials section for details).

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):

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

where 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.

2.5. 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 6844 plots in the Coastal Alaska FIA sample, most of the "access-denied" plots (1808) 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 5036 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 4887, among them 1969 plots were field-measured forested. For 65 forested plots log measurements were not collected in the field due to time limitation, weather conditions, ground cover phenology, snow on plot, or other reasons. Therefore, 1904 plots (represented by 2093 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 1635 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. 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. Out of 1904 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. The disturbance type "Other" included various disturbances such as root disease (10 plots in the Boreal and 9 in the 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.

2.6. 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. 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.

We defined uncertainty as a lack of confidence in a single value (Harmon et al., 2007). Uncertainty of C estimates is essential in determining the upper and lower bounds of forest C sources and sinks with the purpose of assessing forest C sequestration potential. 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), utilizing SE of the

Table 1
Estimates of average biomass and standard error (Mg/ha) by ecoregion and forest type in Coastal Alaska for the measurement time period of 1995–2003.

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)**
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 containing information on log biomass.

mean from literature data (Understory Vegetation and Soils pools) and using Stochastic Uncertainty Estimator – SUE (Goodman, 2002; SUE, 2018) (FWD and Live and Dead Roots pools). Where available (five C pools), SE of the mean was utilized to estimate uncertainty as part of the standard national method for FIA (Bechtold and Patterson, 2005). Where SE of the mean was unavailable (3 C pools), SUE was used. 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 recognized that using 50% of the biomass as C to estimate live tree, snag and log C pools ignored an element of uncertainty. Accounting for this source of uncertainty along with other sources (e.g., spatial variation, volume equations and wood density) (Melson et al., 2011) would certainly increase overall uncertainty estimates.

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 uniform distribution ranging from 15 to 26% (Santantonio et al., 1977; Cairns et al., 1997; Hamburg et al., 1997; Leighty et al., 2006).

The dead Roots C pool was calculated from the CWD C pool using a ratio similar to that for live roots, adjusted for differences in above- and belowground decomposition rates (Harmon et al., 2004) (see details for estimating Dead Roots C pool in the Supplementary Materials section).

Using a similar approach, FWD C pool was estimated based on the CWD C pool as a ratio of 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) (see details for estimating FWD C pool in the Supplementary Materials section).

The understory vegetation C pool and associated uncertainty were estimated based on understory biomass data from Alaback (1982) and the stand age distribution of the 2093 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 (see details for estimating Understory vegetation C pool in the Supplementary Materials section). One value was used for the Understory C pool in the Boreal and the Temperate ecoregions because of our inability to locate understory information for the Boreal ecoregion. To estimate uncertainty in Understory vegetation C pool, we used respective mean biomass and standard error by four age classes (3.93 ± 1.65 Mg/ha for class 1, 0.69 ± 0.25 for class 2, 4.20 ± 2.46 for class 3, and 0.60 ± 0.06 for class 4) (see additional details for estimating the understory vegetation C pool in the Supplementary Materials section).

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. To estimate regional total C store in the upper 1 m of soil and its uncertainty, we multiplied the Boreal and the Temperate ecoregion averages and SE (250 ± 13 Mg/ha and 260 ± 16 Mg/ha, respectively) (Kristofer Johnson, personal communication, 2013) by their respective total areas. 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 et 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.

3. Results

3.1. Biomass distribution

The range of total aboveground biomass (live and dead) 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 (Table 1). 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. In contrast, the highest average biomass in the Boreal ecoregion of 136.7 ± 18.9 Mg/ha found in the black cottonwood forest type was almost one-third that of the highest average biomass in the Temperate ecoregion of 399.0 ± 9.8 Mg/ha found in the western hemlock forest type.

In contrast to total aboveground biomass stores, the CWD (snag and log) stores in forest types of the Boreal and the Temperate ecoregions had similar ranges (Table 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 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).

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 (Tables 1 and 2). 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% of total (live and dead) aboveground woody biomass, whereas in the Temperate ecoregion CWD biomass represented about 21% of total aboveground woody biomass. In the Boreal ecoregion, 67% of CWD biomass consisted of snags compared to 52% in the Temperate ecoregion.

3.2. Disturbance

CWD stores differed between disturbed and undisturbed stands and varied among disturbance types (Table 3). 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). In contrast, the lowest CWD and total biomass stores of 19.3 ± 7.8 Mg/ha and 27.3 ± 8.4 Mg/ha, respectively, were associated with stands disturbed by fire.

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 3). 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 71.4%. The proportion of CWD in stands disturbed by harvest (clearcut and partial harvest) equaled 77.4% and 65.8%, respectively.

Disturbance type and severity had a significant effect on CWD pool partitioning between the snag and log components (Fig. 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 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 (Fig. 4). Spruce bark beetle outbreaks, the disturbance type with the highest regional impact on CWD stores in the Boreal ecoregion, contributed 69 and 13% of overall CWD stores in stands with high and moderate severity spruce bark beetle damage, respectively. In the Temperate ecoregion the majority of CWD (76%) was in undisturbed stands, whereas Clearcuts represented the largest fraction (10%) in overall CWD stores among disturbed stands followed by blowdown stands (6%).

3.3. Carbon pools and uncertainty estimates

The total C stores in Alaskan coastal forests were 183 Tg (lower and upper bounds of 157–209 Tg, respectively) for the Boreal, 1525 Tg (1362–1688 Tg) for the Temperate, and 1708 Tg (1523–1893 Tg) for both ecoregions combined (Table 4). 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 4) indicating the minor role of Boreal C stores in the total Coastal Alaska C stores.

The 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 4) and comprised 63% of total C stores corresponding to 1070 Tg (954–1186 Tg) for the Boreal and the Temperate ecoregions combined. Understory vegetation on the other

Table 2
Estimates of total ecoregion area (ha) and total biomass (Tg) by biomass pools in Coastal Alaska for the measurement time period of 1995–2003.

Ecoregion	Area Thousand ha	Live (SE) Tg	Snags (SE) Tg	Logs (SE) Tg	CWD (SE) Tg	Total (SE) 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 3
Estimates of average biomass and standard error (Mg/ha) by disturbance type in Coastal Alaska for the measurement time period of 1995–2003.

Disturbance Type	Nature of Disturbance	# of plots[c]	Live $\bar{x}$ (SE), Mg/ha	Snags $\bar{x}$ (SE), Mg/ha	Logs $\bar{x}$ (SE), Mg/ha	CWD $\bar{x}$ (SE), Mg/ha	Total $\bar{x}$ (SE), Mg/ha	CWD Proportion % of Total
Clearcut	Human	119	24.6 (3.8)	2.5 (0.8)	82.2 (8.7)	84.7 (8.7)	109.4 (9.3)	77.4
Partial harvest	Human	25	64.2 (14.7)	18.3 (6.6)	104.9 (80.8)	123.2 (80.8)	187.3 (81.3)	65.8
SBB[a] high	Natural	123	30.7 (3.3)	60.4 (4.9)	16.0 (3.6)	76.4 (6.1)	107.0 (7.2)	71.4
SBB[a] moderate	Natural	96	95.9 (8.7)	20.5 (4.3)	13.7 (1.9)	34.2 (4.9)	130.1 (11.8)	26.3
SBB[a] combined[b]	Natural	215	57.6 (4.7)	43.9 (3.7)	15.1 (2.2)	58.9 (4.4)	116.5 (6.5)	50.6
Blowdown	Natural	38	269.9 (32.6)	33.4 (9.3)	110.2 (15.6)	143.6 (17.1)	413.5 (37.8)	34.7
Fire	Unknown	9	8.0 (5.2)	9.2 (5.5)	10.1 (3.8)	19.3 (7.8)	27.3 (8.4)	70.7
Other	Mixed	39	134.2 (18.0)	36.2 (11.3)	21.0 (3.9)	57.2 (12.6)	191.4 (25.6)	29.9
Undisturbed	Not Recent	1502	227.9 (5.0)	29.6 (1.0)	19.7 (1.0)	49.3 (1.6)	277.2 (5.7)	17.8

Clearcut – human-caused disturbance in areas ≥ 2 ha where > 75% of the trees have been cut.
Partial Harvest – human-caused disturbance in areas other than clearcuts where 25–75% of trees have been cut or damaged by tree removal.
SBB high category – natural disturbance representing stands with high severity spruce bark beetle damage, where > 60% of spruce trees in the area were attacked by *Dendroctonus rufipennis* or *Ips* spp.
SBB moderate category – natural disturbance representing stands with moderate severity spruce bark beetle damage, where up to 60% of spruce trees in the area were attacked by *D. rufipennis* or *Ips* spp.
Blowdown – natural disturbance in areas greater than 1 ha in or around subplot with extensive evidence of broken or uprooted trees.
Fire – disturbance type of unknown origin (includes either natural or anthropogenic fires).
Other – a category of mixed (human-caused and natural) disturbances with low number of observations such as root disease, flooding, yellow cedar decline, corridors created along railroads, power lines, gas lines, and canals, drained plots, and land slide plots.
Undisturbed – stands that include areas lacking recent (within 10 years from the field visit) disturbance.
[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 containing information on log biomass.

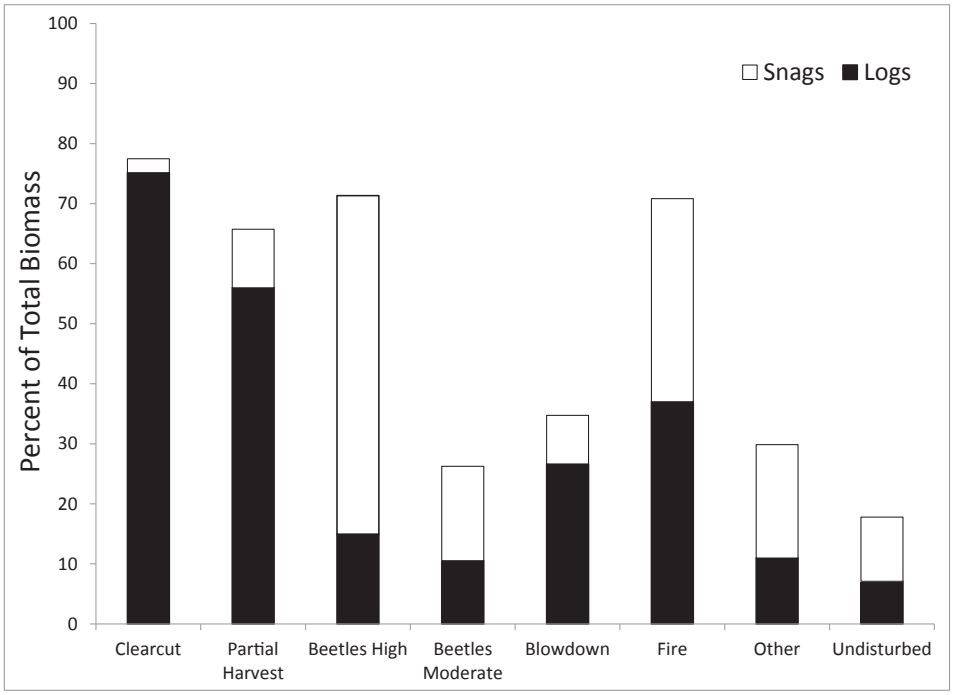


Fig. 3. CWD as percent of aboveground woody (live and dead) biomass by disturbance type for the measurement time period of 1995–2003. For the description of disturbance types refer to Table 3 captions.

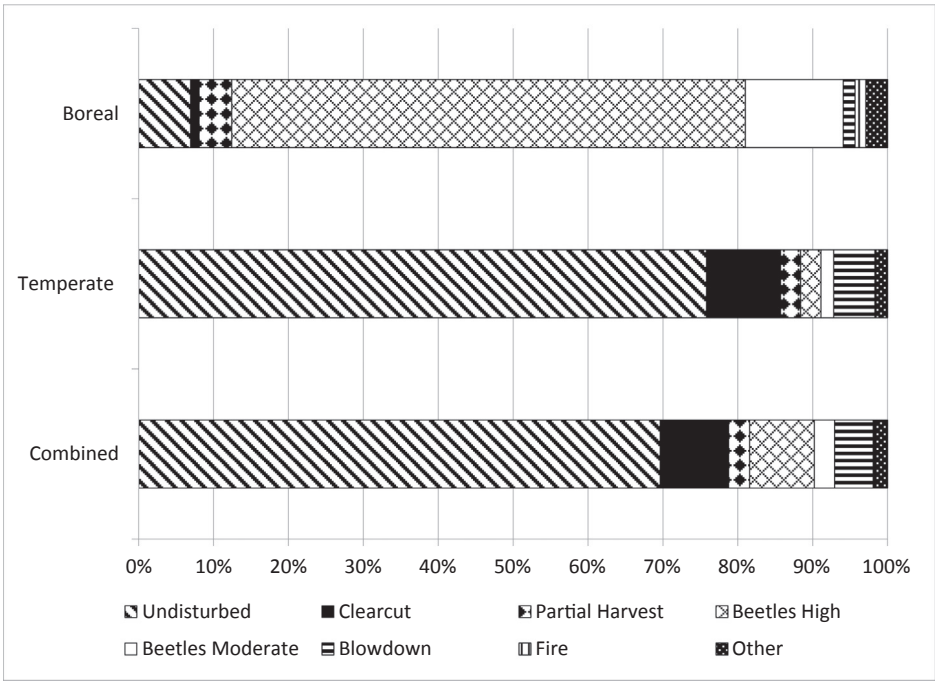


Fig. 4. Contribution of disturbance types to regional CWD stores (% of total CWD mass in ecoregion) for the measurement time period of 1995–2003. For the description of disturbance types refer to Table 3 captions.

hand represented the smallest portion of total C pool with 0.3% for both ecoregions combined. Aboveground C stores were 32% of the total for the region. Among total aboveground components the live tree/sapling portion was the highest, representing 24% of the total C stores and the CWD component was 7% of the total C in both regions. FWD appeared to be fairly insignificant component comprising less than 1% of the 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 4).

The ratios of steady-state masses for the Dead Roots and FWD C pools produced estimates equivalent to 12.4% and 11.4% of the CWD pool, respectively. The uncertainty in these two C pools expressed as percent of the CWD C pool ranged between 7.2% and 17.6% for Dead Roots and 6.6% and 16.2% for FWD C pools. The uncertainty estimates of Live Roots C pool expressed as percent of Live Tree C pool ranged between 13.6% and 26.4%.

4. Discussion

4.1. Biomass distribution

Our study contributes to a 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 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 corresponded well with the difference in the forest area covered by each of the inventories.

Total snag biomass, calculated using average snag biomass by forest type unadjusted for broken tops and density loss was 0.21 ± 0.01 Pg,

Table 4
Estimates of total carbon stores by ecoregion in Coastal Alaska.

C pools	Boreal			Temperate			Combined		
	x̄, Tg	% Total	x̄ ± 2SE, Tg	x̄, Tg	% Total	x̄ ± 2SE, Tg	x̄, Tg	% Total	x̄ ± 2SE, 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 1 m 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.

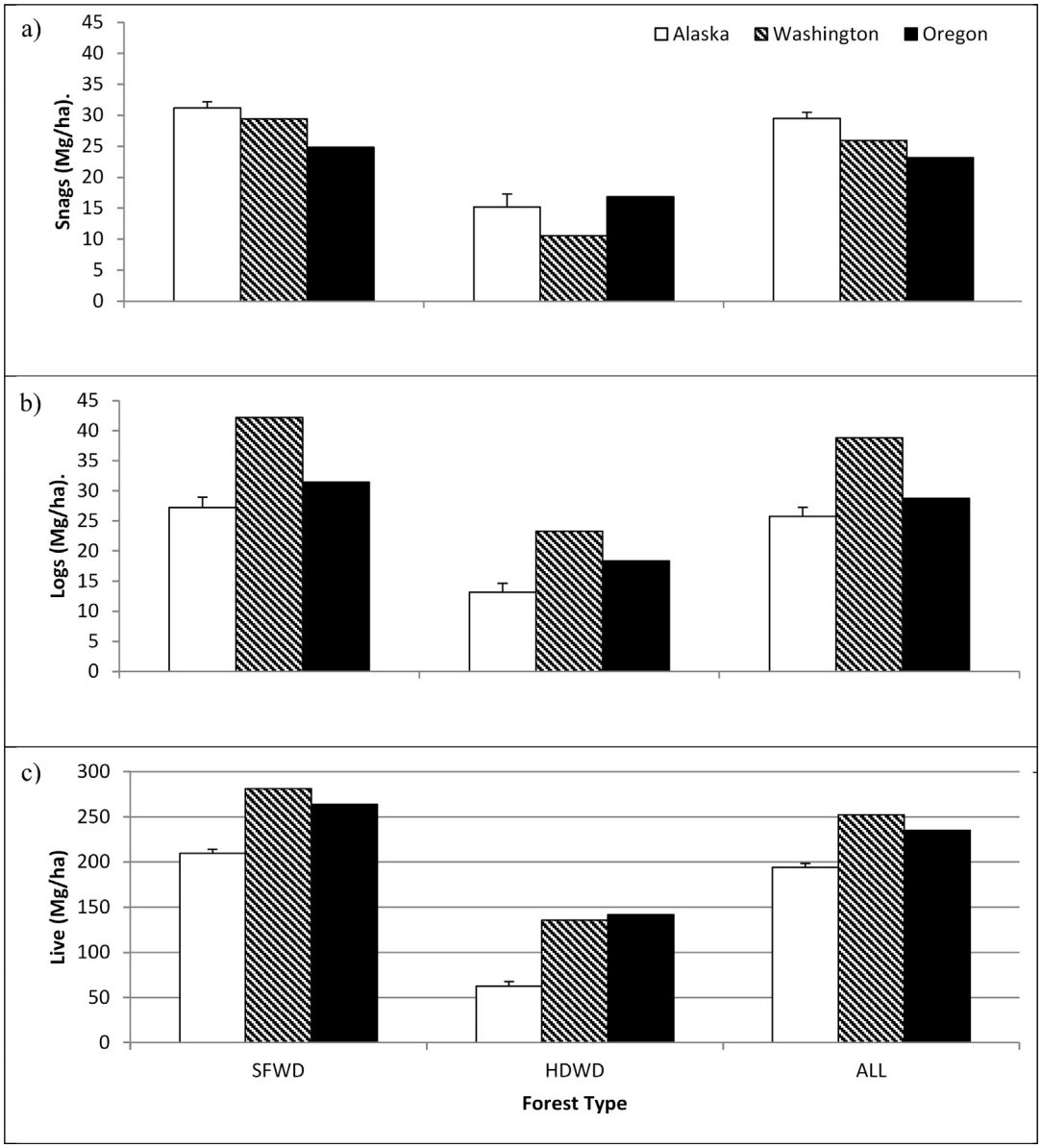


Fig. 5. Comparison of the estimates of average snag (a) log (b) and live biomass (c) among Coastal Alaska and Wester Washington and Oregon in softwood (SFWD), hardwood (HDWD), and all forest type categories.

or 1.4-fold lower than 0.29 ± 0.01 Pg reported by Barrett and Christensen (2011). This difference largely corresponds with the 1.5-fold difference in the land area covered by the periodic and annualized inventories. However, 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 that reported by Barrett and Christensen (2011), reflecting that failure to adjust snags for biomass and density loss could lead to overestimates of snag C stores by up to 60%.

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 Pacific Northwest FIA Annual Inventory Database (PNW-FIADB) 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 despite similar environmental conditions, sampling design and methods (Fig. 5). At the same time the snag biomass was the highest among the three regions in softwoods and all species combined. Upper bounds in live biomass values from Alaska (93 Mg/ha in black cottonwood forests of the Boreal ecoregion and 312 Mg/ha in western hemlock of the Temperate ecoregion) were also lower than values reported in other studies. For example, in the Pacific Northwest, 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 examined 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* (Doug) ex. Loud) 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 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.

High snag biomass in Alaska in comparison to the two PNW states (Oregon and Washington) is likely a result of high mortality rate of spruce-dominated forests damaged by spruce bark beetle outbreaks and Alaska yellow cedar decline as well as potentially slower snag fall rates (Fig. 5). The 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 reflect disturbance characteristics of these regions. The higher snag retention could also be linked to the low proportion of timberland harvested recently in Alaska, resulting in the proportional 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 3).

We also compared our results to the values from Russia, a region that contains about 50% of the world's boreal forest (Kobak, 1988). Our CWD biomass estimates (35.1 Mg/ha and 58.6 Mg/ha, for the Boreal and the Temperate ecoregions, respectively) in general were at the higher end of the ranges for forests in Russia: 14–42 Mg/ha (Tarasov, 1999), 6.6–102.0 Mg/ha (Shorohova and Shorohov, 1999), 7.4–15.0 Mg/ha (Shvidenko and Nilsson, 2000), 34–40 Mg/ha (Moiseev et al., 2000), and 5.7–13.9 Mg/ha (Krankina et al., 2002). We hypothesize that the difference in CWD amounts was due to differences in productivity of the Russian and the Coastal Alaskan forests, although judging by live biomass, 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). 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.

4.2. 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 3) even though fire most certainly increases the amount of CWD. This 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 better approximate 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. The low number of fire plots could be associated with the low fire occurrence during 10-year interval prior to plot visit (time period used by FIA crews to record disturbance on plot) the low density of FIA sampling (1 plot per 2400 ha) compared to fire size and uncertainty dating fire events.

All disturbance types had higher percent CWD in total (live + dead) aboveground biomass than for the Undisturbed category (Fig. 3). However, there was nearly 10-fold difference in CWD biomass range among the disturbance types (Table 3). Biomass extremes in disturbed stands were associated with the Blowdown disturbance on high end and the Fire disturbance on the low end. These results could be explained at least partially by the regional differences. Stands affected by Blowdown disturbance type, located in most cases in the Temperate ecoregion (southeast AK) where this type of disturbance was prevalent, contained high biomass because blowdown primarily affects mature and old-growth stands. Most Undisturbed stands were also located in the Temperate ecoregion, therefore the average biomass totals between Blowdown and Undisturbed stands should have been similar. However, this was not the case because the Blowdown category contained mostly mature and old-growth stands, whereas the Undisturbed category contained many younger stands, therefore the total biomass in Blowdown stands was larger than in Undisturbed stands. In contrast, when compared to biomass in forest types most often associated with the Blowdown disturbance, the average biomass in Blowdown stands (Table 3) was similar to the average biomass in western hemlock and 25% higher than biomass in Sitka spruce forest types (Table 1). The difference with Sitka spruce total average biomass is mostly because of the lower CWD pool size associated with 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). Low stores are potentially the outcome of fires mainly affecting stands with relatively low aboveground tree biomass in the Boreal ecoregion. Therefore, the biomass averages from fire-damaged stands, while being 2–4 times lower (Table 3 versus Table 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 a 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 compared in relative terms (as a ratio or percent of live or total biomass). When expressed as a proportion of total (live + dead) biomass, the lowest proportion of CWD was associated with undisturbed stands, whereas the highest one with clearcut stands. In general, the proportion of CWD in stands disturbed by harvest (clearcut and partial harvest) was relatively high because of large input into CWD pool and the removal of live biomass from site by logging.

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 and 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 into snag and log categories could be linked to the disturbance types based on the nature of the 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 clearcut harvesting despite the total pre- and postharvest CWD volume remaining 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%) 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 (Fig. 3). However, a 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 (Fig. 3). Assuming all clearcut stands prior to disturbance were mature and old-growth with total biomass equivalent to the 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 leaves 40% of biomass partitioned between live and dead biomass pools. Partial Harvest with average total biomass of 187.3 ± 81.3 Mg/ha (Table 3) removed about 32% of total biomass leaving 68% of biomass on site partitioned between live and dead pools. Higher CWD biomass amounts associated with certain disturbance types may indicate 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., 2008b). 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.

4.3. 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 4) 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 estimates.

Some sources of uncertainty have a larger effect on individual C pool estimates than others with sampling error likely high for soils and low for pools estimated by FIA. 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 the soils sample is potentially lacking a representative distribution, may not reflect the full variability in the soils C pool and therefore underestimates actual uncertainty. In contrast, aboveground C pools with systematic FIA sampling have a fairly large number of observations (i.e., 10 times that of soils data). Measurement error is probably low in both cases with quality control measures currently in place.

Model prediction error contributes to overall uncertainty through use of a constant 0.5 biomass-to-C conversion factor. Lamlom and Savidge (2003) reported relative errors of C wood content for North American trees of ± 4% for hardwood species and ± 8% for softwood species. In comparison, relative sampling error of aboveground tree biomass (live, snags, and logs combined) was ± 3.89–11.69% for hardwood species and ± 3.79–15.01% for softwood species in the Temperate and the Boreal ecoregions, respectively. Model prediction error is probably also high for the modelled pools especially Dead Roots, FWD, and Understory given the general nature of the literature-derived ratios and numerous assumptions we made.

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 ≈22%. This form of uncertainty, related to the form of the stem volume model used, was also relatively high for the CWD C estimates. High uncertainty in live aboveground biomass is most likely associated with the inter-regional application of biomass equations (Barrett and Christensen, 2011, table of biomass citations, p. 117) and extrapolation of the allometric equations to diameters larger than they were developed from (Melson et al., 2011).

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 the 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), explicit 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).

5. Conclusions

This study provided estimates of aboveground live and dead biomass 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 as well as mineral soil pools were estimated and uncertainty analysis of these estimates was conducted to explore the ways it could be decreased in future estimates.

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 was generally higher. Overall CWD stores in Coastal Alaska were lower than values reported from 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% of aboveground (live and dead tree) biomass (67% of CWD consisted of snags) as compared to 21% in the Temperate ecoregion (52% of CWD consisted of snags).

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 most CWD stores were found in forest 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. The 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 a whole-ecosystem approach when assessing C stocks within the system.

The relative uncertainty of the individual pools (2 × SE 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 sampling and model selection errors, respectively. To decrease uncertainty in soil C estimates a more representative sampling should be undertaken across Coastal Alaska. To reduce uncertainty in the aboveground live and dead C pools we recommend more attention be paid to accounting for differences in the tree bole form used in volume equations.

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Appendix A. Supplementary material

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